Ecological Preferences of Benthic Foraminifera in the Eastern South Atlantic: Distribution Patterns, Stable Carbon Isotopic Composition, and Paleoceanographic Implications

Ökologische Ansprüche benthischer Foraminiferen im östlichen Südatlantik: Faunenverbreitung, Zusammensetzung stabiler Kohlenstoffisotope und paläozeanographische Bedeutung

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Contents

Introduction

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Abstract

We examined live (Rose Bengal stained) and dead benthic foraminiferal faunas from 23 stations located on a latitudinal transect between 3°N and 32°S along the West-African continental slope. All samples but three were taken from a narrow water-depth range, between 1200 and 1500m, to minimize the influence of different water masses. In addition, stations were chosen in order to completely document the strong gradients in ocean surface productivity caused by several coastal and open-ocean upwelling systems.

The latitudinal distribution of standing stocks, diversity, and foraminiferal assemblages (as defined by Q-mode Principal Component Analysis) shows a clear correspondence with the different primary productivity provinces. Changes in seasonality, quantity, and quality of food supply are the main controlling parameters on the structure and distribution of foraminiferal faunas from the West-African continental margin. The distribution patterns and the composition of dead foraminifera are generally matching the distribution and composition of the live assemblages, an indication that the ecological information obtained from this study can be faithfully used to reconstruct past primary productivity changes, and by extension past changes upwelling variability, in the eastern South Atlantic. Furthermore, it was demonstrated that there are no significant discrepancies in the distribution and species composition of "total" (i.e., including surface and subsurface sediment layers) and "surface" (i.e., in the uppermost cm of sediment) live and dead assemblages. This validates that foraminiferal assemblages from the uppermost centimeter of sediment, commonly used as modern reference data sets for paleoceanographic purposes, do record most of the qualitative ecological information as recorded by the complete faunas. In contrast, subsurface abundance maxima of live foraminifera and dissolution of empty tests might strongly bias quantitative approaches based on the calculation of standing stocks and foraminiferal numbers from the top 1 cm of sediment.

Within the sediment, the clear succession of foraminiferal species into several distinct microhabitats illustrates the interplay between oxygen and food availability. In the less eutrophic Gulf of Guinea and the northern Angola Basin, species are concentrated towards the sediment-water interface to compensate low food supply. Towards the south, the contribution to the fauna and the burial of shallow and deep endobenthic species increase with the establishing of more eutrophic conditions. Highest occurrences of deep endobenthic species (*Globobulimina affinis*, *Fursenkoina mexicana*) characterize the northern Benguela region. Low occurrences of these species in the southern Angola Basin, influenced by oceanic upwelling at the time of sampling, might indicate their longer time-response to strong inputs of fresh phytodetritus compared to more opportunistic shallow endobenthic taxa (e.g. *Bulimina mexicana*).

We found overall a good correlation between species-specific mean $\delta^{13}C$ values and microhabitat preferences, indicating that epibenthic species such as *Fontbotia wuellerstorfi* generally faithfully record the isotopic signature of dissolved inorganic carbon (DIC) of the bottom water, whereas the isotopic composition of endobenthic species mirrors porewater $\delta^{13}C_{DIC}$ values. However, some cibicids (e.g. *Cibicides lobatulus* and *Cibicidoides pachyderma*) are assumed to migrate from an epibenthic to an endobenthic microhabitat at different sites in response to changes in food availability, and may either record bottom or porewater $\delta^{13}C_{DIC}$ values. Within the sediment, our data overall indicate the absence of significant downcore variability of species-specific $\delta^{13}C$ values, which suggests that species might calcify at a preferential level within the sediment, or record an average, site specific-$\delta^{13}C_{DIC}$ porewater signal, dependent on the organic matter flux.

Furthermore, we show that a significant enrichment in ^{13}C of the tests of epibenthic and endobenthic species can occur in high productive areas, where sedimentary carbonate content is low, probably as a result of enhanced fractionation due to carbonate-ion undersaturation.

Introduction

1. General considerations

The increasing concern about global warming has emphasized the necessity to elucidate past climate fluctuations. Two of the key mechanisms implicated in the regulation of climate at large scale are the oceanic overturning and primary productivity, whose variations leave an imprint in the marine sedimentary archives. With respect to these considerations, the South Atlantic can be considered as a sensible wheel in the world climate machinery for two reasons: (1) there is a net heat and salt transfer to the North Atlantic from northward-flowing upper waters; (2) several seasonal and permanent upwelling systems strongly influence surface waters off the West African continental margin, locally resulting in extremely enhanced primary production, and thus exerting a major influence on the global carbon cycle through atmospheric CO_2 draw-down, export and burial of organic carbon. This picture is very dynamic, however, as the South Atlantic experienced major changes in circulation patterns and strong primary productivity fluctuations on glacial-interglacial timescales (e.g. Berger and Wefer, 1996; Wefer et al., 1996, and references therein).

Because of their wide distribution in the world ocean, the good fossilization potential of their calcareous and agglutinated tests, and their long geological record, benthic foraminifera are particularly suitable for the decrypting of the sedimentary record. Therefore, they are extensively used as proxy for changes in organic matter fluxes to the seafloor and bottom-water flow over geological times, which in turn are linked to fluctuations in surface water primary productivity and intensity of the conveyor belt, respectively. For paleoceanographers, the most relevant aspect concerns the sensitivity of these organisms to changes in benthic environmental conditions, indirectly recorded by particular faunal compositions and the presence/absence of specific taxa, and directly in the trace elemental and stable isotopic composition of their calcareous tests. The accurate and reliable interpretation of ecological information conveyed by fossil species distribution and trace elemental and isotopic signature depends, in turn, on the detailed knowledge of the true behavior of modern species with regard to given environmental variables, and on how these factors affect the chemical composition of foraminiferal tests.

In this context, this study investigates the ecological preferences of Recent benthic foraminifera from the eastern South Atlantic continental slope, with emphasis on trophic conditions and the concentration of oxygen in bottom and porewaters. First ecological investigations of benthic foraminiferal surface assemblages in the Gulf of Guinea and the Angola Basin were conducted by Van Leeuwen (1989), based on the analysis of unstained samples from the tops of piston cores and trigger cores. Further investigations were performed on Rose Bengal stained samples recovered by box corer by Schiebel (1992) and Timm (1992) in the northern Gulf of Guinea, and Schmiedl et al. (1997) in the Angola and Cape Basins. For the present study, we investigated high-quality sediment samples collected by multiple corer on a latitudinal transect along the continental margin across the Gulf of Guinea, the Angola and the Cape Basins. Vertical and latitudinal distribution patterns of live (stained) and dead benthic foraminiferal faunas within the sediment are presented, as well as the carbon stable isotopic composition of the principal species from the study area.

2. A brief overview of benthic foraminiferal ecology

Benthic foraminifera (Kingdom PROTOCTISTA Hogg 1860, Phylum GRANULORETICULOSA De Saedeleer 1934, Class FORAMINIFERIDA Eichwald 1830; after Sen Gupta, 1999) are a diverse and successful group of shelled unicellular eukaryotic organisms. Since the first attempt of classification by d'Orbigny (1826), followed by more than one century of taxonomical investigations (e.g. Brady, 1884; Heron-Allen and Earland, 1922; Cushman, 1928), more than 2000 genera have been catalogued (Loeblich and Tappan, 1987) and the number of extant species is estimated to be about 5 000 (Debenay et al., 1996). Present in all aquatic environments, from oceanic abyssal plains to paralic environments (e.g. Debenay, 1990) and freshwater ecosystems (Holzmann and Pawlowski, 2002), benthic foraminifera are especially abundant in the deep sea, where they account for up to 50% or more of the eukaryotic biomass (Gooday et al., 1992).

While early ecological investigations in the deep sea stressed the preponderant influence on foraminiferal faunas of water depth (e.g. Bandy, 1953), and of the physicochemical composition of overlaying water masses (e.g. Streeter, 1973; Schnitker, 1980), it became progressively evident that the organic matter flux to the seafloor is a key control parameter on foraminiferal abundances, diversity, and community structure (e.g. Lutze and Coulbourn, 1984; Mackensen et al., 1985; Corliss and Chen, 1988; Altenbach and Sarnthein, 1989). The discovery of a clear succession of deep-sea foraminiferal species within the sediment, with some species preferentially concentrated over or at the resource- and oxygen-rich surface sediment, and other species well below the sediment-water interface, emphasized the dependence of foraminiferal faunas on the balance of oxygen and food availability in benthic ecosystems (Corliss, 1985; Gooday, 1986; Mackensen and Douglas, 1989; Jorissen et al., 1992; Alve and Bernhard, 1995).

Foraminifera are more tolerant to oxygen-depletion than most metazoan organisms, and many species might have a lower tolerance limit of oxygen depletion in the microxic/dysoxic range (Moodley et al., 1997; Bernhard et al., 1997; Bernhard and Sen Gupta, 1999; Gooday et al., 2001). Increasing observations of the occupancy of anoxic sediments by particular deep endobenthic taxa provided evidence that the intensity of organic matter fluxes, rather than oxygen, influences these species (e.g. Jannink et al., 1998; Jorissen et al., 1998; De Rijk et al., 2000; Schmiedl et al., 2000; Gooday et al., 2001). Other investigations demonstrated that the occupancy of distinct microhabitats by foraminiferal species is not static, but should be regarded as a dynamic strategy to optimize food acquisition (Linke and Lutze, 1993). Field observations of up and down migrations of species within the sediment were reported in response to seasonal fluctuations in the food supply and corresponding changes in the thickness of the oxygenated layer (Barmawidjaja et al., 1992; Kitazato and Ohga, 1995; Ohga and Kitazato, 1997). Other field (Silva et al., 1996; Jannink et al., 1998; Fontanier et al., 2003) and laboratory (Heinz et al., 2001, 2002) investigations reported no significant changes in species vertical distribution following seasonal or simulated phytodetritus pulses, respectively, but increases of species density at all sediment layers. Comparisons between faunal patterns and geochemical gradients within the sediment have shown that deep endobenthic taxa might be closely linked to bacterial suites associated with redox boundaries, whose activity depends on the introduction of organic matter within the sediment and, ultimately, on the organic matter flux (Jorissen et al., 1998; Fontanier et al., submitted). On the basis of these observations, it was suggested that oxygen availability may limit the maximum penetration depth of species within the sediment, whereas intensity and seasonality of organic matter fluxes influence species abundances (Jorissen, 1999a).

The knowledge of benthic foraminiferal microhabitats also opened new perspectives for the utilization of the stable isotopic signature of foraminiferal tests for paleoceanographic purposes. While the stable carbon isotopic composition of epibenthic species, such as cibicids, generally reflect the $\delta^{13}C$ values of the dissolved inorganic carbon (DIC) in overlaying bottom-waters, the $\delta^{13}C$ values of endobenthic species were shown to be influenced by the more negative $\delta^{13}C_{DIC}$ values of porewaters (e.g. Woodruff et al., 1980; Belanger et al., 1981; Grossman, 1987; Mackensen and Douglas, 1989; McCorkle et al., 1990; 1997). This is important for paleoceanographers, since it means that $\delta^{13}C$ values of epibenthic species can faithfully be used as a proxy of deep ocean paleocirculation (e.g. Duplessy et al., 1984, 1988; Curry et al., 1988; Sarnthein et al., 1994; Bickert and Wefer, 1996; Mackensen et al., 2001), while those of endobenthic species give information on the degree of oxidation of the organic matter within the sediment, and in turn, on the organic matter supply to the seafloor (e.g. Woodruff and Savin, 1985; Zahn et al., 1986; Loubere, 1987). On this basis, it was proposed to use the difference between $\delta^{13}C$ values of epibenthic and endobenthic species (benthic $\Delta\delta^{13}C$) as a measure of the organic matter flux (Zahn et al., 1986). However, the influence of productivity (Mackensen et al., 1993b; Mackensen and Bickert, 1999) and methane release (Wefer et al., 1994; Kennett et al., 2000; Rathburn et al., 2000) on the isotopic composition of benthic foraminiferal tests complicates the interpretation of the isotopic record. Furthermore, beside the accurate knowledge of species microhabitat preferences, a prerequisite for such approaches is that for a given species at a given site, there is a low variability of $\delta^{13}C$ values regardless of the actual sediment depth where single specimens are found. Until now, this was demonstrated for rather a few number of species only (Rathburn et al., 1996; McCorkle et al., 1997; Mackensen et al., 2000; Schmiedl et al., 2004).

3. Objectives and outline of this study

The principal aim of this study was to investigate the benthic foraminiferal response to drastic changes in organic matter fluxes to the seafloor, with regard to community structure and stable carbon isotopic composition. Considering that the organic carbon flux is a function of primary productivity and water depth (e.g. Suess, 1980; Berger et al., 1987), one possibility would have been to carry out bathymetrical investigations of benthic foraminiferal faunas. This approach, however, hinders the clear identification of the potential influence of different water masses on benthic foraminifera, which can especially affect epibenthic species (e.g. Schnitker, 1994; Mackensen, 1997). Therefore, in order to minimize the influence of different water mass properties, we investigated stations from a narrow depth interval mostly, and selected such that the strong productivity gradient in surface waters is almost completely documented. This strategy ensures that the flux of organic matter to the seafloor arguably is the most significantly changing environmental variable.

The main objectives of this study were:

- to describe abundance, diversity, composition, and vertical distribution of benthic foraminiferal faunas over distinct productivity provinces in the eastern South Atlantic, characterized by spatially- and seasonally-varying upwelling systems, and identify the main control parameters on these patterns;
- to investigate to which extent foraminiferal dead assemblages, as precursors of fossil assemblages, mirror the imprint of the ecological information as recorded by live faunas;
- to decipher the relationship between $\delta^{13}C$ values of live benthic foraminifera, species-specific microhabitat preferences, and environmental parameters;
- to assess paleoceanographical implications.

These objectives are addressed in four articles, which are published (chapter 1, chapter 2, and chapter 4) or to be submitted for publication (chapter 3).

Chapter 1 "Communities and microhabitat of living benthic foraminifera from the tropical East Atlantic: Impact of different productivity regimes" gives a detailed analysis of changes in species composition and vertical distribution within the sediment of benthic foraminiferal faunas at six stations. Several distinct types of foraminiferal microhabitats are recognized with regard to trophic conditions, and to the gradient of oxygen and nitrate in porewater. A special attention is given to the distribution patterns of *Melonis barleeanum,* an endobenthic species considered to preferentially seek bacterial suites involved in the remineralization of the organic matter within the sediment.

Chapter 2 "Benthic foraminifera off West Africa (1°N to 32°S): Do assemblages from the topmost sediment reliably record environmental variability?" presents a comparison between live and dead foraminiferal assemblages, to assess the extent of the post-mortem alteration of the ecological signal recorded by live species. The reliability of foraminiferal assemblages as estimated from the uppermost centimeter of sediment only, commonly used as modern reference data sets for paleoceanographic purposes, is put to the test.

Chapter 3 "Vertical sediment occupancy by benthic foraminifera between 3°N and 32°S off West Africa and paleoceanographic implications" examines the main changes in the vertical succession of foraminiferal species into distinct microhabitats from the Gulf of Guinea to the Cape Basin, in the view of the insights gained in chapter 1. This chapter includes a description of foraminiferal abundance and diversity patterns in the study area, as well as of the microhabitat preferences of principal species. These patterns are discussed with emphasis on the availability of food and oxygen within the sediment. Implications of these observations for the quantification of past bottom-water oxygenation and the interpretation of fossil stable isotopic signatures are discussed.

Chapter 4 "Carbon isotopes of live benthic foraminifera from the South Atlantic: Sensitivity to bottom water carbonate saturation state and organic matter rain rates" compiles new $\delta^{13}C$ values of benthic foraminifera from the West African continental slope with previously published data of Mackensen et al. (2000), close to Bouvet Island in the Southern Ocean. This paper investigates the influence of changing environmental conditions on the intra- and interspecific variability of the foraminiferal $\delta^{13}C$ record within the sediment and over latitude.

Chapter 5 presents a synthesis of the most important conclusions of this study. Some future perspectives are proposed.

1. Communities and microhabitats of living benthic foraminifera from the tropical East Atlantic: Impact of different productivity regimes

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1.1. Abstract

Living (Rose Bengal stained) benthic foraminifera were collected with a multicorer from six stations between 3°N and 12°S off West Africa. The foraminiferal communities in the investigated area reflect the direct influence of different productivity regimes, which are characterized by a spatially and seasonally varying upwelling activity. At five stations, the foraminiferal abundance coincides well with the gradient of surface productivity. However, at one station off the Congo River, the influence of strong fresh water discharge is documented. Although this station lies directly in the center of an upwelling area, foraminiferal standing stocks are surprisingly low. It is suggested that the Congo discharge may induce a fractionation of the organic matter into small and light particles of low nutritional content, in contrast to the relatively fast-sinking aggregates found in the centers of high productivity areas.

Quality and quantity of the organic matter seem to influence the distribution of microhabitats as well. The flux of organic carbon to the seafloor controls the sequence of degradation of organic matter in sediment and the position of different redox fronts. The vertical foraminiferal stratification within sediment closely parallels the distribution of oxygen and nitrate in porewater, and reflects different nutritive strategies and adaptation to different types of organic matter. The epifauna and shallow infauna colonize oxygenated sediments where labile organic matter is available. The intermediate infauna (*Melonis barleeanum*) is linked to the zone of nitrate reduction in sediments where epifaunal and shallow infaunal species are not competitive anymore, and must feed on bacterial biomass or on metabolizable nutritious particles produced by bacterial degradation of more refractory organic matter. The deep infauna shows its maximum distribution in anoxic sediments, where no easily metabolizable organic matter is available.

1.2. Introduction

The use of fossil benthic foraminifera appears especially promising in the reconstruction of the paleoflux of organic carbon to the seafloor and in the estimation of benthic oxygenation, but the key to the interpretation of fossil records is obviously linked to the knowledge of the ecology of modern foraminifera. The observation of a vertical partitioning of deep-sea foraminifera within sediment (Corliss, 1985) has greatly emphasized the importance of a better understanding of living foraminifera for paleoceanographic reconstructions (Berger and Wefer, 1988), and is essential for a correct interpretation of stable carbon isotope records in benthic foraminifera (Woodruff et al., 1980; Grossman, 1984; McCorkle et al., 1990; Chandler et al., 1996). It also provides important information about surface productivity and ventilation of the deep-sea. Different microhabitat preferences imply adaptation to drastically different environmental conditions within sediment and different nutritive requirements and strategies. It is now widely accepted that the two main parameters controlling benthic foraminiferal vertical distribution and general community structure are the amount of organic matter and the availability of oxygen at the bottom and in porewater.

Global atmospheric CO_2 content is strongly linked to the strength of the "biological pump" in the surface ocean (Volk and Hoffert, 1985). Large changes of productivity during glacial-interglacial cycles have been documented in the low latitude upwelling regions (see e.g. Berger et al., 1994; Rühlemann et al. 1999), which play an important role in the global carbon cycle. In this study, we present a detailed description of six live (Rose Bengal stained) benthic foraminiferal communities off West Africa, sampled in an area characterized by a complex hydrological situation and a highly seasonal system of several oceanic and coastal upwelling zones. Five of the selected stations lie between 1200 and 1300 m water depth, so that water depth effects may be reasonably neglected as a factor influencing the investigated faunas at these stations. Moreover, the effects of water mass properties changes are negligible as well. Foraminiferal standing stocks and assemblages, and the vertical distribution of species in the sediment are examined. Specific microhabitat preferences of assemblages and species are compared to the distribution of oxygen and nitrate in the porewater.

1.3. Environmental setting

1.3.1. Hydrography

The area of investigation is located in the equatorial and tropical eastern South Atlantic Ocean, off West Africa (Fig. 1). Van Bennekom and Berger (1984) and Peterson and Stramma (1991) give detailed descriptions of the surface and subsurface hydrography of the South Atlantic. The surface circulation is complicated by the interaction of the equatorial current system with the main currents of the South Atlantic subtropical gyre.

In the Angola Basin, the wind driven surface circulation is dominated by two major currents. The eastward South Equatorial Counter Current (SECC) flows between 5-14°S, and splits towards the African coast into a southern and a northern branch (Fig. 1). Its southern offshoot, the warm Angola Current (AC), flows along the Angola margin where it meets at around 15-17°S the other main component of the system, the cool and oppositely-directed coastal branch of the Benguela Current (BCC). This results in a convergence zone, the Angola-Benguela-Front (ABF; Shannon et al., 1987), north of which the BCC flows as a narrow subsurface tongue up to 5°S (Van Bennekom and Berger, 1984). The northern part of the SECC mixes with these extensions of the BCC (Van Bennekom and Berger, 1984) and forms a small anticyclonic gyre south of the Congo plume at 7.5°S and 9.5°E (Moroshkin et al., 1970).

Together, the SECC, the AC, and the offshore branch of the Benguela Current (BOC) form the boundaries of a quasi-stationary cyclonic gyre centered in the Angola Basin near 13°S and 5°E (Gordon and Bosley, 1991), which transports warm water of high salinity and low nutrient content to the southeast.

On the western edge of the Gulf of Guinea, the circulation is dominated by the northern boundary of the South Atlantic subtropical gyre, the South Equatorial Current (SEC), which flows westward to South America and is divided into two branches separated by the Equatorial Divergence Zone (EDZ). Underlying the SEC between 50 and 100 m water depth, the Equatorial Undercurrent (EUC) flows as a narrow eastward-flowing current. Together with the North and South Equatorial Undercurrents (NEUC & SEUC respectively, around 100 m water depth), it carries into the Gulf of Guinea relatively nutrient-rich, cold, salt- and oxygen poor South Atlantic Central Water (SACW). Parallel to the coast, the Guinea Current (GC) flows to the east (Van Leeuwen, 1989).

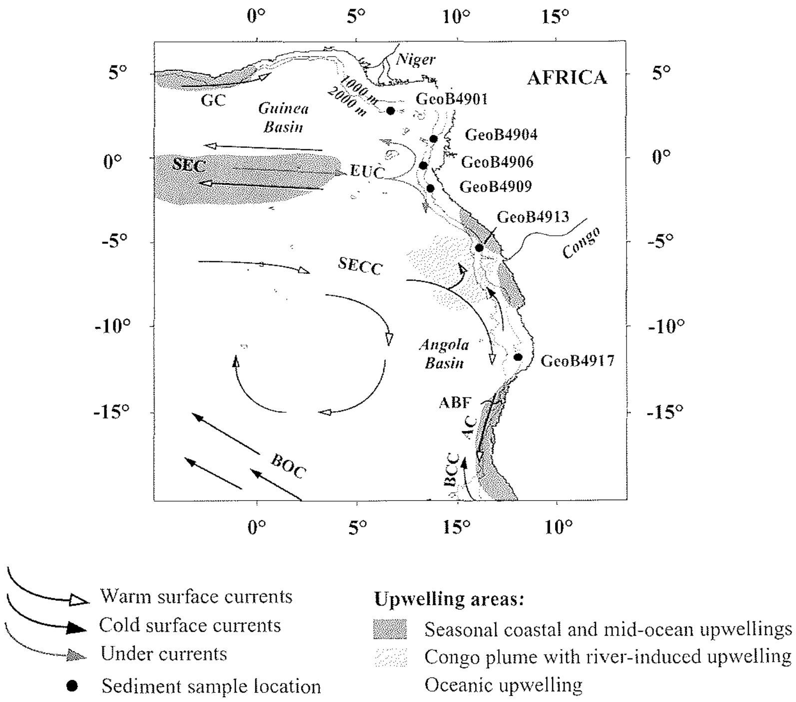

Figure 1. Sample location, surface hydrography, and different upwelling areas in the eastern South Atlantic Ocean. ABF: *Angola-Benguela Front*, AC: *Angola Current*, BCC: *Benguela Coastal Current*, BOC: *Benguela Oceanic Current*, EUC: *Equatorial Under Current*, GC: *Guinea Current*, SEC: *South Equatorial Current*, SECC: *South Equatorial Counter Current* (after Moroshkin et al., 1970, Voituriez and Herbland, 1982; Van Bennekom and Berger, 1984; Lutjeharms and Meeuwis, 1987, Stramma and Schott, 1999).

All samples but one were taken from a narrow interval between 1200 and 1300 m water depth (Table 1). In terms of water masses, these stations are therefore located at the boundary between the Antarctic Intermediate Water (AAIW) and the North Atlantic Deep Water (NADW). The deepest station GeoB4901 is bathed by the NADW (Reid, 1989).

1.3.2. Ocean Surface Productivity

Life on and within oceanic sediments almost entirely depends on the flux of organic matter reaching the ocean floor from the euphotic layer. In the eastern South Atlantic, several systems of permanent and seasonal upwelling cells generate productivities that vary significantly in time and space (Lutjeharms and Meeuwis, 1987). Three high productivity centers can be distinguished in the tropical part of the Angola Basin: the Equatorial Divergence Zone (EDZ), the area of the Congo plume, and the region south of this river mouth (Fig. 1).

At the equator, strong seasonal variations in the trade winds produce a highly fluctuating system. A warm season occurs in the eastern equatorial Atlantic during boreal winter; trade winds cease and SEC speed is at its minimum; slowly upwelled waters provide few nutrients to the photic zone, where productivity is reduced. In boreal summer, trade winds and SEC speed reach their maximum and strong upwelling takes place at the equator, bringing cold and nutrient-rich water to the surface.

As described by Eisma and Van Bennekom (1978), the rapid freshwater outflow of the Congo River at 6°S, forced by a narrow estuary, induces upwelling at the river mouth by entrainment of cool subsurface oceanic waters rich in phosphate and nitrate (Van Bennekom et al., 1978). Around 11°E and large areas off the Congo river in general, the input of nutrients from the river and from river-induced upwelling are assumed to generate a maximum in primary production. Two highly seasonal upwelling cells also take place in coastal waters north and south of the Congo River, at 5° and 7°S, and are considered to be related to the eastward flowing EUC (Voituriez and Herbland, 1982) and to the advection and vertical spreading of SACW (Verstraete, 1987).

Additionally, the complex system of fronts, gyres, and thermal domes generated between 10° and 15°S off Angola by the interaction between SECC, AC and BCC results in seasonal oceanic upwelling (Peterson and Stramma, 1991; Stramma and Schott, 1999). South of the ABF, between 15°-20°S and 34°S, southerly and southeasterly trade winds induce permanent intense coastal upwelling cells (Lutjeharms and Meeuwis, 1987).

This general scheme, schematically illustrated in Fig. 1, is in good agreement with global maps of primary productivity estimates (calculated after Behrenfeld and Falkowski, 1997) based on recent satellite chlorophyll data (maps based on SeaWIFs chlorophyll data from September 1997 to August 1999; http://marine.rutgers.edu/opp/). According to these maps, annual primary productivity values increase from 180 gC m^{-2} y^{-1} in the north Guinea Basin to 450 gC m^{-2} y^{-1} in the Angola Basin. Recent compilations of data from the literature (Berger, 1989) give lower productivity values: from 90-125 gC m^{-2} y^{-1} over large areas off Congo to 180 gC m^{-2} y^{-1} south of 10°S. In the permanent upwelling area, productivity values exceed 200 gC m^{-2} y^{-1} (Hagen et al., 1981).

The remineralization of organic material below the high productivity areas and off the river mouths leads to the formation of an oxygen minimum zone (OMZ), which is strongly developed south of the investigated area. The OMZ reaches its largest extension off the Cunene River (around 17°S), where it extends between 50 and 1200 m water depth with an oxygen minimum value of 1ml l^{-1}. The intensity of the OMZ decreases progressively northward (Schulz and cruise participants, 1992).

1.4. Material and methods

Material for both geochemical and foraminiferal analysis were collected during the cruise M41/1 (February-March 1998; Table 1) of the research vessel *Meteor* in the area of the Niger fan and the Bight of Bonny (Schulz and cruise participants, 1998).

Table 1. Surface sediment samples used for this study with sampling date, number of sampled subcores, position, water depth, organic carbon content, oxygen content of bottom water, and oxygen maximum penetration depth within the sediment.

Station	*Date of sampling (1998)*	*Subcores sampled*	*Latitude*	*Longitude*	*Depth (m)*	*TOC * (%) in the first 0.5 cm*	*Bottom water O_2 (μMol l^{-1})*	*O_2 maximum penetration depth in the sediment (determined from microprofiles)*
GeoB4901-6	26/02	2	2°40.7´N	6°43.2´E	2186	1.46	233	> 8 cm
GeoB4904-7	28/02	1	0°57.6´N	8°52.8´E	1341	-	208.5	2 cm
GeoB4906-5	02/03	2	0°41.4´S	8°22.9´E	1249	3.01	184	2.2 cm
GeoB4909-4	04/03	2	2°04.2´S	8°37.5´E	1308	2.02	183	3 cm
GeoB4913-4	06/03	2	5°30.2´S	11°04.3´E	1297	3.54	194	1.8 cm
GeoB4917-5	10/03	2	11°54.2´S	13°04.4´E	1301	-	189.5	1.6 cm

(* Strotmann personal communication, 1998)

1.4.1. Geochemistry

Oxygen data presented for all stations were obtained in situ (except station GeoB4904) with a 100 μm step resolution and using a benthic profiling lander equipped with oxygen microelectrodes (Gundersen and Jørgensen, 1990; Wenzhöfer et al., 2001). At station GeoB4904, data were obtained by laboratory measurements on multicores incubated at in situ temperature and bottom water oxygen concentration (Rasmussen and Jørgensen, 1992).

The benthic nitrate concentration profiles were determined on porewater samples from multicorers. In order to re-establish in situ temperatures on board after a transient heating during recovery through the water column, the sediments were immediately stored in a cooling laboratory at ca. 4°C. Porewater was extracted using a Teflon squeezer with 0.2 μm membrane filters. Within a few hours after recovery, nitrate (nitrate plus nitrite) concentrations were determined with an autoanalyser using standard photometrical procedures described by Grasshoff et al. (1999). Porewater data are given in Tables A1 and A2 of the appendix.

1.4.2. Counting of benthic foraminifera

We investigated the benthic foraminiferal faunas in undisturbed sediment samples retrieved with a multicorer (Barnett et al., 1984) at six stations off West Africa (Table 1). At all stations (except station GeoB4904), two subcores (with a surface area of 78.5 cm^2 each) were collected and subsampled in 1 cm thick slices. Subsamples corresponding to the same depth in the sediment were put together, stained with a mixture of 95% ethanol and 1g l^{-1} Rose Bengal and kept cool at 4°C until further treatment (Walton, 1952; Lutze, 1964). At station GeoB4904, only one single subcore was subsampled.

Onshore, samples were sieved through 63 and 125 μm mesh screens. Since many paleoceanographic studies use 125 μm as a lower limit, only that size fraction was investigated, keeping in mind that smaller foraminifera, however, may provide additional information (Schröder et al., 1987). Based on different splits, living and dead benthic foraminifera were counted separately from dried samples in the uppermost 10 cm of sediment. About 300 specimens per sample were counted; when less than 300 specimens occured, all individuals were counted. In this paper, we present only the results obtained for the living faunas.

The reliability of the use of the "non vital stain" Rose Bengal (Bernhard and Sen Gupta, 1999) for the quantification of living foraminifera has been extensively discussed (e.g. Bernhard, 1988; Jorissen et al., 1995). This method has been estimated to be appropriate for the recognition of foraminiferal biomass on a level of 97% (Lutze and Altenbach, 1991), and is still the easiest way to quantify living foraminiferal faunas (see Murray and Bowser, 2000, for review).

Another contentious point concerns the quantification of easily fragmented tubular species belonging to arborescent genera such as *Astrorhiza*, *Hyperammina*, *Rhizammina*, *Sacchoriza* or *Tolypammina*. Several authors have counted three to five size-standardized fragments of tubular agglutinated forms to gain a semi-quantitative estimation of the real number of specimens (Mackensen et al., 1993; Schmiedl et al., 1997; Wollenburg and Mackensen, 1998; Kurbjeweit et al., 2000). Because numerous fragments may represent only a small number of individuals, we decided to exclude these species from the total number of individuals per sample in this paper (Jorissen et al., 1995; De Stigter et al., 1998). In the following text, "agglutinated foraminifera" or "agglutinated species" refers exclusively to nontubular forms.

We standardized living foraminifera counts to a surface of 50 cm^2 for standing stock analysis. We used the Shannon-Wiener index H(S) (with S being the maximum number of counted species) and the equitability index E to determine species diversity and equitability, respectively (Buzas and Gibson, 1969).

Species representing more than 5% of the total fauna were considered to be important species, while those representing less than 1% of the total fauna were considered non-significant and omitted from final interpretation (e.g., Mackensen et al., 1990; Schmiedl et al., 1997). Counts and total percentages of significant species are given in the appendix. The index of maximum depth, defined by Shirayama (1984) as the depth of the 95% cumulative abundance, was used for a general overview of foraminiferal vertical distribution. We followed the classification of aquatic environments and corresponding biofaces of Tyson and Pearson (1991) to compare foraminiferal microhabitats and dissolved oxygen in porewater. This classification defines oxic (aerobic biofacies, 8.0-2.0 ml l^{-1} O_2), dysoxic (dysaerobic, 2.0-0.2 ml l^{-1} O_2), suboxic (quasi anaerobic, 0.2-0.0 ml l^{-1} O_2) and anoxic (anaerobic, 0.0 ml l^{-1} O_2) environments. The taxonomic classification follows Schröder (1986), Loeblich and Tappan (1988), and Jones (1994).

1.5. Results

1.5.1. Standing stocks and faunal composition

The main characteristics of the foraminiferal faunas are given in Table 2. Total foraminiferal standing stocks varied between 48 and 930 living (stained) specimens per 50 cm^2 of sediment surface. At stations GeoB4904, GeoB4906, and GeoB4909, an average of 250 specimens/50 cm^2 were counted, whereas at station GeoB4917, from a similar water depth, numbers were more than 3 times higher. At the other extreme, at station GeoB4913 and the deepest site GeoB4901, off the Congo and Niger River fans respectively, we found remarkably low standing stocks of 48 and 67 specimens/50 cm^2 (Fig. 2; Table 2).

The investigated faunas mainly consisted of agglutinated and calcareous perforate foraminifera (Fig. 2; Table 2). Significant numbers of porcellaneous taxa were found at four stations: GeoB4904, GeoB4906, GeoB4909 and particularly GeoB4917. The similarity between stations GeoB4904, GeoB4906 and GeoB4909, where the relative abundance of agglutinated and calcareous perforate taxa in the living fauna is roughly equal to 50%, is remarkable. On the contrary, stations GeoB4901 and GeoB4913 were dominated by agglutinated foraminifera. This is especially true for station GeoB4913, where agglutinated foraminifera made up to 73% of the population. The other extreme is represented by station GeoB4917, which was dominated by perforate species. Here, calcareous species in general (i.e., perforate and porcellaneous taxa together) comprised almost 70% of the foraminiferal fauna.

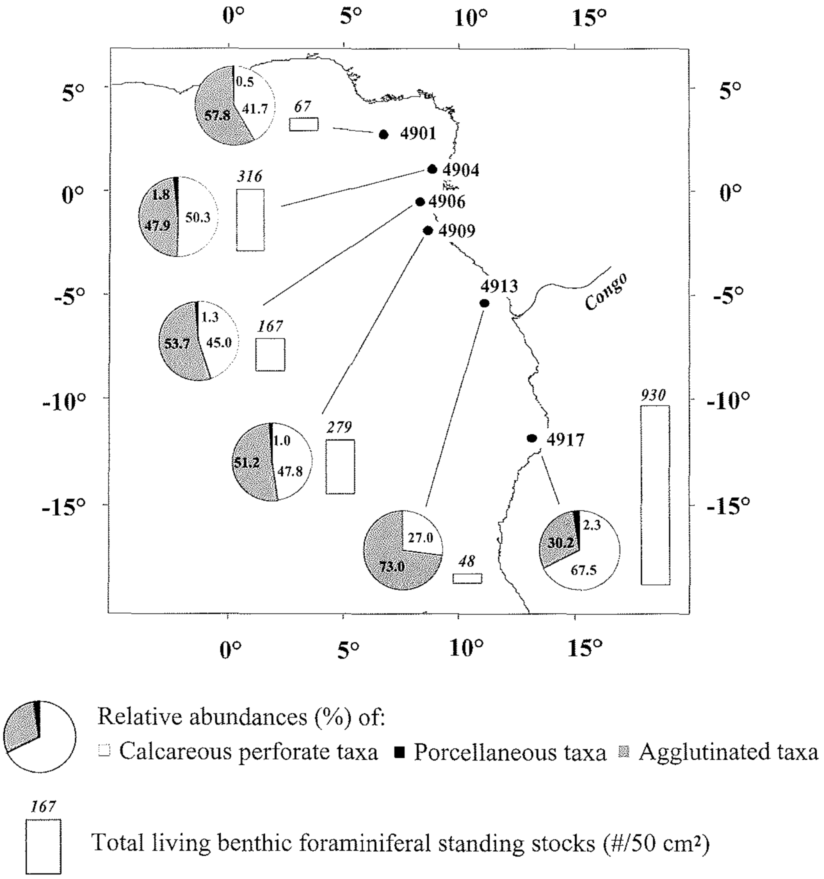

Figure 2. Relative abundances of major taxa groups of benthic foraminifera (%) and total standing stocks (#/50 cm^2; see Table 2).

Stations GeoB4904, GeoB4906, GeoB4909 and GeoB4917 showed no significant differences in ecological parameters (Table 2). Diversity, expressed by the Shannon-Wiener index, as well as the maximum number of species, were very similar. Stations GeoB4901 and GeoB4913 showed, in comparison, a lower diversity, expressed by a significant decrease of both parameters S and H(S).

Table 2. Some characteristics of foraminiferal faunas: foraminiferal counts, standing stocks, number of species, diversity and equitability (calculated after Buzas and Gibson, 1969), relative abundance of perforate, porcellaneous and agglutinated taxa, living maximum depth of total fauna, perforate and agglutinated taxa (calculated after Shirayama, 1984).

	Foraminiferal counts live (>125µm)		*Foraminiferal standing stocks (>125µm)*		*Ecological parameters*			*Relative abundance (%) of :*			*living foraminifera maximum depth (depth of 95% cumulative)*		
GeoB Station	*surface cm*	*down to 8 cm*	*surface cm (50 cm^3)*	*down to 8 cm (50 cm^2)*	*Maximum number of species S*	*Shannon-Wiener index H(S)*	*Equitability index E(S)*	*perforate calcareous taxa*	*porcellaneous taxa*	*agglutinated taxa*	*total fauna*	*perforate calcareous taxa*	*agglutinated taxa*
4901-6	111	211	35	67	27	2.2	0.36	41.7	0.5	57.8	2.7 cm	2.5 cm	2.8 cm
4904-7	201	496	128	316	74	3.6	0.47	50.3	1.8	47.9	6.0 cm	4.8 cm	6.6 cm
4906-5	220	522	70	167	62	3.2	0.42	45.0	1.3	53.7	2.8 cm	2.8 cm	2.8 cm
4909-4	544	875	173	279	76	3.4	0.42	47.8	1.0	51.2	3.1 cm	3.7 cm	3.3 cm
4913-4	71	152	23	48	33	2.8	0.52	29.0	-	73.0	4.3 cm	4.4 cm	4.2 cm
4917-5	1768	2920	563	930	89	3.3	0.30	67.5	2.3	30.2	3.6 cm	3.4 cm	4.1 cm

Important differences in the assemblage composition were found between stations (Table A3 of the appendix). Stations GeoB4901, GeoB4904, GeoB4906 and GeoB4909, all close to the equator, were dominated by *Robertinoides chapmani*, *Reophax scorpiurus*, *Reophax bilocularis* and *Lagenammina difflugiformis*. These four omnipresent species were however associated with different species at each station. At station GeoB4901 for example, *R. scorpiurus* and *R. chapmani* together comprised almost 60% of the total fauna, while *Lagenammina difflugiformis* and *Hoeglundina elegans* were common. Stations GeoB4906 and GeoB4909 were both characterized by the presence of *Uvigerina peregrina*. Station GeoB4906 was also characterized by *Ammomarginulina foliacea* and *Lagenammina tubulata*, whereas *H. elegans*, *Gavelinopsis translucens* and *Ammoscalaria* sp. completed the list of dominant species found at station GeoB4909. GeoB4904 was characterized by *G. translucens, A. foliacea*, and *Melonis barleeanum*.

The fauna at station GeoB4913 differed from the others by the occurrence, in order of importance, of: *Cribrostomoides jeffreysi*, together with *Ammoscalaria* sp., *A. foliacea, Uvigerina peregrina* and *Bulimina alazanensis*. Some of the species common at the other stations were still present in small numbers (*R. scorpiurus, L. difflugiformis, G. translucens*), but others were absent (*R. chapmani, R. bilocularis, M. barleeanum*).

At the southernmost site GeoB4917, *Bulimina mexicana, U. peregrina, L. difflugiformis, Epistominella smithi, R. bilocularis,* and *Valvulineria laevigata* characterized the densest fauna investigated (Table 2).

1.5.2. Vertical distribution within sediment

At sites GeoB4904, GeoB4906, GeoB4909, GeoB4913, and GeoB4917, the profiles of dissolved oxygen in porewater were very similar (Fig. 3). The oxygen concentrations were close to 4ml l^{-1} at the sediment-water interface, and decreased along a steep gradient within sediment. The maximum penetration depth of oxygen in the sediment (defined as the depth where dissolved oxygen value drops to 0) varied from 1.5 cm at stations GeoB4913 and GeoB4917 to slightly more than 2 cm at station GeoB4909 (Table 1). The sediments at station GeoB4901 were better oxygenated (> 5ml l^{-1} at the sediment-water interface). Here oxygen concentration decreased slowly within sediment down to more than 8 cm depth (Fig. 3; Table 1).

At all stations, clear maxima of foraminifera occured in the topmost centimeter, in highly oxygenated sediments, rapidly followed by an exponential decrease that paralleled the decrease of oxygen (Fig. 3). Hence, in the transect from GeoB4904 to GeoB4917, 50% to almost 80% of the total fauna lived in oxic to moderately dysoxic sediment. However, we found significant numbers of stained specimens at deep levels (9% to 24% in strongly to extremely dysoxic sediments; 5% to 15% in suboxic sediments), and even in sediment theoretically devoid of oxygen (5% to 35% in anoxic sediments). This was particularly evident at station GeoB4904, where stained foraminifera occurred down to 8 cm depth (Fig. 3). Also, the maximum habitat depth values obtained at station GeoB4904 were clearly deeper than at the other sites (Table 2). At station GeoB4901, oxygen penetrated so deep in the sediment that almost all living foraminifera occurred in the oxic part of the core (Fig. 3).

The vertical distribution of foraminiferal species within sediment was variable. We recognized several types of vertical profiles in the sediment, and distinguished four basic categories traditionally known from the literature (see Jorissen, 1999, for review): epifauna, shallow infauna, intermediate infauna and deep infauna. Figures

4a to 4d show, for all stations, the vertical distribution of some species typically representative of each category.

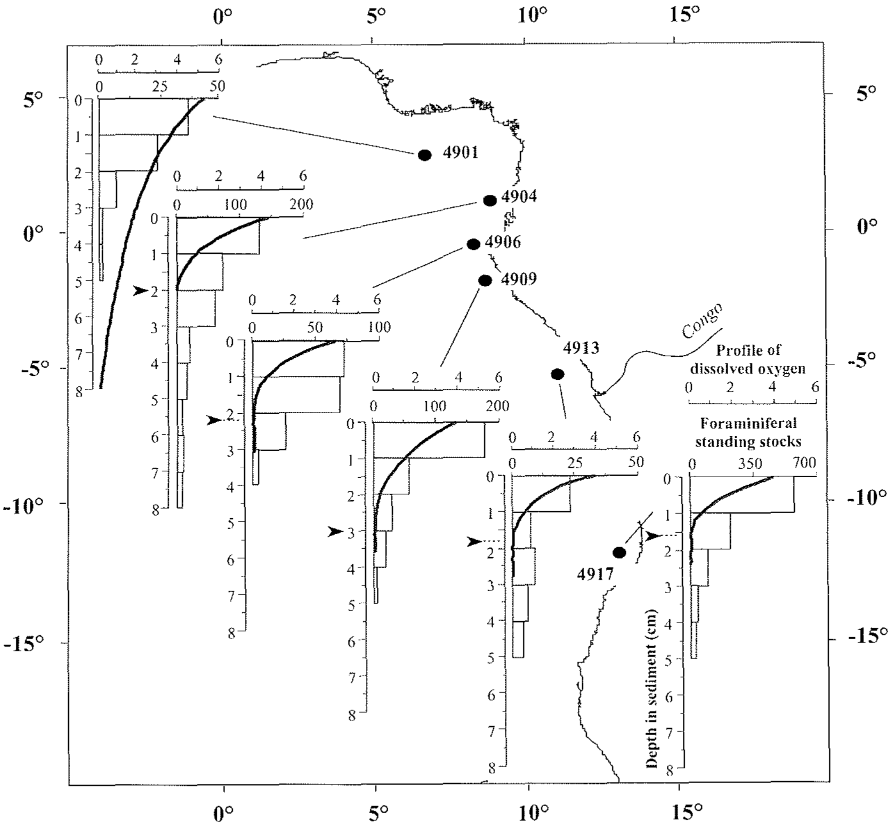

Figure 3. Vertical distribution of foraminiferal standing stocks within the sediment (#/50cm^3) and profiles of dissolved oxygen in pore water (ml l^{-1}). The arrows indicate the sediment depth where dissolved oxygen value drops to zero (Table A1 in the appendix).

Most of the species occurring along the transect consistently showed the same microhabitat preference at all stations (Table A10 in the appendix). The microhabitat label attributed to these species in Table 3 summarizes their average downcore distribution. Species showing occasionally clear preferences for an infaunal niche, such as *B. mexicana and Uvigerina auberiana / hispida* at station GeoB4917, *A. foliacea* at station GeoB4904, or *R. micaceus*, were considered tolerant of conditions found deeper in sediment and therefore classified as shallow infauna.

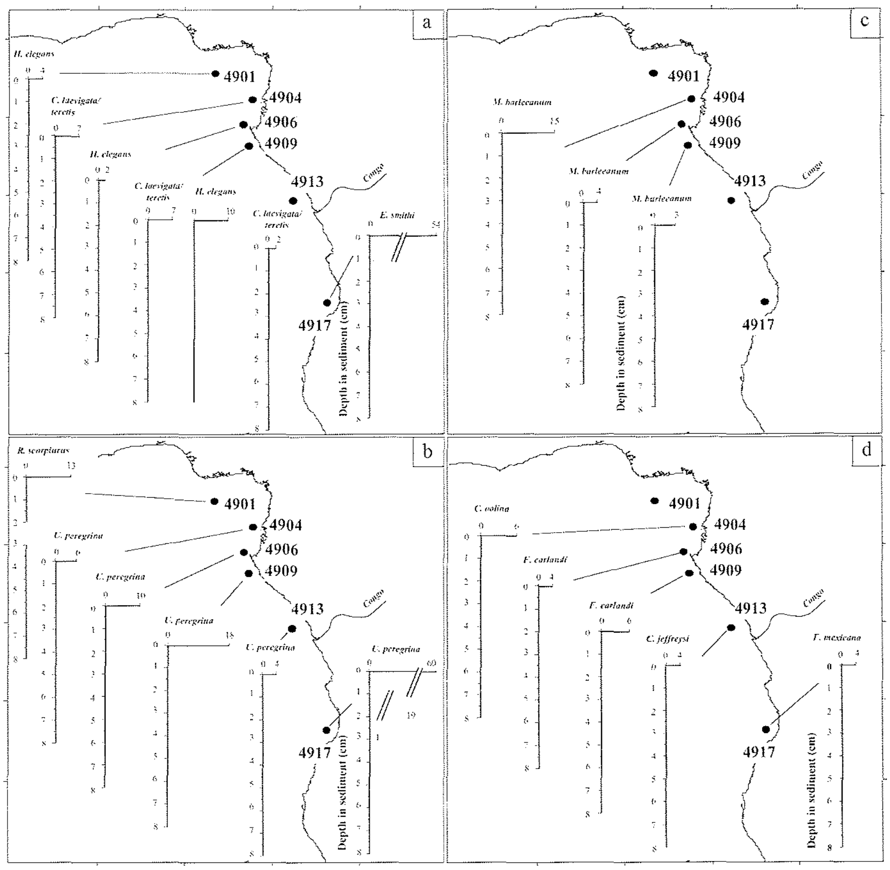

Figure 4. Vertical profiles of foraminiferal standing stocks of typical examples of (a) epifaunal species, (b) shallow infaunal species, (c) intermediate infaunal species, and (d) deep infaunal species (Table 3; Table A10 in the appendix). All stations except GeoB4913: #/50cm^3, station GeoB4913: #/100cm^3.

Applying these concepts, we were able to attribute a microhabitat label to 76% to 91% of all significant species. The relative importance of each microhabitat category at each station is given in Fig. 5. Important shifts in the general distribution of microhabitat categories take place between station GeoB4901 in the north and station GeoB4917 in the south. Epifaunal species were omnipresent along the north-south transect, but showed higher proportions at stations GeoB4901, GeoB4909 and particularly at station GeoB4913. Overall, shallow infaunal species accounted for 60% to more than 80% of the total fauna.

Table 3. Average microhabitat preference of species >2% at least in one station in the studied area. The microhabitat preferences distribution of all significant species occuring at several locations is summarized for the whole transect in Table A10 in the appendix. *Since deep infauna species are important for paleoceanographic reconstruction, *Fursenkoina mexicana* (relative abundance: 1.20% at station GeoB4917) was also listed.

Epifauna	Shallow infauna	Intermediate infauna	Deep infauna
Ammolagena clavata *Cassidulina laevigata / teretis* *Cribrostomoides wiesneri* *Epistominella smithi* *Hoeglundina elegans* *Uvigerina proboscidea*	*Ammodiscus incertus* *Ammomarginulina foliacea* *Ammoscalaria* sp. *Bulimina aculeata* *Bulimina alazanensis* *Bulimina mexicana* *Eggerella scabra* *Gavelinopsis translucens* *Lagenammina difflugiformis* *Lagenammina tubulata* *Reophax bilocularis* *Reophax micaceus* *Reophax scorpiurus* *Robertinoides chapmani* *Sphaeroidina bulloides* *Uvigerina auberiana / hispida* *Uvigerina peregrina* *Valvulineria laevigata*	*Melonis barleeanum* *Reophax dentaliniformis*	*Chilostomella oolina* *Cribrostomoides jeffreysi* *Fursenkoina earlandi* *Fursenkoina mexicana* * *Globobulimina pacifica* *Nouria harrisii*

The scarcity of intermediate and deep infauna in the samples is remarkable. The few species belonging to the intermediate infauna only occurred at stations GeoB4904, GeoB4906 and GeoB4909 near the equator. Although nearly insignificant at station GeoB4901, intermediate species showed highest amounts at station GeoB4904. Their relative abundance was more than halved from station GeoB4904 to station GeoB4906, and then again from station GeoB4906 to station GeoB4909.

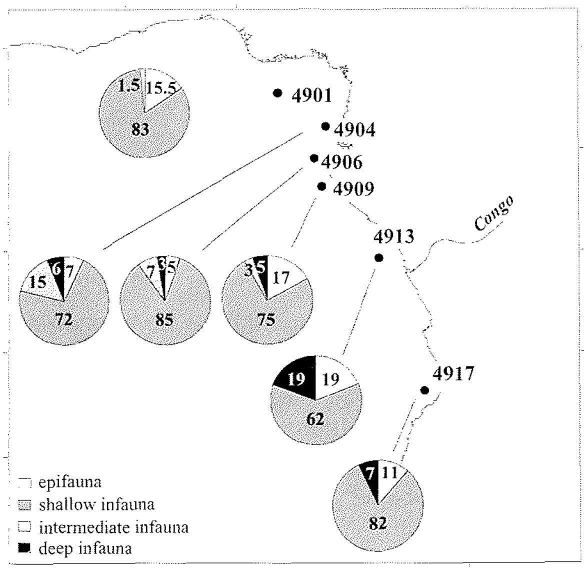

Figure 5. Relative abundances (%) of microhabitat categories along the transect.

The proportion of deep infaunal species also showed great variability between stations. The highest numbers of deep infaunal species were found at station GeoB4913 (ca. 3 times higher than any other site). Deep infaunal species were absent from station Geob4901, but accounted for 3% to 7% at stations GeoB4904, GeoB4906, GeoB4909 and GeoB4917.

1.6. Discussion

1.6.1. Relative importance of food and oxygen

Lutze and Coulbourn (1984) showed that a lateral gradient exists within benthic foraminiferal communities on the continental margin off northwestern Africa. Here, we show that important latitudinal changes take place within deep-sea benthic foraminiferal faunas off equatorial and southwest Africa, in terms of both abundance and faunal composition, and microhabitat occupation.

Food availability appears to exert a major influence on foraminiferal abundance and assemblages (e.g. Van der Zwaan, 1982; Gooday, 1986; Corliss and Chen, 1988; Gooday and Lambshead, 1989; Mackensen et al., 1995), as well as on their vertical distribution in the sediment (e.g. Corliss and Emerson, 1990; Jorissen et al., 1992; Loubere et al., 1993; Jorissen et al., 1995). A close correspondance between foraminiferal density, surface productivity and organic flux to the sea floor has been suggested (Lutze and Coulbourn, 1984; Altenbach and Sarnthein, 1989; Herguera and Berger, 1991; Loubere, 1991; Altenbach, 1992; Loubere, 1994; Fariduddin and Loubere, 1997; Loubere and Fariduddin, 1999), and confirmed by laboratory experiments (Heinz et al., 2001).

The importance of dissolved oxygen content of bottom and/or porewater as a limiting factor for the distribution of species is still controversial. Several field studies suggest that oxygen is not a critical factor for all taxa, since significant standing stocks of foraminifera apparently live in suboxic to anoxic sediments (Bernhard, 1989, 1992; review in Bernhard and Sen Gupta, 1999), and even in the presence of hydrogen sulfide or hydrocarbon seeps (Bernhard, 1993; Moodley et al., 1998a). Laboratory studies tend to confirm this resistance to extreme conditions (Moodley et al., 1998b). On the other hand, oxygen may play a role in determining the lower downward penetration of epifaunal and shallow infaunal species in the sediment. The TROX-model developed by Jorissen et al. (1995) summarizes the close interplay between food availability and oxygen concentration on the control of foraminiferal depth distributions. More recently, Van der Zwaan et al. (1999) proposed a TROX-2 model, which emphasizes the role of the flux of organic matter in regulating processes affecting both foraminiferal distributions and abundances.

In this study, significant numbers of foraminifera were found at depths where the sediment is free of oxygen. Oxic, dysoxic, suboxic, and anoxic sediments, as defined in terms of dissolved oxygen by Tyson and Pearson (1991), were all colonized by foraminifera. However, except at station GeoB4901 where oxygen penetrated very deep into the sediment, the largest changes in oxygen content occurred in the uppermost centimeter of the cores. Since 1 cm was the sampling interval for foraminiferal analysis applied in this study, the parallel between the two parameters (oxygen profile and faunal vertical distribution) was difficult to establish precisely. Therefore, a thinner sample interval would have probably been more appropriate, at least for the first few uppermost centimeters of sediment. Nevertheless, since all stations except GeoB4901 show nearly similar profiles of dissolved oxygen in porewater, we suggest that, in the investigated area, oxygen is not the primary parameter controlling foraminiferal faunas. Moreover, since oxygen and nutritional conditions have been recognized to be the most important factors structuring deep-sea benthic foraminiferal communities, we suggest that food is the principal factor likely explaining the observed change of foraminiferal communities off equatorial and tropical West Africa.

With regard to standing stocks (Fig. 2), faunal composition (Fig.2, Table A3) and microhabitat distribution (Fig. 5), the studied stations can be arranged in three geographically distinct groups: (1) an equatorial group (stations GeoB4901, GeoB4904, GeoB4906, GeoB4909), (2) an off Congo-river group (station GeoB4913), and (3) an Angola Basin group (station GeoB4917). This correlates well with the different upwelling areas. Consequently, our working hypothesis is that these different faunal groups mirror the direct influence of the coastal gradient of productivity, which is affected by different hydrographies.

1.6.2. Foraminiferal standing stocks

At stations near the equator, the lowest standing stocks were recorded at station GeoB4901. Station GeoB4901 is located at a water depth about twice as deep as the other stations of the transect, and is therefore the only station where differences in benthic foraminiferal fauna in comparison to other stations may likely be linked to bathymetry. The influence of water depth on benthic foraminiferal standing stocks has been documented (De Stigter et al., 1998). Assuming that the size of the benthic foraminiferal population is directly related to the export of organic matter from the surface (Altenbach and Sarnthein, 1989), the proportional depth-related decrease of organic matter flux to the sea floor is given by the equation of Berger et al. (1987), which best fits to water depths >1000 m (Berger, 1989):

$$J(z) = (17 * Psw / z) + (Psw / 100),$$

where $J(z)$=the organic matter flux at water depth (z), and Psw=the surface water productivity. $J(z)$ was calculated for all stations from annual primary productivity estimates based on satellite chlorophyll data, and from values taken from the literature. Both types of productivity values and the corresponding calculated fluxes are summarized in Table 4.

Although satellite-based maps give productivity values much higher than Berger (1989), productivity patterns generally agree. Discrepancies occur for stations GeoB4901 and GeoB4913. While Berger's (1989) maps give similar productivity values at all stations but one (GeoB4917), satellite-based maps stations show a productivity gradient increasing progressively from GeoB4901 to GeoB4904, GeoB4906 and GeoB4909, and then again to GeoB4913 and GeoB4917. Since this trend fits well to the distribution of the different upwelling systems in the area (schematically represented in Fig. 1), we will consider satellite-based data only in the following part of the discussion.

In the equatorial group, the calculation of the flux of organic matter to the sea floor gives lower values because of deeper water depth at station GeoB4901 (3.6 gC m^{-2} y^{-1}) than at stations GeoB4904, GeoB4906 and GeoB4909 (from 7.2 to 7.4 gC m-2 y-1). Also, the lowest TOC value in the sediment (1.46 %) was recorded at station GeoB4901, while higher values of TOC within sediment were recorded at stations GeoB4906 and GeoB4909 (3.01% and 2.02%, respectively). Moreover, species such as *M. barleeanum* and *U. peregrina,* known to be associated with high productivity (Lutze and Coulbourn, 1984; Lutze, 1986; Loubere, 1991), occurred at stations GeoB4904, GeoB4906, and GeoB4909. Total foraminiferal standing stocks also followed this trend; while they are very similar at stations GeoB4904, GeoB4906, and GeoB4909, significantly lower standing stocks were recorded in GeoB4901. Note that according to seasonal satellite-based productivity maps (http://marine.rutgers.edu/opp/), the equatorial stations experienced the strongest saisonnality of the transect.

Table 4. Organic carbon content, primary productivity values from satellite-based maps and from Berger (1989), and organic carbon fluxes as calculated after Berger (1989) at all stations.

GeoB Station	*TOC* (%) in the first 0.5 cm*	*Global annual primary productivity values (Psw in gC m^{-2} y^{-1})*		*Calculated organic matter fluxes (J(z) in gC m^{-2} y^{-1})*	
		From satellite chlorophyll data	*From the literature (Berger, 1989)*	*From satellite-based Psw data*	*From literature Psw data*
4901-6	1.46	180 to 225	90 to 125	3.6	2.7
4904-7	-	270 to 360	90 to 125	7.1	3.5
4906-5	3.01	270 to 360	90 to 125	7.4	3.6
4909-4	2.02	270 to 360	90 to 125	7.2	3.5
4913-4	3.54	450	90 to 125	10.4	3.5
4917-5	-	360 to 450	125 to 180	9.3	4.2

(* Strotmann personal communication, 1998)

At station GeoB4913, foraminiferal density dropped drastically, although this station is located directly below the area with the highest productivity values (Table 4). This contrasts with the dramatic increase of foraminifera standing stocks recorded at station GeoB4917. TOC values for station GeoB4913 sediments were the highest of the transect (>3%), and the estimated amount of exported organic matter to the sea-bed exceeds 10 gC m^{-2} y^{-1}. The discrepancy between the apparent high amount of organic matter and benthic foraminiferal total standing stocks coincided with the general meiobenthos distribution in the same area (Soltwedel, 1997).

Both quantity and quality of organic matter have proved to influence benthic foraminiferal faunas (Caralp, 1984, 1989a, 1989b). Furthermore, Soltwedel (1997) suggests that off Congo River, the observed discrepancy between meiofaunal patterns and productivity may result from fractionation of organic matter during its sinking through the water column. Such a mechanism induces the fractionation of organic matter into smaller and lighter particles with longer settling times, causing them to be more degraded by the time they reach the bottom, and thus of lower nutritional content than fast or vertically sinking large aggregates. Such a fractionation has been demonstrated for zooplankton larvae (John et al., 1981; Weikert, 1984), and may affect phytoplankton and particulate detritus as well. In this area, fractionation may likely be mediated by the huge discharge of water by the Congo River (45000 m^3 s^{-1} on average; Eisma and Van Bennekom, 1978) and a possible extension of the BCC north to 3°S (Van Bennekom and Berger, 1984). Moreover, the strong dominance of agglutinated species, which are assumed to be characteristic of relatively oligotrophic ecosystems (Jorissen et al., 1998), is an additional indication of "oligotrophic" conditions (in terms of energy content) at this station. The location of station GeoB4913 on the northern edge of the Congo deep-sea fan raises another hypothesis: high environmental stress due to important sedimentary processes, and input of organic matter of continental origin, leading to low foraminiferal standing stocks.

At station GeoB4917, high foraminiferal standing stock and the dominance of species characteristic of high productivity areas, such as *B. mexicana* in association with *U. peregrina,* suggest an eutrophic situation, which is in agreement with the estimated organic matter flux at this station (>9 gC m^{-2} y^{-1}) which is located in the oceanic upwelling zone. South of the area of investigation, in the high productivity area of the Benguela upwelling system, Schmiedl et al. (1997) described the same species as found at station GeoB4917 (*E. smithi, B. mexicana, V. laevigata*) as being characteristic of different live and dead assemblages of the upper continental margin. These authors showed marked positive correlation of the considered assemblages with the TOC content of the sediment, and negative correlation with the dissolved oxygen concentration of the bottom water mass. In our study, *B. mexicana, V. laevigata* and *E. smithi* co-occurred below 1000 m, out of the influence of the OMZ, and in oxic to anoxic sediments, suggesting that these species are reacting more to a high organic matter content than to a critical level of oxygen.

As showed by Reimers et al. (1992) off California, redistribution of organic matter can be a major process on continental margins. It is very likely that such process occurs on the continental slope off West Africa as well. However, benthic foraminiferal trends we observed matched well to different productivity provinces. This confirms that productivity and corresponding organic matter fluxes are the primary factors controlling benthic foraminiferal communities on the continental slope off West Africa.

1.6.3. Vertical distribution within sediment

In the investigated area, deep-sea benthic foraminiferal species show four different types of microhabitat preference: epifaunal, shallow infaunal, intermediate infaunal, and deep infaunal. The small size of benthic foraminifera and the sampling interval do not sufficiently resolve gradients in the surface sediment, and make it nearly impossible to distinguish true epifaunal species (i.e., species strictly living on top of the sediment) from shallow-dwelling species. As pointed out by Buzas et al. (1993), the separation between epifauna and infauna in soft-bottomed sediments from the deep-sea is probably arbitrary, and even the species living at the surface are probably infaunal. Some authors suggest reserving the term "epifauna" to species living on a hard substrate (Lutze and Thiel, 1987). However, at stations investigated in this study, some species clearly prefer the surface sediment and were considered as epifaunal in comparison to the so-called infaunal species. Moreover, as pointed out by Jorissen (1999), the "scale problem" discussed above emphasizes the necessity to attribute microhabitat preference labels according to the shape of the distribution profiles of the species, and on the relative position of species compared to that of other species, rather than to their precise depth of occurrence in the sediment.

On the other hand, it is unlikely that an undisturbed stratification of oxygen (as well as of other parameters such as other oxidants, food, etc) occurs within sediment. Macrofaunal bioturbation may affect environmental conditions by bringing oxygen and food to deeper sediment layers (Aller and Aller, 1986; Meyers et al., 1987, 1988), and significantly influence foraminiferal vertical distribution within sediment (Thomsen and Altenbach, 1993; Loubere et al., 1995). It is likely that spatial heterogeneity exists on large as well as on small scales (Fenchel and Finlay, 1995). Although no oxygen anomaly was detected in the porewater profile, this may explain the apparent downward progression of fauna in the sediment of GeoB4904, and especially the deeper re-occurrences of *R. scorpiurus* (Fig. 4b) or *L. difflugiformis* and *R. bilocularis*. These species, which are widespread in the study area, show such patterns exclusively at station GeoB4904, which reinforces the hypothesis of the existence of deep oxygenated microenvironments at that site. Moreover, due to increased temperature and microbial activity during recovery, laboratory measurements on decompressed sediment cores show lower oxygen penetration depth than *in situ* measurements (Glud et al., 1994).

The separation of the species in different groups is probably an oversimplification (Linke and Lutze, 1993). The vertical profiles of the main species at each station according to their microhabitat preferences (Fig. 6) show, however, that a clear stratification of benthic foraminiferal species does consistently exist within sediment.

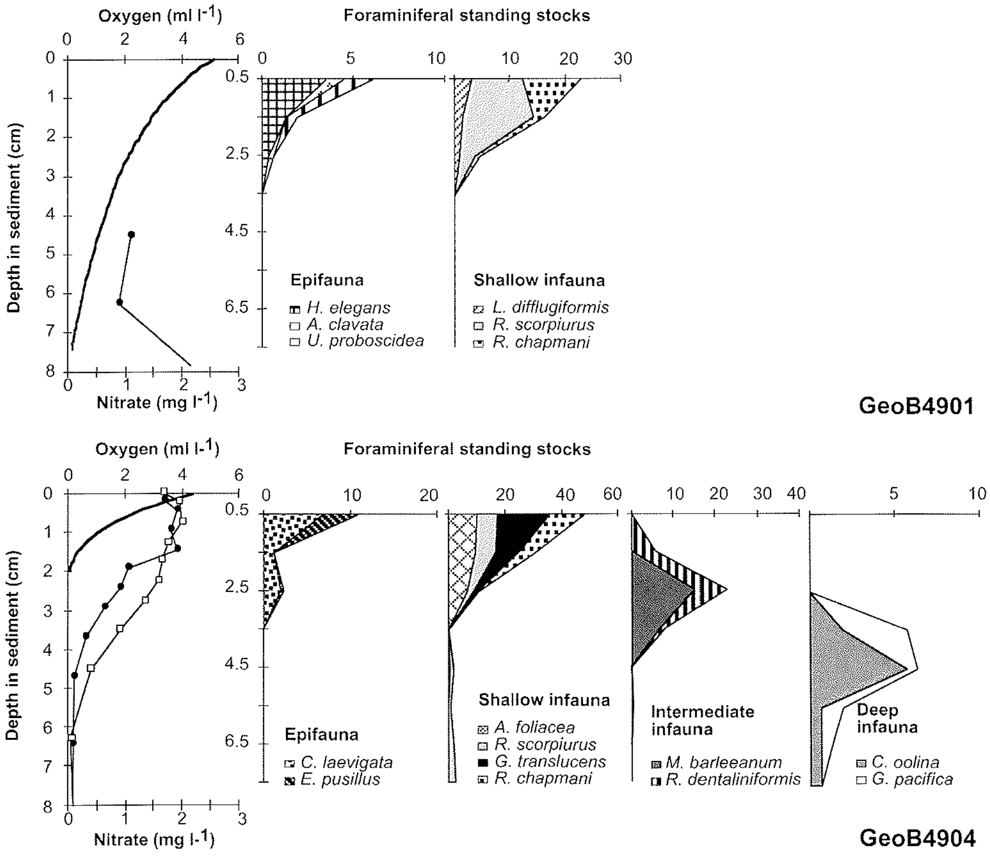

Figure 6. Microhabitat distribution (standing stocks: #/50cm3, except for station GeoB4913: #/100cm3), oxygen (ml l-1, full line) and nitrate (mg l-1, filled circles and squares) profiles within the sediment along the transect. Epifaunal species, shallow infaunal species, intermediate infaunal species, and deep infaunal species are represented separately (Table 3; Table A10 in the appendix). Epifauna, intermediate and deep infauna: all significant species are represented. Shallow infauna: only important species are represented.

The microhabitat distribution along the transect agrees well with the hypothesis of the control of the foraminiferal communities by different productivity regimes. Relative importance of epifaunal and shallow infaunal species remain quite similar along the transect, whereas relative importance of intermediate and deep infaunal species show strong fluctuations, suggesting that the latter species are particularly sensible to the changes of productivity regimes (Fig. 5). The northern site GeoB4901 has a different pattern compared to the other sites. In agreement with the TROX-model of Jorissen et al. (1995), epifaunal species are well represented at this site, whereas intermediate and deep infaunal species are nearly absent and the supply of organic matter is supposed to be especially scarce. The relative importance of infaunal species increases with increasing export flux (Sen Gupta and Machain-Castillo, 1993), and these species occur in significant numbers within sediment at all stations except GeoB4901.

