GEOLOGICA ULTRAIECTINA

Mededelingen van de
Faculteit Aardwetenschappen
Universiteit Utrecht

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Recent and fossil benthic foraminifera in the Adriatic Sea: distribution patterns in relation to organic carbon flux and oxygen concentration at the seabed

H.C. de Stigter

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ISBN 90-5744-002-4

Cover illustration: "Benthic-pelagic coupling":
Benthic foraminifer (*Psammatodendron arborescens*)
anchored in the test of a planktonic foraminifer
(*Globigerina bulloides*). Southern Adriatic Sea,
station AD91-32, 146m). Stereo pair on back cover.

Recent and fossil benthic foraminifera in the Adriatic Sea: distribution patterns in relation to organic carbon flux and oxygen concentration at the seabed

Recente en fossiele benthische foraminiferen in de Adriatische Zee: verspreidingspatronen in relatie tot organisch koolstofflux en zuurstofconcentratie bij de zeebodem

(met een samenvatting in het Nederlands)

Proefschrift

ter verkrijging van de graad van Doctor
aan de Universiteit Utrecht
op gezag van de Rector Magnificus Prof. Dr. J.A. van Ginkel
ingevolge het besluit van het College van Dekanen
in het openbaar te verdedigen op
maandag 28 oktober 1996 des namiddags te 16.15 uur

door

Hendrik Corstiaan de Stigter

geboren op 18 november 1964
te Bennekom

Promotores: Prof. Dr. G.J. van der Zwaan
Prof. Dr. J.E. Meulenkamp
Co-promotor: Dr. F.J. Jorissen

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SUMMARY

Organic matter sinking from the euphotic surface layer of the ocean to the deep sea constitutes the main source of nutrition of organisms living below the photic zone, and as such plays a major role in controlling biological activity in the deep sea. Study of Recent and fossil benthic foraminifera in the Adriatic Sea confirms the importance of the organic carbon flux in determining benthic foraminiferal distribution patterns.

In the Adriatic Sea, living benthic foraminifera decrease in abundance with increasing water depth, reflecting the decreasing flux of organic carbon to the benthos. Enhanced production of foraminifera, observed especially on the upper continental slope, may be related to lateral transport and redeposition of organic carbon by bottom currents. It is suggested that infaunal foraminifera, which may be able to utilize partially degraded organic matter supplied by lateral transport, are largely responsible for the additional foraminiferal production.

A clear distinction of epifauna and infauna could not be made in the Adriatic Sea. Many common species live concentrated at or near the sediment surface, but persist in decreasing abundance down to several centimetres depth in the sediment. Few species are found exclusively at the sediment surface, or exclusively below the surface. Furthermore, the microhabitat of certain species changes with water depth. Comparison of the live and dead abundances of species shows that species which live near the sediment surface, generally are represented by a greater number of empty tests per living individual than deeper-dwelling species. From this observation it is concluded that shallow-dwelling species reproduce more rapidly than deeper-dwelling species. Tentatively, it is suggested that by rapid reproduction epifaunal foraminifera are able to compete for intermittent supplies of fresh organic matter. Since selective feeding on freshly deposited organic matter usually implies occupation of a normal oxic surface habitat, it seems logical to assume that epifaunal species are poorly adapted to oxygen-deficient conditions. More slowly reproducing infaunal species should content themselves with partially degraded organic matter. The reproductive disadvantage of these species may be compensated by a high tolerance to oxygen-deficient conditions, allowing them to exploit organic matter buried below the sediment surface. The lowest reproductive potential, combined with the greatest tolerance to dysoxic or even anoxic conditions, may be found in deep-infaunal species.

Comparison of the Recent distribution of benthic foraminifera in the South

Adriatic Basin with the distribution in fossil sediments recovered in piston cores from the same area shows that the bathymetric range of occurrence of species varied with time, in response to variation in surface water productivity and organic carbon flux.

The devastating effect of prolonged bottom-water anoxia on benthic foraminiferal life is demonstrated by study of foraminiferal assemblages in two fossil sapropels: S1 from the Holocene of the South Adriatic Basin, and C2 from the Upper Pliocene of southern Italy. While benthic foraminifera are completely absent in large parts of the two sapropels, conspicuous low-diverse assemblages, dominated by low-oxygen tolerant infaunal species, are present at certain levels. The presence of these low-diverse faunas indicates periodic reoxygenation of the bottom water, which may have been due to cooling of the surface water. By model simulation of foraminiferal population dynamics it is demonstrated that repeated elimination of foraminiferal communities by anoxia, followed by repopulation, may result in dominance of low-oxygen tolerant opportunistic species in foraminiferal assemblages.

The results of the present study indicate that benthic foraminiferal abundance in Recent and fossil sediments provides a basis for estimation of present and past organic carbon flux at the seabed. Whereas the production of infaunal foraminifera may be enhanced by lateral supply of organic carbon, the abundance of epifaunal foraminifera may be a more reliable measure of the vertical supply of organic carbon. Oxygen deficiency in the bottom water may result in replacement of the normal epifaunal community by a community dominated by low-oxygen tolerant infaunal foraminifera. Under such conditions reliable estimation of the vertical organic flux seems not possible.

CHAPTER 1

Introduction

The sombre forecasts of the possible consequences of rapid man-induced global warming have greatly stimulated research on the mechanisms controlling the earth's climate system. The marked rise in average temperatures observed over the past few decades is commonly attributed to the accumulation of anthropogenic greenhouse gases in the atmosphere, which reduce heat emission from the earth. The concentration of carbon dioxide, considered as one of the important greenhouse gases, has increased dramatically since the middle of the 19th century, mainly as a result of the burning of fossil fuels. Although fluctuations in atmospheric carbon dioxide concentration of comparable amplitude have occurred in the past over glacial-interglacial cycles (e.g. Schneider, 1989), the rate at which the carbon dioxide level changes at present seems unprecedented in recent geological history.

