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Paleoceanographical proxies based on deep-sea benthic foraminiferal assemblage characteristics

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1. Introduction

1.1. General Introduction

The most popular proxies based on microfossil assemblage data produce a quantitative estimate of a physico-chemical target parameter, usually by applying a transfer function, calibrated on the basis of a large data set of recent or core-top samples. Examples are planktonic foraminiferal estimates of sea surface temperature (Imbrie and Kipp, 1971), or reconstructions of sea ice coverage based on radiolarian (Lozano and Hays, 1976) or diatom assemblages (Crosta et al., 1998). These methods are easy to use, apply empirical relationships that do not require a precise knowledge of the ecology of the organisms, and produce quantitative estimates that can be directly applied to reconstruct paleo-environments, and to test and tune global climate models.

Assemblage-based proxy methods that do not yield such fully quantitative results have become less popular over the last decennia, mainly because semi-quantitative or qualitative proxy methods implicitly admit a considerable degree of uncertainty. In many allegedly quantitative proxies, however, the error may be as large, but is concealed by the numerical aspect of the estimate, commonly expressed with of 1 or 2 decimals, suggesting a highly precise and trustworthy reconstruction of the target parameter.

The decreased popularity of assemblage-based proxy methods also affects proxies based on benthic foraminifera, although they have been used to reconstruct a wide range of oceanographic parameters, including water depth, water mass properties, bottom water oxygen content, and the extent and/or seasonality of the organic flux to the ocean floor. Although the use of benthic foraminiferal assemblage compositions has decreased, the use of benthic foraminiferal tests as carriers of geochemical proxy methods (stable isotopes, Mg/Ca, Sr/Ca, etc.) has never been so widespread (e.g. Wefer et al., 1999; Lea, 2004; Lynch-Stieglitz, 2004; Ravizza and Zachos, 2004; Sigman and Haug, 2004).

All geochemical proxies based on the remains of micro-organisms rely on a thorough knowledge of their ecology, that determines when, where, and under what exact conditions the proxy value is fixed in the microfossil test. In the case of benthic foraminifera, their strongly increased application in geochemical studies has led to a renewed interest in ecological studies, in field situations, but also under controlled laboratory conditions (e.g. Heinz et al., 2001; Ernst et al., 2004; Geslin et al., 2004). Due to these studies, and to studies affiliated with the Joint Global Ocean Flux Studies (JGOFS), their ecology is now much better known than 20 years ago, and it has become clear that the composition of benthic foraminiferal faunas is controlled by a limited number of closely interrelated environmental parameters.

In spite of significant advances in foraminiferal ecology, only hesitant attempts to develop or improve proxy methods based on benthic foraminiferal assemblage composition have been undertaken in recent years. The further elaboration of these proxy methods is hampered by a number of problems, most of which are not unique for foraminifera, but are of concern in most commonly used proxy methods:

1) Many of the controlling parameters that the proxy methods aim to reconstruct, are strongly interdependent, making the reconstruction of individual parameters particularly difficult.

2) Recent ecosystems cover only part of the environmental conditions encountered in past oceans. The successful reproduction of non-analog conditions is a critical point for all proxy methods, particularly, because we have no means to test the validity of the proxy estimates in most cases.

3) Laboratory experiments may remedy these two problems, by observing faunal responses to single environmental parameters, and to environmental conditions not encountered in recent ecosystems (e.g. Chandler et al., 1996; Wilson-Finelli et al., 1998; Toyofuku and Kitazato, 2005). Unfortunately, experiments with benthic foraminiferal faunas from open ocean environments are complicated (e.g. Hintz et al., 2004). It appears very difficult to artificially create hospitable environments, in which all foraminiferal species feed, grow and reproduce. Progress in this promising field of research requires important investments, and is consequently rather slow.

4) Our knowledge of taphonomical processes is insufficient. Taphonomical processes are responsible for important compositional differences between living faunas, the subject of ecological studies, and fossil faunas, that are used by proxy methods to reconstruct past environmental parameters. As for many other proxies, a major effort is needed to study the transformations and losses taking place during the transition from a living to a sub-recent (core-top) fauna and finally, to a fossil fauna.

5) A successful proxy method requires calibration with a very large data set, encompassing as many different ecosystems and ecological settings as possible. The best way to develop such a

data set is by cooperation of a large group of scientists, adopting the same methodology, and putting their data in common.

Wefer et al. (1999) give an overview of all commonly used paleoceanographical proxies. The relatively limited attention for benthic foraminiferal assemblages studies in this paper translates their decreased popularity. Following the important progress in foraminiferal ecology in recent years, several papers (e.g. Gooday, 1994; Jorissen, 1999a; Van der Zwaan et al., 1999; Murray, 2001; Smart, 2002) investigate the possibility to apply the new findings in paleoceanography. In a very thorough review, Gooday (2003) presents new ecological concepts, and gives an updated overview of the existing methods using benthic foraminiferal assemblage studies for paleoceanographical reconstructions. The application of benthic foraminifera as carriers of geochemical proxies is reviewed in several chapters (e.g. Lea, 2004; Lynch-Stieglitz, 2004; Ravizza and Zachos, 2004; Sigman and Haug, 2004 by numerous papers in Elderfield (2004).

In the present chapter on paleoceanographical proxies based on deep-sea benthic foraminiferal assemblage characteristics, we do not have the ambition to present a complete treatment of all existing proxy methods, for which we strongly recommend Gooday (2003). Instead, we will give a rather personal view of the three proxy relationships that in our opinion are most promising: those between benthic foraminiferal faunas and benthic ecosystem oxygenation, export productivity and water mass characteristics. For each, we will concentrate on the assets and shortcomings of the existing methods, and try to indicate pathways for future improvements, that will lead to a better application of this potentially very useful group of micro-organisms. A consequence of this approach is that throughout this text, we will highlight the many problems encountered when developing proxies based on benthic foraminiferal assemblage data. We would like to stress that most of these problems are not unique for proxies based on faunal data. We will limit our treatment to the reconstruction of environmental parameters in open marine ecosystems, and will not consider more coastal ecosystems, such as estuaries, inner continental shelf areas, or reef ecosystems.

1.2. Historical overview of the use of benthic foraminiferal assemblages

The practical application of benthic foraminifera started in the beginning of the 20th century, when Joseph Cushman and his co-workers developed their use as biostratigraphic markers, providing age control (Cushman, 1928), and leading to their wide-spread application in oil exploration. In the early 1930's, Natland (1933) first used benthic foraminifera in a strictly paleo-environmental way to determine the depth of deposition of sediments of the Ventura Basin. Sediments originally interpreted as outer shelf deposits later turned out to be turbidity sequences (Natland and Kuenen, 1951), thus confirming Natland's original paleobathymetric estimates. For the next 40 years, benthic foraminifera were used extensively to determine paleobathymetry. At first, efforts concentrated on the recognition of isobathyal species, that were supposed to have the same depth distribution in all oceans (e.g. Bandy, 1953a,b; Bandy and Arnal, 1957; Bandy and Echols, 1964, Bandy and Chierici, 1966, Pujos-Lamy, 1973). In more coastal areas, the ratio between hyaline, porcellaneous and agglutinated taxa was used as an indicator of water depth and salinity (e.g. Bandy and Arnal, 1957; Sliter and Baker, 1972; Murray, 1973; Greiner, 1974). The ratio of planktonic and benthic foraminifera was proposed as a paleobathymetrical tool (Grimsdale and Van Morkhoven, 1955).

In this early period, when multivariate statistical methods were not yet widely available, only relationships of individual species or species groups to single environmental parameters could be analysed, leading to major oversimplification of the complex natural situation, where a host of environmental factors interact and control the foraminiferal ecology. In 1976, Pflum and Frerichs noticed that in front of the Mississippi delta, some "delta-depressed" species showed a lower upper depth limit than in other areas, whereas others, "delta-elevated" taxa, showed the opposite tendency. They suggested that these changed bathymetrical ranges were caused by specific redox conditions, resulting from the input of important amounts of organic matter by river outflow (Pflum and Frerichs, 1976). They were probably first in recognizing the influence of organic input on the bathymetrical range of benthic foraminiferal species.

The early 1970's saw the advent of the water mass concept; different water masses, each characterised by a specific combination of temperature, salinity and pH, were supposed to be inhabited by highly characteristic faunas (e.g. Streeter, 1973, Schrader, 1974, Lohmann, 1978a). On the basis of this hypothesis, it should have become possible to track past variations of the extension of the water masses bathing the ocean floor.

From the 1950's on, research on low oxygen basins off California (e.g. Smith, 1964; Phleger and Soutar, 1973; Douglas and Heitman, 1979) and on Mediterranean sapropels (e.g. Parker, 1958), led to the recognition that recent as well as ancient low oxygen environments were inhabited by very specific faunas, generally with a low diversity, and strongly dominated by some species adapted to these apparently hostile environments (e.g. Cita and Podenzani, 1980; Mullineaux and Lohmann, 1981; Parisi and Cita, 1982; Van der Zwaan, 1982). Bernhard (1986) showed that taxa inhabiting low oxygen environments are characterised by a specific morphology, often with a maximum surface area to volume ratio. An important consequence of these studies was that bottom water oxygenation became gradually accepted as a major environmental factor in many ecosystems.

The work of Lutze's group on the NW Africa upwelling area (Lutze, 1980; Lutze and Coulbourn, 1984; Lutze et al., 1986), probably caused the breakthrough that led to the recent opinion, that the organic flux to the ocean floor is the foremost important parameter controlling benthic life in open ocean ecosystems. Since the 1980's, many efforts have been made to develop reliable proxies of bottom water oxygenation and organic flux to the ocean floor.

1.3. Recent advances in benthic foraminiferal ecology

Although it is outside the scope of this paper to give a complete overview of our present knowledge of deep-sea foraminiferal ecology (recent reviews in Murray, 1991; Sen Gupta, 1999; Van der Zwaan et al., 1999; Gooday, 2003), some of the advances since the 1980's have significantly changed our view of the parameters controlling foraminiferal faunas, and the potential use of fossil faunas as paleoceanographical proxies. Here we will briefly mention the most important new ideas.

1) Since the key papers of Basov and Khusid (1983) and Corliss (1985), and the numerous ecological studies confirming their observations (e.g. Mackensen and Douglas, 1989; Corliss and Emerson, 1990; Corliss, 1991; Barmawidjaja et al., 1992; Rathburn and Corliss, 1994; Kitazato, 1994; Rathburn et al., 1996; Ohga and Kitazato, 1997; De Stigter et al., 1998; Jorissen et al., 1998; Kitazato et al., 2000; Schmiedl et al., 2000; Fontanier et al., 2002; Licari et al., 2003), we know that deep-sea benthic foraminifera do not exclusively live at the sediment surface, but are present alive in the upper 1 to 10 cm of the sediment, in microhabitats that become increasingly oxygen-depleted from the sediment surface downwards. Elaborating ideas proposed by Shirayama (1984), Corliss and Emerson (1990), and Loubere et al. (1993), Jorissen et al. (1995) proposed the so-called TROX model, which explains that the depth of the foraminiferal microhabitat is in oligotrophic ecosystems limited by the availability of food particles within the

sediment, whereas in eutrophic systems, a critical oxygen level decides for most species down to what depth in the sediment they can live (Fig. 1). Although some authors suggested that oxygen concentration is not a major limiting factor for many taxa (e.g. Rathburn and Corliss, 1994; Moodley et al., 1997; 1998a,b), and that competition and predation may interfere (Buzas et al., 1989; Mackensen and Douglas, 1989; Van der Zwaan et al., 1999; Gooday, 2003), the general validity of the TROX concept has been confirmed in many studies. In a recent paper, Carney (2005) suggested that the TROX model may also successfully explain many macrofaunal distribution patterns.

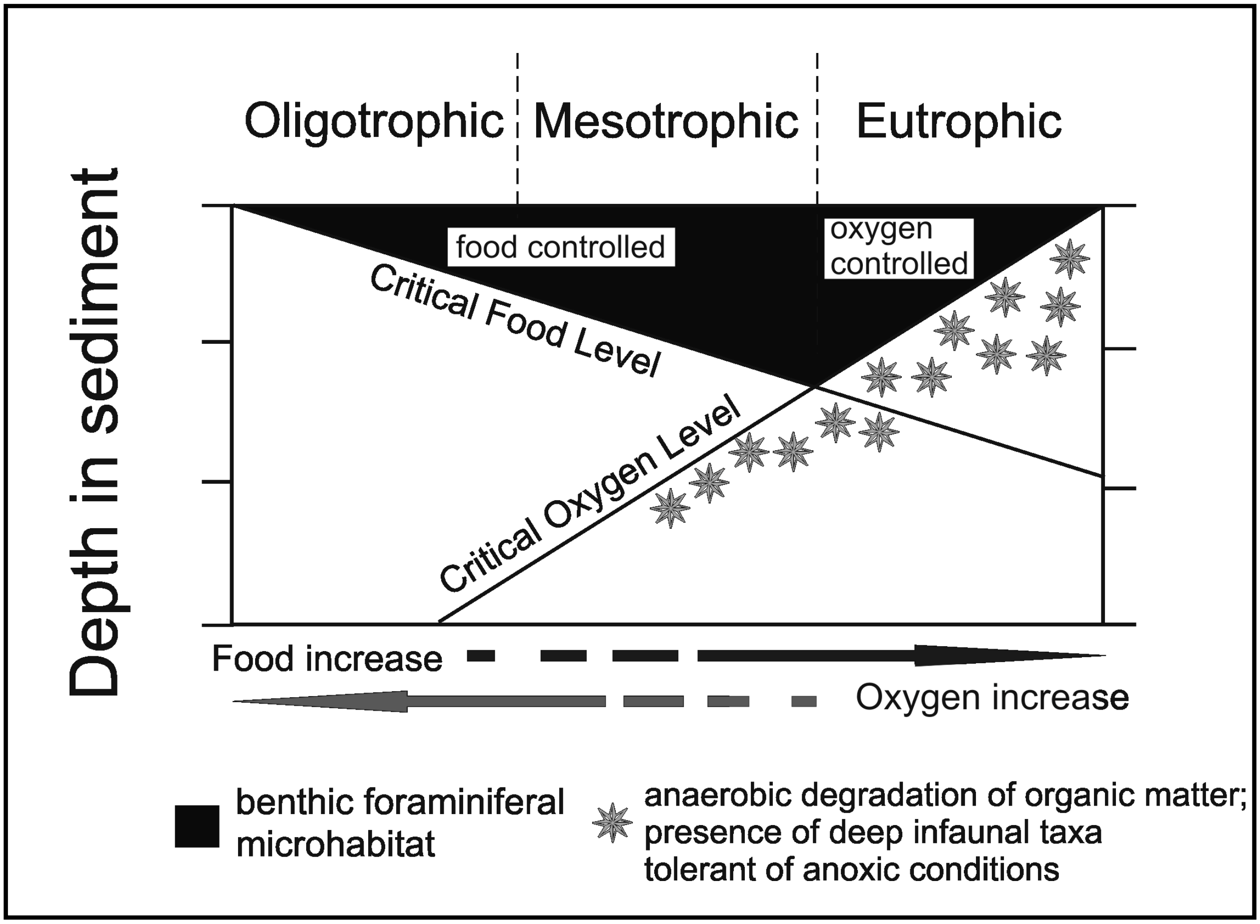

Fig. 1. Trox-model (Jorissen et al., 1995), explaining the depth of the foraminiferal microhabitat by a combination of oxygen penetration and food availability in the sediment. In oligotrophic environments, the microhabitat depth is limited by the low amount of food in the sediment; in eutrophic ecosystems, the penetration depth of most taxa is limited by the shallow level where no more oxygen is present. In mesotrophic areas, microhabitat depth is maximal. Some deep infaunal taxa are not limited by the zero oxygen level, but may participate in anaerobic pathways of organic matter remineralisation at several cm depth in the sediment.

Therefore, the foraminiferal niche is much more variable than was thought previously, with different species inhabiting a wide range of biogeochemically entirely different microenvironments, which succeed each other from the sediment-water interface to several cm depth in the sediment. As a consequence, the trace element and isotopic composition ($\delta^{18}O$, $\delta^{13}C$, Mg/Ca, etc.) of the foraminiferal test can only be interpreted adequately if the microhabitat (and calcification depth) of each investigated species is precisely known. The study of site-specific differences in these parameters opens up new possibilities to reconstruct former redox conditions at and below the sediment-water interface, as well as their controlling parameters.

2) Since the early 1990's, several papers have reported the presence of Rose Bengal stained foraminifera in anoxic environments below the sediment-water interface (e.g. Bernhard, 1989; Bernhard and Reimers, 1991; Loubere et al., 1993; Alve, 1994; Rathburn and Corliss, 1994; Rathburn et al., 1996; Jannink et al., 1998; Jorissen et al., 1998; Fontanier et al., 2002). Rose Bengal is a protein stain (Walton, 1952) that has been widely used for the recognition of living foraminifera. However, some authors have indicated that this colorant will also stain protoplasm in a more or less advanced state of decay (e.g. Bernhard 1988; Corliss and Emerson, 1990; Hannah and Rogerson, 1997; Jorissen, 1999a). As a consequence, its reliability for recognizing living foraminifera has been seriously questioned, especially in anoxic environments, where protoplasm decay may be very slow (e.g., Corliss and Emerson, 1990). Nevertheless, in the last decennia, some studies using more specific vital stains have confirmed that some foraminiferal species can indeed live, and be active, in anoxic sediments (Bernhard and Reimers, 1990; Bernhard, 1993; Bernhard and Alve, 1996). The abundant evidence for populations that are active in low oxygen conditions suggests that oxygen concentration is only a critical factor below a certain threshold value, that for most species appears to be surprisingly low, i.e., below 1 ml/l or even less (Jorissen et al., 1995; Bernhard et al., 1997; van der Zwaan et al., 1999; Levin et al., 2001). This suggests that the quantitative reconstruction of bottom water oxygenation may only be feasible for values below 1 ml/l, and will probably be much more complicated, if not altogether impossible, at higher concentrations (Murray, 2001).

3) Since the key papers of Lutze and co-workers (Lutze, 1980; Lutze and Coulbourn, 1984; Lutze et al., 1986), it has become clear that the flux of organic matter to the deep sea floor is the main parameter structuring benthic foraminiferal faunas, by controlling their density and composition. Many foraminiferal taxa appear to have an optimum range with respect to organic input, in which their competitiveness is maximal. Under such conditions these taxa become dominant faunal elements. If the organic input falls below, or exceeds the optimal flux levels for

some taxa, they are replaced by other taxa that are more competitive under more oligotrophic or more eutrophic conditions. Changes in the bathymetrical range of foraminiferal species under different organic flux regimes were first shown by Pflum and Frerichs (1976) in front of the Mississippi delta, and more recently by de Rijk et al. (2000), who showed a progressive shoaling of the bathymetrical ranges of many species along a W-E transect through the Mediterranean, coincident with a transition from eutrophic to very oligotrophic ecosystems.

The fact that many foraminiferal species depend strongly upon the organic flux must open up new pathways for the reconstruction of paleoproductivity. However, as we will explain in chapter 2.3, the advance of such methods is hampered by calibration problems (Altenbach et al., 1999).

4) Carney (1989) proposed that there exist two independent organic matter remineralisation cycles at the sea floor, fueled by two different types of organic input. Labile organic matter (marine organic matter, phytodetritus), should rapidly be remineralised using aerobic pathways at the sediment water interface, whereas more refractory organic matter (terrestrial organic matter, laterally advected older material) should be remineralised much more slowly in the dysaerobic ecosystems deeper in the sediment. Since this key publication, several authors have speculated on the importance of organic matter quality as a controlling ecological parameter. In several papers, Fontanier et al. (2002; 2005) suggested that most superficially living taxa participate in the aerobic remineralisation, whereas deeper living taxa may contribute to the dysaerobic mineralization of low quality organic matter. In the eastern Atlantic Cap Ferret Canyon, where there is lateral input of large quantities of more refractory organic matter, Fontanier et al. (2005) showed the presence of a very rich deep infauna, in combination with much poorer surface faunas.