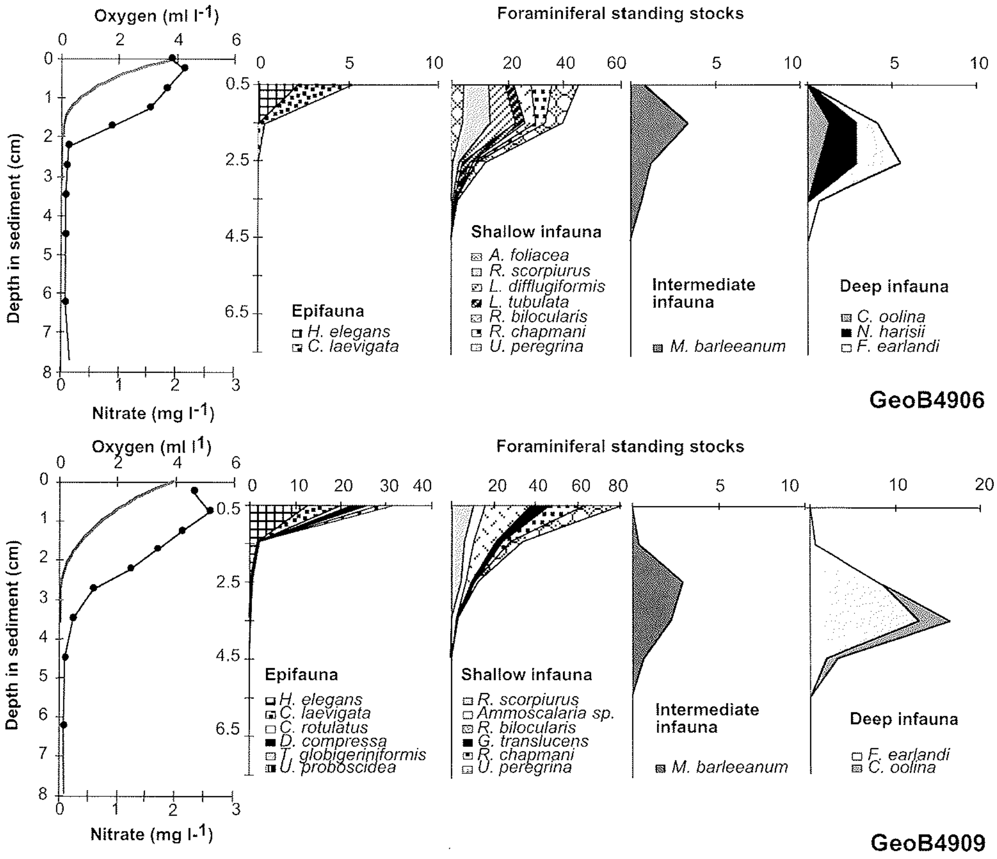

Figure 6 (continued)

The flux of organic matter reaching the seafloor directly controls the sequence of the redox reactions taking place within sediment. A comparison of foraminiferal microhabitats with geochemical parameters such as dissolved oxygen and nitrate in porewater (Fig. 6) reveals a relationship between foraminiferal and chemical stratification in the sediment.

Despite the fact that some individuals of epifaunal and shallow infaunal species were found in anoxic sediment, these taxa generally showed a clear preference for oxygenated sediment. These species probably depend on a certain quality of the organic matter, because most of the labile fraction of the organic matter is consumed at the sediment-water interface and in the uppermost millimeters of sediment (Reimers et al., 1986; Carney, 1989), or on critical levels of dissolved oxygen.

Deeper within sediment, organic matter becomes rapidly refractory and has to be transformed through bacterial activity before it can be consumed by the benthos. In our study, *M. barleeanum* is, together with *R. dentaliniformis*, the only species belonging to the intermediate infauna. Caralp (1989b) showed that *M. barleeanum* is affected by both quantity and quality of the organic matter, and that a high percentage of this species is related to the availabiliy of abundant (but already altered) marine organic matter. At stations GeoB4904, GeoB4906 and GeoB4909, where *M. barleeanum* occurred, the distribution of this species in the sediment coincides with the depth interval where the porewater nitrate starts to be strongly depleted, and corresponds to a maximum of nitrate reduction. The relative abundance of the two intermediate infaunal species is highest at station GeoB4904, where the nitrate reduction zone is particularly well developed. The decrease of *M. barleeanum* in the sediment starts at the depth where nitrate is nearly depleted ($0 < [\mathrm{NO_3^-}] < 0.5$ mg l^{-1}), and intermediate infaunal species are progressively replaced by deep infaunal species.

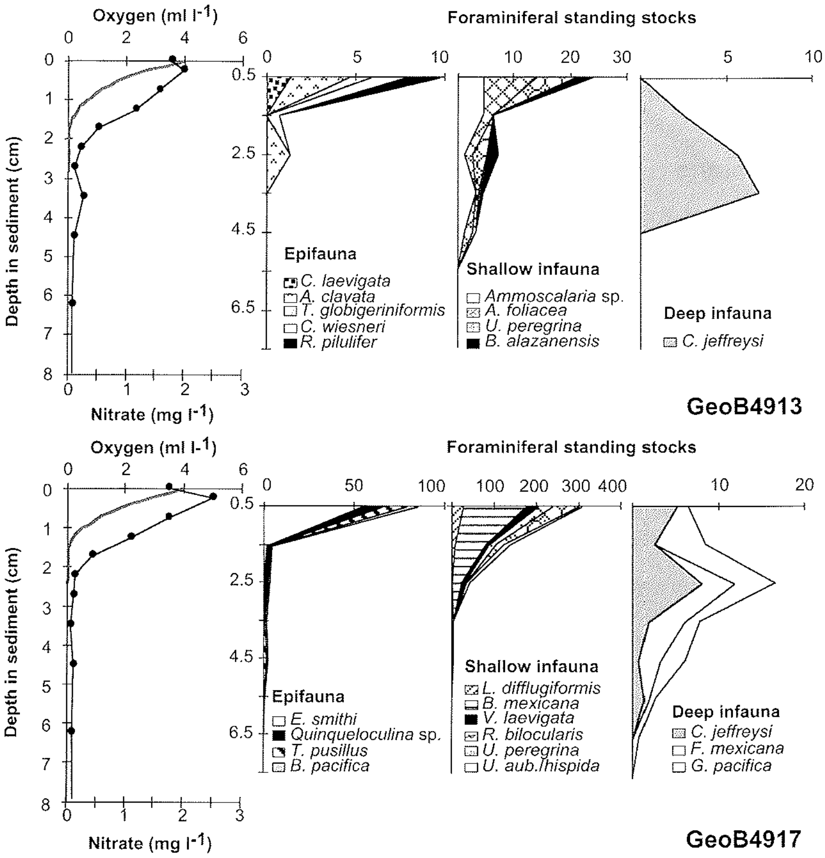

Figure 6 (continued)

Mackensen et al. (2000) suggest that this species prefers a rather stationary position in the sediment, and such a link with the nitrate-reduction zone has been recently shown off Mauritania by Jorissen et al. (1998). Assuming this relationship between biology and chemical processes, the absence of *M. barleeanum,* and intermediate infaunal species, in general, at stations GeoB4913 and GeoB4917 may correspond to the compression of this zone towards the sediment surface at these stations. The species disappears as it is "sandwiched" between strong biological competition at the surface and inhospitable conditions (anoxia) deeper in the sediment. The complete absence of *M. barleeanum*, and of any other species belonging to the intermediate infaunal niche at station GeoB4913 agrees with the hypothesis of an input of extremely low quality organic matter, or of organic matter of continental origin. Moreover, station GeoB4913 shows the highest percentage of the transect of deep infaunal species, indicating that these taxa are obviously not as sensitive as intermediate infauna to the quality of the organic matter. Since the mineralization of the refractory fraction of the organic matter is a slow process, the high percentage of deep infaunal species at station GeoB4913 may also be linked to the presence within sediment of a residual stock of "old refractory" organic matter. Early diagenetic processes are catalyzed by bacteria in the sediment. We suggest that intermediate infaunal species: (1) occur and position themselves in low oxygenated sediment where epifaunal and shallow infaunal species are not competitive anymore; (2) feed on particular metabolizable nutritious particles produced by the bacterial degradation of more refractory organic matter (Jorissen et al., 1998; Van der Zwaan et al., 1999); and (3) are not tolerant to anoxia, and are replaced by deep infaunal species where oxygen concentration drops to zero.

1.7. Conclusions

In the eastern South Atlantic, the observed differences between benthic foraminiferal faunas along a transect of six stations coincide well to different upwelling areas, and reflect the direct influence of a strong gradient of surface productivity. However, station GeoB4913 illustrates that discrepancies between faunal and productivity patterns may exist, and are probably related to the discharge of the Congo River in the ocean. The importance of the quality of the organic matter as a parameter controlling benthic foraminiferal faunas was also documented. A high content of organic matter in the sediment (3% TOC at station GeoB4913) does not give any information about the quality of the organic matter, and does not necessarily imply high foraminiferal standing stocks.

A clear vertical species zonation in sediment was found at all stations. Some species were strongly linked to redox fronts, especially *M. barleeanum* which occurred exclusively in the zone of nitrate reduction. This species stratification within sediment obviously reflects the combined action of several parameters such as competition and redox fronts, which are both regulated by organic flux. These observations are in good agreement with the TROX- and TROX-2 models of Jorissen et al. (1995) and Van der Zwaan et al. (1999).

These results indicate that primary productivity and related organic fluxes are the main parameters controlling both benthic foraminiferal community stucture and microhabitat occupation within sediment on the continental slope off West Africa.

1.8. Acknowledgements

We warmly thank A. Altenbach and an anonymous reviewer for helpful criticism of the manuscript. We would also like to thank G. Cortese for his constructive comments. Acknowlegment is made to the Deutsche Forschungsgemeinschaft which supported this research (Sonderforschungsbereich 261).

1.9. Appendices

Table A1. Dissolved porewater oxygen (ml l^{-1}) measured in situ with microelectrodes (all stations except GeoB4904), or obtained with laboratory measurements (station GeoB4904).

GeoB4901					GeoB4904	GeoB4906	GeoB4909	GeoB4913	GeoB4917
Depth (mm)	O_2 (ml l^{-1})	Depth (mm)	O_2 (ml l^{-1})	Depth (mm)	O_2 (ml l^{-1})	O_2 (ml l^{-1})	O_2 (ml l^{-1})	O_2 (ml l^{-1})	O_2 (ml l^{-1})
0	5.12	40	1.38	0	4.39	3.88	3.89	3.93	3.95
1	4.88	41	1.34	1	3.82	3.38	3.57	3.33	3.49
2	4.66	42	1.3	2	3.43	2.91	3.26	2.79	3.04
3	4.47	43	1.26	3	2.98	2.48	2.97	2.32	2.58
4	4.31	44	1.21	4	2.59	2.11	2.7	1.97	2.16
5	4.2	45	1.18	5	2.25	1.77	2.44	1.66	1.78
6	4.05	46	1.13	6	1.94	1.46	2.22	1.39	1.44
7	3.91	47	1.1	7	1.65	1.21	2	1.14	1.15
8	3.76	48	1.06	8	1.39	1	1.81	0.93	0.91
9	3.62	49	1.02	9	1.16	0.8	1.62	0.75	0.7
10	3.52	50	0.98	10	0.98	0.63	1.44	0.59	0.51
11	3.42	51	0.94	11	0.79	0.49	1.28	0.45	0.35
12	3.3	52	0.91	12	0.64	0.36	1.14	0.34	0.21
13	3.18	53	0.88	13	0.51	0.26	1	0.25	0.11
14	3.07	54	0.84	14	0.38	0.18	0.86	0.17	0.06
15	2.97	55	0.81	15	0.27	0.12	0.74	0.1	0.02
16	2.89	56	0.77	16	0.19	0.09	0.63	0.05	-0.01
17	2.81	57	0.74	17	0.11	0.06	0.53	0.02	0
18	2.73	58	0.71	18	0.06	0.04	0.44	0	0
19	2.63	59	0.68	19	0.02	0.03	0.36	0	0
20	2.59	60	0.65	20	0	0.02	0.29	-0.01	0
21	2.49	61	0.61	21		0.01	0.23	0	-0.01
22	2.43	62	0.59	22		0	0.17	0	-0.01
23	2.33	63	0.55	23		-0.01	0.13	-0.01	0
24	2.26	64	0.52	24		0	0.09	0	-0.03
25	2.18	65	0.49	25		0	0.06	0.01	
26	2.11	66	0.47	26		0	0.04	0	
27	2.05	67	0.44	27		0	0.02	0	
28	1.99	68	0.41	28		0	0.01	0	
29	1.92	69	0.38	29		0	0.01		
30	1.87	70	0.36	30		0	0		
31	1.8	71	0.32	31		0	-0.01		
32	1.75	72	0.3	32			0		
33	1.7	73	0.27	33			0		
34	1.64	74	0.25	34			0		
35	1.6	75	0.23	35			0		
36	1.55	76	0.21	36			0		
37	1.51	77	0.18	37					
38	1.47	78	0.16	38					
39	1.43	79	0.14	39					
		80	0.12						

Table A2. Porewater nitrate concentrations (mg l^{-1}).

depth (mm)	GeoB4901	GeoB4904		GeoB4906	GeoB4909	GeoB4913	GeoB4917
0	-	1.7	1.7	1.9	-	1.8	1.7
2.5	-	1.9	1.9	2.1	2.3	2.0	2.5
7.5	-	2.0	1.8	1.8	2.6	1.5	1.7
12.5	-	1.8	1.9	1.5	2.1	1.1	1.1
17.5	-	1.7	1.0	0.9	1.7	0.5	0.4
22.5	-	1.6	0.9	0.1	1.2	0.2	0.1
27.5	-	1.3	0.6	0.1	0.6	0.1	0.1
35	-	0.9	0.3	0.1	0.2	0.2	0.0
45	1.1	0.4	0.1	0.1	0.1	0.1	0.1
62.5	0.9	0.1	0.1	0.1	0.1	0.1	0.1
87.5	2.9	0.1	0.1	0.2	0.1	0.1	0.1

Table A3. Relative abundances of significant species present at least at one station.

Species	GeoB4901-6	GeoB4904-7	GeoB4906-5	GeoB4909-4	GeoB4913-4	GeoB4917-5
Ammodiscus incertus	x	2.02	x	x	1.97	1.27
Ammolagena clavata	1.90				4.61	
Ammomarginulina foliacea		8.48	4.98	x	14.47	x
Ammoscalaria sp.		x	1.72	5.03	15.13	x
Bolivina pacifica						1.13
Bolivinita pseudothalmanni		x				1.10
Bulimina aculeata		2.22				x
Bulimina alazanensis		1.01	x	x	5.26	
Bulimina mexicana		2.83	2.87	x		25.72
Cassidulina laevigata/teretis		3.23	1.15	2.51	1.32	x
Chilostomella oolina	x	3.03	1.15	x		x
Cribrostomoides jeffreysi			x		15.79	2.09
Cribrostomoides rotulatus				1.03		
Cribrostomoides subglobosus		x	x	1.26	1.97	
Cribrostomoides wiesneri		x	x	x	2.63	
Discammina compressa				1.14		
Eggerella scabra		4.04				x
Epistominella exigua	1.90	x	x			
Epistominella rugosa			x	1.60		
Epistominella smithi						5.89
Eponides pusillus		1.41		x		x
Fursenkoina earlandi			2.68	4.23	1.32	
Fursenkoina mexicana						1.20
Gavelinopsis translucens	x	9.09	4.21	5.14	4.61	1.54
Glaphyrammina americana		1.01				x
Globobulimina pacifica		2.02				1.88
Gyroidinoides polius		x		x	x	1.27
Hoeglundina elegans	7.58	x	1.34	5.26		
Karrerulina compressa				x	1.32	
Lagenammina difflugiformis	8.53	4.65	10.15	4.11	3.95	5.21
Lagenammina tubulata	x	x	6.13	3.20	x	
Melonis barleeanum		7.27	3.83	2.17		x
Nouria harrisii		x	2.30		x	x
Osangularia bengalensis			x		1.32	
Psammosphaera sp.						1.13
Pullenia bulloides	1.90	1.01	x			
Pullenia subcarinata	1.42					
Quinqueloculina spp.		x				1.58
Reophax bilocularis	4.74	2.83	6.70	12.91		5.86
Reophax dentaliniformis	1.42	4.65	x	x		x
Reophax guttifera		1.41	x	x		x
Reophax micaceus	1.42	x	2.30	1.71		1.20
Reophax pilulifer				x	1.97	x
Reophax scorpiurus	37.44	6.67	12.64	9.03	1.97	x
Reophax spp.		1.62				x
Robertinoides chapmani	19.43	6.26	7.28	7.43		
Saccammina sphaerica	x		x	1.14	x	
Sphaeroidina bulloides			2.11	x		1.40
Trochammina globigeriniformis		x	x	1.37	1.32	
Trochamminopsis pusillus						1.75
Uvigerina auberiana/hispida	x	2.02	1.53	2.06		3.60
Uvigerina peregrina	1.42	3.23	11.69	9.03	11.18	8.77
Uvigerina proboscidea	3.32	x		1.03		
Valvulineria laevigata						5.03

Table A4. Counts of significant species of foraminifera for each sediment depth interval at station GeoB4901-6.

Species	Depth interval (cm)				
	0-1	1-2	2-3	3-4	4-5
Ammolagena clavata	3		1		
Epistominella exigua	1	3			
Hoeglundina elegans	11	4	1		
Lagenammina difflugiformis	10	5	3		
Pullenia bulloides	3		1		
Pullenia subcarinata	2	1			
Reophax bilocularis	6	3	1		
Reophax dentaliniformis			2	1	
Reophax micaceus	1	1	1		
Reophax scorpiurus	29	40	9		1
Robertinoides chapmani	33	6	2		
Uvigerina peregrina	1	1	1		
Uvigerina proboscidea	5	2			
Sum others	6	7	1	1	1
Sum all	111	73	23	2	2
Specimens per 50cm^2	35	23	7	1	1

Table A5. Counts of significant species of foraminifera for each sediment depth interval at station GeoB4904-7.

Species	Depth interval (cm)							
	0-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8
Ammodiscus incertus	4	1	4	1				
Ammomarginulina foliacea	16	15	10		1			
Bulimina aculeata	6	3	2					
Bulimina alazanensis	3	1	1					
Bulimina mexicana	10	2			1		1	
Cassidulina laevigata/teretis	11	2	3					
Chilostomella oolina				3	9	1	1	1
Eggerella scabra	10	6	3		1			
Eponides pusillus	6		1					
Gavelinopsis translucens	30	13	2					
Glaphyrammina americana	2	2	1					
Globobulimina pacifica				6	1	2	1	
Lagenammina difflugiformis	9	1			3	3	6	1
Melonis barleeanum			24	11		1		
Pullenia bulloides	1	2	2					
Reophax bilocularis	4	2		2	3		1	2
Reophax dentaliniformis		9	12	2				
Reophax guttifera	3	4						
Reophax scorpiurus	11	11	4		1	1	2	3
Reophax spp.	1			3		2	2	
Robertinoides chapmani	20	10	1					
Uvigerina auberiana/hispida	9	1						
Uvigerina peregrina	9	6				1		
Sum others	36	22	21	2	4	1	1	2
Sum all	201	113	91	30	24	12	15	9
Specimens per 50cm^2	128	72	58	19	15	8	10	6

Table A6. Counts of significant species of foraminifera for each sediment depth interval at station GeoB4906-5.

Species	Depth interval (cm)			
	0-1	1-2	2-3	3-4
Ammomarginulina foliacea	14	11	1	
Ammoscalaria sp.	2	6	1	
Bulimina mexicana	7	8		
Cassidulina laevigata/teretis	4	2		
Chilostomella oolina		4	2	
Fursenkoina earlandi		4	8	2
Gavelinopsis translucens	9	10	2	1
Hoeglundina elegans	7			
Lagenammina difflugiformis	19	29	3	2
Lagenammina tubulata	10	11	10	1
Melonis barleeanum	3	11	4	2
Nouria harrisii		5	7	
Reophax bilocularis	19	13	3	
Reophax micaceus	4	6	2	
Reophax scorpiurus	27	31	7	1
Robertinoides chapmani	23	10	4	1
Sphaeroidina bulloides	10	1		
Uvigerina auberiana/hispida	5	2	1	
Uvigerina peregrina	30	20	10	1
Sum others	27	28	14	
Sum all	220	212	79	11
Specimens per 50cm^2	70	68	25	4

Table A7. Counts of significant species of foraminifera for each sediment depth interval at station GeoB4909-4.

Species	Depth interval (cm)				
	0-1*	1-2	2-3	3-4	4-5
Ammoscalaria sp.	8	14	6	7	1
Cassidulina laevigata/teretis	11				
Cribrostomoides rotulatus	4	1			
Cribrostomoides subglobosus	3	5			
Discammina compressa	5				
Epistominella rugosa	5	3	1		
Fursenkoina earlandi		1	13	20	3
Gavelinopsis translucens	15	9	4	2	
Hoeglundia elegans	20	5	1		
Lagenammina difflugiformis	11	9		4	1
Lagenammina tubulata	10	7	1		
Melonis barleeanum		1	9	7	2
Reophax bilocularis	34	33	11	1	
Reophax micaceus	5	1	3	1	
Reophax scorpiurus	18	22	17	3	1
Robertinoides chapmani	25	13	1		1
Saccammina sphaerica	3	3		1	
Trochammina globigeriniformis	5	1	1		
Uvigerina auberaina/hispida	7	3		1	
Uvigerina peregrina	28	19	4		
Uvigerina proboscidea	4		1		
Sum others	51	22	12	14	4
Sum all	272	172	85	61	13
Specimens per 50cm^2	173	55	27	19	4

* From to 0 to 1cm depth, foraminifera were counted in one half of the sediment sample.

Table A8. Counts of significant species of foraminifera for each sediment depth interval at station GeoB4913-4.

Species	Depth interval (cm)				
	0-1	1-2	2-3	3-4	4-5
Ammodiscus incertus			3		
Ammolagena clavata	5		2		
Ammomarginulina foliacea	15	3	2		2
Ammoscalaria sp.	7	7	2	5	2
Bulimina alazanensis	4		3	1	
Cassidulina laevigata/teretis	2				
Cribrostomoides jeffreysi		4	9	11	
Cribrostomoides subglobosus	2		1		
Cribrostomoides wiesneri	3	1			
Fursenkoina earlandi		1	1		
Gavelinopsis translucens	4			1	2
Karrerulina compressa	1	1			
Lagenammina difflugiformis	1	1		1	3
Osangularia bengalensis	1				1
Reophax pilulifer	3				
Reophax scorpiurus	2	1			
Trochammina globigeriniformis	2				
Uvigerina peregrina	11		4	1	1
Sum others	8	2	2		
Sum all	71	21	29	20	11
Specimens per 50cm^2	23	7	9	6	4

Table A9. Counts of significant species of foraminifera for each sediment depth interval at station GeoB4917-5.

Species	Depth interval (cm)						
	0-1*	1-2**	2-3	3-4	4-5	5-6	6-7
Ammodiscus incertus	4	8	3	2			
Bolivina pacifica	5	1	1	4	3	3	
Bolivina pseudothalmanni	3	1	2	11	5		
Buliminia mexicana	116	105	68	5	4		
Cribrostomoides jeffreysi	4	4	25	6	2	4	
Epistominella smithi	42	2					
Fursenkoina mexicana			12	13	8	2	
Gavelinopsis translucens	10		2	2	1		
Globobulimina pacifica	1	9	15	5	9	2	2
Gyroidinoides polius	6	6	1				
Lagenammina difflugiformis	23	19	4	8	9	1	
Psammosphaera sp.	4	3	7	2	2		
Quinqueloculina spp.	9	3	4				
Reophax bilocularis	27	22	10	4	4		1
Reophax micaceus	3	10		3			
Sphaeroidina bulloides	7	5	3				
Trochamminopsis pusillus	10		4	2	5		
Uvigerina auberiana	7	22	30	3			
Uvigerina peregrina	47	30	4		3	1	
Valvulineria laevigata	21	20	22	1			
Sum others	372	128	57	28	35	4	1
Sum all	442	334	274	99	90	17	4
Specimens per 50cm^2	563	213	87	32	29	5	1

* From to 0 to 1cm depth, foraminifera were counted in one quarter of the sediment sample.

** From to 1 to 2cm depth, foraminifera were counted in one half of the sediment sample.

Table A10. Microhabitat preferences of significant species present at least at one station. Epi = epifauna, S = shallow infauna, I = intermediate infauna, D = deep infauna. x denotes stations where species occur with less than 1%. # denotes stations where species occur with more than 1%, but where microhabitat pattern were not considered to be significant (only 1 living specimen found per sediment slice).

Species	GeoB4901-6	GeoB4904-7	GeoB4906-5	GeoB4909-4	GeoB4913-4	GeoB4917-5
Ammodiscus incertus	x	S	x	x	D	S
Ammolagena clavata	Epi				Epi	
Ammomarginulina foliacea		S	S	x	Epi/S	x
Ammoscalaria sp.		x	S	S	S	x
Bolivina pacifica						Epi
Bolivina pseudothalmanni		x				S
Bulimina aculeata		S				x
Bulimina alazanensis		Epi	x	x	Epi/S	
Bulimina mexicana		Epi	S	x		S
Cassidulina laevigata/teretis		Epi	Epi	Epi	Epi	x
Chilostomella oolina	x	D	I/D	x		x
Cribrostomoides jeffreysi			x		D	D
Cribrostomoides rotulatus				Epi		
Cribrostomoides subglobosus		x	x	S	Epi	
Cribrostomoides wiesneri		x	x	x	Epi	
Discammina compressa				Epi		
Eggerella scabra		S				x
Epistominella exigua	S	x	x			x
Epistominella rugosa			x	Epi/S		
Epistominella smithi						Epi
Eponides pusillus		Epi		x		x
Fursenkoina earlandi			D	D	#	
Fursenkoina mexicana						D
Gavelinopsis translucens	x	Epi/S	S	S	Epi	Epi
Glaphyrammina americana		S				x
Globobulimina pacifica		D				D
Gyroidinoides polius		x		x	x	S
Hoeglundina elegans	Epi/S	x	Epi	Epi		
Karrerulina compressa				x	#	
Lagenammina difflugiformis	S	Epi	S	S	#	S
Lagenammina tubulata	x	x	S	Epi/S	x	
Melonis barleeanum		I	I	I		x
Nouria harisii		x	D		x	x
Osangularia bengalensis			x		#	
Psammosphaera sp.						S
Pullenia bulloides	Epi	S	x			
Pullenia subcarinata	Epi					
Quinqueloculina spp.		x				Epi
Reophax bilocularis	Epi/S	S	S	S		S
Reophax dentaliniformis	I	I	x	x		x
Reophax guttifera		S	x	x		x
Reophax micaceus	#	x	S	Epi		S
Reophax pilulifer				x	Epi	
Reophax scorpiurus	S	S	S	S	Epi	x
Robertinoides chapmani	Epi/S	S	S	S		
Saccammina sphaerica	x		x	S		
Sphaeroidina bulloides			Epi	x		S
Trochammina globigeriniformis		x	x	Epi	Epi	
Trochamminopsis pusillus						Epi
Uvigerina auberiana/hispida	x	Epi	Epi	Epi		S
Uvigerina peregrina	#	S	S	S	Epi/S	S
Uvigerina proboscidea	Epi	x		Epi		
Valvulineria laevigata						S

2. Benthic foraminifera off West Africa (1°N to 32°S): Do live assemblages from the topmost sediment reliably record environmental variability?

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2.1. Abstract

Recent benthic foraminifera (> 125 μm) were investigated from multicorer samples on a latitudinal transect of twenty stations between 1°N and 32°S along the upper slope off West Africa. Samples were selected from a narrow water depth interval, between 1200 and 1500 m, so that changes in water masses are minimized, but changes in surface productivity are important and the only significant environmental variable. Live (Rose Bengal stained) benthic foraminifera were counted from the surface sediment down to a maximum of 12 cm. Dead foraminifera were investigated in the top 5 cm of the sediment only. Five live and five dead benthic foraminiferal assemblages were identified using Q-mode principal component analysis, matching distinct primary productivity provinces, characterized by different systems of seasonal and permanent upwelling. Differences in seasonality, quantity, and quality of food supply are the main controlling parameters on species composition and distribution of the benthic foraminiferal faunas.

To test the sensitivity of foraminiferal studies based on the uppermost centimeter of sediment only, a comparative Q-mode principal component analysis was conducted on live and dead foraminiferal data from the top 1 cm of sediment. It has been demonstrated that, on the upper slope off West Africa, most of the environmental signals as recorded by species composition and distribution of the "total" live and dead assemblages, i.e., including live and dead foraminifera from the surface sediment down to 12 cm and 5 cm, respectively, can be extracted from the assemblages in the top centimeter of sediment only. On the contrary, subsurface abundance maxima of live foraminifera and dissolution of empty tests strongly bias quantitative approaches based on the calculation of standing stocks and foraminiferal numbers in the topmost centimeter.

Keywords: benthic foraminifera ecology, live/dead comparison, eastern South Atlantic, principal component analysis

2.2. Introduction

Benthic foraminifera are a valuable tool for paleoceanographers to estimate changes in past surface productivity (e.g. Thomas et al., 1995; Fariduddin and Loubere, 1997; Den Dulk et al., 1998; Wollenburg et al., 2004). During the last few decades, increasing evidence indicates that benthic foraminifera faunas are strongly controlled by organic carbon flux rates to the sea-floor, which in turn are related to surface primary productivity (e.g. Corliss and Chen, 1988; Jorissen et al., 1992; Mackensen et al., 1995; Loubere and Fariduddin, 1999; Van der Zwaan et al., 1999; Smart, 2002; Gooday, 2003). It has been demonstrated that benthic foraminifera play an important role in benthic carbon cycling (Moodley et al., 2002), but a straightforward connection between benthic foraminiferal faunas and ocean primary productivity is difficult to establish. Some quantitative relationships have been developed (Herguera and Berger, 1991), but their application remains problematic (Naidu and Malmgren, 1995; Schmiedl and Mackensen, 1997).

Off the West African continental margin, seasonal and permanent upwelling systems strongly influence surface waters, locally resulting in extremely enhanced primary productivity, and thus exerting a major influence on the global carbon cycle through atmospheric CO_2 draw-down, export and burial of organic carbon. Therefore, reconstructing the past history of the eastern South Atlantic upwelling systems remains of crucial interest for paleoceanographers. Consequently, to properly interpret the ecological information recorded in benthic foraminiferal fossil assemblages from that area, one aim of this study is to investigate the distribution of live and dead benthic foraminiferal faunas in different primary productivity regions.

A common method to determine the composition of modern benthic foraminiferal faunas is to assume that the assemblages found in the uppermost centimeters of sediment are representative of the whole living community (Lutze and Coulbourn, 1984; Mackensen et al., 1995; Gooday, 1996; Schmiedl et al., 1997; Gooday et al., 2001), although it is known that vertical stratification of species occurs down to several centimeters depth below the sediment surface (Corliss, 1985; Mackensen and Douglas, 1989; Jorissen et al., 1995). Deep-dwelling species are important ecological markers of conditions of low oxygen/high food availability for paleoceanographers (e.g., Sen Gupta and Machain-Castillo, 1993; Baas et al., 1998), and may constitute an important part of faunas below high-productivity areas (e.g. Jorissen et al., 1998). Besides different microhabitat preferences between species, sediment reworking, dissolution due to corrosive bottom-water and acidified pore waters of organic-rich sediments are processes, which affect and alter the composition of the assemblage close to the sediment surface, and cause differences between live and dead assemblages (Loubere, 1989; Mackensen and Douglas, 1989). Therefore, neglecting the foraminiferal content of subsurface sediment might bias determining the faunal composition, and compromise the understanding of the transition from bio- to thanatocoenoses. Consequently, the second aim of this study is to investigate similarities and discrepancies between live and dead assemblages in surface and subsurface sediments from the southeast Atlantic. In the same transect of twenty stations we thus compared the distribution of: (1) live and dead assemblage data obtained from the integration of surface and subsurface sediment samples, referred hereafter as live and dead "total assemblages" respectively, with (2) the corresponding live and dead assemblages obtained from the uppermost 1 cm of surface sediment only, referred hereafter as live and dead "surface assemblages".

2.3. Area of investigation

Multicorer sediment samples were selected from cruises M34/1, M34/2, and M41/1 of the RV *Meteor* on a latitudinal transect parallel to the West African continental margin, which allowed the strong surface productivity gradient along this transect to be almost completely covered (Fig. 1). All stations are from a water-depth interval between 1200 and 1500 m, located within the northward Antarctic Intermediate Water/Upper Circumpolar Deep Water (AAIW and UCDW, respectively) flow field (Reid, 1989; Schulz et al., 1996, 1998; Stramma and Schott, 1999). Therefore changes in conservative water mass properties are negligible, and changes in surface productivity are the only significant environmental variable. Samples were taken during the years 1996 and 1998, between February and March (Table 1).

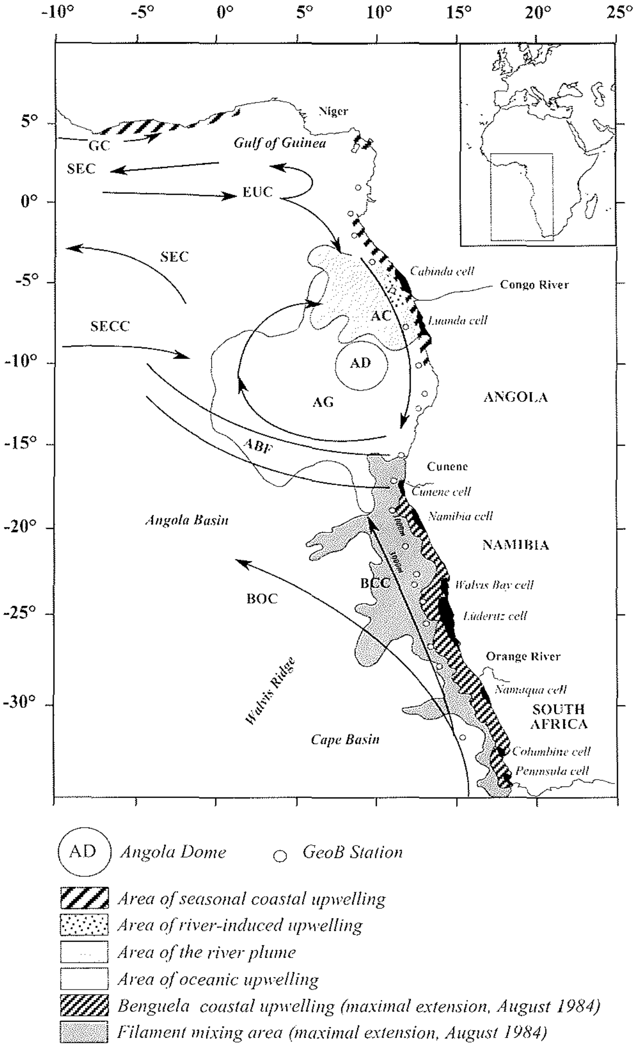

Figure 1. Location of the investigated samples, high-productivity areas, and surface and subsurface hydrography in the eastern South Atlantic. Area of seasonal coastal upwelling is after Voituriez and Herbland (1982). Areas of river plume, oceanic, and river-induced upwelling are after Jansen et al. (1984). Extension of coastal upwelling and adjacent mixing area in southern winter (August) 1984 is after Lutjeharms and Stockton (1897). Upwelling cells are after Lutjeharms and Meeuwis (1987) and Shannon and Nelson (1996). Currents are after Voituriez and Herbland (1982), Van Bennekom and Berger (1984), and Peterson and Stramma (1991). *ABF=Angola-Benguela-Front, AC=Angola Current, AD=Angola Dome, AG=Angola Gyre, BCC=Benguela Coastal Current, BOC=Benguela Oceanic Current, EUC=Equatorial Under Current, GC=Guinea Current, SEC=South Equatorial Current, SECC=South Equatorial Counter Current.*

Table 1. Samples used for this study with sample number, water depth, geographical position, date of sampling, productivity estimates and estimated organic flux, TOC and carbonate content of the sediment, porosity, dissolved oxygen in the overlaying bottom-water, and oxygen penetration depth within sediment (see text for original sources). Standing stocks of benthic foraminifera from the whole community and in the surface centimeter of sediment, percentage of foraminifera living in the surface centimeter, and benthic foraminiferal number from the upper 5 cm and the topmost centimeter of sediment are also given.

GeoB station	Water depth (m)	Lat.	Long.	Sampling date (d/m/y)	Productivity estimates (gC/m^2/y)	Estimated org. carbon flux (gC/m^2/y)	TOC %	Carbonate %	Porosity	Oxygen bottom water (ml/l)	Oxygen penetration depth (cm)	Total standing stocks (#/50cm^2)	Standing stocks in 1cm (#/50cm^2)	Live forams in 1cm (%)	BFN in 5 cm (#/10cm^2)	BFN in 1 cm (#/10cm^2)
4904-7	-1341	0.96	8.88	28/02/98	315	7.1	1.2	9.1	86.5	4.7	2.0	321	129.9	40.5	1008	145
4906-5	-1277	-0.69	8.38	02/03/98	315	7.3	1.5	3.8	84.9	4.1	2.3	168	70.7	42.1	414	66
4909-4	-1313	-2.07	8.63	04/03/98	315	7.2	1.3	10.4	82.4	4.1	3.0	290	177.1	61.0	694	141
4912-4	-1298	-3.73	9.79	06/03/98	450	10.4	1.5	11.4	78.4	4.7	2.4	480	300.6	62.7	3682	411
4913-4	-1300	-5.50	11.07	06/03/98	450	10.4	1.7	0.5	87	4.4	2.0	51	24.5	48.4	194	24
4915-3	-1305	-7.75	11.87	09/03/98	450	10.4	1.3	0.7	86.4	4.7	2.5	156	97.5	62.6	419	69
4916-4	-1300	-10.17	12.69	10/03/98	405	9.3	2.5	1.2	-	4.7	1.7	358	98.1	27.4	555	66
4917-5	-1299	-11.90	13.07	10/03/98	405	9.4	2.2	2.5	81.7	4.2	1.6	932	564.3	60.5	1985	367
4918-4	-1338	-12.84	12.70	11/03/98	405	9.2	2.2	1.3	79.7	4.0	0.9	370	193.9	52.4	896	168
3713-1	-1330	-15.63	11.58	07/02/96	450	10.3	1.6	5.1	87.9	2.9	1.3	827	105.4	12.7	1519	54
3712-1	-1242	-17.19	11.13	06/02/96	450	10.7	2.4	5.7	66.1	3.3	0.7	1645	114.3	7.0	1297	30
3715-1	-1204	-18.95	11.06	09/02/96	450	10.9	4.5	25.6	80.7	3.7	0.9	333	86.3	25.9	2682	284
3711-1	-1214	-19.84	10.77	05/02/96	450	10.8	3.8	66.7	77.8	4.1	1.4	726	189.3	26.1	11080	1184
3708-1	-1283	-21.09	11.83	04/02/96	450	10.5	4.9	52.6	81.2	2.2	1.4	994	264.3	26.6	4270	267
3706-3	-1313	-22.72	12.60	02/02/96	450	10.3	3.7	55.2	89.3	4.4	1.4	580	145.5	25.1	2853	182
3705-2	-1305	-24.30	13.00	02/02/96	450	10.4	4.5	66.0	77.7	4.3	0.8	391	117.5	30.1	3688	237
3703-4	-1376	-25.52	13.23	01/02/96	405	9.1	8.1	55.3	82.9	4.3	0.8	746	287.0	38.5	1855	248
3702-2	-1319	-26.79	13.46	31/01/96	315	7.2	4.7	57.0	75.3	4.3	1.1	247	92.0	37.3	21119	411
3701-1	-1488	-27.95	14.00	31/01/96	315	6.7	1.7	75.1	73.7	4.4	2.6	478	92.7	19.4	4841	156
3604-1	-1512	-31.79	15.49	10/01/96	315	6.7	1.2	78.0	70.4	-	-	279	150.9	54.1	9612	1777

2.3.1. Hydrography and surface water productivity

North of 10°S, the circulation pattern in the surface waters off West Africa is complex, dominated by the interaction of the system of equatorial currents, undercurrents, countercurrents, and significant riverine input from the Congo River (Fig. 1). Strong seasonal upwelling occurs between 4°E and 8°W along the northern coasts of the Gulf of Guinea and in the area between 1°S and 10-13°S (Picaut, 1983; Verstraete, 1985, 1992), where distinct upwelling cells were identified north and south of the Congo river mouth at about 5°S and 7°S (Lutjeharms and Meeuwis, 1987). In this sector of the eastern South Atlantic, the annual upwelling season typically extends from May to September, during the "great cold season" (Verstraete, 1985). A secondary upwelling season (Busalacchi and Picaut, 1983) occurs in December, during the eastern South Atlantic "small cold season" (Verstraete, 1985). Seasonal upwelling in the Equatorial Divergence Zone, river-induced upwelling off the Congo River, and nutrient input from the river also cause locally enhanced productivity in the tropical sector of the eastern South Atlantic (Eisma and Van Bennekom, 1978; Van Bennekom et al., 1978; Voituriez and Herbland, 1982).

Further south, in the Angola Bight, primary productivity is greatly influenced by a system of fronts, domes, cyclonic gyres, and expansions of the adjacent coastal upwelling systems (Jansen et al., 1984), and contributes to the formation of the main oxygen minimum in the southeast Atlantic (Chapman and Shannon, 1985). Seasonal oceanic upwelling related to the uplift of the Angola Dome to the thermocline layer occurs during austral summer, from January to May (Voituriez and Herbland, 1982; Jansen et al., 1984; Peterson and Stramma, 1991). According to Voituriez (1981), the Angola Dome, centered at 10°S 9°E (Mazeika, 1967), is a different structure from the larger-scale Angola Gyre, centered quasi-stationary near 13°S 5°E (Moroshkin et al., 1970; Gordon and Bosley, 1991), and bordered to the east by the southward flowing Angola Current. The influence of the dome can be traced between 8°S and, to some extent, 16°S (Peterson and Stramma, 1991).

The confluence of the Angola Current with the cold northward-flowing Benguela Current results in the Angola Benguela Front (ABF, 14-17°S). The ABF undergoes an annual zonal shift over 2° of latitude, moving farthest north in winter (August) and south in late summer (March). The ABF marks the northern boundary of the semi-permanent Benguela coastal upwelling system, bordered to the south by the Agulhas Retroflection (37°S) (see review in Shannon, 1985; Shannon et al., 1987; Shannon and Nelson, 1996). The Benguela is the most productive of the four upwelling systems linked to eastern boundary currents (Carr, 2002). Six to seven distinct upwelling cells have been identified (Fig. 1), centered along the coast off Angola, Namibia and South Africa near 18°S (Cunene), 19°S (Namibia), 22°S (Walvis Bay), 25°S (Lüderitz), 29°S (Namaqua), 32°S (Columbine), and 34°S (Peninsula). Upwelling is most intense, persistent (frequent), and extends farthest westward than elsewhere in the whole Benguela regime in the Lüderitz cell (Shannon, 1985; Lutjeharms and Meeuwis, 1987; Shannon and Nelson, 1996). According to Shannon (1985), it acts together with the Namaqua cell as a major environmental barrier between a rather perennial northern sub-system north of 31°S, and a highly seasonal southern sub-system south of this latitude (see also Shannon and Nelson, 1996; Strub et al., 1998). During austral winter, the zonal range of the Benguela coastal upwelling and its mixing area is increased as far as 15°S (Lutjeharms and Stockton, 1987).

Between 18°S and 34°S, a well-developed longshore thermal system of upwelling, shelf-break, and oceanic fronts demarcates the seaward extent of the upwelled water, which reaches a westwards extension of 150 km to 250 km on average (Lutjeharms and Stockton, 1987; Shannon and Nelson, 1996). Enhanced productivity is concentrated at frontal features or just outside upwelling fronts (Lutjeharms and Stockton, 1987), and coldwater filaments, plumes and frontal eddies make up an extensive high-productivity outer area extending on average between 300 km and 600 km offshore, and as far as 1000 km during extreme events (Lutjeharms and Stockton, 1987; Lutjeharms et al., 1991).

A strong seasonal component of upwelling events characterizes the southern part of the system, south of 31°S. North of this latitude, upwelling is perennial, but with seasonal maxima (Shannon, 1985). Episodically, warm events comparable to the Pacific El Niños occur in the Benguela area during austral summer. Such Benguela Niños, characterized by reduced upwelling and abnormal intrusion of equatorial and tropical waters eastwards and southwards along the Namibian coast, concern principally the northern Benguela region, and are minimal in the southern part (Shannon et al., 1986).

2.3.2. Oxygen Minimum Zone

The core of the main oxygen minimum layer occurs traditionally between 300 and 600 m water depth. It has its origin largely off Angola, between 7°S and 17°S, from where it horizontally spreads southwards usually no further than 25°S, occasionally as far as 29°S. A second site of formation is located on the shelf in the area of Walvis Bay, separated from the site off Angola by a gap at about 19-21°S or 22°S. This water is probably advected northwards and southwards, and contributes to a subsurface oxygen-minimum off Angola and northern Namibia (Chapman and Shannon, 1985, 1987, and references therein).

With oxygen concentration between 2.2 and 4.7 ml l^{-1} (Hensen et al., 2000; Wenzhöfer et al., 2001; Hensen, pers. comm., 2002; Wenzhöfer and Glud, 2002), bottom-waters overlaying the stations investigated in this study can be regarded as oxygen-depleted, following Chapman and Shannon (1985). Strongest depletion is restricted to a rather limited central area, between 15°S and 21°S, the minimum of oxygen being recorded at station GeoB3708. Both the northern and southern parts of the transect display oxygen concentration of 4 ml l^{-1} or higher (Table 1).

2.3.3. Sediments

Carbonate and total organic carbon content (TOC) of the sediments (Mollenhauer et al., 2002; Wagner et al., submitted; Ferdelman and Strotmann, unpublished data) are given in Table 1. North of the Walvis Ridge, terrigenous material is discharged by the Rivers Niger, the Cunene and especially by the Congo, which leads to typically low carbonate values. The lowest values are found in the vicinity of the Congo River. South of 19°S, carbonate content reaches almost 80%.

Because of several high-productivity systems in surface waters, sediments from the whole area are enriched in TOC. There is an increase of TOC with increasing latitude, and four provinces can be distinguished, matching the distribution of the different productivity systems. Lowest TOC values (1.7% or less) are found below the area of seasonal coastal upwelling in the Gulf of Guinea and the northern Angola Basin, where the fraction of terrigenous organic matter in sediments ranges from 57 to 76% of the bulk organic matter (Wagner et al., 2003). Total organic carbon values increase from the southern Angola Basin to the northern Benguela region, reach maximum values of up to 8% beneath the Lüderitz upwelling cell at about 25°S, and decrease again to the south. In the area of the Benguela upwelling system, the supply of terrigenous organic matter is expected to be minor (Wefer and Fischer, 1993).

2.4. Material and methods

2.4.1. Sample preparation and benthic foraminiferal data

In this paper, we examine foraminiferal data from twenty stations, five of which were presented previously in Licari et al. (2003). The sample positions are plotted in Figure 1, and listed in Table 1 together with environmental and foraminiferal data. Samples were taken with a multicorer (Barnett et al., 1984) between February and March during the years 1996 and 1998, and prepared as in Mackensen and Douglas (1989). At each station, except one, two cores representing 78 cm^2 of sediment surface each were sub-sampled in 1 cm slices. Corresponding sediment layers in both cores were combined and stored at 4°C in a mixture of ethanol and Rose Bengal. On shore, samples were washed over a 2 mm and a 63 μm mesh-screen, the coarse fraction was subsequently dry-sieved over a 125 μm mesh-screen. We examined different splits of the sand fraction (>125 μm) for their contents of live (stained) and dead foraminifera, so that about 300 individuals were counted for each sample. Since less than 300 stained individuals were often found per sample, most samples were examined entirely for their content in live foraminifera.

Branched agglutinated species, mostly belonging to the genera *Hyperammina* and *Rhabdammina*, were counted only if fragments included the proloculus. This is different from the approach used previously in Licari et al. (2003), who omitted these species from quantitative analyses, but it does not substantially affect standing stock calculation and other numerical indices for the five stations considered. Branched species without distinct chambers were not included. This concerns principally the easily breakable *Rhizammina algaeformis*. *Rhizammina* species have been previously described as an important contributor to the benthic foraminiferal fauna on Walvis Ridge and the upper slope off Namibia (Schmiedl et al., 1997). However, according to Cartwright et al. (1989), *R. algaeformis* can form branching strands and interconnected clumps up to 10 cm long. The tubes are fragile and break easily in numerous fragments of varying length, making a realistic estimation of the number of *R. algaeformis* specimens rather difficult.

Standing stocks (live foraminifera) and benthic foraminiferal numbers (dead foraminifera) were calculated and expressed as the number of foraminifera/50 cm^2 and 10 cm^2 surface, respectively.

2.4.2. Statistical treatment

In order to obtain results comparable with previous studies in the southeast Atlantic and the adjacent Southern Ocean (Mackensen et al., 1995; Schmiedl et al., 1997; Schumacher, 2001), foraminiferal assemblages were statistically defined using Q-mode Principal Component Analysis (PCA) with the software SYSTAT 5.2.1©. We deleted rare species with abundances less than 1% or present in only one sample for the statistical analysis, but kept them in the data for calculation of standing stocks and foraminiferal numbers.

Analyses were run for four distinct data sets: (1) "Total Live", (2) "Total Dead", (3) "Surface Live", and (4) "Surface Dead". "Total Live" assemblages were calculated on the basis of all the samples where stained foraminifera were found, that is, from the top 1 cm down to a maximum of 5 cm to 12 cm, depending on the station. For the calculation of the "Total Dead" assemblages, the uppermost 5 cm of sediment were used. Because sedimentation rates of between 4 and 15 cm ky^{-1}, or even higher, have been calculated for this area (e.g., Balsam and McCoy, 1987; Summerhayes et al., 1995; Schmiedl and Mackensen, 1997; Giraudeau et al., 1998; Kirst et al., 1999; Mollenhauer et al., 2002), we assume that the dead assemblages are representative of recent Holocene conditions, and can reasonably be compared with present live foraminiferal assemblages. Finally, "Surface Live" and "Surface Dead" assemblages were calculated on the basis of the top 1 cm of sediment only. The terms "Total Live", "Total Dead", "Surface Live", and "Surface Dead" as used hereafter refer to the data sets and corresponding assemblages described above.

In interpreting the results of the PCA, each PC-loading was squared. The squared PC-loading then represents the proportion of the assemblage information in a sample explained by each component. The sum of these squared loadings (communality) is then the fraction of the sample assemblage explained by the varimax model (Imbrie and Kipp, 1971; Mead and Kennett, 1987).

For the determination of the ecological preferences of the benthic foraminiferal faunas, stepwise multiple regressions with a 95%-confidence limit were used to correlate the PC-loadings (i.e., foraminiferal assemblages) with available environmental parameters. An *F*-test was used to verify the significance of the multiple regressions. Simple linear regressions were subsequently performed between foraminiferal assemblages and single environmental variables for those of the environmental parameters that were identified as significant contributors to the multiple regression. Bottom-water content of dissolved oxygen and oxygen penetration depth within the sediment (Hensen et al., 2000; Wenzhöfer et al., 2001; Hensen, pers. comm., 2002; Wenzhöfer and Glud, 2002), sediment porosity (Müller, unpublished data, 1999), total organic carbon and carbonate contents (Mollenhauer et al., 2002; Wagner et al., submitted; Ferdelman and Strotmann, unpublished data) were selected as possible control parameters. Organic carbon flux rates to the sea floor were calculated on the basis of primary productivity estimates derived from recent satellite-based maps (data available at http://marine.rutgers.edu/opp/), and the equation of Berger (1989) given for water depths greater than 1000 m. All environmental parameters are given in Table 1.

A list of all dominant and associated species contributing to the assemblages is given in Appendix A (Taxonomic appendix) with original designation. Selected species are illustrated in Plates I and II. Varimax principal component loadings and scores derived from the PCA are available in Tables B1 to B4 in the Appendix B. Foraminiferal raw data are given in Appendix C, available as electronic supplement of this paper.

2.5. Results

2.5.1. Foraminiferal total live and dead assemblages

Five live and five dead total assemblages are recognized. The Q-mode model of the biocoenosis explains 67.4% of the total variance of the live data set, while the corresponding model of the thanatocoenosis explains 77.6% of the total variance of the dead data set (Table 2). The distribution patterns of these assemblages, as expressed by squared PC-loadings, are presented for both models in Figure 2. All dominant and important associated species, as indicated by PC-scores, are summarized in Table 2. The faunal assemblages were named according to their most important constituents, and are briefly presented in the following sections (Table 2, Fig. 2).

Total live assemblages

The *Bulimina mexicana* live assemblage (total live PC1), which explains 19% of the total variance of the total live data set, is distributed between 10°S and 17°S. *Bulimina mexicana* is a common species of the biocoenosis in the whole area south of 10°S, with percentages exceeding 3%. The dramatic increase in *B. mexicana* proportions in the central and southern Angola Basin, up to 40%, explains the distribution of this assemblage.

Uvigerina peregrina and *Robertinoides chapmani* equally dominate the second principal component assemblage (total live PC2, 17.2% of the total variance), which dominates the biocoenosis in the Gulf of Guinea and the northern Angola Basin, between 1°N and 8°S.

The *Cibicidoides pachyderma* assemblage (total live PC3) explains close to 12% of the total variance, and typically occurs in the northern Benguela region between 20°S and 24°S.

The *Uvigerina auberiana* assemblage (total live PC5) accounts for nearly 10% of the total variance. It "sandwiches" the *C. pachyderma* assemblage distribution area, and marks its northern and southern boundaries around 19°S and 26°S, respectively. *Uvigerina auberiana* is particularly abundant at the southernmost station, GeoB3703, where it accounts for about half of the fauna. This proportion drops to 8% at station GeoB3715.

The *Sphaeroidina bulloides* assemblage (total live PC4, 9.6% of the total variance) typically emerges south of 26°S and extends towards the southern Benguela region.

Total dead assemblages

The *U. auberiana / B. mexicana* dead assemblage (total dead PC1) explains more than 27% of the total variance of the thanatocoenosis. Its bi-modal distribution, in the northern and the central Benguela region, is mostly generated by high percentages of *U. auberiana* in both areas (up to 40%). The distribution of this assemblage corresponds to the occurrence of the *U. auberiana* and *C. pachyderma* live assemblages mostly, and to a lesser extent to the *B. mexicana* and *S. bulloides* live assemblages.

The *U. peregrina* dead assemblage (total dead PC2) explains 15.7% of the total variance. Its distribution matches the occurrence of the live *U. peregrina* fauna as far south as 5°S, where it is replaced by the *Karrerulina conversa* dead assemblage (total dead PC5), which accounts for less than 10% of the total variance. This assemblage is dominated by agglutinated species.

Gavelinopsis translucens and *Epistominella exigua* (total dead PC3, 13.2% of the total variance) dominate the thanatocoenosis south of 27°S and within the distribution area of the *U. auberiana / B. mexicana* dead assemblage, off Walvis Bay (station GeoB3706).

The *Epistominella smithi* assemblage (total dead PC4, 13.4% of the total variance) characterizes the upper slope off Angola between 10°S and 16°S. The distribution area of this assemblage matches most of the area covered by the total live *B. mexicana* fauna, which extends further south up to station GeoB3712 at 17°S. The *U. auberiana / B. mexicana* total dead assemblage dominates the dead fauna of this station.

Table 2. Species composition of total (1) live and (2) dead foraminiferal assemblages (as expressed by PC-scores). Principal component number, dominant species (as indicated by largest PC-scores), important associated species (i.e., with scores greater than one-fifth of the score of the most dominant species), % of the total variance explained by each factor, and total variance are given.

Dominant species	Score	Associated species	Score	Var.(%)
(1) Live foraminiferal assemblages				
PC1 *Bulimina mexicana*	8.5	*Valvulineria laevigata*	3.2	19.0
		Haplophragmoides bradyi	2.3	
		Reophax bilocularis	1.9	
PC2 *Uvigerina peregrina*	3.9	*Reophax bilocularis*	2.7	17.2
Robertinoides chapmani	3.9	*Ammoscalaria* sp.	2.5	
Gavelinopsis translucens	3.5	*Ammomarginulina foliacea*	2.0	
Lagenammina difflugiformis	3.5	*Melonis barleeanum*	1.8	
Reophax scorpiurus	3.5	*Hoeglundina elegans*	1.3	
PC3 *Cibicidoides pachyderma*	8.5	*Ammoscalaria* sp.	3.1	11.7
		Fursenkoina mexicana	2.2	
PC4 *Sphaeroidina bulloides*	4.6	*Chilostomella oolina*	3.4	9.9
		Reophax bilocularis	2.9	
		Gavelinopsis translucens	2.6	
		Recurvoides contortus	2.3	
		Cribrostomoides subglobosum	1.3	
		Oridorsalis umbonatus	1.3	
		Reophax dentaliniformis	1.3	
		Valvulineria laevigata	1.3	
		Deuterammina montagui	1.3	
		Globocassidulina subglobosa	1.1	
		Reophax micaceus	1.0	
		Cibicidoides pachyderma	1.0	
PC5 *Uvigerina auberiana*	6.5	*Globobulimina affinis*	5.5	9.6
		Fursenkoina mexicana	4.7	
			Total var. (%)	67.4
(2) Dead foraminiferal assemblages				
PC1 *Uvigerina auberiana*	6.4	*Bulimina aculeata*	1.8	27.3
Bulimina mexicana	6.3	*Cassidulina laevigata*	1.3	
PC2 *Uvigerina peregrina*	8.1	*Sphaeroidina bulloides*	2.1	15.7
PC3 *Gavelinopsis translucens*	4.2	*Globocassidulina subglobosa*	3.1	13.2
Epistominella exigua	4.0	*Cassidulina laevigata*	2.8	
		Bulimina mexicana	2.5	
		Cibicidoides pachyderma	2.5	
		Gyroidinoides polius	1.8	
		Eggerella bradyi	1.6	
		Sphaeroidina bulloides	1.3	
		Brizalina subspinescens	1.0	
PC4 *Epistominella smithi*	7.0	*Bulimina mexicana*	3.7	13.4
		Bulimina exilis	3.0	
		Valvulineria laevigata	2.3	
PC5 *Karrerulina conversa*	6.0	*Verneuilinulla propinqua*	3.3	8.0
		Hormosina globulifera	3.1	
		Ammomarginulina foliacea	2.6	
		Ammolagena clavata	2.4	
		Lagenammina difflugiformis	1.8	
		Cribrostomoides subglobosum	1.4	
			Total var. (%)	77.6

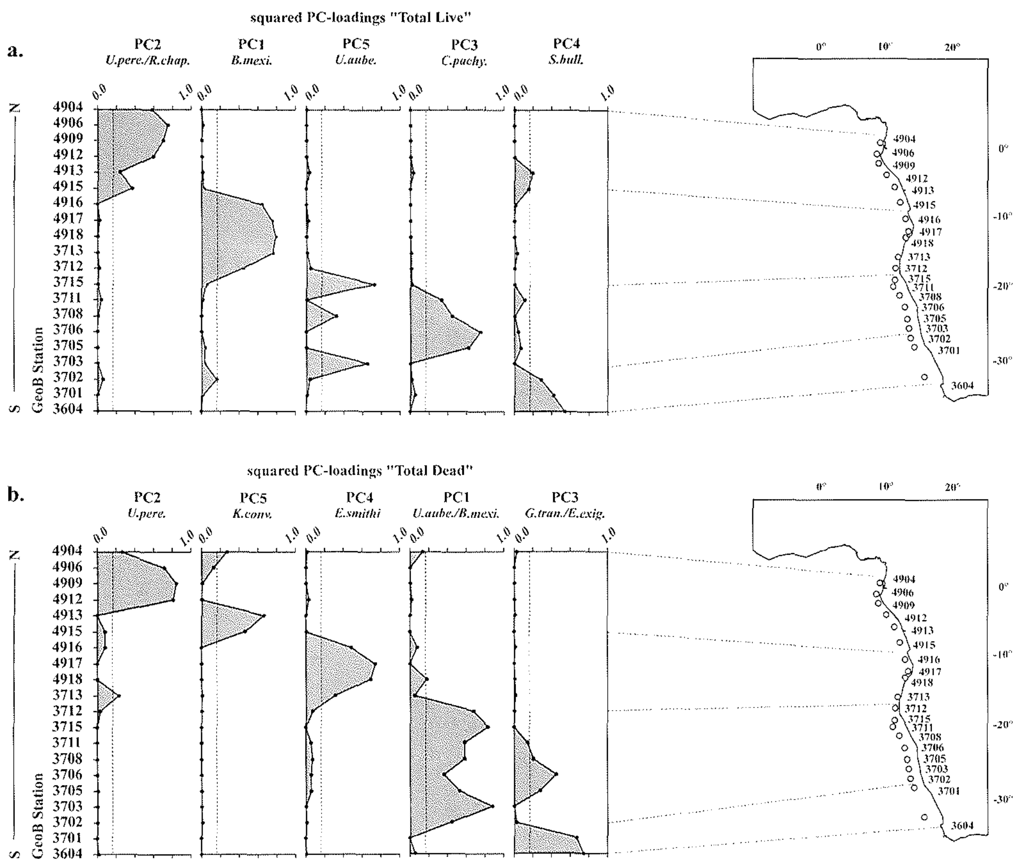

Figure 2. Distribution of total (a) live and (b) dead benthic foraminiferal assemblages, as expressed by squared PC-loadings. Squared loading values greater than 0.2 (hatched line) were considered statistically significant (Malmgren and Haq, 1982). Foraminiferal assemblages are named according to their most important constituents. For convenience, assemblages are sorted according to their geographical appearance and linked to the sample location map. See text for further explanations.

2.5.2. Foraminiferal surface live and dead assemblages

To investigate whether omitting the deeper sediment layers affects the statistical definition of the distribution and species composition of live and dead foraminiferal assemblages, we did the same calculation on the basis of the foraminiferal data from the top 1 cm only. Five live and five dead surface assemblages are recognized, accounting for 70.2% and 75.1% of the live and the dead surface data sets, respectively (Table 3). The species composition and distribution of these assemblages agree extremely well with those from the corresponding total assemblages (Table 3, Fig. 3).

Surface live assemblages

Dissimilarities between the total live and surface live assemblages are primarily due to the different relative importance (as expressed by the component scores) of dominant and associated species in the assemblages, such as the PC2 and PC4 assemblages, and to the statistical disappearance of deep-dwelling species (Tables 2.1 and 3.1). As expected, the most important differences occur in the PC5 assemblage, typically dominated by *U. auberiana* and deep infaunal species in the total biocoenosis. Its corresponding PC5 assemblage in the surface model is typically still dominated by *U. auberiana*, but the preferentially epifaunal species *Cassidulina laevigata* replaces *Globobulimina affinis*, which statistically disappeared, and *Fursenkoina mexicana*, which contributes only marginally to the fauna. Other intermediate and deep infaunal species such as *Melonis barleeanum* (total live PC2), *F. mexicana* (total live PC3), or *Chilostomella oolina* and *Reophax dentaliniformis* (total live PC4) are missing in the surface statistical model as well.

With the exception of station GeoB4915, the distribution of the surface live assemblages perfectly matches the faunal provinces defined from the analysis of the total live data set. The total biocoenosis at GeoB4915 is principally dominated by the *U. peregrina / R. chapmani* assemblage, but it is characterized by a pronounced northern emergence of the *G. translucens / S. bulloides* assemblage in the surface model.

Surface dead assemblages

The differences between total dead and surface dead assemblages are minor, mostly restricted to the PC3 and PC5 assemblages. These dissimilarities principally result from the different relative importance of species in the assemblages (as expressed by the component scores, Tables 2.2 and 3.2). Furthermore, *Bulimina exilis*, an important intermediate infaunal species associated with the total dead PC4, becomes statistically insignificant in the corresponding surface dead PC4. In general, however, deep infaunal species are not important contributors to the total thanatocoenosis.

The distribution areas of the total and surface dead assemblages fit rather well except for the northernmost station of the transect (GeoB4904), where the agglutinated *Verneuilinulla propinqua / K. conversa* assemblage, occurring otherwise off the Congo River, dominates the surface dead fauna instead of the *U. peregrina* assemblage.

Table 3. Species composition of surface (1) live and (2) dead foraminiferal assemblages (as expressed by PC-scores). Principal component number, dominant species (as indicated by largest PC-scores), important associated species (i.e., with scores greater than one-fifth of the score of the most dominant species), % of the total variance explained by each factor, and total variance are given.

	Dominant species	Score	Associated species	Score	Var.(%)
(1) Live foraminiferal assemblages					
PC1	*Bulimina mexicana*	8.7	*Valvulina conica*	2.4	20.0
			Reophax bilocularis	2.2	
PC2	*Uvigerina peregrina*	4.9	*Gavelinopsis translucens*	3.3	17.3
	Robertinoides chapmani	4.5	*Reophax scorpiurus*	2.9	
			Lagenammina difflugiformis	2.7	
			Ammomarginulina foliacea	2.6	
			Reophax bilocularis	2.5	
			Ammoscalaria sp.	2.4	
			Hoeglundina elegans	1.9	
PC3	*Cibicidoides pachyderma*	8.7	*Ammoscalaria* sp.	2.8	12.1
			Pyrgo murrhina	1.9	
PC4	*Gavelinopsis translucens*	5.2	*Globocassidulina subglobosa*	2.2	12.1
	Sphaeroidina bulloides	5.0	*Bulimina mexicana*	1.8	
			Cibicidoides globulosus	1.3	
			Oridorsalis umbonatus	1.2	
			Reophax bilocularis	1.1	
PC5	*Uvigerina auberiana*	7.7	*Cassidulina laevigata*	3.2	8.6
			Gavelinopsis translucens	2.7	
			Hormosina globulifera	2.0	
				Total var. (%)	70.2
(2) Dead foraminiferal assemblages					
PC1	*Uvigerina auberiana*	7.1	*Bulimina mexicana*	5.2	23.8
			Bulimina aculeata	2.2	
PC2	*Uvigerina peregrina*	7.1	*Reophax bilocularis*	2.4	11.5
			Lagenammina difflugiformis	2.4	
			Sphaeroidina bulloides	2.0	
			Cribrostomoides subglobosum	1.6	
			Fissurina spp.	1.5	
PC3	*Gavelinopsis translucens*	3.8	*Eggerella bradyi*	2.2	15.9
	Bulimina mexicana	3.7	*Gyroidinoides polius*	1.4	
	Globocassidulina subglobosa	3.5	*Brizalina subspinescens*	1.3	
	Epistominella exigua	3.4	*Sphaeroidina bulloides*	1.2	
	Cassidulina laevigata	3.0	*Cibicidoides pachyderma*	1.1	
PC4	*Epistominella smithi*	6.5	*Bulimina mexicana*	4.6	16.2
			Valvulineria laevigata	3.0	
			Reophax bilocularis	1.8	
PC5	*Verneuilinulla propinqua*	4.9	*Ammobaculites agglutinans*	2.9	7.8
	Karrerulina conversa	4.0	*Hormosina globulifera*	2.8	
			Cassidulina laevigata	1.5	
			Bulimina mexicana	1.5	
			Ammolagena clavata	1.5	
			Cribrostomoides subglobosum	1.4	
			Lagenammina tubulata	1.4	
			Gavelinopsis translucens	1.1	
				Total var. (%)	75.1

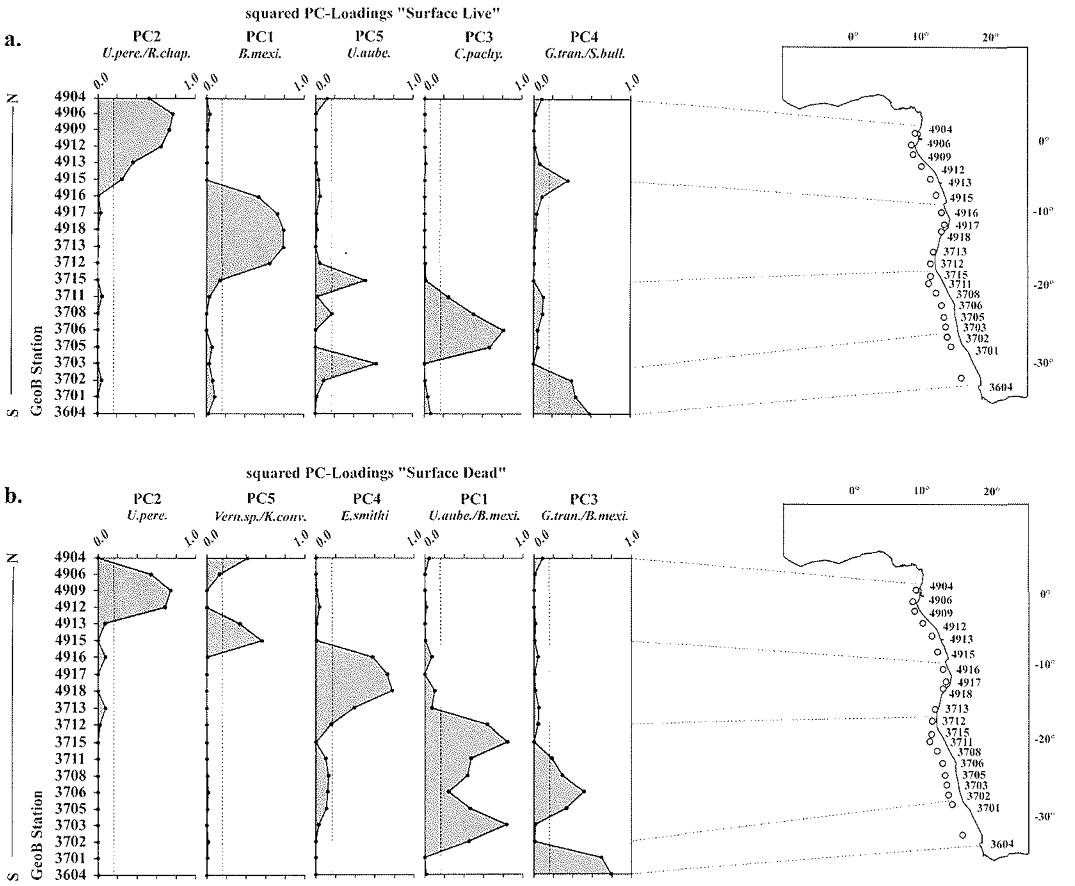

Figure 3. Distribution of surface (a) live and (b) dead benthic foraminiferal assemblages, as expressed by squared PC-loadings. Squared loading values greater than 0.2 (hatched line) were considered statistically significant (Malmgren and Haq, 1982). Foraminiferal assemblages are named according to their most important constituents. For convenience, assemblages are sorted according to their geographical appearance and linked to the sample location map. See text for further explanations.