The search for sources and sinks of carbon dioxide has led to the recognition that there is an important exchange of this gas between the atmosphere and the ocean, the latter constituting a net sink of carbon dioxide. Carbon dioxide is extracted from the atmosphere by its dissolution in the ocean surface water and subsequent photosyn-thetic reduction to organic carbon by phytoplankton. A major part of the carbon thus incorporated in phytoplankton biomass is recycled within the epipelagic foodweb, and returns on a short timescale of usually less than one year as respired carbon dioxide to the ocean water and back to the atmosphere. A minor part of the organic carbon, however, is exported from the euphotic layer of the ocean to deeper water and to the sea bottom, mainly in the form of sinking organic detritus. Most of the exported organic detritus is consumed in the water column by bacteria and bathypelagic higher organisms. A small fraction, decreasing with increasing water depth, reaches the sea bottom and is almost completely consumed by benthic organisms, while only a very small fraction is semipermanently buried in the sediment. Carbon dioxide released by bathypelagic and benthic respiration into the deep water layers is returned on a time-scale in the order of one thousand years to the ocean surface and from there back to the atmosphere by upwelling of deep water. Carbon buried in the sediment is re-turned to the atmosphere on a geological timescale of millions of years by uplift and weathering of sediments, or by subduction of sediments along convergent plate margins, after which carbon is released as volcanic carbon dioxide. The release of sedimentary organic carbon has been speeded up only in recent time by the burning of fossil fuel.

Because the biologically mediated transfer of carbon dioxide from the atmosphere to the deep sea is far more rapid than the release of carbon dioxide from the deep sea back to the atmosphere by ocean circulation and by turnover of sedimentary organic carbon, the capacity of the ocean to absorb the accumulated anthropogenic carbon dioxide from the atmosphere strongly depends on the efficiency of the biological pump. Studies of carbon fluxes in the present-day ocean are therefore central in climatic research, whereas the reconstruction of paleocarbon fluxes provides background values of natural variability against which the impact of human activity on the ocean system can be evaluated.

Paleoproductivity is commonly reconstructed on the basis of analysis of fossil assemblages of pelagic organisms such as planktonic foraminifera, diatoms, radiolaria and dinoflagellates. Also, geochemical productivity tracers like sedimentary organic carbon, biogenic silica, barium and cadmium, and carbon isotopic ratios of inorganic carbon, are widely employed. Alternatively, paleoproductivity may be estimated on the basis of fossil remains of benthic organisms, which may reflect the flux of organic carbon arriving at the sea bottom. Although many benthic groups leave no mentionable trace in the fossil record, benthic foraminifera form a conspicuous exception. This highly diverse group of marine protozoans is well-represented in almost all marine environments, and many species of benthic foraminifera construct tests of calcium carbonate or agglutinated sediment particles which have an excellent preservation potential. Studies of marine benthos which include foraminifera gene-rally agree on the importance of this group in terms of benthic biomass, and indicate the prominent role of foraminifera in the consumption and cycling of organic carbon (Tietjen, 1971; Coull et al., 1977; Shirayama, 1984a; Snider et al., 1984; Gerlach et al., 1985; Gooday, 1986; Alongi and Pichon, 1988; Gooday et al., 1992). Benthic foraminiferal biomass has been reported to correlate well with estimated organic carbon flux (Altenbach and Sarnthein, 1989), whereas the abundance of fossil benthic foraminifera in marine sediments may likewise be correlated with the organic flux, opening new perspectives for paleoproductivity studies (Berger and Diester-Haass, 1988; Van der Zwaan et al., 1990; Herguera and Berger, 1991).

However, in view of the diversity and complexity of marine ecosystems, there are reasons to doubt the general validity of the observed correlation. For example, extreme oxygen depletion in the bottom water almost certainly affects the production of benthic foraminifera, resulting in elimination of foraminiferal life, or instead creating conditions of reduced predation and food competition by benthic macrofauna in which benthic foraminifera may become extremely abundant (e.g. Phleger and Soutar, 1973; Bernhard and Reimers, 1991). Whereas such extreme oxygen depletion of the bottom water occurs only in restricted areas of the ocean, mostly below highly productive upwelling waters along the continental margins or below strongly eu-trophicated coastal waters, oxygen-depleted sediments are present ocean-wide at shallow depth below normal oxic surface sediments. Under a high organic carbon flux the oxygen-depleted subsurface zone may be present below only a few millimetres of oxic sediment, and receive a substantial amount of the organic carbon arriving at the seafloor. Under such conditions, the dysoxic subsurface sediment forms a suitable habitat for infaunal foraminifera which, partly sheltered from competition and predation by metazoan macrofauna, may build up substantial biomass. The oxygen-depleted subsurface sediment zone may not only provide a relatively sheltered habitat to living infaunal foraminifera, but foraminiferal shells produced within this environment may also be better preserved than at the sediment surface (Loubere et al., 1993).