These observations suggest that it should be possible to use the benthic foraminiferal faunal composition to reconstruct not only the quantity, but perhaps also the quality of the organic input. On the basis of the succession of fossil faunas observed in a core off NW Africa, Caralp (1984; 1989) suggested that *Bulimina exilis* is advantaged with respect to other species when there is an input of fresh, labile organic matter, with a high phaeopigment/glucide ratio, whereas *Melonis barleeanus* increased its percentage when the organic input consisted of more refractory, laterally advected organic material. Goldstein and Corliss (1994) observed that diatom frustules were ingested by *U. peregrina*, but not by *Globobulimina* spp., suggesting adaptation to different food types of these taxa. On the basis of a fatty acid analysis in foraminiferal protoplasma, Suhr et al. (2003) concluded that some taxa are more selective than others ones. They suggest that *Globocassidulina subglobosa* may ingest preferentially fresh diatoms, whereas *Thurammina albicans* would feed on degraded material. Nomaki et al. (2005), who performed a field feeding experiment with ^{13}C-labeled algae, show a higher carbon assimilation rate for the shallow infaunal taxa *Uvigerina akitaensis* and *Bulimina aculeata* than for the deeper infaunal species *Textularia kattegatensis* and *Chilostomella ovoidea*. All these observations suggest that different species do not respond in the same way to the input of various types of food particles, and that food preferences may exist.

5) Thanks to long-term observations based on sediment trap deployments, we know that in most areas the organic matter flux to the ocean floor is not constant over time, but has a strong seasonal and interannual variability (e.g. Billett et al., 1983; Berger and Wefer, 1990; Lohrenz et al., 1992). In some areas, episodic events are responsible for most of the organic input, and specialised benthic foraminiferal faunas may rapidly colonize phytodetritus deposits, responding by accelerated growth and/or reproduction (e.g. Gooday, 1988; Gooday and Lambshead, 1989; 1993; 1996; Gooday and Rathburn, 1999; Gooday and Hughes, 2002). These phenomena have been documented most conclusively after episodic phytodetritus falls arrive in otherwise oligotrophic deep oceanic basins, but also appear to control the foraminiferal population dynamics in more eutrophic areas, with a less variable organic input (e.g. Ohga and Kitazato, 1997; Kitazato et al., 2000; Rathburn et al., 2001; Fontanier et al., 2003; 2006). The strong response of some foraminiferal taxa (e.g. *Epistominella exigua*) has led to tentatives to use these taxa as indicators of pulsed organic input (Loubere, 1998; Smart et al., 1994; Thomas et al., 1995; Thomas and Gooday, 1996).

6) Since the early publications of Buzas and co-workers (Buzas and Gibson, 1969; Buzas et al., 1989), it has become increasingly clear that spatial variability at a micro- or mesoscale (patchiness) may be important in the deep ocean (e.g. Gooday and Rathburn, 1999; Hughes and Gooday, 2004). This phenomenon may cause large differences between living faunas collected with multi-corers and fossil samples, in which patchiness has been eliminated by time averaging. Taphonomical processes may be responsible for a partial or even total loss of many foraminiferal taxa and will further increase the differences between fossil and living faunas. It is evident that ecological observations of living faunas are essential for a better understanding of proxy relationships. However, because of the afore-mentioned processes which are responsible for large

differences between living and fossil faunas, we think that a successful calibration of a proxy relationship method is very difficult, if not impossible, on the basis of living faunas. We will argue that once the underlying mechanisms of proxy relations are fully understood, proxy calibration should rather be performed on the basis of sub-recent faunas, in which the transformation of the living fauna to the fossil fauna, due to early diagenetic processes, has been concluded.

2. Benthic foraminiferal proxies: a state of the art

2.1. Overview of proxy methods based on benthic foraminifera assemblage data

In this chapter, we will give a description of the present state of the most commonly used proxy methods based on benthic foraminiferal assemblage data. Benthic foraminiferal assemblage data may be of several types: they may be presence/absence data of various taxa, measures of faunal density, of biodiversity, or even data on the morphology of dominant taxa. All these faunal characteristics have been proposed as paleoceanographical proxies. The reconstructed environmental parameters fall apart into two groups:

a) Physico-chemical parameters, such as temperature, salinity, carbonate saturation, hydrodynamics, or oxygen concentration of the bottom water. Such parameters may be expected to act as limiting factors, deciding whether a foraminiferal species may live somewhere, and if so, if it is capable to feed actively, to grow and to reproduce. If all limiting factors fall within the optimum range for a specific taxon, it will attain maximum competitiveness, and may be expected to reach its maximum abundance. Such a maximum abundance may be very high for opportunistic species, but very low for highly specialised K-selected taxa (e.g. Levinton, 1970; Pianka, 1990; Dodd and Stanton, 1991).

b) Resource parameters, such as the quality and quantity of the organic matter flux, that directly influence the amount of available food. Resources may be expected to act directly on the density of the foraminiferal populations, but since most taxa have a maximal competitiveness in a specific flux range, they will also determine what species will dominate the faunas.

Traditionally, benthic foraminiferal assemblage data have been used to reconstruct water depth. Water depth itself is not a controlling ecological parameter, but most other parameters change with water depth, causing the existence of well-established bathymetrical successions in many ocean basins. Although elaborate bathymetrical distribution schemes have been proposed from the 1950's on, more recent data consistently show important differences in the bathymetrical ranges between various ocean basins, which appear to be at least partially caused by differences in organic flux regime. It has therefore become evident that the reconstruction of paleo water-depth by the use of benthic foraminiferal presence-absence patterns is probably not possible. As a consequence, alternative methods, such as the ratio between planktonic and benthic foraminifera (e.g. Van der Zwaan et al., 1990; Van Hinsbergen et al., 2005), or modern analogue techniques (Hayward, 2004) continue to be explored.

Foraminiferal assemblage characteristics have rarely been used for the reconstruction of bottom water temperature and salinity in open ocean environments. It is thought that the variability of these parameters is in most oceanic basins too limited to cause a significant faunal response. In shallow water environments, on the contrary, where strong temperature and salinity gradients exist, foraminifera have been used successfully to reconstruct these parameters. At present, the combination of stable oxygen isotopes and Mg/Ca values is considered as the most promising method to reconstruct temperature and salinity in deep oceanic environments (e.g. Lear et al., 2000). The combination of bottom water temperature and salinity, however, will of course determine the specific density, and superposition of oceanic water masses. Until the early 1980's, the benthic foraminiferal assemblage composition was thought to reflect these water mass characteristics, and it was thought possible to reconstruct the geographical extension of specific water masses on the basis of the distributional patterns of a number of benthic foraminiferal marker species (e.g. Streeter, 1973; Schnitker, 1974; Gofas, 1978; Lohmann, 1978b; Lutze, 1979; Streeter and Shackleton, 1979; Schnitker, 1979; Corliss, 1979b; Schnitker, 1980; Corliss, 1983a; Caralp, 1987). With the realisation that the spatial and bathymetrical distribution of most foraminiferal taxa is predominantly based on organic flux rates, today many scientists doubt the validity of the so-called "water mass concept". Although small changes in temperature and salinity in deep ocean ecosystems indeed appear to have a minimal influence on benthic foraminiferal assemblages, other parameters related to water masses, such as carbonate saturation (and alkalinity) may have a profound influence on bio-calcification, and in this way structure the live benthic foraminiferal assemblages (e.g. Mackensen et al., 1990; 1995), and the preservation of their tests. Carbonate saturation becomes especially important in deep ecosystems close to the carbonate compensation depth (CCD), where values may become very low.

The reconstruction of the extent of former water masses is still of paramount importance, and today a whole range of geochemical proxies, such as Cd/Ca ratios, Nd and Pb isotopes, or carbon isotopes are used (e.g. Lynch-Stieglitz, 2004). We think therefore that the foraminifera-based "water mass" concept can not be discarded without a serious treatment, which we will present in chapter 2.4.

The organic flux to the ocean floor, and notably its quantity, quality and periodicity, is today considered to be the prevailing environmental parameter structuring deep-sea benthic foraminiferal faunas. It is therefore logical that our best hopes to develop paleoceanographic proxies on the basis of deep-sea benthic foraminiferal assemblages lay in the field of paleo-productivity. We will treat this subject in chapter 2.3., where we will also focus on proxies reconstructing the periodicity of the organic input, and the presence/absence of episodic events.

Although many modern studies suggest that bottom water oxygen concentration is for most species less critical than was thought previously, several foraminiferal proxies of bottom water oxygenation have been proposed, and yield very promising results. In chapter 2.2. we will present the existing methods, and indicate pathways for future improvement.

The observation of a very specific assemblage of benthic foraminifera in areas with elevated current velocities (Schönfeld, 1997; 2002a,b) has led to the tentative development of a proxy of bottom current velocity. This promising new field of proxy development, that could inform us about past variations of the intensity of deep water circulation, is briefly treated in chapter 2.5.

2.2. Proxies of bottom water oxygenation

2.2.1 Introduction

Since the 1960's, abundant live foraminiferal faunas have been reported from various low oxygen environments (e.g. Smith, 1964, Phleger and Soutar, 1973; Douglas and Heitman, 1979). Recent review papers (e.g. Bernhard, 1986; Sen Gupta and Machain-Castello, 1993; Bernhard and Sen Gupta, 1999) agree that faunas from these low oxygen environments have a very characteristic taxonomic composition, generally with a strong dominance of bolivinids, buliminids, globobuliminids and some other typical taxa, at least at concentrations below 1 ml/l.

If, as is apparently the case, the relative proportion of these taxa increases with decreasing bottom water oxygenation, it should be possible to use the composition of fossil faunas to reconstruct ancient bottom water oxygen concentrations. It has been argued, however, that two groups of fundamentally different taxa, with very different life strategies, may profit from the disappearance of less resistant taxa when bottom water oxygen concentration decreases: 1) deep infaunal taxa, which at the onset of bottom water hypoxia migrate from the deeper sediment layers to the sediment surface (Jorissen, 1999), and 2) epifaunal or shallow infaunal taxa which have developed adaptations or tolerance to low oxygen conditions. Unlike the first group, the second group of taxa are usually rare in environments with well oxygenated bottom waters, and are abundant under severely hypoxic conditions.

Before looking at the available proxy methods of paleo bottom water oxygenation based on foraminiferal assemblages, it is necessary to treat the terminology for environments with bottom and/or pore waters undersaturated in oxygen. Unfortunately, there is considerable confusion in the literature concerning the exact meaning of the various descriptors. Fig. 2 presents an inventory of the terms most often encountered in the foraminiferal literature, and their meaning according to various authors. As can be seen in this figure, there is considerable confusion about the exact meaning of the terms “dysoxic” and “suboxic”, that have been used for environments with entirely different oxygen concentrations. The very precise term anoxic (a = without) is sometimes used for environments where oxygen concentrations are below the detection limit, whereas other authors use it for concentrations below 1 ml/l. Bernhard and Sen Gupta (1999) differentiate between anoxic environments with and without sulphate reduction, the latter being termed postoxic. In order to avoid further confusion, we will use the term hypoxic for all environments (without giving a precise range of oxygen concentration) where foraminiferal faunas may potentially be influenced by low oxygen concentrations, and we will use anoxic for all environments without detectable oxygen.

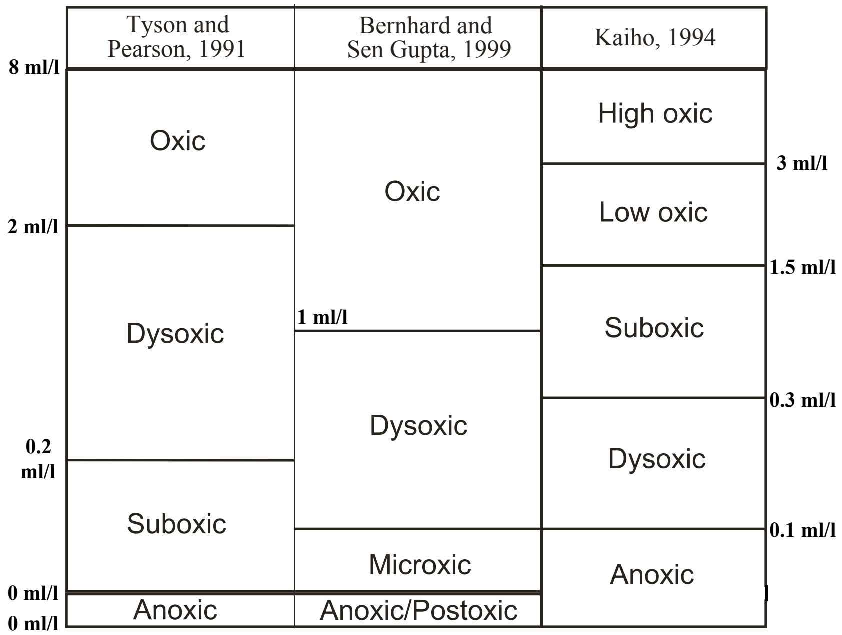

Fig. 2. Classification of environments with different oxygen concentrations, according to Tyson and Pearson (1991), Kaiho (1994) and Bernhard and Sen Gupta (1999).

2.2.2 Potential problems for paleo-oxygenation proxies

Several problems must be considered when benthic foraminiferal assemblages are used to reconstruct bottom water oxygen concentration. Some of these problems (points 1,2, 4 and 5 in the following list) are specific for bottom water oxygenation proxies, whereas others are of a more general nature, and concern most proxies based on microfossil remains:

1. In most benthic ecosystems oxygen concentration is subject to a strong gradient. Starting in the more or less well oxygenated bottom waters, oxygen concentrations show a first decrease at the sediment water interface, followed by a rapid downward decrease in the superficial sediment layer, to become zero at a few mm or cm depth. In most continental slope and margin environments, the depth of the oxic sediment layer rarely exceeds 5 cm. Extreme oxygen penetration, down to 1 m or more, has been observed in the Angola Basin, Weddell Sea and in the West Equatorial Pacific (Rutgers van der Loeff, 1990). In many of the world's oxygen minimum zones, on the contrary, oxygen penetration is limited to the topmost mm of the sediment (e.g. Miao and Thunell, 1993; Levin, 2003).

In environments with strongly changing oxygen concentrations over short vertical distances within the sediment and/or over short time periods, it must be made very clear what the bottom water oxygenation proxy exactly intends to reconstruct: bottom water oxygenation (at some dm above the sediment-water interface), oxygen concentration at the sediment-water interface, or the depth of oxygen penetration into the sediment? These three elements each tell a part of the story, and only the knowledge of all three (which is probably unrealistic) gives a complete picture of benthic ecosystem oxygenation.

2. Benthic foraminiferal faunas often inhabit a several cm deep superficial sediment layer, usually coinciding with the complete range from well oxygenated to strongly hypoxic conditions. Therefore, most faunas collected in environments with well oxygenated bottom waters contain a mixture of taxa that inhabited fully oxic to strongly hypoxic, or even anoxic microhabitats. Although individual species usually have a preference for a specific depth interval (e.g. Corliss, 1985; Jorissen et al., 1998; Fontanier et al., 2002), even taxa considered as “epifaunal” do not exclusively live at the sediment-water interface, but may migrate through the topmost mm or cm of the sediment, and will, as all other taxa, experience a wide range of oxygen concentrations during their life time (e.g. Barmawidjaja et al., 1992; Ohga and Kitazato, 1997).

3. Geological samples, the basis for every paleoceanographic reconstruction, are always time-averaged. In the ideal case (without addition or loss of tests due to lateral transport), a sample will contain a mixture of all faunas that inhabited the site during several decennia. Even in laminated sediments with annual laminae, the fossil fauna found in a single lamina will be representative for the average conditions during a complete season, i.e. about 6 months. If environmental conditions have been stable during the period under consideration, then the composition of the fauna may indeed record bottom water oxygenation very precisely. However, bottom water oxygen concentration (and oxygen penetration depth into the sediment) will very often experience important short-term variability. This may be the case when strong water column stratification, or pulsed phytodetritus deposits, cause seasonal hypoxia/anoxia. Such events may be annual, but can also be highly episodic, occurring once every ten years, or even less often. Of course, in such cases it will be extremely difficult (if not impossible) to extract the precise oxygenation history from the time-averaged faunas. For instance, in cases of anoxic conditions (without fauna) interrupted by short periods with oxic bottom waters, characterised by rich pioneer faunas, a foraminifer-based bottom water oxygenation proxy will probably

overestimate the average long-term bottom water oxygen concentration. In other settings, such as oligotrophic, well-oxygenated ecosystems affected by short-term anoxia, leading to the explosive development of some low-oxygen tolerant taxa, the duration and severity of the periodical hypoxia/anoxia may easily be overestimated.

4. The critical values at which the oxygen concentration starts to have a negative impact on the organism, are probably very low, below 1 ml/l or even below 0.5 ml/l (Levin and Gage, 1988). Many elongated, commonly biserial or triserial taxa have been described as abundant at very low oxygen concentrations. In several papers (e.g. Bernhard, 1986; Corliss and Chen, 1988; Corliss and Fois, 1990; Corliss, 1991) it has been suggested that their morphology corresponds to an infaunal microhabitat. However, not only elongated uniserial, biserial and triserial taxa, but also a wide range of planoconvex to biconvex, planispiral and trochospiral taxa have been found alive in low oxygen environments (Table 1). For example, *C. wuellerstorfi,* usually described as a strictly epifaunal taxon, and considered typical of well oxygenated bottom waters, is present in significant numbers in several stations in the Sulu Sea where bottom water oxygen concentrations are well below 2 ml/l (Rathburn et al., 1994). Many of the planoconvex taxa to biconvex taxa listed in table 1 (e.g. *Cassidulina carinata, Cibicides ungerianus, Cibicidoides wuellerstorfi, Gavelinopsis translucens, Hoeglundina elegans*), have been described in well oxygenated environments, as shallow infaunal or even epifaunal. In some papers (e.g. Kaiho, 1994, Jannink et al., 2001) it was therefore implicitly suggested that these species need elevated oxygen concentrations. Observations of these taxa in strongly hypoxic environments suggest that they are much less sensitive to low oxygen concentrations than generally assumed. We think that their preference for superficial sediment niches should rather be explained by their dependence on a supply of high quality food particles. It should also be realised that no foraminiferal species are exclusively occurring in low-oxygen environments (Sen Gupta and Machain-Castello, 1993). Most taxa indicative for strongly hypoxic conditions can also be found at much higher bottom water oxygenation values. Murray (2001) thus suggested that foraminifera can only be used as proxies for oxygen levels below concentrations of 1 or perhaps 2 ml/l. Above these values, there would no longer be a relationship between oxygen levels and the composition of the foraminiferal faunas (Murray, 2001).

Ammonia batavus	0.3 ml/l	1	*Epistominella smithi*	0.1 ml/l	3
Anomalina sp.	0.2 ml/l	4	*Epistominella vitrea*	0.8 ml/l	5
Cancris auriculus	0.3 ml/l	6	*Eponides antillarum*	0.9 ml/l	9
Cancris inaequalis	0.2 ml/l	7	*Eponides leviculus*	0.2 ml/l	3
Cancris oblongus	0.2 ml/l	4	*Eponides regularis*	0.1 ml/l	6
Cancris panamensis	0.6 ml/l	9	*Gavelinopsis lobatulus*	2.1 ml/l	4
Cancris sagra	0.4 ml/l	9	*Gavelinopsis translucens*	0.0 ml/l	8
Cassidulina carinata	0.3 ml/l	4	*Gyroidina io*	0.2 ml/l	3
Cassidulina crassa	0.3 ml/l	6	*Gyroidina lamarckiana*	0.1 ml/l	6
Cassidulina cushmani	0.3 ml/l	9	*Gyroidina multilocula*	0.4 ml/l	9
Cassidulina delicata	0.1 ml/l	3,7	*Gyroidina parva/pulchra*	0.9 ml/l	4
Cassidulina depressa	0.5 ml/l	4	*Gyroidina rotundimargo*	0.3 ml/l	9
Cassidulina laevigata	0.2 ml/l	7	*Gyroidina umbonata*	0.4 ml/l	4
Cassidulina limbata	1.0 ml/l	3	*Gyroidinoides neosoldanii*	0.5 ml/l	2
Cassidulina minuta	0.6 ml/l	9	*Gyroidinoides soldanii*	0.1 ml/l	6
Cassidulina oblonga	0.6 ml/l	9	*Hanzawaia boueana*	0.8 ml/l	5
Cassidulina sgarellae	0.3 ml/l	6	*Hanzawaia concentrica*	0.3 ml/l	6
Cassidulina subcarinata	0.2 ml/l	3	*Hoeglundina elegans*	0.2 ml/l	3
Cassidulina subglobosa	0.2 ml/l	4	*Hyalinea balthica*	0.3 ml/l	4
Cassidulina teretis	0.5 ml/l	3	*Islandiella subglobosa*	0.2 ml/l	3
Cassidulina tumida	0.4 ml/l	9	*Islandiella sp.*	0.3 ml/l	6
Cibicides bradyi	0.3 ml/l	4	*Lenticulina articulata*	0.3 ml/l	6
Cibicides fletcheri	0.4 ml/l	7	*Oridorsalis umbonatus*	0.4 ml/l	4
Cibicides refulgens	0.3 ml/l	2	*Osangularia culter*	0.3 ml/l	4
Cibicides ungerianus	2.1 ml/l	4	*Osangularia rugosa*	0.0 ml/l	8
Cibicidoides wuellerstorfi	1.6 ml/l	2	*Planulina ariminensis*	0.2 ml/l	7
Elphidium albiumbilicatulum	0.0 ml/l	1	*Planulina exorna*	0.6 ml/l	9
Elphidium excavatum	0.1 ml/l	1	*Planulina limbata/ornata*	0.3 ml/l	9
Elphidium incertum	0.1 ml/l	1	*Pullenia* sp.	0.4 ml/l	4
Elphidium tumidum	2.4 ml/l	9	*Valvulineria araucana*	0.2 ml/l	3
Epistominella decorata	0.1 ml/l	6	*Valvulineria javana*	0.2 ml/l	4
Epistominella exigua	0.3 ml/l	6	*Valvulineria oblonga*	0.3 ml/l	9

Table 1 : Observations of planoconvex planispiral and trochospiral taxa generally considered as typical of well oxygenated bottom waters in low oxygen environments. The second column gives the lowest bottom water oxygen concentration at which living (Rose Bengal stained) specimens have been described. The third column gives the reference: 1. Alve, 1990; 2. Bernhard, 1992; 3. Douglas and Heitman, 1979; 4. Jannink et al., 1998; 5. Jorissen et al., 1992; 6. Maas, 2000; 7. Mackensen and Douglas, 1989; 8. Sen Gupta et al., 1997; 9. Smith; 1964.