2.5.3. Correlations to environmental parameters

Although regression coefficients might differ, results of multiple and simple regression analysis from total and corresponding surface assemblages are generally comparable (Table 4). For reasons of convenience, the outcome of the different analyses will be presented simultaneously.

Table 4. Simple linear regression coefficients (r) between single foraminiferal assemblages (i.e. PC-loadings) and single environmental variables for those environmental parameters that significantly influence the foraminiferal faunas, as indicated by stepwise multiple regression analysis (with a 95% confidence-limit), are given in the upper part of table. Multiple regression coefficients (R) of stepwise multiple regression between single foraminiferal assemblages and all environmental parameters, *F* and probability of *F* (*p*), and the number of samples (n) included in the analysis are given in the lower part.

	a) Live total assemblage					b) Dead total assemblage				
	PC1	**PC2**	**PC3**	**PC4**	**PC5**	**PC1**	**PC2**	**PC3**	**PC4**	**PC5**
	B.mexi.	*U.pere.*	*C.pachy.*	*S.bull.*	*U.aube.*	*U.aube.*	*U.pere.*	*G.tran.*	*E.smit.*	*K.conv.*
Latitude		0.79				-0.53				0.62
Longitude						0.17	-0.74			
Organic Flux			0.41							
TOC	-0.09				0.75	0.81		0.00		
Carbonate			0.56		0.15			0.79		
Porosity										
Oxygen Bottom Water										
Oxygen Penetration Dept	-0.43	0.73				-0.83				
R	0.69	0.87	0.77		0.79	0.96	0.74	0.91		0.62
n	19	19	20		20	19	20	20		20
F	7.3	25.0	12.4		14.5	39.3	22.2	43.4		11.5
p (F-Test)	0.006	<0.001	<0.001		<0.001	<0.001	<0.001	<0.001		0.003

	c) Live surface assemblage					d) Dead surface assemblage				
	PC1	**PC2**	**PC3**	**PC4**	**PC5**	**PC1**	**PC2**	**PC3**	**PC4**	**PC5**
	B.mexi.	*U.pere.*	*C.pachy.*	*G.tran.*	*U.aube.*	*U.aube.*	*U.pere.*	*G.tran.*	*E.smit.*	*V.pro.*
Latitude		0.84								0.59
Longitude				0.54			-0.64			
Organic Flux			0.34	-0.58						
TOC	-0.10				0.70	0.83		0.07		
Carbonate		-0.52	0.63		0.01			0.78		
Porosity										
Oxygen Bottom Water										
Oxygen Penetration Dept	-0.44					-0.82				
R	0.70	0.91	0.79	0.77	0.80	0.91	0.64	0.86		0.59
n	19	20	20	20	20	19	20	20		20
F	7.9	39.5	14.1	12.0	14.6	37.5	12.2	23.1		9.4
p (F-Test)	0.004	<0.001	<0.001	0.001	<0.001	<0.001	0.003	<0.001		0.007

With the exception of three assemblages (*S. bulloides* total live assemblage and *E. smithi* total and surface dead assemblages), the multiple regression coefficients show that there is generally a clear environmental control on benthic foraminiferal total and surface biocoenosis (multiple R > 0.69) and thanatocoenosis (multiple R > 0.59). However, foraminiferal assemblages exhibit rather few significant correlations to single environmental parameters. With the exception of the Guinea Basin and the northern Angola Basin (*U. peregrina* total live assemblage), benthic foraminiferal assemblages show a negative correlation to the oxygen penetration depth within the sediment (*B. mexicana* total and surface live assemblage, *U. auberiana / B. mexicana* total and surface dead assemblage). Relation to the sediment is indicated below the Benguela upwelling system by positive correlation to the carbonate content for *C. pachyderma* and *U. auberiana* total and surface live assemblages and *G. translucens / E. exigua* total and surface dead assemblages. These assemblages occur in environments characterized by sedimentary carbonate contents typically higher than 50%. In the Guinea Basin and the northern Angola Basin, the *U. peregrina* surface live assemblage negatively correlates to the carbonate content. Benthic foraminiferal faunas especially from the northern part of the upwelling system positively correlate to organic matter fluxes to the sea-floor and TOC content of the sediment (*C. pachyderma* and *U. auberiana* total and surface live assemblages, *U. auberiana / B. mexicana* total and surface dead assemblage). On the contrary, in the southern Benguela area, the *G. translucens / S. bulloides* surface live assemblage exhibits a negative correlation to the organic matter flux. None of the assemblages shows significant correlation either to bottom water oxygen content or porosity.

2.5.4. Standing stocks and numbers of empty tests

Benthic foraminiferal total standing stocks vary between 51 and 1645 stained individuals per 50 cm^2 for the total live data set, and are distributed following a latitudinal trend (Table 1, Fig. 4). Standing stocks increase from low values in the northern Angola Basin to the highest values close to 17°S, and then decrease progressively to the south. The lowest values are found in the vicinity of the Congo River mouth. Standing stocks recorded at both the northern and the southern extremities of the investigated area are in the same order of magnitude, varying around 200 to 400 specimens per 50 cm^2. With values from 25 to 564 live foraminifera per 50 cm^2 (Table 1), standing stocks calculated for the upper centimeter of sediment are much lower than those integrating the deeper layers. In Figure 4, total and surface standing stocks are plotted versus latitude. North of 15°S, 50% of the total fauna on average inhabits the topmost centimeter of sediment, and the latitudinal variation of surface standing stocks closely follows that of total standing stocks. In the southern part of the area, the proportion of foraminifera found at the surface drops to close to 30% of the total fauna, but surface standing stocks still vary in agreement with total standing stocks. Strong discrepancies are observed in the center of the study area, between 15°S and 17°S, where the highest total standing stocks were observed. Here, only 7 to 12% of the total live fauna were found in the top 1 cm of sediment (Fig. 4).

Similar observations can be made when comparing total numbers of empty tests (that is, in 5 cm of sediment) with numbers of empty tests in the surface sediment only (Table 1, Fig. 4). Total numbers of empty tests increase sharply from 194-3682 empty tests per 10 cm^2 north of 18°S, to 1855-21119 empty tests per 10 cm^2 south of this latitude, related to the increase of carbonate content in the sediment (Fig. 4). Although this trend is smoothed when considering the surface sediment only, this latitude still marks a boundary, south of which the uppermost sediment contains on average less than 10% of the empty tests found within 5 cm of sediment. North of 15°S, this proportion is on average 15%. Discrepancies occur in the central area (between 15°S and 17°S) as well as between 26°S and 28°S, with percentages less than 4% in both areas.

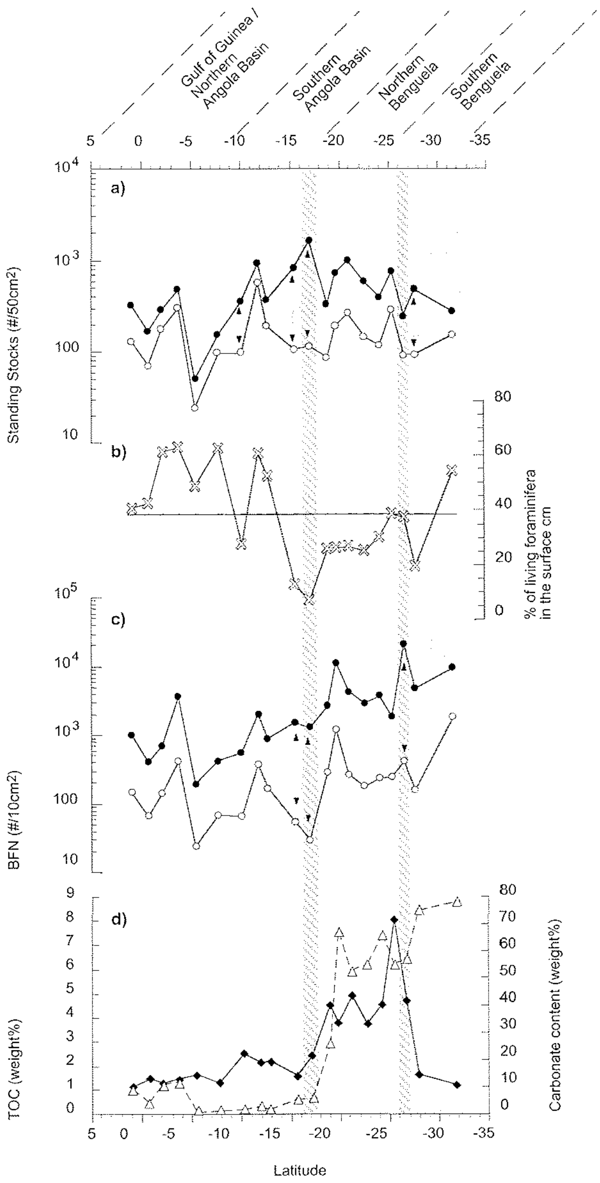

Figure 4. Distribution versus latitude of (a) foraminiferal total standing stocks (filled circles) and in the uppermost sediment (open circles), (b) percentages of live foraminifera found in the surface centimeter (crosses), (c) benthic foraminiferal number (BFN) in five (filled circles) and one centimeter (open circles) sediment, and (d) TOC (filled diamonds) and carbonate content (open triangles) of the sediment. Foraminiferal provinces (shaded areas) are indicated for comparison. Hatched areas indicate where live and dead assemblages have different distribution pattern (see text for further explanations).

2.6. Discussion

2.6.1. Distribution of total benthic foraminiferal assemblages

The West African upper slope is influenced by several oceanic and coastal upwelling cells strongly variable in time and space (Fig. 1). The distinct geographical distribution of these events generates a strong latitudinal gradient of productivity in the surface waters. Live and dead benthic foraminiferal assemblages show a latitudinal succession matching these productivity provinces fairly well (Fig. 2). These results demonstrate that changes in organic carbon fluxes have the strongest control on the faunal changes, as changes in water masses are minimized due to our sampling strategy, i.e., samples were taken from a narrow water depth interval. We believe that only a minor portion of the species geographic patterns may also have partly been influenced by the different sampling campaigns used for sample collection. Consequently, we focused our discussion on the influence of trophic conditions on the composition and distribution of total benthic foraminiferal assemblages.

Gulf of Guinea and northern Angola Basin

Below the area of seasonal coastal upwelling in the Gulf of Guinea and the northern Angola Basin (Fig.1), sediments are typically inhabited by the highly diverse *U. peregrina / R. chapmani* total live assemblage (Table 2, Fig. 3).

The period of sampling (March 1998) coincides with the eastern tropical Atlantic warm season, when coastal upwelling has not yet taken place in the surface waters. Intensity and timing of upwelling in the eastern tropical Atlantic decrease in certain years, and according to Signorini et al. (1999), the December bloom was abnormally reduced in 1997. From the analysis of satellite images, these authors showed that the chlorophyll signature from the Congo River plume was very pronounced in January 1998, and peaked in August 1998. Previous investigations (Licari et al., 2003), in agreement with data on other groups of meiobenthic organisms (Soltwedel, 1997), suggest, however, that little labile marine organic matter probably reaches the sea-floor below the area influenced by the Congo discharge. Sampling for this study thus occurred at a time where supply of fresh marine organic matter to the benthos was, even if temporarily, possibly reduced in the Gulf of Guinea and the northern Angola Basin.

These observations, and the apparent lack of correlation between the *U. peregrina* assemblage and TOC content or the organic carbon flux (Table 4), might primarily appear to contrast with the published ecological preferences of *U. peregrina*, which is commonly used as an indicator of enhanced organic matter flux conditions (e.g. Lutze and Coulbourn, 1984; Lutze, 1986; Hermelin and Shimmield, 1990; Mackensen et al., 1995; Fariduddin and Loubere, 1997; Schmiedl and Mackensen, 1997; De Rijk et al., 1999; Kuhnt et al., 1999; Schmiedl et al., 2000; Huang et al., 2002). Hermelin and Shimmield (1990), and Jannink et al. (1998) described *U. peregrina* in severely oxygen-depleted areas from the Arabian Sea, which suggests a distribution not clearly limited by oxygen deficiency. Schmiedl et al. (1997) suggested, however, that in the southern Angola Basin and the Cape Basin, *U. peregrina* avoids strong oxygen depletion, and occurs preferentially in TOC-rich sediments (>1%) from the lower slope, characterized by moderate oxygen deficiency (>2 ml l^{-1}). Such conditions occur on the upper slope below the area of seasonal coastal upwelling, where bottom-water oxygen concentration typically exceeds 4 ml l^{-1}, and sediments are moderately enriched in TOC (between 1.2% and 1.7%, Table 1). Additionally, the *U. peregrina* fauna is positively correlated to the oxygen penetration depth within the sediment (Table 4).

Other important contributors to the fauna such as *Lagenammina difflugiformis* and *Reophax scorpiurus* (Table 2) have been described in the seasonal coastal upwelling area from the northern Gulf of Guinea by Schiebel (1992) and Timm (1992), in sediments from the shelf to abyssal with TOC content ranging from 0.1% to about 3%. These species occur in other environments influenced by seasonally high organic carbon fluxes, in sediments generally moderately TOC-enriched (Harloff and Mackensen, 1997; Schmiedl et al., 1997; Wollenburg and Mackensen, 1998; Kurbjeweit et al., 2000; Ohkushi and Natori, 2001).

The occurrence of low standing stocks (Fig. 4) further corroborates the hypothesis that the supply of fresh organic matter was moderate in that area shortly before sampling. Foraminifera possibly fed on old organic matter remaining from a precedent high-productivity event, of terrestrial origin, or transported downslope from the shelf. The significant occurrence of *M. barleeanum* in the live fauna from that area (Table 2) concurs with the conclusions of Caralp (1989), who demonstrated that this species avoids areas permanently influenced by upwelling, and preferentially feeds on altered organic matter.

In contrast to live assemblages, which represent a snapshot of foraminiferal faunas in a particular environmental context, dead assemblages correspond to a time-averaged image of foraminiferal faunal patterns, smoothed or transformed by (destructive) taphonomic processes. Different degrees of carbonate corrosiveness of the ambient waters explain the occurrence of a dead fauna largely dominated by *Karrerulina conversa* and other agglutinated species in the vicinity of the Congo River (Table 2, Fig. 2). There, high sedimentation rates and large amounts of terrestrial organic detritus generate highly corrosive pore-waters and carbonate dissolution (Jansen et al., 1984; Van Leeuwen, 1989). An external organic coating protects the test of live calcareous foraminifera against dissolution in carbonate-aggressive environment, but empty tests rapidly dissolve (Mackensen et al., 1993; Debenay et al., 1996). Further north, *U. peregrina* strongly dominates the dead fauna. Rapid post-mortem disintegration probably causes the disappearance of agglutinated species such as *Lagenammina difflugiformis* and *Reophax scorpiurus*, and selective destruction of easily dissolvable aragonite is a possible explanation for the loss of *R. chapmani*. However, the effect of population dynamics should not be excluded. Fontanier et al. (2003) demonstrated that *U. peregrina* strongly responds to seasonal inputs of fresh organic matter in the Bay of Biscay. Potentially important changes in the composition of the fauna probably follow the establishment of more favorable trophic conditions in the eastern South Atlantic. A stronger *U. peregrina*-dominated live fauna during periods of increased food availability, resulting in turn in a strong *U. peregrina* signal in the dead fauna, is a realistic scenario.

Accordingly, we suggest that the *U. peregrina*-dominated faunas on the upper slope in the tropical part of the eastern South Atlantic are adapted to seasonally high fluxes of marine phytodetritus, and tolerate low-quality organic matter from marine or terrestrial origin. The characteristic species of these assemblages possibly avoid the most eutrophic areas of the southern regions, where they might be outcompeted by more opportunistic species. These results support previous observations from Jannink et al. (1998) and Fontanier et al. (2002), who proposed that *U. peregrina* might be adapted to more degraded organic matter and lower food levels than typical high-productivity species (such as e.g. *Bulimina* spp. and *Bolivina* spp.).

Southern Angola Basin

Bulimina mexicana strongly dominates the biocoenosis in the southern Angola Basin, in the frontal zone separating the cold Benguela Current and warm South Equatorial Counter Current water masses (Fig. 1). The assemblage extends from 10°S to 17°S (Fig. 2), which marks the southernmost limit of the meridional shift of the ABF.

Coastal upwelling does not characterize the area corresponding to the *B. mexicana* fauna, but the sequence of events in the surface waters certainly influences primary productivity, possibly resulting in a succession of high-productivity episodes in the Angola Basin through the year. Specifically, samples from that area were taken between February and March (Table 1), that is, a couple of months after the influence of the Angola Dome reaches the euphotic layer. According to investigations of deep-sea sediments and culture experiments, the temporal reaction of benthic foraminifera to the input of fresh organic matter is of the order of several weeks (Heinz et al., 2002; Fontanier et al., 2003). Therefore, we interpret the relative increase of standing stocks in that area as the direct response to significant supply of fresh organic matter from the surface, in relation to oceanic upwelling activity. This is corroborated by the appearance of *B. exilis*, known to thrive under conditions of high input of fresh phytodetritus (Caralp, 1989; Jannink et al., 1998). The influence of the Dome could especially explain the peak in total standing stocks recorded at station GeoB4917 at about 12°S. Why standing stocks sharply increase at station GeoB3712 at about 17°S is less clear. The situation is certainly complex at this latitude, which marks the approximate summer position of the ABF at the time of sampling (austral summer). Station GeoB3712 is located some distance from the Dome area, but could be influenced by locally enhanced primary productivity linked to other frontal features, or to nutrient input from the Cunene River.

Bulimina mexicana appears to be a typical species of high-productivity faunas on the continental slope (Loubere, 1999; Loubere and Fariduddin, 1999). Schmiedl et al. (1997) reported this species as part of assemblages in the southern Angola Basin and the northern part of the Benguela system, showing a positive correlation to TOC contents, and a negative one to the dissolved oxygen concentration of bottom waters. Similarly, sibling species (*B. costata*, *B. inflata*) have been repeatedly reported from eutrophic environments (e.g. Jorissen et al., 1998). According to our study, *B. mexicana* typically inhabits sediments where TOC contents generally exceed 2%, but there was no positive correlation between the *B. mexicana* fauna and the TOC content of the sediment or the organic carbon flux to the sea-floor (Table 4). Oxygen concentrations at the time of sampling were of the same order of magnitude than in the Gulf of Guinea and northern Angola Basin, between 3 and 4 ml l^{-1}. Thus, it can be reasonably excluded that the lack of oxygen explains the replacement of the *U. peregrina / R. chapmani* fauna by the *B. mexicana* fauna. In our view, these important faunal changes result from the different trophic conditions.

The occurrence of a dead fauna strongly dominated by *E. smithi* together with *B. mexicana* (Table 2, Fig. 2) indicates, however, that oxygen availability might at some times greatly influence the composition of the southern Angola Basin assemblage. *Epistominella smithi* has been extensively described in oxygen minimum zones, in a wide range of dysoxic (2.0-0.2 ml.l^{-1}) to suboxic (0.2-0.0 ml.l^{-1}) environments (Sen Gupta and Machain-Castillo, 1993; Silva et al., 1996). In Pleistocene and Upper Pleistocene sediments from the Benguela upwelling system, Brüchert et al. (2000) found this species in dark sediment layers which probably formed during periods of intense upwelling, enhanced carbon export, and very low benthic oxygenation. As suggested by the weak negative correlation between the live fauna and oxygen penetration depth (Table 4), *B. mexicana* probably tolerates oxygen depletion, a characteristic shared by most species typically found in high productivity areas (review in Sen Gupta and Machain-Castillo, 1993; Bernhard and Sen Gupta, 1999). Denne and Sen Gupta (1991) reported *B. mexicana* in the Gulf of Mexico in an assemblage from environments with slightly lower oxygen concentrations than those recorded in this study, between 2.5 and 2.9 ml l^{-1}. Off Southwest Africa, Schmiedl et al. (1997) showed that *B. mexicana* typically occurs in organic rich sediments located below the area of strongest oxygen depletion, whereas *E. smithi* characterizes organic rich sediments within the core of the OMZ. In agreement with these observations, we suggest that *B. mexicana* does not tolerate strong oxygen deficiency, and that the dominance of *E. smithi* in the dead fauna mirrors episodes of strong oxygen depletion in the southern Angola Basin, possibly connected to periods of enhanced organic matter fluxes, and/or of vertical expansion of the main oxygen minimum layer. Empty tests of *E. smithi* might have been transported downslope from shallower depths influenced by the OMZ. The absence of significant numbers of specimens of allochthonous species in the fauna indicates, however, that most likely this phenomenon remains of secondary importance. Moreover, the strong opportunistic behavior observed for many species belonging to the genus *Epistominella* (Gooday, 1988, 1993, 1996; Wollenburg and Kuhnt, 2000) supports our suggestion of a strong reproduction event of *E. smithi* in response to the establishment of favorable conditions.

We interpret the shift of the southernmost limit of the dead fauna at 15°S, which approximately marks the winter position of the ABF, as the imprint of the seasonal influence of the Benguela system. South of this latitude, the dead fauna is typically dominated by *B. mexicana* together with *U. auberiana*, a species characteristic of the northern region of the Benguela area (see below).

We thus suggest that the benthic foraminiferal assemblages found in the southern Angola Basin mirror more regular supplies of fresh organic matter than in the Gulf of Guinea and the northern Angola Basin. Important changes in the faunal composition are expected to occur seasonally, related to changes in oxygen concentrations and/or organic matter fluxes.

Benguela coastal upwelling system

Uvigerina auberiana, *C. pachyderma*, and *S. bulloides* dominate three distinct live assemblages found north of 31°S in the area of the Benguela upwelling system (Fig. 2). These three foraminiferal live assemblages can be grouped into a northern and a southern faunal province. The *C. pachyderma* and *U. auberiana* assemblages characterize the persistent high-productivity area of the central Lüderitz cell and the northern region between 19°S and 26°S, whereas *S. bulloides* and *C. oolina* dominate the biocoenosis south of 27°S, towards the Namaqua cell and the seasonal Columbine cell (Fig. 2).

The boundary between the faunal provinces lies between the Lüderitz and Namaqua cells, and not south of Namaqua as might have been expected from the description of the upwelling regions (e.g., Shannon, 1985). Our data concur with the observation that shelf sediments between 19°S and 26°S are strongly enriched in TOC, especially in three provinces underlaying the highly productive Namibia, Walvis Bay, and Lüderitz upwelling cells (Mollenhauer et al., 2002). Also, sedimentary TOC maxima on the upper slope at 25.5°S and about 19°S may be possibly related to enhanced productivity due to jets and eddies offshore, downwelling transport of organic particles related to a shelf break front with maximum in productivity, and/or downslope transport of TOC-rich material from the shelf. In contrast, the high productivity observed at Namaqua is not recorded in the sediment, even though this upwelling cell corresponds to a secondary center of perennial upwelling (Lutjeharms and Meeuwis, 1987). One possible explanation is the prevalence of regenerated production in that area, and the southern subsystem in general, further characterized by consistently lower TOC content than in the northern region (Mollenhauer et al., 2002, and references therein). Accordingly, trophic conditions at the sea-floor are expected to be different in the northern and the southern provinces.

Most of the benthic foraminiferal species in the strongly TOC-enriched sediments (about 4% or higher) from the northern area are known to tolerate and/or require high food supply. *Cibicidoides pachyderma* has been described in a wide range of trophic conditions (Rathburn and Corliss, 1994; Almogi-Labin et al., 2000; Schmiedl et al., 2000; Fontanier et al., 2002). Off northwest Africa, *Cibicides kullenbergi*, closely related to *C. pachyderma*, flourishes in environments permanently influenced by upwelling (Jorissen et al., 1998). According to Altenbach et al. (1999), *Cibicidoides pseudoungerianus* (a synonym of *C. pachyderma*; Jones, 1994) is linked to fluxes and primary productivity ranges comparable to those required by uvigerinid species.

Uvigerina auberiana has been extensively described from organic-rich/low-oxygen environments (Loubere, 1991; Sen Gupta and Machain-Castillo, 1993; Schmiedl et al., 1997). In sediments from the Bight of Angola, Pérez et al. (2001) reported this species and *Fursenkoina mexicana* associated with *Bolivina dilatata* during periods of higher upwelling intensity, and speculated that these species might require sustained fluxes of organic matter, in agreement with our results. The *Uvigerina auberiana* fauna typically shows a bi-modal distribution, north and south of the area dominated by *C. pachyderma.* Its northern occurrence, at about 18-19°S near the Namibia cell, coincides with the maximal northern extension of the upwelling regime during austral summer (time of sampling), when the system is displaced to the south (Shannon and Nelson, 1996). This area corresponds to a secondary perennial center of upwelling-favorable winds, with maxima in autumn and spring. Filaments and plumes forming the highly productive offshore area tend to extend farthest offshore there, as well as off the Lüderitz and the Namaqua cells (Lutjeharms and Stockton, 1987). The *U. auberiana* fauna at about 26°S coincides with the area of the permanently active Lüderitz cell, and approximately matches the southern boundary of the area with highest primary productivity (Berger et al., 2002).

In addition to *C. pachyderma* and *U. auberiana*, high percentages (up to about 18%) of *Globobulimina affinis* and *F. mexicana* characterize the biocoenosis in the northern province. Species belonging to these genera usually occur in deep infaunal habitats, associated with high organic carbon fluxes (e.g. Mackensen and Douglas, 1989; Rathburn and Corliss, 1994; Silva et al., 1996; De Stigter et al., 1998; Jorissen et al., 1998; De Rijk et al., 1999, 2000; Licari et al., 2003).

The dominant species from the southern province, *S. bulloides* and *C. oolina*, are generally considered typical of high-productivity areas (Loubere, 1996; Gooday, 2003, and references therein). Upwelling is rather perennial north of 31°S, but is restricted to the period between September and March in the area further south (Shannon, 1985). However, significantly lower foraminiferal standing stocks (Fig. 4) indicate the absence or limited amount of fresh organic matter in the southern Benguela region. We frequently found live *S. bulloides* completely embedded in a thick sediment ball (10 in Plate 2). Linke and Lutze (1993) also observed encysted *S. bulloides* specimens in the northern Guinea Basin, where this species especially occurs on the slope which is seasonally influenced by coastal upwelling (Schiebel, 1992; Timm, 1992). It has been suggested that encystment, which protects foraminifera from chemical or physical disturbances, provides additional food sources from enhanced bacterial growth within the cyst (Linke and Lutze, 1993; Goldstein and Corliss, 1994). Accordingly, we interpret the construction of cysts by *S. bulloides* in the southern Benguela province as a feeding strategy to optimize food acquisition, in an area characterized by seasonal input of organic matter and lower carbon export than in the north. *Chilostomella oolina*, the second dominant species of the fauna, and other species belonging to this genus, have been commonly reported from deep infaunal habitats in eutrophic environments (e.g. Corliss and Emerson, 1990; De Rijk et al., 2000; Schumacher, 2001). *Chilostomella oolina*, in contrast with *Globobulimina affinis*, might be associated with the availability of labile organic matter (Kurbjeweit et al., 2000; Fontanier et al., 2002). Our results apparently contradict these observations, but corroborate new results of laboratory and *in situ* feeding experiments made on *G. affinis* and another *Chilostomella* species, *C. ovoidea*, in the Sagami Bay, Japan (Nomaki, 2002, and Kitazato et al., in press, as quoted in Gooday, 2003). In these studies, *C. ovoidea* did not respond to the addition of algae to the sediment, whereas *G. affinis* migrated upwards and ingested fresh algae.

These conclusions are generally confirmed by the data on composition and distribution of corresponding dead faunas (Table 2, Fig. 2). In the northern region, *U. auberiana* dominates the thanatocoenosis together with *B. mexicana*, which overprints the contribution of *Cibicidoides pachyderma* to the dead fauna. We found numerous juveniles of *C. pachyderma* in the live fauna and interpret the strong dominance of this species as the result of a recent reproduction event. The zonal extension of the dead fauna increased as compared to the live assemblages, approximately matching the area of maximum latitudinal expansion of the upwelling system. *Gavelinopsis translucens* and *Epistominella exigua* characterize the dead assemblages in the southern area. *Epistominella exigua* is a typical opportunistic species, highly adapted to strongly pulsed phytodetritus events (Gooday, 1993; Smart and Gooday, 1997).

We therefore suggest that the foraminiferal assemblages from the north Benguela region are associated with high and sustained organic matter fluxes. In contrast, species from the southern region are adapted to lower trophic conditions, characterized by a high seasonal component and overall lower export production.

2.6.2. Total versus surface assemblages

Although minor differences do exist, the species composition and distribution of foraminiferal live and dead surface assemblages from the eastern South Atlantic upper slope reflect those of the total faunas (i.e., including deeper sediment layers) extremely well (Table 3, Fig. 3). This implies that most of the qualitative ecological information obtained from the faunal analysis of the total assemblages, i.e., absence/presence of species and geographical occurrences of the faunas, can be gained from the investigation of the topmost centimeter of sediment only. The principal reasons for this include (1) generally no significant numbers of strictly epibenthic species in the fauna, (2) low numbers of strictly intermediate and deep endodenthic species in comparison to shallow endobenthic species, and (3) the dominance of the same species in the surface sediment down to deeper layers.

In contrast with the correspondence in species composition and distribution between foraminiferal surface and total assemblages, we occasionally found important discrepancies between surface and total standing stocks, and foraminiferal numbers (Fig. 4). At three stations from the southern Angola Basin and one from the southern Benguela area, total standing stocks increase by a factor of 2 compared to adjacent stations, whereas surface standing stocks remain of the same order of magnitude, or even decrease. At these stations, the percentage of the whole fauna in the uppermost 1 cm of sediment is low (between 7 and 19%), and vertical profiles of standing stocks within the sediment typically show a clear subsurface maximum (Mackensen and Licari, 2003). Similar distribution patterns are reported by Bernhard and Bowser (1992), Rathburn and Corliss (1994), Kitazato and Ohga (1995), and Rathburn et al. (2000). Generally, however, the vertical distribution of deep-sea benthic foraminifera is characterized by a clear maximum in the topmost interval, and an exponential downward decrease (review in Jorissen, 1999). The stratification of species into distinct microhabitats in our samples indicates that these subsurface maxima are not the result of rapid burial events through bioturbation, or other disturbance processes (Licari and Mackensen, unpublished). Foraminiferal species can avoid hostile conditions at the surface (e.g., enhanced corrosiveness due to high organic matter supply, stronger competition) by residing below the uppermost sediment and, at the same time, take advantage of organic matter within the sediment (Rathburn et al., 1996; Jorissen, 1999).

The numbers of empty tests in the uppermost centimeter strongly decrease at three stations, GeoB3713, GeoB3712, and GeoB3702. These were otherwise characterized by an increase of total numbers of empty tests compared to adjacent samples. Two of these stations are located off the Cunene River, and we interpret these differences as the result of enhanced dissolution at the surface sediment.

Overall we conclude that quantitative calculation of standing stocks and foraminiferal numbers based on the topmost centimeter of sediment, for example as used for the calibration of the Benthic Foraminiferal Accumulation Rate (Herguera and Berger, 1991; Herguera, 1992), may be occasionally biased.

2.7. Conclusions

Between 1°N and 32°S on the upper slope off West Africa, variations in live foraminiferal faunas and standing stocks can be plausibly attributed to trophic conditions. Five assemblages of living foraminifera are distinguished, coinciding with distinct primary productivity provinces. *Uvigerina peregrina* and *Robertinoides chapmani* are characteristic for the seasonal coastal upwelling area in the Gulf of Guinea and the northern Angola Basin, but *Bulimina mexicana* dominates the fauna in the area of seasonal oceanic upwelling in the southern Angola Basin. *Uvigerina auberiana*, *Cibicidoides pachyderma*, and endobenthic species such as *Globobulimina affinis* and *Fursenkoina mexicana* characterize the northern region of the Benguela upwelling system and its mixing area, where upwelling is rather perennial. Towards the southern Benguela subsystem, where seasonality is high and export production lower, the fauna is dominated by *Sphaeroidina bulloides* and *Chilostomella oolina*.

This live distribution pattern generally resembles the distribution and composition of the dead assemblages, which indicates that the ecological information obtained from this study can be faithfully used to reconstruct past variability of upwelling, and by extension past primary productivity changes in the eastern South Atlantic. Discrepancies between live and dead faunas occur off the Congo River, where calcite dissolution strongly biases the dead foraminiferal record.

High abundances of *Epistominella smithi* and *Epistominella exigua* in the dead assemblages from the southern Angola Basin and the southern Benguela area, respectively, indicate that important faunal changes possibly triggered by seasonality may occur there. Further investigations on samples taken at different seasons are thus necessary.

Finally, we document that there are no significant discrepancies in the distribution and species composition of total (i.e., including deeper sediment layers) and surface (i.e., in the top 1 cm of sediment) live and dead assemblages. To the authors' knowledge, this is the first study, which validates that foraminiferal assemblages from the uppermost centimeter of sediment record most of the qualitative ecological information as recorded by the complete faunas. However, this might not be the case in other oceanic regions, e.g., with different primary productivity patterns, and at different seasons.

In contrast, subsurface abundance maxima of live foraminifera and dissolution of empty tests might strongly bias quantitative approaches based on the calculation of standing stocks and foraminiferal numbers from the top 1 cm of sediment. Furthermore, the results obtained from the analysis of the total assemblages corroborate that some intermediate and deep species, such as *Bulimina exilis* and *Melonis barleeanum*, which are often absent from the surface sediment or present at low abundances, may be useful indicators of the quality of the organic matter, and are therefore important for a better understanding of the processes locally influencing trophic conditions.

2.8. Acknowledgements

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Appendix A. Taxonomic appendix.

All dominant and associated species from the assemblages described in this study are listed. Scanning Electron Microscope (SEM) pictures of selected dominant species and associated species are represented in Plates I and II. We followed taxonomical concepts of Loeblich and Tappan (1988), Mackensen et al. (1990, 1993), Jones (1996), and Schmiedl et al. (1997).

Order FORAMINIFERIDA Eichwald 1830

Suborder TEXTULARIINA Delage & Hérouard 1896

Ammobaculites agglutinans (d'Orbigny) = *Spirolina agglutinans* d'Orbigny 1846
Ammolagena clavata (Jones & Parker) = *Trochammina irregularis* var. *clavata* Jones & Parker 1860
Ammomarginulina foliacea (Brady) = *Haplophragmium foliaceum* Brady 1881
Ammoscalaria pseudospiralis (Williamson) = *Proteonina pseudospiralis* Williamson 1858
Cribrostomoides subglobosum (M. Sars) = *Lituola subglobosa* M. Sars 1868
Deuterammina montagui Brönimann & Whittaker 1988
Eggerella bradyi (Cushman) = *Verneuilina bradyi* Cushman 1911
Haplophragmoides bradyi (Robertson) = *Trochammina bradyi* Robertson 1891
Hormosina globulifera Brady 1879
Karrerulina conversa (Grzybowski) = *Gaudryina conversa* Grzybowski 1901
Lagenammina difflugiformis (Brady) = *Reophax difflugiformis* Brady 1879
Lagenammina tubulata (Rhumbler) = *Saccammina tubulata* Rhumbler 1931
Recurvoides contortus Earland 1934
Reophax bilocularis Flint 1899
Reophax dentaliniformis Brady 1881
Reophax micaceus Earland 1934
Reophax pilulifer Brady 1884
Reophax scorpiurus de Montfort 1808
Valvulina conica (Parker & Jones) = *Valvulina triangularis* var. *conica* Parker & Jones 1865
Verneuilinulla propinqua (Brady) = *Verneuilina propinqua* Brady 1884

Suborder MILIOLINA Delage & Hérouard 1896

Pyrgo murrhina (Schwager) = *Biloculina murrhina* Schwager 1866

Suborder LAGENINA Delage & Hérouard 1896

Fissurina Reuss 1850

Suborder ROBERTININA Loeblich & Tappan 1984

Hoeglundina elegans (d'Orbigny) = *Rotalia elegans* d'Orbigny 1826
Robertinoides chapmani (Heron-Allen & Earland) = *Robertina chapmani* Heron-Allen & Earland 1922

Suborder ROTALIINA Delage & Hérouard 1896

Brizalina subspinescens (Cushman) = *Bolivina subspinescens* Cushman 1922
Bulimina aculeata d'Orbigny 1826
Bulimina exilis (Brady) = *Bulimina elegans* var. *exilis* Brady 1884
Bulimina mexicana (Cushman) = *Bulimina inflata* var. *mexicana* Cushman 1922
Cassidulina laevigata d'Orbigny 1826
Chilostomella oolina Schwager 1878
Cibicidoides globulosus (Chapman & Parr) = *Anomalina globulosa* Chapman & Parr 1937
Cibicidoides pachyderma (Rzehak) = *Truncatulina pachyderma* Rzehak 1886
Epistominella exigua (Brady) = *Pulvinulina exigua* Brady 1884
Epistominella smithi (Stewart & Stewart) = *Pulvinulinella smithi* Stewart & Stewart 1930
Fursenkoina mexicana (Cushman) = *Virgulina mexicana* Cushman 1922
Gavelinopsis translucens (Phleger & Parker) = *Rotalia translucens* Phleger & Parker 1951
Globobulimina affinis (d'Orbigny) = *Bulimina affinis* d'Orbigny 1839
Globocassidulina subglobosa (Brady) = *Cassidulina subglobosa* Brady 1881

Gyroidinoides polius (Phleger & Parker) = *Eponides polius* Phleger & Parker 1951
Melonis barleeanum (Williamson) = *Nonionina barleeana* Williamson 1858
Oridorsalis umbonatus (Reuss) = *Rotalina umbonata* Reuss 1851
Sphaeroidinoides bulloides Deshayes 1832
Uvigerina auberiana d'Orbigny 1839
Uvigerina peregrina Cushman 1923
Valvulineria laevigata Phleger & Parker 1951

Plate I. Scale bar = 100 μm (see page 58)

1, 2. *Uvigerina peregrina* Cushman, samples GeoB4909 (0-1 cm), GeoB4912 (0-1 cm)
3. *Robertinoides chapmani* (Heron-Allen & Earland), sample GeoB4912 (0-1 cm)
4. *Lagenammina difflugiformis* (Brady), sample GeoB4912 (0-1 cm)
5-7. *Gavelinopsis translucens* (Phleger & Parker) - spiral (5), umbilical (6), and apertural (7) view, samples GeoB3703 (1-2 cm), GeoB3712 (2-3 cm)
8. *Reophax scorpiurus* de Montfort, sample GeoB4912 (0-1 cm)
9. *Karrerulina conversa* (Grzybowski), sample GeoB4913 (0-1 cm)
10, 11. *Melonis barleeanum* (Williamson) - side (10) and apertural (11) view, sample GeoB3725 (2-3 cm)
12, 13. *Bulimina mexicana* (Cushman), samples GeoB3713 (1-2 cm), GeoB3706 (0-1 cm)
14-16. *Epistominella smithi* (Stewart & Stewart) - spiral (14), umbilical (15), and apertural (16) view, samples GeoB4918 (1-2 cm), GeoB3713 (0-1 cm)
17, 18. *Bulimina exilis* (Brady) - side views, sample GeoB3713 (2-3 cm)

Plate II. Scale bar = 100 μm (see page 59)

1-3. *Cibicidoides pachyderma* (Rzehak) - spiral (1), umbilical (2), and apertural (3) view, sample GeoB3706 (1-2 cm)
4, 5. *Uvigerina auberiana* d'Orbigny, sample GeoB3703 (1-2 cm)
6. *Globobulimina affinis* (d'Orbigny), sample GeoB3703 (1-2 cm)
7, 8. *Fursenkoina mexicana* (Cushman), sample GeoB3708 (2-3 cm)
9. *Sphaeroidina bulloides* Deshayes, sample GeoB3701 (0-1 cm)
10. Encysted *Sphaeroidina bulloides* (the last chamber was broken while opening the cyst), sample GeoB3701 (0-1 cm)
11, 12. *Chilostomella oolina* Schwager - samples GeoB4904 (4-5 cm) and GeoB3725 (4-5 cm)
13-15. *Epistominella exigua* (Brady) - spiral (13), umbilical (14), and apertural (15) view, samples GeoB3604 (0-1 cm), GeoB3701 (1-2 cm)

Plate I

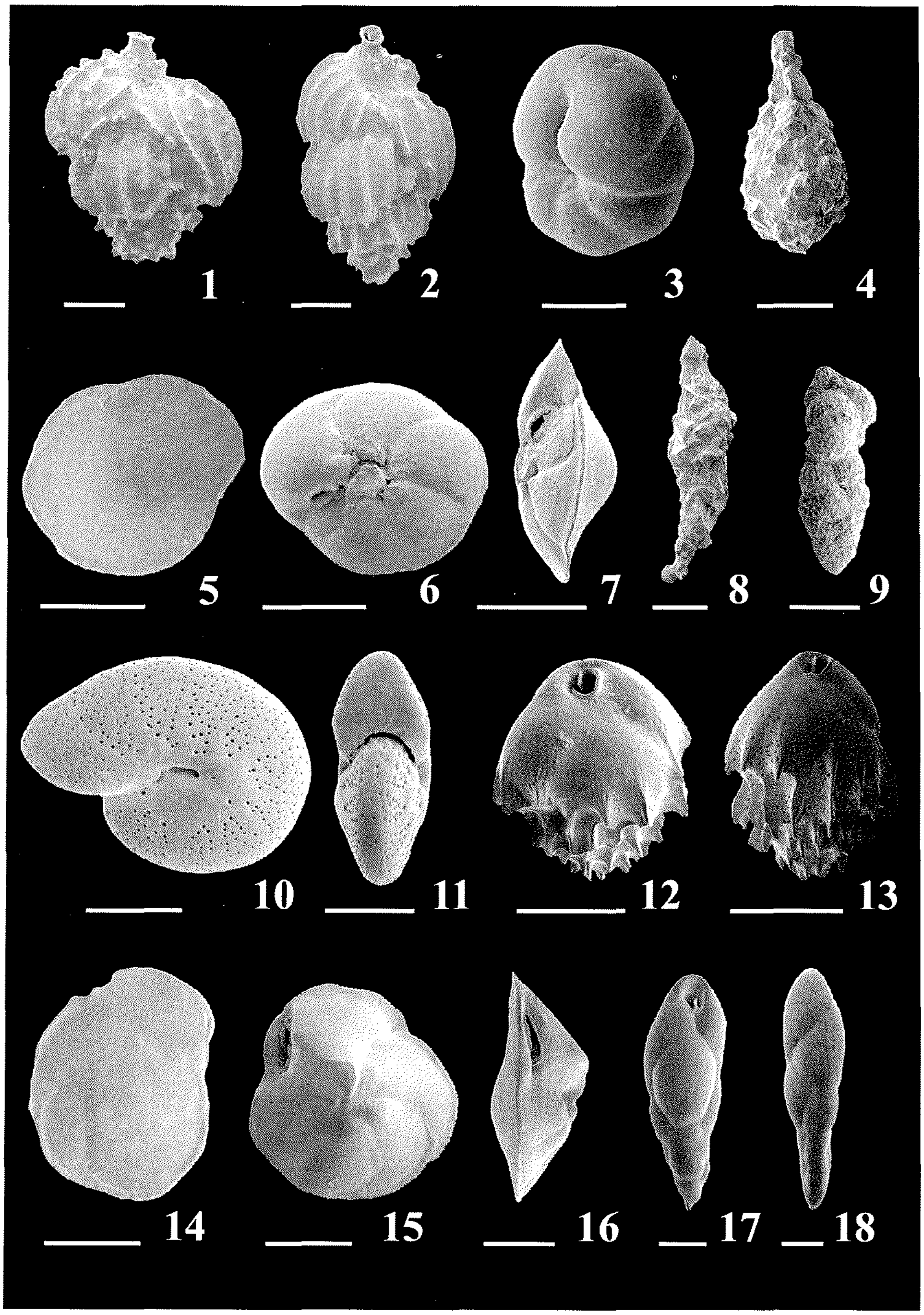
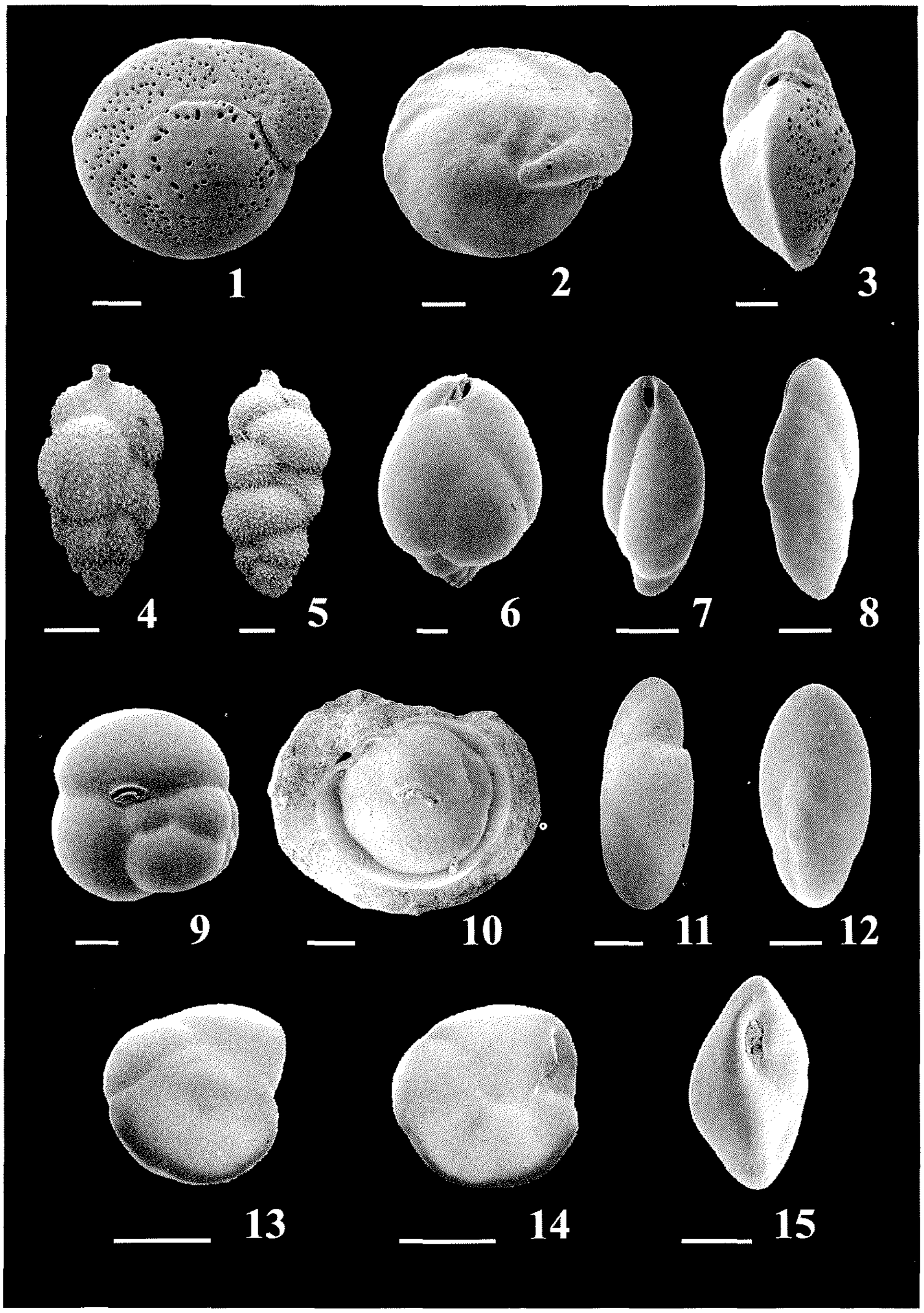


Plate II



Appendix B.

Table B1.1.

Varimax PC-loadings of total live foraminiferal assemblages

GeoB Station	PC1	PC2	PC3	PC4	PC5	Communality
4904-7	0.07	0.77	-0.06	0.11	0.10	0.62
4906-5	0.13	0.87	0.00	0.01	-0.03	0.78
4909-4	0.07	0.84	0.06	0.04	-0.01	0.71
4912-4	-0.03	0.77	-0.01	0.01	0.01	0.60
4913-4	0.09	0.50	0.19	-0.43	-0.17	0.51
4915-3	0.16	0.61	0.02	0.41	0.02	0.56
4916-4	0.80	0.02	0.00	0.15	0.05	0.67
4917-5	0.87	0.16	0.09	0.05	0.16	0.82
4918-4	0.89	0.01	0.09	-0.03	0.04	0.80
3713-1	0.87	0.07	0.10	0.19	0.11	0.82
3712-1	0.67	0.14	0.12	0.07	0.22	0.53
3715-1	0.24	-0.02	0.13	-0.05	0.85	0.80
3711-1	0.14	0.22	0.58	-0.33	0.10	0.53
3708-1	0.07	-0.09	0.66	0.11	0.59	0.81
3706-3	0.00	-0.06	0.88	0.22	-0.02	0.83
3705-2	0.21	0.00	0.79	0.29	0.00	0.75
3703-4	0.18	0.05	-0.04	-0.01	0.80	0.68
3702-2	0.39	0.25	0.13	0.54	0.21	0.57
3701-1	0.15	0.05	0.22	0.67	-0.09	0.52
3604-1	0.07	0.10	0.08	0.75	-0.04	0.58

Table B1.2.

Varimax PC-loadings of total dead foraminiferal assemblages

GeoB Station	PC1	PC2	PC3	PC4	PC5	Communality
4904-7	0.38	0.52	0.19	0.14	0.52	0.74
4906-5	0.05	0.85	0.06	0.04	0.37	0.86
4909-4	0.00	0.92	-0.02	0.05	0.10	0.86
4912-4	0.13	0.90	0.06	0.18	0.07	0.87
4913-4	-0.06	0.05	-0.10	-0.08	0.82	0.69
4915-3	-0.06	0.30	0.00	0.12	0.68	0.57
4916-4	0.29	0.30	0.12	0.70	-0.01	0.67
4917-5	0.05	0.01	-0.06	0.86	0.07	0.75
4918-4	0.43	0.02	0.09	0.83	0.07	0.89
3713-1	0.23	0.48	0.14	0.56	-0.12	0.63
3712-1	0.83	0.18	0.05	0.28	-0.01	0.80
3715-1	0.92	0.01	-0.07	0.06	0.00	0.85
3711-1	0.77	0.06	0.38	0.25	0.01	0.80
3708-1	0.77	0.07	0.46	0.27	0.03	0.87
3706-3	0.60	0.07	0.67	0.25	0.03	0.89
3705-2	0.73	0.09	0.53	0.25	0.02	0.89
3703-4	0.94	0.05	-0.02	0.08	0.03	0.89
3702-2	0.67	0.08	0.15	0.10	-0.09	0.49
3701-1	-0.01	-0.02	0.82	-0.08	-0.05	0.68
3604-1	0.24	0.12	0.87	0.09	-0.01	0.83

Table B2.1.

Varimax PC-loadings of surface live foraminiferal assemblages

GeoB Station	PC1	PC2	PC3	PC4	PC5	Communality
4904-7	0.05	0.73	0.01	0.29	0.35	0.74
4906-5	0.18	0.88	-0.03	0.12	-0.06	0.83
4909-4	0.12	0.86	-0.01	0.07	0.02	0.76
4912-4	0.02	0.81	0.01	0.09	-0.06	0.66
4913-4	0.01	0.60	0.09	-0.25	-0.04	0.44
4915-3	-0.04	0.50	-0.01	0.60	0.17	0.64
4916-4	0.73	0.09	0.06	0.31	0.22	0.69
4917-5	0.85	0.18	0.06	0.19	0.11	0.81
4918-4	0.89	-0.05	0.08	0.15	0.12	0.84
3713-1	0.89	0.10	0.05	0.12	0.05	0.82
3712-1	0.81	0.07	0.10	-0.10	0.22	0.72
3715-1	0.37	0.01	0.13	-0.02	0.72	0.67
3711-1	0.18	0.21	0.50	-0.33	0.12	0.45
3708-1	0.03	-0.01	0.71	0.31	0.41	0.77
3706-3	-0.06	-0.02	0.90	0.21	-0.02	0.86
3705-2	0.25	-0.03	0.82	0.22	-0.06	0.79
3703-4	0.18	0.00	0.02	0.02	0.79	0.66
3702-2	0.26	0.21	0.10	0.63	0.30	0.61
3701-1	0.30	-0.05	0.21	0.66	-0.12	0.59
3604-1	0.16	0.03	0.26	0.77	-0.08	0.69

Table B2.2.

Varimax PC-loadings of surface dead foraminiferal assemblages

GeoB Station	PC1	PC2	PC3	PC4	PC5	Communality
4904-7	0.22	0.06	0.29	0.05	0.65	0.56
4906-5	0.07	0.74	0.09	0.08	0.36	0.69
4909-4	0.01	0.87	0.04	0.12	-0.03	0.77
4912-4	0.13	0.83	0.05	0.19	0.06	0.75
4913-4	-0.08	0.28	-0.13	-0.09	0.58	0.45
4915-3	-0.09	-0.02	-0.11	0.10	0.76	0.60
4916-4	0.27	0.29	0.22	0.76	0.09	0.80
4917-5	0.02	0.07	-0.10	0.86	-0.03	0.75
4918-4	0.33	0.00	0.14	0.88	0.04	0.91
3713-1	0.28	0.28	0.24	0.63	0.03	0.61
3712-1	0.80	0.17	0.22	0.40	0.04	0.87
3715-1	0.92	0.02	-0.04	0.06	-0.02	0.85
3711-1	0.69	0.03	0.43	0.32	0.07	0.77
3708-1	0.67	0.05	0.54	0.36	0.12	0.88
3706-3	0.50	0.06	0.72	0.35	0.12	0.91
3705-2	0.68	0.07	0.59	0.34	0.10	0.93
3703-4	0.92	0.05	0.14	0.19	0.07	0.90
3702-2	0.67	0.06	0.09	0.02	-0.12	0.48
3701-1	0.07	0.02	0.83	-0.03	-0.10	0.71
3604-1	0.14	0.12	0.89	0.08	-0.03	0.84

Table B3.1. Varimax PC-scores of total live assemblages

Species	PC1	PC2	PC3	PC4	PC5
Ammobaculites filiformis	-0.28	0.26	-0.43	-0.07	-0.15
Ammodiscus incertus	0.51	-0.10	-0.33	-0.51	-0.12
Ammolagena clavata	-0.17	-0.33	0.38	-0.75	-0.55
Ammomarginulina foliacea	-0.15	2.01	0.14	-1.81	-0.62
Ammoscalaria sp	0.60	2.46	3.11	-4.59	-0.80
Astrorhiza sp	-0.32	-0.32	-0.26	0.17	-0.30
Biloculinella spp.	-0.30	-0.57	-0.09	-0.36	-0.13
Bolivina albatrossi	-0.08	-0.19	-0.38	-0.24	-0.26
Bolivina pacifica pseudopunctata	0.05	-0.59	-0.36	-0.43	-0.29
Bolivina pseudothalmanni	-0.16	-0.53	-0.32	-0.42	-0.22
Brizalina subspinescens	-0.34	-0.54	-0.09	-0.27	0.04
Bulimina aculeata	-0.20	-0.25	-0.39	-0.34	-0.13
Bulimina alazanensis	-0.24	0.44	-0.17	-0.50	-0.43
Bulimina exilis	0.16	-0.64	-0.09	-0.37	0.30
Bulimina mexicana	8.49	-0.68	1.12	0.27	0.91
Cassidulina laevigata	-0.21	0.54	-0.39	-0.25	1.16
Cassidulinoides tenuis	0.63	-0.71	-0.49	-0.41	-0.44
Chilostomella oolina	-0.41	0.27	-0.76	3.39	0.20
Cibicides lobatulus	-0.46	-0.55	0.80	0.41	-0.12
Cibicidoides bradyi	-0.36	-0.44	-0.34	0.45	-0.29
Cibicidoides globulosus	-0.32	-0.57	-0.30	0.79	-0.37
Cibicidoides pachyderma	-1.36	-0.96	8.52	1.01	-0.40
Cribostomoides jeffreysi	1.28	0.72	0.48	-0.95	-0.92
Cribrostomoides subglobosum	-0.45	0.15	-0.14	1.32	-0.42
Cribrostomoides wiesneri	-0.33	0.10	-0.16	-0.32	-0.37
Crithionina spp.	-0.19	-0.30	-0.12	0.55	0.56
Cyclammina cancellata	-0.23	-0.48	0.15	0.07	-0.15
Cystammina pauciloculata	-0.41	0.10	-0.32	-0.44	-0.15
Deuterammina montagui	-0.37	-0.43	-0.46	1.27	-0.23
Discammina spp	-0.22	-0.02	-0.33	-0.41	-0.17
Eggerella bradyi	-0.38	-0.42	0.89	0.52	-0.51
Epistominella exigua	-0.38	0.06	-0.43	0.48	-0.22
Epistominella rugosa	-0.29	-0.31	-0.29	-0.42	-0.23
Epistominella smithi	0.90	-0.67	-0.37	-0.73	-0.49
Eponides pusillus	-0.31	-0.29	-0.34	-0.37	-0.16
Fissurina spp.	-0.16	-0.55	-0.16	-0.35	0.20
Fontbotia wuellerstorfi	-0.19	-0.30	0.24	-0.07	-0.24
Fursenkoina earlandi	-0.32	0.35	-0.22	-0.51	-0.33
Fursenkoina mexicana	-0.25	-0.54	2.17	-0.21	4.66
Gavelinopsis translucens	-0.55	3.51	0.76	2.62	0.28
Glandulina ovula	-0.03	-0.56	-0.30	-0.44	-0.22
Globobulimina affinis	-0.62	0.13	-0.56	-0.02	5.52
Globocassidulina subglobosa	-0.40	-0.52	0.08	1.06	-0.19
Gyroidinoides polius	-0.06	0.04	-0.06	0.96	-0.13
Gyroidinoides soldanii	-0.23	-0.43	-0.22	0.27	0.08
Gyroidinoides umbonatus	-0.15	-0.48	-0.31	-0.06	-0.13
Haplophragmoides bradyi	2.29	-0.97	-0.67	-0.47	-0.89
Haplophragmoides coronatum	-0.27	-0.54	-0.27	-0.08	-0.29
Haplophragmoides sphaeriloculus	-0.30	-0.24	-0.35	-0.18	-0.19
Hoeglundina elegans	-0.58	1.32	-0.35	-0.26	-0.13
Hormosina globulifera	-0.08	0.19	1.14	-0.98	0.68
Hyperammina elongata	-0.11	-0.05	0.05	-0.95	-0.53
Karreriella bradyi	-0.27	-0.55	-0.32	-0.19	-0.23
Karrerulina conversa	-0.31	0.31	-0.33	-0.06	-0.26
Lagenammina difflugiformis	0.91	3.48	-0.62	0.45	0.29
Lagenammina tubulata	-0.31	0.81	-0.27	-0.53	-0.28
Melonis barleeanum	0.38	1.76	-0.77	0.21	-0.17
Miliolidae spp	-0.31	-0.54	0.01	-0.23	-0.12
Nonion spp.	-0.18	-0.33	-0.25	-0.44	-0.24
Nouria harrisii	-0.04	-0.11	1.47	-0.09	-0.59
Oolina spp.	-0.26	-0.52	-0.33	-0.33	0.02
Oridorsalis umbonatus	-0.16	-0.27	0.95	1.32	0.68
Osangularia culter	-0.28	-0.13	-0.28	-0.40	-0.27
Paratrochammina challengeri	-0.19	-0.48	-0.33	-0.20	-0.21
Placopsilinella aurantiaca	-0.26	-0.48	-0.32	-0.44	0.16
Portatrochammina spp	-0.03	-0.55	-0.29	-0.34	-0.13
Praecystammina globigeriniformis	-0.21	-0.54	-0.30	-0.26	-0.26
Psammosphaera fusca	0.18	-0.56	-0.34	-0.28	-0.22
Psammosphaera sp	0.26	-0.56	-0.33	-0.44	-0.20
Pseudogaudryina sp.	-0.36	-0.56	-0.34	0.58	-0.31
Pullenia bulloides	-0.40	-0.06	-0.03	0.29	0.23
Pullenia subcarinata	-0.37	-0.51	-0.37	0.79	-0.27
Pyrgo depressa	-0.40	-0.57	0.35	-0.28	0.15
Pyrgo elongata	-0.24	-0.50	-0.20	-0.40	-0.20
Pyrgo murrhina	-0.28	-0.47	0.94	-0.25	-0.50
Pyrgo serrata	-0.25	-0.50	0.02	-0.56	-0.23
Pyrgoella sphaera	-0.49	-0.66	0.97	-0.32	0.42
Quinqueloculina spp.	-0.15	-0.35	-0.03	-0.23	-0.19
Recurvoides contortus	0.53	0.24	0.11	2.34	-0.01
Recurvoides scitulum	0.28	-0.50	-0.25	-0.20	-0.23
Reophax agglutinatus	-0.23	-0.56	-0.28	-0.21	-0.26
Reophax bilocularis	1.94	2.68	1.17	2.90	-0.30
Reophax dentaliniformis	-0.28	0.60	-0.49	1.31	-0.10
Reophax distans	-0.24	-0.55	-0.31	-0.33	-0.22
Reophax guttifera	-0.06	-0.15	-0.25	-0.30	-0.01
Reophax micaceus	-0.25	0.08	-0.16	1.02	-0.36
Reophax pilulifer	0.72	-0.22	-0.28	-0.41	-0.42
Reophax scorpiurus	-0.40	3.45	-0.48	-0.61	-0.10
Reophax spp.	0.03	-0.12	-0.30	-0.24	-0.14
Rhabdammina spp.	-0.23	-0.34	-0.31	-0.17	-0.18
Robertinoides chapmani	-1.02	3.85	-0.63	0.19	0.16
Saccammina sphaerica	0.09	-0.31	-0.16	0.02	-0.28
Saccorhiza ramosa	-0.32	-0.30	-0.36	-0.29	-0.15
Sigmoilopsis schlumbergeri	-0.35	-0.57	-0.26	0.58	-0.32
Siphotextularia spp.	-0.30	-0.54	-0.25	-0.03	-0.24
Sphaeroidina bulloides	-0.24	0.27	0.43	4.57	-0.85
Spirosigmoilina spp.	-0.31	-0.56	-0.28	-0.42	0.45
Subreophax aduncus	-0.07	-0.51	-0.31	-0.36	-0.23
Textularia conica	-0.28	-0.53	-0.12	0.03	-0.21
Triloculina sp.	-0.24	-0.51	-0.22	-0.12	0.04
Trochammina spp.	0.20	-0.06	0.03	0.16	-0.05
Trochamminopsis pusillus	-0.05	-0.56	-0.32	-0.45	-0.24
Uvigerina auberiana	-0.25	0.43	-0.66	-0.62	6.52
Uvigerina peregrina	0.45	3.87	0.12	-1.75	-0.76
Uvigerina proboscidea	-0.30	-0.32	-0.31	-0.38	-0.20
Uzbekistania charoides	-0.31	-0.49	-0.31	0.08	-0.27
Valvulina conica	1.32	-0.57	-0.29	-0.81	0.52
Valvulineria laevigata	3.19	-0.30	-0.58	1.30	0.02
Verneuilinulla propinqua	-0.38	0.18	-0.47	0.04	-0.07

Table B3.2. Varimax PC-scores of the total dead assemblages

Species	PC1	PC2	PC3	PC4	PC5
Adercotryma glomerata	-0.24	-0.35	-0.40	-0.01	-0.57
Ammobaculites agglutinans	-0.17	-0.26	-0.39	-0.32	-0.47
Ammobaculites filiformis	-0.10	-0.12	-0.33	-0.36	0.39
Ammodiscus incertus	-0.11	-0.42	-0.39	-0.20	0.50
Ammolagena clavata	-0.07	-1.10	-0.40	-0.35	2.44
Ammomarginulina ensis	-0.17	-0.24	-0.36	-0.08	0.09
Ammomarginulina foliacea	-0.08	-0.50	-0.37	-0.43	2.61
Ammoscalaria sp.	-0.15	0.19	-0.47	-0.32	0.18
Angulogerina angulosa	-0.24	-0.27	0.04	-0.32	-0.33
Atlantica atlantiella	-0.09	-0.43	-0.45	-0.16	-0.46
Bolivina albatrossi	-0.21	0.15	-0.40	-0.06	-0.35
Bolivina dilatata	-0.23	-0.09	-0.26	0.49	-0.94
Bolivina pacifica pseudopunctata	-0.23	-0.39	-0.37	0.00	-0.44
Bolivina pseudothalmanni	-0.26	-0.52	-0.38	0.06	-0.38
Bolivina spp.	-0.21	-0.32	-0.38	-0.13	-0.55
Brizalina subspinescens	0.14	-0.50	1.05	-0.42	-0.43
Bulimina aculeata	1.80	0.28	0.34	-1.08	-1.31
Bulimina alazanensis	-0.09	0.07	-0.19	-0.14	-0.02
Bulimina exilis	-0.42	0.21	-0.54	2.98	-1.32
Bulimina marginata	0.69	-0.60	-0.12	-0.40	-0.33
Bulimina mexicana	6.30	1.09	2.52	3.74	0.86
Cassidulina laevigata	1.29	0.26	2.75	-0.81	0.62
Cassidulinoides tenuis	-0.21	-0.40	-0.42	0.32	-0.58
Chilostomella oolina	-0.14	0.89	-0.06	-0.33	0.09
Cibicides lobatulus	-0.12	-0.47	0.18	-0.33	-0.49
Cibicides refulgens	-0.21	0.62	-0.44	-0.56	-0.31
Cibicidoides bradyi	-0.39	-0.28	0.34	-0.17	-0.38
Cibicidoides globulosus	-0.45	-0.45	0.73	-0.32	-0.51
Cibicidoides kullenbergi	-0.21	-0.18	-0.30	-0.36	-0.44
Cibicidoides pachyderma	-0.02	-0.52	2.48	-0.27	-0.44
Cibicidoides robertsonianus	-0.22	-0.14	-0.25	-0.36	-0.50
Cribostomoides jeffreysi	-0.16	-0.37	-0.44	0.17	0.17
Cribrostomoides subglobosum	-0.31	1.10	-0.40	-0.66	1.42
Cribrostomoides wiesneri	-0.22	-0.10	-0.37	-0.32	-0.04
Cyclammina cancellata	-0.19	-0.39	-0.35	-0.24	-0.14
Cystammina galeata	-0.16	-0.54	-0.38	-0.29	-0.10
Deuterammina grahami	-0.17	-0.40	-0.39	-0.31	-0.13
Deuterammina montagui	-0.28	-0.40	-0.33	0.09	0.42
Discammina spp.	-0.18	-0.08	-0.42	-0.23	-0.49
Discorbina sp.	-0.21	-0.44	-0.22	-0.29	-0.49
Earlandammina inconspicua	-0.24	-0.45	-0.36	-0.10	0.02
Eggerella bradyi	-0.29	0.90	1.59	-0.03	-0.47
Epistominella exigua	-1.37	-0.43	3.97	-0.50	-0.43
Epistominella rugosa	-0.19	0.00	-0.43	-0.37	-0.64
Epistominella smithi	-1.04	-2.10	-1.26	7.02	0.36
Fissurina spp.	-0.08	0.80	-0.09	-0.56	-0.30
Fontbotia wuellerstorfi	-0.10	0.26	-0.15	-0.36	-0.10
Fursenkoina earlandi	-0.21	0.12	-0.38	-0.41	-0.43
Fursenkoina mexicana	1.04	-0.46	0.80	0.91	-0.75
Gavelinopsis translucens	0.05	0.24	4.23	-0.40	0.94
Globobulimina affinis	0.28	-0.37	-0.56	0.88	-0.05
Globocassidulina subglobosa	-0.62	-0.54	3.06	-0.49	-0.41
Glomospira gordialis	-0.17	-0.42	-0.38	-0.26	-0.50
Gyroidinoides polius	-0.19	-0.06	1.80	-0.34	-0.34
Gyroidinoides soldanii	0.07	-0.13	-0.19	-0.37	-0.23
Gyroidinoides umbonatus	-0.21	-0.37	-0.01	-0.22	-0.47
Haplophragmoides bradyi	-0.25	-0.33	-0.39	0.14	-0.55
Haplophragmoides sphaeriloculus	-0.17	-0.39	-0.34	-0.27	-0.32
Hoeglundina elegans	-0.22	0.51	-0.47	-0.46	-0.73
Hormosina globulifera	-0.11	-0.92	-0.36	-0.31	3.07
Hyperammina elongata	-0.15	-0.47	-0.38	-0.30	-0.01
Karrerulina conversa	-0.30	0.06	-0.24	-0.34	6.00
Labrospira ringens	-0.21	-0.46	-0.39	-0.18	-0.06
Lagena spp.	-0.04	0.36	-0.27	-0.11	-0.06
Lagenammina difflugiformis	-0.14	1.10	-0.62	0.57	1.82
Lagenammina tubulata	-0.25	0.19	-0.37	-0.32	0.49
Martinotiella communis	-0.03	-0.26	-0.48	-0.11	-0.70
Melonis barleeanum	-0.37	1.32	-0.50	0.63	-0.96
Nonion spp	-0.20	-0.29	0.01	-0.10	-0.54
Nonionella spp.	-0.27	-0.05	-0.26	-0.21	-0.39
Oridorsalis umbonatus	0.75	0.34	0.78	0.34	-0.22
Osangularia culter	-0.13	0.14	-0.30	-0.38	0.32
Paratrochammina challengeri	-0.23	-0.38	-0.33	-0.11	-0.34
Paratrochammina spp.	-0.09	-0.19	-0.43	0.05	-0.55
Praecystammina globigeriniformis	-0.18	-0.42	-0.36	-0.20	-0.21
Psammosphaera fusca	-0.18	-0.21	-0.44	0.08	-0.54
Pullenia bulloides	0.06	0.23	0.09	-0.12	-0.29
Pullenia salisburyi	-0.18	-0.41	-0.33	-0.29	-0.49
Pullenia subcarinata	-0.33	-0.21	0.71	-0.38	-0.34
Pyrgo spp.	-0.14	-0.36	-0.11	-0.12	-0.36
Recurvoides contortus	-0.21	-0.21	-0.29	0.03	0.64
Reophax bilocularis	-0.04	1.33	-0.67	0.58	-0.14
Reophax pilulifer	-0.16	-0.30	-0.45	0.04	-0.16
Reophax scorpiurus	-0.19	0.24	-0.44	-0.28	-0.44
Reophax spp.	-0.11	0.38	-0.35	0.02	0.09
Robertinoides chapmani	-0.12	1.01	-0.26	-0.49	0.42
Saccammina sphaerica	-0.17	-0.07	-0.40	-0.04	0.14
Sigmoilopsis schlumbergeri	-0.16	-0.20	0.35	-0.39	-0.38
Sphaeroidina bulloides	-0.55	2.09	1.30	0.81	0.35
Textularia spp	-0.06	-0.59	0.98	-0.03	0.35
Trochammina spp.	-0.20	0.13	-0.44	-0.01	0.97
Uvigerina auberiana	6.41	-0.33	-2.83	-2.41	-0.30
Uvigerina peregrina	-0.97	8.06	-0.90	0.64	0.07
Valvulina conica	0.32	-0.27	-0.73	-0.03	-0.68
Valvulineria laevigata	0.15	0.17	0.27	2.29	-0.79
Verneuilinulla propinqua	-0.43	-0.49	-0.12	0.40	3.28