If, on the basis of foraminiferal abundance, a reasonably accurate estimate can be made of the benthic flux of organic carbon, it may not always be possible to reconstruct the productivity of the surface water on this basis. First, there is the possibility that part of the benthic organic flux is not derived from vertical settling of organic detritus, but rather arrives by lateral transport. Especially on the continental slope the resuspension and lateral transport of particulate matter may result in significant redistribution of organic carbon (Walsh, 1991; 1992). It needs verification, however, whether the organic carbon transported laterally within bottom nepheloid layers is of the same nutritional quality as the carbon which settles vertically from the water column. Another complication is that the benthic organic flux represents only a fraction of what is produced in and exported from the euphotic surface layer. A large part of the primary production is retained within the surface water, whereas most of the exported organic carbon is remineralised during the first few hundreds of metres of descent to the bottom. Empirical equations which describe the organic carbon flux as a function of surface primary production and water depth (Suess, 1980; Betzer et al., 1984; Berger et al., 1987; Martin et al., 1987) differ on some points and may not be applicable under all circumstances. The exported fraction of primary production is not linearly proportional to the annual average primary production, but increases exponentially with increasing primary production (Eppley and Peterson, 1979; Betzer et al., 1984), and with increasing seasonality or intermittency of the primary production (Berger and Wefer, 1990). Furthermore, the decrease of the organic flux with water depth depends on a variety of factors, such as the sinking speed of organic particles, the quality and hence degradation rate of the organic matter, and the characteristics of the water column. A high water temperature is likely to increase the degradation rate of organic matter, by stimulating microbial enzymatic activity. A strong temperature-dependence of enzymatic degradation of organic detritus in the deep sea has been experimentally confirmed by Meyer-Reil and Köster (1992). Midwater anoxia on the other hand may lead to an enhanced carbon flux to the benthos, by limiting the abundance of bathypelagic consumers of organic matter (e.g. Wishner et al., 1990).

This thesis deals with the question how various aspects of live communities and fossil assemblages of benthic foraminifera may be related to environmental conditions prevailing at the seabed, with special emphasis on the benthic flux of organic carbon and the concentration of oxygen in the bottom water. Most of the work presented in this thesis is based on the study of living (Rose Bengal stained) foraminifera collected from surface sediment samples from the southern Adriatic Sea, and fossil foraminifera collected from box and piston cores of Recent to latest Pleistocene sediments from the same area.

In the next Chapter (Ch. 2) the potential of planktonic/benthic foraminiferal ratios for paleobathymetric reconstruction is discussed, with reference to published data on planktonic and benthic foraminiferal abundance in the Adriatic Sea. Central in the discussion is the dependency of benthic foraminiferal production on the vertical flux of organic carbon, and the possible effects of lateral supply of organic carbon.

Chapter 3 gives a detailed account of the distribution of living benthic foraminifera in sediments of the South Adriatic Basin; this includes description of the variation in benthic foraminiferal abundance with water depth and with depth in the sediment, and also of the bathymetric zonation and microhabitat characteristics of common foraminiferal species. The role of the organic carbon flux and of oxygen concentration in the sediment in controlling foraminiferal distribution is discussed. A more general discussion of the relation between benthic foraminiferal microhabitats and the distribution of food and oxygen in the sediment is presented in Chapter 4, with reference to observed distribution patterns of living foraminifera in the Central and South Adriatic Basin.

In Chapter 5, live foraminiferal communities from the South Adriatic Basin are compared with corresponding dead foraminiferal assemblages, with the purpose of assessing differences in reproduction rate between benthic foraminiferal species.

In Chapter 6 it is investigated how variation in organic carbon flux in the southern Adriatic Sea over the past 18,000 years affected the bathymetric distribution of benthic foraminiferal species. Changes in the bathymetric distribution of benthic foraminifera are inferred from a comparison between the Recent distribution and the distribution in two piston cores from the same area. Accumulation rates of planktonic and benthic foraminifera in the two piston cores are used as proxies of paleoproductivity and paleocarbon flux.

Chapters 7 and 8 give a reconstruction of the depositional history of, respectively, sapropel S1 from the Holocene of the South Adriatic Basin, and sapropel C2 from the Upper Pliocene of southern Italy, based on analysis of planktonic and benthic foraminiferal assemblages. The anomalous benthic foraminiferal assemblages present in the two sapropels testify to the profound effect of bottom-water anoxia on benthic foraminifera.

A model simulation of benthic foraminiferal population dynamics under seasonally fluctuating bottom-water oxygen concentration is presented in Chapter 9.

A synthesis of the most important conclusions of this study, concerning the question how benthic foraminiferal distribution is related to organic carbon flux and oxygen concentration at the seabed, is presented in the last Chapter (Ch. 10).

CHAPTER 2

The depth dependency of planktonic/benthic foraminiferal ratios: Constraints and applications*

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Abstract Study of the ratio between planktonic and benthic foraminifera in a great number of areas shows that variation of this ratio with depth can be described using organic matter flux equations. Essentially, the share of benthic foraminifera in the total association is inversely proportional to depth, as is the amount of organic matter resulting from primary productivity reaching the sea bottom.
Variation in the *P/B* ratio from area to area appears to be strongly dependent on the amount of inbenthic living foraminifera. If the ratios are corrected for this, the regressions between the proportion of planktonic foraminifera (%*P*) and depth appear to be near-identical in the Gulf of Mexico, the Gulf of California, the west coast of the USA and the Adriatic Sea. This regression can be described by:

$$Depth = e^{(3.58718+(0.03534\%P))}$$

A study of the behaviour of this function in nine cores from the Adriatic Upper Quaternary reveals that the palaeodepth reconstructions are not influenced by fluctuations in productivity and temperature but that they are significantly influenced by redeposition of fine-grained deposits.

Introduction

Palaeobathymetry is of growing importance in palaeoceanography and basin analysis, its main importance being in the reconstruction of the uplift and subsidence history of sedimentary basins. In addition to this, increasing attention is being paid to the construction of sea-level curves. This followed the first publication (Vail et al., 1977) pertaining to the until then unknown and unappreciated magnitude and rhythm of relative sea-level movements. Although the model originally put forward by Vail et al. has been contested (e.g. Cloetingh et al., 1985; Cloetingh, 1988), this first attempt to evaluate the magnitude and effects of relative sea-level movements has

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* *Marine Geology, 95 (1990) 1-16*

functioned as a catalyst for further research (e.g. Haq et al., 1988). In this context it is not surprising that the demand for more accurate palaeobathymetrical techniques - has increased. However, this demand has by no means been satisfied. The presently - most widely employed and probably most accurate palaeobathymetrical techniques are of a micropaleontological nature. In these techniques, use is made of the distribution patterns of mainly benthic species, which in younger Cenozoic deposits are mostly foraminifera or ostracods. Although a reasonable consensus has been developed concerning the notion that benthic species are roughly arranged along a depth gradient, it is evident that a number of problems prevent accurate reconstructions of palaeobathymetry:

(1) There is only a little understanding of the fundamental factors which decide the ultimate bathymetric distribution of benthic species.