5. In recent benthic ecosystems, there is a complex interplay between export productivity (organic flux to the sea floor) and oxygenation of bottom and pore waters. The competitive ability of most species appears to be determined by one or both of these parameters. Jorissen et al. (1995) suggested that deep infaunal taxa, often considered indicative of hypoxic conditions, are only present when the organic flux is sufficiently high to have organic detritus within the sediment that can be used metabolically. In areas with lower flux rates, most organic matter is consumed at the sediment-water interface, and deeper sediment layers are too poor in organic matter to be inhabited by deep infaunal taxa (Fig. 1). This means that a sudden appearance, or a relative frequency increase, of these deep infaunal taxa in the fossil record may very well be the result of an increased organic flux, and not of lowered bottom water oxygen concentrations. Oxygen concentrations have a direct impact on the faunal composition only in areas where bottom water concentrations become so low that they cause a diminished competitive ability

and/or reproductive potential of the more superficially living taxa. In such cases, one may expect that less resistant taxa will disappear, and that deep infaunal taxa, that are perfectly adapted to live in low oxygen environments, will take over niches at the sediment surface and dominate the foraminiferal assemblages (Jorissen, 1999b). But such conditions will only occur when the oxygen concentrations fall below a threshold level critical for the surface dwelling taxa (1 ml/l or less; Murray, 2001). Finally, even faunas that are strongly dominated by deep infaunal taxa may form in environments with well oxygenated bottom waters. For instance, at a 2800 m deep station in Cap Ferret Canyon (north-eastern Atlantic) oxygenated bottom waters are well oxygenated (5 ml/l), but deep infaunal taxa were dominant, probably because of intensive degradation of large quantities of low quality organic matter by anaerobic bacterial stocks deeper in the sediment (Fontanier et al., 2005).

6. There is always an important difference between the living fauna, and the fossil faunas accumulating at the same site (e.g. Murray, 1991; Jorissen and Wittling, 1999; Walker and Goldstein, 1999). This difference is caused by early diagenetic processes, causing a preferential loss of the more fragile taxa, but also by biological parameters, such as large interspecific differences in test production, or selective predation on some foraminiferal species (e.g. Culver and Lipps, 2003). Additionally, transport by bottom currents may be responsible for the addition of allochthonous foraminifera and/or the removal of small autochthonous elements. Since paleoceanographic reconstructions are based on fossil material, that has been seriously modified by taphonomic processes, it is probably not logical to use living faunas for the calibration of paleoceanographical proxies. Individuals living at any specific moment of sample collection do not necessarily reflect a fauna as averaged over a full seasonal cycle, for instance. We think that proxy relationships between faunal characteristics and oceanographical parameters should rather be calibrated by a comparison of the recent values of the target parameter with "subfossil" faunas, that represent recent environmental conditions, but that have fully concluded the suit of diagenetic processes, and will undergo no more post-mortem compositional changes. Unfortunately, in most ocean basins, it takes several thousands of years before a fauna has passed through the biologically active top part of the sediment, where most of the diagenetic processes and losses of foraminiferal tests take place (e.g. Walker and Goldstein, 1999). It is very improbable that the Holocene fossil faunas collected below this topmost sediment layer, where early diagenesis is taking place, can directly be compared with the recent (man-influenced) environmental conditions, a procedure that cannot be avoided when a proxy relationship has to be

calibrated. However, these problems can at least partly been solved by a careful, high resolution study of the succession of Holocene faunas in areas with high sedimentation rates.

7. Most oceanic environments are much less stable then was previously thought. Even abyssal environments experience episodic phytodetritus inputs, provoking a strong response of some highly opportunistic taxa, that may rapidly attain very high densities (e.g. Gooday, 1988; 1993, Gooday and Lambshead, 1989). Other unpredictable events such as whale falls, or pulsed food input from hydrothermal vents may equally have a profound impact on benthic foraminiferal faunas, although hydrothermal vent regions and cold seep areas do not contain endemic benthic assemblages (e.g.,Rathburn et al., 2003; Barberi and Panieri, 2004). At present, it can not be excluded that in many parts of the ocean, an important part of the fossil faunas is formed during such ephemeral events. If true, then the fossil fauna should not be representative of average conditions, but rather for the very specific conditions associated with the short periods of high productivity.

In spite of these problems, there appear to be significant differences in tolerance for low oxygen levels between species, and therefore, oxygen concentration must have an impact on the assemblage composition, at least at low to very low oxygenation levels. The possibility to estimate former oxygen levels with a high precision in the 0-1 ml/l range is important, because it will open up the possibility to reconstruct the history of oxygen minimum zones (OMZ's). These continental margin environments potentially play an important role in the global carbon cycle as organic carbon sinks. Furthermore, the reconstruction of the variability of the intensity of OMZ's through time may give insight into the dynamics of intermediate and deeper water masses.

2.2.3 Existing proxies of bottom water oxygenation

The proposed methods for the reconstruction of ancient bottom water oxygenation concentrations on the basis of benthic foraminiferal assemblage characteristics fall into four categories:

1. Most often, a number of taxa is considered as indicative of hypoxic conditions, and the relative frequency of these taxa (expressed as a percentage of the total benthic foraminiferal fauna) is used as a semi-quantitative index of bottom water oxygenation. The best example of this

method is the widely applied benthic foraminiferal oxygen index (BFOI) of Kaiho (1991; 1994; 1999). In this oxygen index, the subdivision of taxa into categories of dysoxic, suboxic or oxic indicators is made rather arbitrarily, is mainly based on test morphology, and differs between the 1991 paper, that deals with Paleogene faunas, and the 1994 and 1999 papers, that try to calibrate the method on the basis of recent faunas. It is surprising to see that for many species adult individuals (≥ 350µm) are considered as "oxic" indicators, whereas smaller individuals (< 350 µm) of the same species are considered as "suboxic" indicators (Kaiho 1994; 1999). The hypothesis underlying the method is that in well oxygenated bottom waters, dysoxic indicators live in poorly oxygenated deep infaunal microhabitats. In the case of hypoxic conditions at the sediment-water interface, less resistant taxa would disappear, and the "dysoxic indicators" would become dominant. However, among these "dysoxic" indicators (21 taxa listed by Kaiho, 1994) only few have actually been observed alive in intermediate or deep infaunal microhabitats. The suggested microhabitat separation between oxic and suboxic indicators (Kaiho, 1994, fig. 1) is not supported by data. In its latest version (Kaiho, 1999), Kaiho's oxygen index distinguishes between 5 classes of bottom water oxygenation (fig. 1), and at levels above 3.2 ml/l, the index is no longer correlated with bottom water oxygenation. Other authors have slightly modified the attribution of taxa to the categories of dysoxic, suboxic or oxic indicators (e.g. Baas et al., 1998), in order to better fit the method (and results?!) to their ideas.

2. The method proposed by Jannink et al. (2001) is interesting because it follows an inverse approach. Taxa that are systematically found living in the topmost sediment are considered as oxiphylic, and their cumulative percentage is considered as a proxy for bottom water oxygenation. The rationale behind this procedure is that with increasing bottom water oxygenation, oxygen penetration into the sediment supposedly increases, leading to an increased volume of the niche potentially occupied by allegedly oxiphylic taxa. The problem with this method is how to determine which species are oxiphylic. A species living close to the sediment-water interface may prefer this microhabitat because it does not tolerate the lower oxygen concentrations deeper in the sediment, but it may also prefer high quality food particles, that have the highest concentration at the sediment-water interface, as indicated by an increasing number of data (e.g. Kitazato et al., 2003; Fontanier et al., 2003; 2006; Ernst et al., 2005; Nomaki et al., 2005).

3. Several authors (e.g. Loubere, 1994; 1996; Morigi et al., 2001) have attempted to link subrecent faunal assemblages to bottom water oxygenation values by multivariate statistical methods, withsome encouraging results for recent faunas. It is very difficult to know, however, whether application of these relationships to fossil material would yield reliable results, because the investigated data sets contain a rather limited array of combinations of oxygen concentration and organic flux (and of other environmental parameters). Non-analog conditions thus may not be correctly reconstructed. An additional problem is the fact that in order to be robust, the multivariate statistical methods need many more data (samples) than variables (taxa) (e.g. Tabachnick and Fidell, 1983). At present, the size of the analysed data sets is small in comparison with the number of species.

4. Finally, Schmiedl et al. (2003) proposed a method based on a combination of the relative proportion of low-oxygen tolerant marker species and a diversity index, counting each for 50% of the final score of his oxygen index, because all hypoxic environments show a lower biodiversity than well oxygenated settings. By adding a factor independent of taxonomic composition, the proxy method may become more robust, and applicable in an array of areas with very different faunal compositions.

Unfortunately, all four procedures suffer from one or more of the pitfalls outlined before. The main problem is the fact that all species simultaneously respond to bottom and pore water oxygenation as well as to the organic flux level. Many taxa that have been proposed as low oxygen indicators should probably rather be considered as high productivity markers. Although these taxa are indeed abundantly present in many low oxygen environments, they may also dominate faunas in high productivity areas with fairly high bottom water oxygen concentrations, such as the upwelling area off NW Africa (e.g. Jorissen et al., 1995; Morigi et al., 2001). And inversely, in areas where export production is slightly lower, benthic environments with low oxygen concentrations are not necessarily dominated by "low oxygen indicators" (e.g. Rathburn and Corliss, 1994).

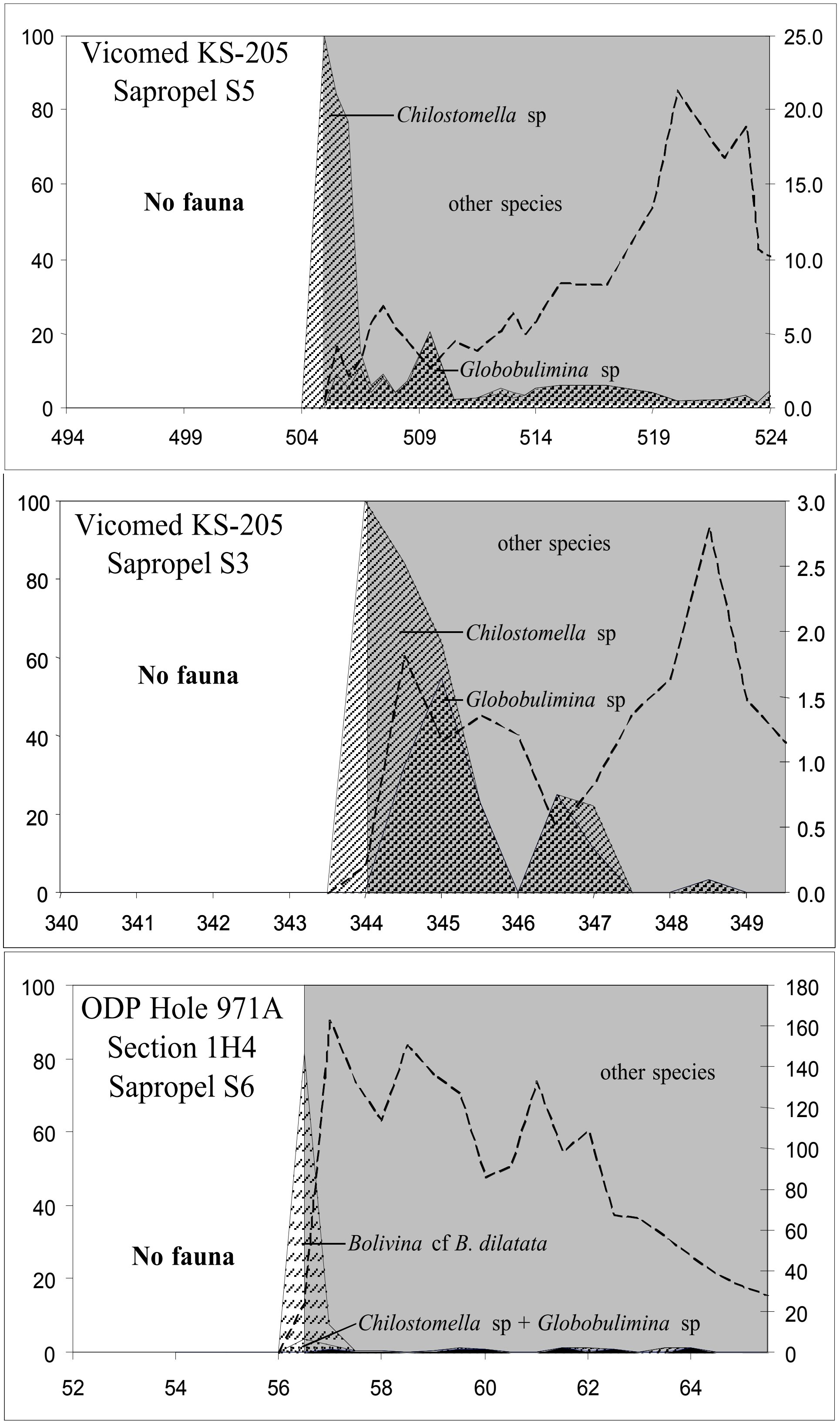

Fig. 3: Relative frequency of deep infaunal taxa (percentage, scale on the left), in the centuries before deposition of sapropels S5, S3 (both from core Vicomed KS205, 38°11,86'N, 18°08,04'E, 2345 m) and S6 (ODP Hole 971A, section 1H4, 33°42,19'N, 24°42.81'E, 2143 m) and total faunal density (interrupted line, in number of foraminifera per gram dry weight, scale on the right), in function of depth in the core (in cm, scale below). Note the abrupt

frequency increase to a total dominance in the last cm before azoic sediments, that coincides with the disappearance of almost all other taxa. In all three cases this frequency increase is accompanied by a strong drop in faunal density. Sapropel S5 shows a preliminary frequency increase (at 510 cm) about 5 cm before this ultimate frequency increase. Sapropel S6 does not show such a phenomenon. Ionian Sea core Vicomed KS205 (38°11,86'N, 18°08,04'E, 2345 m).

2.3.4 Future developments of bottom water oxygenation proxies

Some of the best examples of past changes in bottom water oxygenation have been preserved in Mediterranean sapropels (e.g. Jorissen, 1999b; Schmiedl et al., 2003). A detailed study of the faunal succession at the transition from homogeneous sediments characteristic of oxygenated bottom waters to the laminated sediments associated with anoxic conditions can yield essential information about the tolerance levels of the various species. Especially at the onset of the anoxic periods, that lasted for several thousands of years, rapid faunal changes took place (Fig. 3). The faunas of the centuries immediately preceding the azoic sediments indicative of total anoxia systematically contain a low diversity fauna, strongly dominated by taxa (e.g. *Globobulima* spp., *Chilostomella* spp.), that in recent ecosystems have been described in deep infaunal microhabitats. Apparently, surface dwellers adapted to strongly hypoxic conditions, such as appear in Santa Barbara Basin (e.g. *Epistominella smithi, Nonionella stella* and *Cassidulina delicata;* Mackensen and Douglas, 1989; Bernhard et al., 1997) were absent in the late Quaternary Mediterranean.

Fig. 3 shows the relative frequencies of deep infaunal taxa immediately before sapropels S5 and S6. In the rather oligotrophic environments of the central Mediterranean, *Globobulima* spp., *Chilostomella* spp. and other deep infaunal taxa are rare or even absent at this water depth (De Rijk et al., 2000). These taxa increase dramatically in relative abundance in the one to two cm below the azoic sapropelic sediments (in this case coinciding with 1 to 2 centuries), to attain dominance in the last fauna-containing sample (Fig. 3). In these examples, the increase in deep infaunal taxa to percentages of 80-100% is accompanied by a strong decrease in the number of foraminiferal tests per gram dry sediment. This suggests that this increase in relative abundance is mainly caused by the disappearance of other taxa, which are less resistant to low oxygen concentrations.

In some sapropels this takeover of the benthic faunas by deep infaunal taxa is preceded by a preliminary increase in relative abundance of these taxa (510 cm for sapropel S5, 347 cm for sapropel S3), but in other sapropels this is not the case (Fig. 3: sapropel S6). This first increase of deep infaunal taxa is not accompanied by a disappearance of less resistant taxa. Two explanations are possible:

1) an increased organic flux to the ocean floor may have opened up niches deeper in the sediment for deep infaunal taxa.

2) a short-term strong decrease in bottom water oxygenation may have caused mixing of deep infaunal taxa with the more diverse faunas deposited before and/or after this short hypoxic event

Since the first frequency increase of deep infaunal taxa at both S3 and S5 is accompanied by a temporary decrease of overall faunal density, the second possibility seems most probable.

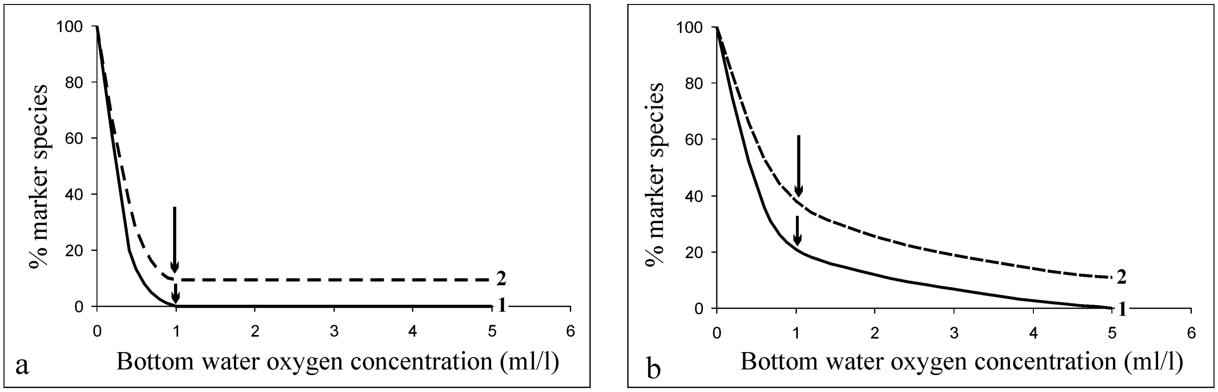

Fig. 4. Hypothetical curves showing the percentage of deep infaunal, low-oxygen marker species as a function of bottom water oxygen concentration and organic flux to the ocean floor. Fig. 4a: the decrease of bottom water oxygenation is not accompanied by an increase in organic flux. Fig. 4b: the decrease of bottom water oxygenation is accompanied by an increase of organic flux to the ocean floor. Figs 4a/b: curve 1): oligotrophic setting without deep infaunal taxa in the background fauna. Curve 2): more eutrophic setting with about 10% deep infaunal taxa in the background fauna.

The curves in Fig. 4 present different scenarios during a strong decrease of bottom water oxygenation. In Fig. 4a the decrease of bottom water oxygenation is not accompanied by an increase in organic flux, and could occur because of stratification of the water column, or a long-term lack of renewal of deep waters. The percentage of deep infaunal taxa will initially remain stable, until a critical point (indicated by arrow), at which taxa less resistant to hypoxic conditions start to disappear, here arbitrarily placed at 1 ml/l. With a further decrease of bottom water oxygenation, deep infaunal taxa rapidly take over hypoxic niches at the sediment-water interface, and their abundance will increase exponentially, reaching 100% at about 0,01 ml/l. The initial percentage of deep infaunal taxa (the horizontal lines to the right of the threshold point in Fig. 4a) is determined by the organic flux level. Curve (1) depicts an oligotrophic setting without deep infaunal taxa, where only the sediment-water interface is inhabited. Curve (2) characterizes more eutrophic settings where the organic flux can sustain a fauna living at several cm depth in the sediment. Curve (1) corresponds to the situation observed in sapropel S6 of ODP hole 971A (Fig. 3); curve (2) corresponds to the succession observed below sapropel S5 of core Vicomed KS-205 (Fig. 3).