Table B4.1. Varimax PC-scores of surface live assemblages

Species	PC1	PC2	PC3	PC4	PC5
Ammobaculites agglutinans	-0.08	-0.43	-0.32	-0.38	-0.28
Ammobaculites filiformis	-0.38	0.30	-0.54	0.30	-0.07
Ammodiscus incertus	0.29	-0.34	-0.39	-0.23	0.32
Ammolagena clavata	-0.29	0.07	0.45	-0.78	-0.47
Ammomarginulina foliacea	-0.33	2.60	0.20	-1.49	-0.24
Ammoscalaria sp.	0.94	2.35	2.76	-4.23	0.04
Angulogerina angulosa	-0.28	-0.22	-0.37	-0.17	-0.13
Astrorhiza sp.	-0.23	-0.25	-0.30	0.07	-0.44
Bolivina albatrossi	-0.06	-0.16	-0.42	-0.13	-0.29
Bolivina dilatata	-0.05	-0.44	-0.34	-0.34	-0.28
Bolivina pacifica pseudopunctata	-0.11	-0.43	-0.34	-0.33	-0.25
Bolivina spp.	-0.12	-0.43	-0.32	-0.28	-0.28
Brizalina subspinescens	-0.51	-0.46	0.28	0.06	0.35
Bulimina aculeata	-0.27	-0.15	-0.40	-0.19	0.03
Bulimina alazanensis	-0.51	0.73	-0.42	0.11	-0.04
Bulimina exilis	-0.29	-0.46	-0.05	-0.32	0.05
Bulimina mexicana	8.74	-0.72	1.26	1.83	1.39
Cassidulina laevigata	-0.14	0.87	-0.27	-0.16	3.16
Cassidulinoides tenuis	0.00	-0.47	-0.39	-0.25	-0.12
Chilostomella oolina	-0.17	-0.47	-0.34	-0.06	-0.24
Cibicides lobatulus	-0.37	-0.59	1.23	1.03	-0.52
Cibicidoides bradyi	-0.32	-0.43	-0.32	0.57	-0.45
Cibicidoides globulosus	-0.17	-0.69	-0.28	1.33	-0.83
Cibicidoides pachyderma	-1.17	-0.56	8.73	0.22	-0.87
Cribostomoides jeffreysi	0.24	-0.45	-0.41	0.43	0.47
Cribrostomoides subglobosum	-0.34	0.01	-0.01	0.80	-0.47
Cribrostomoides wiesneri	-0.27	0.10	-0.18	-0.53	-0.30
Crithionina sp.	-0.09	-0.53	0.40	0.54	1.28
Cyclammina cancellata	-0.22	-0.41	0.23	-0.09	-0.13
Deuterammina montagui	-0.22	-0.29	-0.37	-0.21	-0.06
Discammina spp	-0.10	0.21	-0.28	-0.45	-0.39
Earlandammina inconspicua	-0.07	-0.42	-0.30	-0.38	-0.21
Eggerella bradyi	-0.24	-0.33	1.60	0.68	-0.98
Epistominella exigua	-0.66	0.11	-0.64	0.86	0.06
Epistominella rugosa	-0.23	-0.10	-0.31	-0.39	-0.30
Epistominella smithi	1.27	-0.52	-0.50	-0.34	-0.62
Eponides pusillus	-0.36	-0.03	-0.37	-0.25	0.03
Fissurina spp.	-0.20	-0.50	0.07	-0.29	0.84
Fontbotia wuellerstorfi	-0.35	-0.17	0.33	0.22	-0.09
Fursenkoina mexicana	-0.54	-0.55	0.63	-0.27	1.31
Gavelinopsis translucens	-1.61	3.28	0.89	5.23	2.66
Glandulina ovula	-0.04	-0.44	-0.33	-0.38	-0.14
Globobulimina affinis	-0.25	-0.48	-0.31	-0.43	0.48
Globocassidulina subglobosa	-0.39	-0.73	0.27	2.16	-0.57
Globulotuba sp.	-0.08	-0.44	-0.32	-0.38	-0.23
Gyroidinoides polius	-0.14	-0.23	-0.16	0.82	-0.25
Gyroidinoides soldanii	-0.29	-0.38	-0.22	-0.11	0.09
Gyroidinoides umbonatus	-0.13	-0.40	-0.42	0.25	-0.14
Haplophragmoides bradyi	0.39	-0.52	-0.45	-0.20	-0.24
Haplophragmoides sphaeriloculus	-0.25	-0.16	-0.34	-0.26	-0.24
Hoeglundina elegans	-0.31	1.86	-0.30	-0.46	-0.76
Hormosina globulifera	-0.09	0.00	1.39	-1.16	2.03
Hyperammina elongata	-0.16	0.31	-0.02	-0.89	-0.38
Karreriulina conversa	-0.46	0.23	-0.48	0.23	-0.12
Lagena spp.	-0.06	-0.45	-0.35	-0.09	0.09
Lagenammina difflugiformis	1.39	2.71	-0.65	0.73	0.30
Lagenammina tubulata	-0.16	0.91	-0.33	-0.44	-0.39
Laticarinina pauperata	-0.30	-0.35	-0.35	-0.21	-0.18
Melonis barleeanum	0.12	-0.32	-0.37	-0.35	-0.33
Miliolidae spp.	-0.23	-0.46	0.30	-0.03	-0.41
Nonion spp	-0.19	-0.31	-0.27	-0.39	-0.28
Nonionella spp	-0.28	-0.26	-0.29	-0.20	-0.21
Oolina spp.	-0.26	-0.44	-0.37	-0.19	0.23
Oridorsalis umbonatus	-0.21	-0.40	0.60	1.23	1.28
Osangularia culter	-0.35	-0.08	-0.34	-0.20	-0.17
Paratrochammina challengeri	-0.01	-0.44	-0.31	-0.17	-0.26
Praecystammina globigeriniformis	-0.15	-0.51	-0.31	0.01	-0.42
Psammosphaera fusca	0.44	-0.40	-0.40	-0.27	-0.40
Psammosphaera sp.	0.50	-0.42	-0.31	-0.62	-0.37
Pseudogaudryina sp	-0.28	-0.59	-0.26	0.84	-0.62
Pullenia bulloides	-0.42	-0.20	-0.10	0.47	0.06
Pullenia subcarinata	-0.28	-0.50	-0.30	0.27	-0.37
Pyrgo depressa	-0.51	-0.49	0.91	-0.17	0.36
Pyrgo lucernula	-0.24	-0.40	-0.10	-0.44	-0.22
Pyrgo murrhina	-0.08	-0.17	1.93	-0.70	-0.71
Pyrgo serrata	-0.24	-0.38	-0.13	-0.48	-0.19
Pyrgoella sphaera	-0.59	-0.53	0.84	-0.22	0.61
Quinqueloculina spp.	-0.12	-0.23	0.28	-0.18	-0.21
Recurvoides contortus	0.15	-0.12	0.03	1.01	-0.09
Recurvoides scitulum	0.51	-0.28	-0.15	-0.70	-0.32
Reophax agglutinatus	-0.17	-0.50	-0.31	-0.03	-0.39
Reophax bilocularis	2.23	2.47	0.30	1.09	-0.90
Reophax dentaliniformis	-0.03	-0.17	-0.21	-0.36	-0.22
Reophax guttifera	-0.11	-0.06	-0.14	-0.19	0.06
Reophax micaceus	-0.15	-0.06	-0.30	0.19	-0.45
Reophax pilulifer	1.52	-0.14	-0.22	-1.13	-0.47
Reophax scorpiurus	0.03	2.91	-0.46	-0.45	-0.56
Reophax spp.	0.07	-0.33	-0.23	-0.28	-0.19
Rhabdammina spp.	-0.28	-0.29	-0.47	0.29	0.09
Robertinoides chapmani	-0.77	4.55	-0.59	0.47	-0.43
Saccammina sphaerica	0.24	-0.31	-0.19	0.41	-0.11
Saccorhiza ramosa	-0.31	-0.26	-0.33	-0.25	-0.12
Sigmoilopsis schlumbergeri	-0.27	-0.47	-0.29	-0.02	-0.26
Siphotextularia spp.	-0.27	-0.44	-0.22	-0.08	-0.30
Sphaeroidina bulloides	0.04	-0.10	0.25	4.99	-2.04
Spirophthalmidum pusillum	-0.23	-0.24	-0.32	-0.36	-0.29
Spirosigmoilina spp.	-0.19	-0.53	-0.22	-0.50	1.00
Subreophax aduncus	0.35	-0.39	-0.34	-0.51	-0.40
Textularia conica	-0.24	-0.47	-0.21	0.21	-0.33
Triloculina sp.	-0.39	-0.47	-0.06	0.26	0.49
Trochammina spp.	0.46	0.13	0.01	0.17	0.37
Trochamminopsis pusillus	0.07	-0.41	-0.31	-0.43	-0.29
Uvigerina auberiana	-0.86	0.10	-0.09	-0.77	7.71
Uvigerina peregrina	0.73	4.86	-0.11	-1.08	-1.34
Uvigerina proboscidea	-0.27	-0.14	-0.31	-0.31	-0.24
Uzbekistania charoides	-0.29	-0.37	-0.32	-0.12	-0.19
Valvulina conica	2.36	-0.46	-0.16	-1.67	0.18
Valvulineria laevigata	1.32	-0.49	-0.72	0.82	0.78
Verneuilinulla propinqua	-0.46	0.17	-0.54	0.41	0.21

Table B4.2. Varimax PC-scores of the surface dead assemblages

Species	PC1	PC2	PC3	PC4	PC5
Adercotryma glomerata	-0.18	-0.44	-0.36	-0.06	-0.51
Ammobaculites filiformis	-0.12	-0.68	0.09	-0.55	2.86
Ammodiscus incertus	-0.13	-0.32	-0.37	-0.17	0.94
Ammolagena clavata	-0.12	-0.26	-0.51	-0.51	1.51
Ammomarginulina ensis	-0.21	-0.55	-0.22	-0.02	0.62
Ammomarginulina foliacea	-0.16	-0.08	-0.31	-0.38	0.95
Ammoscalaria sp.	-0.09	0.16	-0.44	-0.11	-0.44
Angulogerina angulosa	-0.22	-0.50	0.07	-0.35	-0.05
Atlantica atlantiella	-0.15	-0.55	-0.29	-0.18	-0.19
Bolivina alata	-0.09	-0.54	-0.30	-0.09	-0.55
Bolivina dilatata	-0.27	-0.41	-0.30	0.38	-0.64
Bolivina spp.	-0.15	-0.27	-0.36	0.13	-0.51
Brizalina subspinescens	-0.08	-0.38	1.31	-0.48	-0.71
Bulimina aculeata	2.19	0.18	0.21	-1.39	-1.47
Bulimina alazanensis	-0.15	0.05	-0.14	-0.18	0.46
Bulimina exilis	-0.12	-0.34	-0.23	1.06	-0.64
Bulimina marginata	1.30	-0.63	-0.20	-0.48	-0.62
Bulimina mexicana	5.18	0.99	3.74	4.61	1.53
Cassidulina laevigata	0.58	0.05	3.03	-0.46	1.54
Cassidulinoides tenuis	-0.30	-0.45	-0.35	0.51	-0.58
Chilostomella oolina	-0.26	-0.23	-0.09	-0.10	-0.34
Cibicides lobatulus	-0.09	-0.51	0.19	-0.31	-0.60
Cibicides refulgens	-0.15	0.03	-0.30	-0.36	-0.26
Cibicidoides globulosus	-0.41	-0.48	0.49	-0.32	-0.68
Cibicidoides kullenbergi	-0.14	-0.11	-0.34	-0.32	-0.41
Cibicidoides pachyderma	-0.14	-0.37	1.10	-0.04	-0.61
Cibicidoides robertsionanus	-0.21	-0.50	-0.08	-0.26	-0.59
Cribostomoides jeffreysi	-0.02	-0.63	-0.54	0.26	0.46
Cribrostomoides subglobosum	-0.22	1.60	-0.48	-0.69	1.44
Cribrostomoides wiesneri	-0.18	-0.25	-0.37	-0.22	-0.08
Cyclammina cancellata	-0.16	-0.37	-0.37	-0.23	-0.15
Cystammina pauciloculata	-0.15	0.02	-0.34	-0.33	-0.49
Deuterammina grahami	-0.14	-0.23	-0.37	-0.33	-0.19
Deuterammina montagui	-0.31	-0.45	-0.47	0.16	0.71
Discammina spp.	-0.13	-0.45	-0.38	-0.02	-0.59
Earlandammina inconspicua	-0.14	-0.32	-0.44	-0.15	-0.09
Eggerella bradyi	-0.47	0.77	2.20	-0.37	-0.60
Epistominella exigua	-1.27	-0.38	3.37	-0.69	-1.04
Epistominella rugosa	-0.17	0.48	-0.36	-0.36	-0.78
Epistominella smithi	-1.24	-1.63	-1.71	6.45	-1.01
Eponides pusillus	-0.13	-0.37	-0.19	-0.35	0.11
Fissurina spp.	0.09	1.46	-0.06	-0.63	-0.49
Fontbotia wuellerstorfi	-0.06	0.04	-0.21	-0.28	-0.30
Fursenkoina earlandi	-0.17	0.21	-0.36	-0.30	-0.71
Fursenkoina mexicana	0.65	-0.62	0.60	1.00	-0.35
Gavelinopsis translucens	-0.40	0.21	3.83	-0.75	1.10
Globobulimina affinis	0.27	-0.41	-0.48	0.21	-0.47
Globocassidulina subglobosa	-0.90	-0.38	3.49	-0.75	-0.79
Gyroidinoides polius	-0.22	0.29	1.36	-0.34	-0.84
Gyroidinoides soldanii	0.21	-0.45	-0.25	-0.33	-0.11
Gyroidinoides umbonatus	-0.12	-0.02	-0.03	-0.31	-0.47
Haplophragmoides bradyi	-0.20	-0.50	-0.35	0.05	-0.57
Hoeglundina elegans	-0.18	0.84	-0.40	-0.39	-0.63
Hormosina globulifera	-0.24	0.47	-0.66	-0.47	2.77
Karreriella conversa	-0.36	0.82	-0.73	-0.51	3.98
Labrospira ringens	-0.22	-0.51	-0.42	-0.04	0.12
Lagena spp	0.09	0.37	-0.36	-0.32	0.23
Lagenammina difflugiformis	-0.20	2.38	-0.56	0.48	0.18
Lagenammina tubulata	-0.26	0.56	-0.54	-0.23	1.36
Melonis barleeanum	-0.24	0.75	-0.34	0.53	-0.48
Miliolidae spp.	-0.11	-0.59	-0.33	-0.10	-0.25
Nonion spp	-0.16	-0.43	-0.04	-0.10	-0.48
Nonionella spp	-0.21	0.03	-0.28	-0.22	-0.78
Oridorsalis umbonatus	0.82	0.23	0.14	0.31	-0.62
Osangularia culter	-0.16	-0.46	-0.25	-0.19	-0.22
Paratrochammina challengeri	-0.18	-0.57	-0.36	-0.09	-0.21
Psammosphaera fusca	-0.22	-0.30	-0.35	0.42	-0.45
Pullenia bulloides	0.06	0.04	-0.09	0.00	-0.66
Pullenia salisburyi	-0.16	-0.51	-0.24	-0.25	-0.57
Pullenia subcarinata	-0.40	-0.20	0.88	-0.39	-0.62
Pyrgo spp.	0.03	-0.04	-0.08	-0.19	-0.43
Quinqueloculina spp.	-0.12	-0.14	-0.33	-0.24	-0.46
Recurvoides contortus	-0.22	0.15	-0.31	0.04	0.10
Recurvoides scitulum	-0.08	0.68	-0.53	-0.46	0.89
Reophax bilocularis	-0.54	2.43	-0.69	1.75	-0.22
Reophax guttifera	-0.21	-0.23	-0.29	-0.10	0.17
Reophax micaceus	-0.17	0.02	-0.28	-0.33	-0.29
Reophax pilulifer	-0.17	-0.16	-0.40	0.13	-0.59
Reophax scorpiurus	-0.18	0.59	-0.31	-0.09	-0.07
Reophax spp.	-0.09	-0.52	-0.38	-0.11	0.48
Robertinoides chapmani	-0.17	0.09	-0.22	-0.32	-0.03
Saccammina sphaerica	-0.10	-0.24	-0.32	-0.14	0.45
Sigmoilopsis schlumbergeri	-0.13	0.00	0.07	-0.31	-0.70
Siphotextularia spp.	-0.13	-0.56	0.05	-0.25	-0.54
Sphaeroidina bulloides	-0.61	1.98	1.16	0.26	0.03
Subreophax aduncus	-0.16	-0.41	-0.26	-0.24	0.22
Textularia spp.	-0.06	-0.88	0.83	-0.16	0.22
Trochammina spp	-0.44	0.48	-0.55	0.64	0.62
Uvigerina auberiana	7.06	-0.24	-2.33	-2.05	-0.56
Uvigerina peregrina	-0.58	7.10	-0.87	0.53	-0.40
Uzbekistania charoides	-0.13	-0.63	-0.15	-0.32	0.11
Valvulina conica	0.26	-0.46	-0.52	-0.03	-0.62
Valvulineria laevigata	-0.05	-0.72	-0.10	2.97	0.29
Verneuilinulla propinqua	-0.47	-1.70	-0.44	0.25	4.94

Appendix C.

Table C1.1 Relative abundances of benthic foraminifera species of the total live fauna

Species	GeoB4904-7	GeoB4906-5	GeoB4909-4	GeoB4912-4	GeoB4913-4	GeoB4915-3	GeoB4916-4	GeoB4917-5	GeoB4918-4	GeoB3713-1	GeoB3712-1	GeoB3715-1	GeoB3711-1	GeoB3708-1	GeoB3706-3	GeoB3705-2	GeoB3703-4	GeoB3702-2	GeoB3701-1	GeoB3604-1
Ammobaculites filiformis	0.8	0.2	0.4	2.0		2.9	0.1	0.8		0.3	0.2									
Ammodiscus incertus	2.0	0.8	0.1	0.1	1.9	0.6	1.9	1.3	5.8	0.1	1.1	1.1	0.2	0.3	0.2		0.3	1.3		
Ammolagena clavata		0.6			4.4		0.1				0.7				3.7	0.3		0.1	0.1	0.3
Ammomarginulina foliacea	8.3	4.9	0.2	0.7	13.8			0.4	0.3	0.3	0.0									
Ammoscalaria sp.	1.0	1.7	4.8	5.0	14.5		0.8	0.2	2.4	0.8	3.7	2.0	29.1				0.0			
Astrorhiza sp.		0.2	0.4	1.3							0.2								2.7	0.5
Biloculinella spp.														1.0	0.1	0.7			0.1	
Bolivina albatrossi	0.2	0.8	0.5	0.2		1.6	0.4	1.4	0.7	0.6	0.0									
Bolivina pacifica pseudopunctata							1.9	1.4		0.1										
Bolivina pseudothalmanni	0.2							1.1												
Brizalina subspinescens			0.2											2.0	0.1	0.1	0.1	0.5	0.1	0.2
Bulimina aculeata	2.2					0.2	0.2	0.6	0.1	0.1	0.4									
Bulimina alazanensis	1.0	0.9	0.4	0.3	5.0	3.5	0.2			0.1										
Bulimina exilis						0.2	1.0	0.3		3.9	0.1	1.8	0.1	2.9	0.1					
Bulimina mexicana	2.8	2.8	0.5	0.3		1.4	16.1	25.9	40.0	16.8	9.7	9.9	5.5	5.7	5.3	8.2	12.4	4.0	5.9	3.3
Cassidulina laevigata	3.2	1.1	2.4	0.7	1.3	0.8	1.2	1.0		0.4	0.8	5.9	0.3	1.0			2.0	0.8	0.3	0.5
Cassidulinoides tenuis							7.9	0.6	1.5	0.1		0.2						0.1		
Chilostomella oolina	3.0	1.1	0.9	0.3		0.2	1.2	0.1		0.7	0.2		0.1			0.6	2.0	6.0	0.1	11.9
Cibicides lobatulus												0.2	3.1	2.3	4.0	1.1	0.1	0.9	1.9	2.2
Cibicidoides bradyi				0.3		0.8													1.5	2.0
Cibicidoides globulosus								0.5										0.1	3.3	2.6
Cibicidoides pachyderma				0.5			0.2		0.1	0.1			8.5	14.1	36.6	18.2	0.1	0.8	3.5	1.9
Cribostomoides jeffreysi		0.6		0.3	15.1	3.1	0.6	2.1	8.3	0.3	5.0	0.2	0.3	0.1	1.4	0.4	0.6	4.2	0.1	1.8
Cribrostomoides subglobosum	0.6	0.6	1.2	1.3	1.9	1.4	0.2		0.2	0.2			0.2	0.5	0.6			0.4	4.0	4.4
Cribrostomoides wiesneri	0.2	0.4	0.4	2.8	2.5	0.2				0.1									1.7	0.3
Crithionina spp.				1.5	0.6	0.4	2.4				0.6	3.7	0.1	1.5	1.0	0.6	0.1	2.2	0.6	2.4
Cyclammina cancellata	0.2			0.1		0.6	0.2		0.1	0.3	0.4		0.1	1.3	0.1	2.5		0.8	0.6	0.4
Cystammina pauciloculata			0.2	4.6							0.1									
Deuterammina montagui	0.4					0.6	0.2	0.2		0.5	0.2	0.3	0.2		0.1			0.1	0.1	6.8
Discammina spp.	0.6		1.1	2.3		0.2		0.6	0.1	0.5	0.5		0.1							
Eggerella bradyi		0.9	0.4	0.4						0.1				0.4	3.7	5.6		0.9	1.4	1.6
Epistominella exigua	0.2	0.2		0.7		4.5												0.1	1.2	0.3
Epistominella rugosa		0.4	1.5																	
Epistominella smithi							0.4	5.9	7.4	0.5										
Eponides pusillus	1.4		0.7																	
Fissurina spp.	0.2						0.5		0.6	0.1	0.8	2.1	0.4	0.6	0.4	0.4	0.3	0.1	0.1	0.3
Fontbotia wuellerstorfi		0.2		0.2		1.8				1.2			2.0	0.6	2.2	0.9	0.0	0.9	0.2	0.2
Fursenkoina earlandi		2.7	4.1		1.3															0.5
Fursenkoina mexicana						0.6	2.3	1.2	0.2	2.7	2.0	15.6	6.8	17.3	1.1	2.8	2.4	4.8		
Gavelinopsis translucens	8.9	4.2	4.9	2.5	4.4	10.7	1.9	1.6	0.3	0.3	0.7	0.2	5.0	2.9	5.5	1.5	1.3	5.3	4.3	3.6
Glandulina ovula				0.1			0.2	0.6		1.4		0.1	0.4				0.3			
Globobulimina affinis	2.0			2.3		1.0	0.3	1.9	0.2	2.0	0.0	19.3	0.0	5.0	0.5		18.4	1.3	0.1	4.6
Globocassidulina subglobosa	0.2					0.4	0.2				0.1		0.2	0.9	1.6	1.4	0.4	1.6	1.5	0.3
Gyroidinoides polius	0.6		0.3	1.1	0.6	2.7	1.3	1.3	0.3	0.4	0.5		0.6	0.9	0.6	1.5	0.3	2.6	1.5	2.0
Gyroidinoides soldanii				0.3						0.1	0.1	0.6	0.5	0.6	0.2	0.1		3.5	0.9	
Gyroidinoides umbonatus			0.2	0.1			0.4	0.7				0.3	0.3		0.2	0.1		1.6		0.6
Haplophragmoides bradyi				0.1			11.2	1.0	5.4	9.2	0.1	0.1								
Haplophragmoides coronatum	0.2						0.1												1.8	
Haplophragmoides sphaeriloculus	0.2			1.3		1.0		0.1		0.1	0.3								0.1	0.3
Hoeglundina elegans	0.2	1.3	5.0	6.4		1.8	0.2												0.1	
Hormosina globulifera	0.2	0.2	0.4	0.5	0.6	3.3	0.8	0.8	0.1	0.9	1.1	5.2	12.0	1.7	2.7	0.1		0.1	0.1	0.3
Hyperammina elongata		0.2	1.2	0.1	5.7			0.1		0.4	0.1	0.1			0.3		0.0		0.3	0.2
Karreriella bradyi										0.1										1.0
Karrerulina conversa			0.3	3.3	1.3	3.1	0.3	0.7		0.1									0.7	
Lagenammina difflugiformis	4.6	10.1	4.0	9.0	1.9	4.7	3.6	5.2	6.7	1.4	2.7	0.5	0.2	1.4		0.3	1.0	6.0		
Lagenammina tubulata	0.6	6.1	3.1	0.9	0.6	0.2				0.2	0.3		0.3					0.1	0.2	
Melonis barleeanum	7.1	3.8	2.1	3.3		3.9	3.5	0.6	3.8	3.6	0.1								0.7	
Miliolidae spp.				0.3				0.2				0.2	0.2	1.0	0.5	1.0	0.1	0.1	0.4	0.3
Nonion spp	0.2	0.4	0.1	0.7	0.6	0.2	0.4	0.5	0.0	0.0	0.2	0.1	0.0	0.0	0.0	0.4	0.0	0.0	0.1	0.0
Nouria harrisii	0.8	2.3		1.0	0.6	0.4	0.1	0.5		1.6	0.9	0.2	0.5	0.6	3.6	9.8		0.8		
Oolina spp						0.2		0.1			0.1	1.3			0.1			0.4		
Oridorsalis umbonatus	0.6		0.5	0.2		1.8	0.5	0.7	0.6	0.6	1.9	4.6	0.5	2.8	5.0	3.7	0.4	3.5	4.6	0.6
Osangularia culter	0.2	0.8		0.8	1.3	1.2			0.1											
Paratrochammina challengeri	0.2	0.2	1.3	0.3	1.3	0.2	0.2			0.2	0.5		0.0					0.4	0.1	0.5
Placopsilinella aurantiaca			0.5								0.4	2.2								

Table C1.1. (continued)

Species	GeoB4904-7	GeoB4906-5	GeoB4909-4	GeoB4912-4	GeoB4913-4	GeoB4915-3	GeoB4916-4	GeoB4917-5	GeoB4918-4	GeoB3713-1	GeoB3712-1	GeoB3715-1	GeoB3711-1	GeoB3708-1	GeoB3706-3	GeoB3705-2	GeoB3703-4	GeoB3702-2	GeoB3701-1	GeoB3604-1
Portatrochammina spp.							0.1	0.1		0.5	1.7	0.2	0.1	0.1	0.1			0.7		
Praecystammina globigeriniform	0.2						0.4	0.3											0.8	
Psammosphaera fusca		0.2					0.6			2.1	1.6	0.1	0.1		0.2			0.8	0.1	
Psammosphaera sp.								1.1		0.9	3.7		0.1						0.1	
Pseudogaudryina sp																			1.5	
Pullenia bulloides	1.0	0.2		1.0		2.0	0.1			0.3	0.2		0.2	2.8	0.7	0.3	0.7	1.4	0.6	
Pullenia subcarinata				0.3						0.1	0.0							0.5	1.2	3.9
Pyrgo depressa						0.4					0.1			3.8	0.1	2.0				
Pyrgo elongata						0.2					0.2		1.1	0.1	0.1		0.1	0.3	0.1	
Pyrgo murrhina	0.6		0.2	0.6							0.0		1.2	0.3	1.1	7.6		0.3		
Pyrgo serrata													3.0	0.3					0.5	
Pyrgoella sphaera								0.1			0.2	0.1	0.5	6.5	0.1	4.1	0.1			
Quinqueloculina spp.	0.6	0.2	0.4	0.1		0.4	0.1	1.6		0.2	0.0	0.2	0.3	0.3	1.6	0.7		0.5	0.1	0.2
Recurvoides contortus	0.6		0.4	3.9		1.4	3.7	0.0	0.8	4.0	2.5	0.7	1.5	1.1	3.2	1.2	0.1	7.3	4.1	3.5
Recurvoides scitulum				0.1	0.6	0.4	0.1			3.9	1.2		0.2	0.6	0.2			0.9		0.3
Reophax agglutinatus								0.1			0.3								1.2	
Reophax bilocularis	2.8	6.6	12.4	1.5		4.9	2.1	5.9	0.1	10.6	9.4	1.6	1.5	0.3	2.3	12.4	1.9	6.1	3.3	5.8
Reophax dentaliniformis	5.2	0.4	0.7	0.7		2.5	0.3	0.4		0.7	1.9		1.1					0.3	2.8	3.8
Reophax distans											0.3									0.3
Reophax guttifera	1.4	0.2	0.9	0.6		0.2	0.2	0.8		1.0	1.1	0.9	0.8	0.3	0.2			0.1	0.7	0.2
Reophax micaceus	0.6	2.3	1.6	0.7	0.0	0.2	0.0	1.2	0.0	0.1	0.1	0.0	0.0	0.3	0.1	0.4	0.0	1.4	5.9	1.0
Reophax pilulifer			0.4	0.1	1.9	2.3	1.9	0.5	5.3	1.2	2.8		0.6	0.1				0.9		
Reophax scorpiurus	6.5	12.5	8.7	2.9	1.9	1.0	1.6	0.2	0.3	0.7	0.3	0.3						0.1		
Reophax spp.	2.2	0.2	0.1	0.3	0.0	1.0	0.4	0.2	0.0	1.7	1.5	0.1	1.1	0.1	0.1	0.1	0.0	0.0	0.4	0.2
Rhabdammina spp.	0.0	0.2	0.1	0.8	0.6	0.0	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.6	0.1	0.2
Robertinoides chapmani	6.2	7.2	7.1	11.3		3.3	0.1												0.2	1.0
Saccammina sphaerica		0.2	1.1	0.5	0.6				3.2	0.8	0.3		0.0		0.1	1.1	0.2	2.3	0.5	0.4
Saccorhiza ramosa	1.6		0.1	0.3																0.4
Sigmoilopsis schlumbergeri													0.0	0.1	0.2	0.1	0.1	0.1	2.5	2.4
Siphotextularia spp	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.1	0.2	0.2	0.0	0.0	0.0	1.1	0.8
Sphaeroidina bulloides		2.1	0.3	2.7		3.3	1.0	1.4	0.1	1.6	1.4		0.7	1.2	2.8	1.8		1.8	16.4	6.4
Spirosigmoilina spp.										0.1		3.5		0.3		0.4	0.4	0.1		
Subreophax aduncus	0.2		0.2					0.1		0.8	1.1								0.3	
Textularia conica	0.2	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.1	0.5	0.0	0.3	1.2	0.6	0.0	0.0	0.0	1.8	0.5
Triloculina sp.												0.6	0.3	0.5	0.1	0.3	0.2	1.8		0.2
Trochammina spp.	0.2	0.0	0.7	0.5	0.0	0.6	1.4	0.6	0.8	0.5	3.1	1.1	0.7	0.0	0.7	1.2	0.8	1.4	1.9	0.9
Trochamminopsis pusillus								1.8		0.3	0.2		0.1							
Uvigerina auberiana	2.0	1.5	2.0	0.5		0.2	0.3	3.6	0.2	0.5	5.5	8.0	2.8	6.1	0.2	0.4	47.6	1.2	0.1	
Uvigerina peregrina	3.2	11.6	8.7	5.6	10.7	2.0	0.6	8.8	0.1	1.1			0.5	0.2	0.2				0.1	
Uvigerina proboscidea	0.4		1.0	0.4																0.2
Uzbekistania charoides	0.6																		1.6	0.8
Valvulina conica								0.9	0.9	3.1	12.9	3.7	1.5							
Valvulineria laevigata		0.2		0.7		4.5	19.2	5.1	2.6	6.0	5.6	0.1	0.2	2.2	2.4	1.1	3.7	7.7	0.1	0.2
Verneuilinulla propinqua	4.0			0.4		1.6	0.2	0.0	0.1	0.1									0.8	
Sum all others (<1%)	4.8	3.8	7.9	2.9	2.5	4.5	0.9	2.8	0.7	3.5	3.6	1.0	1.8	1.4	1.2	2.4	1.3	3.8	2.5	4.5
Total counted	504	527	633	1034	159	489	1123	1263	1163	1493	2074	1045	1646	1465	1691	1091	1328	775	1116	756

Table C1.2. Relative abundances of benthic foraminifera species of the total dead fauna

Species	GeoB4904-7	GeoB4906-5	GeoB4909-4	GeoB4912-4	GeoB4913-4	GeoB4915-3	GeoB4916-4	GeoB4917-5	GeoB4918-4	GeoB3713-1	GeoB3712-1	GeoB3715-1	GeoB3711-1	GeoB3708-1	GeoB3706-3	GeoB3705-2	GeoB3703-4	GeoB3702-2	GeoB3701-1	GeoB3604-1
Adercotryma glomerata			0.1	0.2		0.1	0.1	1.0		0.9	0.0									
Ammobaculites agglutinans	0.2	0.5	0.4	0.1							0.1									
Ammobaculites filiformis	2.7	0.6	0.4	0.6	0.9	0.7	0.1	0.1		0.1	0.0			0.0						
Ammodiscus incertus	1.3	0.3	0.2	0.1	2.1	0.9	0.6	0.2	0.3	0.0	0.6		0.0		0.0					
Ammolagena clavata	0.8		0.1		10.5	0.2	0.0			0.1	0.3			0.0	0.1					
Ammomarginulina ensis	2.1	0.1	0.4	0.2	0.1	0.8	0.6	0.7	0.5	0.3	0.1									
Ammomarginulina foliacea	2.4	2.3		0.5	9.5	0.3	0.2	0.3	0.1	0.2	0.1									
Ammoscalaria sp.	0.1	1.3	1.5	2.3	3.1	0.2	0.7		0.1	0.3	0.6	0.1	0.3							
Angulogerina angulosa	0.9	0.3	0.4			0.0		0.2												2.1
Cibicidoides globulosus								0.2		0.1			0.0						2.9	3.5
Atlantica atlantiella	0.2			0.0		0.1	0.1	0.7		0.1	1.2	0.1	0.0							
Bolivina dilatata						0.1	0.3	1.0	0.3	4.6		0.3	2.4		0.7	0.3		0.1		0.0
Bolivina pacifica pseudopunctata	0.5	0.1					0.6	1.1		0.5								0.1		0.1
Bolivina albatrossi	1.1	0.7	1.0	1.2	0.1	0.5	0.3	0.7	0.3	1.2	0.3		0.1		0.1	0.1		0.0		
Bolivina pseudothalmanni	0.2					0.1		2.4												0.2
Bolivina spp.			0.1	0.1		0.3		0.1	0.1	1.0	0.0			0.1						
Brizalina subspinescens	0.1	0.1	0.3	0.2		0.1							0.9	2.9	3.7	4.8	0.2	3.4	2.3	2.1
Bulimina aculeata	0.3		0.1	5.0		0.1	0.1	0.1	0.0	0.1	4.5	2.3	6.7	0.3	2.2	2.7	0.0	31.1	4.4	1.3
Bulimina alazanensis	2.1	0.6	0.9	1.0	0.5	0.4	0.2	1.0	0.1	1.0	0.3	0.3	0.5	0.2	0.6	0.6		0.9	0.3	0.4
Bulimina exilis		0.3		0.5		0.3	14.2	3.2	3.4	5.8	1.3	2.7	1.4	1.4	0.4	0.7	0.1	1.1		
Bulimina marginata		0.1		0.2	0.6		0.1		0.1	0.1	0.6	3.3	10.5	0.4	1.7	0.8		1.8	0.1	0.0
Bulimina mexicana	8.2	3.3	3.3	8.8	0.5	2.1	11.4	8.6	31.8	8.1	16.7	20.7	21.0	24.2	19.4	20.4	34.4	17.3	3.1	9.3
Cassidulina laevigata	3.6	2.6	1.7	1.6	0.8	1.0	1.3	1.0	0.1	0.4	0.9	6.9	11.8	6.7	5.1	8.5	2.4	6.9	5.9	6.9
Cassidulinoides tenuis				0.1			3.6	0.2	1.0	0.1	0.2	0.4	0.3			0.1		0.2		
Chilostomella oolina	3.3	3.1	1.7	1.6	0.1	0.4	1.3	0.3		1.0	0.2	0.2	0.2	0.3	0.0	0.7	0.7	0.5	0.3	1.3
Cibicidoides bradyi	0.2			0.7		1.0	0.2		0.1	1.0	0.2		0.1						2.0	2.2
Cibicidoides kullenbergi		1.2	0.3		0.0														0.4	0.1
Cibicides lobatulus							0.0	0.1			0.6	0.6	0.9	0.4	0.7	0.2	0.1	0.2	1.3	1.6
Cibicidoides pachyderma				1.2		0.1	0.3		0.2	0.8	1.1	0.2	1.1	8.5	8.5	1.9	0.2	0.2	5.9	4.5
Cibicides refulgens	0.6	2.7	3.0		0.6															
Cibicidoides robertsonianus	0.1	0.7	0.9					0.0											0.2	0.6
Cribostomoides jeffreysi		0.1	0.4		0.0	3.4	0.4	0.6	1.4	1.0	1.9		0.0		0.2			0.0		0.0
Cribrostomoides subglobosum	0.3	5.0	4.9	0.7	5.6	2.5	0.1	0.1	0.2	0.3	0.2	0.0	0.0	0.1	0.1				0.3	0.1
Cribrostomoides wiesneri	0.4	0.5	1.2	0.4	0.4	1.5		0.1		0.0									0.1	
Cyclammina cancellata	0.2	0.3	0.1	0.1	0.4	0.9	0.2		0.1	0.1	0.1			0.1	0.1				0.1	
Cystammina galeata		0.1			1.5															
Deuterammina grahami		0.5	0.2		1.3					0.0										
Deuterammina montagui	0.7	0.3			0.6	2.9	1.0	0.7		0.7							0.1			0.0
Discammina spp.	0.3	0.5	0.7	1.1		0.2	0.0	0.0	0.7	0.3	0.3									
Discorbina sp.				0.1							0.0								0.6	0.3
Earlandammina inconspicua				0.4		2.3	0.5	0.3		0.0	0.1	0.0							0.0	
Eggerella bradyi	2.5	1.4	2.8	0.9	0.0	0.5		0.1	0.2	4.6	1.2		0.2	2.0	4.8	2.8	0.1	0.1	2.0	5.7
Epistominella exigua		0.1	1.1	0.2		0.6	0.4	1.7				0.0	0.4	0.5	1.4	0.3	0.1	0.1	21.7	4.7
Epistominella rugosa		0.1	2.1																	
Epistominella smithi				0.1		0.3	4.1	30.8	27.9	1.5	0.8	3.9	1.9	0.1	0.1	0.1		4.5	0.1	
Fissurina spp	1.3	2.0	3.6	1.3	0.6	0.3	0.2	0.1	0.1	0.4	0.3	1.9	0.7	0.8	0.4	0.3	0.2	0.1	0.7	1.4
Fontbotia wuellerstorfi	0.4	2.8	1.3	0.1	0.6	0.6	0.6	0.4	0.1	0.2	0.6	0.8	0.5	0.5	1.0	0.7	0.4	0.1	1.0	0.1
Fursenkoina earlandi		1.6	1.5		0.3		0.1		0.1											0.2
Fursenkoina mexicana				0.3		0.0	4.0	1.8	1.1	3.9	0.9	3.2	5.3	11.5	5.2	10.0	2.4	2.3	0.0	0.1
Gavelinopsis translucens	3.1	2.9	1.7	1.9	1.1	1.9	2.5	1.0	0.1	0.1	0.0	0.4	4.2	7.4	9.1	10.1	1.7	1.8	10.1	7.7
Globobulimina affinis	1.4			1.0		1.2	3.4	2.6	4.8	1.4	0.3	3.9	0.4	1.8	0.4	1.2	5.4	0.6	0.0	0.3
Globocassidulina subglobosa	0.1	0.1	0.1				0.1						0.2	0.8	5.0	3.0	0.3	0.3	5.8	10.0
Glomospira gordialis			0.1					0.0		0.1	0.1									
Gyroidinoides polius	0.6	0.3	1.3	1.5	0.2	0.8	0.7	0.4	0.4	0.6	0.8	0.6	2.3	1.8	3.1	2.6	0.7	2.2	6.3	4.3
Gyroidinoides soldanii	1.7	0.4	0.7	0.2		0.1	0.2			0.4	0.3	0.6	0.8	0.6	0.7	0.8	1.5	0.5	0.5	0.2
Gyroidinoides umbonatus		0.4	0.1	0.1	0.0		0.0	0.7	0.1	0.1	0.1		0.3	0.3	0.3	0.4		0.6	0.6	1.3
Haplophragmoides bradyi	0.1			0.1		0.3	1.5	0.2	0.5	1.1	0.1									
Haplophragmoides sphaeriloculus	0.4			0.3		0.5		0.0		0.1	0.0								0.1	0.1
Hoeglundina elegans	0.1	0.5	3.6	1.2		0.2	0.0													
Hormosina globulifera	1.6	1.2	0.2	0.1	12.2	0.2		0.8		0.4	0.0		0.0	0.1	0.4					
Hyperammina elongata	0.4	0.1	0.2		1.4	0.2		0.0												
Karreriulina conversa	4.8	4.4	2.0	1.4	12.3	10.0		1.4		0.1									0.1	
Labrospira ringens		0.4	0.1	0.0	1.1	0.5	0.3	0.5		0.0										
Lagena spp.	1.1	1.4	1.5	1.5	1.1	0.9	0.9	0.5	0.1	1.5	1.3	0.9	0.4	0.8	0.6	0.6	0.4	0.1	0.3	0.5
Lagenammina difflugiformis	2.9	2.7	3.6	4.3	3.5	5.8	4.8	2.0	2.1	0.5	3.6	0.1	0.0	0.5	0.1	0.0	0.6		0.0	0.0
Lagenammina tubulata	0.5	2.4	1.1	0.5	0.7	3.0	0.2	0.1		0.3	0.2					0.1				
Martinotiella communis			0.1							1.5	2.3								0.1	0.1

Table C1.2. (continued)

Species	GeoB4904-7	GeoB4906-5	GeoB4909-4	GeoB4912-4	GeoB4913-4	GeoB4915-3	GeoB4916-4	GeoB4917-5	GeoB4918-4	GeoB3713-1	GeoB3712-1	GeoB3715-1	GeoB3711-1	GeoB3708-1	GeoB3706-3	GeoB3705-2	GeoB3703-4	GeoB3702-2	GeoB3701-1	GeoB3604-1
Melonis barleeanum	1.8	0.7	4.1	3.5		0.4	2.1	1.7	1.9	4.2	1.1		0.3		0.2				0.1	0.1
Nonion spp.	0.1			0.6		0.3	0.3	0.4		1.1	0.3	0.1	0.2	0.3	0.2	0.6	0.7	0.2	0.7	1.3
Nonionella spp.	0.1	0.6	1.6		0.1	0.6		1.0		0.2								0.2	0.2	0.7
Oridorsalis umbonatus	0.8	2.4	2.0	1.5	0.4	0.8	3.9	2.7	2.7	0.9	2.5	6.7	3.7	5.0	3.9	4.5	2.2	3.7	3.0	2.6
Osangularia culter	2.7	1.8		1.4	0.6	0.5	0.1	0.3		0.1			0.0			0.0		0.0		0.2
Paratrochammina challengeri				0.2		1.0	0.6			0.5									0.0	0.2
Paratrochammina spp.			0.1	0.2		1.0	0.6			2.0	2.3								0.1	0.3
Praecystammina globigeriniformis	0.4					0.9	0.0	0.1	0.1	0.3	0.1								0.0	
Psammosphaera fusca		0.1	0.2	0.0	0.8	0.1	0.2	0.3	0.2	2.4	1.1				0.1					
Pullenia bulloides	2.0	0.2	1.3	1.5		0.8	0.2	0.1	0.4	2.0	1.3	0.2	1.2	2.0	0.9	1.4	0.7	0.8	1.5	0.5
Pullenia salisburyi	0.1		0.1																0.2	0.1
Pullenia subcarinata	1.1	0.5	0.1	0.5				0.1		0.4	0.3	0.0	0.8	0.1	0.3	0.1	0.1	0.2	2.9	3.1
Pyrgo spp.	0.1	0.5	0.4	0.1	0.2	0.1	0.4	1.0	0.3	0.1	0.0	0.0	0.8	0.8	0.3	1.2	0.4	0.0	0.8	0.3
Recurvoides contortus	1.1	0.9	0.1	0.5	2.0	2.3	1.5	0.0	0.3	1.0	0.6	0.1		0.1	0.1	0.1	0.1		0.4	0.1
Reophax bilocularis	0.7	2.9	5.4	0.9	2.7	0.9	2.4	3.8	0.6	3.2	5.3	0.1	0.2	0.2	0.4	1.1	0.6	0.0	0.1	0.4
Reophax pilulifer	0.3	0.6	0.2	0.2	0.6	0.8	1.0	0.5	1.1	0.4	1.0	0.0								
Reophax scorpiurus	0.7	0.8	2.1	0.6	0.3	0.1	1.0	0.0	0.1	0.1	0.3									
Reophax spp.	2.4	1.0	1.1	1.5	0.3	1.6	1.0	0.9		1.7	1.9		0.1	0.1		0.2	0.1	0.1	0.3	0.3
Robertinoides chapmani	5.2	2.7	2.0	1.9		0.4	0.1	0.2		1.1										0.3
Saccammina sphaerica	0.6	0.8	0.7	0.4	0.2	2.6	0.8	0.5	0.2	0.8	1.2	0.3	0.0			0.0	0.1		0.2	0.0
Sigmoilopsis schlumbergeri	0.4	0.5	0.4	1.0	0.1	0.2	0.1	0.0	0.0	0.0	0.5	0.4	0.9	0.8	1.1	0.4	0.0	0.4	2.3	1.4
Sphaeroidina bulloides	2.7	5.6	1.3	5.3	2.3	3.0	3.0	1.4	1.4	7.5	4.3	0.1	0.9	0.6	1.6	0.6		0.3	1.8	7.5
Textularia spp.				0.1	0.1	3.5	0.1			1.4	0.1		3.6	2.0	6.6	1.2		0.5	1.7	1.4
Trochammina spp.	0.7	2.2	1.6	0.7	3.9	2.0	1.2	1.2	0.1	0.9	1.2	0.0	0.0	0.2	0.0	0.1	0.1	0.0	0.1	0.0
Uvigerina auberiana	1.9	0.9	0.7	0.4		0.0	0.2	0.6	1.2	0.1	10.7	35.8	6.4	8.4	2.7	6.2	39.8	11.4	0.2	0.1
Uvigerina peregrina	5.5	11.0	15.5	25.7	2.5	6.0	5.1	6.1	3.2	5.4	0.8	0.1	0.3	0.1	0.2	0.1		1.7	0.1	0.3
Valvulina conica	0.1		0.1	0.2			0.2	0.2	1.5	0.9	6.2	0.0	0.0							0.0
Valvulineria laevigata		0.1		2.0	0.1	2.3	7.7	3.1	4.8	6.5	4.7	0.5	2.7	3.2	3.1	4.7	2.0	2.1	1.0	1.3
Verneuilinulla propinqua	3.8			0.5		13.1	1.9	0.9	0.4	0.1									0.2	
Sum all others (<1%)	8.8	10.1	5.6	2.6	8.2	3.1	1.8	3.1	0.9	5.8	6.4	1.3	1.8	1.5	1.9	2.6	1.4	1.2	2.1	3.7
Total counted	1669	1620	1362	2143	952	1700	2306	3689	1893	1813	1991	2552	2677	2226	2111	2416	2064	3093	2233	2358

Table C2.1. Relative abundances of benthic foraminifera species of the surface live fauna

Species	GeoB4904-7	GeoB4906-5	GeoB4909-4	GeoB4912-4	GeoB4913-4	GeoB4915-3	GeoB4916-4	GeoB4917-5	GeoB4918-4	GeoB3713-1	GeoB3712-1	GeoB3715-1	GeoB3711-1	GeoB3708-1	GeoB3706-3	GeoB3705-2	GeoB3703-4	GeoB3702-2	GeoB3701-1	GeoB3604-1
Ammobaculites agglutinans										1.2	0.3									
Ammobaculites filiformis	1.0	0.5		3.0		4.6	0.3	1.1		0.3	0.3									
Ammodiscus incertus	2.0					0.3	1.9	0.9	5.1		1.4	1.5	0.2	0.2	0.2		0.3	0.7		
Ammolagena clavata					6.5										4.5	0.3				0.3
Ammomarginulina foliacea	7.9	6.3	0.4	0.6	19.5			0.2		0.3										
Ammoscalaria sp.	1.0	0.9	2.9	5.7	9.1		0.6	0.2	1.5	0.3	5.1	2.7	34.9							
Angulogerina angulosa	1.0		0.7			0.7	0.3	0.2												0.3
Astrorhiza sp.		0.5		1.7														0.4	1.8	0.9
Bolivina albatrossi		1.4	0.4			1.6	0.3	1.1	0.7	0.9										
Bolivina dilatata							0.6	0.2		1.2										
Bolivina pacifica pseudopunctata							0.6	1.1												
Bolivina spp.								1.6												0.3
Brizalina subspinescens			0.4											4.5		0.3		1.4	0.4	0.3
Bulimina aculeata	3.0					0.3		0.9	0.2	0.3										
Bulimina alazanensis	1.5	1.8	0.7	0.4	5.2	5.6	0.3			0.3										
Bulimina exilis										0.6		0.4		2.0						
Bulimina mexicana	4.9	3.2	0.7	0.4		1.6	18.8	26.5	43.8	19.1	12.7	10.8	5.9	6.0	4.5	10.3	16.6	6.0	12.4	5.4
Cassidulina laevigata	5.4	1.8	4.0	1.1	2.6	1.3	2.3	1.1		0.9	1.1	13.5	0.8	1.5			3.6	2.1	0.7	0.9
Cassidulinoides tenuis							3.6					0.4								
Chilostomella oolina							1.3											0.4		0.9
Cibicides lobatulus													4.0	2.5	5.3	2.7		2.1	5.1	3.7
Cibicidoides bradyi				0.4		1.0													0.7	3.1
Cibicidoides globulosus								0.5										0.4	5.1	4.9
Cibicidoides pachyderma				0.8			0.6		0.2				6.9	12.9	37.6	19.8		0.4	3.3	3.1
Cribostomoides jeffreysi						0.7	1.3	0.9	2.1	0.3	2.8	0.8	0.4		1.1	0.3	1.2	5.7		0.3
Cribrostomoides subglobosum		0.5	1.1	1.1	2.6	1.6			0.2	0.9				1.2	0.9			0.7	0.7	4.3
Cribrostomoides wiesneri	0.5		0.7	0.6	3.9	0.3														0.3
Crithionina sp.				1.5			4.2				1.1	6.9		3.0	2.4	1.2	0.3	2.1		3.1
Cyclammina cancellata				0.2		1.0			0.2	0.9	0.6			2.2		2.1				0.6
Deuterammina montagui	1.0					1.0		0.2		0.9		0.4	0.2							
Discammina spp.			1.8	3.4		0.3		0.2		0.6	0.8		0.2							
Earlandammina inconspicua						0.3					1.7									0.3
Eggerella bradyi		1.4	0.7	0.4										1.0	5.8	8.8		1.8	3.3	2.3
Epistominella exigua		0.5		1.1		7.2												0.4		0.6
Epistominella rugosa		0.9	1.8																	
Epistominella smithi							1.3	9.6	10.8	0.3										
Eponides pusillus	3.0		1.1																	
Fissurina spp.	0.5						0.6		0.5	0.3	0.3	4.6	0.8	1.5	0.2	0.9	0.9	0.4	0.4	0.6
Fontbotia wuellerstorfi		0.5		0.2		3.0				1.2			2.4	0.7	3.3	1.5		1.8	0.4	0.3
Fursenkoina mexicana							0.3				0.6	3.1	0.8	6.7			1.2	0.7		
Gavelinopsis translucens	14.8	4.1	5.4	3.8	5.2	15.1	5.8	2.3	0.5	0.6	0.3	0.8	4.2	7.9	8.0	2.1	2.4	11.0	4.0	6.3
Glandulina ovula							0.3	0.7		1.2		0.4	0.2				0.9			
Globobulimina affinis								0.2			0.3	1.9		0.2			3.3			
Globocassidulina subglobosa						0.7							0.2	1.2	2.0	2.1	0.9	3.2	5.5	6.3
Globulotuba sp.										1.5		0.4								
Gyroidinoides polius			0.4	0.6	1.3	1.6	1.0	1.4	0.5	0.3	0.6		0.4	0.7	0.4	0.6		2.1		3.4
Gyroidinoides soldanii				0.4								0.8	0.8	0.5	0.2			1.8	0.4	
Gyroidinoides umbonatus			0.4	0.2			1.3	0.9										2.1		1.1
Haplophragmoides bradyi							5.2	0.7	3.9											
Haplophragmoides sphaeriloculus	0.5			1.7		0.7				0.6										
Hoeglundina elegans		3.2	7.2	8.5		1.0														
Hormosina globulifera			0.4	0.6	1.3	2.3	1.6	1.4	0.2	0.3	1.1	10.0	11.5	3.7	3.6					0.6
Hyperammina elongata			1.1		7.8			0.2		0.3		0.4								0.3
Karreriulina conversa			0.4	2.1	1.3	4.9		0.9												
Lagena spp.						0.7	0.3	0.2		0.6	1.1	1.2		0.2			0.3	1.1	1.1	
Lagenammina difflugiformis	4.4	8.6	4.0	10.4	1.3	3.3	5.8	5.3	7.4	4.3	3.7	1.5	0.8	1.7		0.3	1.2	6.7		
Lagenammina tubulata	1.5	4.5	3.6	1.3	1.3	0.3				0.3	0.6							0.4		
Laticarinina pauperata				0.2		1.0														
Melonis barleeanum		1.4					1.3	0.5	2.6	0.3	0.3									
Miliolidae spp.				0.4				0.2					0.2	1.0	0.9	2.7	0.3		1.8	0.6
Nonion spp.				0.2	1.3		0.3	0.2											0.4	
Nonionella spp.	1.0	0.5	0.4													0.3				0.6
Oolina spp.						0.3		0.2				1.9						1.1		
Oridorsalis umbonatus	0.5		0.7	0.2		3.0	0.6	0.7	0.8	0.9	1.1	6.6	0.4	2.2	4.2	3.5	0.9	4.9	4.4	1.1
Osangularia culter	0.5			1.1	1.3	1.6			0.2											
Paratrochammina challengeri				0.2			0.6				1.7							0.4	0.4	0.9
Praecystammina globigeriniformis								0.5											3.3	

Table C2.1. (continued)

Species	GeoB4904-7	GeoB4906-5	GeoB4909-4	GeoB4912-4	GeoB4913-4	GeoB4915-3	GeoB4916-4	GeoB4917-5	GeoB4918-4	GeoB3713-1	GeoB3712-1	GeoB3715-1	GeoB3711-1	GeoB3708-1	GeoB3706-3	GeoB3705-2	GeoB3703-4	GeoB3702-2	GeoB3701-1	GeoB3604-1
Psammosphaera fusca		0.5					0.6			4.9	0.8		0.2					1.1	0.4	
Psammosphaera sp.								0.9		3.1	2.8		0.2							
Pseudogaudryina sp.																			1.1	4.9
Pullenia bulloides	0.5			1.5		1.6	0.3			0.3			0.4	1.5	0.9	0.3	0.6	1.8	1.5	0.6
Pullenia subcarinata																		0.4		2.6
Pyrgo depressa						0.7					0.6			6.2		2.9				
Pyrgo lucernula													1.2	0.2		0.6				
Pyrgo murrhina	1.0		0.4	0.4							0.3		4.8	0.5	2.0	12.1		0.7		
Pyrgo serrata													2.0	0.2						
Pyrgoella sphaera											0.3	0.4	0.2	7.2		1.2				
Quinqueloculina spp.	1.0		0.7	0.2				2.1		0.3	0.3		0.4	0.7	2.4	2.1		1.1		0.3
Recurvoides contortus	1.0			3.2		0.7	5.2		1.0	1.2	0.3	1.5	1.6	0.5	1.1	1.8		2.5		4.3
Recurvoides scitulum					1.3	0.7	0.3			3.4	3.4		0.8	0.2	0.4					
Reophax agglutinatus								0.2											2.9	
Reophax bilocularis	2.0	8.6	12.2	1.9		4.9	3.6	6.2	0.2	12.0	5.4	2.3	0.6	0.5	0.4	8.3	1.5	4.6	1.5	3.7
Reophax dentaliniformis	1.0		0.7	0.6				0.7			1.7		1.2							0.9
Reophax guttifera	1.5		1.4	0.6		0.3	0.6	0.5		0.6	0.8	0.8	1.0	1.0	0.2			0.4	1.1	0.3
Reophax micaceus		1.8	1.8			0.3		0.7		0.3				0.2	0.2			0.7	1.8	1.1
Reophax pilulifer			0.7		3.9		3.2	0.2	7.1	2.8	6.8		0.4							
Reophax scorpiurus	5.4	12.2	6.5	4.0	2.6	1.3	1.6	0.2	0.2	1.2	1.1									
Reophax spp.	0.5					0.3	1.0			0.3	1.7		1.2						0.4	
Rhabdammina spp.				1.3			0.3				0.3							4.2		
Robertinoides chapmani	9.9	10.4	9.0	14.8		3.3	0.3													1.7
Saccammina sphaerica			1.1	0.6					4.4	1.9	0.8				0.2	2.4	0.6	4.9		0.6
Saccorhiza ramosa	1.5			0.4																0.3
Sigmoilopsis schlumbergeri															0.2		0.3	0.4	0.4	1.1
Siphotextularia spp.				0.2									0.2	0.2	0.2				0.4	1.1
Sphaeroidina bulloides		4.5	0.4	3.4		4.6	0.6	1.6	0.2	0.9	0.3		0.4	2.0	2.7	1.8		2.5	24.1	8.3
Spirophthalmidum pusillum		1.4	0.4																	
Spirosigmoilina spp.										0.6		6.2		0.2		0.6	0.9	0.4		
Subreophax aduncus			0.4					0.2		3.7	1.4									
Textularia conica	0.5					0.3					0.3			0.5	0.4				2.9	0.9
Triloculina sp.								0.2				1.2	0.6	1.7	0.4	0.6	0.3	3.9		0.3
Trochammina spp.	0.5	0.5	2.9		2.6	0.7	1.3	0.5	0.3	1.2	3.7	2.3	0.6	0.7	0.7	0.6	0.9	3.5	1.1	0.9
Trochamminopsis pusillus								2.3		0.3	0.8		0.2							
Uvigerina auberiana	4.4	2.3	2.5	0.8		0.3		1.6			3.4	9.3	1.8	5.2	0.4	0.3	53.3	1.4		
Uvigerina peregrina	4.4	13.5	10.1	7.2	14.3	3.3	1.3	10.7	0.2	1.5			0.4	0.2	0.2				0.4	
Uvigerina proboscidea	0.5		1.4	0.6																0.3
Uzbekistania charoides	1.0																			0.9
Valvulina conica								0.9	1.1	9.6	11.9	4.2	2.0							
Valvulineria laevigata						3.3	14.3	4.8	3.6	2.5	1.1			2.0	0.2		5.9	2.1		0.3
Verneuilinulla.propinqua	4.9			0.6		2.6	0.3		0.2	0.6									1.8	
Sum all others (<1%)	3.0	2.7	6.5	2.8	3.9	2.0	1.0	2.3	0.3	4.0	10.2	0.8	1.8	2.5	1.1	5.0	1.8	1.8	2.9	7.3
Total counted	204	222	278	472	77	306	308	443	609	331	359	271	520	415	457	369	338	289	291	355

Table C2.2. Relative abundances of benthic foraminifera species of surface total dead fauna

Species	GeoB4904-7	GeoB4906-5	GeoB4909-4	GeoB4912-4	GeoB4913-4	GeoB4915-3	GeoB4916-4	GeoB4917-5	GeoB4918-4	GeoB3713-1	GeoB3712-1	GeoB3715-1	GeoB3711-1	GeoB3708-1	GeoB3706-3	GeoB3705-2	GeoB3703-4	GeoB3702-2	GeoB3701-1	GeoB3604-1
Adercotryma glomerata				0.5		0.4		0.6		1.0										
Ammobaculites filiformis	9.9	0.8		1.8	1.4	2.6		0.1						0.4						
Ammodiscus incertus	2.2	0.8	0.4	0.3	3.2	1.9	0.8	0.1	0.3	0.5	0.9									
Ammolagena clavata	1.1				11.7	0.4	0.3							0.4						
Ammomarginulina ensis	3.7		0.4	0.5	0.7	0.8	0.8	0.9	0.9	0.5										
Ammomarginulina foliacea	2.6	1.5		0.5	5.0		0.5	0.2		0.5										
Ammoscalaria sp.			0.7	3.3	0.7	0.8	1.3				0.9		0.5							
Angulogerina angulosa	2.2		0.4																	1.7
Atlantica atlantiella	1.1			0.3		0.4	0.3	0.3												
Bolivina alata							0.8		0.3				1.6							
Bolivina dilatata								1.2		4.5					0.3	0.5				
Bolivina pseudothalmanni								0.3												
Bolivina spp.	0.4	0.4	0.4	0.5			0.8	0.9	0.9	1.0	0.9				0.3					
Brizalina subspinescens			0.7	0.5									1.6	2.8	3.6	4.5	0.4	2.5	5.2	2.4
Bulimina aculeata	0.7			3.1				0.2			3.7	1.2	5.9	0.8	2.1	1.4	0.2	36.7	5.9	1.4
Bulimina alazonensis	2.9	0.8	2.2	0.3	0.7	1.1	0.5	0.4	0.3	1.0		0.4	0.5		1.5	0.2		0.3		
Bulimina exilis							3.7	0.4	0.9	6.5	0.9	1.2	1.8	2.0	0.3	0.9				
Bulimina marginata					0.4		0.3				2.8	6.2	11.9		1.2	1.4		4.9	1.5	
Bulimina mexicana	6.6	5.4	2.9	8.9	0.4	1.5	13.5	10.6	31.1	12.4	17.6	18.9	19.7	26.0	24.6	23.9	38.3	14.8	8.1	10.0
Cassidulina laevigata	6.6	1.5	2.9	0.8	2.1	0.8	3.2	0.7		0.5	1.9	2.3	11.3	7.7	6.8	9.0	2.7	2.2	7.0	6.0
Cassidulinoides tenuis							4.0	0.2	1.2	0.7			0.2							
Chilostomella oolina	0.7	0.4	0.7	0.3		0.4	1.3	0.1		0.2				0.4						1.2
Cibicides lobatulus							0.3					1.9	0.4	1.2	0.6	0.2	0.2		0.4	2.6
Cibicides refulgens	0.7	1.9	0.7																	
Cibicidoides globulosus								0.4											1.5	3.6
Cibicidoides kullenbergi		1.5	0.4		0.4															
Cibicidoides pachyderma				1.3			0.5			2.5	0.5	0.8	1.5	4.1	3.9	2.7	0.2	0.3	1.9	3.8
Cibicidoides robertsonianus								0.1												1.4
Cribostomoides jeffreysi		0.4			0.4	4.2	0.3	0.7	1.2	1.5	3.2				0.3					
Cribrostomoides subglobosum	1.1	6.9	2.2	1.8	4.3	3.0		0.1		0.2		0.4								
Cribrostomoides wiesneri	0.4	0.4	1.1	0.3		1.9		0.2												
Cyclammina cancellata		0.8			1.1	0.8	0.3													
Cystammina pauciloculata		1.5	0.7	0.3																
Deuterammina grahami		1.1			1.8															
Deuterammina montagui		1.1			1.4	4.2	1.6	0.7		0.7										
Discammina spp.				0.8			0.3	0.2	1.8		0.5									
Earlandammina inconspicua				2.3		2.3		0.4			0.5									
Eggerella bradyi	0.7	1.9	3.6		0.4					2.7	2.3			3.3	7.7	2.7		0.3	5.2	6.2
Epistominella exigua			0.4	0.3		0.8	1.3	0.1					0.4	0.8	2.1	0.2			20.0	4.5
Epistominella rugosa		0.8	3.3																	
Epistominella smithi						0.4	4.8	32.2	28.0	2.0	0.9	2.7	2.4			0.2		3.3	0.4	
Eponides pusillus	2.9		1.1																	
Fissurina spp.	0.4	3.8	4.4	0.8		0.4	0.3	0.2			0.9	3.5	0.9		0.3	1.6	0.2		0.4	1.9
Fontbotia wuellerstorfi		2.7		0.3	0.4			0.6	0.3	0.2	0.5	0.8	0.5		0.9	0.5	0.2		0.7	
Fursenkoina earlandi		0.4	2.5		0.4				0.3											
Fursenkoina mexicana				0.3			3.2	1.2	0.6	5.7	2.3	1.9	3.3	11.4	5.3	6.3	1.9	0.8		0.2
Gavelinopsis translucens	5.5	1.9	1.8	2.6	1.1	0.8	1.1	0.2	0.3	0.2			3.1	7.3	9.5	7.0	1.9	1.4	7.4	9.8
Globobulimina affinis	0.4			1.0		0.4	2.6	1.4	1.2	0.5		4.2	0.2	0.8	0.3	0.7	3.3	1.1	0.7	
Globocassidulina subglobosa	0.4	0.4	0.4				0.3						0.2	1.6	5.6	4.5	0.8	0.8	10.4	10.0
Gyroidinoides polius		0.4	2.2	1.0	0.4	0.4	1.1	0.4	0.6	0.5	1.9	0.8	1.5	1.2	1.2	3.2	0.8	1.6	4.1	6.0
Gyroidinoides soldanii	1.8		0.7				0.3				0.5	1.2	0.5	1.6		0.9	2.3	0.3		
Gyroidinoides umbonatus		1.5	0.7		0.4				0.6		0.9		0.9		0.3	0.5				1.7
Haplophragmoides bradyi							1.3	0.3	0.6	0.2										
Hoeglundina elegans		1.1	3.3	2.3		0.8														
Hormosina globulifera	1.8	2.3		1.3	17.1	1.1		2.0		1.2					0.3					
Karrerulina conversa	1.8	5.4	1.1	2.0	11.0	9.1		1.2												
Labrospira ringens		0.4		0.3	0.7	2.3	0.5	0.7		0.2										
Lagena spp.	1.1	1.5	1.8	1.0	2.1	1.1	0.3	0.2		1.0	0.9	2.3	0.5	0.4	1.2		0.4	0.3		0.2
Lagenammina difflugiformis	2.9	2.7	4.4	8.4	3.2		4.5	2.9	1.8	1.2	2.8			0.4	0.3		0.4			
Lagenammina tubulata		3.8	1.8	0.8	2.1	6.0	0.5	0.4		0.2	0.5					0.5				
Melonis barleeanum	2.2		3.3	2.8			1.1	1.1	1.8	5.0	1.4		0.4							
Miliolidae spp.	0.4				0.4	0.8	0.3		1.2		0.5	0.4				0.2				0.2
Nonion spp.	0.4			0.8			0.5	0.4		0.5			0.2	0.4	1.2	0.7	0.6			1.0
Nonionella spp.			2.2					0.8											0.4	0.2
Oridorsalis umbonatus	0.4	0.8	1.8	2.0		0.4	2.9	3.0	2.1	1.0	2.3	8.1	4.4	3.3	2.4	3.8	2.5	1.9	1.9	1.9
Osangularia culter	1.1			0.8		0.4	0.3	0.1		0.2										0.2
Paratrochammina challengeri						1.5				1.0										

Table C2.2. (continued)

Species	GeoB4904-7	GeoB4906-5	GeoB4909-4	GeoB4912-4	GeoB4913-4	GeoB4915-3	GeoB4916-4	GeoB4917-5	GeoB4918-4	GeoB3713-1	GeoB3712-1	GeoB3715-1	GeoB3711-1	GeoB3708-1	GeoB3706-3	GeoB3705-2	GeoB3703-4	GeoB3702-2	GeoB3701-1	GeoB3604-1
Psammosphaera fusca		0.4				0.8	0.5	0.2		5.2	0.9									
Pullenia bulloides			1.5	1.3		0.4	0.5		0.3	2.2	0.9	0.4	1.3	1.6	0.3	2.3	0.4	0.8	0.7	0.2
Pullenia salisburyi																			0.4	0.2
Pullenia subcarinata	0.4	0.8		0.5						1.0	0.9	0.4	0.7					0.3	2.6	5.0
Pyrgo spp.	0.4	0.4	1.5	0.8	0.7			1.2			0.9		0.5	2.0	0.9	2.5	0.4		0.4	0.2
Quinqueloculina spp.	0.7		1.1	0.8	0.4		0.5	0.1									0.4	0.3		
Recurvoides contortus	1.1	1.9	0.4	1.3	1.4	0.4	2.6	0.1	0.9		0.5					0.2				0.2
Recurvoides scitulum		4.6			7.5			0.1	0.3	1.2	1.4									
Reophax bilocularis	0.4	1.9	9.1	1.3	2.5	3.4	7.9	6.5	1.5	4.2	3.7	0.4				1.1		1.1	0.7	0.2
Reophax guttifera	1.8	0.8	0.7	0.5		1.1	1.3	0.4												
Reophax micaceus	0.7	1.1	1.1	0.5		0.4		0.1												0.2
Reophax pilulifer		0.8	0.7				0.8	1.1	0.9	1.0	0.9									
Reophax scorpiurus	1.8	1.5	2.9	0.8		0.8	1.9			0.7	0.9									
Reophax spp.	1.5		0.4	0.8		3.0	0.5			0.2	1.4									
Robertinoides chapmani	1.8	1.1	1.1	1.3		0.4	0.3			0.2										0.2
Saccammina sphaerica	1.8	0.8	0.7	0.8	0.4	2.3	0.3	0.6		0.5	1.4		0.2							0.2
Sigmoilopsis schlumbergeri			1.1	1.8		0.4	0.3	0.1		0.2		0.4	1.6			0.5	0.2	0.8	1.9	1.0
Siphotextularia spp.														2.8	0.6				1.1	0.5
Sphaeroidina bulloides		6.9	1.5	2.6	2.8	0.4	2.1	0.8	0.9	6.9	2.8	0.4	1.6	0.8	0.9	0.2			2.6	6.9
Subreophax aduncus	1.8	0.8	0.4			1.1		0.1		0.5			0.2							
Textularia spp.						3.0				0.5			4.8	1.2	6.8	1.4		1.1	3.7	0.2
Trochammina spp.	0.7	1.9	1.8	1.3	3.2	2.6	4.0	3.6		1.2		0.4	0.2		0.3			0.3		
Uvigerina auberiana	1.5	0.4	1.1	0.5				0.3	1.5	0.5	9.7	37.8	6.4	8.1	2.4	8.4	38.8	16.7	0.4	0.2
Uvigerina peregrina	1.8	6.9	10.9	24.0	3.2	2.3	4.0	6.3	2.1	4.0	0.9		0.5					2.2	0.4	0.5
Uzbekistania charoides	2.6																			0.2
Valvulina conica								0.4	0.6	0.5	5.1									
Valvulineria laevigata				0.8		4.2	8.2	3.6	11.3	6.7	4.6	0.8	3.5	2.4	3.9	3.4	0.8	2.7		1.2
Verneuilinulla propinqua	5.5			0.3		17.0	0.8	0.5		0.5										
Sum all others (<1%)	4.8	6.9	4.7	1.8	2.8	2.6	1.3	4.0	0.9	3.7	9.7	0.0	2.0	2.4	0.0	2.0	1.5	0.3	2.2	3.8
Total counted	284	261	277	403	284	271	387	1441	329	424	234	279	581	262	357	465	487	403	306	436

3. Vertical sediment occupancy by benthic foraminifera between 3°N and 32°S off West Africa and paleoceanographic implications

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3.1. Abstract

We investigated multicorer samples on a latitudinal transect of twenty-three stations between 3°N and 32°S along the continental slope off West Africa, in order to decipher the influence of several seasonally and spatially varying primary productivity provinces on the occupancy of distinct microhabitats within the sediment by benthic foraminifera. The total abundance and diversity of foraminifera exhibit a clear relationship with the primary productivity gradient in surface waters. Eight assemblages of benthic foraminiferal species were recognized by Q-mode Principal Component Analysis, indicating a clear succession of distinct groups of epibenthic, shallow, intermediate, and deep endobenthic species (1) within the sediment and (2) over latitude, matching well the distinct primary productivity provinces. While species are concentrated towards the sediment-water interface in the less eutrophic Gulf of Guinea and the northern Angola Basin, the contribution to the fauna and the burial of shallow and deep endobenthic species towards the south increases with the establishing of more eutrophic conditions. Highest occurrences of deep endobenthic species (*Globobulimina affinis*, *Fursenkoina mexicana*) characterize the northern Benguela region. The absence of these species in the southern Angola Basin, influenced by oceanic upwelling at the time of sampling, might indicate their longer time-response to strong inputs of fresh phytodetritus compared to more opportunistic shallow endobenthic taxa (e.g. *Bulimina mexicana*). The dominance of *Chilostomella oolina* in the southern Benguela region, where food supplies are lower than in the northern Benguela region, suggests differential ecological preferences of deep endobenthic species. The mean stable carbon isotopic composition of foraminiferal species generally decreases with increasing habitat depth within the sediment. Lowest mean enrichment in ^{12}C is observed for cibicids (*Cibicidoides globulosus*, *Cibicidoides pachyderma*, *Cibicides lobatulus*). Our data suggest that *C. pachyderma* and *C. lobatulus* migrate from an endobenthic niche towards the sediment-water interface at different sites, depending on food availability, and so either reflect the $\delta^{13}C$ signal of dissolved inorganic carbon of the bottom water or the porewater.