(2) Bathymetric ranges of species differ considerably from area to area, apparently depending on rather badly defined and poorly understood factors. A good example is provided by the so-called delta-depressed or delta-elevated species described by Pflum and Frerichs (1976).

(3) There is no consensus as to whether species are isobathyal in time or whether they may be able to change their bathymetrical range through time. The implicit assumption in most palaeobathymetrical analyses is that species, or even homeomorphic species, inhabit constant depth ranges through time. However, there is evidence that following particular environmental changes some species have changed their depth habitats (e.g. Douglas and Woodruff, 1981; Miller, 1982).

The need for a better quantitative measure of palaeodepth stimulated the search for tools other than species distribution patterns. In 1955, Grimsdale and Van Morkhoven published their classical study on the application of the ratio between planktonic and benthic foraminifera (*P/B* ratio) in palaeodepth reconstructions. Their work followed the study of Phleger (1951), who also pointed to the relationship between *P/B* ratios and depth. They found that the proportion of planktonic foraminifera of the total association (*P*) increased fairly systematically towards deeper water. In spite of the general tendency of increasing *P*-values with depth, Grimsdale and Van Morkhoven (1955) observed an extremely wide data scatter. Later, the *P/B* ratio was applied in a number of studies (e.g. Uchio, 1960; Poag, 1972; Kafescioglu, 1975; Murray, 1976; Van Marle et al., 1987). Although the *P/B* ratio seemed to be a fair measure of depth in nearly all cases, the scatter in *P*-values versus depth in modern environments (Parker, 1954; Uchio, 1960; Wilcoxon, 1964; Lutze, 1974) remains a worrying factor, rendering the method difficult to apply.

In this paper we will present *P/B* data from a number of areas and discuss their application to palaeobathymetry. Most of these data are derived from the literature.

We will discuss the sources of the wide data scatter and present a refined method for quantitatively using the *P/B*-ratio elaborating upon the results of Berger and Diester-Haass (1988). In this method we will stress the dependence of the abundance of benthic foraminifera on the organic flux exported from the photic zone. In numerical experiments we will show the effects of variation in this flux on foraminiferal abundance patterns.

The ratio between planktonic and benthic foraminifera

There is no clear consensus in the literature regarding the cause of the increase in the number of planktonic foraminifera (*P*) with depth (or, more precisely, with increasing distance from the coast) (Berger and Diester-Haass, 1988). However, the reason for the increase is partly evident: with increasing distance from the coast the turbidity decreases, enabling primary production to increase. Furthermore, the complex pelagic ecosystem, with many nutrient chains and recycling loops, is only fully developed at a certain water depth encompassing the total photic zone (Rohling and Gieskes, 1989). With a continued increase in water depth the mesopelagic and bathypelagic planktonic foraminifera enter the ecosystem (Hemleben and Spindler, 1983; Hemleben et al., 1989), thus completing the pelagic system and adding to the total pelagic biomass. As the input of nutrients from the continent decreases, one would expect the pelagic biomass to decrease again at a certain distance from the coast.

The benthic biomass follows less predictable patterns, sometimes being extremely high in unexpected places such as in anoxic basins (e.g. Uchio, 1960; Phleger and Soutar, 1973). The general pattern, however, is that the benthic foraminiferal number increases from the nearshore area to the continental edge; further seaward it decreases rather drastically towards low values at bathyal depths (compare Douglas and Woodruff, 1981). In many respects the benthic biomass and thus the benthic foraminiferal number follows the global distribution pattern of organic carbon in the sediment (Romankevich, 1984; Pearson and Rosenberg, 1987) which is highest in shelf seas and at the continental edge, and rapidly decreasing towards greater depths. In this respect, both the benthic and planktonic foraminiferal abundance patterns appear to be to a great extent a function of food and nutrients. Many other factors, such as temperature, salinity, substrate and circulation pattern also play a role, but in most cases clearly a subordinate one (compare Pearson and Rosenberg, 1987).

Berger and Diester-Haass (1988) used the planktonic/benthic foraminiferal ratio as a productivity index. They showed that the flux of primary produced organic matter plays a crucial role in this respect. If we assume that the main source of food for benthic organisms consists of organic matter raining down through the water column, the amount reaching the bottom at a particular depth can be calculated by:

$$J(d) = (k\ PP/d) + (r\ PP) \tag{2.1}$$

where $J(d)$ is the amount of organic matter arriving at the bottom, k and r are constants, d is the water depth/100 and PP the primary production (see Suess, 1980; Berger and Diester-Haass, 1988). Berger and Diester-Haass argue that the second term is of no importance in this context. It represents the amount of refractory organic matter and r is close to 0.01. The first term indicates the amount of non-refractory organic matter arriving at the bottom at depth D. They estimate the export factor k at about 0.2, instead of the original estimate of Suess of 0.4.