In the curves in Fig. 4b the decrease in bottom water oxygenation is at least partially accompanied by an increase of the organic flux , as in places where hypoxia is caused by eutrophication. Deep infaunal taxa are then expected to show a first increase in abundance due to an increased food availability within the sediment. With a further decrease of bottom water oxygenation, less resistant taxa will start to disappear (vertical arrows in Fig. 4), and their increase will strongly accelerate. From this threshold point on, the percentage of deep infaunal taxa is mainly determined by bottom water oxygenation, and no longer by the organic flux. The initial percentage of deep infaunal taxa will depend on the organic flux, with curve (1) depicting an oligotrophic setting (no deep infaunal taxa), curve (2) a more eutrophic ecosystem.

This theoretical example illustrates that the interplay between organic flux and bottom water oxygenation, which controls the percentage of deep infaunal taxa, may be rather complex. As soon as oxygenation levels fall below a certain threshold value, further increase of the percentage of deep infaunal taxa seems to be largely due to the disappearance of taxa less resistant to low oxygen conditions, and therefore, mainly to bottom water oxygenation. At such low bottom water oxygenation levels, it should be possible to use the percentage of deep infaunal taxa to estimate bottom water oxygenation. For this approach it must be determined precisely at what oxygenation level the various less resistant taxa start to disappear from the ecosystem, and the percentage of deep infaunal taxa starts its final increase. In Fig. 4, this level has arbitrarily been placed at 1 ml/l, but a different threshold value would not significantly change the shape of the curves. At bottom water oxygenation levels above this critical boundary, on the contrary, the percentage of deep infaunal taxa may be determined by a combination of bottom water concentration and organic flux level, and the reconstruction of bottom water oxygenation is more difficult. However, when longer records are available (such as the sapropel records presented before), it may be possible to constrain the organic flux level by other methods (chapter 2.3.), making it possible to gain insight into bottom water oxygenation at slightly higher concentrations.

Summarising, it appears that in spite of the complexity of the interplay between bottom water oxygenation and organic matter flux, there is a potential to develop a quantitative proxy method for bottom water oxygenation, on the basis of the relative proportions of a group of indicator species that replace taxa less resistant to low oxygen concentrations below a critical threshold value. The calibration of such a proxy has to be based on the rigorous application of the following conditions:

1) Indicator species for low oxygen conditions should be selected on the basis of observations in recent low oxygen ecosystems. All deep infaunal taxa (e.g. *Chilostomella* spp., *Globobulimina* spp.) qualify as marker species. Other taxa observed to be abundant in low oxygen settings have a planoconvex morphology (e.g., *Epistominella smithi, Nonionella stella* and *Cassidulina delicata)* that suggests an adaptation to a microhabitat close to the sediment-water interface (e.g. Mackensen and Douglas, 1989; Bernhard et al., 1997).

2) In order to take taphonomical processes into account, the proxy method should be calibrated by a comparison between upper Holocene fossil faunas (if existing) and the recent value of the proxy parameter. The calibration should concentrate on many different settings (especially in different productivity regimes) with oxygenation values between 0 and 2 ml/l. Above 2 ml/l, benthic foraminiferal assemblage composition is probably not influenced by bottom water oxygenation (Murray, 2001).

3) It should be tested whether the addition of a diversity index (Schmiedl et al., 1995) can make the proxy method more robust, and more globally applicable. However, diversity responds in a very similar way to an increase in organic flux as to a decrease in oxygen concentration. In both cases a lowering of all diversity indices is the result.

If the relationship between the percentage of deep infaunal taxa, bottom water oxygen concentration and downward organic flux can be successfully calibrated for a wide range of recent and/or subrecent environments, a precise proxy of bottom water oxygenation may be obtained for the range of 0 to 1 ml/l. Potential success of this approach is suggested by Martinez et al. (1999), who documented similarity between the percentage of deep infaunal taxa with Mo/Al (Molybdenum/Aluminium) ratios (a geochemical oxygenation index). After the development of a reliable proxy for bottom water oxygenation, the next challenge will be the reconstruction of the redox conditions within the superficial sediments.

2.3. Paleoproductivity proxies

2.3.1 Introduction

Knowledge of past changes in primary production and the subsequent transport of organic matter to the ocean floor is essential for the understanding of the response of the biological carbon pump to climate change. Paleoproductivity proxies, which address these complex phenomena, may have several objectives: in some cases they try to reconstruct surface water primary production, whereas in other cases a less ambitious, but equally valuable approach is followed, aiming to reconstruct the flux of organic carbon to the ocean floor. A major complication is the fact that most paleoproductivity proxies based on responses to the organic carbon flux to the ocean floor (e.g., sedimentary organic carbon flux, benthic ecosystem response, $\delta^{13}C$) will not only be influenced by the quantity of organic matter arriving at the sea floor, but also by other aspects of the organic flux, such as the quality of the organic matter, and the timing (invariable versus pulsed) of the organic input. Another problem is that the mechanisms of organic material transport from the surface waters to the ocean floor are still badly known. If we are able to gain insight into these secondary aspects of paleoproductivity, then we will of course also largely improve our understanding of the functioning of surface water phytoplankton communities and the biological carbon pump in past oceans.

The use of benthic foraminifera as markers of export productivity to the sea floor has become conceivable since the 1970's, when it became progressively clear that not water depth, temperature and salinity ("water masses"), but rather organic input and bottom water oxygenation are the main environmental parameters controlling faunal patterns in open ocean benthic ecosystems. In the majority of open ocean benthic ecosystems, the flux of organic matter from the productive surface waters to the ocean floor constitutes the main food source for benthic organisms. Although hydrocarbon seeps and hydrothermal vents have received much attention in the past decennia because of their rich and often spectacular faunas, in the present oceans their cumulative surface area is probably small in comparison with sea floor areas which depend on the input of organic detritus produced in the surface waters. Unfortunately, there is still considerable uncertainty about the transport of particulate organic carbon to the ocean floor. Since the late 1970's, sediment trap data have been used to develop equations describing the downward organic flux through the water column (e.g. Eppley and Peterson, 1979; Suess, 1980; Betzer et al., 1984; Martin et al., 1987; Pace et al., 1985; Berger et al., 1989; Berger and Wefer, 1990). In all these equations, the downward organic flux is described as a function of primary production in the surface waters and water depth. More recent data, however, suggest that many other parameters interfere:

- Several authors (e.g. Eppley and Peterson, 1979; Berger et al., 1989; Berger and Wefer (1990) have suggested that the organic flux to the ocean floor should be much more important in unstable settings (such as in ecosystems with a high seasonal variability in primary production). Recently, however, François et al. (2002) described a decreasing particle flux with higher seasonality.
- The amount of particulate organic carbon transported from the surface waters to deeper layers seems also to depend on the structure and functioning of the pelagic food webs (e.g. Wassmann, 1993). For instance, Boyd and Newton (1995) describe a twofold increase of the primary organic carbon flux as a function of community structure. In general, vertical transport of large particles, such as marine snow (Turley 2002), diatom aggregates (e.g. Kemp et al., 1995; 2000) or zooplankton fecal pellets, is much more efficient than transport of small particles.
- Ballasting of organic particles with siliceous or carbonate tests (François et al., 2002), terrigenous dust (Ittekot, 1993) or tunicate feeding structures (Robinson et al., 2005) may significantly increase the efficiency of organic matter transport to deeper parts of the water column. Armstrong et al. (2002) suggest that ballast minerals are largely responsible for the deep-water (> 1800 m) POC fluxes.
- Particle organic carbon fluxes through the water column appear to be strongly modulated by biological, physical and chemical transformation processes. Unfortunately, the various mechanisms of POC degradation in the water column are still badly known (Jackson and Burd, 2002), and the potentially important role of dissolved organic carbon (DOC) is not taken into account in many organic flux studies.
- In many parts of the ocean, and especially in ocean margin settings, lateral advection, either by intermediate or deep water currents, or by slope failure and turbidity

currents, is a major factor responsible for the transport of particulate organic carbon to the ocean floor (e.g. Antia et al., 1999). Laterally advected organic matter is often aged, with the more labile, easily consumable components stripped off. As a consequence, laterally advected organic matter will be only partially remineralised in the oxic ecosystems at the sediment-water interface. The more refractory parts, however, may trigger intensive early diagenetic processes in the anaerobic ecosystems deeper in the sediment (Carney, 1989; Fontanier et al., 2005).

In spite of these many complicating factors, an important part of the particle rain appears to fall vertically (e.g., Berelson et al., 1997; Nelson et al., 2001), and at least down to about 1000 depth, the POC flux appears to vary as a function of the primary production in the surface waters (Fischer et al., 2000). The afore-mentioned flux equations can therefore be useful as a first approximation of the quantity of particulate organic matter arriving at the ocean floor.

One of the major problems inhibiting a more precise knowledge of the quantity (and quality) of organic matter arriving at the ocean floor is the difficulty to obtain reliable measurements. Empirical flux formula are useful, but can only give a rough, long-term estimate of the organic flux to the ocean floor. More precise estimates can be obtained by measuring the amount of organic matter remineralisation in the benthic ecosystem. This can be done by *in situ* measurements of oxygen consumption by benthic landers (e.g. Reimers, 1987; Gundersen and Jørgensen, 1990; Epping and Helder, 1998) or in benthic chambers (e.g. Tengberg et al., 1995). Measurements in multi-cores, aboard of the ship, are easier to perform, but are generally considered less reliable. In order to have a more complete picture of the extent of organic matter degradation, including mineralisation in anaerobic conditions, vertical profiles of important redox species (e.g. nitrate, manganese, reactived iron-oxides and sulfate) can be measured in the superficial sediment and pore waters (Froehlich et al., 1979). Models integrating the downcore concentration profiles of all major redox species can provide accurate estimates of the total amount of organic matter remineralised in the benthic ecosystem (e.g. Jahnke et al., Rabouille and Gaillaurd, 1991; Soetaert et al., 1996; Kelly-Gerreyn et al., 2005).

Although these approaches may provide reliable data about the remineralisation of labile organic matter, the data concern rather short periods of time (days to weeks). Such measurements do not necessarily reflect the long term, average conditions, represented by a fossil benthic foraminiferal fauna, or by any other proxy carrier. Furthermore, these measurements mostly represent the labile, highly reactive part of the organic matter, but not the more refractory components, that are degraded in the anaerobic ecosystems deeper in the sediment, over time spans of months to years, or are fossilised, to become sedimentary organic matter.

Problems concerning the quantification of the downward organic flux, and the relative importance of laterally advected material, do not only complicate reconstructions based on benthic foraminiferal faunas, but concern most paleoproductivity proxies. If we want to successfully apply benthic foraminiferal assemblages as quantitative paleoproductivity proxies we need to understand in detail how recent assemblages are structured by the input of various amounts of organic matter of different quality. In addition, we have to understand how low oxygen concentrations may modify the foraminiferal response to different organic flux regimes.

Several foraminiferal proxies for paleo-export production have been proposed during the last decennia, based on three different approaches:

1) Most are based on supposed relationships between faunal composition and organic carbon flux rates. In several areas, preferred flux regimes have been tentatively determined for dominant benthic foraminiferal taxa (e.g. Altenbach et al., 1999; 2003; De Rijk et al., 2000; Schönfeld et al., 2005). For example, *Uvigerina mediterranea* and *U. peregrina* are typical for flux rates above 2,5 g/m^2/year, whereas *Cibicides wuellerstorfi, Gyroidina altiformis* and *G. orbicularis* are almost exclusively found below this flux range (Altenbach et al., 1999; de Rijk et al., 2000). However, important inconsistencies appear to exist between studied areas (Schönfeld and Altenbach, 2005), and some important taxa, such as *Epistominella exigua* (Altenbach et al. (1999) or *Melonis* spp. (Altenbach et al., 1999; de Rijk et al., 2000) occur in areas with very different flux regimes, and appear to be much less dependent of a specific organic flux level. These inconsistencies may be due to inadequate estimates of export production, but also to the impact of other ecological factors that may interfere with the foraminiferal dependence on export production. Until today, observed flux regimes for individual taxa have not systematically been used to reconstruct paleo-productivity.

2) Multivariate statistical methods have been applied in order to investigate the response of the foraminiferal assemblage composition to different flux regimes (e.g. Loubere, 1991; 1994; 1996; 1998; Fariduddin and Loubere, 1997; Kuhnt et al., 1999; Loubere and Fariduddin, 1999; Wollenberg and Kuhnt, 2000; Morigi et al., 2001). Loubere (1998) and Loubere and Fariduddin

(1999) have presented multiple regression functions that quantitatively relate the foraminiferal assemblage composition to primary production values in the surface waters. Other studies (e.g. Kuhnt et al., 1999; Wollenburg et al., 2001) have tried to use these statistical relationships observed in recent ecosystems to reconstruct paleoproductivity on the basis of fossil faunas.

3) Herguera and Berger (1991) and Herguera (1992) proposed a paleoproductivity proxy on the basis of the accumulation rate of the benthic foraminiferal fossil fauna larger than 150 μm. They presented data from the western equatorial Pacific, showing that for stations with primary production ranging from 40 to 135 g/m^2/year, the benthic foraminiferal accumulation rate (BFAR) varied linearly with export production, so that for every mg of organic carbon reaching the ocean floor, one foraminiferal shell larger than 150 μm is deposited. The striking simplicity of this idea is appealing but also discouraging, since somehow we feel that nature can not be that simple. It can hardly been imagined that faunas subject to much higher flux regimes characteristic of more eutrophic areas will have identical test production rates per unit of organic carbon as those described by Herguera (1992), and such a non-linear response to increasing export production has been suggested by Schmiedl and Mackensen (1997). Naidu and Malmgren (1995) showed that in low oxygen environments from the Oman margin Oxygen Minimum Zone (OMZ), the BFAR does not reflect surface-water productivity. In spite of these problems, BFARs have tentatively been applied to reconstruct paleo-productivity semi-quantitatively (e.g. Den Dulk et al., 2000; Herguera, 2000; Wollenburg and Kuhnt, 2000), but since no objective tests to check the reliability of the results are available (a problem for all paleo-productivity proxies), we are still in doubt about the reliability of this method.

2.3.2 Paleoproductivity proxies based on flux-dependency of individual species

The realisation that foraminiferal species may be dependant on specific organic flux rates dates from the 1970's when Lutze and co-workers (Lutze, 1980; Lutze and Coulbourn, 1984) conclusively showed that some foraminiferal taxa (e.g. *Uvigerina* spp.) appear with increased relative densities in areas with high organic input. Until today, only very few studies have tried to quantify the flux-dependency of the various benthic foraminiferal taxa.

In a study of the morphology of benthic foraminifera in a series of core top samples from the Norwegian Sea, Corliss and Chen (1988) observed a rapid shift, at a water depth of about

1500 m, from faunas dominated by morphotypes considered as typical of epifaunal lifestyles (trochospiral, milioline) to faunas dominated by morphotypes considered typical of infaunal microhabitats (rounded planispiral, flattened ovoid, tapered cylindrical, spherical, tapered flattened). They estimate that this important change in morphotype dominance takes place at an organic flux level of 3-6 g C/m^2/year. Although Buzas et al. (1993) indicate that microhabitat assignments on the basis of morphology had only a 75% accuracy, the data of Corliss and Chen (1988) clearly indicate the existence of a major faunal change related to a rather specific organic flux level.

In a new analysis of the large data sets of the Lutze-team, Altenbach et al. (1999) investigated the dependence on specific organic flux rates for various foraminiferal taxa. Rather disappointingly, the range of most foraminiferal taxa appears to be very large. For almost all taxa, correlation coefficients between their percentage in the total fauna, and the organic flux rates at the stations where they are found, are very weak. Altenbach et al. (1999) conclude that down to 2000 m, the succession of faunal species seems to be related mainly to bathymetry, whereas only below 2000 m a relation with export production becomes visible, as confirmed in faunas from the Gulf of Guinea (Altenbach et al., 2003). Altenbach et al. (1999) concluded that the presence or absence of a taxon does not seem to be a valuable measure for the reconstruction of flux rates. In spite of these rather disappointing results, they suggest that an organic flux rate of about 2-3 g organic carbon per m^2 per year is an important threshold limit for many species, as confirmed by Jian et al. (1999), De Rijk et al. (2000) and Weinelt et al. (2001). De Rijk et al. (2000) observed that such a faunal threshold occurs at an estimated input of labile organic matter of about 2.5 g/m^2/year in the Mediterranean. This level is at about 1500 m water depth in the eutrophic Western Mediterranean, and shoals to about 400 m depth in the much more oligotrophic eastern Mediterranean. Morigi et al. (2001) used a multivariate statistical analysis of recent foraminiferal thanatocoenoses in the upwelling area off Cap Blanc, a part (19-27°N) of the much larger area (Arctic Ocean, Norwegian-Greenland Sea, NW Africa, and Guinea Basin) investigated by Altenbach et al. (1999), to subdivide frequent taxa into 6 groups, each of which has a preference for a rather narrow range or organic flux rates.

In view of these studies, we think that Altenbach et al. (1999), who studied a huge area, may have been too pessimistic when they concluded that the presence or absence of foraminiferal species cannot be used to reconstruct organic flux levels. Taxa with a preference for a rather narrow range of flux levels will necessarily display a weak correlation coefficient with organic flux when their percentage distribution is compared with the total range of observed flux rates in a huge area.

The direct application of the afore-mentioned observed flux-dependencies is hampered by three problems:

1) in all previously mentioned studies, the estimated organic flux values to the ocean floor were based on a combination of (usually satellite-image derived) PP values and empirical flux equations. As a consequence, the resulting Jz (organic flux arriving at a water depth of z meters) values are very approximate, and it is difficult to compare flux-dependencies between different regions. The obvious solution would be to calibrate these calculated flux values by a comparison with actual flux data observed in sediment traps in the same areas. Unfortunately, sediment trap data are still scarce, in many areas even non existent, and we do not have measured flux data for larger sets of stations. However, sediment trap data for only one or two stations in each investigated area would already allow us to verify the correctness of the order of magnitude of values provided by the flux equations, and, when necessary, to apply corrections for nearby stations. Successful proxy calibration depends on the acquisition of reliable flux data for many open ocean and continental margin areas.

2) Presently most scientists may agree that the organic flux is a main parameter structuring open ocean benthic faunas, but it is evident that it is not the only one. Other factors may modify the foraminiferal response to varying flux levels, especially when presence/absence patterns are concerned. Therefore, proxy calibration efforts should not only consider the relationships of faunal characteristics and Jz, but should take other environmental factors (such as bottom water oxygenation, current velocity or sediment grain-size) into account.

3) Foraminifera have a wide range of ecological strategies. Species vary from K-selected, highly specialised taxa, occupying very specific and narrow ecological niches, to much more opportunistic, r-selected taxa, occupying a wide range of ecological niches. The group of r-selected taxa will show a strong response to strongly episodic phytodetritus deposits, but will probably be weakly dependent upon annual flux rates. Good marker species for annual organic flux rates should be found in the group of K-selected species.

These problems are serious, but we do not think that they are insoluable. Tentative quantifications of preferred flux regimes for individual species are still scarce, but in our opinion, the first results are encouraging. A large research effort is needed to improve the quantification of the flux of organic matter to the benthic ecosystem, and to determine upper and lower tolerance limits as well as the optimum flux range for many foraminiferal taxa. We are convinced that such an inventory could be the basis of a reliable paleoproductivity proxy.