3.2. Introduction

Deep-sea benthic foraminifera do not live exclusively at the sediment-water interface, but can be found up to tens centimeters depth within the sediment. The first descriptions of a clear succession of foraminiferal deep-sea species within the sediment (Corliss, 1985; Gooday, 1986; Mackensen and Douglas, 1989) demonstrated that some species preferentially live close to the resource-rich, oxygenated surface sediment, whereas others show maxima well below the sediment-water interface. Since then, a number of publications have confirmed these observations and provided essential information on the ecological preferences of distinct species with regard to oxygen and trophic conditions, which are considered to be the most important controlling factors on foraminiferal vertical distribution (e.g. Corliss and Chen, 1988; Jorissen et al., 1995; Schmiedl et al., 2000; Fontanier et al., 2002). This information is essential for a proper interpretation of foraminiferal fossil assemblages with regard to changes of primary productivity and deep-sea ventilation during geological times (e.g. Thomas et al., 1995; Den Dulk et al., 1998; Wollenburg et al., 2004). The close interrelation of these parameters, however, often hinders the clear separation between their respective influences and the development of accurate quantitative proxies.

The knowledge of foraminiferal microhabitats is also crucial for the reliable utilization of the foraminiferal fossil $\delta^{13}C$ record. Some epibenthic species, mostly cibicids, were shown to overall faithfully record the isotopic signature of bottom-water dissolved inorganic carbon, whereas others, assumed to preferentially occupy an endobenthic niche within sediment, were shown to be largely influenced by the more negative $\delta^{13}C_{DIC}$ values of the porewater (e.g. Woodruff et al., 1980; Belanger et al., 1981; Grossman, 1987; Rathburn et al., 1996; McCorkle et al., 1997; Mackensen et al., 2000). In other words, the $\delta^{13}C$ values of epibenthic species can be used as a reliable proxy for deep ocean paleocirculation (e.g. Duplessy et al., 1984, 1988; Curry et al., 1988; Sarnthein et al., 1994; Mackensen et al., 2001; Bickert and Mackensen, 2003), while those of endobenthic species give information on the intensity of the organic carbon fluxes to the seafloor (e.g. Woodruff and Savin, 1985; Zahn et al., 1986; Loubere, 1987). Mackensen et al. (1993b), however, demonstrated that even the strict epibenthic *Fontbotia wuellerstorfi*, if collected from areas characterized by strongly pulsed production, exhibits lower $\delta^{13}C$ values than the ambient seawater. Furthermore, many questions remain open on the exact relationships between foraminiferal $\delta^{13}C$ record, specific ecological preferences, and porewater chemistry of the surrounding water.

In the eastern South Atlantic, several seasonal and permanent upwelling systems strongly influence surface waters, locally resulting in extremely enhanced primary production. In a previous study investigating the transition from live to dead benthic foraminiferal assemblages from a narrow water-depth range (between 1300 and 1500 m), Licari and Mackensen (2005) demonstrated that differences in seasonality, quantity, and quality of food supply are the main controlling parameters on species composition and distribution of faunas over the distinct primary productivity provinces. To investigate to which extent the vertical sediment occupancy of benthic foraminifera in the eastern South Atlantic is controlled by these factors, we examine in this paper a compilation of foraminiferal microhabitat preferences at 23 stations on a latitudinal transect between 3°N and 32°S along the West African slope. Q-mode principal component analysis was used to recognize the main distribution patterns of principal foraminifera species versus sediment depth and latitude, also taking in consideration the insights gained from the detailed analysis of foraminiferal microhabitat distribution at six stations by Licari et al. (2003). This approach differs from that used in most regional studies dealing with the vertical partitioning of benthic foraminifera, generally based on the detailed description of a few cores.

Subsequently, the implication of microhabitats for the utilization of some foraminiferal proxies is discussed. A detailed investigation of the fluctuations of the foraminiferal isotopic signal with respect to carbonate saturation state and organic matter fluxes was presented by Mackensen and Licari (2004) at sixteen stations from the transect investigated in this study. In this paper, we briefly examine these data in the view of new stable isotope data from six additional stations with emphasis on species microhabitat preferences.

3.3. Area of investigation

Main patterns of hydrography and surface water primary productivity are described in detail in Licari and Mackensen (2005), and are schematically represented in Figure 1. The study area can be divided in several distinct provinces, characterized by different upwelling regimes.

Strong seasonal coastal upwelling occurs from May to September between 4°E and 8°W along the northern coasts of the Gulf of Guinea and in the northern Angola Basin between 1°S and 10°S (Verstraete, 1992), where distinct upwelling cells were identified north and south of the Congo river mouth at about 5°S and 7°S (Lutjeharms and Meeuwis, 1987). Seasonal upwelling in the Equatorial Divergence Zone, river-induced upwelling off the Congo River, and nutrient input from the river also account for locally enhanced productivity in the tropical sector of the eastern South Atlantic (Eisma and Van Bennekom, 1978; Van Bennekom et al., 1978; Voituriez and Herbland, 1982).

In the southern Angola Basin, primary productivity patterns are influenced by a complex system of cyclonic gyres, domes and fronts, and by the extension of the adjacent coastal upwelling systems. Seasonal oceanic upwelling occurs during austral summer in connection to the uplift to the thermocline layers of the Angola Dome (AD), one of the principal features of this area (Voituriez and Herbland, 1982; Jansen et al., 1984; Van Bennekom and Berger, 1984; Peterson and Stramma, 1991). The AD, centered at approximately 10°S 9°E (Mazeika, 1967), is itself embedded in another cyclonic circulation structure at larger scale, the Angola Gyre (AG), centered quasi stationary near 13°S 5°E (Moroshkin et al., 1970; Gordon and Bosley, 1991).

At 14-17°S, the Angola-Benguela-Front (ABF, Shannon et al., 1987) marks the northern boundary of the semi-permanent Benguela coastal upwelling system, bordered at its southern extremity by the Agulhas Retroflection (37°S). Upwelling occurs preferentially in six to seven specific upwelling cells centered on the shelf and shelf edge along the coast off Angola, Namibia and South Africa (Figure 1). This system can be subdivided in a southern subsystem, where upwelling is highly seasonal, and a northern subsystem, where upwelling is mostly perennial, but with seasonal maxima. Upwelling is most intense and most frequent at the Lüderitz cell (centered at about 25°S), which marks the boundary between the two distinct subsystems (Shannon, 1985; Shannon et al., 1987; Shannon and Nelson, 1996; Strub et al., 1998). Between 18°S and 34°S, a well-developed longshore thermal system of upwelling, shelf-break, and oceanic fronts demarcates the seaward extent of the upwelled water, which reaches a westwards extension of 150 to 250 km on average (Lutjeharms and Stockton, 1987; Shannon and Nelson, 1996). Enhanced productivity is concentrated at frontal features or just outside upwelling fronts (Lutjeharms and Stockton, 1987), and coldwater filaments, plumes and frontal eddies make up an extensive high-productive outer area extending on average between 300 and 600 km offshore, and as far as 1000 km during extreme events (Lutjeharms and Stockton, 1987; Lutjeharms et al., 1991).

With regard to benthic environment trophic levels, the less eutrophic conditions are encountered in the Gulf of Guinea and the northern Angola Basin, where sampling (March 1998) occurred outside of the main upwelling season, generally extending from May to September during the "great cold season" (Verstraete, 1985). In this area, influenced by riverine discharges from the Rivers Niger and Congo, the input of detritic organic matter from continental origin is expected to be high (Wagner et al., 2003). The southern Angola Basin and the northern Benguela region correspond to more favorable trophic conditions. In the southern Angola Basin, the benthos is expected to be mainly influenced by freshly deposited phytodetritus

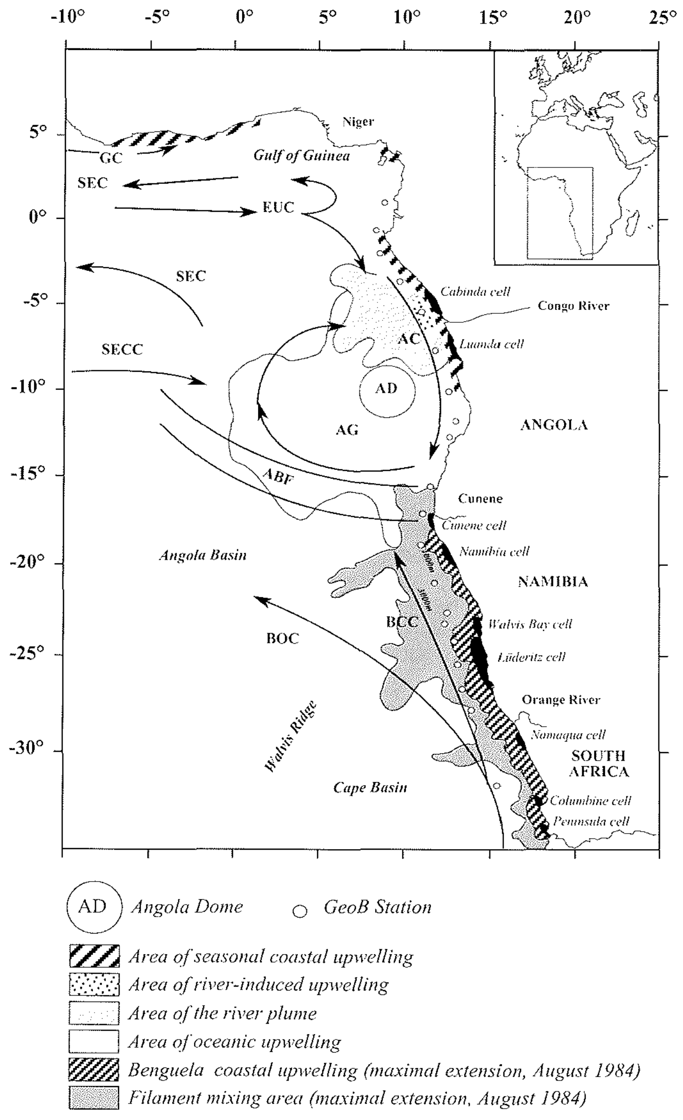

Figure 1. Location of the investigated samples, high-productivity areas, and surface and subsurface hydrography in the eastern South Atlantic. Area of seasonal coastal upwelling is after Voituriez and Herbland (1982). Areas of river plume, oceanic, and river-induced upwelling are after Jansen et al. (1984). Extension of coastal upwelling and adjacent mixing area in southern winter (August) 1984 is after Lutjeharms and Stockton (1897). Upwelling cells are after Lutjeharms and Meeuwis (1987) and Shannon and Nelson (1996). Currents are after Voituriez and herbland (1982), Van Bennekom and Berger (1984), and Peterson and Stramma (1991). *ABF=Angola-Benguela-Front, AC=Angola Current, AD=Angola Dome, AG=Angola Gyre, BCC=Benguela Coastal Current, BOC=Benguela Oceanic Current, EUC=Equatorial Under Current, GC=Guinea Current, SEC=South Equatorial Current, SECC=South Equatorial Counter Current.*

of marine origin at the time of sampling, connected to oceanic upwelling. Towards the south, there is again a decrease of food availability in the southern Benguela region, in relation to the highly seasonal character of upwelling events and possibly reduced carbon export in that area (see Licari and Mackensen, 2005, and references therein). In contrast to the Gulf of Guinea and the northern Angola Basin, terrestrial inputs of organic matter are minor in the Benguela upwelling system (Wefer and Fisher, 1993; Romero et al., 2002).

3.4. Material and methods

3.4.1. Sampling and processing

We selected sediment samples recovered by a multicorer at 23 stations during cruises M20/2, 34/1, 34/2, and 41/1 of R.V. *Meteor* to be located on a latitudinal transect along the eastern South Atlantic slope, such that the strong surface productivity gradient is almost completely documented (Figure 1, Table 1). All samples were taken between January and March during years 1992, 1996, and 1998 (Table 1). Shortly after recovering, each core was sub-sampled every centimeter down to 15 cm depth, and sub-samples were subsequently fixed and stained with a mixture of alcohol and Rose Bengal in order to differentiate live benthic foraminifera from empty tests, following Mackensen and Douglas (1989). A detailed description of sampling and processing protocol is presented in Licari and Mackensen (2005).

3.4.2. Foraminiferal data

For each core, foraminiferal total standing stocks were calculated for the complete fauna and single species from the >125 μm grain-size fraction for all sediment intervals from the top 1 cm down to 12 cm depth, and standardized for 50 cm^3 sediment volume. Total standing stocks per core were expressed as number of stained specimens per 50 cm^2 sediment surface (Table 1). We used the Shannon-Wiener index H(S) and the equitability index E, where S is the number of species, to estimate the diversity and equitability, respectively (Buzas and Gibson, 1969).

The stable carbon isotopic composition of foraminiferal tests was determined for selected epibenthic and endobenthic species, which were abundant enough for isotopic analysis, according to the method described in Mackensen and Licari (2004).

3.4.3. Statistical analysis

Q-mode Principal Component Analysis (PCA) was carried out on the foraminiferal data set using SYSTAT 5.2.1©. Our aim was to recognize the principal foraminiferal species and their main distribution patterns (1) within the sediment, and (2) with increasing latitude. Therefore, each single sediment sample from each single core where more than 15 stained foraminifera were counted was considered as a single object in the input matrix. This strategy should allow us to statistically recognize distinct groups of species within the sediment, ideally corresponding to distinct microhabitat types, and latitudinal changes in the vertical distribution patterns of these groups. With the exception of three deeper stations, bathed by the North Atlantic Deep Water (NADW), all stations are located within the Antarctic Intermediate Water (AAIW)/Upper Circumpolar Deep Water (UCDW) flowing path (Reid, 1989; Schulz et al., 1996, 1998).

Table 1. Samples used for this study (sorted according to the latitude) with sample number, water depth, geographical position, date of sampling, productivity estimates (data available at http://marine.rutgers.edu/opp/) and estimated organic carbon flux (calculated after Berger, 1989). Sedimentary data (total organic carbon and carbonate contents) are from the data archive PANGAEA (http://www.pangaea.de, originally published or compiled by Balsam and McCoy. 1987; Archer, 1996; Lochte et al., 2000; Mollenhauer et al., 2002, 2004; Wagner et al., submitted) and from Timm (1992). Italic values indicate extrapolation from measurements at nearby stations, using Ocean Data View software (Schlitzer, 2002). Dissolved oxygen concentration in the overlaying bottom-water, and oxygen penetration depth within sediment are from Schulz et al. (1992) and Hensen et al. (2000) (data available at www.pangaea.de), Wenzhöfer and Glud (2002), Hensen (pers.comm. 2002), Licari et al. (2003). Benthic foraminiferal total standing stocks, Average Living Depth (total ALD) (after Jorissen et al., 1995) and Maximum Habitat Depth (total MD) (after Shirayama, 1984), species number S, diversity H(S), and equitability E (Buzas and Gibson, 1969) are also given for the complete fauna.

GeoB station	**water depth** m	**Lat.**	**Long.**	**Sampling date** (d/m/y)	**Productivity estimates** (gC/m^2/y)	**Estimated total org. carbon flux** (gC/m^2/y)	**TOC** %	**Carbonate** %	**Oxygen bottom water** (ml l^{-1})	**Oxygen penetration depth** (cm)	**Total Standing Stocks** (#/50cm^2)	**Total ALD** (cm)	**Total MD** (cm)	**S**	**H(S)**	**E**
4901-6	2188	2.68	6.72	26/02/98	203	3.6	0.8	*9.6*	5.2	8.9	67	1.1	2.2	25	2.2	0.4
4904-7	1341	0.96	8.88	28/02/98	315	7.1	1.2	*12.9*	4.7	2.0	321	1.6	5.5	74	3.6	0.5
4906-5	1277	-0.69	8.38	02/03/98	315	7.3	1.5	*16.5*	4.1	2.3	168	1.3	2.3	58	3.2	0.4
4909-4	1313	-2.07	8.63	04/03/98	315	7.2	1.3	*5.2*	4.1	3.0	290	1.1	2.9	71	3.4	0.4
4912-4	1298	-3.73	9.79	06/03/98	450	10.4	1.5	*3.0*	4.7	2.4	480	1.2	3.4	91	3.6	0.4
4913-4	1300	-5.50	11.07	06/03/98	450	10.4	1.7	*4.0*	4.4	2.0	51	1.4	3.8	32	2.8	0.5
4915-3	1305	-7.75	11.87	09/03/98	450	10.4	1.3	*20.5*	4.7	2.5	156	1.7	4.4	69	3.7	0.6
4916-4	1300	-10.17	12.69	10/03/98	405	9.3	2.5	*15.8*	4.7	2.0	358	1.7	3.5	69	3.0	0.3
4917-5	1299	-11.90	13.07	10/03/98	405	9.4	2.2	*15.5*	4.2	1.6	932	1.1	3.1	82	3.2	0.3
4918-4	1338	-12.84	12.70	11/03/98	405	9.2	2.2	*20.0*	4.0	1.2	370	1.4	3.8	41	2.3	0.2
3713-1	1330	-15.63	11.58	07/02/96	450	10.3	1.6	5.1	2.9	1.3	827	2.4	4.0	92	3.4	0.3
3712-1	1242	-17.19	11.13	06/02/96	450	10.7	2.4	5.7	3.3	0.7	1645	2.2	5.1	94	3.5	0.3
3715-1	1204	-18.95	11.06	09/02/96	450	10.9	4.5	25.6	3.7	0.9	333	2.6	6.2	48	2.8	0.4
3711-1	1214	-19.84	10.77	05/02/96	450	10.8	3.8	66.7	4.1	1.4	726	2.1	5.1	72	2.9	0.2
3708-1	1283	-21.09	11.83	04/02/96	450	10.5	4.9	52.6	2.2	1.4	994	1.9	4.2	61	3.0	0.3
3706-3	1313	-22.72	12.60	02/02/96	450	10.3	3.7	55.2	4.4	1.4	580	2.1	4.4	60	2.8	0.3
3725-1	1980	-23.32	12.37	17/02/96	405	7.5	2.1	76.4			283	2.3	5.8	61	3.2	0.4
3705-2	1305	-24.30	13.00	02/02/96	450	10.4	4.5	66.0	4.3	0.8	391	1.7	3.7	53	3.0	0.4
3703-4	1376	-25.52	13.23	01/02/96	405	9.1	8.1	55.3	4.3	0.8	746	2.2	7.3	41	1.9	0.2
3702-2	1319	-26.79	13.46	31/01/96	315	7.2	4.7	57.0	4.3	1.1	247	1.5	3.2	67	3.6	0.5
3701-1	1488	-27.95	14.00	31/01/96	315	6.7	1.7	75.1	4.4	2.6	478	1.7	3.3	84	3.6	0.4
1720-3	2004	-29.00	13.84	17/01/92	315	5.8	0.8	77.6	5.0	>0.9	268	1.4	3.4	72	3.6	0.5
3604-1	1512	-31.79	15.49	10/01/96	315	6.7	1.2	78.0			279	1.4	3.4	73	3.6	0.5

The counting of 15 individuals might appear insufficient, as in most quantitative foraminiferal studies it is generally considered that the counting of a poll of about 100 to 300 individuals provides a reliable representation of the whole assemblages (e.g. Imbrie and Kipp, 1971). In our study, lowest foraminiferal counts characterize the deepest sediment samples, where foraminiferal faunas tend towards monospecificity. While the average observed species number ranges between about 30 and 60 in the first few centimeters of sediment, it drops to less than 5 in the deepest layers (Figure 2). Parallel to the decrease in diversity with increasing sediment depth, the number of individuals encountered rapidly decreases from the sediment surface downcore (Figure 2). Therefore, we assume that counting only tens of individuals is sufficient to properly describe the abundance relationship between the few species present at this depth. As demonstrated by Fatela and Taborda (2002), counting ten specimens is already statistically reliable to describe abundance patterns of species representing about 20% of the assemblage at a 95% confidence level. Furthermore, we removed rare species with abundances less than 1% or present in only one sample for the statistical analysis, but kept them in the data for calculation of standing stocks and foraminiferal numbers.

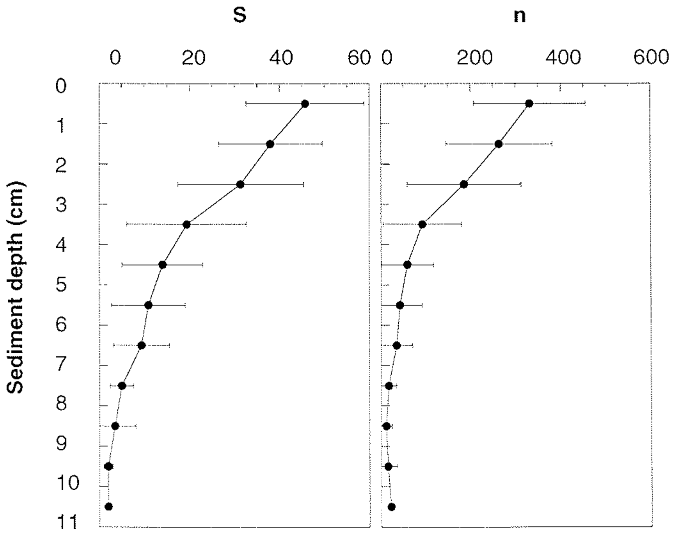

Figure 2. Average number of species (S) and individuals (n) encountered within the sediment.

Squared PC-loading values greater than 0.2, i.e. corresponding to non-squared loading values greater than 0.4, were regarded as significant (Malmgren and Haq, 1982).

A list of all dominant and associated species contributing to the assemblages is given in appendix A. Varimax principal component loadings and scores derived from the PCA are given in appendix B. Foraminiferal background data (standing stocks) are reported in appendix C.

3.4.4. Calculation of Maximum habitat Depth and Average Living Depth

For the quantitative determination of benthic foraminiferal microhabitat preferences, we estimated the Maximum habitat Depth (MD) (Shirayama, 1984) for the complete fauna, and the Average Living Depth (ALD) (Jorissen et al., 1995) for the complete fauna and principal single species (as defined from PCA). The MD corresponds to the maximum depth were living individuals are found within the sediment, and was graphically obtained from the curve of cumulative total percentages of foraminifera versus sediment depth, as the intercept value (in cm) corresponding to 95%.

The ALD corresponds to the average depth (in cm) of all live specimens found, and is calculated according to

$$ALD_x = \sum_{i=1,x} (n_i \times D_i) / N,$$

where x is the lower boundary (in cm) of the deepest sample, n_i the number of live specimens in sediment interval i, D_i the midpoint (in cm) of sediment interval i, and N the total number of specimens in all intervals.

The ALD is heavily influenced by foraminiferal deep occurrences within the sediment. Therefore, isolated specimens separated from the bulk of the main population by more than 1 cm of "sterile" sediment (that is, without live specimens), were considered as outliers and omitted from the calculation (Jorissen et al., 1995). In this paper, ALD values of single taxa are given for the cores where species are present with percentages greater than 1%. Furthermore, only species with percentages greater than 1% were included in the calculation of the total ALD per core (that is, the ALD of the complete live fauna at one core).

In order to allow comparison between MD and ALD, cumulative values were plotted at the mid-point of the sediment interval (e.g. 0.5 cm = 0-1 cm). This is different from Licari et al. (2003), where the lower boundary of the sediment interval was taken as indicative of the whole sampling interval (i.e., 1 cm = 0-1 cm). Consequently, MD values estimated for this study are different from those presented for six stations in Licari et al. (2003).

3.4.5. Correlation to environmental parameters at the seafloor and within the sediment

To decipher the relationships between environmental parameters and the occurrence and vertical distribution of benthic foraminifera, we compiled data of *in situ* and laboratory measurements of bottom water and porewater oxygen content (Schulz et al., 1992; Hensen et al., 2000; Wenzhöfer and Glud, 2002; Hensen, pers.com., 2002; Licari et al., 2003), and data of sedimentary carbonate and total organic carbon (TOC) content (Balsam and McCoy, 1987; Timm, 1992; Archer, 1996; Lochte et al., 2000; Mollenhauer et al., 2002, 2004; Wagner et al., 2004). Estimated organic carbon flux rates to the sea floor were calculated on the basis of primary productivity estimates interpolated from recent satellite-based chlorophyll distribution maps (available at http://marine.rutgers.edu/opp/) and the equation of Berger (1989) given for water depths greater than 1000 m.

Stepwise multiple regression with a 95%-confidence limit was carried out to correlate foraminiferal total standing stocks, MD, ALD, and the relative abundance of principal single species to available environmental data. Simple linear regression analysis was subsequently performed to correlate foraminiferal data and each of the environmental variable that were identified as significant contributors to the multiple regression.

3.5. Results

3.5.1. Foraminiferal total standing stocks, MD, ALD, and diversity indices

Foraminiferal total standing stock patterns over latitude match well with the main productivity provinces (Licari and Mackensen, 2005; Figure 3). Standing stocks increase from low values (between 51 and 480 individuals per 50 cm^2) in the Gulf of Guinea and the northern Angola Basin to highest values (up to 1645 individuals per cm^2) in the southern Angola Basin, and then progressively decrease towards the south, where standing stocks are of the same order of magnitude as in the northern province (between 247 and 478 individuals per 50 cm^2). Lowest values are found in the vicinity of the Congo River mouth at about 5°S (GeoB4913, 51 individuals per 50 cm^2) and in the deep northernmost station (GeoB4901, 67 individuals per 50 cm^2).

Within the sediment, foraminiferal total standing stocks decrease more or less rapidly with increasing depth. Three main types of vertical distribution were identified for the total fauna, represented in Figure 4 for selected stations. Type (1) is characterized by a rapid exponential decrease of standing stock values from the surface down to deeper sediment layers, parallel to the decrease of dissolved oxygen. Type (2) exhibits one or two distinct subsurface peaks in dysoxic to anoxic sediments (according to Tyson and Pearson's nomenclature, 1991), following a surface minimum. Finally, type (3) displays maximum density within the top few centimeters of sediment, in oxic to anoxic sediments.

The latitudinal variation of the total ALD (Figure 3) shows some similarities with that of total standing stocks. From the northern area to the mid-Angola Basin at about 13°S, the ALD generally exhibits a gradual increase, varying from 1.1 to 1.7 cm. Between 15 and 19°S, it abruptly increases to values up to 2.6 cm, reflecting the burial of the fauna within the sediment, and then progressively decreases again to the south. Values encountered at both the northern and southern extremities of the transect are of the same order of magnitude, varying around 1.4 cm. Average Living Depth and MD change rather similarly over latitude (Figure 3), the highest MD values are found where ALD values are maximal. It should be noted that the amplitude of variations of the MD corresponds to a scale of several centimeters, while ALD values vary by about 1 centimeter around a central value.

In the area north of 20°S, we could not identify any clear trend in species number and diversity, as expressed by S and H(S), respectively (Figure 5). Diversity is generally higher than average, but fluctuates strongly. South of this latitude, diversity fluctuations are reduced. Generally low diversities characterize the northern Benguela region, while the southern Benguela region displays higher than average diversities. On the contrary, equitability allows to separate the study area in clearly distinct provinces. Higher than average equitabilities are found in the northern province and the southern Benguela region, while the Angola Basin and the northern Benguela region are characterized by lower than average equitabilities.

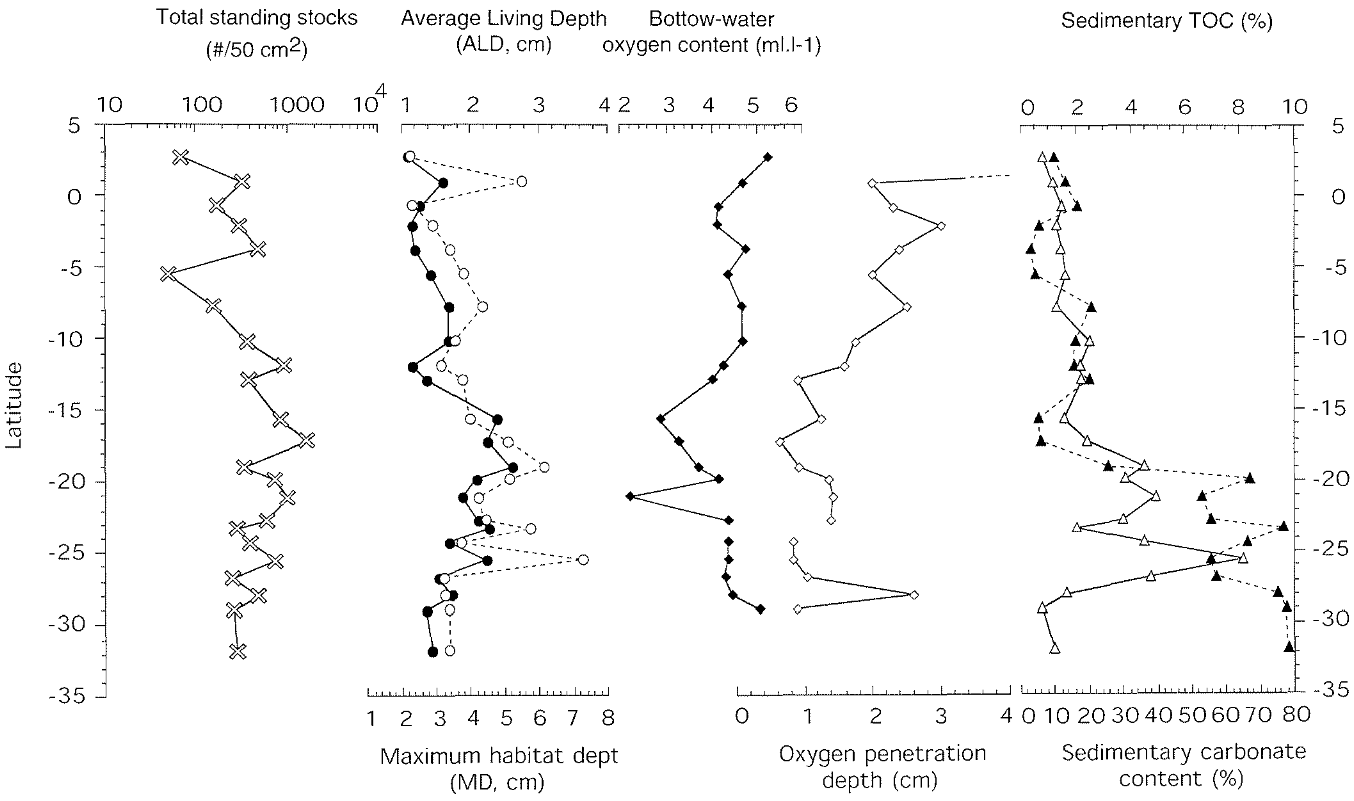

Figure 3. Distribution of foraminiferal total standing stocks (crosses), total ALD (filled circles) and MD (open circles), bottom-water oxygen content (filled diamonds), oxygen penetration depth within the sediment (open diamonds), TOC (open triangles) and carbonate content (filled triangles) of the sediment versus latitude. Shaded areas approximately mark the geographic extent of the different primary productivity and upwelling provinces.

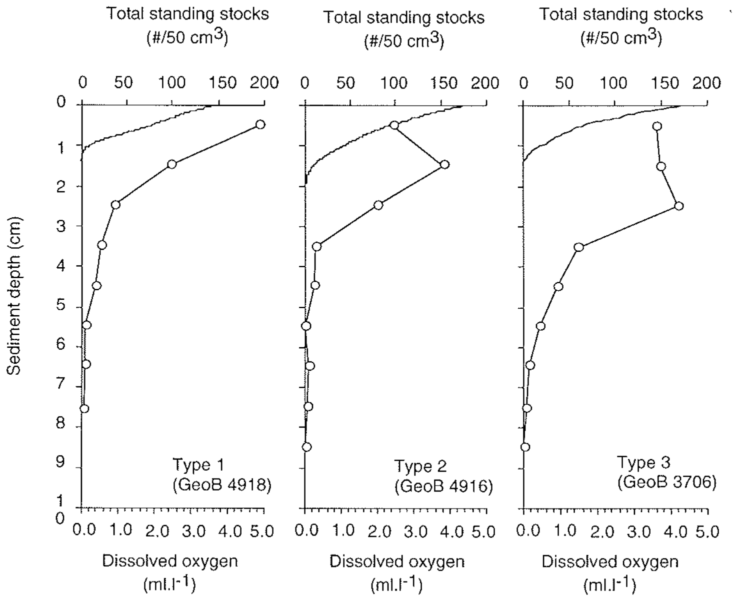

Figure 4. Typical examples of the principal types of vertical profiles of total standing stocks (open circles). Oxygen profiles are plotted for comparison.

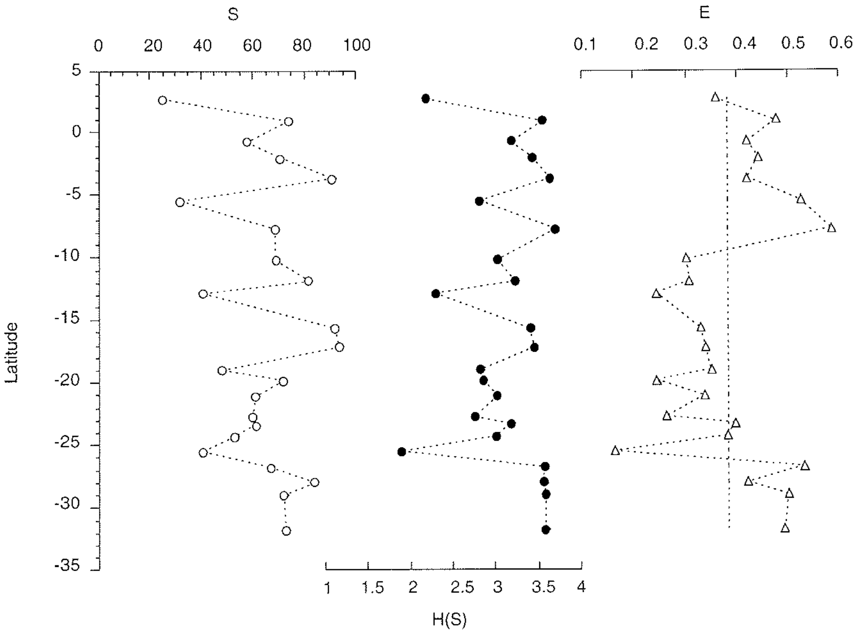

Figure 5. Distribution of species number S, diversity H(S), and equitability E of the total fauna versus latitude (vertical hatched lines indicate average values).

3.5.2. Foraminiferal statistical assemblages

We identified eight foraminiferal assemblages by means of PCA. These explain 64.3% of the total variance of the foraminiferal data set and are named hereafter according to their most important constituent species. All dominant and important associated species, as indicated by statistically significant PC-scores, are summarized in Table 2. The distribution patterns of these assemblages (as expressed by squared PC-loadings) are plotted in Figure 6 versus depth and latitude, and briefly described below. For convenience, the assemblages are ranged according to the distribution of species within the sediment, and to their geographical appearance.

Table 2. Species composition of foraminiferal assemblages (as expressed by PC-scores). Principal component number, dominant species (as indicated by highest PC-scores), important associated species (i.e., with scores greater than one-fifth of the score of the most dominant species), % of the total variance explained by each factor, and total variance are given.

	Dominant species	Score	Associated species	Score	Var.(%)
PC1	*Globobulimina affinis*	12.4			12.7
PC2	*Bulimina mexicana*	10.3	*Valvulineria laevigata*	3.1	11.5
			Reophax bilocularis	3.1	
			Uvigerina auberiana	2.8	
PC3	*Reophax scorpirus*	7.1	*Reophax bilocularis*	5.1	7.2
			Robertinoides chapmani	4.2	
			Lagenammina difflugiformis	4.2	
			Uvigerina peregrina	3.6	
			Gavelinopsis translucens	2.6	
			Hoeglundina elegans	1.8	
PC4	*Cibicidoides pachyderma*	10.6	*Gavelinopsis translucens*	2.5	7.2
			Sphaeroidina bulloides	2.1	
PC5	*Melonis barleeanum*	11.4			6.9
PC6	*Ammoscalaria* sp	9.1	*Cribrostomoides jeffreysi*	7.5	4.8
PC7	*Chilostomella oolina*	10.5	*Reophax bilocularis*	3.8	5.5
			Nouria harrisii	3.1	
			Deuterammina montagui	2.1	
PC8	*Fursenkoina mexicana*	11.8			8.4
				Total var. (%)	64.3

The *Reophax scorpiurus* assemblage (PC3, 7.2% of the total variance) is the most diverse assemblage and typically occurs between 3°N and 4°S (stations GeoB4901, GeoB4904, GeoB4906, GeoB4909, GeoB4912), from the sediment surface down to 3 cm depth. Associated species for this assemblage are, by order of importance, *Reophax bilocularis*, *Robertinoides chapmani*, *Lagenammina difflugiformis*, *Uvigerina peregrina*, *Gavelinopsis translucens*, and *Hoeglundina elegans*.

The *Bulimina mexicana* assemblage (PC2, 11.5% of the total variance) is strongly dominated by this species, associated with *Valvulineria laevigata*, *Reophax bilocularis*, and *Uvigerina auberiana*. This assemblage especially inhabits sediments between 10°S and 19°S (stations GeoB4916, GeoB4917,

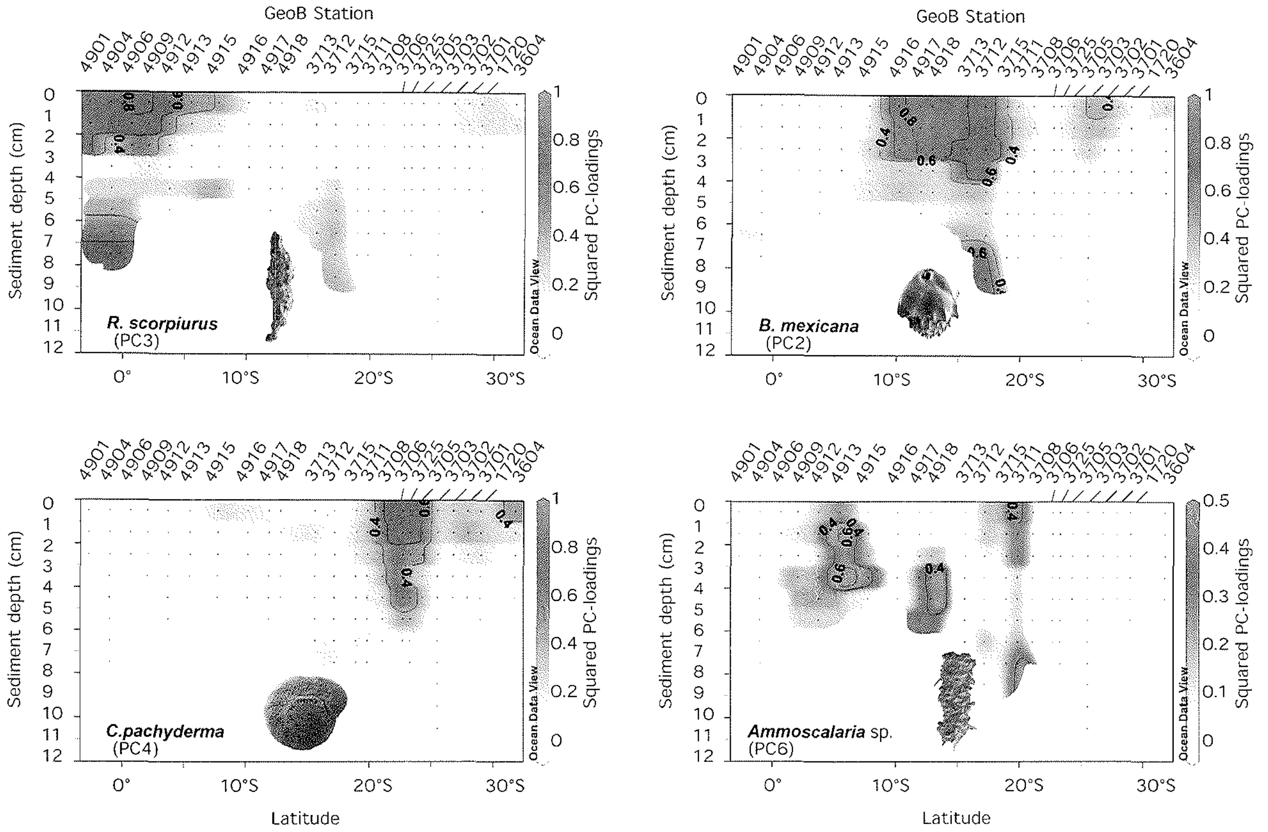

Figure 6. Distribution of benthic foraminiferal assemblages versus sediment depth and latitude, as expressed by squared PC-loadings (plotted using Ocean Data View software, Schlitzer, 2002). Foraminiferal assemblages are named according to their most important constituents.

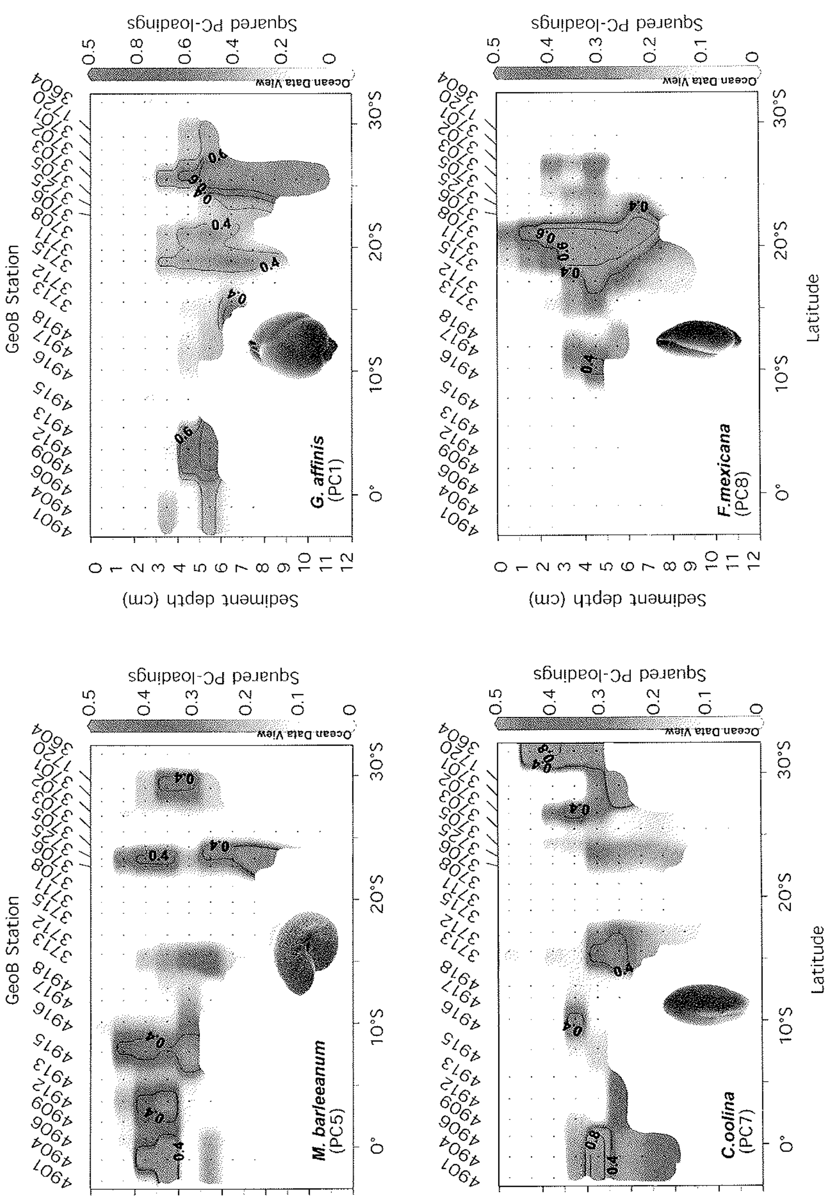

Figure 6 (continued)

GeoB4918, GeoB3713, GeoB3712, GeoB3715), from the topmost sediment down to 4 cm depth.

The *Cibicidoides pachyderma* assemblage (PC4, 7.2% of the total variance) is particularly dominant between 21° and 24°S (stations GeoB3708, GeoB3706, GeoB3725, GeoB3705), from the topmost sediment down to 5 cm depth. Further species belonging to this assemblage are *G. translucens* and *Sphaeroidina bulloides*. Reoccurrences of this assemblage are observed at the sediment surface in the southern part of the area (GeoB3701 and GeoB3604).

The *Ammoscalaria* sp. assemblage (PC6, 4.8% of the total variance), occurs at stations GeoB4913, GeoB4918, and GeoB3711, at various depths within the sediment. This assemblage is further characterized by the agglutinated species *Cribrostomoides jeffreysi.*

The *Melonis barleeanum* assemblage (PC5, 6.9% of the total variance), exclusively dominated by this species, characterizes subsurface and deeper sediments (between 2 and 5 cm) at stations GeoB4904, GeoB4912, and GeoB4915. This assemblage is especially dominant at station GeoB3725, where it occurs down to 8 cm depth within the sediment.

The *Globobulimina affinis* assemblage (PC1, 12.7% of the total variance) is exclusively dominated by this species. This assemblage characterizes stations GeoB4912, GeoB3715, GeoB3708, and especially GeoB3703, where it repeatedly occurs in sediments deeper than 4 cm depth (down to 11 cm sediment depth).

The *Chilostomella oolina* assemblage (PC7, 5.5% of the total variance) is present at stations GeoB4916 and GeoB3713, but shows strongest occurences at station GeoB4904, GeoB3702, GeoB1720, and especially GeoB3604. It typically occurs between 2 and 5 cm depth within the sediment. The agglutinated species *R. bilocularis*, *Nouria harrisi*, and *Deuterammina montagui* further characterize this assemblage.

Fursenkoina mexicana is the only statistically significant species of the PC8-assemblage (8.4% of the total variance). This assemblage is particularly dominant in deep sediments (from 2 cm down to 7 cm depth) between 18°S and 22°S (stations GeoB3715, GeoB3711, GeoB3708).

3.5.3. Correlation to environmental parameters

Environmental conditions at the seafloor and within the sediment

Oxygen and sedimentary data are given in Table 1 (along with the original sources) and plotted in Figure 3 versus latitude. Bottom- and porewater oxygen data were available at twenty-one stations. The oxygen concentration of the overlaying bottom-waters ranges from 2.2 to 5.2 ml l^{-1}. Lowest values are documented between 15°S and 21°S, at stations GeoB3713, GeoB3712, and especially GeoB3708, whereas both the northernmost and southernmost parts of the transect display oxygen concentration of 4 ml l^{-1} or higher. Within the sediment, there is a rapid consumption of dissolved oxygen, usually in the first centimeters below the sediment-water interface. The oxygen penetration depth generally ranges between less than 1 cm and 2.5 cm, except at station GeoB4901. By opposition to the oxygen content of bottom waters, there is a clear decrease of the oxygen penetration within the sediment with increasing latitude. Shallowest zero levels of oxygen within the sediment are documented at stations GeoB3712, GeoB3715, GeoB3705, GeoB3703, and GeoB1720.

Low carbonate values characterize the area north of Walvis Ridge, at about 19°S, while south of this latitude, carbonate content reaches almost 80%. The distribution of TOC content over latitude matches well the different productive systems (Figure 3). Lowest TOC values (0.8% or less) are documented in the area of seasonal coastal upwelling in the Gulf of Guinea and the northern Angola Basin. Total organic carbon values increase then from the southern Angola Basin to the northern Benguela, where they reach maximum values (up to 8%) close to the Lüderitz upwelling cell at about 25°S, and decrease again further south.

Correlation coefficients

Correlation coefficients from the multiple (R) and simple linear (r) regression analysis are given in Table 3. As shown from multiple regression coefficients ranging from 0.6 to 0.8, there is a rather clear influence of the combination of selected environmental variables on the faunal parameters calculated for the complete fauna (total standing stocks, H(S), E, ALD, and MD) (Table 3a). While a clear negative dependence of total standing stocks on the oxygenation at the seafloor is indicated by a negative correlation to the bottom water oxygen content (r=-0.64), ALD and MD positively correlate with food availability, as expressed by the estimated organic carbon flux to the seafloor and the TOC content, respectively. On the contrary, diversity and equitability negatively correlate with the TOC content (r=-0.51 and r=-0.48, respectively).

When considering ALD values of most dominant single species, significant multiple regression coefficients are obtained for a few species only (Table 3b). Multiple R values greater than 0.8 are found for *G. affinis* and *U. auberiana*. While the combined influence of oxygen penetration depth and especially TOC content (r=0.54) is documented for *G. affinis*, *Uvigerina auberiana* correlates well (r=0.82) with the estimated organic carbon flux to the seafloor. Furthermore, both *B. mexicana* and *R. bilocularis* exhibit fair negative correlations with the oxygenation at the seafloor (r=-0.62 and r=-0.66, respectively).

A significant control of the selected environmental variables on foraminiferal relative abundances is documented for more species by multiple regression coefficients >0.6 (Table 3c). *Reophax scorpiurus* and *R. chapmani* exhibit highest multiple R values (>0.9). More specifically, a relation to the availability of oxygen is indicated for *R. scorpiurus*, *Fursenkoina mexicana*, and *R. chapmani* by a strong positive correlation to the oxygen penetration depth within the sediment (r=0.94), a negative (r=-0.66) and a weak positive correlation (r=0.46) to the bottom-water oxygen content, respectively. Furthermore, while *R. scorpiurus* correlates negatively to the estimated organic carbon flux to the seafloor (r=-0.62), *F. mexicana* shows a positive correlation to the TOC content (r=0.55). Strongest dependence of foraminiferal relative abundance on food availability is indicated for *G. affinis* (r=0.65) and especially *U. auberiana* (0.74) by a positive correlation to the TOC content.

3.5.4. Foraminiferal $\delta^{13}C$ values

The foraminiferal stable carbon isotopic composition has been determined for twelve distinct species (*Bulimina mexicana, Chilostomella oolina, Cibicides lobatulus, Cibicidoides globulosus, Cibicidoides pachyderma, Fursenkoina mexicana, Globobulimina affinis, Hoeglundina elegans, Melonis barleeanum, Robertinoides chapmani, Uvigerina auberiana*, and *Uvigerina peregrina*) (Mackensen and Licari, 2004; this study). Strong interspecific differences are observed (up to 2.6‰), and the total range of mean $\delta^{13}C$ values of all species

Table 3. Multiple (R) and simple (r) linear regression coefficients between: a) quantitative parameters of the total fauna, b) ALD values, and c) relative abundances of principal single species and environmental variables (for those species showing a significant correlation to environmental variables). Simple linear regression coefficients (r) for those environmental parameters that significantly influence the foraminiferal faunas, as indicated by stepwise multiple regression analysis, are given in the upper part of tables. Multiple regression coefficients (R) of stepwise multiple regression between single foraminiferal parameters and all environmental parameters, and the number of samples (n) included in the analysis are given in the lower part.

a.

	Total st.stocks (#/50cm2)	Total ALD (cm)	Total MD (cm)	S	H(S)	E
Depth						
Latitude		-0.45				
Long		0.22				
Bottom water oxygen	-0.64					
Oxygen penetration depth					-0.23	
Carbonate						
TOC			0.59		-0.51	-0.48
Organic carbon flux		0.51				
R	0.64	0.77	0.59	0.00	0.70	0.48
n	21	23	23		23	23

b.

	ALD (cm) of				
	G. affinis	*B. mexi.*	*L.difflug.*	*R. biloc.*	*U.aube.*
Depth					
Latitude			-0.55	-0.48	
Long	-0.34				
Bottom water oxygen		-0.62		-0.66	
Oxygen penetration dept	-0.27				
Carbonate			0.08		
TOC	0.54				
Organic carbon flux					0.82
R	0.95	0.62	0.74	0.76	0.82
n	11	17	15	17	10

c.

	Relative abundance (%) of									
	C. pachy.	*F.mexi.*	*G.affinis*	*L. difflug.*	*M.barlee.*	*R. scorp.*	*R. chapm.*	*S.bull.*	*U. aube.*	*U. pere.*
Depth							-0.47			
Latitude				0.74	0.12					0.56
Long						-0.74	-0.75			
Bottom water oxygen		-0.66					0.46			
Oxygen penetration depth					-0.01	0.94				
Carbonate	0.43							0.44		
TOC		0.55	0.65					-0.22	0.74	
Organic carbon flux					-0.15	-0.62				
R	0.43	0.74	0.65	0.74	0.77	0.97	0.94	0.58	0.74	0.56
n	23	21	11	23	21	21	21	23	23	23

varies between 0.65‰ and –1.97‰ VPDB (Table 4). Intraspecific fluctuations of mean δ^{13}C values were observed over latitude for most species, as illustrated in the present study for *C. lobatulus* and *C. pachyderma* in Table 5.

Isotopic analysis of the endobentic *Melonis barleeanum* were performed at three stations. Although δ^{13}C values could only be estimated at two or three sediment depth levels due to the lack of sufficient specimens, our data indicate a low downcore variability of the isotopic signal of this species (Table 6).

Table 4. Mean δ^{13}C (‰VPDB) and ALD (cm) values, as well as standard deviations, of the principal foraminiferal species, as averaged for all stations. Bottom water $\delta^{13}C_{DIC}$ values (derived from Mackensen and Licari, 2004, and references therein) are substracted.

	mean δ^{13}C		mean ALD	
	(per mil VPDB)	stdev	(cm)	stdev
B.mexicana	-1.38	0.35	1.51	0.42
C.globulosus	-0.26	0.13	0.81	0.37
C.lobatulus	-0.18	0.18	1.31	0.61
C.oolina	-1.97		2.53	
C.pachyderma	-0.27	0.25	1.53	0.48
F.mexicana	-1.20	0.28	3.46	0.75
G.affinis	-1.56	0.25	4.10	1.33
H.elegans	0.96	0.34	0.74	0.14
M.barleeanum	-1.94	0.32	2.69	0.53
R.chapmani	0.65	0.36	0.79	0.14
U.auberiana	-1.26	0.30	1.37	0.56
U.peregrina	-1.11	0.38	1.04	0.32

Table 5. Mean δ^{13}C (‰VPDB) values and standard deviations of *C. pachyderma* and *C. lobatulus*, as averaged at each station.

GeoB station	*C.pachyderma*	stdev	*C.lobatulus*	stdev
3711-1	-0.01	0.09	0.13	0.14
3708-1	-0.03	0.08	0.00	0.08
3706-3	0.12	0.06	0.26	0.05
3725-1	0.10	0.40	0.14	
3705-2	-0.28	0.13	0.15	
3701-1	0.48	0.01	0.47	0.06
3604-1	0.55	0.09	0.58	0.03

Table 6. Sediment depth (cm), standing stocks (#/50cm^3), and δ^{13}C (‰VPDB) values of *Melonis barleeanum* at three stations.

	GeoB4904-7		GeoB4912-4		GeoB3725-1	
sed. depth (cm)	st. stocks #/50cm^3	δ^{13}C (per mil VPDB)	st. stocks #/50cm^3	δ^{13}C (per mil VPDB)	st. stocks #/50cm^3	δ^{13}C (per mil VPDB)
0.5	0.0		0.0		0.3	
1.5	0.0		4.5	-1.43	10.5	-1.19
2.5	15.3	-1.86	6.7	-1.47	18.2	-1.31
3.5	7.0	-1.75	4.5	-1.31	15.3	-1.19
4.5	0.0		0.3		2.2	
5.5	0.6		0.0		3.8	
6.5	0.0				2.5	
7.5	0.0				2.5	
8.5					0.6	

3.6. Discussion

3.6.1. Main trends of foraminiferal abundance, diversity, and vertical distribution

Benthic foraminiferal abundances are considered to largely reflect food availability in benthic ecosystems, principally connected to organic carbon fluxes to the seafloor, which in turn depend on surface waters primary production (e.g. Herguera and Berger, 1991; Altenbach et al., 1999; Loubere and Fariddudin, 1999a; Van der Zwaan et al., 1999; Kurbjeweit et al., 2000). Total foraminiferal densities found in the present study are in the same range as those reported for a comparable sediment size fraction in bathyal environments from other mesotrophic to eutrophic continental margins (e.g. Mackensen and Douglas, 1989; Rathburn et al., 1996; Jorissen et al., 1998; Rathburn et al., 2001; Fontanier et al., 2002). In such environments, increased rates of biological metabolism frequently lead to more or less strong and durable oxygen depletion at the sediment-water interface and in the sediment. Reported abundances of foraminifera from low-oxygen areas are often high, possibly in relation to the decrease of predation pressure from metazoans, more severely affected by oxygen depletion (Douglas, 1981; Bernhard and Sen Gupta, 1999).

Despite the apparent lack of correlation between standing stocks and sediment TOC contents or estimated organic matter fluxes (Table 3), our results are in good agreement with these considerations. Total standing stocks exhibit a fair negative correlation with bottom-water oxygen content, and their latitudinal distribution matches well the distinct upwelling provinces (Licari and Mackensen, 2005; Figure 3). Lowest densities are documented at the stations from the transect where trophic conditions are most unfavorable, either because of lower organic carbon fluxes, like at deep station GeoB4901, or because of the input of mostly degraded organic matter (GeoB4913) (Licari et al., 2003). Highest densities are recorded at station GeoB3712. Although the bottom water overlaying the sediment at this station is not strongly oxygen-depleted (3.7 ml l^{-1}), like at most stations of the transect, the dissolved oxygen content in porewater (directly influencing organisms living within the sediment like endobenthic foraminifera) sharply decreases.

As for the standing stocks, the diversity of foraminiferal communities, and of the benthic meio- and macrofauna in general, is strongly related to trophic and oxygen conditions (Levin et al., 2001). As summarized by Gooday (2003), diversity exhibits a parabolic relation to food supply. Diversity is expected to be lowest in oligotrophic ecosystems such as the Arctic Ocean (e.g. Wollenburg and Mackensen, 1998b), well oxygenated but limited in food supply, and in eutrophic habitats such as Oxygen Minimum Zones (e.g. Gooday et al., 2000). Highest diversities are reached at intermediate levels between these extremes, that is, in oxic/mesotrophic environments. According to Gooday (2003, and references therein), the diversity is considered to be more related to oxygenation (oxygen depletion eliminating for instance the most oxiphilic species), while the dominance is principally influenced by food availability. As a matter of fact, the combination of high organic matter fluxes and low oxygen conditions in eutrophic environments generally leads to less diverse/highly dominated fauna, characterized by a few dysoxia-tolerant species flourishing in response to an abundant food supply (e.g. Sen Gupta and Machain-Castillo, 1993).

The trends of diversity (as expressed by H(S)) and equitability (E, that is, dominance) (Figure 5), as well as the results from multiple regression analysis (Table 3) found in this study generally confirm these observations. Repeatedly low diversity and high dominance (i.e., low E values) characterize the northern Benguela region, where coastal upwelling is mostly perennial (Shannon, 1985; Shannon and Nelson, 1996). More specifically, lowest H(S) and E values along the transect are found at station GeoB3703, located in the vicinity of the intense upwelling cell of Lüderitz, and characterized by highest sedimentary TOC content (>8%). Although bottom-water overlaying the sediment at this station is well oxygenated (>4 $ml\ l^{-1}$), oxygen penetration depth within the sediment is among the shallowest (Table 1, Figure 3). In the southern Angola Basin, influenced by oceanic upwelling related to the Angola Dome at the time of sampling, foraminiferal faunas are generally more diverse than in the northern Benguela, but similarly high dominated. At the opposite, high diversity/low dominance faunas characterize both the more oligotrophic northern and southern areas of the transect.

In many of the stations investigated in this study, maximum foraminiferal densities occur in the first or the first few centimeters of sediment, indicating the preference of most species for labile organic matter and/or well oxygenated environments. This is in agreement with many other observations in deep-sea sediments, where the vertical distribution of benthic foraminifera is generally characterized by a clear maximum in the topmost interval followed by an exponential downward decrease (e.g. Jorissen, 1999a; Schumacher, 2001; Fontanier et al., 2002, 2003; Heinz and Hemleben, 2003). At several locations, however, vertical profiles of standing stocks exhibit intriguing subsurface density maxima (Mackensen and Licari, 2004; Type 2, Figure 4). At these stations (GeoB4916, GeoB3713, GeoB3712, GeoB3711, GeoB3708, GeoB3705, and GeoB3701), most shallow endobenthic taxa exhibit type 2-distribution patterns, whereas other taxa show a "typical" type 1-distribution. Moreover, since a clear microhabitat stratification exists at these stations and, furthermore, some species (e.g. *R. bilocularis*) repeatedly exhibit type 2-distribution profiles at other stations, we assume that these patterns are not an artifact of a rapid burial event or other disturbance processes.

Rathburn et al. (2000) reported similar observations from foraminiferal faunas associated to methane seeps on the northern Californian margin, and hypothesized that foraminifera might be attracted to subsurface depth by enhanced food supply (such as reducing bacteria), or are influenced by a chemical zone or boundary at this level. In our study, these patterns are especially pronounced at stations GeoB3713 and GeoB3712, in the southern Angola Basin, where the low proportions of the complete fauna living in the uppermost centimeter (7 and 12% respectively, Licari and Mackensen, 2005) explains the high ALD values of the total fauna (Figure 3). These two stations, located north of and in front of the Cunene river mouth, are characterized by moderate oxygen depletion at the sediment-water interface, sharp oxygen gradients in porewater, and extremely low sedimentary carbonate content (about 5%, Table 1). In general, these distribution patterns characterize especially the high-productive southern Angola Basin and northern Benguela region (Figure 7). Therefore, following Rathburn et al. (1996), we think that in the high-productive areas from the eastern South Atlantic, low-oxygen tolerant species avoid hostile conditions at the sediment surface (e.g. enhanced corrosiveness due to high organic matter supply, stronger competition at the well oxygenated water-sediment interface) by residing below the uppermost sediment, and at the same time, take advantage of the enhanced input of organic matter into the sediment.