In our further reasoning we will assume that the number of planktonic foraminiferal tests is proportional to the primary production and that the number of benthic foraminifera is proportional to $J(d)$. The term (k PP) would then be equivalent to (k(number of planktonic foraminifera)) and represent the export productivity. This is evidently a simplification, but at the moment we find it an acceptable assumption. However, before these terms in the equation can be replaced by their biotic counterparts, another problem must be solved, i.e. how efficient benthic foraminifera are compared with planktonic foraminifera in the use of food. Clearly, it is not acceptable to assume that from a given amount of food the same number of progeny arises for planktonic and benthic foraminifera alike. We must take an efficiency factor into account, which is estimated by Berger and Diester-Haass to be about 3; i.e. benthic foraminifera are three times more efficient in the use of organic matter than planktonic foraminifera are as secondary producers. We calculated various options for k and efficiency factor E (Fig. 2.1). From this Figure it appears that the calculated percentage of planktonic foraminifera in the total association follows a semi-linear relationship with Ln(D) at depths greater than 100 m. As stated earlier, Berger and Diester-Haass assume the export factor to be 0.2, instead of the original 0.4 estimated by Suess. The different factors of k, however, have a relatively minor effect on the proportion of planktonic foraminifera in the total association. It should be appreciated that Eppley and Peterson (1979) and Betzer et al. (1984) propose that the export factor k is dependent on PP. For instance, the relationship described by Betzer et al. would result in a variation in k from about 0.2 to 0.3 under conditions of intermediate to high-primary productivity. For the time being, we also consider this variation in k to be of no importance. Although various models estimate different export productivities, the decay below the mixed layer is described by all as essentially inversely proportional to depth.

From the $J(d)$ equation it follows that the P/B ratio varies directly with depth,

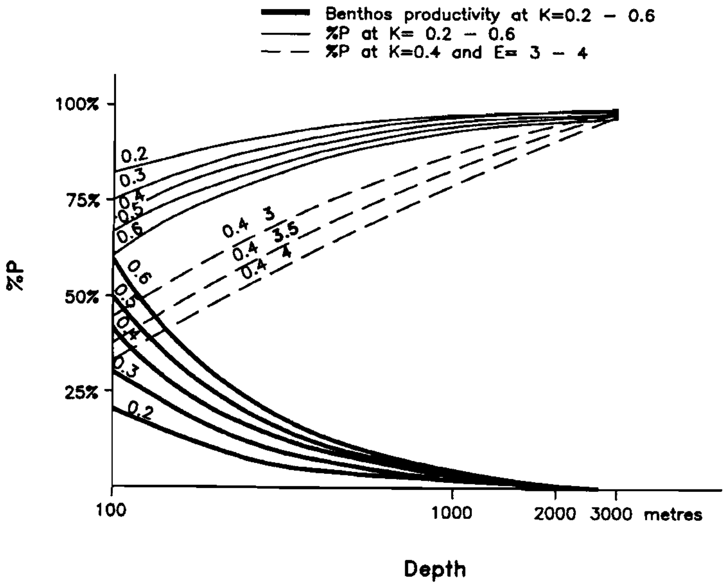


Fig. 2.1. Relationship between number of benthic foraminifera, %*P* and depth, calculated on the basis of the *J*(*d*) equation and constant primary productivity. The %*P* versus depth relationship is calculated for *k* = 0.2-0.6 and for *k* = 0.4 with varying efficiency factors *E* = 3-4. For explanation, see text.

because it can be rewritten as:

$$D = 100\ k\ P/B \tag{2.2}$$

From the value of the %*P* in Fig. 2.1 it follows that in deeper waters the values of the *P*/*B* ratio strongly increase and eventually approach infinity. This implies that in the depth range of 0-1000 m the *P*/*B* ratio increases from 0 to 10, but then rapidly from 20 to ∞. Regression analysis is strongly influenced by this tail. Moreover, the *P*/*B* ratio in this depth range is highly sensitive to small changes in *B*, which could easily be artificial and induce inaccuracy. Therefore, we decided to use the %*P* instead of the *P*/*B* ratio. From Fig. 2.1 it is clear that in the greater part of the depth range below 1500 m the relationship between depth and %*P* is almost log-linear and can be described as:

$$Ln(D) = a + b\ \%P \tag{2.3}$$

This type of equation was earlier empirically found by Wright (1977) and employed by Van Marle et al. (1987).

In Fig. 2 we have depicted a number of curves of %*P* versus depth derived from various areas. For sake of convenience we have depicted the curves here on a non-logarithmic depth scale to better demonstrate the gradual variation in regression from area to area. The regressions have varying degrees of correlation, most being significant but showing an extremely great data scatter. What is more worrying is the difference in regression from area to area, which strongly limits the general applicability of the method. This variability has already been observed by Wright (1977) and Van Marle et al. (1987). In the context of the *J*(*d*) flux equation, however, this variability can only be explained by variation in *k* from area to area, a variation which far exceeds the expected variation determined by *PP* (Betzer et al., 1984), or by assuming that the equation is not valid in the context of our problem. Therefore, we have decided to analyze the data from various areas from which extensive faunal data sets existed in more detail, mainly focussing on the Gulf of Mexico, the Gulf of California, the western coast of the United States and the Adriatic Sea.