2.3.2 Paleoproductivity proxies based on flux-dependency revealed by multivariate statistical methods

Since the early 1990's Loubere and co-workers (Loubere, 1991; 1994; 1996; 1998; Fariduddin and Loubere, 1997; Loubere and Fariduddin, 1999) built up a large set of core top data on benthic foraminiferal distribution in the Atlantic and Pacific Ocean, and developed a multiple regression function linking the composition of the foraminiferal faunas to the primary production in the overlying surface waters. For their samples from a fairly narrow bathymetrical range (2800-3500 m), the correlation between bottom water oxygenation and primary production was very weak, so that apparent reactions to different organic flux rates cannot be caused by covarying oxygen concentrations. In the 1994 and 1996 papers, Loubere presents a Pacific Ocean data set of 74 samples. The multiple regression analysis shows a very strong correlation coefficient with surface water primary production values. Fariduddin and Loubere (1997) present a similar analysis for an 84 station Atlantic Ocean data set. Productivity seems to be the most important ecological factor. In 1998, Loubere presented a paper in which the Pacific multiple regression function was tested with Indian Ocean core top material (water depth 2400-3500 m). Although in general the Pacific regression function reproduced the Indian Ocean primary production values rather well, the Indian Ocean benthic foraminiferal fauna differed by much higher percentages of *Epistominella*, interpreted as a response to the more seasonal aspect of the organic matter flux in the Indian Ocean. In 1999, Loubere and Fariduddin presented a multiple regression analysis of a 207 station sample set from the Pacific, Indian and Atlantic Oceans, from water depths between 2300 and 3700 m. Again, the correlation coefficients between primary production, seasonality and other parameters are weak.

Kuhnt et al. (1999) applied correspondence analysis to data on benthic foraminiferal faunas in 43 box cores from the South China Sea. The first factor of their correspondence analysis has a very strong correlation with the estimated organic carbon flux to the ocean floor. This relationship was then used to reconstruct the organic carbon flux to the ocean floor for the last glacial-interglacial cycle. In a study of 37 Rose-bengal stained samples from the Laptev Sea, Wollenburg and Kuhnt (2000) again found a strong positive correlation between their first factor and the organic flux to the ocean floor. This relationship was used by Wollenburg et al. (2001) to reconstruct a paleoproductivity record on the basis of faunal successions found in two piston cores from the Arctic Ocean.

Although these multivariate statistical approaches are promising, they suffer from the general weaknesses of such methods. First of all, multiple regression analyses ideally need, in order to be reliable, about twenty times more samples than variables (Tabachnick and Fidell, 1983). Even the final, 207 station data set of Loubere and Fariduddin (1999) is far too small in view of the large number of variables (species abundances) used. Next, all described regression functions are strictly empirical equations, thus not based on understanding of the ecological mechanisms controlling the faunal distribution. With other words, the statistical relationships are black boxes, with no underlying logic to explain the results. Recurrent combinations between environmental parameters observed in today's oceans (e.g., low temperature and high primary production, or high organic flux and low oxygen concentrations), may not have existed, or may have been different in the past, causing different responses of faunal composition to the target parameter. The application of statistical relationship observed in recent ecosystems becomes especially hazardous when extrapolation is used to reconstruct conditions not present in the data set used for calibration. Such non analog conditions include extreme primary production regimes (higher or lower than today), or combinations of environmental parameters (organic flux, oxygenation, quality of organic matter, etc.) that are not encountered in the recent ocean. For instance, in the geological past deep ocean temperatures were considerably higher than today, and it has been speculated that the resulting increased metabolic activity would lead to increased organic matter mineralisation in the water column (and a lower flux to the ocean floor). Benthic faunas would probably have required higher food fluxes to sustain a similar biomass (Thomas, 2006).

Finally, as for most proxies, we can only check the validity of the results by comparing them to estimates obtained by independent (e.g., . geochemical) proxy methods. In spite of our instinctive mistrust when confronted with methods not based on a mechanistical understanding of observed ecological patterns, we agree that multivariate statistical methods are a promising pathway to a useful paleoproductivity proxy. It is therefore important to continue the efforts to increase the size of available data sets, and to extend this type of study to a wider range of continental slope and open ocean environments.

2.3.3 Paleoproductivity proxies based on the benthic foraminiferal accumulation rate (BFAR)

In 1991, Herguera and Berger proposed the Benthic Foraminiferal Accumulation Rate (BFAR, number of benthic foraminifera per unit of area per unit of time) as a paleoproductivity proxy. The underlying hypothesis of the method is that for every mg of organic carbon reaching the ocean floor, a fixed number of fossil foraminiferal tests is deposited. In their 1991 benchmark paper, Herguera and Berger indicated that such a concept has to be based on four conditions: 1) a linear relationship between the organic matter flux and the number of fossilised foraminifera, 2) the flux of organic matter arriving at the ocean floor must in a linear way depend on surface water primary production, 3) the clastic sedimentation rate must be invariable or known in sufficient detail to detect eventual changes, 4) there must be no significant carbonate dissolution. The authors suggest that probably none of these assumptions is fully met.

Herguera and Berger (1991) investigated two series of cores in the western equatorial Pacific, from oligotrophic to mesotrophic areas with primary production rates of 65-80, and 105-135 g/m^2/yr, respectively. After calculation of the flux of organic matter to the ocean floor by applying a flux equation based on sediment trap data, and a comparison with the accumulation rates of foraminifera in core tops, they arrived at the conclusion that for every mg of organic carbon reaching the ocean floor, about 1 foraminiferal test larger than 150 µm is fossilised. Herguera (1992) exploits various flux formulas, and concludes that the BFAR is becoming unreliable below a water depth of about 4000 m, due to carbonate dissolution. Naidu and Malmgren (1995), who tested the BFAR in the Oman Margin Oxygen Minimum Zone, concluded that the proxy does not work in a low oxygen setting.

Although BFAR has been applied as a semi-quantitative proxy of paleo-productivity (e.g. Nees et al., 1997, Schmiedl and Mackensen, 1997; Den Dulk et al., 2000; Herguera, 2000;

Wollenburg and Kuhnt, 2000), most authors have refrained to use the BFAR concept to obtain quantitative estimates of primary production, or even of the organic flux to the ocean floor. The main reason for this is probably the presence of the problems outlined by Herguera and Berger (1991), and the absence of a reliable calibration of the method, either in the western equatorial Pacific or in regions with different patterns of productivity.

Such a calibration is needed, since it is very improbable that in different flux regimes a similar number of foraminifera will be deposited per gram organic carbon arriving at the ocean floor (Schmiedl and Mackensen, 1997). One could expect that in eutrophic areas, with a high export production, faunas will be dominated by rather opportunistic taxa, that may produce much more offspring per mg organic carbon, than the more K-selected taxa encountered in more oligotrophic areas. The scheme presented in fig. 5 presents the successive steps for the calibration of a paleoproductivity proxy based on the BFAR.

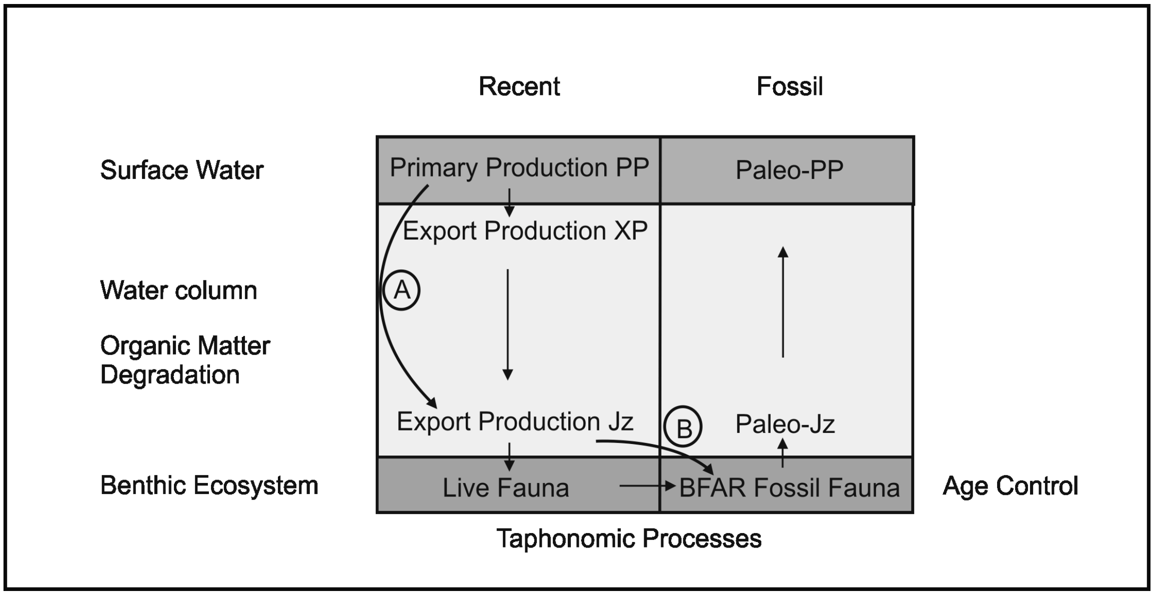

Fig. 5. Scheme indicating the various steps and potential problems involved in the calibration of the BFAR as a paleoproductivity proxy. See text for further explanation.

The first problem (A in fig. 5) is the quantitative relationship between primary production in the surface waters (PP), the quantity of organic matter that leaves the productive surface layer (Export Production, XP), and the flux of organic matter to the sea floor at a water depth of z meters (Jz). As outlined in section 2.3.1, equations quantitatively describing these relationships have been developed on the basis of a comparison of primary production values measured in surface waters with sediment trap data. In paleoceanography, once the paleo-Jz (flux to the sea floor) has been reconstructed, these flux equations can theoretically be used to calculate paleo-PP (past primary production). However, it is evident that all trials to translate a reconstructed paleo-Jz into a paleo-PP value should accept a wide error margin, due to the uncertainties of the flux equations, and the possibility of a significant contribution of laterally advected material. Since only a minor portion (0.01 to 1%) of the total primary production is transported to the ocean floor (e.g. Murray et al., 1996), even small changes in the transport mechanism may have a large impact on the amount of organic matter finally arriving at the sea floor. It seems therefore judicious to limit the use of the BFAR concept in a first time to the reconstruction of the organic flux to the ocean floor (paleo-Jz).

For calibration purposes, the characteristics of the benthic fauna have to be compared quantitatively with recent Jz values. In most cases recent Jz values have been calculated by introducing satellite-derived PP-values into the afore-mentioned flux equations, adding another source of uncertainty. Difficulties to obtain precise Jz values, needed to quantify its impact on the foraminiferal faunas, have seriously hampered the development of the BFAR concept.

A next problem is the calibration of the BFAR, by comparison with recent Jz values (B in fig. 5). When more or less accurate estimates of Jz are available, they can easily be compared with the density of a living foraminiferal fauna (e.g. Fontanier et al., 2002). However, it is much more complicated to compare Jz with an accumulation rate of fossil foraminifera. In order to do so, it is first of all imperative to have a precise knowledge of the sediment accumulation rate. Such a knowledge requires a very detailed age control for the topmost sediment layer, that in ideal cases may, and for the last ~ 100 years, may be obtained by downcore profiles of excess ^{210}Pb and/or ^{237}Cs profiles (e. g., Nittrouer et al., 1984). However, bioturbation activities and/or sediment resuspension after deposition may significantly alter the ^{210}Pb-profiles, and can lead to incorrect sediment accumulation rates. In aquatic environments, assumptions must also be made about the exact transfer process of the radionuclides from atmosphere to sea floor (e.g., Appleby and Oldfield, 1992). Next, the loss of foraminiferal tests due to taphonomical processes should be extremely well constrained. Unfortunately, our present knowledge of taphonomical processes is far too fragmentary to have any realistic hope to calibrate the BFAR method by comparing Jz with recent, or core top, foraminiferal faunas, for which taphonomical processes have not been finished. An additional problem is the fact that recent faunas may show important seasonal variability, and are therefore not always representative for longer periods.

We thus are left with the option to calibrate the BFAR on the basis of (sub-)recent material, for which two essential conditions have been met: 1) taphonomical processes have been terminated, and 2) the fauna is representative of recent environmental conditions. Unfortunately, it is very difficult, if not impossible, to be certain that both conditions are fulfilled. In recent or very modern faunas, faunal transformations due to taphonomical processes have not been finished (as discussed above in the section on problems with paleo-oxygenation problems). For fossil faunas it is uncertain whether the environmental parameters by which they were structured were similar to the recent conditions observed at the site. The best solution seems to calibrate the proxy relationship by using faunas deposited during the early Holocene or other recent interglacial periods with environmental conditions (as far as we know them) relatively comparable to modern ones. A considerable uncertainty will be the result, thus paleo-Jz estimates resulting from BFAR will always have a large error margin.

A final problem is the quality of the organic flux to the ocean floor. Fresh marine organic matter (phytodetritus) is directly consumed by benthic foraminifera, and its availability in large quantities may lead to the production of a relatively large number of produced tests per mg of organic carbon (e.g. Gooday, 1988; 1993). Aged, or continental organic matter, on the contrary, will contain more refractory components, and only a small part can be directly consumed by the benthic fauna. As a consequence, fewer foraminifera will be produced per mg organic carbon when refractory organic carbon accounts for an important part of the input. There are as yet no methods available that are routinely used to describe the nutritious value of organic matter, and it may be particularly complicated to take this parameter into account.

Core	Latitude	Longitude	Water depth	Age at Bottom core	Number of Age control points	Primary Production	Jz total C_{org} flux	Jz Labile component
KS04	20°34.70'N	18°08.80'W	1000 m	MIS7	8	200 $g/m^2/year$	7.9 $g/m^2/year$	5.65 $g/m^2/year$
Sed20bK	25°01.70'N	16°39.02'W	1445 m	MIS5d	12	100 $g/m^2/year$	2.7 $g/m^2/year$	1.3 $g/m^2/year$
Sed17aK	25°16.80'N	17°06.45'W	2975 m	MIS6	15	65 $g/m^2/year$	1.1 $g/m^2/year$	0.35 $g/m^2/year$

Table. 2. Cores KS04, Sed20bK and Sed 17aK: geographical position, water depth, age at the bottom of the core (indicated as MIS: marine isotopic stage), number of age control points, primary production (according to Schemainda et al., 1975), total estimated organic carbon flux to the sea floor, and its labile component (calculated according to equation one, after Herguera (1992).

Below, we use data from piston cores (Table 2) for three sites from the continental margin off Cape Blanc (NW Africa) to illustrate some of the calibration problems. Core Sed17aK was sampled in an oligotrophic area, at 2975 m depth. Core KS04 was sampled at 1000 m depth in an area of strong coastal upwelling, whereas core Sed20bK comes from a site at 1445 m depth, presently outside the direct influence of upwelling. For all three cores, age control is based on stable isotope analyses of planktonic foraminifera (*G. bulloides* for Sed17aK and Sed20bK; *G. inflata* for KS04). We will use core Sed20bK, which has the highest time resolution, as an example (Fig. 6).

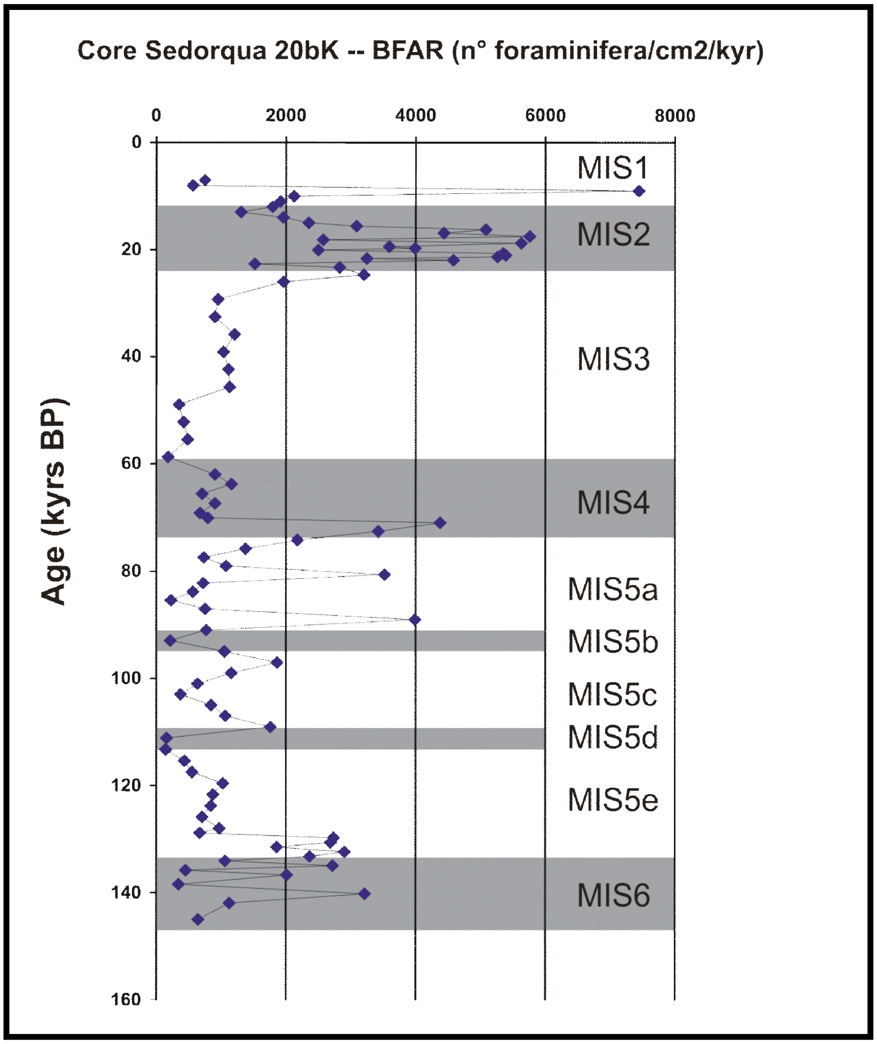

Fig. 6. Variation of BFAR in NW Africa core Sed20bK (25°01.70'N, 16°39.02'W, 1445 m), over the last 2 glacial-interglacial cycles. After Guichard et al., 1999.

As is often the case for piston cores, in all three cores the topmost sediment layer has been lost, and in all three cores only the lower part of the Holocene is present. In core Sed20bK (as well as in the other cores) the BFAR (of the >150 µm size fraction of benthic foraminifers, following Herguera and Berger, 1991) shows a strong variability, with peak values about 10 times higher than the baseline (Fig. 6). Such peaks are present in glacial and interglacial periods, and may be due to rapid changes in sediment accumulation rate, which are not recognized due to the imperfect time resolution or they may be real, and due to the occurrence of long-lived benthic foraminiferal bloom periods in response to upwelling events, that have resulted in periods with large-scale phytodetritus deposition. Because the topmost sediment layer has not been recovered, we do not know whether the present organic flux to the ocean floor corresponds to 1) a peak of BFAR, 2) Holocene background BFAR values or 3) some intermediate BFAR value. The only acceptable solution is to consider the two extreme situations, and use those to define an error envelope. Guichard et al. (1999) decided to compare recent Jz values with BFAR values of Marine Isotope Stage (MIS) 5a, an interglacial period with climatic conditions more or less comparable to the Holocene. With the exception of the peak value observed at about 9000 BP, BFAR values observed in MIS5a cover the range of values observed in the lowerHolocene part of the core.

Today, primary production at site SED20bK is about 100 gC/m^2/year (Schemainda et al., 1975). For the calculation of the flux to the sea floor, we use the flux equation proposed by Herguera (1992):

$$J_z = \left(2\sqrt{PP} \times {PP}/{z}\right) + \left(5\sqrt{PP} \times {PP}/{\sqrt{z}}\right) \qquad (1)$$

in which Jz is the total organic flux to the sea floor at water depth of z meter, and PP is primary production in the surface waters. We prefer this flux equation over other ones (review in Herguera, 1992), because it distinguishes between a labile component (first term), that rapidly diminishes with water depth, and a more refractory component (second term), that is much more constant with water depth.

For site KS20bK, the estimated total Jz is 2.7 gC/m^2/year; the labile component is estimated at 1.4 gC/m^2/year, the more refractory component 1.3 gC/m^2/year. Three different hypotheses can now be tested. Estimated Recent flux rates:

1) correspond to the background (minimal) BFAR values observed in MIS 5a,
2) correspond to the average BFAR values during MIS 5
3) correspond to the peak values during MIS 5, which seems improbable in view of the moderate recent primary production value.

Next, for these three different hypotheses (recent PP corresponds to minimum, average or peak BFAR) the BFAR values can be compared with the estimated values of the total organic flux to the sea floor, and with its labile component. The result is the number of foraminifera deposited per mg of organic carbon (total or labile) arriving at the sea floor (Table 3); for core Sed20bK this number varies from 2.9 to 28 foraminifera per mg for total organic carbon, and from 5.6 to 54 foraminifer per mg if only the labile component is considered.

This first estimate produces values that differ by an order of magnitude, but it seems very improbable that the recent primary production value (very moderate for the Cap Blanc region) corresponds to peak BFAR values (Fig. 6), which probably represent periods of intensified upwelling. It seems more probable that recent PP values correspond to a BFAR value between the minimum and average value, which would mean that for every mg of organic carbon arriving at the ocean floor, 2.9 to 5.6 fossil foraminifera > 150 µm are preserved (or 5.6-10.7 per mg labile organic carbon).