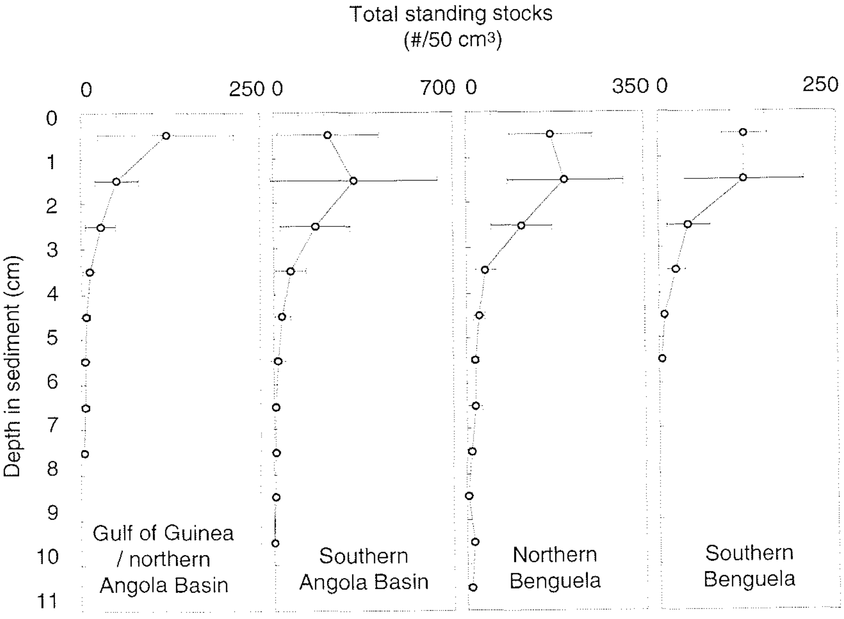

Figure 7. Vertical profiles of foraminiferal total standing stocks (with standard deviation) within the sediment, as averaged for each primary productivity province.

3.6.2. Statistical assemblages and microhabitat occupancy

On the continental margin off West Africa, we recognized four main types of microhabitats, traditionally known from the literature (review in Jorissen, 1999a) and described in detail at six stations by Licari et al. (2003): (1) epibenthic, (2) shallow, (3) intermediate, and (4) deep endobenthic species. As suggested by Jorissen (1999a), we considered the shape of the species vertical profiles within the sediment and the relative position of the species. These preferences are overall well mirrored by the estimated ALD.

It is widely accepted that food and oxygen availability are the main parameters controlling benthic foraminifera vertical distribution patterns within the sediment (e.g. Corliss and Chen, 1988; Mackensen and Douglas, 1989; Barmawidjaja et al., 1992; Jorissen et al., 1992; Rathburn and Corliss, 1994; Alve and Bernhard, 1995). The dependence of the occupancy of microhabitats by foraminifera on the balance between these two parameters has been schematized in a conceptual model (TROX-model, TRophic condition and OXygen concentration) by Jorissen et al. (1995) (see also Van der Zwaan et al., 1999). According to this model, in well-oxygenated but food-limited oligotrophic environments, benthic foraminiferal species are concentrated near the surface, as the scarcity of organic matter available within the sediment prevents the burial of shallow endobenthic species and the development of an important stock of deep endobenthic species. On the contrary, when the supply of food is high, oxygen is rapidly strongly limiting for many species. Therefore, maximum penetration and microhabitat structure are expected in intermediate environments, where both oxygen and food are available well below the sediment/water interface. These predictions are supported by increasing field evidence (e.g. De Stigter et al., 1998; Wollenburg and Mackensen, 1998a; Schmiedl et al., 2000; Schumacher, 2001; Fontanier et al., 2002, 2003; Heinz and

Hemleben, 2003). In the following section, we will discuss the distribution of these faunal assemblages with regard to the microhabitat preference of their main constituents and the availability of food and oxygen within sediment, tightly connected to regionally varying production patterns. Overall, there is good coincidence of our data with the assumptions of the TROX-model.

Epibenthic and shallow endobenthic species assemblages

While PCA allowed for the identification of several distinct groups of shallow, intermediate, and deep endobenthic species (Figure 6), we could not statistically recognize any group of species strictly inhabiting epibenthic microhabitats (that is, preferentially concentrated in the topmost sediment). This is in contrast to the findings of Kurbjeweit et al. (2000) in the Arabian Sea. One of the likely principal reasons for this is the sampling interval (1 cm) we used, inadequate to resolve gradients in the first millimeters of sediment, and necessary to recognize truly epibenthic species. Another reason is the strong dominance, over most of the study area, of species known to prefer a shallow endobenthic microhabitat, which eclipse overall the contribution of strictly epibenthic species to the fauna in surface samples (Schmiedl et al., 1997; Licari et al., 2003; Licari and Mackensen, 2005). Therefore, species showing a preferential affinity to the uppermost sediment are only expected to be found as associated constituent of assemblages otherwise dominated by shallow endobenthic species.

In fact, statistically significant occurrences of epibenthic species such as *H. elegans* are restricted to the *R. scorpiurus* assemblage (PC3) in the Gulf of Guinea and the northern Angola Basin (Table 2, Figure 6), that is, the most oligotrophic province of the transect. Another important species in that area is *Robertinoides chapmani*. According to new data, we believe that this species should be regarded as epibenthic rather than shallow endobenthic, as previously suggested by Licari et al., (2003). Typically low ALD values (generally <1 cm, Table 7) for both species indicate their preference for the uppermost part of the sediment column, in oxic sediments. This agrees with many observations depicting similar vertical distribution patterns for *H. elegans*, and is generally regarded as a strategy to optimize food acquisition in oligotrophic environments, where most of labile organic compounds are concentrated close to the sediment-water interface (e.g. Corliss and Emerson, 1990; Corliss, 1991; Rathburn and Corliss, 1994; Schönfeld, 2001; Fontanier et al., 2002). Extreme epibenthic lifestyles have been reported for several cibicids, preferentially occupying elevated positions above the sediment-water interface, suggesting that these species benefit from suspended food particles from streaming bottom waters (e.g. Lutze and Thiel, 1989; Linke and Lutze, 1993; Schmiedl et al., 2000; Schönfeld, 2002).

It is generally considered that epibenthic species are less tolerant to oxygen-depletion than endobenthic species (Gooday, 1994). Since the overlaying bottom waters and the uppermost sediments are consistently well oxygenated in that part of the study area, we could not investigate the influence of oxygenation on the distribution of *H. elegans* and *R. chapmani*. Previous observations of *H. elegans* in low-oxygen settings (Hermelin and Shimmield, 1990; Kaiho, 1994; Rathburn and Corliss, 1994) indicate, however, that this species might tolerate oxygen concentrations close to 1 ml l^{-1}. A weak correlation between the abundance patterns of *R. chapmani* and the bottom-water oxygen content might indicate higher oxygen requirements for this species.

Table 7. Average Living Depth (ALD) values of principal foraminiferal single species (as estimated from PCA) at all stations (note that stations are listed according to latitude).

	GeoBstation																						
	4901-6	4904-7	4906-5	4909-4	4912-4	4913-4	4915-3	4916-4	4917-5	4918-4	3713-1	3712-1	3715-1	3711-1	3708-1	3706-3	3725-1	3705-2	3703-4	3702-2	3701-1	1720-3	3604-1
Ammoscalaria sp		1.3	1.4	1.7	1.1	2.0				2.3		2.7	1.4	2.2									
Bulimina mexicana		0.7	1.0				0.5	1.5	1.0	1.1	2.0	2.3	1.6	1.7	1.7	2.1	1.0	1.4	1.2	1.2	1.2	0.7	0.6
Chilostomella oolina		4.7	1.8					2.3									4.9		5.4	2.8		5.3	2.5
Cibicidoides pachyderma														2.0	1.7	2.0	1.9	1.4			1.3		0.6
Cribostomoides jeffreysi						2.8	3.2		2.2	2.9		1.8				1.9				1.2			2.7
Fursenkoina mexicana								3.2	3.5		3.1	4.0	3.7	4.2	2.4	5.8	4.2	3.9	4.0	3.1			
Gavelinopsis translucens		0.9	1.3	1.0	0.5	0.5	0.5	0.7	0.8					1.8	0.8	1.5	1.9	1.9	0.8	1.6	1.6		0.6
Globobulimina affinis		4.3		4.0	4.0		2.3		2.7		3.9		4.9		3.9		5.4		5.6	3.3		2.7	2.7
Hoeglundina elegans			0.5	0.7	0.8		0.8															0.8	
Lagenammina difflugiformis	1.1	0.6	1.3	0.8	0.9	1.0	1.5	1.4	1.2	1.3	1.7	2.6			1.4				1.3	1.5			
Melonis barleeanum		2.8	1.8	3.0	2.5		2.8	3.6		2.1	3.2						3.3					3.9	
Nouria harrisii			2.1		3.7						3.3	4.9				4.6		3.4					
Reophax bilocularis	1.0	0.8	1.0	1.0	0.7		0.7	1.2	1.0		2.3	3.0	1.4	2.1		2.4	1.4	1.5	1.3	1.4	1.7		1.2
Reophax scorpiurus	1.2	1.2	1.2	1.4	0.8	0.8	0.5	1.5															
Robertinoides chapmani	0.7	0.9	1.1	0.7	0.8		0.7															0.8	0.6
Sphaeroidina bulloides			0.6		0.7		0.6	1.8	0.9		2.4	2.1			1.0	1.9		1.3		1.1	1.4	0.8	0.8
Uvigerina auberiana		0.6	1.0	0.7					1.6			2.2	1.6	2.1	1.4				1.2	1.4			
Uvigerina peregrina	1.5	0.9	1.2	0.8	0.9	0.5	0.5		0.8		1.5						1.0					0.8	
Valvulineria laevigata							1.5	1.6	1.1	2.5	2.5	2.3			1.6	2.6	2.3	1.8	1.3	1.6			

Reophax scorpiurus and the other important contributors to the fauna can be regarded as mostly inhabiting shallow endobenthic habitats (see also Licari et al., 2003), which concurs with previous observations made on these species in other deep-sea areas (e.g. De Stigter et al., 1998; Schumacher, 2001; Schmiedl et al., 2000; Fontanier et al., 2002). The confining of *R. scorpiurus* to the Gulf of Guinea and northern Angola Basin and the results of the regression analysis emphasize the preference of this species for low food supply/high oxygen conditions, as encountered in the deep station GeoB4901 where its abundance is highest (Licari et al., 2003).

Towards the south, the statistical and actual elimination of epibenthic species from the fauna, and the increased vertical extension of the assemblages within the sediment, confirm the more eutrophic character of the benthic environment. Our data indicate the overall preference of *B. mexicana* (PC2) for a shallow endobenthic habitat, and are in agreement with similar observations concerning this species and other *Bulimina* spp. (e.g. McCorkle et al., 1990; Jorissen et al., 1998; Schmiedl et al., 2000; Schumacher, 2001). While the occurrence of the *B. mexicana*-dominated fauna (PC2) in the southern Angola Basin can be regarded as reflecting enhanced supplies of fresh organic matter shortly before sampling, a *C. pachyderma* fauna (PC4) dominates the northern Benguela region, characterized by regular organic matter fluxes over time (Licari and Mackensen, 2005). The preference of *C. pachyderma* for an endobenthic lifestyle, as depicted in this study, stresses that not all cibicids are strictly epifaunal, and validates laboratory observations from Bornmalm et al. (1997), and field evidence from Rathburn and Corliss (1994), and Wollenburg and Mackensen (1998a).

The faunal changes associated to the increase of food supply over latitude are accompanied by a clear burial of shallow endobenthic species, as expressed by the deepening of species ALD values in the southern Angola Basin and the northern Benguela region (Table 7). At several stations from the most eutrophic provinces, increased ALD mirrors type 2-vertical distributions of shallow endobenthic species. This deepening of foraminifera within the sediment is especially evident when looking at ALD fluctuations of species common along most of the transect, such as *B. mexicana* or *R. bilocularis* (Figure 8). High proportions of a species probably more closely mirror its environmental optimum

(Altenbach et al., 1999). Consequently, to estimate critical oxygen values of *B. mexicana* and *C. pachyderma* (i.e., the range of oxygen concentrations tolerated by these species), we considered, at the stations where they are dominant, the oxygen concentration in porewater at the upper and lower boundaries of the sediment sample where maxima of these species were found.

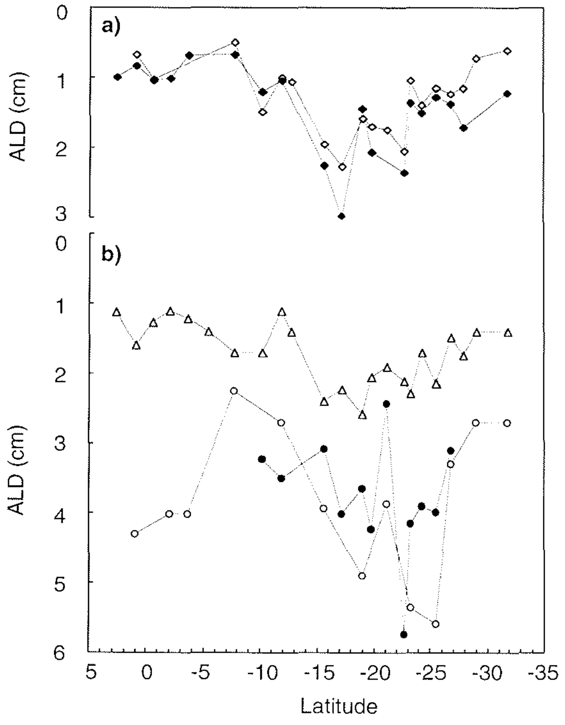

Figure 8. Average Living Depth values of selected a) shallow (filled diamonds *R. bilocularis*, open diamonds *B. mexicana*, and b) deep (filled circles *F. mexicana*, open circles *G. affinis)* endobenthic species versus latitude. The ALD of the total fauna (open triangle) is given for comparison)

As discussed by Licari et al. (2003), the resolution of the sampling interval of the sediment (1 cm) does not allow the precise comparison of foraminiferal vertical distribution patterns with oxygen gradients in porewater, obtained from *in situ* and laboratory microelectrode measurements at a high spatial resolution (order of millimeter). Another factor hindering an accurate comparison is that in most stations, important changes in pore-water oxygen concentration already occur in the first few centimeters of sediment (Table 1). Nevertheless, we think that these observations provide good indication on the environmental conditions tolerated and/or required by foraminiferal species. We found overall a lower oxygen concentration threshold of about 0.4 ml l^{-1} for *B. mexicana* and 0.2 ml l^{-1} for *C. pachyderma,* although both species occasionally exhibit peaks of density in anoxic sediments. Since oxygen measurements were performed in other multiple subcores that those used for the faunal analysis, we can not exclude that the actual porewater gradients in the sediments we investigated are different. Furthermore, as suggested by Bernhard et al. (2003), a mosaic of chemically heterogeneous microhabitats probably exists in both the vertical and horizontal dimensions within sediment. Foraminifera could also acquire oxygen by extending their pseudopodia towards oxygenated sediments (Bernhard and Sen Gupta, 1999). Therefore, we think that most shallow endobenthic species dominant in the southern Angola Basin and in the northern Benguela region tolerate dysoxic to suboxic conditions and, in agreement with several other authors (e.g. McCorkle et al., 1997; Jorissen et al., 1998; Fontanier et al., 2002), that the zero oxygen level limits their maximum penetration depth within the sediment.

Intermediate and deep endobenthic species

Species found deeper in the sediment are generally regarded as indicators of low oxygen/high food availability in benthic ecosystems (e.g. Sen Gupta and Machain-Castillo, 1993; Jorissen, 1999b; De Rijk et al., 2000; Schmiedl et al., 2003). In this study, marked latitudinal differences in the distribution of distinct intermediate and deep endobenthic species, comparable to those described for shallow endobenthic taxa, suggest differential responses to changes in trophic conditions over latitude. With regard to the importance of deep endobenthic species for the interpretation of fossil assemblages, we will focus our discussion on the ecological preferences of calcareous species.

The occurrence of *M. barleeanum* in the Gulf of Guinea, the northern Angola Basin, and on the lower slope off the Benguela coastal upwelling area support evidences that this species might be related to the availability of refractory organic matter (Caralp, 1989b). In the Gulf of Guinea and northern Angola Basin, *M. barleeanum* (PC5) characterizes the sediment layer between 2 and 5 cm. Average Living Depth values ranging from 1.8 to 3.0 cm (Table 7) indicate the preference of this species for the sediment close to or immediately below the depth of zero oxygen, which is in good agreement with similar observations made in other areas (e.g. Corliss and Emerson, 1990; Mackensen et al., 2000; Schumacher, 2001). These results confirm that, as suggested by Jorissen et al. (1998) and corroborated by observations of Fontanier et al. (2002) and Licari et al. (2003), this species might actively seek bacterial consortia involved in the degradation of organic compounds at the base of the oxic sediment layer. At station GeoB3725, where highest densities of *M. barleeanum* along the transect are recorded, this species flourishes principally over a broad sediment interval centered around 3 cm, but exhibits significant occurrences as deep as 7 cm within the sediment. The absence of oxygen measurements unfortunately hinders the investigation of whether the positioning of *M. barleeanum* with regard to redox boundaries at this site is consistent. In agreement with Caralp (1989b), we believe that the important stock of *M. barleeanum* at this station from the lower slope reflects increased supplies of degraded organic matter from marine origin in comparison to the Gulf of Guinea and the northern Angola Basin. This species disappears at the adjacent shallowest stations from the northern Benguela area, more directly influenced by the coastal upwelling system and its filamentous mixing area. These observations are consistent with previous observations in the same area from Schmiedl et al. (1997).

Globobulimina affinis (PC1), *C. oolina* (PC7), and *F. mexicana* (PC8) consistently exhibit downcore maxima below the zero oxygen level, as indicated by ALD values generally ranging from 2 to 5 cm and deeper (Table 7, Figure 8). Similar observations in deep endobenthic microhabitats have been repeatedly reported, providing evidence that these species might permanently occupy anoxic sediment (e.g. Kitazato, 1994; Jannink et al., 1998; De Stigter et al., 1998; Schumacher, 2001; Schönfeld, 2001) and probably are facultative anaerobes (Bernhard, 1993, 1996). Therefore, the availability of food stored in the sediment, rather than oxygen, is probably the main agent controlling these taxa (e.g. Jorissen et al., 1998; Van der Zwaan et al., 1999; De Rijk et al., 1999, 2000). Like for *M.*

barleeanum, *C. oolina*, *F. mexicana*, and *G. affinis* may be associated to specific bacterial consortia involved in the degradation of the refractory organic matter within the sediment (Fontanier et al., submitted), and either directly feed on bacterial biomass or on their breakdown products (e.g. Bernhard and Reimers, 1991), or live in symbiosis with these organisms (Bernhard, 2003). In this study, *G. affinis* and *F. mexicana* occur preferentially in the northern Benguela region, whereas *C. oolina* principally dominates in the southern Benguela and in the Gulf of Guinea and northern Angola Basin, suggesting different trophic requirements. The good correlation between the ALD and the abundance of *G. affinis*, and the abundance of *F. mexicana* with sedimentary TOC content suggests that these species might be more dependent on high availability of buried organic material in the sediment, and in turn increased bacterial activity, than *C. oolina* (Table 3). We interpret the clear burial of *G. affinis* and *F. mexicana* in the northern Benguela region, as indicated by the downward broadening of the sediment depth interval where these species are statistically represented (Figure 6) and increased ALD values (Table 7, Figure 8), as reflecting the higher introduction of organic matter into the sediment. In our opinion, the statistical near-absence of these species in the southern Angola Basin is linked to their longer time-response to the deposition of fresh phytodetritus than more opportunistic taxa, such as *B. mexicana* (Ohga and Kitazato, 1997; Kitazato et al., 2000; Fontanier et al., 2003).

3.6.3. Implication of foraminiferal microhabitats for paleoreconstructions

Deep endobenthic species and estimates of bottom-water oxygen content

The knowledge of the ecological preferences of benthic foraminiferal species, applied to the interpretation of fossil assemblages, provides a powerful tool to recognize past changes of trophic and oxygen conditions (e.g. Thomas et al., 1995; Schmiedl and Mackensen, 1997; Den Dulk et al., 1998; Jorissen, 1999b; Loubere and Fariddudin, 1999b; Wollenburg et al., 2001; Schmiedl et al., 2003). Based on the good correlation of bottom water oxygen content and the relative abundance of "oxic", "dysoxic", and "suboxic" taxa, Kaiho (1994) developed a proxy for bottom-water oxygenation (Benthic Foraminiferal Oxygen Index, BFOI). While our data do confirm the preference of endobenthic species (belonging to Kaiho's "dysoxic" group) for sediments characterized by strongly oxygen-depleted *porewater,* strong abundances of these species are not indicative of low oxygen in *bottom water.* At stations GeoB3715 and GeoB3703, for example, where *G. affinis* accounts for about 20% of the total live fauna, oxygen gradients in porewater are steep, but overlaying waters exhibit oxygen concentrations close to 4 ml l^{-1}. Similar observations in other well-oxygenated environments (e.g. McCorkle et al., 1997; Jorissen et al., 1998; Schmiedl et al., 2000; Gooday et al., 2001; Fontanier et al., 2002) confirm the problematic aspect of the BFOI approach (see also Gooday, 2003). According to these observations, high abundances of deep endobenthic species in such environments should therefore be interpreted as indicating increased food supply.

Microhabitat and stable isotopic composition

The stable isotopic signal recorded in benthic foraminiferal calcareous tests is an essential tool in paleoceanography, as it may represent a direct record of porewater and bottom water conditions. In particular, the stable carbon isotopic composition of benthic foraminifera is extensively used as a proxy to reconstruct past changes of bottom water circulation and downward organic carbon fluxes (e.g. Duplessy et al., 1984; Curry et al., 1988; Sarnthein et al., 1994; Bickert and Wefer, 1996; Mackensen et al., 2001; Bickert and Mackensen, 2003). As for the proper interpretation of fossil assemblages, the reliability of these investigations closely depends on the accurate knowledge of the behavior of the species (i.e. specific isotopic record) with regard to a given environmental variable (i.e. isotopic composition of the surrounding bottom- or porewater, depending on the species microhabitat). In the following section, we briefly examine, with respect to species-specific microhabitat preferences, the data published by Mackensen and Licari (2004) in the view of new stable isotope data from six additional stations.

As a result of the decay of isotopically light organic matter in the sediment, sharp $\delta^{13}C$ gradients are found in the porewater, which becomes enriched in ^{12}C with increasing depth (McCorkle et al., 1985). While epibenthic species such as *Fontbotia wuellerstorfi* are considered to faithfully mirror the $\delta^{13}C$ of bottom-water dissolved inorganic carbon (DIC), the isotopic composition of shallow and endobenthic species is influenced by that of the porewater (e.g. McCorkle et al., 1997; Rathburn et al., 1996; Mackensen et al., 2000). In agreement with these considerations, and similarly to the results reported by Schmiedl et al. (2004), there generally is a clear decrease of the mean $\delta^{13}C$ of the principal epibenthic and endobentic species investigated in this study with increasing ALD (Figure 9), reflecting a dominant microhabitat signal. Contrasting with the results of McCorkle et al. (1997) and Schmiedl et al. (2004), however, our results indicate a rather small offset between the $\delta^{13}C$ values of the shallow endobenthic species and the endobenthic species *G. affinis,* and in particular *F. mexicana.* Strongest enrichments in ^{12}C are recorded for *C.oolina* and *M. barleeanum.* Strongly positive values, as recorded for both *H. elegans* and *R. chapmani*, are characteristic for aragonitic species (Grossman, 1987; McCorkle et al., 1997; Corliss et al., 2002).

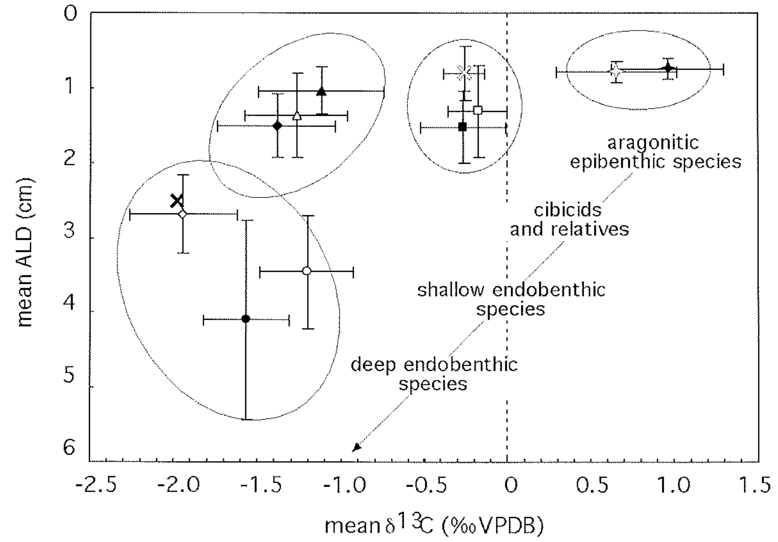

Figure 9. Mean $\delta^{13}C$ (‰VPDB) values of *B. mexicana* (filled diamond), *C. globulosus* (open cross), C. *lobatulus* (open square), *C. pachyderma* (filled square), *C. oolina* (filled cross), *F. mexicana* (open circle), *G. affinis* (filled circle), *H. elegans* (filled star), *M. barleeanum* (open diamond), *U. auberiana* (open triangle), *U. peregrina* (filled triangle), and *R. chapmani* (filled star) versus mean ALD (cm). Bottom water $\delta^{13}C_{DIC}$ values (after Mackensen and Licari, 2004, and references therein) are substracted.

Large standard deviations indicate strong intraspecific fluctuations between sites of the isotopic signal displayed by epibenthic and endobenthic species (about 1‰ or greater), probably reflecting the influence of the saturation state of surrounding waters in carbonate-ion and of the organic carbon decomposition rate (Mackensen and Licari, 2004).

The shift in the mean $\delta^{13}C$ record of *C. pachyderma* and *C. lobatulus* from negative values in the northern Benguela area towards values close to a 1:1 relationship with bottom water in the southern Benguela is noteworthy (Figure 10).

Although at station GeoB3701, the ALD is not significantly shallower than at the stations from the northern Benguela (Table 5), we think that these changes mirror the migration within sediment of both species from a shallow endobenthic microhabitat towards the sediment-water interface, to compensate lower food supply in the southern region. Although further data are needed, our results strongly suggest that these species may either record the bottom water or porewater isotopic $\delta^{13}C_{DIC}$ signal.

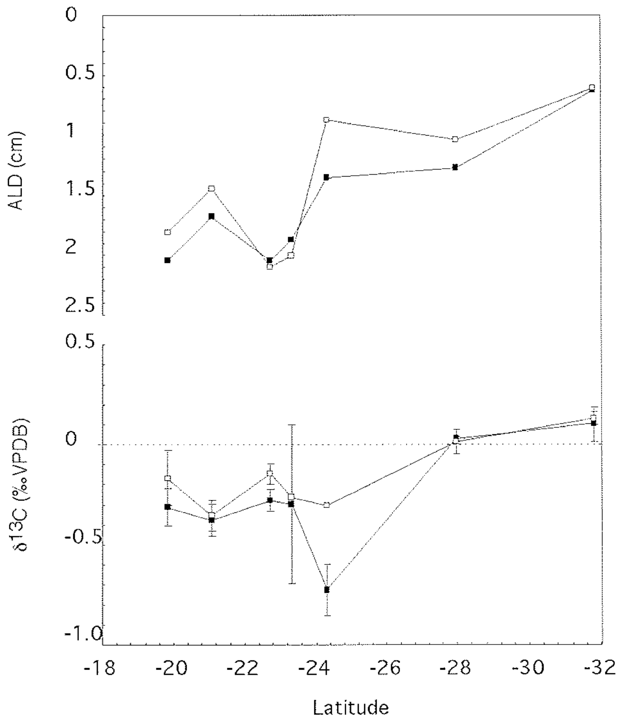

Figure 10. Average Living Depth (cm) and mean $\delta^{13}C$ (‰VPDB) values of *C. pachyderma* (filled squares) and *C. lobatulus* (open squares) versus latitude, and standard deviation. Bottom water $\delta^{13}C_{DIC}$ values at each station (after Mackensen and Licari, 2004, and references therein) are substracted.

As for the variability of the $\delta^{13}C$ signal of benthic foraminifera according to their distribution within the sediment, there is increasing evidence that, at a given site, all specimens of a given species exhibit consistent $\delta^{13}C$ signal (Rathburn et al., 1996; McCorkle et al., 1997; Mackensen et al., 2000; Tachikawa and Elderfield, 2002;

Schmiedl et al., 2004). This is important for paleoceanographers, since it implies that fossil benthic foraminiferal $\delta^{13}C$ values represent one signal at one particular time at one particular site. Furthermore, in an ecological context, this provides indications on the species-specific calcification depths within the sediment (McCorkle et al., 1997; Tachikawa and Elderfield, 2002). Contrasting with these results, Mackensen et al. (2000) found a consistent decrease of *M. barleeanum* $\delta^{13}C$ with increasing depth within the sediment, indicating that this species might prefer a static way of life and calcify at fix depths within the sediment. This does not seem to be the case in the eastern South Atlantic, as indicated by consistent $\delta^{13}C$ values throughout the sediment (Figure 11).

These results indicate the need for further isotopic investigations on live foraminifera for a better understanding of the relationship between $\delta^{13}C$ values of foraminiferal species, and their specific microhabitat preference and environments.

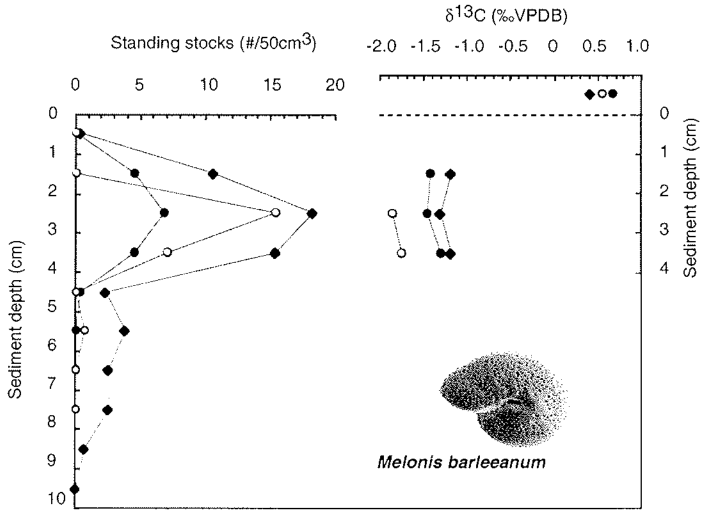

Figure 11. Vertical distribution of standing stocks (#/50cm^3) and $\delta^{13}C$ (‰VPDB) values of *M. barleeanum* at three stations (open circles: GeoB4904; filled circles: GeoB4912; filled diamonds: GeoB3725). The bottom water $\delta^{13}C_{DIC}$ values (after Mackensen and Licari, 2004, and references therein) are indicated (plotted above the sediment-water horizon).

3.7. Conclusion

Significant changes in foraminiferal abundances, diversity, and vertical partinion within the sediment at single sites and between sites between 3°N and 32°S on the continental slope off West Africa, can be interpreted as depending on distinct ecological preferences of foraminiferal species with regard to food and oxygen availability.

In general agreement with the conceptual model of Jorissen et al. (1995), our data indicate that in the more oligotrophic Gulf of Guinea and the northern Angola Basin, foraminiferal species compensate low food supply by moving towards the sediment-water interface, where the organic matter is concentrated. With increasing food supplies towards the south, the contribution of species such as *H. elegans* and *R. chapmani* to the fauna decreases, whereas that of low-oxygenation tolerant shallow and deep endobenthic species increases, accompanied by a significant burial of these species within the sediment. While the opportunistic *B. mexicana* dominates the shallow endobenthic niche in the southern Angola Basin, influenced by seasonal oceanic upwelling at the time of sampling, this species is replaced by *C. pachyderma* in the northern Benguela subsystem, influenced by semi-permanent upwelling. There, the occupation of the deep, anoxic sediments by *F. mexicana* and *G. affinis* is highest. Towards the southern Benguela region, we interpret the decreased participation of these deep endobenthic species to the fauna and their replacement by *C. oolina,* as well as the overall shallowing of all foraminiferal species in the sediment, as linked to the return to lower food availability.

Significant occurrences of deep endobenthic species at sites overlaid by well-oxygenated bottom waters indicate that estimates of past oxygen conditions at the seafloor based on the Benthic Foraminiferal Oxygen Index might be strongly biased, and underestimate actual conditions of past deep-sea ventilation.

Benthic foraminiferal $\delta^{13}C$ values are overall consistent with species-specific microhabitat preferences. Strongest enrichments in ^{12}C are found for shallow and deep endobenthic species, indicating the strong influence of the porewater $\delta^{13}C$ gradient on the isotopic signature of these species. Our results indicate that *C. pachyderma* and *C. lobatulus*, which occupy different microhabitats at different sites in response to changes in food availability, either mirror bottom or porewater $\delta^{13}C_{DIC}$ values, which might complicate the interpretation of the fossil isotopic signature.

3.8. Acknowledgements

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Appendix A. Taxonomic appendix.

All dominant and associated species from the assemblages described in this study are listed. Scanning Electron Microscope (SEM) pictures of selected dominant species and associated species are represented in Plates I and II. We followed taxonomical concepts of Loeblich and Tappan (1988), Mackensen et al. (1990, 1993), Jones (1996), and Schmiedl et al. (1997).

Order FORAMINIFERIDA Eichwald 1830

Suborder TEXTULARIINA Delage & Hérouard 1896

Ammoscalaria sp.
Cribrostomoides jeffreysi (Williamson 1858)
Deuterammina montagui Brönimann & Whittaker 1988
Lagenammina difflugiformis (Brady 1879)
Nouria harrisii Heron-Allen & Earland 1914
Reophax bilocularis Flint 1899
Reophax scorpiurus de Montfort 1808

Suborder ROBERTININA Loeblich & Tappan 1984

Hoeglundina elegans (d'Orbigny 1826)
Robertinoides chapmani (Heron-Allen & Earland 1922)

Suborder ROTALIINA Delage & Hérouard 1896

Bulimina mexicana (Cushman 1922)
Chilostomella oolina Schwager 1878
Cibicidoides globulosus (Chapman & Parr 1937)
Cibicidoides pachyderma (Rzehak 1886)
Fursenkoina mexicana (Cushman 1922)
Gavelinopsis translucens (Phleger & Parker 1951)
Globobulimina affinis (d'Orbigny 1839)
Melonis barleeanum (Williamson 1858)
Sphaeroidina bulloides Deshayes 1832
Uvigerina auberiana d'Orbigny 1839
Uvigerina peregrina Cushman 1923
Valvulineria laevigata Phleger & Parker 1951

Appendix B.

Table B1. Varimax PC-loadings of the foraminiferal assemblages.

GeoB station	depth (cm)	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	Communality
4901-6	0-1	0.01	-0.04	0.75	-0.05	0.01	-0.07	-0.03	0.00	0.6
	1-2	0.00	-0.04	0.70	-0.07	-0.01	-0.09	0.02	0.02	0.5
	2-3	-0.01	-0.02	0.77	-0.07	0.02	-0.07	0.04	0.01	0.6
4904-7	0-1	0.03	0.19	0.59	0.11	-0.01	0.07	-0.14	-0.04	0.4
	1-2	0.00	0.00	0.63	0.06	0.03	0.07	-0.12	-0.03	0.4
	2-3	-0.07	-0.04	0.13	-0.06	0.78	0.04	-0.04	0.01	0.6
	3-4	0.38	0.01	0.02	-0.03	0.79	-0.01	0.25	0.01	0.8
	4-5	0.11	0.09	0.23	0.06	0.04	-0.02	0.89	0.03	0.9
	5-6	0.44	0.03	0.38	-0.10	0.25	0.05	0.24	-0.02	0.5
	6-7	0.16	0.22	0.50	-0.07	0.04	0.03	0.25	0.01	0.4
	7-8	-0.03	0.08	0.70	-0.03	0.00	-0.09	0.40	0.04	0.7
4906-5	0-1	0.01	0.16	0.89	0.04	0.04	0.01	-0.02	-0.02	0.8
	1-2	-0.01	0.16	0.84	-0.02	0.19	0.12	0.11	0.03	0.8
	2-3	-0.02	-0.05	0.61	0.01	0.18	0.07	0.15	0.04	0.4
4909-4	0-1	-0.01	0.13	0.85	0.06	-0.01	0.06	0.02	0.01	0.7
	1-2	-0.03	0.14	0.86	0.06	0.01	0.14	0.10	0.05	0.8
	2-3	-0.07	0.01	0.65	-0.02	0.29	0.11	0.09	0.06	0.5
	3-4	-0.03	-0.05	0.20	-0.05	0.27	0.26	0.23	0.05	0.2
4912-4	0-1	0.03	0.00	0.72	0.05	0.04	0.19	-0.12	0.00	0.6
	1-2	-0.02	0.01	0.42	-0.01	0.37	0.13	-0.11	-0.01	0.3
	2-3	0.12	-0.01	0.12	-0.04	0.66	0.02	-0.06	0.00	0.5
	3-4	0.38	0.00	0.13	-0.03	0.77	0.07	-0.03	-0.03	0.8
	4-5	0.73	-0.01	0.23	0.05	0.10	0.25	0.05	0.07	0.7
	5-6	0.85	-0.02	-0.03	0.05	0.08	0.16	0.39	-0.03	0.9
4913-4	0-1	0.01	-0.05	0.35	0.00	0.00	0.35	-0.13	-0.01	0.3
	1-2	-0.01	-0.01	0.17	-0.08	-0.02	0.87	-0.01	0.08	0.8
	2-3	0.01	0.05	0.06	-0.07	0.02	0.67	0.05	-0.07	0.5
	3-4	0.01	0.08	0.01	-0.07	0.02	0.86	0.07	-0.03	0.8
4915-3	0-1	-0.01	0.15	0.44	0.22	0.04	0.03	-0.08	-0.07	0.3
	1-2	-0.02	0.18	0.20	-0.01	0.51	0.07	0.03	0.05	0.3
	2-3	0.27	0.29	0.04	-0.03	0.57	0.16	-0.01	0.07	0.5
	3-4	-0.03	0.23	0.15	-0.07	0.48	0.43	0.12	-0.03	0.5
	4-5	-0.08	0.20	0.41	0.04	0.52	0.12	0.17	0.01	0.5
4916-4	0-1	-0.03	0.83	0.11	0.15	0.15	0.02	0.04	-0.02	0.7
	1-2	-0.05	0.67	-0.04	0.04	0.19	-0.05	0.02	0.03	0.5
	2-3	-0.03	0.64	-0.09	0.04	0.17	-0.04	0.01	0.05	0.5
	3-4	-0.01	0.34	0.06	-0.05	0.13	-0.02	0.57	0.20	0.5
	4-5	0.23	0.40	-0.03	-0.06	0.32	-0.01	0.09	0.51	0.6
4917-5	0-1	0.02	0.82	0.17	0.12	0.00	0.02	0.00	-0.05	0.7
	1-2	0.09	0.90	0.13	0.12	-0.01	0.00	0.01	-0.03	0.9
	2-3	0.20	0.88	-0.03	0.08	0.00	0.13	0.04	0.11	0.8
	3-4	0.24	0.33	0.14	-0.09	0.04	0.11	0.14	0.55	0.5
	4-5	0.44	0.29	0.19	-0.12	0.25	0.03	0.08	0.39	0.5
	5-6	0.36	0.10	0.00	-0.14	0.04	0.39	0.07	0.24	0.4
4918-4	0-1	0.00	0.85	-0.03	0.09	0.04	0.04	0.00	-0.04	0.7
	1-2	0.01	0.85	-0.06	0.09	0.06	0.05	0.00	-0.04	0.7
	2-3	-0.01	0.82	-0.09	0.04	0.07	0.24	0.04	-0.05	0.8
	3-4	0.03	0.21	-0.02	-0.11	0.18	0.72	0.11	-0.06	0.6
	4-5	0.00	0.24	-0.04	-0.11	0.11	0.74	0.11	-0.06	0.6
3713-1	0-1	-0.04	0.83	0.20	0.10	-0.04	-0.03	0.14	-0.02	0.8
	1-2	-0.02	0.87	0.12	0.19	0.05	-0.04	0.06	-0.02	0.8
	2-3	-0.02	0.77	0.09	0.07	0.21	-0.09	0.16	0.15	0.7

Table B1. (continued)

GeoB station	depth (cm)	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	Communality
	3-4	0.09	0.57	0.01	0.00	0.27	-0.07	0.12	0.25	0.5
	4-5	0.25	0.35	0.07	0.03	0.38	-0.04	0.47	0.31	0.7
	5-6	0.27	0.19	0.16	0.01	0.41	0.06	0.50	0.08	0.6
	6-7	0.74	0.39	0.13	0.07	0.14	-0.05	0.23	-0.02	0.8
3712-1	0-1	-0.02	0.71	0.11	0.01	-0.07	0.24	0.07	0.04	0.6
	1-2	-0.04	0.62	0.09	0.03	-0.03	0.24	0.09	0.01	0.5
	2-3	-0.02	0.83	0.03	0.08	-0.02	0.17	0.02	0.02	0.7
	3-4	-0.02	0.78	0.16	0.11	0.02	0.10	0.09	0.24	0.7
	4-5	-0.05	0.39	0.32	0.06	-0.04	0.08	0.28	0.55	0.7
	5-6	-0.05	0.33	0.40	0.06	-0.03	0.09	0.42	0.37	0.6
	6-7	-0.06	0.30	0.51	0.08	0.01	0.27	0.28	0.29	0.6
	7-8	-0.03	0.78	0.29	0.12	-0.04	0.10	0.18	0.12	0.8
	8-9	-0.04	0.66	0.40	0.06	0.24	-0.01	0.11	0.13	0.7
3715-1	0-1	0.10	0.54	0.01	0.09	-0.08	0.11	-0.11	0.15	0.4
	1-2	0.26	0.63	-0.02	0.07	-0.08	0.04	-0.12	0.35	0.6
	2-3	0.25	0.63	-0.05	0.03	-0.08	-0.02	-0.07	0.49	0.7
	3-4	0.72	0.02	-0.04	-0.06	0.03	-0.05	-0.02	0.66	1.0
	4-5	0.81	0.04	-0.04	-0.05	0.04	-0.06	-0.01	0.55	1.0
	5-6	0.87	0.03	-0.03	-0.04	0.05	-0.04	-0.02	0.47	1.0
	6-7	0.97	0.03	-0.02	-0.02	0.06	-0.03	0.00	0.19	1.0
	7-8	0.97	0.01	-0.02	-0.03	0.05	0.02	-0.01	0.19	1.0
3711-1	0-1	-0.02	0.10	0.08	0.23	-0.05	0.72	-0.08	0.19	0.6
	1-2	-0.02	0.15	0.09	0.37	-0.04	0.62	-0.09	0.18	0.6
	2-3	-0.02	0.12	0.07	0.31	-0.05	0.69	-0.08	0.23	0.7
	3-4	0.05	0.08	0.02	0.09	-0.05	0.33	0.00	0.88	0.9
	4-5	0.04	0.01	0.03	0.16	-0.03	0.35	-0.06	0.87	0.9
	5-6	0.06	0.00	0.01	0.09	-0.02	0.33	-0.04	0.89	0.9
	6-7	0.03	0.13	-0.01	0.24	0.00	0.36	-0.08	0.79	0.8
	7-8	-0.01	-0.04	0.09	0.00	-0.06	0.71	-0.05	0.24	0.6
3708-1	0-1	0.03	0.23	-0.01	0.67	-0.01	0.01	-0.12	0.36	0.6
	1-2	0.12	0.23	-0.08	0.55	-0.01	-0.04	-0.10	0.63	0.8
	2-3	0.14	0.13	-0.11	0.38	0.02	-0.05	-0.06	0.82	0.9
	3-4	0.50	0.10	-0.08	0.35	0.04	-0.05	-0.01	0.74	0.9
	4-5	0.71	-0.01	-0.04	0.11	0.04	-0.06	0.01	0.66	1.0
	5-6	0.78	0.06	-0.03	-0.02	0.05	-0.06	-0.01	0.58	1.0
	6-7	0.57	0.13	-0.06	-0.02	0.02	-0.05	-0.03	0.76	0.9
3706-3	0-1	0.00	-0.03	-0.05	0.93	0.02	0.09	-0.05	0.06	0.9
	1-2	-0.01	0.04	-0.01	0.94	0.04	0.09	-0.04	0.06	0.9
	2-3	-0.01	0.06	-0.05	0.92	0.04	0.08	-0.01	0.07	0.9
	3-4	-0.02	-0.01	-0.05	0.92	0.04	0.06	0.01	0.13	0.9
	4-5	-0.01	-0.06	-0.01	0.83	0.01	0.04	0.13	0.24	0.8
	5-6	0.09	-0.02	-0.03	0.63	-0.02	0.01	0.18	0.21	0.5
	6-7	0.23	0.00	-0.04	-0.06	0.00	-0.09	0.05	0.92	0.9
3725-1	0-1	-0.01	0.25	0.00	0.65	0.07	0.00	-0.08	-0.01	0.5
	1-2	-0.07	0.24	0.02	0.46	0.66	-0.01	-0.04	0.03	0.7
	2-3	-0.01	0.04	-0.04	0.08	0.92	0.01	0.00	0.03	0.9
	3-4	0.04	0.04	-0.06	0.00	0.94	0.02	0.11	0.05	0.9
	4-5	0.18	-0.02	-0.11	0.54	0.49	0.06	0.47	0.16	0.8
	5-6	0.36	-0.06	-0.06	0.18	0.77	0.01	0.34	0.14	0.9
	6-7	0.54	0.00	-0.05	0.15	0.65	0.01	0.37	0.06	0.9
	7-8	0.37	-0.03	-0.06	-0.02	0.83	0.00	0.24	-0.02	0.9

Table B1. (continued)

GeoB station	depth (cm)	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	Communality
3705-2	0-1	-0.03	0.26	0.03	0.80	-0.02	0.00	0.04	0.04	0.7
	1-2	-0.05	0.26	0.15	0.78	0.00	-0.03	0.15	0.10	0.7
	2-3	-0.05	0.21	0.14	0.66	-0.02	-0.03	0.32	0.23	0.7
	3-4	-0.02	-0.01	0.05	0.23	-0.05	-0.05	0.26	0.43	0.3
	4-5	-0.02	0.01	0.03	0.17	-0.05	-0.05	0.25	0.36	0.2
3703-4	0-1	0.11	0.49	-0.01	0.03	-0.09	0.00	-0.12	0.07	0.3
	1-2	0.13	0.40	0.00	0.02	-0.09	-0.01	-0.09	0.07	0.2
	2-3	0.25	0.41	0.00	0.02	-0.08	-0.02	-0.09	0.10	0.3
	3-4	0.91	0.30	-0.02	0.03	0.01	0.01	-0.04	-0.03	0.9
	4-5	0.97	0.07	-0.04	-0.01	0.07	-0.03	0.06	0.18	1.0
	5-6	0.99	0.01	-0.02	0.00	0.07	-0.02	0.09	0.00	1.0
	6-7	0.99	-0.01	-0.02	-0.01	0.07	-0.02	0.11	0.04	1.0
	7-8	0.97	0.00	-0.02	-0.01	0.07	-0.03	0.17	0.10	1.0
	8-9	0.98	0.00	-0.03	-0.01	0.08	-0.02	0.14	0.06	1.0
	9-10	0.98	0.02	-0.01	0.00	0.06	-0.01	0.00	-0.05	1.0
	10-11	0.98	-0.01	0.00	0.01	0.06	-0.01	0.00	-0.05	1.0
3702-2	0-1	-0.01	0.44	0.26	0.25	0.04	0.17	0.02	-0.04	0.4
	1-2	-0.05	0.42	0.16	0.24	0.21	0.02	0.10	-0.03	0.3
	2-3	0.15	0.15	0.08	-0.01	0.09	-0.02	0.61	0.54	0.7
	3-4	0.12	0.01	-0.03	-0.04	0.03	-0.01	0.76	0.40	0.8
	4-5	0.45	0.14	-0.06	-0.05	0.04	-0.07	0.42	0.61	0.8
3701-1	0-1	0.01	0.36	0.05	0.39	-0.02	-0.09	-0.08	-0.08	0.3
	1-2	-0.01	0.23	0.16	0.51	0.03	-0.10	-0.07	-0.07	0.4
	2-3	-0.04	0.14	0.15	0.24	0.20	-0.13	-0.07	-0.09	0.2
	3-4	-0.05	-0.03	0.08	0.04	0.20	-0.07	-0.02	-0.05	0.1
	4-5	0.12	0.03	0.07	0.15	0.27	-0.06	0.21	-0.09	0.2
1720-3	0-1	0.03	0.06	0.28	0.14	0.00	-0.06	-0.17	-0.09	0.1
	1-2	0.02	0.02	0.22	0.18	0.07	-0.10	-0.19	-0.11	0.1
	2-3	-0.01	0.01	0.09	0.15	0.18	-0.10	-0.14	-0.09	0.1
	3-4	-0.04	-0.03	0.01	0.01	0.55	-0.05	-0.12	-0.03	0.3
	4-5	0.50	-0.06	-0.06	-0.03	0.50	-0.04	0.29	-0.05	0.6
	5-6	0.43	-0.07	-0.06	0.01	0.16	-0.01	0.75	-0.05	0.8
3604-1	0-1	-0.02	0.27	0.16	0.48	0.05	-0.09	-0.03	-0.09	0.3
	1-2	0.00	0.11	0.20	0.18	0.09	-0.09	0.62	-0.06	0.5
	2-3	0.17	-0.05	-0.07	0.00	0.08	0.08	0.84	-0.07	0.8
	3-4	0.10	-0.05	-0.08	-0.02	0.00	0.10	0.64	-0.07	0.4
	4-5	0.01	-0.05	-0.08	-0.01	-0.03	0.01	0.51	-0.05	0.3

Table B2. Varimax PC-scores of the foraminiferal assemblages

Species	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8
Adercotryma glomerata	-0.09	-0.24	-0.25	-0.27	-0.23	-0.15	-0.07	-0.09
Ammobaculites agglutinans	-0.10	-0.22	0.26	-0.23	-0.16	-0.09	-0.14	-0.08
Ammobaculites filiformis	-0.12	-0.20	-0.21	-0.30	-0.17	-0.13	-0.05	-0.07
Ammodiscus incertus	-0.27	0.62	-0.36	-0.31	0.35	0.43	-0.10	-0.06
Ammodiscus spp.	-0.09	-0.24	-0.32	-0.28	-0.23	-0.14	-0.08	-0.11
Ammolagena clavata	-0.02	-0.39	-0.08	0.38	-0.32	0.26	-0.11	-0.27
Ammomarginulina ensis	-0.04	-0.20	-0.18	-0.28	-0.24	-0.13	-0.12	-0.11
Ammomarginulina foliacea	0.03	-0.49	0.13	-0.32	0.06	1.10	-0.60	-0.26
Ammoscalaria sp.	-0.23	-0.43	0.23	0.01	-0.69	9.13	-0.59	2.11
Angulogerina angulosa	-0.09	-0.23	-0.24	-0.25	-0.25	-0.15	-0.09	-0.11
Astrorhiza sp.	-0.06	-0.21	-0.08	-0.05	-0.21	-0.20	-0.19	-0.21
Atlantica atlantiella	-0.10	-0.20	-0.33	-0.25	-0.25	-0.12	-0.07	-0.10
Biloculinella spp.	-0.11	-0.26	-0.34	-0.12	-0.24	-0.19	-0.10	-0.03
Bolivina albatrossi	-0.12	-0.04	-0.08	-0.30	-0.05	-0.19	-0.18	-0.14
Bolivina dilatata	-0.11	-0.15	-0.34	-0.29	-0.24	-0.17	-0.06	-0.11
Bolivina pacifica	-0.07	0.03	-0.40	-0.59	-0.20	0.12	0.24	0.16
Bolivina pseudopunctata	-0.09	-0.20	-0.35	-0.27	-0.25	-0.14	-0.07	-0.13
Bolivina pseudothalmanni	-0.06	-0.09	-0.19	-0.50	-0.20	-0.17	-0.10	0.26
Bolivina sp.	-0.08	-0.24	-0.32	-0.26	-0.12	-0.14	-0.12	-0.14
Brizalina subspinescens	-0.10	-0.23	-0.32	0.00	-0.25	-0.18	-0.17	0.01
Bulimina aculeata	-0.11	-0.18	-0.13	-0.29	-0.17	-0.16	-0.08	-0.10
Bulimina alazanensis	0.04	-0.30	0.15	-0.18	-0.27	0.46	-0.25	-0.32
Bulimina exilis	-0.13	0.53	-0.51	-0.74	0.54	-0.57	0.18	1.19
Bulimina marginata	-0.09	-0.27	-0.27	-0.26	-0.25	-0.13	-0.09	-0.12
Bulimina mexicana	0.22	10.27	-0.84	1.62	-0.47	-0.35	-0.25	-0.42
Cancris oblungus	-0.21	-0.28	-0.41	-0.43	-0.36	-0.31	0.78	0.37
Cassidulina crassa	-0.11	-0.26	-0.31	-0.27	-0.16	-0.14	-0.10	-0.11
Cassidulina laevigata	0.09	0.45	0.32	-0.03	-0.26	0.01	-0.62	0.03
Cassidulinoides tenuis	-0.30	0.61	-0.65	-0.49	-0.07	-0.34	0.28	-0.08
Chilostomella oolina	0.60	-0.88	-0.86	0.16	0.63	-0.15	10.51	-0.46
Cibicidoides bradyi	-0.06	-0.22	-0.21	0.01	-0.22	-0.24	-0.04	-0.25
Cibicidoides globulosus	-0.01	-0.12	-0.12	0.21	-0.26	-0.35	-0.28	-0.34
Cibicides lobatulus	-0.12	-0.35	-0.39	1.36	-0.10	0.26	-0.24	0.08
Cibicidoides pachyderma	-0.06	-1.75	-1.03	10.59	0.33	0.93	-0.04	1.20
Cibicidoides robertsionanus	-0.10	-0.26	-0.30	-0.24	-0.20	-0.14	-0.11	-0.13
Cornuspira spp.	-0.11	-0.26	-0.26	-0.17	-0.16	-0.15	-0.11	-0.13
Cribostomoides jeffreysii	0.14	1.22	-1.32	-1.14	0.54	7.54	1.33	-1.21
Cribostomoides rotulatus	-0.09	-0.26	-0.24	-0.26	-0.26	-0.15	-0.07	-0.12
Cribostomoides weddellensis	-0.10	-0.25	-0.29	-0.26	-0.24	-0.14	-0.06	-0.12
Cribrostomoides sp.	-0.10	-0.26	-0.30	-0.20	-0.26	-0.14	-0.05	-0.11
Cribrostomoides subglobosum	-0.12	-0.19	0.41	0.31	0.37	-0.28	-0.17	-0.30
Cribrostomoides wiesneri	-0.04	-0.42	0.09	-0.17	1.82	0.02	-0.70	-0.23
Crithionina sp.	-0.05	0.40	-0.09	0.20	-0.10	-0.10	-0.33	-0.01
Cyclammina cancelata	-0.07	-0.12	-0.26	0.22	-0.27	-0.25	0.03	-0.11
Cystammina pauciloculata	-0.13	-0.46	-0.02	-0.37	1.90	-0.25	-0.97	-0.11
Dentalina spp.	-0.12	-0.21	-0.26	-0.24	-0.17	-0.16	-0.10	-0.10
Deuterammina montagui	-0.12	-0.29	-0.65	-0.15	-0.72	0.15	2.07	-0.52
Discammina spp.	0.00	-0.11	0.10	-0.39	-0.17	9.07	0.04	0.01
Earlandammina inconspicua	-0.09	-0.18	-0.31	-0.27	-0.19	-0.12	-0.08	-0.12

Table B2. (continued)

Species	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8
Eggerella bradyi	-0.03	-0.28	-0.02	1.64	-0.13	-0.34	-0.19	-0.39
Epistominella exigua	0.01	-0.27	0.25	0.09	-0.19	-0.32	-0.42	-0.28
Epistominella rugosa	-0.09	-0.28	-0.10	-0.26	-0.26	-0.15	-0.08	-0.12
Epistominella smithi	-0.01	0.37	-0.46	-0.31	-0.28	0.10	-0.06	-0.40
Eponides pusillus	-0.08	-0.26	-0.17	-0.25	-0.22	-0.15	-0.13	-0.13
Eponides tumidulus	-0.11	-0.23	-0.32	-0.29	-0.22	-0.15	-0.07	-0.04
Fissurina spp.	-0.06	0.04	-0.37	-0.06	-0.16	-0.15	-0.27	0.03
Fontbotia wuellerstorfi	-0.03	-0.19	-0.27	0.69	-0.02	0.05	-0.22	-0.17
Fursenkoina earlandi	-0.27	-0.60	0.57	-0.41	0.17	0.59	0.35	-0.05
Fursenkoina mexicana	0.81	0.20	-0.57	-1.18	-0.02	-1.04	-0.31	11.75
Gavelinopsis translucens	0.14	-0.06	2.57	2.47	0.40	0.76	-1.07	-0.39
Glandulina ovula	-0.11	-0.05	-0.35	-0.29	-0.13	-0.16	-0.01	-0.13
Glandulonodosaria calomorpha	-0.06	-0.26	-0.31	-0.26	-0.23	-0.12	-0.06	-0.13
Globobulimina affinis	12.37	-0.06	-0.13	0.01	0.77	-0.09	0.05	-0.61
Globocassidulina subglobosa	-0.06	-0.08	-0.19	0.66	-0.21	-0.32	-0.12	-0.30
Globulotuba sp.	-0.10	-0.14	-0.33	-0.26	-0.25	-0.18	-0.06	-0.14
Glomospira gordialis	-0.11	-0.16	-0.29	-0.29	-0.22	-0.13	0.05	-0.06
Gyroidinoides polius	-0.16	0.08	-0.06	0.41	1.23	-0.26	-0.60	-0.15
Gyroidinoides soldanii	-0.26	-0.09	-0.47	0.42	0.82	-0.25	-0.28	-0.03
Gyroidinoides umbonatus	-0.08	-0.07	-0.27	-0.12	-0.21	-0.13	-0.14	-0.14
Haplophragmoides bradyi	-0.50	1.71	-0.95	-0.82	0.50	-0.53	0.50	0.03
Haplophragmoides coronatum	-0.15	-0.28	-0.27	-0.22	0.00	-0.26	-0.16	-0.12
Haplophragmoides sp	-0.09	-0.24	-0.33	-0.27	-0.19	-0.14	-0.09	-0.13
Haplophragmoides sphaeriloculus	-0.03	-0.25	0.03	-0.16	-0.13	-0.18	-0.23	-0.21
Hoeglundina elegans	0.19	-0.48	1.78	-0.04	0.40	-0.15	-0.84	-0.35
Hormosina globulifera	-0.06	0.26	-0.28	0.61	0.03	1.57	-0.85	0.43
Hyperammina elongata	-0.03	-0.30	0.02	-0.18	-0.23	0.49	-0.18	-0.21
Karreriella bradyi	-0.11	-0.25	-0.32	-0.23	-0.24	-0.17	0.06	-0.14
Karrerulina conversa	-0.08	-0.28	0.19	-0.19	0.07	0.08	-0.41	-0.18
Labrospira ringens	-0.12	-0.27	-0.29	-0.27	-0.17	-0.09	-0.04	-0.11
Lagena spp	-0.06	-0.12	-0.27	-0.16	-0.25	-0.14	-0.07	-0.15
Lagenammina difflugiformis	0.23	1.33	4.21	-1.19	0.40	1.13	1.12	0.27
Lagenammina spiculata	-0.11	-0.19	-0.33	-0.26	-0.24	-0.17	-0.06	-0.13
Lagenammina tubulata	-0.09	-0.38	1.04	-0.23	-0.20	-0.13	-0.15	-0.10
Laticarinina pauperata	-0.12	-0.25	-0.24	-0.26	-0.14	-0.13	-0.08	-0.12
Lenticulina spp.	-0.12	-0.26	-0.27	-0.18	-0.24	-0.10	-0.05	-0.04
Martinotiella communis	-0.10	-0.25	-0.30	-0.20	-0.16	-0.19	-0.12	-0.14
Melonis barleeanum	-0.80	-0.12	-0.43	-0.69	11.44	0.18	-0.14	0.35
Miliolidae sp.	-0.04	-0.23	-0.32	0.08	-0.27	-0.18	-0.15	-0.09
Nodosaria spp.	-0.09	-0.27	-0.30	-0.24	-0.18	-0.14	-0.09	-0.13
Nonion commune	-0.13	-0.25	-0.22	-0.29	-0.08	-0.06	0.03	-0.05
Nonion sp.	-0.02	-0.19	-0.33	-0.33	0.17	-0.20	0.02	-0.09
Nouria harrisii	-0.51	-0.80	0.52	1.83	-0.63	-0.37	3.06	2.06
Oolina spp.	-0.07	-0.15	-0.31	-0.29	-0.27	-0.18	-0.16	0.03
Oridorsalis umbonatus	0.21	0.49	0.32	1.90	-0.31	-0.40	-0.72	-0.23
Osangularia culter	-0.10	-0.28	-0.10	-0.26	-0.13	-0.02	-0.13	-0.15
Placopsilinella aurantiaca	-0.10	-0.02	-0.34	-0.34	-0.30	-0.19	-0.13	0.05
Paratrochammina challengeri	-0.12	-0.12	-0.28	-0.24	-0.20	-0.14	-0.01	-0.13
Planularia sp.	-0.10	-0.26	-0.27	-0.26	-0.24	-0.14	-0.07	-0.12

Table B2. (continued)

Species	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8
Portatrochammina spp.	-0.11	-0.10	-0.35	-0.24	-0.23	-0.10	-0.04	-0.13
Praecystammina globigeriniformis	-0.07	-0.16	-0.39	0.32	0.19	-0.24	-0.25	-0.29
Praecystammina sp.	-0.09	-0.25	-0.29	-0.20	-0.22	-0.16	-0.08	-0.15
Psammosphaera fusca	-0.17	0.22	-0.23	-0.29	-0.17	-0.20	0.28	-0.10
Psammosphaera sp.	-0.10	0.24	-0.33	-0.40	-0.30	-0.04	0.08	-0.11
Pseudogaudryina sp.	-0.06	-0.21	-0.12	0.10	-0.11	-0.36	-0.24	-0.28
Pseudonodosinella nodulosa	-0.10	-0.27	-0.27	-0.27	-0.23	-0.13	-0.06	-0.12
Pullenia bulloides	-0.07	-0.22	0.16	0.19	0.26	-0.08	-0.29	0.28
Pullenia subcarinata	0.01	-0.30	-0.15	0.10	0.12	-0.36	0.62	-0.35
Pyrgo depressa	-0.11	-0.24	-0.31	0.29	-0.29	-0.25	-0.18	0.20
Pyrgo elongata	-0.14	-0.25	-0.35	-0.19	-0.16	0.14	-0.10	-0.02
Pyrgo lucernula	-0.15	-0.28	-0.34	-0.13	-0.15	-0.06	-0.16	0.06
Pyrgo murrhina	-0.09	-0.30	-0.23	0.84	-0.34	-0.03	0.07	-0.24
Pyrgo serrata	-0.11	-0.29	-0.33	-0.11	-0.26	0.23	-0.16	0.00
Pyrgo sp.	-0.08	-0.23	-0.33	-0.26	-0.25	-0.15	-0.08	-0.12
Pyrgo williamsoni	-0.06	-0.27	-0.30	-0.23	-0.25	-0.11	-0.09	-0.13
Pyrgoella sphaera	-0.14	-0.25	-0.38	0.67	-0.30	-0.34	-0.27	0.49
Quinqueloculina spp.	-0.09	-0.14	-0.17	0.16	-0.23	-0.03	-0.13	-0.12
Recurvoides contortus	-0.21	0.71	0.27	1.57	1.85	-0.48	-0.85	-0.46
Recurvoides scitulum	-0.11	0.26	-0.35	-0.26	-0.25	-0.16	0.28	-0.11
Reophax agglutinatus	-0.08	-0.21	-0.32	-0.18	-0.26	-0.17	-0.09	-0.16
Reophax bilocularis	-0.91	3.06	5.07	1.24	-0.20	-0.96	3.79	0.67
Reophax dentaliniformis	-0.37	-0.20	0.70	-0.14	1.05	-0.24	0.42	-0.16
Reophax distans	-0.08	-0.24	-0.25	-0.14	-0.14	-0.24	-0.23	-0.18
Reophax fusiformis	-0.03	-0.27	-0.21	-0.29	-0.20	-0.12	-0.01	-0.16
Reophax gaussicus	-0.10	-0.20	-0.34	-0.31	0.01	-0.08	-0.17	-0.11
Reophax guttifera	0.01	0.07	0.10	-0.18	-0.19	-0.02	-0.13	-0.02
Reophax micaceus	-0.06	-0.09	0.85	0.27	0.27	-0.62	-0.28	-0.28
Reophax nodulosus	-0.11	-0.22	-0.33	-0.26	-0.17	-0.15	-0.10	-0.12
Reophax pilulifer	-0.33	0.94	-0.06	-0.59	0.21	0.53	0.38	-0.09
Reophax scorpiurus	-0.09	-0.73	7.09	-0.84	-0.16	-1.10	0.21	0.30
Reophax spp.	0.06	0.13	0.17	-0.37	0.00	-0.04	0.43	-0.12
Rhabdammina abyssorum	-0.08	-0.19	-0.28	-0.20	-0.26	-0.08	-0.08	-0.18
Rhabdammina linearis	-0.08	-0.25	-0.27	-0.25	-0.26	0.01	0.00	-0.17
Robertinoides chapmani	0.29	-0.79	4.24	-0.06	0.20	-0.33	-1.33	-0.25
Saccammina sphaerica	-0.10	0.07	0.00	0.01	-0.21	-0.06	-0.09	-0.29
Saccorhiza ramosa	-0.08	-0.28	-0.11	-0.23	-0.22	-0.15	-0.12	-0.14
Sigmoilopsis schlumbergeri	-0.15	-0.28	-0.28	-0.01	-0.02	-0.28	0.19	-0.23
Siphotextularia sp	-0.09	-0.23	-0.28	-0.13	-0.20	-0.21	-0.10	-0.10
Sphaeroidina bulloides	0.09	0.50	0.80	2.12	0.15	-0.95	-0.59	-0.71
Spiroloculina spp.	-0.06	-0.27	-0.25	-0.22	-0.25	-0.11	-0.09	-0.13
Spirophthalmidium pusilla	-0.09	-0.27	-0.20	-0.26	-0.26	-0.16	-0.08	-0.12
Spirosigmoilina spp.	-0.05	0.06	-0.39	-0.24	-0.34	-0.18	-0.23	0.01
Subreophax aduncus	-0.14	0.01	-0.31	-0.31	-0.21	-0.18	0.09	-0.10
Textularia conica	-0.11	-0.19	-0.26	0.00	-0.23	-0.05	-0.16	0.01
Tholosina sp.	-0.14	0.04	-0.33	-0.34	-0.35	-0.02	0.01	-0.10
Triloculina spp.	-0.11	-0.13	-0.31	-0.03	-0.22	-0.08	-0.04	-0.09
Triloculinella spp.	-0.09	-0.26	-0.32	-0.26	-0.17	-0.15	-0.07	-0.13

Table B2. (continued)

Species	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8
Trochammina inflata	-0.05	-0.20	-0.34	-0.06	0.03	-0.18	-0.02	-0.26
Trochammina nana	-0.09	-0.24	-0.31	-0.21	-0.24	-0.17	-0.09	-0.14
Trochammina spp.	-0.01	0.35	0.02	-0.01	-0.03	0.01	-0.01	0.01
Trochammina tricamerata	-0.07	-0.26	-0.26	-0.22	-0.23	-0.18	-0.14	-0.15
Trochamminopsis pusillus	-0.06	-0.04	-0.29	-0.38	-0.21	-0.16	-0.10	-0.01
Uvigerina auberiana	0.66	2.83	-0.09	-0.19	-1.24	-0.03	-1.47	0.80
Uvigerina peregrina	0.51	-0.14	3.65	0.05	0.05	0.72	-1.12	-0.60
Uvigerina proboscidea	-0.10	-0.32	0.21	-0.28	-0.33	-0.28	0.04	-0.10
Uzbekistania charoides	-0.02	-0.30	0.08	0.15	0.39	-0.56	-0.66	-0.33
Valvulina conica	-0.18	1.81	-0.49	-0.62	-0.74	0.44	0.11	-0.06
Valvulineria laevigata	-0.48	3.13	-0.84	0.26	1.96	-0.46	-0.14	-0.03
Vanhoeffenella gaussi	-0.09	-0.27	-0.31	-0.27	-0.26	0.04	-0.07	-0.13
Verneuilinulla propinqua	-0.06	-0.25	0.16	-0.16	-0.16	-0.19	-0.17	-0.18

Appendix C. Foraminiferal standing stocks (#/50cm^3) in all sediment samples (for species with abundances>1%)