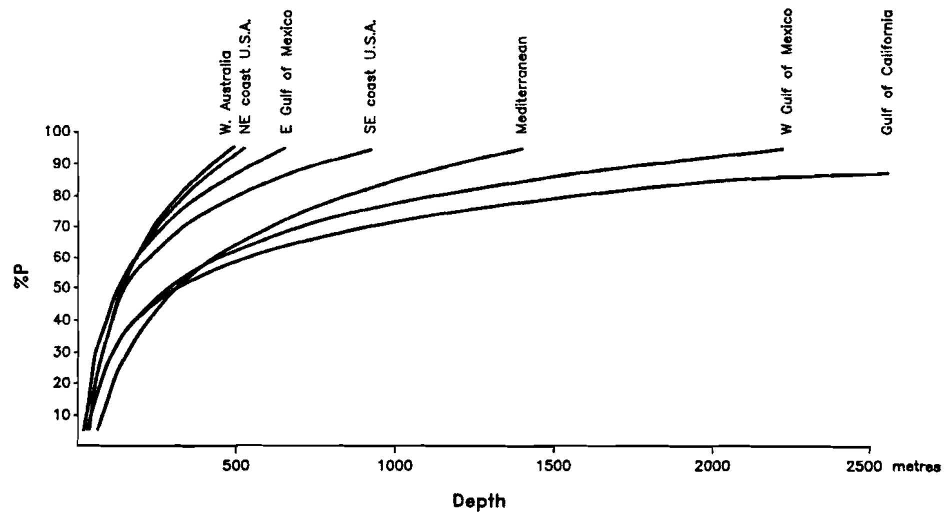


Fig. 2.2. Regression curves of %*P* versus depth based on the following data: Western Australia (Betjeman, 1969); northeastern coast of the USA (Kafescioglu, 1975); eastern Gulf of Mexico (Parker, 1954); southeastern coast of the USA (Wilcoxon, 1964); Mediterranean (Parker, 1958; Todd, 1958; Jorissen, 1988); western Gulf of Mexico (Phleger, 1951); Gulf of California (Uchio, 1960). For regression analysis, the general equation $\mathrm{Ln}(D) = a + b\ \%P$ was used.

The dependence of %*P* on depth

In the Gulf of Mexico we analyzed in detail a number of transects previously studied by Phleger (1951; transects 1-12) and by Parker (1954; transects 1-7). The plot of all the raw *P* data versus depth (Fig. 2.3) shows the enormous data scatter which occurs in this area. Figures 2.4 and 2.5 show the plot of the number of benthic and planktonic foraminifera respectively versus depth. The number of planktonic foraminifera steadily increases with depth, and the number of benthic foraminifera shows a very vague trend towards decreasing values. These total numbers are of course not corrected for differences in sedimentation rate. The Figures show, however, that the trend of increasing %*P* with increasing depth is clearly caused by the opposite trends in numbers of the two groups.

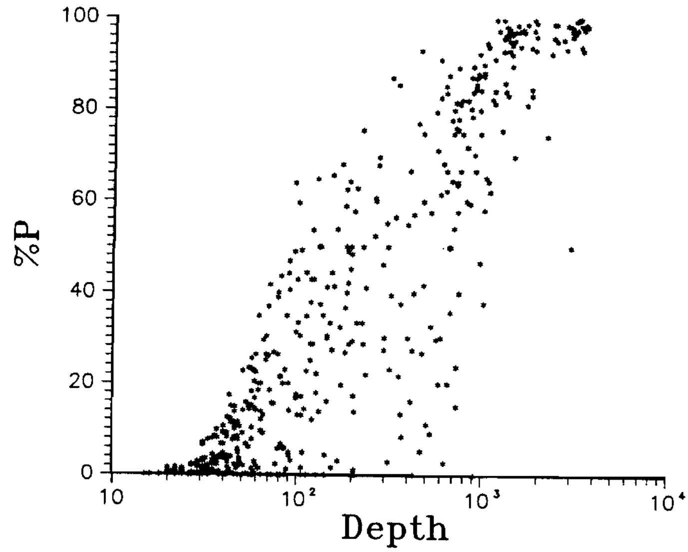


Fig. 2.3. Raw data (n = 517) from transects 1-12 of Phleger (1951) and transects 1-7 of Parker (1954) from the Gulf of Mexico. All samples containing less than 100 foraminifera per sample are deleted.

In many of the transects studied the trend of increasing %*P*-values with depth is rather pleasing and regular. In some transects, however, notably those from areas in front of the Rio Grande River and the Mississippi River, this trend is highly irregular, causing the large data scatter in Fig. 2.3.

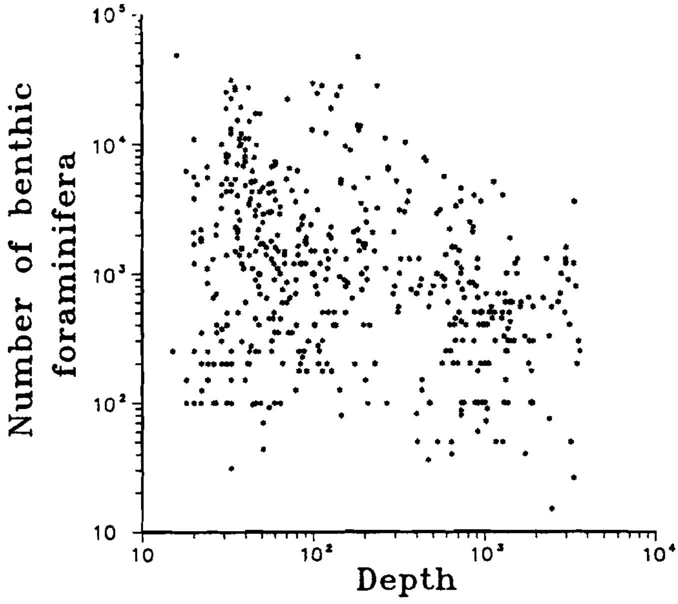


Fig. 2.4. Number of benthic foraminifera versus depth from the Gulf of Mexico (see caption Fig. 2.3).