Core Sed20bK–1445 m	**BFAR**	**Total C_{org} flux (2.7 gC/m^2/year)**	**C_{org}, labile component (1.4 gC/m^2/year)**
Background BFAR	780 forams/cm^2/kyr	2.9 forams/mg C_{org}	5.6 forams/mg labile C_{org}
Average BFAR	1500 forams/cm^2/kyr	5.6 forams/mg C_{org}	10.7 forams/mg labile C_{org}
Peak values BFAR	4000-7500 forams/cm^2/kyr	15-28 forams/mg C_{org}	28-54 forams/mg labile C_{org}
Core KS04--1000 m	**BFAR**	**Total C_{org} flux (7.9 gC/m^2/year)**	**C_{org}, labile component (5.65 gC/m^2/year)**
Background BFAR	17000 forams/m^2/yr	2.2 forams/mg C_{org}	3.0 forams/mg labile C_{org}
Average BFAR	24800 forams/m^2/yr	3.1 forams/mg C_{org}	4.4 forams/mg labile C_{org}
Peak values BFAR	50000 forams/m^2/yr	6.3 forams/mg C_{org}	8.8 forams/mg labile C_{org}
Core Sed17aK--2975 m	**BFAR**	**Total C_{org} flux (1.1 gC/m^2/year)**	**C_{org}, labile component (0.35 gC/m^2/year)**
Background BFAR MIS5a	450 forams/m^2/yr	0.4 forams/mg C_{org}	1.3 forams/mg labile C_{org}
Peak value BFAR MIS1	4000 forams/m^2/yr	3.6 forams/mg C_{org}	11 forams/mg labile C_{org}

Table 3. Cores Sed20bK, KS04 and Sed17aK: Comparison of observed Benthic Foraminiferal Accumulation rates (BFAR, according to three hypotheses) with the estimated flux of organic carbon to the sea floor (total flux and labile component). Three scenarios are tested, and the numbers of foraminifera > 150 µm preserved in the sediment are given for each case.

For cores KS04 (water depth 1000 m) and Sed17aK (water depth 2975 m), also from off NW Africa (Guichard et al., 1997), a similar procedure was followed (Table 3). The flux rates were estimated by introducing primary production measurements of Schemainda et al. (1975) into flux equation (1) formula (Herguera, 1992). Next, the number of fossil foraminifera per mg organic carbon was calculated for each of the three afore-mentioned hypotheses, once using the total organic flux, and once using only the labile component (Table 3).

From these tentative BFAR calibrations we observe:

1) The tentative value of 1 foraminifer larger than >150 µm deposited per 1 mg organic matter reaching the sea floor, as suggested by Herguera and Berger (1991), has the right order of magnitude, but appears too low for our 2 continental margin cores. If we do not consider the rather improbable numbers based on hypothesis 3 (recent situation corresponds to peak BFAR), we find that 0.4 – 5.6 fossilised foraminifera > 150 µm are deposited per mg total organic carbon arriving at the sea floor off NW Africa.

2) The values for our deepest core (Sed17aK; Table 3) correspond rather well to the values proposed by Herguera and Berger (1991), whereas our two continental margin cores, that represent much more eutrophic ecosystems, show much higher values (2.2 - 5.6 foraminifera deposited per mg total organic carbon arriving at the ocean floor). This suggests that the relationship between Jz and BFAR is not linear. More eutrophic areas appear indeed to be inhabited by more opportunistic taxa, that produce more tests per unit of organic carbon.

3) By only considering the labile component of the downward organic flux, the differences between our deep oligotrophic site, and our shallower, more eutrophic sites diminish slightly (Table 3). This suggests that it may be judicious to consider only the labile part of the organic flux to the ocean floor.

We think that this example documents that BFAR is a promising proxy for paleo-Jz. We need to develop a large data-basis of BFAR records in well-dated cores from regions with different patterns of primary productivity (oligotrophic to eutrophic, highly seasonal to less seasonal), in order to determine the way in which BFAR responds to various organic flux regimes.

2.3.4 Reconstructing the quality of the downward organic flux

Benthic foraminifera, as well as most other benthic organisms, will mainly respond to the flux to the ocean floor of labile organic particles that are easily metabolized. Terrigenous, or old marine organic particles (refractory organic matter), have only a limited nutritious value, and will commonly bypass the oxic niches at the sediment-water interface. Only in the anaerobic environments deeper in the sediment, part of this material is recycled (e.g. Fenchel and Finlay, 1995), whereas the remainder will be preserved as sedimentary organic matter. The absolute quantities and relative proportions of these two types of organic matter (labile versus refractory) will differ as a function of the amount of terrigenous input (usually determined by the distance from land) and the local biological and sedimentological conditions (and geographic – distance away from land – terrigenous input). At sites with an influx of predominantly labile organic matter, most will be consumed by the benthic fauna at the sediment water interface, whereas at sites with more refractory components, a larger part of the organic matter will become preserved in the sediments. It thus seems unlikely that sedimentary organic flux rates (the amount of fossilised C_{org} per surface area per year) can provide a reliable paleoproductivity proxy (Wefer et al., 1999). Nevertheless, the sedimentary organic carbon content has often been used to reproduce past biological production (e.g. Müller and Suess, 1979; Sarnthein et al., 1987; 1988).

In our opinion, the differential response of benthic foraminiferal faunas to influx of these two types of organic matter could be used to gain insight into the character of past organic particle supply, but more information is required about the dependence of various species on food quality. Surface-dwelling taxa have been said to rely on labile organic matter, whereas intermediate and deep infaunal taxa would tolerate more refractory food particles made available by partial recycling under anaerobic conditions (e.g. Jorissen, 1999a; Fontanier et al., 2005).

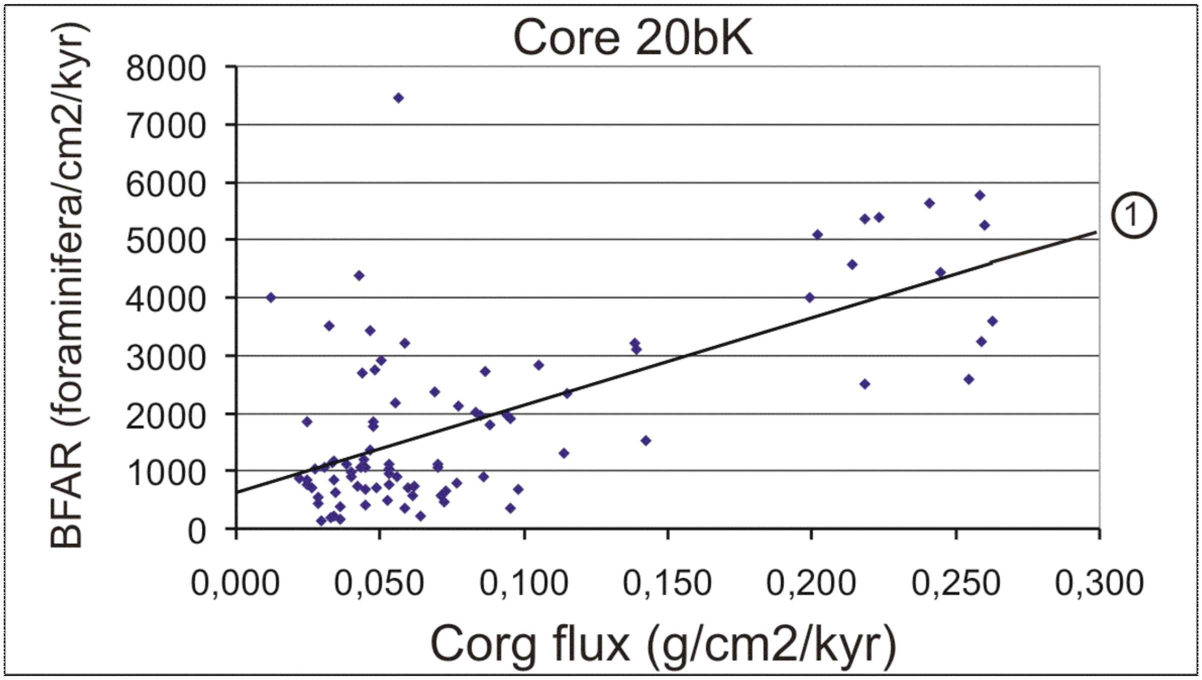

Fig. 7. Core Sed20bK; comparison between BFAR and sediment Corg flux (after Guichard et al., 1999); 88 samples; regression line (1): BFAR = 15160 * C_{org} + 616.5 ($r^2 = 0.42$).

In order to gain insight into the organic matter quality, Guichard et al. (1999) combined data on BFAR and sedimentary organic matter flux (Fig. 7). The underlying idea is that the BFAR varies as a function of the labile organic carbon input, but is rather insensitive to the input of refractory organic carbon. It may be expected that the quality of the organic matter flux changed considerably over time. During periods with intensified upwelling, large amounts of labile organic matter must have reached the sea floor, where they undoubtedly triggered biological production, and high BFAR's. During prolonged periods without sustained upwelling (as is the case today at this site), on the contrary, the quality of the organic input was probably much lower, a larger proportion was preserved in the sediment, leading to a relatively low BFAR with respect to the sedimentary C_{org} flux.

Sedimentary C_{org} flux is positively correlated to BFAR, but there is a wide scatter around regression line (1), which represents the average ratio between the BFAR and sedimentary C_{org} flux (of 15 foraminiferal tests per 1 mg sedimentary organic carbon), and thus an average quality of organic matter. Samples with minimal BFAR values probably represent periods when the quality of the organic influx was poor (i.e., minimal labile fraction). Points high above the regression line represent samples with a very high BFAR relative to the sedimentary organic carbon flux, suggesting an organic matter flux dominated by labile components, in this region possibly representing periods with strongly intensified upwelling. The variability of BFAR is not only a response to a varying organic input, but may be partially caused by short term variability of the sediment accumulation rate, not recognised due to the limits on the resolution of the age model. In spite of these complications, we think that this approach deserves to be further explored.

2.3.5 Reconstructing the periodicity of the downward organic flux

Studies on the Porcupine abyssal plane (Levitt, 1985; Gooday, 1988; Lambshead and Gooday, 1990) have conclusively shown the huge importance of massive phytoplankton deposits in the deep ocean, to which the benthic fauna responds by a period of intense biological activity, for many taxa leading to accelerated growth and/or reproduction (Pfannkuche et al., 1993). Benthic foraminifera are among the organisms with the strongest response to such events (e.g.

Gooday, 1988; 1993; 1996; Gooday et al., 1992; Gooday and Hughes, 2002). Several small taxa (e.g. *Alabaminella weddellensis, Epistominella exigua, Epistominella pusilla, Fursenkoina* spp., *Globocassidulina subglobosa*) as well as soft-shelled forms rapidly colonise the phytodetritus, producing abundant offspring, leading to the prediction that these taxa will probably become dominant elements in the fossil assemblages at sites with episodic phytodetritus deposits. Smart et al. (1994) applied this concept to Miocene and Quaternary deep sea cores; Thomas et al. (1995) to two mid-latitude North Atlantic sediment cores (last 45 kyr). They interpreted the abundance of phytodetritus species and increased BFAR during the last deglaciation, as the result of increased surface primary production, and subsequent transport of phytodetritus to the ocean floor in response to a northward migration of the polar front (Thomas et al., 1995). Thomas and Gooday (1996) argued that phytodetritus deposition increased strongly at the establishment of the Antarctic ice sheet (earliest Oligocene), leading to the occurrence of lower diversity assemblages with dominant phytodetritus species at high latitudes. Several other papers follow a very similar approach to reconstruct past phytodetritus flux events (e.g. Nees et al., 1997; 1999; Nees and Struck, 1999; Ohkushi et al., 2000).

A potential problem is the fact that most of the indicator species of these pulsed phytodetritus deposits are small (63-150 µm), have therefore not been studied very often, and may be sensitive to dissolution. In a recent paper, Sun et al. (2006) showed that the *E. exigua-A. weddellensis* assemblage was positively correlated with the seasonality of primary production, whereas individual species of this assemblage did not show such a relationship. In fact, all opportunistic taxa will be advantaged by instable conditions, such as episodic transport of phytodetritus to the ocean floor, but some opportunistic species can show a strong response to phytodetritus input in an oligotrophic deep ocean setting, whereas other taxa may be typical for similar conditions in a more eutrophic continental slope context. For instance, at 550 m water depth in the Bay of Biscay large (adult specimens >150 µm) *Uvigerina peregrina* and *Uvigerina mediterranea* show (together with *E. exigua*) a marked increase in abundance in response to phytodetritus deposits following phytoplankton blooms (Fontanier et al. (2003). These observations are in contrast with the situation in the open-ocean environments of the northwestern Pacific (Ohkushi et al., 2000), where *Uvigerina* spp. reacted very differently from *E. exigua*. These results show that we can not validly extrapolate from observations at one location to large areas, and that more observations of faunal variability over time are needed to further understand the periodicity of the past organic matter flux.

2.4 The water mass concept

As described in section 2.1, the 'water mass concept' implied that the differences in physico-chemical parameters in various water masses were responsible for the fact that they could be characterised by a specific benthic foraminiferal fauna. Below we will discuss arguments that led to the rejection of the fixed bathymetry concept, then consider the pros and cons of the water mass concept, and discuss the present ideas of the relations between foraminiferal assemblage structure and the physico-chemical characteristics of bottom waters.

2.4.1. Deep-sea foraminifera as indicators of bathymetry

Attempts to compare bathymetrical species distributions in various oceans led to the conclusion that for many species important differences in bathymetrical distribution existed. For instance, Pujos-Lamy (1973) compared the bathymetrical species succession for shelf to abyssal environments on the French continental margin (Bay of Biscay, NE Atlantic; Caralp et al., 1970) with successions in other ocean basins such as the western Pacific (Polski, 1959), the north-western Pacific (Stschedrina, 1957), the north Pacific (Saidova, 1961), the Californian margin (Bandy, 1961) and the Gulf of Mexico (Phleger, 1960). At water depths of less than 2000 m at least some cosmopolitan taxa showed comparable depth distributions in the Pacific and Atlantic Oceans, but below that depth limits separating the successive faunal associations occurred at significantly different depths. Pujos-Lamy (1973) (in agreement with Boltovskoy, 1965) concluded that these differences in bathymetrical distribution could be explained by the existence of different oceanic provinces, thereby preparing the ground for the water mass theory.

Many subsequent papers (e.g. Streeter, 1973; Schnitker, 1974, Lohmann, 1978a; Schnitker, 1980; Douglas and Woodruff, 1981; Bremer and Lohmann, 1982; Corliss, 1983b; Mackensen et al., 1990; 1995; Schmiedl et al., 1997) confirmed that the upper and lower depth limits of many foraminiferal species show significant differences between various ocean basins , although bathymetrical species successions may be very similar.. Many papers on the distribution of living and fossil deep-sea foraminiferal faunas (e.g. Corliss, 1985; Woodruff, 1985; Thomas, 1986; Mackensen and Douglas, 1989; Woodruff and Savin, 1989; Corliss and Emerson, 1990; Corliss, 1991; Barmawidjaja et al., 1992; Rathburn and Corliss, 1994; Kitazato, 1994; Rathburn et al., 1996; Ohga and Kitazato, 1997; de Stigter et al., 1998; Jorissen et al., 1998; Jannink et al., 1998; Kitazato et al., 2000; Schmiedl et al., 2000; Fontanier et al., 2002; Licari et al., 2003; Hess et al., 2005) show that cosmopolitan species, such as *Nuttallides umboniferus, Epistominella exigua* or *Cibicidoides wuellerstorfi*, thrive in all deep-sea basins, without showing a clear preference for a specific bathymetrical range or bio-province.

2.4.2. Deep-sea foraminifera as water mass indicators?

In the 1970's and early 1980's deep-sea foraminiferal assemblages were related to specific water masses, and various authors (e.g. Streeter, 1973; Schnitker, 1974; Lagoe, 1977; Lohmann, 1978a; 1978b, Gofas, 1978; Corliss, 1978; 1979; Streeter and Shackleton, 1979; Osterman and Kellogg, 1979; Schnitker, 1980; Belanger and Streeter, 1980; Miller and Lohmann, 1982; Streeter et al., 1982; Bremer and Lohmann, 1982; Weston, 1982; Corliss, 1983a; 1983b, Peterson, 1984; Woodruff, 1985; Murray et al., 1986) investigated whether their past spatial distribution could be used to reconstruct deep-sea circulation patterns (i.e., the geographical distribution of water masses). In most of these papers, the presence of foraminiferal species in some deep-sea environments, and their absence in other ones, was explained by their dependence on water-mass characteristics rather than by their bathymetrical preferences. Several "index species", or a "specific combination of benthic foraminiferal species" were related to the specific physical and chemical properties of present water masses, in some cases rather subjectively, in others by using statistical methods (Appendix 1). Most of these data pertained to foraminiferal thanatocoenoses sampled in core-tops (of piston, gravity, trigger-weight and grab cores), considered representative of the living faunas. However, the use of thanatocoenoses to determine a possible correlation between foraminiferal distribution and the geographical extension of water masses is highly problematic (e.g., Mackensen et al., 1990; Douglas and Woodruff, 1981). In most cases the uppermost material does not contain Recent assemblages, because the sediment-water interface is only rarely sampled by these methods. Taphonomical processes, such as carbonate dissolution below the lysocline or in organic-rich sediments, differential disintegration of fragile tests, deposition of reworked material, or winnowing of autochthonous species, may cause strong differences between living and fossil faunas (e.g. Corliss and Honjo, 1981; Mackensen et al., 1990; 1995). In some of the studies documenting the water mass concept (Lohmann, 1978a; Schnitker, 1979; Streeter and Shackleton, 1979), agglutinated and porcellaneous foraminifera were excluded from the faunal counts, leading to less reliable correlations between water mass distribution and foraminiferal assemblages. Moreover, as underlined by several authors (e.g. Thomas et al., 1995; Gooday, 2003), the use of different size fractions between most of these studies (>125 µm, or >150 µm or >250 µm) created important methodology-related faunal discrepancies between the various study areas.

One of the major problems of the water mass concept is the fact that in most of the classical papers, water mass characteristics are presented very simplistically. For instance, the physico-chemical definition of North Atlantic deep Water (NADW) is very complex (e.g., Frew et al., 2000; Van Aken, 2000). NADW can be subdivided in a number of regional water masses (e.g. LSW, DSOW, ISOW, NEADW, NWADW) with a large variability in physico-chemical parameters (temperature, salinity, nutrient concentrations, oxygen concentration, etc.). In the "Southern Ocean", some physico-chemical water mass properties such as oxygenation, alkalinity, nutrient concentration and corrosiveness progressively change along their pathways along the ocean floor (e.g., Peterson, 1984; Mackensen et al., 1995). Appendix 1 thus does not show clear-cut physico-chemical differences between the various water masses, and one cannot pinpoint the exact water mass properties that limit the occurrence of a specific group of taxa. Furthermore, many environmental parameters defining a specific water mass are cross-correlated (temperature, salinity, pressure, oxygen concentration, nutrient concentration, alkalinity/acidity, current velocity, sedimentological patterns, etc.), posing another obstacle to efforts to determine which physico-chemical parameter(s) control the distribution of the foraminiferal assemblages. We are therefore of the opinion that the water mass concept has lost much of its credibility over the last 20 years.

The alleged relation between faunal composition and water masses has been used to reconstruct the Quaternary history of bottom water circulation (e.g. Streeter, 1973; Schnitker, 1974; Schnitker, 1976; Gofas, 1978; Lohmann, 1978b; Streeter and Shackleton, 1979; Schnitker, 1979; Corliss, 1979; Schnitker, 1980; Caralp et al. 1982; Peterson and Lohmann, 1982; Corliss, 1983a; Peterson, 1984; Caralp, 1984; Caralp, 1987; Murray et al., 1986; Murray, 1988). In our opinion, the interpretations of the data presented in these studies are no longer valid.