GeoB station	Sediment depth	*Adercotryma glomerata*	*Ammobaculites agglutinans*	*Ammobaculites filiformis*	*Ammodiscus incertus*	*Ammodiscus spp.*	*Ammolagena clavata*	*Ammomarginulina ensis*	*Ammomarginulina foliacea*	*Ammoscalaria sp.*	*Angulogerina angulosa*	*Astrorhiza sp.*	*Atlantica atlantiella*	*Bilocullinella spp.*	*Bolivina albatrossi*	*Bolivina dilatata*	*Bolivina pacifica*	*Bolivina pseudopunctata*	*Bolivina pseudothalmanni*	*Bolivina sp.*	*Brizalina subspinescens*	*Bulimina aculeata*	*Bulimina alazanensis*	*Bulimina exilis*	*Bulimina marginata*	*Bulimina mexicana*	*Cancris oblungus*	*Cassidulina crassa*	*Cassidulina laevigata*	*Cassidulinoides tenuis*	*Chilostomella oolina*	*Cibicidoides bradyi*	*Cibicidoides globulosus*	*Cibicides lobatulus*	*Cibicidoides pachyderma*	*Cibicidoides robertsionanus*	*Cornuspira spp.*	*Cribostomoides jeffreysii*	*Cribostomoides ratulatus*	*Cribostomoides weddellensis*	*Cribrostomoides sp.*	*Cribrostomoides subglobosum*
4901-6	0-1				0.3		1.0																		0.6																	
	1-2																																									
	2-3						0.3																																			
4904-7	0-1			1.3	2.5				10.2	1.3	1.3											3.8	1.9			6.4		0.6	7.0												0.6	
	1-2				0.6			1.9	9.6	1.3									0.6			1.9	0.6			1.3			1.3													1.3
	2-3			1.3	2.5				6.4	0.6					0.6							1.3	0.6					1.3	1.9								0.6					0.6
	3-4				0.6																										1.9											
	4-5								0.6																	0.6					5.7											
	5-6																														0.6											
	6-7																									0.6					0.6											
	7-8																														0.6											
4906-5	0-1			0.3					4.5	0.6		0.3			1.0								1.3			2.2			1.3													0.3
	1-2			1.0	0.6				3.5	1.9					0.3								0.3			2.5			0.6		1.3					0.3	0.6	0.6				
	2-3	0.3			0.3				0.3	0.3																					0.6							0.3		0.3		0.6
4909-4	0-1	0.6						0.6	0.6	5.1	1.3				0.6						0.6		1.3			1.3			7.0								0.6		2.5			1.9
	1-2	0.3	0.6		0.3					4.5		1.3			1.0											0.3													0.3			1.6
	2-3		0.3	1.3						1.9																																
	3-4		0.3							2.2																					1.9											
4912-4	0-1			8.9		0.6			1.9	17.2		5.1											1.3			1.3			3.2			1.3			2.5							3.2
	1-2		0.6	0.3	0.3			0.3	1.0	3.8		0.6			1.0																											2.9
	2-3		0.6		0.3				0.3	0.6		0.3								0.3						0.3					0.3							0.3				
	3-4									0.3										0.6											0.3							0.6				0.3
	4-5			0.3				0.3		1.9													0.3																			
	5-6									0.3																					1.0							0.3				
4913-4	0-1						1.6		4.8	2.2													1.3		0.3				0.6													0.6
	1-2								1.0	2.2																												1.3				
	2-3				1.0		0.6		0.6	0.6													1.0															2.9				0.3
	3-4									1.6													0.3															3.5				
4915-3	0-1			4.5	0.3						0.6				1.6							0.3	5.4			1.6			1.3			1.0				0.3		0.6				1.6
	1-2				0.6										0.3																							0.3				
	2-3														0.3											0.3												0.6				0.6
	3-4																							0.3		0.3												1.9				
	4-5																																					0.6				
4916-4	0-1			0.3	1.9					0.6	0.3				0.3	0.6	0.6						0.3			18.5			2.2	3.5	1.3				0.6			1.3				
	1-2				2.9			0.3		1.3					1.0		2.9					0.3	0.3	0.3		24.2			2.2	8.9	0.6											
	2-3				1.6		0.3			1.0						0.3	1.9							0.6		12.4				14.3	0.3							0.3				0.3
	3-4				0.3												1.0					0.3		0.3		1.0				1.3	1.6							0.3				0.3
	4-5																							1.9		1.3					0.3							0.3				
4917-5	0-1			6.4	5.1			2.5	1.3	1.3	1.3		2.5		6.4	1.3	6.4		3.8	5.1		5.1				147.8			6.4				2.5					5.1				
	1-2	0.6		0.6	5.1			1.3	1.3	0.6					1.3		0.6	0.6	0.6							66.9			1.9	3.8			1.9					2.5				
	2-3	0.3			1.0				1.0						0.3		0.3	1.6	0.6					0.3		21.7				1.3	0.3							8.0				
	3-4				0.6			0.3	0.3		0.3		0.3			0.3	1.3		3.5							1.6				0.3	0.3							1.9				
	4-5	0.3	0.3			0.3		0.3									1.0		1.6			0.3		2.5		1.3			0.3									0.6				
	5-6																1.0							0.3					0.3									1.3				
4918-4	0-1				9.9			0.3		2.9					1.3							0.3				85.0									0.3			4.1				0.3
	1-2		0.3		7.3				0.6	1.3					1.3	1.0										47.1				4.1								4.5				
	2-3				3.5					1.3																13.7				1.3								5.4				0.3
	3-4				1.0					1.9																1.0												9.6				
	4-5								0.3	1.6																1.0												6.7				
3713-1	0-1		1.3	0.3				0.6	0.3	0.3					1.0	1.3						0.3	0.3	0.6		19.7			1.0									0.3		0.3		1.0
	1-2			0.6	0.6					2.5					0.6								0.6	0.6		58.0			1.3						0.6			0.6				
	2-3		0.8	0.8					1.7	0.8					3.4	0.8						0.8		15.3		40.8			0.8		0.8							0.8				
	3-4			0.5				0.5	0.5	1.5						0.5	0.5							9.7		15.3			0.5	0.5	0.5							0.5				1.0
	4-5									0.6														4.1		1.9					2.9											
	5-6									0.6														0.6		0.3					1.3											
	6-7																							0.3		1.0					0.3											
3712-1	0-1		0.3	0.3	1.6			0.3		5.7																14.3			1.3									3.2				
	1-2				7.6		10.2			22.9			5.1									5.1				66.2			10.2									58.6		2.5		
	2-3	0.8	0.8		1.7	0.8	0.8			12.7		3.4	0.8									0.8				53.5												14.4				
	3-4			0.6	3.5		0.3	0.3		5.4														0.6		13.7			0.3		0.3							2.9				
	4-5		0.6	1.3	1.9				0.3	4.5														0.3		3.8												1.9				
	5-6		0.6	1.0	1.3					4.5														0.6		1.9			1.0		2.9							0.6			1.0	
	6-7			0.6						3.2																0.6			0.3													
	7-8									1.0																3.2																
	8-9									0.3					0.3											2.2																
3715-1	0-1				1.3					2.2														0.3		8.9			11.1	0.3								0.6				
	1-2				1.0					1.9														2.5		10.5			5.7													
	2-3				1.3					1.3			0.3											1.0		11.5			1.6	0.3				0.6								
	3-4									0.3																			0.3													
	4-5																							1.0		0.3			0.3													
	5-6									0.3																0.3																
	6-7																							1.0		0.3																
	7-8									0.3																																

Appendix C. (continued)

GeoB station	Sediment depth	*Adercotryma glomerata*	*Ammobaculites agglutinans*	*Ammobaculites filiformis*	*Ammodiscus incertus*	*Ammodiscus* spp.	*Ammolagena clavata*	*Ammomarginulina ensis*	*Ammomarginulina foliacea*	*Ammoscalaria* sp.	*Angulogerina angulosa*	*Astrorhiza* sp.	*Atlantica atlantiella*	*Biloculinella* spp.	*Bolivina albatrossi*	*Bolivina dilatata*	*Bolivina pacifica*	*Bolivina pseudopunctata*	*Bolivina pseudothalmanni*	*Bolivina* sp.	*Brizalina subspinescens*	*Bulimina aculeata*	*Bulimina alazanensis*	*Bulimina exilis*	*Bulimina marginata*	*Bulimina mexicana*	*Cancris oblungus*	*Cassidulina crassa*	*Cassidulina laevigata*	*Cassidulinoides tenuis*	*Chilostomella oolina*	*Cibicidoides bradyi*	*Cibicidoides globulosus*	*Cibicides lobatulus*	*Cibicidoides pachyderma*	*Cibicidoides robertsonianus*	*Cornuspira* spp.	*Cribostomoides jeffreysi*	*Cribostomoides rotulatus*	*Cribostomoides weddellensis*	*Cribrostomoides* sp.	*Cribrostomoides subglobosum*
3711-1	0-1				0.4					64.1																10.9			1.5					7.3	12.7			0.7				
	1-2									56.1			1.0													15.3								7.1	22.4	1.0	1.0	1.0				1.0
	2-3				0.6					48.4																10.2			0.3					4.8	15.6							
	3-4									8.0														0.6		1.0					1.0			0.6	2.2							
	4-5									9.9																0.6								0.6	3.8							
	5-6									6.7																0.3								0.6	2.2			0.3				0.3
	6-7				0.3					1.9																0.6								0.3	1.0							
	7-8									7.6																								0.3								
3708-1	0-1				0.6								0.6								11.5			5.1		15.3			3.8					6.4	33.1							3.2
	1-2				1.3									6.4							2.5			10.2		22.9			2.5					11.5	59.9							1.3
	2-3	0.6			0.6									3.2							3.8			10.8		9.6			3.2					3.2	27.4			0.6				
	3-4													0.3							0.6			0.3		3.5								1.0	8.9							0.3
	4-5																							0.3		0.3									2.9							
	5-6																							0.3		0.6									0.3							
	6-7																									1.0									0.3			0.3				
3706-3	0-1				0.3		6.4																			6.4								7.6	53.8			1.6			1.0	1.3
	1-2						7.3														0.3					8.0								2.5	49.0			2.5			0.3	1.0
	2-3				0.4		4.7						0.4	0.4												12.3								7.6	68.8			3.4				1.3
	3-4				0.3		1.3							0.3												2.2								2.9	23.2			0.3			0.6	
	4-5						1.3																			1.0								1.9	11.5			0.3				
	5-6						0.3																			1.0								0.6	4.5							
	6-7																							0.3																		
3725-1	0-1				0.6																					8.3			1.3					0.6	11.5							0.3
	1-2				2.2																					3.8			0.3		0.3			2.2	6.4		0.6					
	2-3				1.6																					0.6			0.3		1.0			1.0	1.6			0.3				0.3
	3-4				0.3																			0.3		0.3					2.5				0.6			0.6				
	4-5				0.3																					0.3			0.6		2.9			0.6	3.2			0.3				
	5-6																														1.9				1.3							
	6-7																									0.3					1.9				0.6							
	7-8																														1.0											
3705-2	0-1						0.3							1.0							0.3					11.1								2.9	21.3		1.0	0.3				
	1-2						0.4							1.7												12.7					0.4			0.8	34.4		0.8	0.4				
	2-3						0.3																			4.1					1.3			0.3	8.9			0.6				
	3-4																									0.6					0.3				1.0							
	4-5																									1.0					0.3				0.3							
3703-4	0-1				0.8																					47.6			10.2									3.4				
	1-2				0.7																0.7					32.8			4.4		2.9			0.7	0.7			0.7				
	2-3				0.6																					7.6					1.0			0.3								
	3-4									0.3																2.9																
	4-5																									0.6					0.6											
	5-6																									0.3					1.9											
	6-7																														4.5											
	7-8																														2.5											
	8-9																														1.3											
	9-10																									0.3																
	10-11																																									
3702-2	0-1				0.6							0.3									1.3					5.4			1.9		0.3		0.3	1.9	0.3			5.1				0.6
	1-2				2.2		0.3						0.3												0.3	3.2				0.3	1.6			0.3	1.6			3.5				
	2-3				0.3																					0.3	3.5				7.0							1.3				0.3
	3-4																									0.3	1.3				4.1							0.3				
	4-5																									0.6	1.0				1.6											
3701-1	0-1											1.6	0.3								0.3					10.8			0.6			0.6	4.5	4.5	2.9							0.6
	1-2						0.6					8.9														12.7			0.6			5.7	9.6	3.2	12.1							5.1
	2-3											1.3														1.9							0.3	0.6	0.3							7.0
	3-4													0.3																												4.8
	4-5																														0.6	0.3										
1720-3	0-1						1.0					0.3							1.3				1.0			3.5			2.5			0.6	6.1	0.6			0.6				0.3	2.9
	1-2						0.3																0.6			1.0			0.6				1.6			0.3						0.6
	2-3																																				0.3					0.3
	3-4																																			0.3						0.6
	4-5																														1.0											
	5-6																														2.9											
3604-1	0-1						0.4				0.4	1.3								0.4	0.4					8.1			1.3		1.3	4.7	7.2	5.5	4.7	0.4	0.4	0.4				6.4
	1-2						0.3																			1.0					11.1	1.0		0.6	0.6			0.6				5.7
	2-3																														8.9							1.6				
	3-4																														8.3							2.2				
	4-5																														3.2											

Appendix C. (continued)

GeoB station	Sediment depth	*Cribrostomoides wiesneri*	*Crithionina* sp.	*Cyclammina cancelata*	*Cystammina pauciloculata*	*Dentalina* spp	*Deuterammina montagui*	*Discammina* spp.	*Earlandammina inconspicua*	*Eggerella bradyi*	*Epistominella exigua*	*Epistominella rugosa*	*Epistominella smithi*	*Eponides pusillus*	*Eponides tumidulus*	*Fissurina* spp.	*Fontbotia wuellerstorfi*	*Fursenkoina earlandi*	*Fursenkoina mexicana*	*Gavelinopsis translucens*	*Glandulina ovula*	*Glandulonodosaria calomorpha*	*Globobulimina affinis*	*Globocassidulina subglobosa*	*Globulotuba* sp.	*Glomospira gordialis*	*Gyroidinoides polius*	*Gyroidinoides soldanii*	*Gyroidinoides umbonatus*	*Haplophragmoides bradyi*	*Haplophragmoides coronatum*	*Haplophragmoides* sp.	*Haplophragmoides sphaeriloci*	*Hoeglundina elegans*	*Hormosina globulifera*	*Hyperammina elongata*	*Karreriella bradyi*	*Karrerulina conversa*	*Labrospira ringens*	*Lagena* spp.	*Lagenammina difflugiformis*	*Lagenammina spiculata*
4901-6	0-1										0.3																						0.3	3.5							3.2	
	1-2										1.0									0.3													0.3	1.3							1.6	
	2-3																																	0.3							1.0	
4904-7	0-1	0.6					1.3							3.8		0.6				19.1													0.6								5.7	
	1-2							1.9			0.6									8.3															0.6						0.6	
	2-3			0.6		0.6								0.6						1.3							1.9				0.6			0.6								
	3-4																						3.8																			
	4-5																						0.6																		1.9	
	5-6																						1.3																		1.9	
	6-7																						0.6																		3.8	
	7-8																																								0.6	
4906-5	0-1									1.0	0.3	0.6					0.3			2.9														2.2							6.1	
	1-2	0.3								0.3								1.3		3.2															0.3					0.3	9.2	
	2-3	0.3								0.3								2.5		0.6																0.3					1.0	
4909-4	0-1	1.3			0.6			3.2		1.3		3.2		1.9						9.6							0.6		0.6					12.7	0.6	1.9		0.6			7.0	
	1-2					0.3						1.0						0.3		2.9							0.3							1.6	0.3	1.0					2.9	
	2-3											0.3						4.1		1.3														0.3		0.6		0.3				
	3-4																	6.4		0.6															0.3				1.0		1.3	
4912-4	0-1	1.9	4.5	0.6	0.6			10.2		1.3	3.2						0.6			11.5							1.9	1.3	0.6				5.1	25.5	1.9			6.4			31.2	
	1-2	2.5	1.9		11.8	0.3				0.3							0.3			0.3		0.3					1.6	0.3					1.0	2.9	0.3			8.3			9.2	
	2-3	5.7	0.6		8.6			0.3	0.3	0.3													2.2				1.6			0.3				0.6	0.3	0.3		1.0			1.0	
	3-4	2.9			1.3				0.3												0.3		2.9				0.3					0.3		0.6							0.3	
	4-5	0.3						0.3														0.3	4.1										0.3	1.0							1.3	
	5-6																						1.9																			
4913-4	0-1	1.0																		1.3							0.3								0.3	1.9		0.3			0.3	
	1-2	0.3	0.3															0.3																		0.6		0.3			0.3	
	2-3																	0.3																		0.3						
	3-4																			0.3																					0.3	
4915-3	0-1	0.3		1.0			1.0	0.3	0.3		7.0						2.9			14.6				0.6			1.6						0.6	1.0	2.2			4.8	0.6	0.6	3.2	
	1-2		0.6																0.3	0.3			0.3				1.9						1.0	0.3	1.9				0.3		1.9	
	2-3																		0.3				1.0				0.6							0.3	1.0						1.0	
	3-4																			0.3														0.6							1.0	
	4-5																			0.6														0.6								
4916-4	0-1		4.1										1.3			0.6			0.3	5.7	0.3						1.0		1.3	5.1					1.6					0.3	5.7	
	1-2		4.1	0.6			0.6								0.3	0.3	0.3		2.5	0.6							1.9			25.8	0.3			0.3	1.3			1.0			4.8	
	2-3		0.3													0.6			1.9	0.3	0.3		0.3	0.3			1.6		0.3	7.6		0.3		0.3							1.3	
	3-4																		0.6					0.3						1.0											0.3	
	4-5															0.3			1.6				0.6																		0.6	
4917-5	0-1						1.3	1.3					53.5							12.7	3.8		1.3				7.6		5.1	3.8		1.3			7.6	1.3		5.1		1.3	29.3	
	1-2							1.3					1.3								1.3		5.7				3.8			2.5			0.6					1.3			12.1	
	2-3						1.0	0.6	0.3										3.8	0.6	0.3		4.8				0.3		1.0	0.6								0.3			1.3	
	3-4							0.3	0.3						1.0				4.1	0.6			1.6						0.6	0.3											2.5	
	4-5							1.0											2.5	0.3			2.9			0.3															2.9	
	5-6							0.3											0.6				0.6																		0.3	
4918-4	0-1			0.3									21.0			1.0				1.0							1.0			7.6					0.3						14.3	
	1-2												1.6			1.3							0.3							7.0											4.8	
	2-3												1.0																	4.1											1.6	
	3-4												0.6										0.3							0.6											2.5	
	4-5												1.0																	0.6											1.3	
3713-1	0-1			1.0			1.0	0.6					0.3			0.3	1.3			0.6	1.3				1.6	0.3	0.3					0.3	0.6		0.3	0.3				0.6	4.5	0.6
	1-2	0.6		0.6			1.9		0.6				2.5				7.6		0.6	1.3	2.5		0.6		4.5		1.3	0.6		7.6					3.2						1.3	2.5
	2-3			0.8			0.8	0.6								0.8			9.3		4.2		3.4		0.8		1.7			34.8					3.4	1.7	0.8				4.2	2.5
	3-4							2.0		0.5			0.5				0.5		9.7	0.5	3.1		6.1		0.5					30.1						1.5		0.5			1.0	
	4-5																		1.9		0.3	0.3	2.9			0.3				1.9					0.6						0.3	
	5-6							1.0													0.3		1.3			0.3				0.6										0.3		
	6-7			0.3									0.3										2.2																			
3712-1	0-1		1.3	0.6				1.0	1.9							0.3			0.6	0.3			0.3			1.0	0.6								1.3					1.3	4.1	
	1-2			5.1			2.5	2.5								10.2			5.1	10.2							5.1						5.1		12.7					2.5	22.9	
	2-3		6.8	1.0	1.7		0.8	1.7								1.7			0.8	0.8				0.8		1.7	1.7	0.8		0.8					2.5	0.8					5.1	
	3-4			0.3				1.3	0.3										6.1	0.3						1.0	1.3								1.0	0.3					2.5	
	4-5		0.6				0.3	0.6											11.8							1.3	0.3														1.9	
	5-6							0.3								0.3			6.1																0.3						3.5	
	6-7		0.3					0.6											1.0	0.3						0.3															2.9	
	7-8		0.3																0.3																						1.0	
	8-9		0.6			0.3													0.3																						0.6	
3715-1	0-1		5.7				0.3									3.8			2.5	0.6	0.3		1.6		0.3			0.6							8.3	0.3				1.0	1.3	
	1-2		1.0													1.6			6.4				4.1					1.3	1.0	0.3					6.7					0.6		
	2-3		2.5													0.6			10.5				4.1												1.3							
	3-4		1.0																10.2				9.6												0.6							
	4-5		1.6				0.3									0.3			8.6				10.8																			
	5-6		0.3													0.3			7.3				11.5																			
	6-7						0.3												3.5				13.7																		0.3	
	7-8																		1.3				5.1																			

Appendix C. (continued)

GeoB station	Sediment depth	*Cribrostomoides wiesneri*	*Crithionina* sp.	*Cyclammina cancellata*	*Cystammina pauciloculata*	*Dentalina* spp.	*Deuterammina montagui*	*Discammina* spp.	*Earlandammina inconspicua*	*Eggerella bradyi*	*Epistominella exigua*	*Epistominella rugosa*	*Epistominella smithi*	*Eponides pusillus*	*Eponides tumidulus*	*Fissurina* spp.	*Fontbotia wuellerstorfi*	*Fursenkoina earlandi*	*Fursenkoina mexicana*	*Gavelinopsis translucens*	*Glandulina ovula*	*Glandulonodosaria calomorpha*	*Globobulimina affinis*	*Globocassidulina subglobosa*	*Globulotuba* sp.	*Glomospira gordialis*	*Gyroidinoides polius*	*Gyroidinoides soldanii*	*Gyroidinoides umbonatus*	*Haplophragmoides bradyi*	*Haplophragmoides coronatum*	*Haplophragmoides* sp.	*Haplophragmoides sphaeriloculum*	*Hoeglundina elegans*	*Hormosina globulifera*	*Hyperammina elongata*	*Karreriella bradyi*	*Karrerulina conversa*	*Labrospira ringens*	*Lagena* spp.	*Lagenammina difflugiformis*	*Lagenammina spiculata*
3711-1	0-1						0.4	0.4									1.5	4.4		1.5	7.6	0.4			0.4			0.7	1.5								21.1						1.5	
	1-2			1.0		1.0	1.0									1.0	7.1		2.0	18.3	2.0			1.0				2.0	2.0						40.8								
	2-3		0.6													0.6	2.2		3.2	5.1	0.6						2.2									19.7								
	3-4																		12.4	1.0								0.6	0.3								1.6								
	4-5																	0.3		14.6	2.2								0.3									1.3								
	5-6							0.3										0.3		11.1	0.6			0.3					0.3									0.3								
	6-7																		2.5	0.3																	0.3								
	7-8																		0.6																									
3708-1	0-1		7.6	5.7		0.6				2.5					0.6	3.8	1.9		17.2	20.4			0.6	3.2			1.9	1.3								9.6					0.6	4.5	
	1-2		5.1	3.8													1.3		58.6	5.1			7.6	3.8			5.1	2.5								1.3						6.4	
	2-3		1.3	2.5		0.6				1.3						1.3	0.6		47.1	1.3			5.7	1.3			1.3	1.3								5.1					0.6	0.6	
	3-4															0.6	1.9		16.2	0.3			9.9				0.3	0.3								0.3						0.3	
	4-5															0.3			11.1				11.1																		0.3	0.3	
	5-6									0.3									6.1				7.0	0.3																	0.3	
	6-7																		5.7				3.5																				
3706-3	0-1		3.5							8.3						0.3	4.8			11.5					2.9			0.6	0.3								5.1								
	1-2		1.6			0.3	0.3			5.4						0.3	3.5			13.1					1.9			1.0		0.6							4.5	0.6				1.0		
	2-3		0.4	0.4						3.8						0.8	3.0			3.8					4.2			1.3	0.8								4.7	0.8				0.4		
	3-4			0.3			0.3			1.9						0.3	1.3		1.0	1.9					0.3			0.3		0.3							0.6	0.3				0.3		
	4-5									1.3						0.3	0.3		1.3	1.6			0.3				0.3										0.3								
	5-6									0.3									0.3				1.0													0.3								
	6-7																		3.2				0.6																					
3725-1	0-1		1.3							6.7	1.0					0.3	4.5			3.8				1.0		0.3	0.6	5.7	0.3									1.0						
	1-2	1.0								2.9	0.3					0.3	2.5		0.3	3.5				1.3			2.2	9.2	0.6														
	2-3	1.3								0.6						0.3	1.3	0.3		0.3	0.6			1.3				4.5	4.1											0.3						
	3-4																		0.6	0.6			1.6				1.0	1.0																
	4-5																		0.6				1.0					0.3															
	5-6																	0.3		0.6				1.9																			
	6-7																	0.3		0.3	0.6			2.2																			
	7-8																							1.3					0.3															
3705-2	0-1		1.3	2.2						9.6						1.0	1.6			2.2				2.2			0.6														0.3	
	1-2		0.8	5.1		0.4				7.6							0.8		0.8	0.8				2.1			3.0	0.4	0.4						0.4						0.8	
	2-3			1.9						2.5						0.3	0.6		1.6	1.0				0.3			1.9																
	3-4									0.6							0.3		2.9	0.6																						
	4-5																		2.2	0.3				0.3																			
3703-4	0-1		0.8			1.7										2.5			3.4	6.8	2.5		9.3	2.5																	0.8	3.4	
	1-2						1.5												2.9	2.2			13.8				1.5														1.5	2.2	
	2-3																		2.2	0.3			7.0	0.3			0.6															1.3	
	3-4																							9.9														0.3						0.3	
	4-5																	0.3		1.9				7.3																			
	5-6																		1.0				18.5																			
	6-7																		3.2	0.3			31.8																			
	7-8																		2.2				13.1																			
	8-9																		1.0				7.6				0.3															
	9-10																							12.1																			
	10-11																			0.3			6.7																			
3702-2	0-1		1.9							1.6	0.3					0.3	1.6		0.6	9.9				2.9			1.9	1.6	1.9													1.0	6.1	
	1-2		3.5	1.3						0.6							0.6			2.9			0.3	1.0			3.8	5.7	1.9						0.3						4.5	
	2-3			0.6														6.7	0.3			1.3				0.6	1.0															2.9	
	3-4						0.3												2.2				0.3																		1.0	
	4-5																		2.2				1.3					0.3															0.3	
3701-1	0-1									2.9						0.3	0.3			3.5				4.8		0.3		0.3														1.0		
	1-2	0.6	0.6	1.9					0.6	2.5	3.8							0.6			13.4				1.3			5.1	3.2						0.6		0.6	0.6		1.3		0.6		
	2-3	3.2	1.6	0.6		0.3				0.6	1.0					0.3				0.3				0.6			1.6	0.3			1.0			0.3		0.6		1.9		0.3		
	3-4	3.5										0.6									0.6								0.3			7.0											
	4-5	0.3					0.3														1.0			0.3																		
1720-3	0-1	0.3							0.6	4.5	5.7					1.9	0.3			0.3				1.6			1.9	0.6						6.7	20.1						0.6	0.6	
	1-2	1.0								2.2	3.8						0.3			0.6				1.0			2.9		0.6					2.5	5.7		0.3				0.3		
	2-3	0.3			1.9																			0.3			1.3							1.3								
	3-4	1.0			4.8																																						
	4-5				1.0																			1.3				0.6															
	5-6																							1.3												0.3								
3604-1	0-1	0.4	4.7	0.8					0.4	3.4	0.8				0.4	0.8	0.4			9.3				9.3			5.1		1.7							0.8	0.4	0.4						
	1-2		1.9	0.3					0.3	1.0										0.6			0.6	1.0			0.3							0.6				2.2						
	2-3	0.3					0.6																	1.3											0.3									
	3-4						11.5											1.3						1.3																			
	4-5						6.7																																				

Appendix C. (continued)

GeoB station	Sediment depth	Lagenammina tubulata	Laticarinina pauperata	Lenticulina spp.	Martinotiella communis	Melonis barleeanum	Miliolidae sp.	Nodosaria spp.	Nonion commune	Nonion sp.	Nouria harrisii	Oolina spp.	Oridorsalis umbonatus	Osangularia culter	Placopsilinella aurantiaca	Paratrochammina challengeri	Planularia sp.	Portatrochammina spp.	Praecystammina globigerinifo	Praecystammina sp.	Psammosphaera fusca	Psammosphaera sp.	Pseudogaudryina sp.	Pseudonodosinella nodulosa	Pullenia bulloides	Pullenia subcarinata	Pyrgo depressa	Pyrgo elongata	Pyrgo lucernula	Pyrgo murrhina	Pyrgo serrata	Pyrgo sp.	Pyrgo williamsoni	Pyrgoella sphaera	Quinqueloculina spp.	Recurvoides contortus	Recurvoides scitulum	Reophax agglutinatus	Reophax bilocularis	Reophax dentaliniformis	Reophax distans
4901-6	0-1												0.3												1.0	0.6													1.9		
	1-2	0.3																								0.3													1.0		
	2-3																								0.3														0.3	0.6	
4904-7	0-1	1.9		0.6									0.6	0.6											0.6					1.3					1.3	1.3			2.5	1.3	
	1-2												1.3												1.3										0.6	0.6			1.3	5.7	
	2-3					15.3				0.6									0.6						1.3					0.6										7.6	
	3-4					7.0					0.6																												1.3	1.3	
	4-5										1.9																												1.9	0.6	
	5-6					0.6																																			
	6-7																																						0.6		
	7-8																																						1.3		
4906-5	0-1	3.2				1.0															0.3			0.3															6.1		
	1-2	3.5				3.5					1.6			1.0										0.6	0.3														4.1		
	2-3	3.2				1.3			0.6		2.2			0.3																					0.3				1.0	0.6	
4909-4	0-1	6.4		0.6									1.3		1.3		1.3													0.6					1.3				21.7	1.3	
	1-2	2.2				0.3							0.3																							1.3			10.5		
	2-3	0.3				2.9		0.3									0.3																						3.5	0.6	
	3-4					2.2									0.3									0.3															0.3		
4912-4	0-1	3.8	0.6	1.9			1.3			0.6			0.6	3.2		0.6									4.5					1.3			1.3		0.6	9.6			5.7	1.9	
	1-2	0.6				4.5			0.3	0.6	0.3			0.3		1.0				1.0						0.6										7.0			1.3	1.0	
	2-3		0.3			6.7			0.3	1.0	1.3			0.3											0.3											0.6	0.3		0.3	0.6	
	3-4					4.5		0.3	0.3		0.6															0.3										1.0					
	4-5					0.3					2.2															0.3							0.3			0.3					
	5-6										0.3		0.3																							0.3	0.3				
4913-4	0-1	0.3							0.3					0.3																							0.3				
	1-2																																								
	2-3										0.3																														
	3-4																																								
4915-3	0-1	0.3	1.0									0.3	2.9	1.6											1.6		0.6									0.6	0.6		4.8		
	1-2					2.2										0.3																				1.0			1.0	3.2	
	2-3					1.3																														0.3				0.3	
	3-4					1.3			0.3		0.3			0.3											0.6			0.3							0.3				0.3		
	4-5		0.3			1.3																			0.3														1.6		
4916-4	0-1					1.3				0.3			0.6			0.6					0.6				0.3											5.1	0.3		3.5		
	1-2					3.2				0.3			0.3					0.3	1.0		0.6														0.3	6.1			2.9	0.6	
	2-3					1.9							1.0						0.3		1.0															1.9			0.6	0.3	
	3-4					0.3			0.3	0.3	0.3																												0.3		
	4-5					1.0																																			
4917-5	0-1					2.5	1.3			1.3		1.3	3.8					1.3	2.5			5.1										2.5			11.5			1.3	34.4	3.8	
	1-2						0.6		0.6	0.6	1.3		2.5									1.9												0.6	1.9				14.0		
	2-3					0.3				0.6	2.5		0.3									2.2										0.3			1.3	0.3			3.2		
	3-4					0.3				1.0	1.0											0.6																	1.3		
	4-5					1.6			0.3	0.3									0.3			0.6																	1.3		
	5-6																																								
4918-4	0-1					5.1							1.6	0.3																						1.9			0.3		
	1-2					4.1							0.6																							1.0					
	2-3					1.0																																			
	3-4					1.6																																			
	4-5					0.6																																			
3713-1	0-1	0.3				0.3							1.0								5.1	3.2			0.3							0.3			0.3	1.3	3.5		12.4		
	1-2					1.9					1.3		0.6			0.6					1.3	0.6			1.3											23.6	7.0		24.2	1.3	
	2-3	1.7				12.7					5.1		2.5			0.8		3.4			7.6	0.8			0.8										0.8	5.9	17.0		32.3	4.2	
	3-4					9.2					2.5		0.5								1.5	2.0				0.5									0.5	1.0	4.6		10.7	0.5	
	4-5					3.2					3.2					0.3		0.3			0.3															0.3			3.5		
	5-6					1.6					0.6										1.0	0.3																	1.9		
	6-7					0.3																																	1.3		
3712-1	0-1	0.6				0.3					0.3		1.3			1.9					1.0	3.2					0.6	0.3		0.3				0.3	0.3	0.3	3.8		6.1	1.9	
	1-2	2.5								2.5			15.3			5.1		28.0			20.4	56.1			2.5			2.5						2.5		25.5	10.2	5.1	66.2	22.9	5.1
	2-3	0.8										0.8	8.5		5.9	0.8					1.7															10.2	4.2		21.3	4.2	
	3-4	0.3	0.3								1.6		3.2		0.3	1.0					0.3	0.3			0.3											3.2			14.3	0.3	
	4-5	0.3									7.3		1.6								1.0	1.0														0.6	0.3		17.8		
	5-6										4.1		0.6		0.6						1.0						0.3								0.3		0.3		18.5	1.3	
	6-7					0.3					1.9		0.6								0.3				0.6	0.3	0.3												5.1	1.0	
	7-8																																						2.9		
	8-9					1.0															0.3				0.3														1.3		
3715-1	0-1											1.6	5.4																					0.3		1.3			1.9		
	1-2											1.9	4.5					0.6																	0.3	0.3			1.6		
	2-3									0.3			3.8		7.0																				0.3	0.6			1.6		
	3-4										0.3	0.3																													
	4-5						0.3				0.3	0.3	0.3								0.3																				
	5-6												0.6																			0.3									
	6-7						0.3						0.3																												
	7-8																																								

Appendix C. (continued)

GeoB station	Sediment depth	*Lagenammina tubulata*	*Laticarinina pauperata*	*Lenticulina* spp.	*Martinotiella communis*	*Melonis barleeanum*	*Miliolidae* sp.	*Nodosaria* spp.	*Nonion commune*	*Nonion* sp.	*Nouria harrisii*	*Oolina* spp.	*Oridorsalis umbonatus*	*Osangularia culter*	*Placopsilinella aurantiaca*	*Paratrochammina challengeri*	*Planularia* sp.	*Portatrochammina* spp.	*Praecystammina globigerinifor*	*Praecystammina* sp.	*Psammosphaera fusca*	*Psammosphaera* sp.	*Pseudogaudryina* sp.	*Pseudonodosinella nodulosa*	*Pullenia bulloides*	*Pullenia subcarinata*	*Pyrgo depressa*	*Pyrgo elongata*	*Pyrgo lucernula*	*Pyrgo murrhina*	*Pyrgo serrata*	*Pyrgo* sp.	*Pyrgo williamsoni*	*Pyrgoella sphaera*	*Quinqueloculina* spp.	*Recurvoides contortus*	*Recurvoides scitulum*	*Reophax agglutinatus*	*Reophax bilocularis*	*Reophax dentaliniformis*	*Reophax distans*
3711-1	0-1						0.4						0.7								0.4	0.4			0.7			0.4	2.2	8.7	3.6			0.4	0.7	2.9	1.5		1.1	2.2	
	1-2	2.0		1.0			1.0				1.0		2.0															4.1			10.2			3.1		4.1			5.1	4.1	
	2-3										0.3		0.6			0.3		1.0							0.3			2.9	1.6		6.1			0.3	0.3	2.5			3.2	1.0	
	3-4										1.0																		0.3		1.0				0.6				1.0		
	4-5										1.0																								0.3	0.3			0.3		
	5-6										0.3														0.3			0.3	0.3		0.3					0.3			0.3	0.3	
	6-7			0.3																					0.3			0.3	0.3							0.3					
	7-8																																								
3708-1	0-1						2.5						5.7					1.3							3.8		15.9	0.6	0.6	1.3	0.6		1.3	18.5	1.9	1.3	0.6		1.3		
	1-2						5.1						16.6												11.5		12.7		1.3		1.3			25.5	1.3	3.8	5.1		1.3		
	2-3						1.3				1.3		3.2												3.2		5.1		1.9		0.6			14.6		5.1					
	3-4						0.3		0.3		1.9		1.3												1.0		1.0				0.3			2.2		0.3			0.3		
	4-5						0.3				2.2														2.5		0.3							0.3							
	5-6																								1.0																
	6-7																								0.3		0.3							0.3							
3706-3	0-1						1.3						6.1												1.3			0.3		2.9					3.5	1.6	0.6		0.6		
	1-2						0.3				0.6		10.2					0.6			0.6				0.3					1.9				0.6	3.5	7.3	0.6		4.1		
	2-3						1.3				1.3		6.8												1.7		0.4			0.8					1.7	6.4			5.9		
	3-4										2.5		4.1												0.3					0.6					0.3	1.9			1.6		
	4-5										8.6		1.6								0.3															1.0			1.0		
	5-6										6.4														0.3										0.3						
	6-7										1.0	0.3																													
3725-1	0-1					0.3	0.6			0.3			1.6						12.4		0.3					0.6		0.6	0.3	0.3				1.3	1.3	4.8			1.3		
	1-2	0.3		0.3		10.5							1.6						0.6						0.3	0.6										5.4			2.9		
	2-3					18.2							1.0						2.2						0.6	0.6			0.6							2.2	0.3		0.6		
	3-4					15.3							0.3															0.3	0.3							1.3					
	4-5					2.2																			0.6					0.3						0.3			0.3		
	5-6					3.8																																	0.3		
	6-7					2.5																			0.3																
	7-8					2.5													0.3																	0.3					
3705-2	0-1			0.6			2.9	0.6					3.8												0.3		3.2		0.6	13.1				1.3	2.2	1.9			8.9		
	1-2						0.8		0.4		2.1		6.4												0.8		3.4			10.6				11.9		1.7			27.2		
	2-3								0.3		12.4		3.2														0.6			2.9				1.3		0.6			8.3		
	3-4								0.3		9.6																		0.3	0.6				0.3	0.3				0.6		
	4-5								0.3		10.2																														
3703-4	0-1			0.8			0.8						2.5												1.7			0.8											4.2		
	1-2			0.7																					2.9									0.7		0.7			8.0		
	2-3								0.3				0.6												0.3														1.3		
	3-4																																								
	4-5																																								
	5-6																																								
	6-7																																								
	7-8																																						0.3		
	8-9																																								
	9-10																																								
	10-11																																								
3702-2	0-1	0.3		0.3								1.0	4.5			0.3					1.0				1.6	0.3		0.3		0.6					1.0	2.2			4.1		
	1-2			0.3			0.3						3.8			0.3		1.6			0.6				1.9											14.0	1.0		8.6	0.3	
	2-3										1.3		0.3								0.3					0.6		0.3							0.3	1.6	1.0		2.2		
	3-4			0.3							0.6					0.3																					0.3			0.3	
	4-5																									0.3															
3701-1	0-1						1.6			0.3			3.8			0.3			2.9		0.3		1.0		1.3													2.5	1.3		
	1-2												14.0									0.6	3.8		1.3	1.3		0.6	1.3		1.3	0.6			0.6	8.3		2.5	9.6	0.6	
	2-3	1.0			1.3	1.3							1.9			0.3			0.3				1.0			2.2			0.6		0.6					8.6			2.5	5.1	
	3-4				0.6	1.3							0.3										1.0			0.3					0.3					1.0			1.0	6.1	
	4-5					0.3													0.3							1.0										0.3				0.6	
1720-3	0-1	0.3			0.3					0.6		1.0	18.8			1.9			1.6				7.0		1.0					0.6					2.2				1.0		0.6
	1-2			0.3						0.6			5.7										1.3		1.0	1.0			0.3	0.6					0.3	3.8					1.3
	2-3									0.3			0.3										0.3			0.6			0.3							5.1					2.5
	3-4				0.3	2.5				0.3													0.6													2.5					
	4-5					1.0				1.0																0.6															
	5-6					0.3																																			
3604-1	0-1			1.3	1.3		0.8						1.7			1.3				2.1			7.2		0.8	3.8									0.4	6.4			5.5	1.3	0.8
	1-2																			0.3		0.3	1.3			5.7										2.9	1.0		9.9	7.3	
	2-3																									1.3										0.3			0.3	1.0	
	3-4																																						0.3	1.0	
	4-5																																								

Appendix C. (continued)

GeoB station	Sediment depth	*Reophax fusiformis*	*Reophax gaussicus*	*Reophax guttifera*	*Reophax micaceus*	*Reophax nodulosus*	*Reophax pilulifer*	*Reophax scorpiurus*	*Reophax* spp.	*Rhabdammina abyssorum*	*Rhabdammina linearis*	*Robertinoides chapmani*	*Saccammina sphaerica*	*Saccorhiza ramosa*	*Sigmoilopsis schlumbergeri*	*Siphotextularia* sp.	*Sphaeroidina bulloides*	*Spiroloculina* spp.	*Spirophthalmidium pusilla*	*Spirosigmoilina* spp.	*Subreophax aduncus*	*Textularia conica*	*Tholosina* sp.	*Triloculina* spp.	*Triloculinella* spp.	*Trochammina inflata*	*Trochammina nana*	*Trochammina* spp.	*Trochammina tricamerata*	*Trochamminopsis pusillus*	*Uvigerina auberiana*	*Uvigerina peregrina*	*Uvigerina proboscidea*	*Uzbekistania charoides*	*Valvulina conica*	*Valvulineria laevigata*	*Vanhoeffenella gaussi*	*Verneuilinulla propinqua*	*Sum others*	*Total counted*
4901-6	0-1				0.3			9.2				10.5																				0.3	1.6						0.3	111
	1-2				0.3			12.7				1.9							0.3												0.3	0.3	0.6						0.6	73
	2-3				0.3			2.9				0.6	0.3																			0.3							0.0	23
4904-7	0-1			1.9				7.0	0.6			12.7		1.9								0.6			0.6			0.6			5.7	5.7	0.6	1.3				6.4	2.5	204
	1-2			2.5	1.3			7.0				6.4		2.5														0.6			0.6	3.8		0.6				3.8	1.9	117
	2-3					0.6		2.5				0.6		0.6							0.6																	1.9	1.9	93
	3-4								1.9																0.6														0.0	30
	4-5							0.6																														0.6	0.0	24
	5-6	0.6						0.6	1.3																							0.6							0.0	12
	6-7				0.6			1.3	1.3																														0.0	15
	7-8							1.9																									0.6						0.6	9
4906-5	0-1	0.3			1.3			8.6				7.3					3.2	0.3	1.0									0.3			1.6	9.6					0.3		0.6	222
	1-2			0.3	1.9			9.9			0.3	3.2	0.3				0.3	0.6													0.6	6.4				0.3			0.3	214
	2-3				0.6			2.2				1.3																			0.3	3.2							0.0	80
4909-4	0-1			2.5	3.2		1.3	11.5				15.9	1.9				0.6		0.6		0.6							5.1			4.5	17.8	2.5						1.9	278
	1-2				0.3			7.0			0.3	4.1	1.0	0.3			0.3		0.3									0.3			1.0	6.1							1.3	189
	2-3				1.0			5.4				0.3																0.3				1.3	0.3						0.6	92
	3-4	0.3			0.3			1.0					0.3																		0.3								0.0	61
4912-4	0-1			1.9				12.1		0.6	3.2	44.6	1.9	1.3		0.6	10.2	0.6													2.5	21.7	1.9					1.9	3.2	240
	1-2			1.0	0.3		0.6	1.3				7.0	0.3				1.9											1.0				2.5				0.3			0.3	79
	2-3				2.9	0.3		1.3				0.6				0.3										0.6		0.3				0.6				1.0			0.0	52
	3-4							0.3				1.3					0.3									0.3						1.3				1.3			0.0	46
	4-5											0.6					0.3	0.3														1.0				0.6			0.0	30
	5-6																																						0.0	10
4913-4	0-1						1.0	0.6																				0.6				3.5							0.6	77
	1-2							0.3																													0.3		0.0	23
	2-3												0.3																			1.3							0.0	30
	3-4										0.3																					0.3							0.0	21
4915-3	0-1			0.3	0.3			1.3	0.3			3.2					4.5					0.3						0.6			0.3	3.2				3.2		2.5	1.0	306
	1-2		0.6				2.2					0.6					0.3											0.3								1.6			0.3	77
	2-3		0.6				0.3																													1.6			0.0	33
	3-4						0.3					0.3																								0.3			0.3	30
	4-5						0.6	0.3				0.3																								0.3			0.0	22
4916-4	0-1			0.6			3.2	1.6	1.0		0.3	0.3					0.6									0.6		1.3				1.3				14.0		0.3	0.3	308
	1-2						1.9	2.9	0.6								1.0									0.6		1.3				1.0				36.9		0.3	0.0	480
	2-3						1.3	0.3									1.6									0.3		0.6			1.0					17.5			0.0	247
	3-4						0.3	0.6																															0.0	35
	4-5																0.3											0.3											0.0	27
4917-5	0-1			2.5	3.8		1.3	1.3									8.9				1.3			1.3				2.5		12.7	8.9	59.9			5.1	26.8			2.5	443
	1-2	0.6		3.2	6.4		2.5		0.6		1.3						3.2														14.0	19.1			1.9	12.7			3.2	336
	2-3						0.3	0.3	0.3								1.0							0.3				0.6		1.3	9.6	1.3			1.0	7.0			1.0	274
	3-4			0.6	1.0		0.3	0.3																				0.6		0.6	1.0					0.3			0.0	99
	4-5			0.6			0.3																					1.3		1.6		1.0			0.3			0.3	0.0	90
	5-6			0.3																												0.3							0.0	17
4918-4	0-1						13.7	0.3					8.6				0.3											0.6				0.3			2.2	7.0		0.3	0.3	609
	1-2						2.5	0.3					3.2															0.6			0.6				0.3	1.3			0.6	307
	2-3						1.3																			1.0		0.3								1.3			0.0	116
	3-4						1.0																																0.0	63
	4-5						1.0																												0.3				0.0	45
3713-1	0-1			0.6	0.3		2.9	1.3	0.3				1.9				1.0			0.6	3.8							1.3		0.3		1.6			9.9	2.5		0.6	1.6	331
	1-2			3.2	0.6	0.6	3.8	3.2	5.1				0.6				4.5				1.3	0.6								1.3	1.3	5.7			7.6	10.2			1.3	347
	2-3			2.5		0.8	0.8	0.8	1.7				3.4				3.4											1.7		0.8	1.7	1.7			6.8	22.9			2.5	350
	3-4	0.5		0.5			1.5	0.5	3.1				0.5				4.6											1.0			1.0				0.5	10.7			0.0	288
	4-5			1.0			0.3		0.6												1.6														0.6	2.2			0.0	112
	5-6			0.6			0.3		0.6																														0.0	43
	6-7						0.3		0.3																														0.0	22
3712-1	0-1			1.0			7.6	1.3	1.9	0.3			1.0				0.3				1.6	0.3	7.6					4.1		1.0	3.8				13.4	1.3			1.9	359
	1-2			12.7		2.5	20.4		12.7				2.5				15.3				12.7	7.6						35.7			43.3				135.0	40.8			5.1	350
	2-3			1.7	0.8	1.7	5.9						1.7			0.8	3.4				1.7		9.3					5.1		1.7	27.2				50.1	30.6			2.5	382
	3-4			0.6	0.6		1.3	0.6	1.3				0.3			0.3	2.9				1.3	0.3	1.0					1.0		0.3	12.4				6.4	15.9			1.9	365
	4-5			0.3			3.5	1.3	0.6							0.3	0.6				0.6		2.9					3.2			1.0				5.7	1.9			0.6	266
	5-6			1.0	0.6		5.1		1.9								0.3				0.3	0.3						1.0			1.3				1.3	0.6			0.0	209
	6-7						0.6	0.3	0.6								0.3							0.3							0.6					0.3			0.0	75
	7-8						1.0		0.3													0.3									0.3					0.3			0.0	34
	8-9				0.3			1.3	0.3																														0.0	30
3715-1	0-1		0.3	0.6																5.1				1.0				1.9			7.6				3.5				0.3	271
	1-2			1.3				0.6												3.2				0.3				0.3			9.9				1.9				0.3	234
	2-3			0.6				0.3												3.2				0.6				1.3			7.0				6.4	0.3			0.0	225
	3-4																														0.6								0.0	75
	4-5			0.3																											0.3								0.0	81
	5-6																																						0.0	67
	6-7																														0.3								0.0	63
	7-8																																		0.3				0.0	23

Appendix C. (continued)

GeoB station	Sediment depth	*Reophax fusiformis*	*Reophax gaussicus*	*Reophax guttifera*	*Reophax micaceus*	*Reophax nodulosus*	*Reophax pilulifer*	*Reophax scorpiurus*	*Reophax* spp.	*Rhabdammina abyssorum*	*Rhabdammina linearis*	*Rhizammina algaeformis*	*Robertinoides chapmani*	*Saccammina sphaerica*	*Saccorhiza ramosa*	*Sigmoilopsis schlumbergeri*	*Siphotextularia* sp.	*Sphaeroidina bulloides*	*Spiroloculina* spp.	*Spirophthalmidium pusilla*	*Spirosigmoilina* spp.	*Subreophax aduncus*	*Textularia conica*	*Tholosina* sp.	*Triloculina* spp.	*Triloculinella* spp.	*Trochammina inflata*	*Trochammina nana*	*Trochammina* spp.	*Trochammina tricamerata*	*Trochamminopsis pusillus*	*Uvigerina auberiana*	*Uvigerina peregrina*	*Uvigerina proboscidea*	*Uzbekistania charoides*	*Valvulina conica*	*Valvulineria laevigata*	*Vanhoeffenella gaussi*	*Verneuilinulla propinqua*	*Sum others*	*Total counted*
3711-1	0-1		0.4	1.8			0.7		2.2								0.4	0.7	0.4						1.1				1.1		0.4	3.3	0.7			3.6				2.2	520
	1-2			3.1			3.1		4.1									2.0							1.0				1.0			7.1	2.0			4.1	1.0			0.0	254
	2-3		0.3	0.6			0.3							0.3		0.3		1.0							0.3				1.6			4.5	0.6			2.5				0.3	469
	3-4								0.3														0.3									3.5								0.3	123
	4-5																	0.6					0.3						0.3			1.3								0.0	120
	5-6																						0.3						0.3							0.3				0.0	86
	6-7								0.3									0.3																			0.3			0.0	32
	7-8																						1.0																	0.0	30
3708-1	0-1			2.5	0.6												0.6	5.1	0.6		0.6		1.3		4.5				1.9			13.4	0.6				5.1			0.6	415
	1-2				2.5													5.1	1.3		1.3		1.3						2.5			36.9	1.3				8.9			1.3	308
	2-3			0.6			1.3									0.6	1.3				0.6		3.2		0.6							5.7					4.5			0.6	311
	3-4																	0.3					0.3									0.3	0.3				1.3			0.0	219
	4-5																															0.3								0.0	104
	5-6																																							0.0	51
	6-7																0.3	0.3					0.3									0.3								0.0	41
3706-3	0-1			0.3	0.3									0.3		0.3	0.3	3.8					0.6		0.6				1.0			0.6	0.3				0.3			0.3	457
	1-2															0.3	0.3	4.5					1.3				0.3		0.6			0.3	1.0				3.5			0.6	469
	2-3			0.4													0.4	6.4					1.3						1.7								5.5			0.4	394
	3-4			0.6					0.3									0.6									0.3										3.5			0.0	183
	4-5															0.3		0.3									0.3										0.6			0.0	113
	5-6																	0.3					0.3														0.3			0.0	52
	6-7																																							0.0	17
3725-1	0-1											0.2		0.3				0.3			0.3				1.6				1.0			0.3	3.2				0.3			1.3	264
	1-2											0.0		0.6				0.6							0.3		0.6		1.3			0.3	1.3				5.4			1.0	233
	2-3																								1.0		0.3					0.3	0.6				1.6			0.0	164
	3-4				0.3																																2.2			0.0	94
	4-5																												0.3								0.6			0.0	47
	5-6																																							0.0	32
	6-7																												0.3											0.0	30
	7-8																																							0.0	18
3705-2	0-1													2.5				1.9	0.6		0.6				0.6		1.0		0.6			0.3								1.0	369
	1-2				1.3									1.3				3.8			0.4				0.4				2.5			0.4					2.5			2.1	406
	2-3				0.3				0.3					0.3		0.3		0.6			0.3								0.3			0.6					1.3			0.6	197
	3-4																																							0.0	58
	4-5																																							0.0	47
3703-4	0-1													1.7		0.8					2.5				0.8				2.5			152.9					17.0			1.7	338
	1-2																				0.7								1.5			163.1					6.6			0.7	350
	2-3																								0.6				1.6			34.7					1.9			0.0	197
	3-4																															3.8					0.3			0.0	56
	4-5																										0.3		0.3								0.3			0.0	37
	5-6																																				0.6			0.0	70
	6-7																															0.6					0.3			0.0	128
	7-8																																				0.3			0.0	58
	8-9																																				0.3			0.0	33
	9-10																																							0.0	39
	10-11																																							0.0	22
3702-2	0-1			0.3	0.6					3.8				4.5		0.3		2.2			0.3				3.5		0.3		3.2			1.3					1.9			0.6	289
	1-2				2.5		1.9							1.0				1.6							0.3							0.6					14.0			0.0	298
	2-3				0.3		0.3	0.3						0.3				0.6							0.3							1.0					2.9			0.0	126
	3-4																								0.3															0.0	38
	4-5																																							0.0	24
3701-1	0-1			1.0	1.6				0.3							0.3	0.3	21.0					2.5					0.3	1.0				0.3						1.6	1.6	291
	1-2			1.9	16.6				0.6				0.6	1.9		4.5	3.2	39.5				1.3	2.5				0.6	3.2	0.6						2.5				1.3	1.3	385
	2-3				5.1	0.6					0.3		0.3	0.3		1.6	0.6	9.6					1.3				0.3	0.3	0.3			0.3			2.5					0.3	272
	3-4				1.6											3.5	0.6	1.3					1.6												1.9				0.6	0.0	131
	4-5				0.6													0.6									1.0										0.6			0.0	26
1720-3	0-1			5.1	2.5								6.1	0.3			0.3	3.5									0.3	0.3	1.0	3.2			11.8		3.8					3.8	460
	1-2			1.3	3.5								2.9	0.6			0.3	2.9											0.3	1.3		0.3	2.9		8.9					0.6	215
	2-3				1.3									0.3		0.3		2.5											0.3				0.6		3.5					0.0	76
	3-4													0.3		1.3																	0.3		1.9					0.3	54
	4-5																												0.3						0.3					0.0	22
	5-6																												0.3											0.0	16
3604-1	0-1			0.4	1.7							1.0	2.5	0.8	0.4	1.7	1.7	12.3					1.3		0.4				1.3					0.4	1.3		0.4			3.4	355
	1-2				0.6						0.3	0.6	0.3	0.3	0.6	3.2	0.3	5.4											0.3						1.0					0.6	230
	2-3				0.3						0.3					1.3																								0.0	57
	3-4															0.3	0.3																							0.0	83
	4-5																																							0.0	31

4. Carbon isotopes of live benthic foraminifera from the South Atlantic: Sensitivity to bottom water saturation state and organic matter rain rates

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4.1. Abstract

Live (Rose Bengal stained) and dead benthic foraminifera of surface and subsurface sediments from 25 stations in the eastern South Atlantic Ocean and the Atlantic sector of the Southern Ocean were analyzed to decipher a potential influence of seasonally and spatially varying high primary productivity on the stable carbon isotopic composition of foraminiferal tests. Therefore, stations were chosen so that productivity strongly varied, whereas conservative water mass properties changed only little. To define the stable carbon isotopic composition of dissolved inorganic carbon ($\delta^{13}C_{DIC}$) in ambient water masses, we compiled new and previously published $\delta^{13}C_{DIC}$ data in a section running from Antarctica through Agulhas, Cape and Angola Basins, via the Guinea Abyssal Plain to the Equator.

We found that intraspecific $\delta^{13}C$ variability of all species at a single site is constantly low throughout their distribution within the sediments, i.e. species specific and site dependent mean values calculated from all subbottom depths on average only varied by ±0.09 ‰. This is important because it makes the stable carbon isotopic signal of species independent of the particular microhabitat of each single specimen measured and thus more constant and reliable than has been previously assumed. So-called vital and/or microhabitat effects were further quantified: (1) $\delta^{13}C$ values of endobenthic *Globobulimina affinis*, *Fursenkoina mexicana*, and *Bulimina mexicana* consistently are by between -1.5 and -1.0 ‰ VPDB more depleted than $\delta^{13}C$ values of preferentially epibenthic *Fontbotia wuellerstorfi*, *Cibicidoides pachyderma*, and *Lobatula lobatula*. (2) In contrast to the Antarctic Polar Front region, at all stations except one on the African continental slope *Fontbotia wuellerstorfi* records bottom water $\delta^{13}C_{DIC}$ values without significant offset, whereas *L. lobatula* and *C. pachyderma* values deviate from bottom water values by about -0.4‰ and -0.6‰, respectively. This adds to the growing amount of data on contrasting cibicid $\delta^{13}C$ values which on the one hand support the original 1:1-calibration of *F. wuellerstorfi* and bottom water $\delta^{13}C_{DIC}$, and on the other hand document severe depletions of taxonomically close relatives such as *L. lobatula* and *C. pachyderma*.

At one station close to Bouvet Island at the western rim of Agulhas Basin, we interpret the offset of -1.5 ‰ between bottom water $\delta^{13}C_{DIC}$ and $\delta^{13}C$ values of infaunal living *Bulimina aculeata* in contrast to about -0.6 ± 0.1 ‰ measured at eight stations close-by, as a direct reflection of locally increased organic matter fluxes and sedimentation rates. Alternatively, we speculate that methane locally released from gas vents and related to hydrothermal venting at the mid-ocean ridge might have caused this strong depletion of ^{13}C in the benthic foraminiferal carbon isotopic composition. Along the African continental margin, offsets between deep infaunal *Globobulimina affinis* and epibenthic *Fontbotia wuellerstorfi* as well as between

shallow infaunal *Uvigerina peregrina* and *F. wuellerstorfi,* $\delta^{13}C$ values tend to increase with generally increasing organic matter decomposition rates. Although clearly more data are needed, these offsets between species might be used for quantification of biogeochemical paleogradients within the sediment and thus paleocarbon flux estimates. Furthermore, our data suggest that in high-productivity areas where sedimentary carbonate contents are lower than 15 weight %, epibenthic and endobenthic foraminiferal $\delta^{13}C$ values are strongly influenced by ^{13}C enrichment probably due to carbonate-ion undersaturation, whereas above this sedimentary carbonate threshold endobenthic $\delta^{13}C$ values reflect depleted pore water $\delta^{13}C_{DIC}$ values.

4.2. Introduction

Benthic foraminifera are the only abundant and ubiquitous benthic marine protists of the deep sea that, due to their mostly calcareous tests, have a great potential to become fossilized. They record paleoenvironmental conditions directly in the trace elemental and isotopic composition of their calcareous test, and indirectly by particular faunal compositions specifically adapted to environmental parameters such as food supply, oxygen content, hydrodynamic and physicochemical conditions of bottom water masses. For paleoceanographic purposes it is most interesting to know what specific environmental conditions are recorded by benthic foraminifera and how sensitive their response is to changes in these parameters.

Since the work of Corliss (1985) and the detailed analyses of Gooday (1986) it is agreed that specific deep-sea benthic foraminifera do live in stratified depths within the sediment down to a depth of 10-15 cm below the seafloor. After a decade of intensive research and collecting high-quality samples using multiple corers, there is no doubt that food availability and oxygen content of the interstitial waters most substantially control the benthic foraminiferal microhabitat (e.g. Mackensen and Douglas, 1989; Gooday and Turley, 1990; Bernhard, 1992; Jorissen et al., 1992; Rathburn and Corliss, 1994; Alve and Bernhard, 1995; Wollenburg and Mackensen, 1998a). Generally, it is assumed that the oxygen penetration depth controls the maximum habitat depth as long as food is available. Consequently, a model was proposed that determines the microhabitat depth in eutrophic environments by a critical oxygen level within the sediment, and by a critical level of food supply in case of oligotrophic environments (Corliss and Emerson, 1990; Jorissen et al., 1995). It was further suggested that the vertical foraminiferal distribution of species within the sediments reflects the presence of various populations of anaerobic and sulfate- and nitrate-reducing bacteria, which the foraminifera are thought to feed on directly. Otherwise they might selectively depend on the state of bacterial organic matter degradation (Caralp, 1989b; Jorissen et al., 1998). Since the pore-water oxygen content and food availability, including bacterial communities, are coupled to seasonal fluctuations in the ocean's surface productivity, this implies that microhabitat depth preferences do not only vary between different species, but also within a single species, depending on season and food supply (cf. Linke and Lutze, 1993).

In most oceans, a linear correlation is observed between the stable carbon isotopic composition of the dissolved inorganic carbon ($\delta^{13}C_{DIC}$) values and nutrient contents of deep and bottom water masses because the distribution of both are controlled by the interaction of biological uptake at the sea surface and decomposition in deeper water masses with the general circulation of the ocean (Kroopnick, 1980; Kroopnick, 1985). This is important because the carbon isotopic composition of foraminiferal carbonate exhibits consistent relationships with the isotopic composition of dissolved inorganic carbon in ambient waters at the time of precipitation (Woodruff et al., 1980; Graham et al., 1981). Thus the $\delta^{13}C$ signal of the water masses is recorded in epibenthic foraminifera and as such is extensively used as a nutrient proxy to reconstruct deep ocean paleocirculation (e.g. Duplessy et al., 1984; Curry et al., 1988; Oppo et al., 1990; Raymo et al., 1990; Boyle, 1992; Sarnthein et al., 1994; Mackensen et al., 2001).

Some species assumed to live within the sediment were detected to reflect by their carbon isotopic test composition the amount of organic carbon fluxes to the seafloor (Woodruff and Savin, 1985; Zahn et al., 1986; Loubere, 1987; McCorkle et al., 1994). Other species known for their epibenthic lifestyle, such as *Fontbotia wuellerstorfi*, were shown to record the isotope signal of dissolved inorganic carbon in bottom water (Duplessy et al., 1984; Grossman, 1987). Even the carbon isotopic composition of epibenthic *F. wuellerstorfi*, however, if collected from areas prone to seasonal plankton blooms and subsequent rapid sedimentation and the development of a phytodetritus layer at the sea floor, significantly deviates from the bottom water isotope signal, thus making the interpretation of fossil tests more difficult and ambiguous (Mackensen et al., 1993b; Mackensen and Bickert, 1999).

Generally, only few species of the marine calcareous macrobenthos and meiobenthos precipitate calcite in equilibrium with the isotopic composition of dissolved inorganic carbon in ocean bottom water (Wefer and Berger, 1991). Basically two mechanisms are responsible for carbon isotope disequilibria seen in benthic foraminifera: so called vital (physiological) and microhabitat effects. Vital effects can be further subdivided into two categories: metabolic and kinetic isotope effects (McConnaughey, 1989a, 1989b). Metabolic effects reduce the $\delta^{13}C$ values due to the incorporation of respired CO_2 into the foraminiferal test (Spero and Lea, 1996; McConnaughey et al., 1997; Wilson-Finelli et al., 1998). In addition, kinetic fractionation can occur during stages of rapid shell calcification and would result in even more depleted $\delta^{13}C$ values. The term 'microhabitat effect' summarizes both equilibrium as well as kinetic fractionation during calcification within the sediment porewater or other specific microhabitats, for instance, within a phytodetrital layer directly on the sediment surface (see above). Generally, porewater $\delta^{13}C_{DIC}$ values rapidly decrease with increasing depth in the sediment within the top centimeter. Calcitic tests of infaunal species are therefore expected to generally display low $\delta^{13}C$ values (Grossman, 1984b; McCorkle et al., 1985). Studies of Rathburn et al., (1996) and Mackensen et al., (2000), however, revealed that most taxa caught over a depth range within the sediment do not show consistent gradients in $\delta^{13}C$ as would be expected if carbon isotopic composition were influenced only by the average porewater environments in which they had been found. The saturation state of the ambient water with respect to carbonate may also influence the isotopic signal recorded in the benthic foraminiferal shell. Culturing experiments revealed that the stable isotopic composition of planktic foraminiferal tests responds to changes in seawater carbonate ion concentration (Spero et al., 1997). Recently, this 'Carbonate Ion Effect' was applied to interpret severe deviations of $\delta^{13}C_{DIC}$ values of planktic foraminifera *Neogloboquadrina pachyderma* from surface water $\delta^{13}C_{DIC}$ values in the Ochotsk Sea (Bauch et al., 2002). If the responses of benthic and planktic foraminifera are similar, a decrease in carbonate ion concentration by 10 μmol/kg would be equivalent to an increase in calcitic test $\delta^{13}C$ of 0.1 ‰ (Lea et al., 1999).

Relatively few studies from deep-sea environments are available that relate live (Rose Bengal stained) benthic foraminiferal test isotopic composition to ambient bottom and pore water dissolved inorganic carbon isotopes (Grossman, 1984a, 1984b, 1987; Mackensen and Douglas 1989; McCorkle et al. 1990; Mackensen et al. 1993b; Rathburn et al. 1996; McCorkle et al. 1997; Mackensen and Bickert 1999; Mackensen et al. 2000). Therefore, in this study we further address the relationship between $\delta^{13}C$ values of live (Rose Bengal stained) benthic foraminifera and their specific microhabitat preferences and environments to increase the reliability and substantiate the use of benthic foraminiferal test $\delta^{13}C$ as a proxy for paleoceanographic reconstructions. Benthic $\delta^{13}C$ data, due to their dependency on ocean surface productivity as well as air-sea gas exchange, provide crucial insight into the links between upper ocean climate and deep water circulation.

4.3. Material

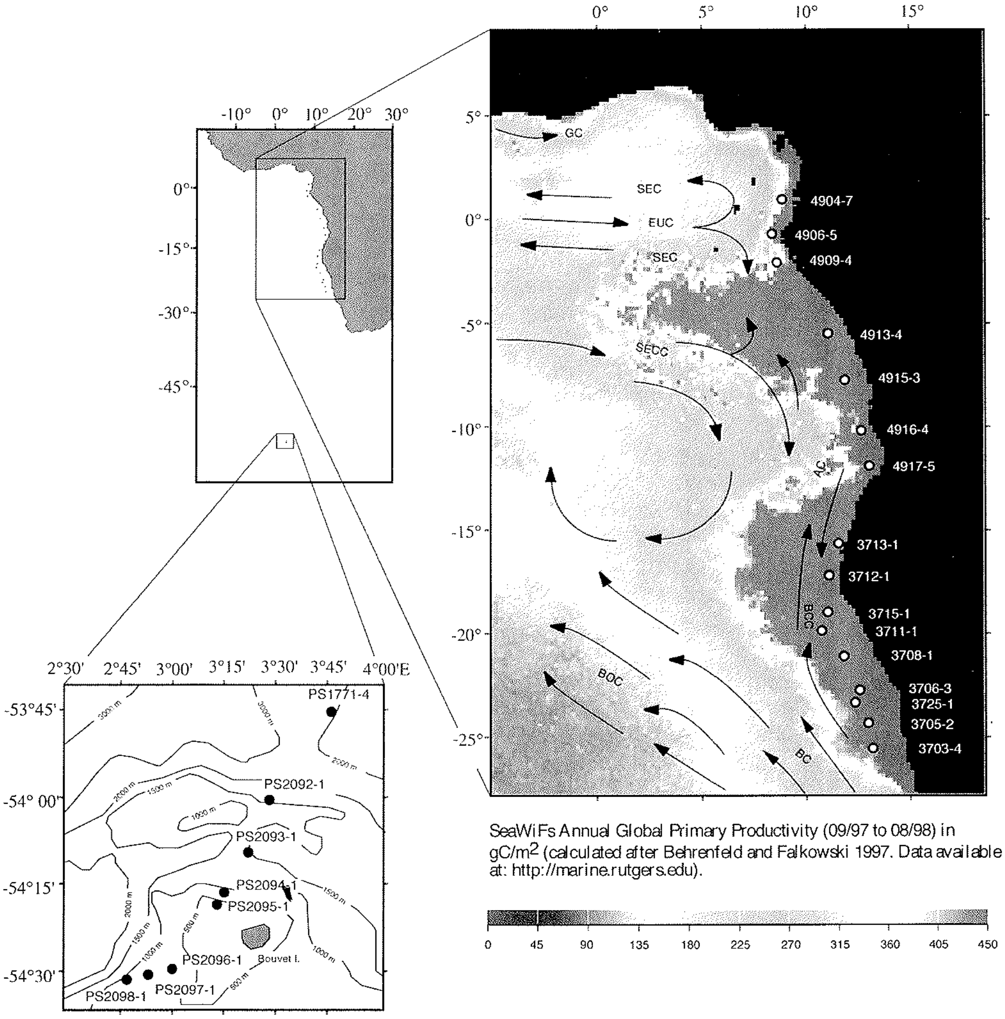
Live (Rose Bengal stained) and dead benthic foraminifera of surface and subsurface sediments from 25 stations in the eastern South Atlantic Ocean and the Atlantic sector of the Southern Ocean were analyzed in order to decipher a potential influence of seasonally and spatially varying high primary productivity on the stable carbon isotopic composition of foraminiferal tests (Fig. 1; Table 1). We have chosen two sample sets out of more than 250 samples from the South Atlantic Ocean, most of which have been investigated earlier for their benthic foraminiferal content and ecological preferences (Mackensen et al., 1990; Mackensen et al., 1993a; Mackensen et al., 1995; Harloff and Mackensen, 1997; Schmiedl et al., 1997; Mackensen et al. 2000; Schumacher 2001; Licari et al., 2003).