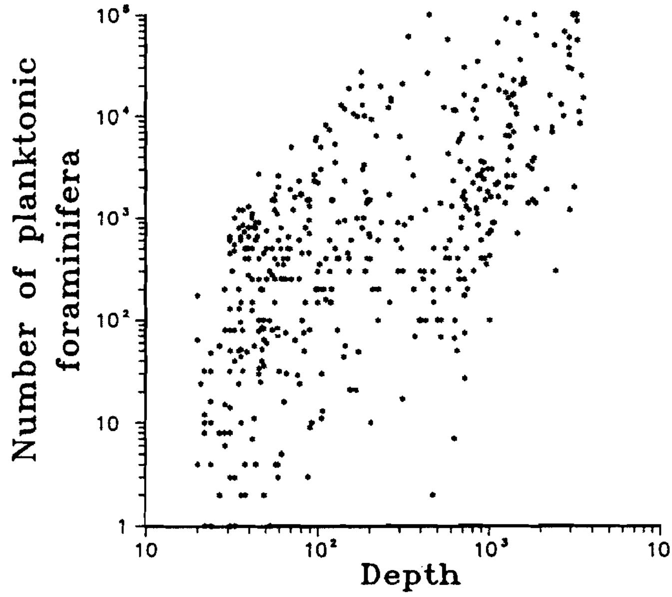


Fig. 2.5. Number of planktonic foraminifera versus depth from the Gulf of Mexico (see caption Fig. 2.3).

We have recently concluded (Van der Zwaan and Jorissen, 1989) that in these areas high numbers of the benthic genera *Bulimina*, *Globobulimina*, *Bolivina*, *Uvigerina*, and *Fursenkoina* occurred. We suggested that these species all have aninfaunal habitat, i.e. are not directly dependent on the supply of organic matter and food from the overlying water layers. Instead, they would be deposit-feeders, relying on the food within the sediment. In Fig. 2.6 we have plotted the cumulative frequencies of species belonging to the above-mentioned genera versus depth. It can be seen that this group reaches highest frequencies between 50 and 800 m. Comparison with Fig. 2.3 suggests that also in this interval a high number of deviant, low *P*-values occur.

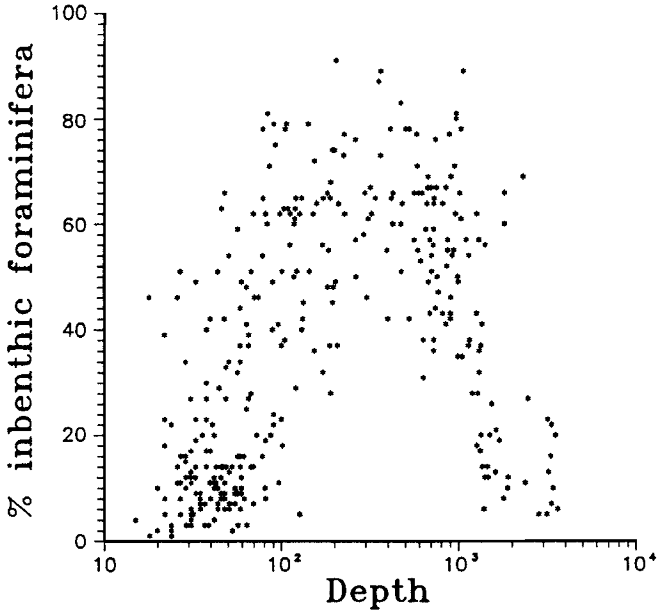


Fig. 2.6. Cumulative frequencies of infaunal benthic species (see text) versus depth (n = 517; see caption Fig. 2.3).

Assuming that the $J(d)$ model describes primarily the relationship between planktonic foraminifera and epibenthic foraminifera (Fig. 2.7), we calculated new %P-values, omitting the inbenthic species. We made conservative groupings in this case; i.e. we only excluded taxa which are generally agreed upon as being inbenthic (see Grossman, 1984a, b; Corliss, 1985; Van der Zwaan et al., 1986; Verhallen, 1987; Jorissen, 1988; Mackensen and Douglas, 1989). This newly calculated ratio, hereafter called %P^*, is depicted in Fig. 2.8. It can be seen that the regression is greatly improved by disregarding the infaunal elements, especially between 100 and

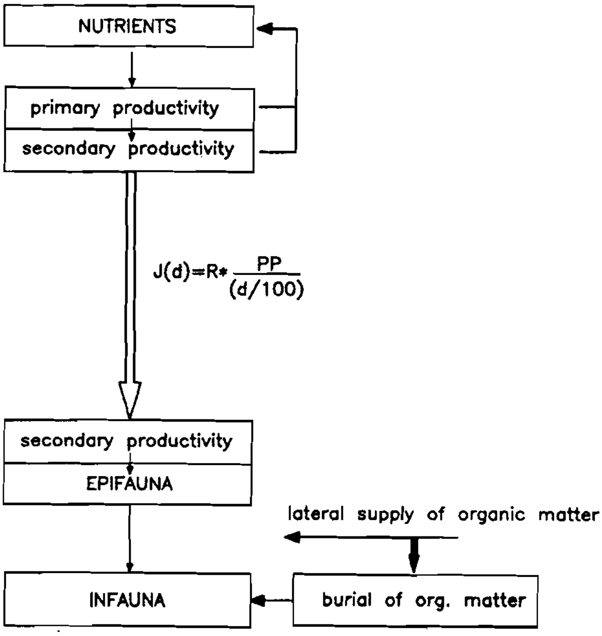


Fig. 2.7. Theoretical model of food flux from surface layers to the benthic environment, with separate boxes for epifaunal and infaunal benthic species.

800 m, but still we have a relatively high degree of data scatter. Returning to the original data sets of Parker and Phleger, it is striking to note that especially Parker mentions dissolution of carbonate in the organic-rich sediments in front of the Mississippi River. In particular, transects 1, 2, 3 and 4 of Parker, and also 1 and 2 of Phleger, seem to be prone to dissolution. Moreover, in these and some other transects *Hoeglundina elegans*, an aragonitic species, is not present at the depths where it is present in the neighbouring transects. We believe it is likely that selective dissolution plays an important role and thus we removed the above-mentioned transects from the data set. The resulting Figure (Fig. 2.9) shows that the data scatter is greatly reduced, although still not at a minimum. However, we must keep in mind that effects of downslope transport or reworking have not yet been taken into account. The effects of resedimentation could be especially important, although we have no means of tracing them without restudying the sample material. We will return to this problem later.