2.4.3. Deep-sea foraminifera as indicators of complex environmental conditions

A number of ecological studies, mainly based on living (Rose Bengal stained) foraminiferal faunas (e.g. Mackensen et al., 1990; 1995; Schmiedl et al., 1997; Murray, 2001), have shown that the composition of deep-sea benthic foraminiferal faunas is related to a complex of environmental parameters. The faunal composition appears to be mainly determined by the food supply, the characteristics of the sediment and of the overlying surface waters, whereas water mass properties appear to play at best only a minor role. For example, Mackensen et al. (1990) show that the distribution of live foraminiferal faunas in the eastern Weddell Sea is related to parameters such as sediment granulometry, current velocity, organic matter deposits and the corrosiveness of bottom and interstitial waters. The interplay of four main environmental parameters controls the distribution of benthic foraminiferal taxa in a large, South Atlantic Ocean database (Mackensen et al. ,1995):

1) the organic carbon content of the sediment and the exported organic matter flux to the sea-floor
2) the hydrodynamical properties of the benthic environment, and the related sediment grain size.
3) the bottom water oxygenation
4) the bottom water carbonate saturation

The abundance of *Fontbotia (=Cibicidoides) wuellerstorfi* is related to the occurrence of young and well ventilated (NADW-like) bottom waters, where the organic carbon flux does not exceed 1 gCm-_year^{-1}. *Cassidulina laevigata*, *Uvigerina peregrina* and some buliminids and bolivinids are correlated with higher organic carbon flux rates (> 3 gC m^{-}_ year^{-1}), whereas assemblages dominated by *Epistominella exigua* occur in the low salinity core of NADW, where primary production shows a large seasonal contrast. *Angulogerina angulosa* is well correlated with coarse-grained sediment in environments characterised by strong bottom currents. *Nuttallides umboniferus* is found above the CCD, but below the lysocline (Mackensen et al., 1995). Schmiedl et al. (1997) related the spatial distribution of 7 living and dead assemblages to the dissolved oxygen content of the bottom water, the organic carbon flux, the organic carbon content of the surface sediment, the nature of the substrate and the related porosity.

2.5 Benthic foraminiferal faunas as indicators of current velocity

Intensified bottom water currents (contour, tidal or slope currents) have been shown to influence the microhabitats and composition of the benthic foraminiferal fauna (Lutze and Altenbach, 1988; Lutze and Thiel, 1989; Linke and Lutze, 1993; Schönfeld. 1997; 2002a, 2002b). Under high current velocities (20-50 cm s^{-1}), some species may live preferentially on elevated substrates, or within sedimentary objects (such as pteropod shells). Elevated substrates include large biogenic objects (coarse shell debris, sponges, crinoids, hydroids, etc.), large terrigenous particles (pebbles) or living arborescent benthic foraminifera (e.g. *Rhabdammina* spp.). At some mm or cm above the sediment-water interface, specialized epibenthic foraminifera may catch suspended organic matter particles (suspension-feeders). Mackensen et al. (1995) recognized a faunal association dominated by *Angulogerina angulosa*, correlated with very coarse–grained sediments (sand-gravel) and putatively with strong bottom currents. On the southern Portuguese continental margin, Schönfeld (1997) described common *Cibicides lobatulus, Planulina ariminensis, Discanomalina* spp. and *Epistominella exigua* living on elevated substrates, and suggested that these taxa thus maximize the acquisition of suspended organic compounds. A similar assemblage of sessile epifaunal and/or epibenthic suspension feeders was found on the Spanish continental margin, influenced by high velocity bottom currents related to the Mediterranean Outflow Water (Schönfeld, 2002a). Using data from Gulf of Cadiz and the southern Portuguese margin, Schönfeld (2002b) showed a linear correlation between the percentage of taxa thought typical for elevated microhabitats and bottom water current velocity, and used this relationship to reconstruct the Holocene history of bottom current velocity.

The use of the composition of benthic foraminiferal assemblages as a proxy for past current regimes is complicated by the fact that active currents may constitute one of the main taphonomical factors, causing resuspension and/or transport at the sediment–water interface, leading to winnowing of or addition of components. Schönfeld (1997) recommended the use of the >250 μm fraction benthic foraminifera in a proxy for bottom current regimes because tests in this large size fraction may be least affected by transport.

The development of such a current velocity proxy requires more ecological studies based on living and subfossil faunas, in order to understand taphonomical modifications, and the recording of the faunal response to current regimes in the sediments (Schönfeld, 1997; 2002b). Moreover, the calibration of such proxies is hampered by the lack of precise and highly detailed measurements of bottom current velocities in regions where information on benthic foraminiferal assemblages is available. For example, no precise current measurements are available for the Bay of Biscay, where foraminiferal ecology has been well studied (e.g. Fontanier et al., 2002; 2003; 2005; 2006; Hess et al., 2005). In the absence of current measurements, various non-faunal proxies for current activity could be used, such as grain size analysis, X-Ray photographs and ^{210}Pb and/or ^{234}Th profiles of the upper sediment layers (Fontanier et al., 2005). Direct observations of sedimentary structures in core material, photographic/video surveys of the seafloor and parasound records, may also give information on sedimentary processes and the associated current flow regimes (Schönfeld, 1997). Finally, a potential problem of this proxy method is the fact that we do not have observations that the benthic foraminifera living on elevated substrates are indeed suspension feeders. At least some species considered to be indicators of high current velocities (Schönfeld, 1997; 2002a,b) also occur in shallow infaunal microhabitats (e.g. *Cibicidoides* spp. in Corliss, 1985; Rathburn and Corliss; 1994; Fontanier et al., 2002; *Planulina ariminensis* in De Stigter et al., 1998). Species such as *Cibicides lobatulus, Planulina ariminensis,* and especially *Epistominella exigua* are common in areas where we have no indications of significant bottom currents. Most of these species appear to be typical of rather oligotrophic environments, where a microhabitat close to the sediment-water interface and perhaps a suspension-feeding life strategy, may be advantageous.

We thus suggest that the method proposed by Schönfeld should be used with caution, and may not be useful in all open ocean environments. In a well constrained local context, on the contrary, this method could be used to provide valuable information about past current regimes, but more research is needed.

3. Conclusions

The main environmental parameters structuring benthic foraminiferal faunas appear to be the organic flux to the ocean floor (its quantity, quality, and periodicity), and bottom water oxygenation (especially at very low ranges). To a lesser degree, sediment grain size and current velocity may act as limiting factors (e.g., Miller et Lohmann, 1982, Lutze and Coulbourn, 1984; Mackensen et al., 1990; Mackensen et al., 1995; Schmiedl et al., 1997). Conservative water mass properties such as salinity and temperature play only a minor role. Only in the deepest part of ocean basins, where strongly oligotrophic conditions prevail, the corrosiveness of the bottom waters (highest in waters such as AABW), may control the distribution of a few cosmopolitan taxa, such as *Nuttallides umboniferus* or *Oridorsalis tener* (e.g. Bremer and Lohmann, 1982; Mackensen et al., 1990; Mackensen et al., 1995; Schmiedl et al., 1997).

One of the first conclusions of this overview of the most important paleoceanographic proxy methods based on benthic foraminiferal assemblage characteristics could be that the scientific community working on benthic foraminiferal assemblages has been too modest. Many recent ecological studies conclusively show that under most circumstances the composition of deep sea benthic foraminiferal assemblages is controlled by a rather limited number of environmental factors. Our understanding of the often complex interactions between these factors, and of the way in which they structure the faunal composition, has made much progress over the last twenty years. Once we understand how environmental parameters influence the faunal composition, it should be possible to use this relationship in the reverse way, i.e., to use fossil faunas for the reconstruction of the controlling environmental parameters in the past, although more research is needed in order to establish for which part of earth history conditions resembled those in the present oceans sufficiently for this approach to work.

Methods to reconstruct past values of the essential oceanographic parameters of organic flux to the sea floor and bottom water oxygenation have largely remained qualitative, or at best semi-quantitative. In spite of the indisputable presence of a number of problems (which are shared with other, e.g., geochemical, proxy methods), some of the proposed proxies are based on firm ecological observations. Other physico-chemical parameters, such as current velocity, water corrosiveness to $CaCO_3$, temperature and/or salinity appear less important, except perhaps in some specific environmental contexts, where benthic foraminiferal proxies may provide adequate reconstructions of their past variability.

The available proxies based on benthic foraminiferal assemblage composition show that they have a major potential, but further research is needed to add or improve the quantitative aspects (Table 4). In many cases (e.g., bottom water oxygenation, and C_{org} flux to the ocean floor) this can be done by significantly increasing the size of existing data bases. In others (e.g., periodicity of the organic flux), time series observations are necessary. A major obstacle is our insufficient knowledge of the differences between recent and fossil faunas, due to taphonomical alterations. This phenomenon, of importance for all paleoceanographic proxies, can to some extent be solved relatively easily in the case of foraminiferal assemblages, by detailed studies of their vertical succession in sediments deposited in the last 5000 years, when environmental conditions were probably rather invariable in many areas. Unfortunately, such taphonomical studies are extremely time-consuming. Finally, we want to stress that scientists working with benthic foraminiferal assemblages should try to quantify the very complex relationships observed in nature. If a single proxy reconstruction has a large degree of uncertainty, a multi-proxy approach, with as many independent proxies as possible, may successfully reduce the uncertainty related to each single method. Proxies based on foraminiferal assemblage composition are fundamentally different from all geochemical proxies, and thus may provide independent reconstructions of essential oceanographic parameters. We conclude that benthic foraminiferal proxies deserve to be much more widely applied than they are today.

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Parameter	**Method**	**Problems and remedies**
Bottom water oxygenation	Marker species approach	Needs a more objective choice of marker species and a better calibration, probably only feasible for low O_2 concentrations
Bottom water oxygenation	Marker species + faunal diversity index	Needs further testing
Organic matter flux to the sea floor (Jz)	Flux dependency of species or species groups	Needs better estimates of Jz, needs calibration in many more areas
Organic matter flux to the sea floor (Jz)	BFAR	Needs calibration, using a large number of cores from different PP regimes
Primary Production (PP)	BFAR, flux dependency	Needs better knowledge of relations between PP and Jz
Quality of organic input	Marker species approach	Needs much more data on the geochemical composition of organic matter
Quality of organic input	BFAR/Corg flux	Needs more research
Periodicity of the organic flux		Needs more time series studies in various productivity contexts
Physico-chemical characteristics of water masses		May work in oligotrophic abyssal environments; more research needed
Current velocity		More current velocity measurements needed; probably only feasible in areas with high current velocities

Table 4. Overview of proxy methods based on benthic foraminiferal assemblage characteristics, their problems and possible remedies.

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Figure captions

Table 1 : Observations in low oxygen environments of planoconvex planispiral and trochospiral taxa, that are generally considered as typical of well oxygenated bottom waters. The second column gives the lowest bottom water oxygen concentration at which living (Rose Bengal stained) specimens have been described. The third column gives the reference: 1. Alve, 1990; 2. Bernhard, 1992; 3. Douglas and Heitman, 1979; 4. Jannink et al., 1998; 5. Jorissen et al., 1992; 6. Maas, 2000; 7. Mackensen and Douglas, 1989; 8. Sen Gupta et al., 1997; 9. Smith; 1964.

Fig. 2. Classification of environments with different oxygen concentrations, according to Tyson and Pearson (1991), Kaiho (1994) and Bernhard and Sen Gupta (1999).

Fig. 3: Relative frequency of deep infaunal taxa (percentage, scale on the left), in the centuries before deposition of sapropels S5, S3 (both from core Vicomed KS205, 38°11,86'N, 18°08,04'E, 2345 m) and S6 (ODP Hole 971A, section 1H4, 33°42,19'N, 24°42.81'E, 2143 m) and total faunal density (interrupted line, in number of foraminifera per gram dry weight, scale on the right), in function of depth in the core (in cm, scale below). Note the abrupt frequency increase to a total dominance in the last cm before azoic sediments, that coincides with the disappearance of almost all other taxa. In all three cases this frequency increase is accompanied by a strong drop in faunal density. Sapropel S5 shows a preliminary frequency increase (at 510 cm) about 5 cm before this ultimate frequency increase. Sapropel S6 does not show such a phenomenon. Ionian Sea core Vicomed KS205 (38°11,86'N, 18°08,04'E, 2345 m).

Fig. 4. Hypothetical curves showing the percentage of deep infaunal, low-oxygen marker species as a function of bottom water oxygen concentration and organic flux to the ocean floor. Fig. 4a: the decrease of bottom water oxygenation is not accompanied by an increase in organic flux. Fig. 4b: the decrease of bottom water oxygenation is accompanied by an increase of organic flux to the ocean floor. Figs 4a/b: curve 1): oligotrophic setting without deep infaunal taxa in the background fauna. Curve 2): more eutrophic setting with about 10% deep infaunal taxa in the background fauna.

Fig. 5. Scheme indicating the various steps and potential problems involved in the calibration of the BFAR as a paleoproductivity proxy. See text for further explanation.

Fig. 6. Variation of BFAR in NW Africa core Sed20bK (25°01.70'N, 16°39.02'W, 1445 m), over the last 2 glacial-interglacial cycles. After Guichard et al., 1999.

Fig. 7. Core Sed20bK; comparison between BFAR and sediment Corg flux (after Guichard et al., 1999); 88 samples; regression line (1): BFAR = 15160 * C_{org} + 616.5 ($r^2 = 0.42$).

Table Captions:

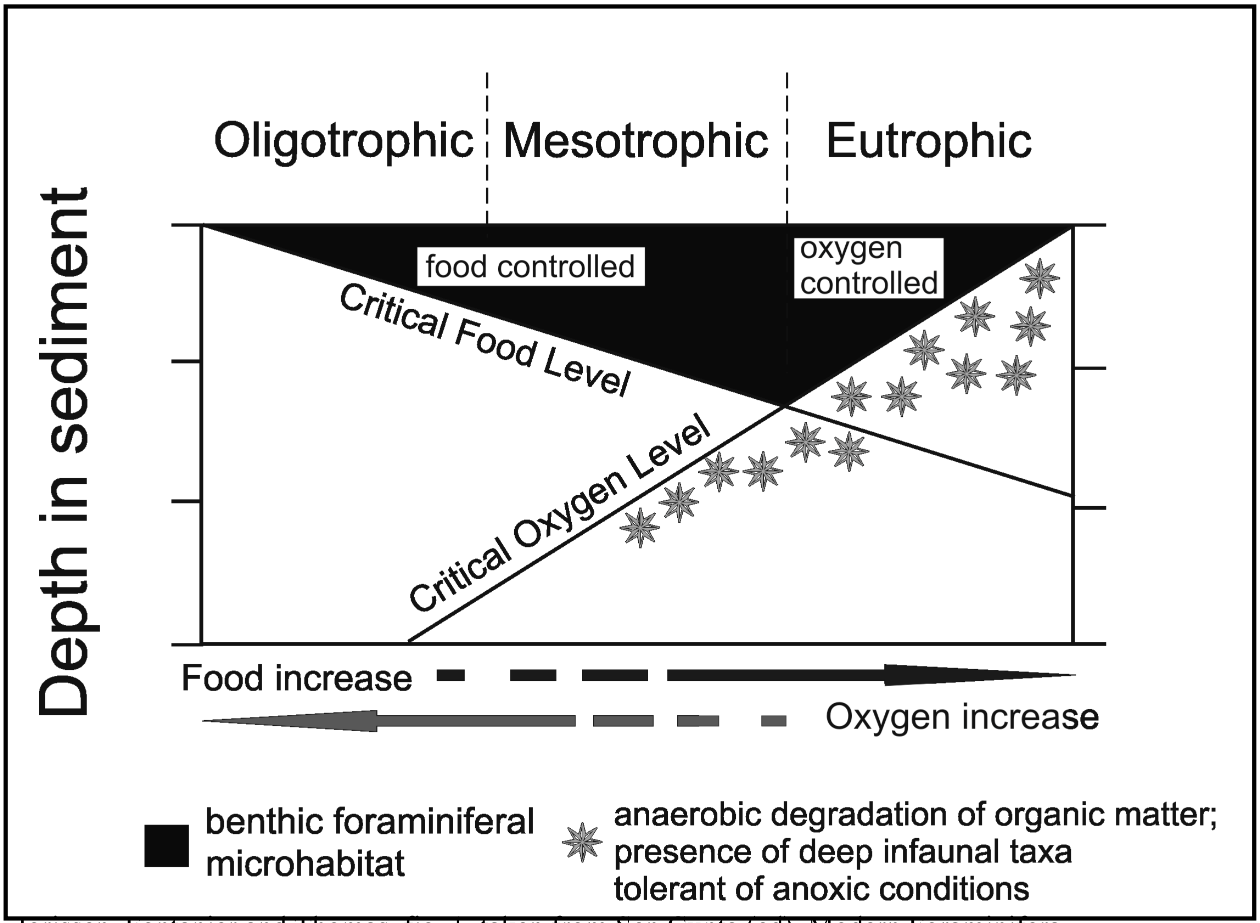
Table 1 : Observations of planoconvex planispiral and trochospiral taxa generally considered as typical of well oxygenated bottom waters in low oxygen environments. The second column gives the lowest bottom water oxygen concentration at which living (Rose Bengal stained) specimens have been described. The third column gives the reference: 1. Alve, 1990; 2. Bernhard, 1992; 3. Douglas and Heitman, 1979; 4. Jannink et al., 1998; 5. Jorissen et al., 1992; 6. Maas, 2000; 7. Mackensen and Douglas, 1989; 8. Sen Gupta et al., 1997; 9. Smith; 1964.

Table. 2. Cores KS04, Sed20bK and Sed 17aK: geographical position, water depth, age at the bottom of the core (indicated as MIS: marine isotopic stage), number of age control points, primary production (according to Schemainda et al., 1975), total estimated organic carbon flux to the sea floor, and its labile component (calculated according to equation one, after Herguera (1992).

Table 3. Cores Sed20bK, KS04 and Sed17aK: Comparison of observed Benthic Foraminiferal Accumulation rates (BFAR, according to three hypotheses) with the estimated flux of organic carbon to the sea floor (total flux and labile component). Three scenarios are tested, and the numbers of foraminifera > 150 µm preserved in the sediment are given for each case.

Table 4. Overview of proxy methods based on benthic foraminiferal assemblage characteristics, their problems and possible remedies.

Appendix 1. Summarize of early studies dealing with putative relationship between foraminiferal assemblages and water mass properties and/or bathymetry. Note the differences between papers concerning the water mass characteristics and the faunas inhabiting specific water masses. References are numbered in the first column and listed below. Water mass nomenclature is also detailed below. “nbd” means “no bathymetric data” available in the related note. Taxonomic names are not homogenised between studies. Reference list: (1) Caralp et al. (1970) and Pujos-Lamy (1973); (2) Streeter (1973); (3) Schnitker (1974); (4) Lagoe (1977); (5) Gofas (1978); (6) Gofas (1978); (7) Corliss 1978a; (8) Corliss (1978b; 1979); (9) Osterman and Kellogg (1979); (10) Schnitker (1980); (11) Belanger and Streeter (1980) and Streeter et al. (1982); (12) Burke (1981); (13) Corliss (1981; 1983b); (14) Miller and Lohmann (1982); (15) Peterson (1983-84); (16) Weston (1982) and Murray et al. (1986). Water mass nomenclature: CPDW/CDW/Circumpolar Deep Water; NADW/North Atlantic Deep Water; AABW/Antarctic Bottom Water; ABW/Arctic Bottom Water; NSOW/Norwegian Sea Overflow Water; AAIW/Antarctic Intermediate Water; IDW/Indian Deep Water; IBW/Indian Bottom Water; PBW/Pacific Bottom Water; PDW/Pacific Deep Water; MW/Mediterreanean Water; NEADW/North East Atlantic Deep Water.



Jorissen, Fontanier and Thomas, fig. 1, taken from Sen Gupta (ed). Modern Foraminifera.