One set of nine surface sediment samples is from a transect across a mid-ocean ridge close to Bouvet Island, roughly between 48°S and 55°S (Mackensen et al., 1993a; Mackensen et al., 2000). Ecologically this area is characterized by a locally and seasonally highly varying ocean surface productivity associated with the Antarctic Polar Frontal Zone between the Subantarctic and the Polar Fronts (Peterson and Stramma, 1991; Orsi et al., 1995).

Another set of 16 samples is from the South African continental slope between the equator and about 30°S, from a water depth of approximately 1300 m, chosen to assure that conservative water mass characteristics change only little and most sample positions are bathed by Antarctic Intermediate Water or Upper Circumpolar Deep Water, except one dominated by North Atlantic Deep Water (Mackensen et al., 1995; Schmiedl et al., 1997; Licari et al., 2003). The sample positions in the eastern South Atlantic are ecologically dominated by several systems of permanent and seasonal upwelling cells which generate productivities that vary significantly in time and space (Lutjeharms and Meeuwis, 1987).

At the equator, strong seasonal variations in the trade winds produce a highly fluctuating ocean surface productivity system. At 6°S, in addition to an enhanced nutrient supply from Congo River outflow, the rapidity of this freshwater outflow forced by a narrow estuary, induces upwelling at the river mouth by entrainment of cool subsurface oceanic waters which are rich in phosphate and nitrate (Van Bennekom et al., 1978). Between 10°S and 15°S off Angola, a complex system of fronts, gyres, and thermal domes induces highly seasonal oceanic upwelling (Stramma and Schott, 1999). Between 15-20°S, southerly and southeasterly trade winds induce permanent intense coastal upwelling cells (Lutjeharms and Meeuwis, 1987).

This general scheme, schematically illustrated in Fig. 1, is in good agreement with global maps of primary productivity estimates (calculated after Behrenfeld and Falkowski (1997), based on recent satellite chlorophyll data (SeaWIFs chlorophyll data from September 1997 to August 1998; http://marine.rutgers.edu/opp/). According to these maps, annual primary productivity values increase from 180 gC m^{-2} y^{-1} in the northern part of the Guinea Basin to 450 gC m^{-2} y^{-1} in the Angola Basin.



SeaWiFs Annual Global Primary Productivity (09/97 to 08/98) in gC/m^2 (calculated after Behrenfeld and Falkowski 1997. Data available at: http://marine.rutgers.edu).

Figure 1. Positions of sites investigated in this study close to Bouvet in the Southern Ocean Island and in the South Atlantic Ocean off the southwest African continental margin. Bathymetry is after GEBCO and surface hydrography according to Voituriez and Herbland (1982) and Peterson and Stramma (1991). AC = Angola Current, BC = Benguela Current, BCC = Benguela Coastel Current, BOC = Benguela Oceanic Current, EUC = Equatorial Under Current, GC = Guinea Current, SEC = South Equatorial Current, SECC = South Equatorial Counter Current

Table 1. Station list with sample numbers, geographical position, water depth, standing stocks of benthic foraminifera, as well as total organic carbon and carbonate contents of the sediment, and stable carbon isotopic composition of dissolved inorganic carbon of bottom water. Numbers in italics indicate extrapolation from measurements at nearby stations. Sample PS1777-7 is omitted in Figure 1 for graphical reasons. Sediment data are from www.pangaea.de originally published by Mollenhauer et al. (2002), and Wagner et al. (submitted).

Sample	Latitude [°]	Longitude [°]	Water depth [m]	Stocks [#/50cm^2]	TOC [%]	Carbonate [%]	$\delta^{13}C_{DIC}$ [‰VPDB]
GeoB4904-7	0.96	8.88	1341	315	1.2	*12.9*	0.53
GeoB4906-5	-0.69	8.38	1277	166	1.5	*16.5*	0.70
GeoB4909-4	-2.07	8.63	1313	279	1.3	*5.2*	0.67
GeoB4913-4	-5.50	11.07	1300	48	1.7	*4.0*	0.65
GeoB4915-3	-7.75	11.87	1305	156	1.3	*20.5*	*0.63*
GeoB4916-4	-10.17	12.69	1300	357	2.5	*15.8*	*0.61*
GeoB4917-5	-11.90	13.07	1299	930	2.2	*15.5*	0.63
GeoB3713-1	-15.63	11.58	1330	827	1.6	5.1	*0.35*
GeoB3712-1	-17.19	11.13	1242	1647	2.4	5.7	*0.25*
GeoB3715-1	-18.95	11.06	1204	332	4.5	25.6	*0.30*
GeoB3711-1	-19.84	10.77	1214	726	3.8	66.7	*0.30*
GeoB3708-1	-21.09	11.83	1283	994	4.9	52.6	*0.35*
GeoB3706-3	-22.72	12.60	1313	580	3.7	55.2	*0.40*
GeoB3725-1	-23.32	12.37	1980	356	2.1	76.4	*0.40*
GeoB3705-2	-24.30	13.00	1305	391	4.5	66.0	*0.45*
GeoB3703-4	-25.52	13.23	1376	749	8.1	55.3	*0.45*
PS1777-7	-48.23	11.03	2556	595	0.4	63.0	0.64
PS1771-4	-53.77	3.78	1811	205	0.6	1.6	0.28
PS2092-1	-54.02	3.48	1897	275	0.3	2.7	0.32
PS2093-1	-54.17	3.38	1441	345	0.2	3.2	0.45
PS2094-1	-54.28	3.27	937	880	0.4	3.9	0.33
PS2095-1	-54.32	3.23	486	800	0.1	3.8	0.33
PS2096-1	-54.5	3.02	502	1695	0.2	3.2	0.27
PS2097-1	-54.52	2.9	1020	335	0.3	3.1	0.21
PS2098-1	-54.53	2.8	1500	180	0.3	2.2	0.38

Remineralization of organic material below the high productivity areas and off the river mouths leads to the formation of an oxygen minimum zone (OMZ), which reaches its largest extension off the Cunene River (around 17°S), where it extends between water depths of 50 and 1200 m with an oxygen minimum value of 1ml l^{-1}. The intensity of the OMZ decreases progressively northward (Chapman and Shannon, 1985, 1987; Schulz and cruise participants, 1992).

4.4. Methods

Surface sediment samples were taken with the aid of a multiple corer down to a subbottom depth of 15 cm, preserved in a mixture of alcohol and Rose Bengal (1 g Rose Bengal dissolved in 1L 96%-ethanol) and kept cool at 4 °C until further treatment (Walton, 1955; Lutze, 1964; Mackensen and Douglas, 1989). From each station, at least four of twelve multiple corer subcores (6 cm diameter), or two of ten (10 cm diameter) were analyzed, selected according to quality, i.e., clarity of the supernatant water, and position, i.e., maximum distance between subcores. This way we achieved to obtain replicates from the surface area covered by a multiple corer, i.e.of about one m^2, by just one deployment of the sampling gear. This allows for a reasonable treatment of patchiness in benthic foraminiferal abundance patterns on a spatial scale from tens of centimeters to about one meter. On shore, samples were wet sieved over 63 μm and the dried fraction >125 μm was investigated for its benthic foraminiferal content. Live (stained) and dead assemblages were counted separately. The stable isotopic composition of live and dead benthic foraminifera was determined with a Finnigan MAT251 isotope ratio gas mass spectrometer directly coupled to an automatic carbonate preparation device (Kiel I) and calibrated via NIST 19 to the VPDB (Vienna Pee Dee Belemnite) scale. The number of specimens analyzed in a single measurement varied between two and five for cibicids and uvigerinids, between five and eight for *Bulimina aculeata*, and nine and 25 for all other species. All values are reported as δ-notation versus VPDB. The overall precision of the measurements based on repeated analyses of a laboratory standard (Solnhofen limestone) over a one year period was better than 0.06 ‰ and 0.09 ‰ for carbon and oxygen, respectively.

The water column was sampled with the aid of Niskin bottles mounted on a water-sampling rosette. The bottom water from directly above the sediment/water interface was sampled from one of the multiple corer tubes. Although sub-sampled immediately after recovery on board, the bottom water in the sub-cores of the multiple corer was nevertheless influenced by shipboard handling that may have led to the release of porewater into the bottom water (Mackensen et al., 1993b). Dissolved inorganic carbon was either manually extracted in a preparation line following Mook et al. (1974), or automatically extracted with a Finnigan Gas Bench using gas chromatography to purify CO_2. The stable isotopic composition of resulting purified CO_2 was determined with a Finnigan MAT252 isotope ratio gas mass spectrometer and calibrated to the VPDB scale. The precision of carbon measurements, including CO_2 extraction, is better than 0.1 ‰. All samples including gas extraction were processed in duplicate.

4.5. Results

4.5.1. Water column $\delta^{13}C_{DIC}$

To define the range of water depths in which conservative water mass properties and $\delta^{13}C_{DIC}$ values vary only slightly, we compiled new $\delta^{13}C_{DIC}$ data measured in this study and data published earlier in a section from Antarctica through the Agulhas Basin, crossing the middle oceanic ridge at Bouvet Island, the Walvis Ridge between Cape and Angola Basins and eventually, via the Guinea Abyssal Plain, the Equator (Oestlund et al., 1987; Mackensen et al., 1993b; Mackensen et al., 1996; Bickert and Wefer, 1999; Mackensen, 2001). All of the stations investigated in this study are bathed by waters with $\delta^{13}C_{DIC}$ values ranging from 0.2 to 0.7 ‰ VPDB, i.e. AAIW and UCDW (Fig. 2, Table 1).

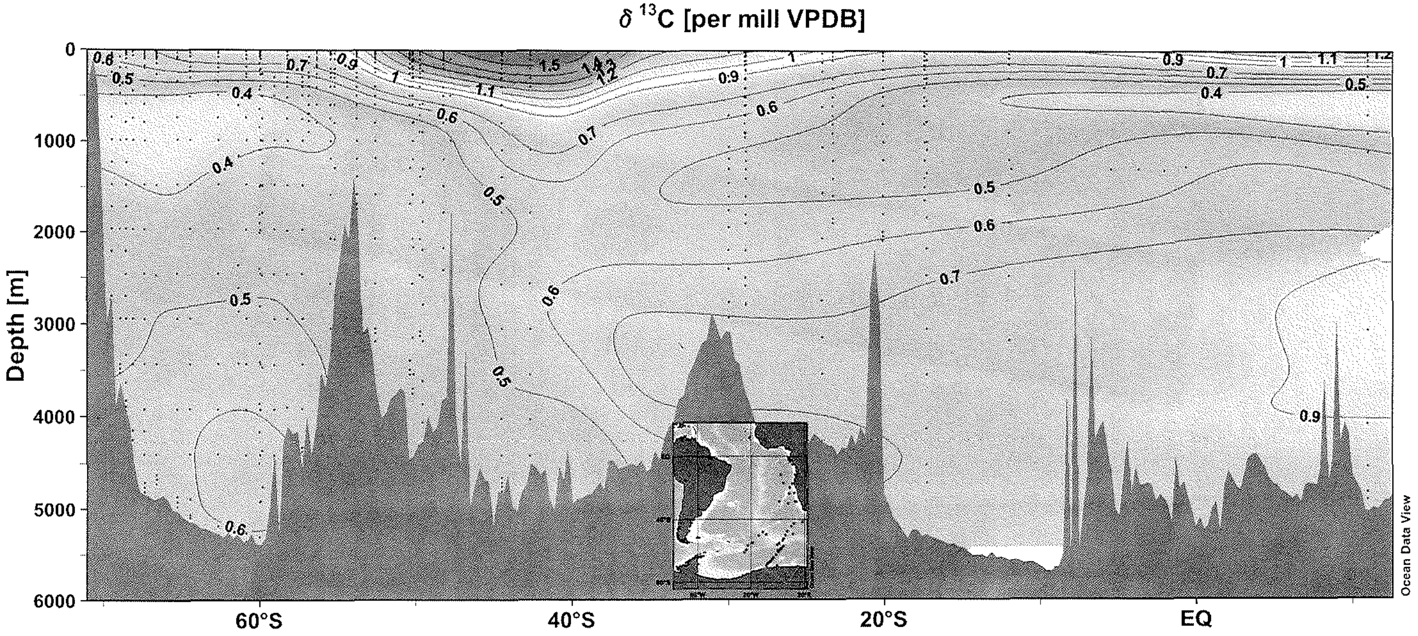


Figure 2 . Distribution of $\delta^{13}C_{DIC}$ (‰ VPDB) on a section from 70°S at the Antarctic continental margin along the African continental slope to 10°N. Data are compiled from Mackensen et al. (1993b, 1996, 2001), Bickert und Wefer (1999), and Oestlund et al. (1987) using Ocean Data View visualization software (Schlitzer 2002).

4.5.2. Microhabitats and foraminiferal $\delta^{13}C$

In accordance with the distribution of benthic foraminiferal faunal provinces characterized by specific assemblage compositions (Mackensen et al., 1993a; Mackensen et al., 1995; Schmiedl et al., 1997; Schumacher, 2001; Licari et al., 2003), we present and discuss in this paper faunal and isotopic data in the order of the following geographic positions of sites (Fig. 1, Table 1): (1) samples from sites PS1771 to PS2098 from near Bouvet Island between 48 and 55°S (hereinafter referred to as Agulhas Basin samples), (2) samples south of Walvis Ridge including GeoB3711-1 (hereinafter referred to as Cape Basin samples), (3) samples from north of Walvis Ridge from site GeoB3715 to site GeoB4916 (hereinafter referred to as Angola Basin samples), and (4) north of 10°S (hereinafter referred to as Guinea Abyssal Plain samples).

The number of live (stained) benthic foraminifera in the >125 μm size fraction generally decreases from Bouvet Island in the south at about 50°S, via the Cape Basin and Angola Basin to the Guinea Abyssal Plain in the north near the equator (Fig. 3). Interestingly, in Cape Basin and Angola Basin samples, highest standing stock values are found between one and two cm below the sediment surface, in contrast to the expected exponential decrease from the sediment surface down to 11 cm subbottom depth as found off Bouvet Island and at the Guinea Abyssal Plain continental slope.

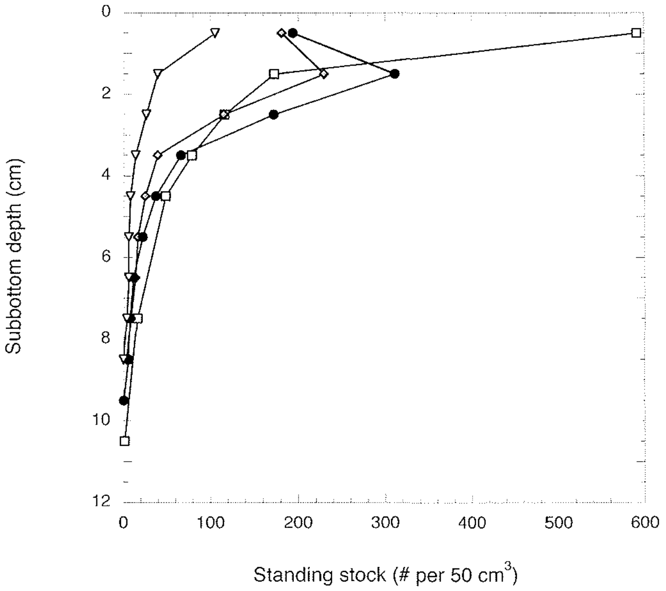


Figure 3. Mean total benthic foraminiferal standing stocks of nine stations from Agulhas Basin (squares), and of six and five stations from the African continental slopes of Cape (diamonds) and Angola Basins (dots), respectively, as well as five stations from Guinea Abyssal Plain slope (triangles).

Agulhas Basin

At the mid-ocean ridge, which Bouvet Island is part of, the benthic foraminiferal fauna is characterized by the presence of *Bulimina aculeata* and *Angulogerina angulosa* (Mackensen et al., 1994). At all stations except one the number of live specimens of these two species exponentially decreases from the uppermost surface sediment down to about five centimeters subbottom depth (Fig. 4). At station PS2094, however, live specimens are found at a water depth of 937 m down to a subbottom depth of 11 cm, and surface values decrease from 59 individuals per 10 cm^3 in the top centimeter to four in the second sediment slice, then increasing to a second subsurface maximum at a subbottom depth of 3-5 cm (Fig. 4).

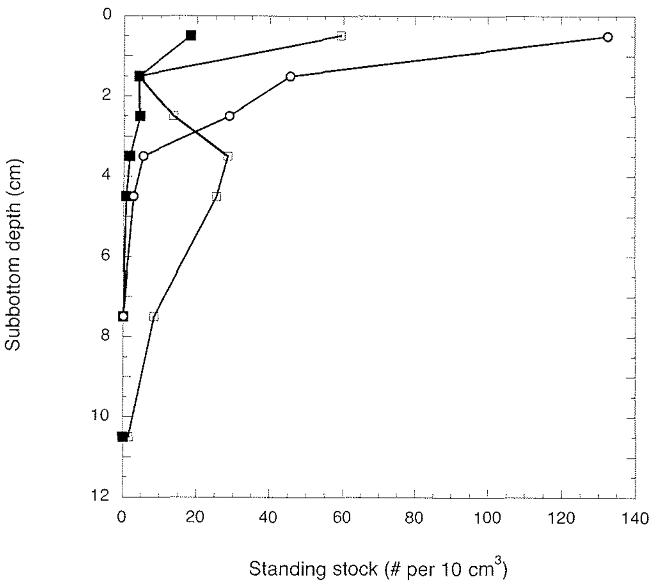


Figure 4. Mean standing stocks of live *Bulimina aculeata* (filled squares) from eight stations and one single station PS2094 (open squares) off Bouvet Island are plotted versus sediment depth. Mean standing stock of live *Angulogerina angulosa* (dots) from two of the eight stations is given for comparison.

The stable carbon isotope offset of preferentially infaunal *B. aculeata* from bottom water $\delta^{13}C_{DIC}$ at all stations investigated rather constantly varies around -0.6 ± 0.1 ‰ throughout the sediment, except at station PS2094 where the $\delta^{13}C$ values are consistently lower, varying around -1.5 ± 0.2 ‰ (Mackensen et al., 2000). The $\delta^{13}C$ values of live and dead specimens of *A. angulosa* vary around the same mean within the standard deviation of the *B. aculeata* values (Fig. 5). *Angulogerina angulosa* does not thrive in water depths beyond 800 m in this area and thus is not found at station PS2094. The stable carbon isotopic composition of dissolved inorganic carbon was determined in multiple corer water and checked with $\delta^{13}C_{DIC}$ measurements from the water column (Mackensen et al., 1993b; Mackensen et al., 1996). According to this, $\delta^{13}C_{DIC}$ values from multiple corer water may underestimate the actual bottom water $\delta^{13}C_{DIC}$ by 0.2 ‰ at the most (see Methods section).

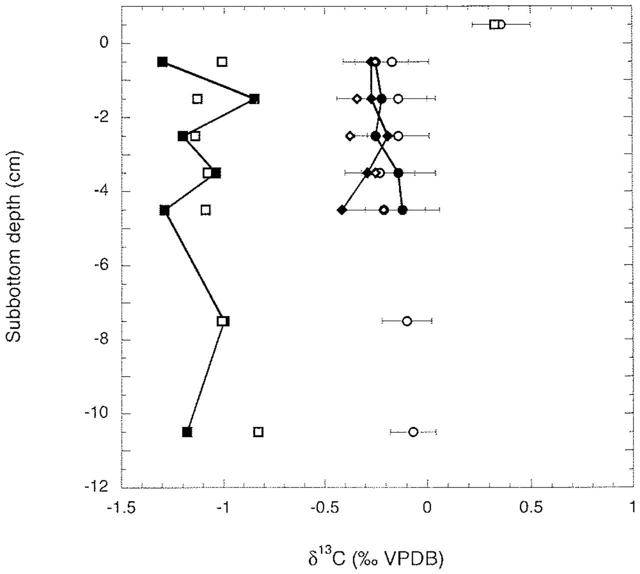


Figure 5. δ^{13}C values of live and dead *Bulimina aculeata* (filled and open circles, respectively) from eight stations and one single station PS2094 off Bouvet Island (squares) are plotted versus sediment depth, as well as δ^{13}C values of live and dead *Angulogerina angulosa* from two of the eight stations for comparison (filled and open diamonds, respectively). Error bars indicate the standard deviation of the mean of eight and two stations, respectively. In addition, the $\delta^{13}C_{DIC}$ values of the bottom water are indicated, as determined in multiple corer water simultaneously sampled (for graphic reasons plotted 0.5 cm above sediment/water interface).

Cape and Angola Basins

The live benthic foraminiferal fauna at the African upper continental slope between 30 and 10°S is characterized by assemblages either dominated by *Fontbotia wuellerstorfi* or *Uvigerina auberiana*, mainly depending on substrate composition and organic matter fluxes (Schmiedl et al. 1997). Further north *Uvigerina peregrina* becomes a more dominant component of the live fauna, in addition to species such as *Globobulimina turgida* and *G. affinis*, as well as *Fursenkoina earlandi* and *F. mexicana* that were found associated discontinuously along the entire continental slope at this water depth (Mackensen et al. 1995; Schmiedl et al. 1997; Licari et al. 2003). Although total benthic foraminiferal standing stocks at the slopes of both Cape Basin and Angola Basin clearly show a shallow subsurface maximum between one and two centimeters within the sediment (Fig. 3), the preferentially epibenthic living *F. wuellerstorfi* mostly is restricted to the first centimeter and is on average equally distributed within the top two sediment centimeters at all stations in Cape Basin. On the contrary, deeply infaunal species such as *G. affinis* and *F. mexicana* exhibit a subsurface distributional maximum between five and seven, and three and six centimeters, respectively (Fig. 6).

All mean δ^{13}C values of the various epifaunal and infaunal species under investigation do not significantly vary or obviously decrease with increasing depth within the sediment (Fig. 7, Table 2). The data vary only slightly around a mean value for each single species at each single site, no matter what habitat the species prefer and at what subbottom depth the particular specimens were caught. The preferentially epibenthic living species *F. wuellerstorfi*, *Lobatula lobatula* and *Cibicidoides pachyderma*, however, can be clearly differentiated by δ^{13}C values more than 1 ‰ higher than the values applying to the deep and shallow infaunal *G. affinis, F. mexicana,* and *B. mexicana.*

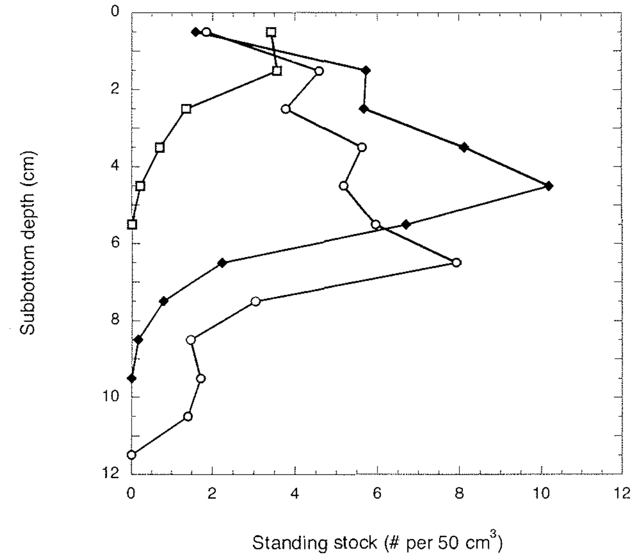


Figure 6. Mean standing stock of *Fontbotia wuellerstorfi* (squares) from four stations in the Cape Basin, of *Globobulimina affinis* from six stations in Cape and Angola Basins (dots), and of *Fursenkoina mexicana* (diamonds) form two stations in Angola Basin plotted versus sediment depth.

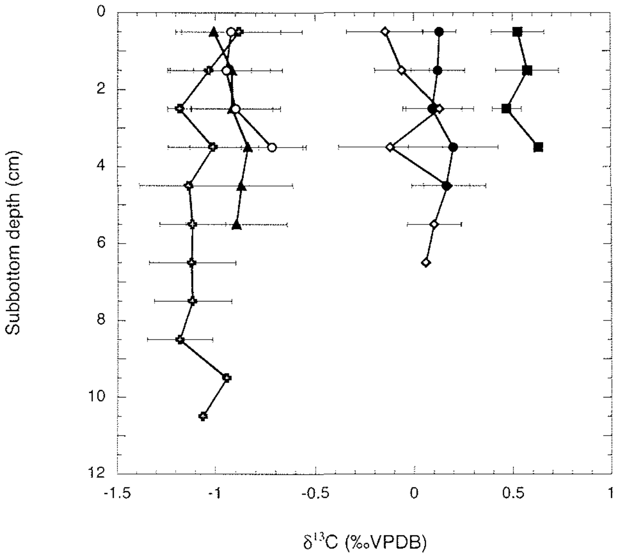


Figure 7. Mean δ^{13}C values of live *Fontbotia wuellerstorfi* (squares), *Cibicidoides pachyderma* (diamonds), and *Lobatula lobatula* (dots) from five stations in Cape Basin, as well as δ^{13}C values of live *Globobulimina affinis* (crosses), *Fursenkoina mexicana* (triangles), and *Bulimina mexicana* (open circles) from seven, four, and ten stations, respectively, from Cape and Angola Basins plotted versus sediment depth. Error bars give standard deviations of means of stations used for the particular species. Bottom water δ^{13}C$_{DIC}$ values (not plotted) at stations lie exactly within the range of *F. wuellerstorfi* δ^{13}C, i.e. between .45 and .65 ‰.

Table 2. Mean $\delta^{13}C$ (‰ VPDB) values and standard deviations of live (upper part) and dead (lower part) species from the sediment surface and all subbottom depths at every single station.

Sample	*L. lobatula*	stdev	*C. pachyderma*	stdev	*F. wuellerstorfi*	stdev	*B. mexicana*	stdev	*G. pacifica*	stdev	*F. mexicana*	stdev	*U. auberiana*	stdev	*U. peregrina*	stdev
GeoB4904-7													-0.48		-0.95	0.12
GeoB4906-5							-1.05						-0.49		-0.94	0.03
GeoB4909-4													-0.19		-0.66	0.08
GeoB4913-4															-0.76	
GeoB4915-3			0.44		0.63				-0.93						-0.55	
GeoB4916-4							-1.25	0.03								
GeoB4917-5							-1.22	0.05	-1.02	0.13			-1.03	0.09	-0.38	0.16
GeoB3713-1					1.01		-0.82	0.07	-0.86	0.08					0.03	
GeoB3712-1							-0.44	0.11			-0.49	0.03	-0.63	0.08		
GeoB3715-1							-0.85	0.08	-0.98	0.24	-0.84	0.10	-0.93	0.05		
GeoB3711-1	0.13	0.14	-0.01	0.09	0.39	0.02	-1.08	0.03			-1.06	0.03	-1.21	0.03	-0.71	
GeoB3708-1	0.00	0.08	-0.03	0.08	0.48	0.05	-0.92	0.14	-1.27	0.04	-1.04	0.02	-1.15	0.01		
GeoB3706-3	0.26	0.05	0.12	0.06	0.64	0.11	-0.74	0.10	-1.15	0.20						
GeoB3725-1	0.14		0.10	0.40	0.60	0.07			-1.30	0.13					-0.86	
GeoB3705-2	0.15		-0.28	0.13	0.45		-0.98	0.07								
GeoB3703-4							-1.04	0.06	-1.00	0.14			-1.09	0.14		
GeoB4904-7															-0.62	0.11
GeoB4906-5															-1.03	0.17
GeoB4909-4															-0.64	0.10
GeoB4915-3					0.75				-1.33						-0.28	
GeoB4916-4							-1.14	0.06								
GeoB4917-5							-1.09	0.04	-1.03	0.16					-0.44	0.01
GeoB3713-1							-0.84	0.06	-0.95	0.32					-0.20	0.10
GeoB3712-1							-0.75	0.07			-0.55	0.07	-0.77	0.08		
GeoB3715-1							-0.96	0.02	-1.22	0.20	-0.85	0.04	-0.98	0.14		
GeoB3711-1	0.04	0.11	0.01	0.16	0.37	0.17	-0.98	0.04			-0.93	0.06	-1.09	0.05		
GeoB3708-1	-0.01	0.04	-0.07	0.10	0.55	0.05	-1.10	0.06	-1.28	0.15	-1.07	0.05	-1.31	0.06		
GeoB3706-3	0.15	0.14	0.09	0.09	0.58	0.17	-1.03	0.05	-1.34	0.26						
GeoB3725-1	0.25		0.17	0.23	0.34	0.22			-1.14	0.19						
GeoB3705-2			-0.18	0.31	0.53	0.15	-1.06	0.03								
GeoB3703-4									-0.89	0.13						

Guinea Abyssal Plain

Standing stock values at Guinea Abyssal Plain are the lowest of all stations investigated in this study (Fig. 3). Consequently, mean standing stock values of single taxa are low as well, and only few specimens are available for stable isotope determinations. This is in particular the case for preferentially infaunal species. One of the most common taxa in these samples is *Uvigerina peregrina* (Licari et al. 2003). Although generally considered as a shallow infaunal species, it clearly has its distribution maximum within the top centimeter of the sediment. In the second and third centimeter within the sediment, however, about half of the total number of live specimens is still found (Fig. 8). The $\delta^{13}C$ values of stained and empty *U. peregrina* tests vary between stations by ±0.25 ‰, regardless of the bottom water $\delta^{13}C_{DIC}$ values, but they do not significantly change with increasing subbottom depths (Fig. 8, Table 2).

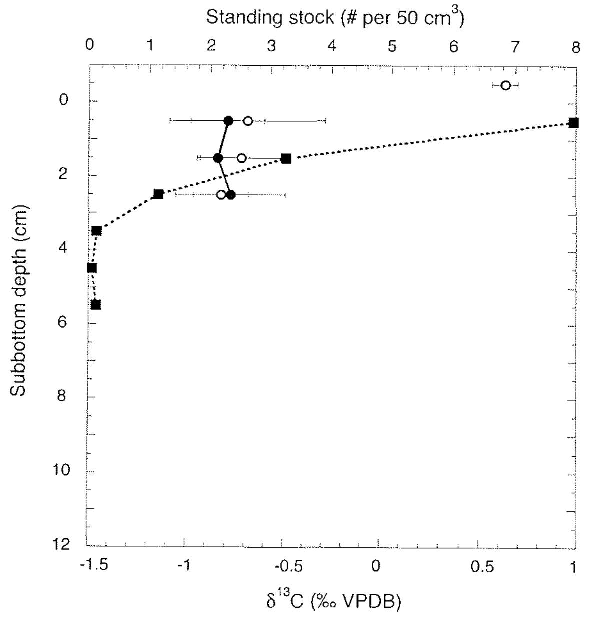


Figure 8. Mean $\delta^{13}C$ values of live and dead *Uvigerina peregrina* (dots and open circles, respectively), as well as standing stocks (squares) from five stations at the Guinea Abyssal Plain continental slope are plotted versus sediment depth. Error bars give standard deviations of means of stations used. $\delta^{13}C_{DIC}$ values of the bottom water are indicated, as determined from simultaneously sampled Multiple corer water (for graphic reasons plotted 0.5 cm above the sediment/water interface).

4.6. Discussion

4.6.1. Intraspecific $\delta^{13}C$ variability at single sites

In all four series of samples from stations in Agulhas Basin, Cape Basin and Angola Basins as well as the Guinea Abyssal Plain, $\delta^{13}C$ values of all species vary on average ±0.09 ‰ (range of standard deviations: 0.01 – 0.40 ‰) around a species specific and site dependent mean value calculated from all subbottom depths (Figs. 5, 7, 8; Table 2). This simply reflects that at each station live specimens of each particular species have about the same stable carbon isotopic composition, regardless of the actual sediment depth they were caught in. This in turn means that no matter which habitat depth the different species prefer, all specimens of the same species record the same $\delta^{13}C$ signal. This was shown earlier for some of the species discussed here (Mackensen and Douglas 1989; McCorkle et al. 1990; McCorkle and Keigwin 1994; Rathburn et al. 1996; Mackensen et al. 2000), but to our knowledge it has not been clear yet that obviously most, if not all benthic foraminiferal species behave like this.

This means further that if specimens of particular species vertically migrate within the sediment, as is known from culture experiments (Severin, 1987; Moodley, 1992; Ernst et al., 2002) they obviously do not record different $\delta^{13}C$ signals in accordance with the stratified and downwards rapidly decreasing $\delta^{13}C$ values of pore water DIC. Based on a limited data set comprising values merely pertaining to *B. aculeata* , it was suggested that by moving within the sediment, individuals of infaunal species either record an average isotope signal of the pore water or the signal of one specific calcification depth level (Mackensen et al., 2000). Now more data from different species being at hand, it is safe for paleoceanographers to interpret fossil benthic foraminiferal $\delta^{13}C$ values as representing one signal at one particular site at one particular time. In other words, if there is strong variation within fossil specimens of the same species at one site in a sample of one particular age, mechanisms other than migration of specimens and subsequent recording of different $\delta^{13}C$ signals during lifetime have to be considered as an explanation. The most common possibilities should include reworking of older sediments, or lateral and down-slope transport from elsewhere.

4.6.2. Interspecific $\delta^{13}C$ differences at single sites

Generally, at all sites along the African continental slope, $\delta^{13}C$ values of live and dead *Fontbotia wuellerstorfi, Cibicidoides pachyderma*, and *Lobatula lobatula* differ consistently and significantly from $\delta^{13}C$ values of live and dead *Globobulimina affinis*, *Fursenkoina mexicana*, and *Bulimina mexicana* by 1.5 to 1.0 ‰ (Fig. 7, Table 2). This finding is in good agreement with the hypothesis that lower $\delta^{13}C$ values of *G. affinis, B. mexicana* and *F. mexicana* — species generally considered to dwell in deep or shallow infaunal microhabitats (Kitazato, 1994; Jorissen et al., 1998) — simply reflect a calcification depth within the sediment and its depleted $\delta^{13}C_{DIC}$ porewater values (Woodruff et al., 1980; Grossman, 1984b; Mackensen and Douglas, 1989; McCorkle et al., 1990; Rathburn et al., 1996). Moreover, depleted $\delta^{13}C$ values of *C. pachyderma* and *L. lobatula* additionally reflect that cibicids and in particular *C. pachyderma* are not strictly epifaunal in contrast to *F. wuellerstorfi* (Wollenburg and Mackensen, 1998a). Alternatively, different taxa may feed on different diets or may even live in symbiosis with bacteria, instead of eating them (Bernhard and Bowser, 1992; Jorissen et al., 1995; Kitazato and Ohga, 1995; Bernhard et al., 2000). This eventually, via the metabolism of the foraminifera, affects the stable carbon isotopic composition of their calcareous tests.

It also appears that *F. wuellerstorfi* records bottom water $\delta^{13}C_{DIC}$ values almost perfectly, without any significant offset, whereas *L. lobatula* and *C. pachyderma* values deviate from bottom water values by about -0.4‰ and -0.6‰, respectively (Fig. 7). This adds to the growing data on contrasting cibicid $\delta^{13}C$ values which on the one hand supports the original calibration between *F. wuellerstorfi* and bottom water $\delta^{13}C_{DIC}$ (Duplessy et al., 1984; McCorkle and Keigwin, 1994), and on the other hand documents severe depletions of *L. lobatula* which was shown just recently to reliably record $\delta^{13}C_{DIC}$ values in the Nordic seas (Hald and Aspeli, 1997; Mackensen et al., 2000). Moreover, the confirmation of *F. wuellerstorfi* as a reliable recorder of bottom water $\delta^{13}C_{DIC}$ values at the Cape Basin continental slope supports the view that explains negative deviations in *F.*

wuellerstorfi tests of up to -0.6 ‰ close to the Antarctic Polar Front (Mackensen et al., 1993b; Mackensen et al., 2001) and in other high sedimentation rate environments (McCorkle, pers. comm.) as being mainly due to a highly seasonal ocean surface production and the subsequent deposition of ephemeral phytodetritus layers. A closer look on a satellite-based primary productivity map of the ocean at the positions of the seven stations investigated here for *F. wuellerstorfi* $\delta^{13}C$ values, shows that most of them are situated not below the belt of highly seasonal coastal upwelling, but are rather influenced by sustained ocean surface productivity and constant rain rates (Fig. 1) (Behrenfeld and Falkowski, 1997; Schmiedl et al., 1997). However, because of the paramount importance of *F. wuellerstorfi* and other epibenthic cibicids for paleoceanographic reconstruction more research is demanded to assess the $\delta^{13}C$ fidelity of these taxa.

4.6.3. Intraspecific $\delta^{13}C$ differences between sites

Generally, site specific $\delta^{13}C$ values of epibenthic foraminiferal species can be influenced by (1) the $\delta^{13}C_{DIC}$ values of the bottom water mass (Duplessy et al., 1984; Curry et al., 1988), (2) the saturation state of bottom water with respect to calcite, which may influence the isotopic signal either by *post mortem* dissolution or by altering the fractionation during calcification (McCorkle et al., 1995; Boyle and Rosenthal, 1996; Spero et al., 1997; Mackensen et al., 2000), and (3) highly seasonal ocean surface productivity with high-sedimentation rates and the subsequent development of an ephemeral phytodetritus layer at the sea floor. This phytodetrital layer may influence the isotopic signal either by inducing the animals to calcify test chambers when plenty of food is available but fluffy layer $\delta^{13}C_{DIC}$ values are depleted in ^{13}C due to increased organic decomposition rates, or by altering fractionation coefficients during the more rapid calcification processes (Mackensen et al., 1993b; Mackensen and Bickert, 1999; Mackensen et al., 2000).

In addition to the environmental conditions that affect $\delta^{13}C$ values of epibenthic foraminifera, endobenthic species further can be influenced by (1) the $\delta^{13}C_{DIC}$ gradients in the pore water, which in turn depend on the decomposition rate of sedimentary organic matter, which again is largely driven by the rain rate of particulate organic matter to the sea floor (Belanger et al., 1981; Woodruff and Savin, 1985; Zahn et al., 1986; McCorkle et al., 1990), and (2) by the release of methane into the pore water, which either significantly lowers the pore water $\delta^{13}C_{DIC}$ values via the pathway of bacterial oxidation to CO_2, or which favor benthic foraminifera to feed directly on methane consuming bacteria and thus alter the isotopic fractionation in the course of their metabolism (Wefer et al., 1994; Kennett et al., 2000; Bernhard et al., 2001).

In the Agulhas Basin data, we interpret the offset of 1.5 ± 0.2 ‰ between bottom water $\delta^{13}C_{DIC}$ and $\delta^{13}C$ values of *B. aculeata* at one single station in contrast to about 0.6 ± 0.1 ‰ at all other stations, as a direct reflection on locally increased organic matter fluxes and sedimentation rates (Fig. 9). This particular station PS2094 exhibiting lower $\delta^{13}C$ values in live and dead *Bulimina aculeata* calcite at about 1 ‰ compared to the rest of the stations, displays similar total organic carbon contents of the sediments but shows a specific high-productivity/low-oxygen conditions indicating deep infaunal *Fursenkoina earlandi* component and very high standing stocks (Mackensen et al., 1993a; Mackensen et al., 2000). Alternatively, from the one station with low values in contrast to eight stations close-by with significantly higher values, all of them overlain by the same general productivity regime, one may speculate that this strong depletion of ^{13}C in the composition of isotopic carbon in benthic foraminifera may have been caused by methane which could have been locally released from gas vents, such as reflecting hydrothermal activities at the mid-ocean ridge (cf. Rathburn et al., 2000). It is worth mentioning that the $\delta^{18}O$ values of *B. aculeata* from station PS2094 do not differ from the $\delta^{18}O$ values of *B. aculeata* at the rest of the stations.

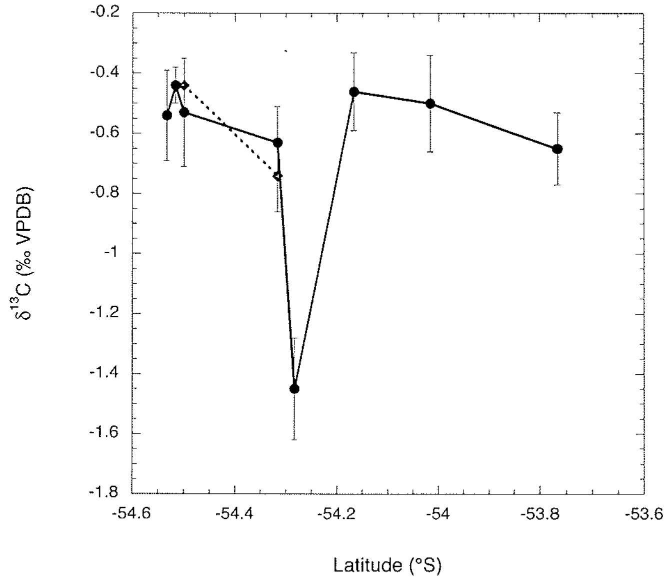


Figure 9. Mean $\delta^{13}C$ values of live *Bulimina aculeata* (dots) and *Trifarina angulosa* (diamonds) from all stations in Agulhas Basin plotted versus latitude. Error bars indicate standard deviations of means of all downcore values at each single station. Bottom water $\delta^{13}C_{DIC}$ values at each of the stations are subtracted.

We plotted mean $\delta^{13}C$ values of live *Fontbotia wuellerstorfi*, *Lobatula lobatula*, *Cibicidoides pachyderma*, *Bulimina mexicana*, *Globobulimina affinis*, *Fursenkoina mexicana*, *Uvigerina auberiana*, and *U. peregrina* as well as $CaCO_3$ contents of the sediments from all stations along the African continental margin versus latitude (Fig. 10). Mean $\delta^{13}C$ values of live and dead preferentially epibenthic *F. wuellerstorfi* reduced by station specific $\delta^{13}C_{DIC}$ values, vary between 0 and 0.2‰, i.e. well within the ±0.2 ‰ range of variation around the expected 1:1 relationship between foraminiferal calcite and bottom water $\delta^{13}C$ values (Figs. 10, 13), except at station GeoB3713 at 15°S where $\delta^{13}C$ values exceed $\delta^{13}C_{DIC}$ values of bottom water by 0.7‰ (Fig. 10).

Comparing $\delta^{13}C$ values of all species from all stations in a more generalized view, it becomes obvious that all species exhibit significantly higher values between 19 and 15°S, centered at stations Geob 3712 and 3713 (Figs. 10, 13). This particular area off Angola coincides with low $CaCO_3$ and organic carbon contents of the sediments. Further north, both sedimentary carbonate and organic carbon contents increase again between 16 and 7°S, to finally decrease to lowest values in the Guinea Abyssal Plain samples. Below the equator, carbonate values of the continental slope in a water depth of 1300 m then increase to about 17 weight% (Fig. 11).

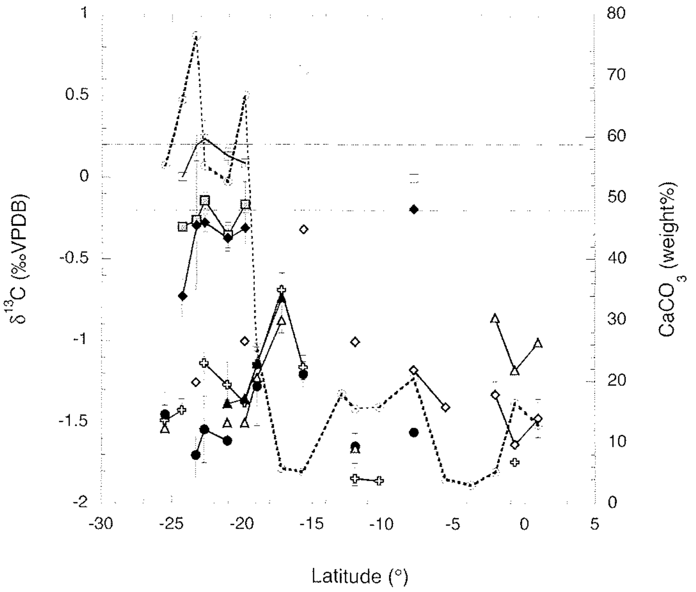


Figure 10. Mean $\delta^{13}C$ values of live *Fontbotia wuellerstorfi* (open squares), *Lobatula lobatula* (filled squares), *Cibicidoides pachyderma* (filled diamonds), *Bulimina mexicana* (crosses), *Globobulimina affinis* (dots), *Fursenkoina mexicana* (filled triangles), *Uvigerina auberiana* (open triangles), and *U. peregrina* (open diamonds), as well as $CaCO_3$ contents (open circles) of the sediments from all stations along the African continental margin plotted versus latitude. Error bars indicate standard deviations of means of all down-core values at each single station. Bottom water $\delta^{13}C_{DIC}$ values are subtracted. Horizontal lines at ±0.2 ‰ give range of 1:1 relationship between $\delta^{13}C$ values of bottom water DIC and foraminiferal calcite as commonly tolerated for paleonutrient reconstructions.

The low sedimentary carbonate contents are at least partially related to the oxidation of particulate organic matter within the water column, which is confirmed by a well developed oxygen minimum zone, as well as by the organic matter decomposition in the sediments of the continental slope beneath. Both processes cause the water to become more acidic and lower the carbonate saturation state through the consequent decrease in $[CO_3^{2-}]$, the carbonate ion concentration, which results in highly carbonate aggressive bottom and pore waters. A low carbonate ion concentration results in enhanced isotopic fractionation during calcification of foraminiferal tests in this environment (Spero et al., 1997; Bijma et al., 1999), or an initial dissolution of calcitic tests as early as during the lifetime of the organisms. Although both of these processes induce a shift toward higher $\delta^{13}C$ values, the latter process, however, seems rather unlikely, since most benthic foraminifera protect their calcitic tests with an outer organic lining against dissolution in a carbonate aggressive microenvironment. We, therefore, interpret the enriched calcite $\delta^{13}C$ values as mainly reflecting a severe undersaturation of bottom water and pore waters.

Although there is some scattering of data due to the lack of sufficient specimen numbers applied in the stable isotope determinations of all species in each sample, *U. auberiana,* and partly *U. peregrina* , corroborate our interpretation as both exhibit higher values which coincide with the low carbonate contents of the sediment (Figs. 10, 11). Furthermore, the mean $\delta^{18}O$ value of live *F. wuellerstorfi* at station GeoB3713 is enriched by 0.47 ‰, relative to the lowest value of Station

GeoB3705 from the same water depth and displaying about the same conservative water mass properties, and by 0.22‰ as compared to the mean of all stations. This supports the interpretation of an isotope fractionation effect caused by low carbonate ion concentrations as was first discussed by Lea et al. (1999) with regard to benthic foraminifera and which up to now has been observed under natural conditions only for planktonic foraminifera (Bauch et al. 2002).

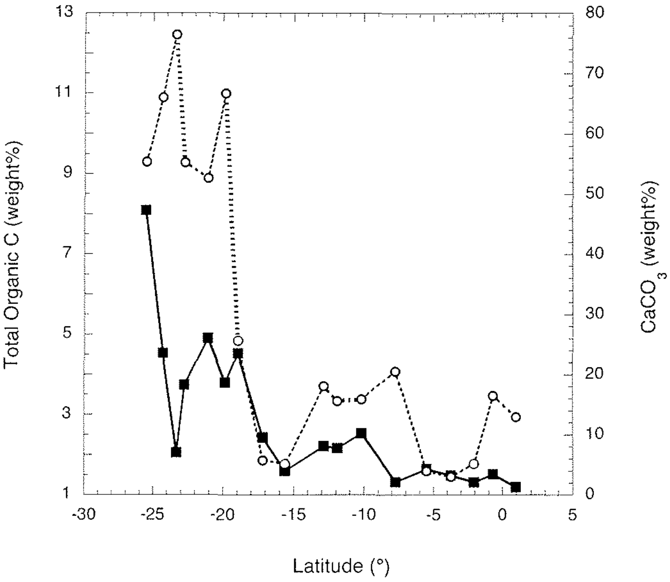


Figure 11. Sediment $CaCO_3$ (dots) and total organic carbon (squares) contents from along the African continental slope of surface sediment samples investigated in this study plotted versus latitude.

A scatter plot of the sedimentary carbonate content versus the mean $\delta^{13}C$ values of *F. wuellerstorfi*, *F. mexicana* and *U. auberiana* further illustrates that, below a threshold of about 15% sedimentary carbonate content, $\delta^{13}C$ values are enriched by up to 0.7‰ relative to values of samples containing 50-80% carbonate (Fig. 12). Above we discussed a significant depletion in ^{13}C of *B. aculeata* tests at one single station off Bouvet Island with respect to all other stations in this area as probably being caused by an enhanced local deposition of organic matter and subsequent low pore water $\delta^{13}C_{DIC}$ values. On the contrary, on the African continental slope between 19 and 15 °S, we have shown that if the decomposition of organic matter within the intermediate water column and the interstitial waters is not compensated for by a sufficient supply of carbonate from the oceanic surface layer, the carbonate ion concentration decreases below a threshold that finally results in a ^{13}C enrichment of epibenthic *F. wuellerstorfi* and different preferentially infaunal species, although pore water $\delta^{13}C_{DIC}$ values must still be low. This is no contradiction, but just the reflection of processes with opposing effects on the stable isotopic composition of benthic foraminiferal tests in areas with generally high ocean surface productivity and organic matter rain rates. This may be best illustrated by the shallow infaunal *Bulimina mexicana*: Mean $\delta^{13}C$ values from stations between 26 and 20 °S with >50 % sedimentary $CaCO_3$ content, vary between -1.2 and -1.5 ‰, between 19 and 15 °S with <5% $CaCO_3$ values increase to –0.7

and –1,2 ‰, and between 12 °S and the equator with >15 % carbonate, values decrease again below -1.7 ‰ (Fig. 10). As suggested above, in areas with a generally high productivity below the sedimentary carbonate threshold of 15 weight%, epibenthic and endobenthic $\delta^{13}C$ values are predominantly influenced by ^{13}C enrichment due to carbonate ion undersaturation, whereas above this threshold $\delta^{13}C$ values of endobenthic species reflect the influence of the strongly depleted pore water $\delta^{13}C_{DIC}$ values.

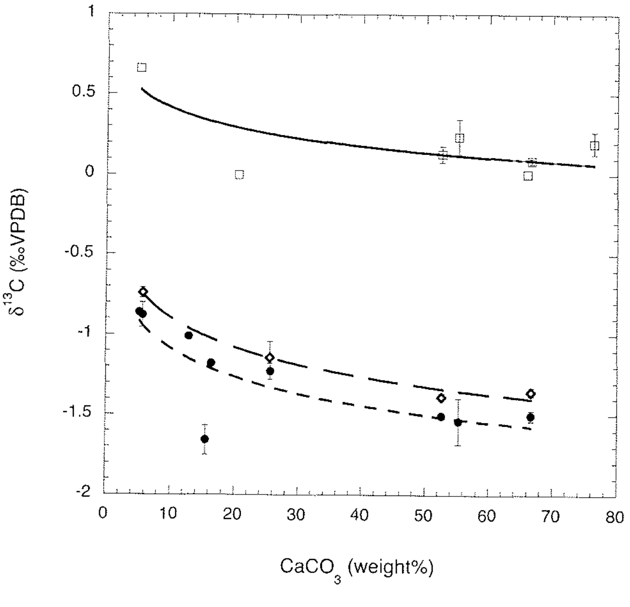


Figure 12. Mean $\delta^{13}C$ values of live *Fontbotia wuellerstorfi* (squares), *Fursenkoina mexicana* (diamonds), and *Uvigerina auberiana* (circles) are plotted versus $CaCO_3$ contents of the sediments from all stations along the African continental margin. Error bars indicate standard deviations of means of down-core values at each single station. Bottom water $\delta^{13}C_{DIC}$ values are subtracted. Curve fit is logarithmic with y=0.81-0.39*log(x) and R=0.74 for *F. wuellerstorfi*, y=-0.28-0.62*log(x) and R=0.99 for *F. mexicana*, and y=-0.49-0.59*log(x) and R=0.81 for *U. auberiana*, reflecting virtually no response in $\delta^{13}C$ values on decreasing carbonate values below the threshold of 15 % $CaCO_3$.

Although the dead assemblage represents a longer period of time than the live assemblage, good agreement between live and dead benthic stable isotope values has often been observed (McCorkle et al. 1990; Mackensen et al. 1993b). To broaden the data base and help to assess the persistence of the features observed in the living assemblage, we plotted mean $\delta^{13}C$ values of dead *Fontbotia wuellerstorfi*, *Lobatula lobatula*, *Cibicidoides pachyderma*, *Bulimina mexicana*, *Globobulimina affinis*, *Fursenkoina mexicana*, *Uvigerina auberiana*, and *U. peregrina* as well as $CaCO_3$ contents of the sediments from all stations along the African continental margin versus latitude (Fig. 13). Although the variability within some species at single stations tends to be increased, the isotopic composition of empty tests generally corresponds perfectly to the pattern observed within the live data set. This corroborates our speculation that postmortem calcite dissolution does not play a major role in shaping the variability of benthic $\delta^{13}C$ values between the stations.

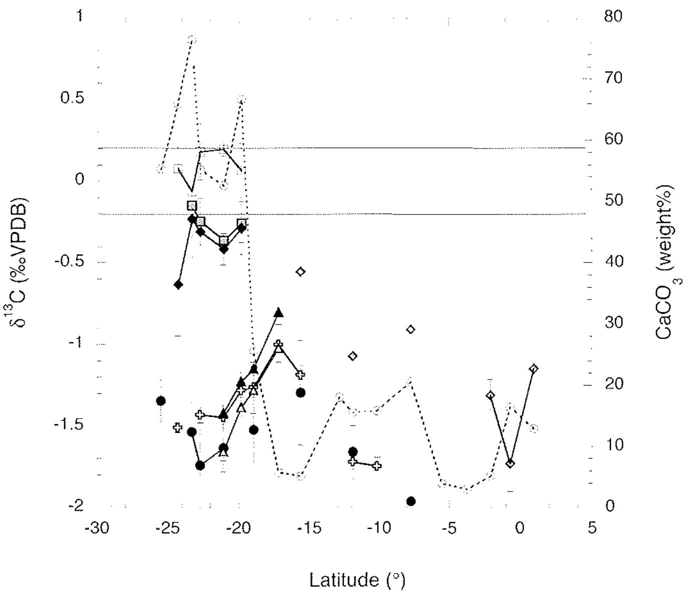


Figure 13. Mean $\delta^{13}C$ values of dead *Fontbotia wuellerstorfi* (open squares), *Lobatula lobatula* (filled squares), *Cibicidoides pachyderma* (filled diamonds), *Bulimina mexicana* (crosses), *Globobulimina affinis* (dots), *Fursenkoina mexicana* (filled triangles), *Uvigerina auberiana* (open triangles), and *U. peregrina* (open diamonds), as well as $CaCO_3$ contents (open circles) of the sediments from all stations along the African continental margin plotted versus latitude. Error bars indicate standard deviations of means of downcore values at each single station. Bottom water $\delta^{13}C_{DIC}$ values are subtracted. Horizontal lines at ±0.2 ‰ show the range of 1:1 relationship between $\delta^{13}C$ values of bottom water DIC and foraminiferal calcite, which is commonly tolerated for paleonutrient reconstructions.

4.6.4. $\delta^{13}C$ differences between epi- and endobenthic species at different sites

Since Zahn et al. (1986) it is known that infaunal benthic $\delta^{13}C$ values depend on the organic carbon decomposition rate within the sediment and thus on the organic matter rain rate from the upper ocean to the sediment surface. On the other hand, epibenthic species such as *F. wuellerstorfi* in general reliably record the bottom water $\delta^{13}C_{DIC}$ ratios in their tests (Duplessy et al. 1984). Consequently, it has long been suggested that decreasing rain rates should be mirrored by decreasing differences between epi- and infaunal benthic $\delta^{13}C$ values, and *vice versa* (Woodruff and Savin 1985; Zahn et al. 1986; McCorkle et al. 1994). However, it was argued that because of the expected down-core ^{13}C depletion of live specimens of infaunal taxa corresponding with the gradient of organic matter decomposition, the difference between epifaunal and infaunal $\delta^{13}C$ values randomly depends on how many specimens per sample were analyzed in the mass spectrometer and how sedimentation rates varied. This new study now corroborates earlier findings of Rathburn et al. (1996) and Mackensen et al. (2000) in suggesting that indeed most, if not all infaunal species have relatively consistent $\delta^{13}C$ values throughout their distribution within the sediments. Thus, we investigated whether the offsets between epifaunal cibicids and deeply infaunal globobuliminids or shallow infaunal uvigerinids vary with latitude (Fig. 14).

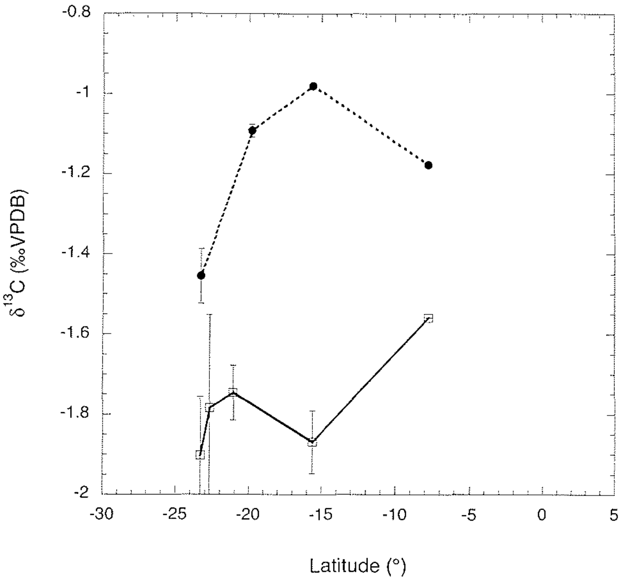


Figure 14. Offset between deep infaunal *G. affinis* and epifaunal *F. wuellerstorfi* (squares) and between shallow infaunal *U. peregrina* and *F. wuellerstorfi* (circles) mean $\delta^{13}C$ values plotted versus latitude. Error bars give propagated standard deviations of differences between means of downcore values at each single station. Bottom water $\delta^{13}C_{DIC}$ values are subtracted.

The variation with latitude of the offsets between *G. affinis* as well as *U. peregrina* and *F. wuellerstorfi* $\delta^{13}C$ values around means of −1.77 ±0.13 and −1.18 ±0.20 ‰, respectively, is not significant, given the widely accepted overall margin of reliability of ±0.2 ‰ typical of this kind of investigation. However, there, might be a visible trend indicating an increase of absolute differences from the north to the south and, in particular, at the southernmost station which would comply with the hypothesis of increasing differences with increasing organic matter rain rates and subsequent decomposition rates, if corroborated by further investigations (Figs. 11, 14).

4.7. Conclusions

Summarizing the above discussion in terms of paleoceanographic applicability, we conclude:

(1) All species investigated display relatively consistent $\delta^{13}C$ values throughout their distribution within the sediments.

(2) The $\delta^{13}C$ values of *Bulimina aculeata* from a location close to Bouvet Island reflect ocean surface water productivity in the sense that high organic carbon fluxes result in low $\delta^{13}C$ values of tests of live specimens. Alternatively, methane locally released from gas vents and related to hydrothermal venting at the mid-ocean ridge may have caused the strong depletion of ^{13}C in the benthic foraminiferal carbon isotopic composition.

(3) If the decomposition of organic matter within the Oxygen Minimum Zone of the intermediate water column and within the interstitial waters is not

compensated for by a sufficient supply of carbonate from the oceanic surface production, the carbonate ion concentration drops below a threshold that finally results in a ^{13}C enrichment of epibenthic *F. wuellerstorfi* and even of preferentially infaunal species, although pore-water $\delta^{13}C_{DIC}$ values are low.

(4) The offsets between deep endobenthic *Globobulimina affinis* and *Fontbotia wuellerstorfi* as well as between shallow endobenthic *Uvigerina peregrina* and *F. wuellersorfi* $\delta^{13}C$ values tend to increase from north to south, in parallel with generally increasing rates of organic matter decomposition. Although clearly more data are needed, these offsets between species might be used for the quantification of biogeochemical paleogradients within the sediment and thus for paleocarbon flux estimates as was previously suggested.

Generally this study confirms that further detailed investigations of quantifying the dependence of $\delta^{13}C$ values of infaunal species from organic carbon fluxes are urgently needed to derive reliable paleoproductivity proxies.

4.8. Acknowledgements

We are grateful to the crews and shipboard scientific parties of RV "Meteor" for the recovery of virtually undisturbed surface sediment samples, as well as to M. Warnkroß and H. Röben for sample preparation and picking of stained specimens. We thank G. Traue, M. Matura and G. Meyer for running and supervising the mass spectrometers. The final version of this manuscript profited from thorough reviews and helpful suggestions of F. Jorissen and S. Heß. This is Special Research Project 261 publication no. 370. Data are available under www.pangaea.de/Projects/SFB261.

5. Synthesis and future perspectives

In this thesis, we could identify the principal ecological characteristics of benthic foraminiferal faunas from a latitudinal transect running along the continental margin from the Gulf of Guinea through the Angola Basin to the Cape Basin.

While oxygen conditions over and within sediment overall fluctuate within a restricted range between sites, we could show that drastic changes in the structure and distribution of benthic foraminiferal faunas occur over latitude. On the basis of these results and the close correspondence between distinct faunal and upwelling provinces, we could demonstrate the preponderant influence of intensity, seasonality, and quality of the trophic resources on abundance, diversity, and species composition of foraminiferal live faunas in the study area (chapter 2 and 3). The live distribution patterns are in general corroborated by the distribution and composition of the dead assemblages, which indicates that the ecological information obtained from this study can be faithfully used to reconstruct past primary productivity changes in the eastern South Atlantic. An important result of this study is the documentation of no significant discrepancies in the distribution and species composition of total and surface live and dead assemblages. This validates that foraminiferal assemblages from the uppermost centimeter of sediment, commonly used as modern reference data sets for paleoceanographic purposes, do record most of the qualitative ecological information as recorded by the complete faunas (chapter 2). On the contrary, subsurface maxima of live foraminifera and dissolution of empty tests might bias quantitative approaches based on the calculation of foraminiferal standing stocks and foraminiferal numbers from the uppermost centimeter of sediment.

Within sediment, we could identify a clear stratification of foraminiferal species into four principal types of microhabitats, indicating differential ecological requirements of species with regard to food and oxygen availability (chapter 1 and 3). In areas with a limited food supply, species are concentrated towards the surface, where most of the organic matter is available. The contribution of shallow and deep endobenthic species to the fauna increases with the establishing of more eutrophic conditions. Although many endobenthic species exhibit high abundances in sediment layers that already are severely depleted in oxygen, the depth of the zero oxygen level appears to limit their maximum vertical penetration. This suggests that these species probably tolerate low-oxygen conditions and at the same time take advantage of the introduction of labile or low degraded organic compounds into the first few centimeters of sediment. A clear estimation of species-specific critical oxygen concentrations was, however, hindered by the different sampling interval for faunal and oxygen analysis. Furthermore, oxygen measurements were not performed in the same multicorer subcores as those used for the faunal investigations. Consistent occurrences of characteristic taxa (*Chilostomella oolina*, *Fursenkoina mexicana, Globobulimina affinis*) well below the zero oxygen level support other studies indicating the tolerance of these taxa to anoxia, and their ability to feed on rather refractory organic compounds or on bacterial suites involved in the remineralization of the organic matter. Our results indicate differential ecological preferences of these species with regard to trophic resources. *Fursenkoina mexicana* and *G. affinis* appear to be more dependent on the availability of organic matter in the sediment than *C. oolina* .

Placed in a paleoceanographical context, these results provide essential information for the interpretation of fossil benthic assemblages in terms of trophic conditions, linked to organic matter fluxes to the seafloor and, ultimately, to primary productivity. For example, high abundances of *Hoeglundina elegans* and *Robertinoides chapmani* are a marker of low organic matter fluxes. *Bulimina* *mexicana*, *Cibicidoides pachyderma,* and *Uvigerina auberiana* indicate higher organic matter fluxes, in well-oxygenated to low oxygen conditions. Due to the rather good oxygenation of bottom water encountered at all sites, we could not investigate the impact of severe oxygen-depletion on the composition of live faunas. On the basis of the investigation of the dead fauna, we suggest *Epistominella smithi* as potential indicator for high fluxes/low oxygen conditions. However, it would be mistaken to systematically interpret high abundances of deep endobenthic species such as *F. mexicana* or *G. affinis* as indicator of strong oxygen depletion in a context of high organic matter fluxes. Significant occurrences of these deep endobenthic species at sites overlaid by well-oxygenated bottom waters indicate that estimates of past oxygen conditions at the seafloor based on the Benthic Foraminiferal Oxygen Index might be strongly biased, and underestimate past conditions of oxygenation at the seafloor (chapter 3).

With regard to the stable carbon isotopic composition of foraminiferal tests (chapter 3 and 4), we found overall a good correlation between specific mean $\delta^{13}C$ values and microhabitat preferences, indicating that epibenthic species such as *Fontbotia wuellerstorfi* generally faithfully record the isotopic signature of dissolved inorganic carbon (DIC) of the bottom water, whereas the isotopic composition of endobenthic species mirrors the imprint of porewater $\delta^{13}C_{DIC}$ values. However, species migrating from an endobenthic microhabitat toward the surface sediment at different sites in response to changes in food availability, such as *Cibicidoides pachyderma* and *Cibicides lobatulus*, might either record bottom or porewater $\delta^{13}C_{DIC}$, which surely complicates the interpretation of the fossil isotopic signature. Furthermore, we could show that a significant enrichment in ^{13}C of the tests of epibenthic and endobenthic species can occur in high productive areas where sedimentary carbonate content is low, and probably result of enhanced isotopic fractionation due to low carbonate-ion concentration. Within the sediment, our data indicate overall the absence of significant downcore variability of species- specific $\delta^{13}C$ values, which suggests that species might calcify at a preferential level within the sediment, or record an average, site-specific $\delta^{13}C_{DIC}$ porewater signal, dependent on the organic matter flux. This is important, since it means that, at one site, the difference between epibenthic $\delta^{13}C$ values and endobenthic $\delta^{13}C$ values (benthic $\Delta\delta^{13}C$) is not arbitrarily affected by the actual living position of foraminiferal specimens within sediment, but pictures the isotopic gradient between bottom water and porewater. Although more data are clearly needed, our results suggest that the benthic $\Delta\delta^{13}C$ might be useful for the reconstruction of the degree of oxidation of the organic matter within the sediment, and by extension the intensity of the organic matter flux.

Still, several questions remain open that need further study to increase the reliability of paleoceanographic reconstructions based on benthic foraminiferal investigations:

1) In order to accurately determine species-specific critical oxygen concentrations and for a better resolution of the vertical succession of species at small scale (especially in the first few centimeters of sediment), a sediment sampling resolution in the order of millimeters should be achieved. Furthermore, oxygen measurements in the sediment should be performed on the same samples as used for foraminiferal investigations. Parallel to this, a detailed comparison of the vertical zonation of deep endobenthic species and the major geochemical gradients within sediment could help to resolve many uncertainties on the exact trophic requirements of these species, and in particular their relationship to specific bacterial consortia involved in the early diagenetic processes within sediment.

2) To verify and refine the accuracy of our conclusions concerning species preferences with regard to food and oxygen conditions, seasonal investigations of the community structure and vertical distribution of foraminiferal faunas should be performed along the same transect of stations at different times of the year. In this study, dedicated to the determination of foraminiferal ecological preferences for paleoceanographical purposes, we did not investigate the sediment grain-size fraction $<125\mu m$. For a better understanding of foraminiferal seasonal dynamics, the sediment fraction $63\text{-}125\mu m$ should be analysed as well. This faunal survey should be coupled to a seasonal survey of geochemical gradients within the sediment.

3) To confirm and refine the relationships between foraminiferal species $\delta^{13}C$ records, specific microhabitat preferences, and environmental conditions, further detailed investigations of the isotopic composition of live specimens need to be conducted (1) within the sediment and (2) over latitudinal or bathymetric gradients of environmental parameters. These investigations should include the analysis of the isotopic composition of bottom water and porewater as well. To investigate potential ontogenetic influences on the isotopic composition of species, isotopic measurements could be performed on several size classes. Furthermore, to assess the potential influence on the benthic foraminiferal isotopic record of changes of environmental conditions over time, in particular of organic carbon fluxes, seasonal investigations of species-specific isotopic composition should be performed in connection to the seasonal faunal survey described in point 2.

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