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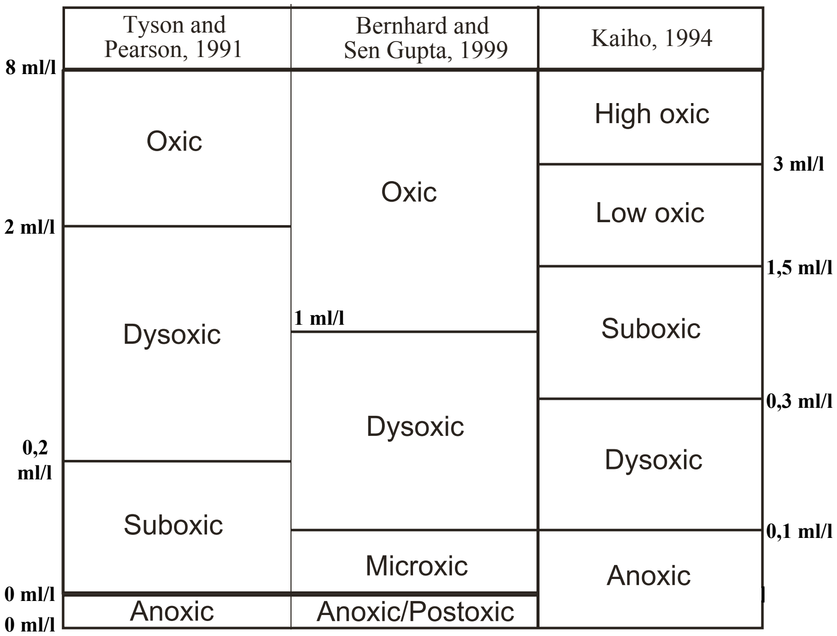
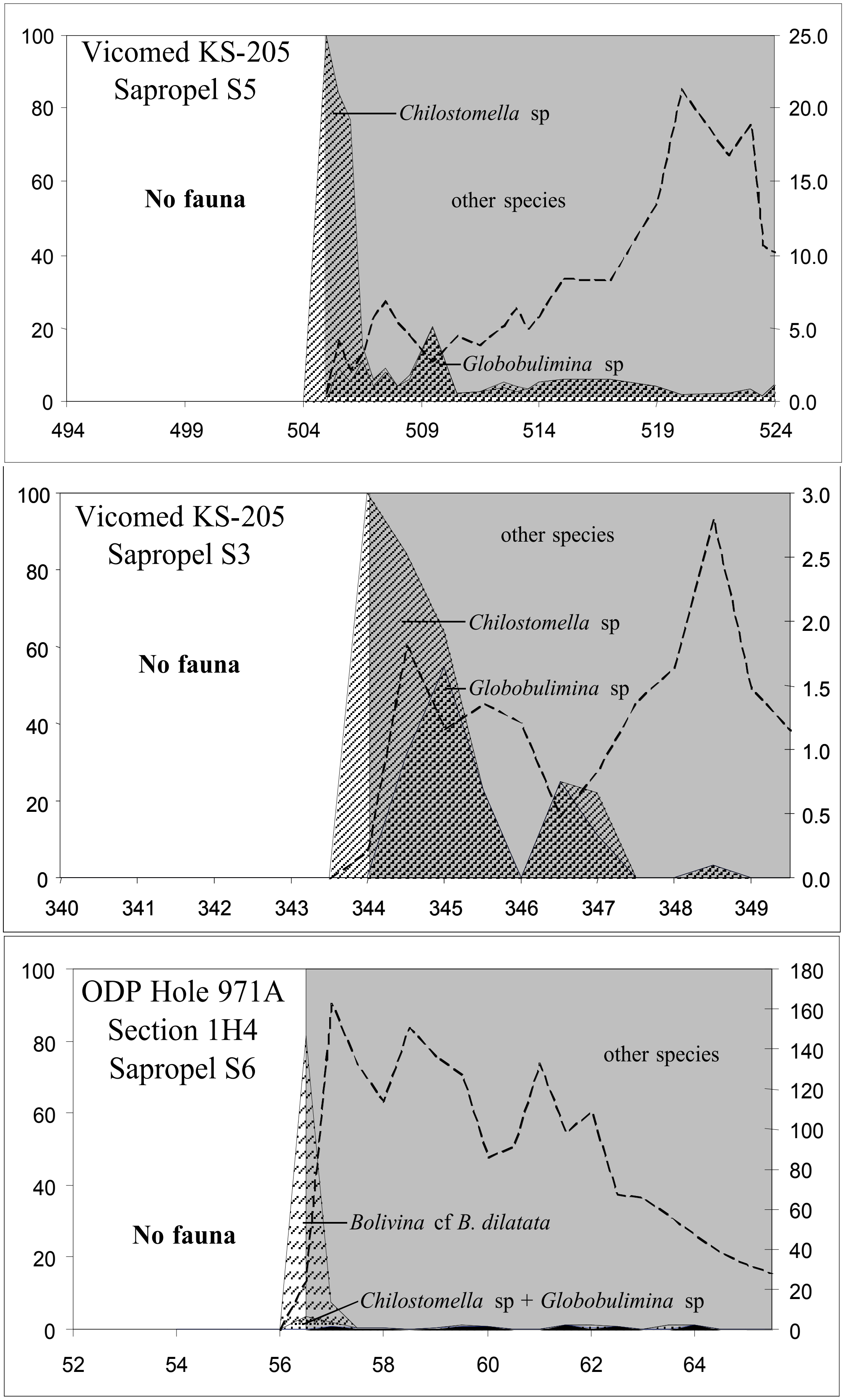
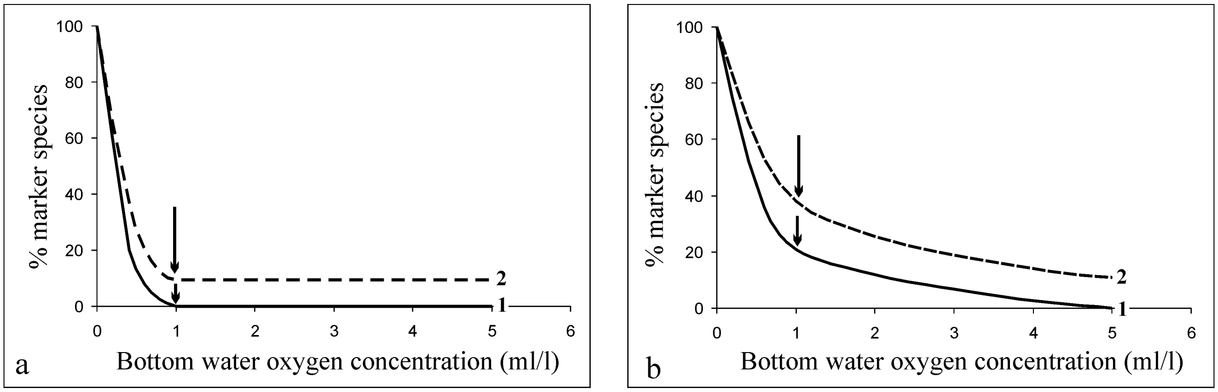


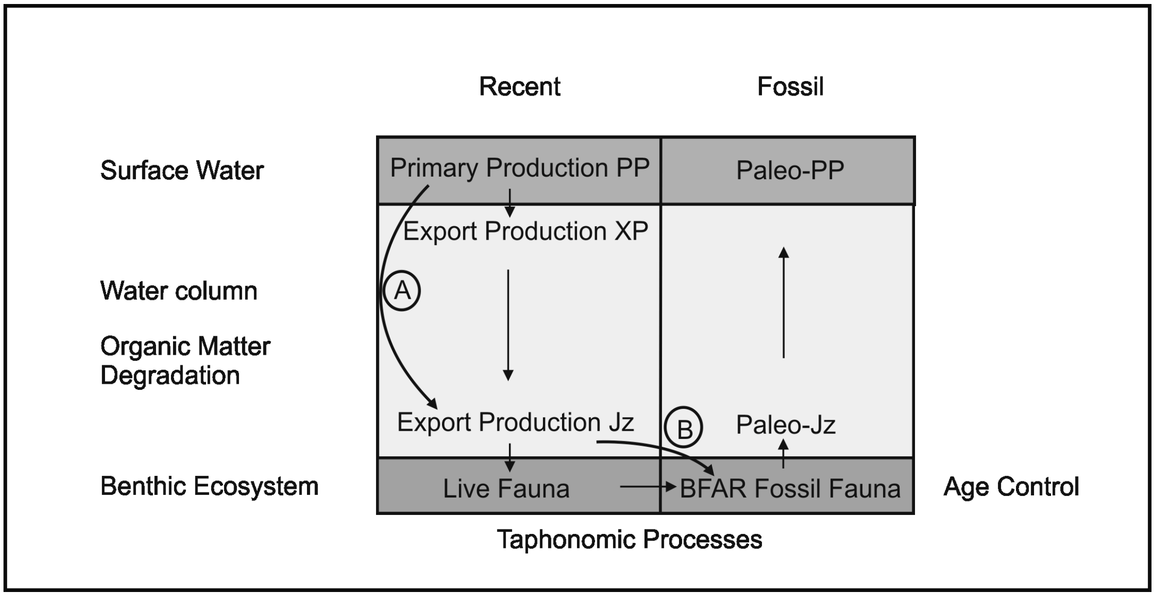
Jorissen, Fontanier and Thomas, fig. 2



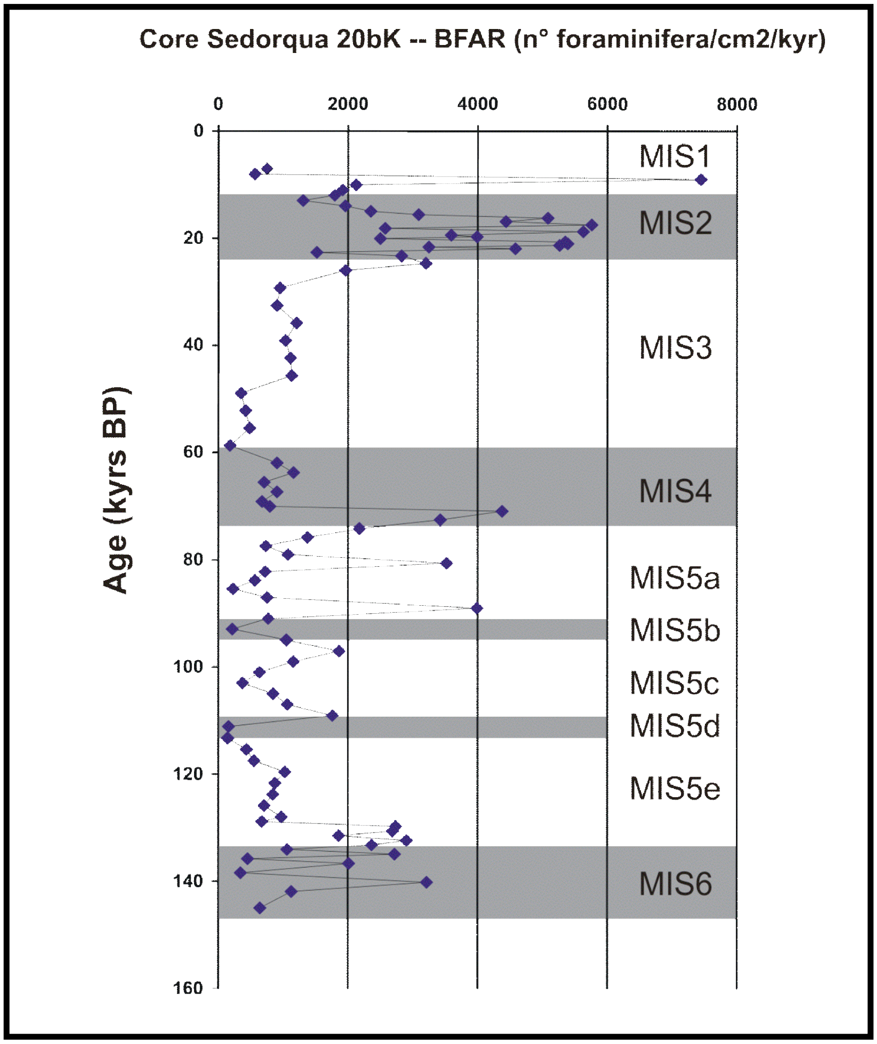
Jorissen, Fontanier and Thomas, fig. 3



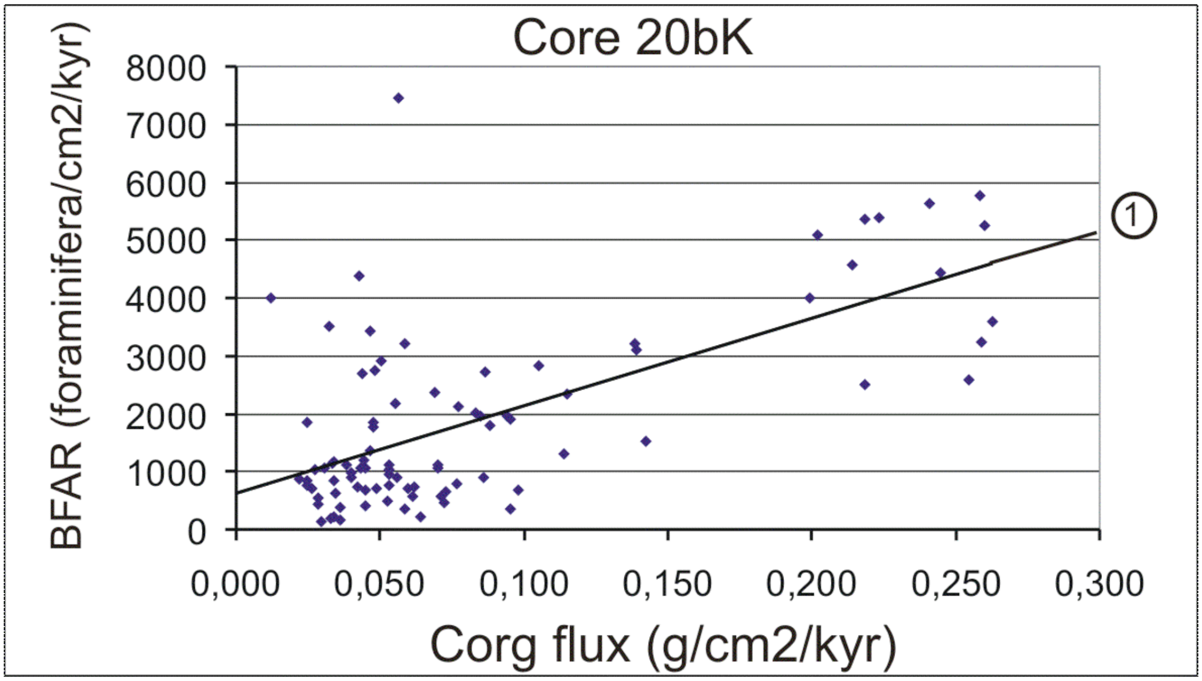
Jorissen, Fontanier and Thomas, fig. 4.



Jorissen, Fontanier and Thomas, fig. 5



Jorissen, Fontanier and Thomas, fig. 6.



Jorissen, Fontanier and Thomas, fig. 7.

Ammonia batavus	0.3 ml/l	1	*Epistominella smithi*	0.1 ml/l	3
Anomalina sp.	0.2 ml/l	4	*Epistominella vitrea*	0.8 ml/l	5
Cancris auriculus	0.3 ml/l	6	*Eponides antillarum*	0.9 ml/l	9
Cancris inaequalis	0.2 ml/l	7	*Eponides leviculus*	0.2 ml/l	3
Cancris oblongus	0.2 ml/l	4	*Eponides regularis*	0.1 ml/l	6
Cancris panamensis	0.6 ml/l	9	*Gavelinopsis lobatulus*	2.1 ml/l	4
Cancris sagra	0.4 ml/l	9	*Gavelinopsis translucens*	0.0 ml/l	8
Cassidulina carinata	0.3 ml/l	4	*Gyroidina io*	0.2 ml/l	3
Cassidulina crassa	0.3 ml/l	6	*Gyroidina lamarckiana*	0.1 ml/l	6
Cassidulina cushmani	0.3 ml/l	9	*Gyroidina multilocula*	0.4 ml/l	9
Cassidulina delicata	0.1 ml/l	3,7	*Gyroidina parva/pulchra*	0.9 ml/l	4
Cassidulina depressa	0.5 ml/l	4	*Gyroidina rotundimargo*	0.3 ml/l	9
Cassidulina laevigata	0.2 ml/l	7	*Gyroidina umbonata*	0.4 ml/l	4
Cassidulina limbata	1.0 ml/l	3	*Gyroidinoides neosoldanii*	0.5 ml/l	2
Cassidulina minuta	0.6 ml/l	9	*Gyroidinoides soldanii*	0.1 ml/l	6
Cassidulina oblonga	0.6 ml/l	9	*Hanzawaia boueana*	0.8 ml/l	5
Cassidulina sgarellae	0.3 ml/l	6	*Hanzawaia concentrica*	0.3 ml/l	6
Cassidulina subcarinata	0.2 ml/l	3	*Hoeglundina elegans*	0.2 ml/l	3
Cassidulina subglobosa	0.2 ml/l	4	*Hyalinea balthica*	0.3 ml/l	4
Cassidulina teretis	0.5 ml/l	3	*Islandiella subglobosa*	0.2 ml/l	3
Cassidulina tumida	0.4 ml/l	9	*Islandiella sp.*	0.3 ml/l	6
Cibicides bradyi	0.3 ml/l	4	*Lenticulina articulata*	0.3 ml/l	6
Cibicides fletcheri	0.4 ml/l	7	*Oridorsalis umbonatus*	0.4 ml/l	4
Cibicides refulgens	0.3 ml/l	2	*Osangularia culter*	0.3 ml/l	4
Cibicides ungerianus	2.1 ml/l	4	*Osangularia rugosa*	0.0 ml/l	8
Cibicidoides wuellerstorfi	1.6 ml/l	2	*Planulina ariminensis*	0.2 ml/l	7
Elphidium albiumbilicatulum	0.0 ml/l	1	*Planulina exorna*	0.6 ml/l	9
Elphidium excavatum	0.1 ml/l	1	*Planulina limbata/ornata*	0.3 ml/l	9
Elphidium incertum	0.1 ml/l	1	*Pullenia* sp.	0.4 ml/l	4
Elphidium tumidum	2.4 ml/l	9	*Valvulineria araucana*	0.2 ml/l	3
Epistominella decorata	0.1 ml/l	6	*Valvulineria javana*	0.2 ml/l	4
Epistominella exigua	0.3 ml/l	6	*Valvulineria oblonga*	0.3 ml/l	9

Jorissen, Fontanier and Thomas, table 1.

Core	Latitude	Longitude	Water depth	Age at Bottom core	Number of Age control points	Primary Production	Jz total C$_{org}$ flux	Jz Labile component
KS04	20°34.70’N	18°08.80’W	1000 m	MIS7	8	200 g/m^2/year	7.9 g/m^2/year	5.65 g/m^2/year
Sed20bK	25°01.70’N	16°39.02’W	1445 m	MIS5d	12	100 g/m^2/year	2.7 g/m^2/year	1.3 g/m^2/year
Sed17aK	25°16.80’N	17°06.45’W	2975 m	MIS6	15	65 g/m^2/year	1.1 g/m^2/year	0.35 g/m^2/year

Jorissen, Fontanier and Thomas, table 2.

Core Sed20bK–1445 m	**BFAR**	**Total C$_{org}$ flux (2.7 gC/m^2/year)**	**C$_{org}$, labile component (1.4 gC/m^2/year)**
Background BFAR	780 forams/cm^2/kyr	2.9 forams/mg C$_{org}$	5.6 forams/mg labile C$_{org}$
Average BFAR	1500 forams/cm^2/kyr	5.6 forams/mg C$_{org}$	10.7 forams/mg labile C$_{org}$
Peak values BFAR	4000-7500 forams/cm^2/kyr	15-28 forams/mg C$_{org}$	28-54 forams/mg labile C$_{org}$
Core KS04--1000 m	**BFAR**	**Total C$_{org}$ flux (7.9 gC/m^2/year)**	**C$_{org}$, labile component (5.65 gC/m^2/year)**
Background BFAR	17000 forams/m^2/yr	2.2 forams/mg C$_{org}$	3.0 forams/mg labile C$_{org}$
Average BFAR	24800 forams/m^2/yr	3.1 forams/mg C$_{org}$	4.4 forams/mg labile C$_{org}$
Peak values BFAR	50000 forams/m^2/yr	6.3 forams/mg C$_{org}$	8.8 forams/mg labile C$_{org}$
Core Sed17aK--2975 m	**BFAR**	**Total C$_{org}$ flux (1.1 gC/m^2/year)**	**C$_{org}$, labile component (0.35 gC/m^2/year)**
Background BFAR MIS5a	450 forams/m^2/yr	0.4 forams/mg C$_{org}$	1.3 forams/mg labile C$_{org}$
Peak value BFAR MIS1	4000 forams/m^2/yr	3.6 forams/mg C$_{org}$	11 forams/mg labile C$_{org}$

Jorissen, Fontanier and Thomas, table 3.

Parameter	**Method**	**Problems and remedies**
Bottom water oxygenation	Marker species approach	Needs a more objective choice of marker species and a better calibration, probably only feasible for low O_2 concentrations
Bottom water oxygenation	Marker species + faunal diversity index	Needs further testing
Organic matter flux to the sea floor (Jz)	Flux dependency of species or species groups	Needs better estimates of Jz, needs calibration in many more areas
Organic matter flux to the sea floor (Jz)	BFAR	Needs calibration, using a large number of cores from different PP regimes
Primary Production (PP)	BFAR, flux dependency	Needs better knowledge of relations between PP and Jz
Quality of organic input	Marker species approach	Needs much more data on the geochemical composition of organic matter
Quality of organic input	BFAR/Corg flux	Needs more research
Periodicity of the organic flux		Needs more time series studies in various productivity contexts
Physico-chemical characteristics of water masses		May work in oligotrophic abyssal environments; more research needed
Current velocity		More current velocity measurements needed; probably only feasible in areas with high current velocities

Jorissen, Fontanier and Thomas, table 4.