The same procedure as outlined above has been applied to the data sets from the Gulf of California (Figs. 2.10, 2.11 and 2.12; data Uchio, 1960), the west coast of the United States (Figs. 2.13 and 2.14; data Wilcoxon, 1964) and the Adriatic Sea (Figs. 2.15 and 2.16; data Jorissen, 1988). All data sets are based on counts in the

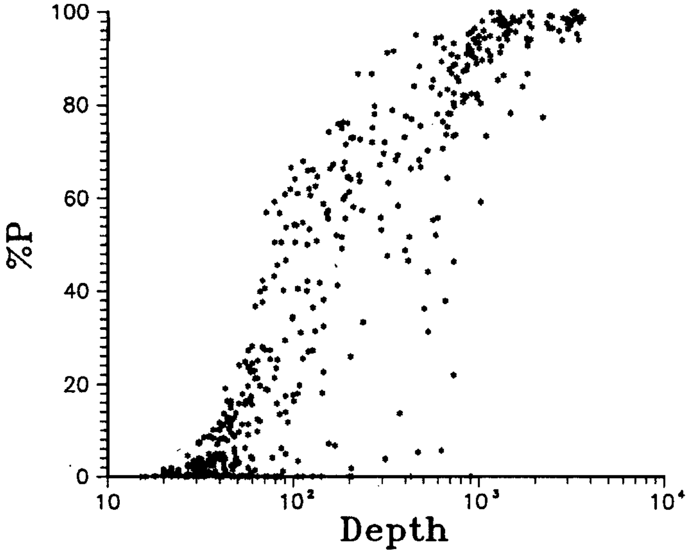


Fig. 2.8. Data from Fig. 2.3, now with recalculated %*P*-values, disregarding infaunal benthic taxa.

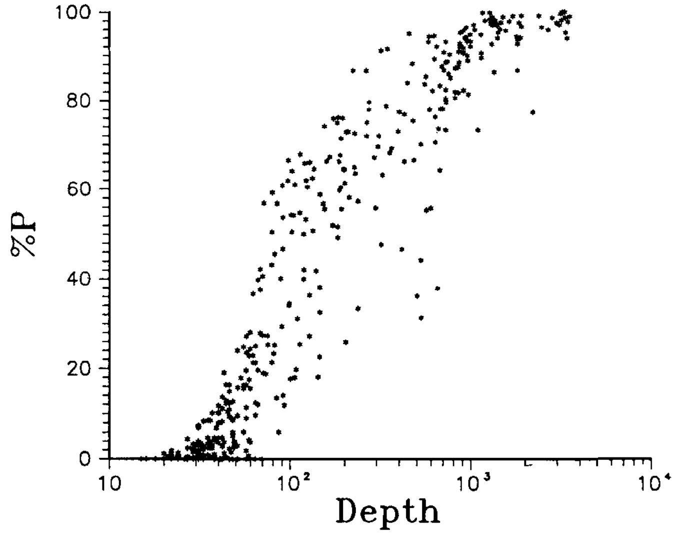


Fig. 2.9. Data from Fig. 2.8, now without transects 1 and 2 from Phleger (1951) and 1, 2, 3 and 4 from Parker (1954) in which dissolution is suspected.

63 μm size fraction, except for the Adriatic Sea where the 150 μm size fraction was employed. In the case of the Gulf of California we omitted the deeper samples, because Uchio suggests that these samples are considerably affected by downslope contamination. Further, Schrader et al. (1983) found considerable effects of dissolution in these deeper basins. All samples available from the Adriatic Sea were critically re-examined in view of possible reworking and downslope contamination effects; this resulted in a particularly tight regression.

The data of Wilcoxon are most difficult to assess in view of possible downslope transport. If we consider his data matrix, the probability of downslope mixing and reworking seems to be high, especially in rather shallow waters. We present his data however, because they represent an example of an association with a minor proportion of infauna. Therefore, the %P^*-values approximate the original ones, which in turn are close to the corrected values from the other areas. In view of the uncertainty regarding the possibility of displacement, however, we omitted the data in the end from the total analysis.

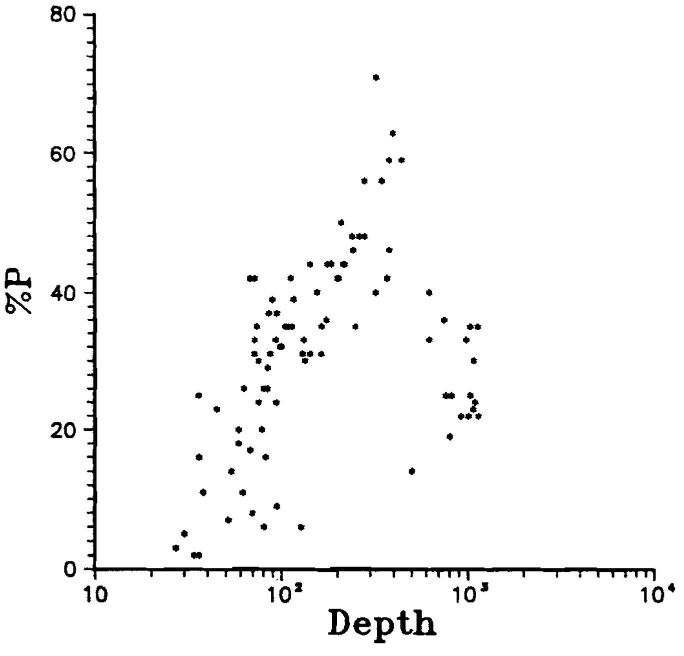


Fig. 2.10. Raw data of %P versus depth from the Gulf of California (Uchio, 1960; $n = 94$).

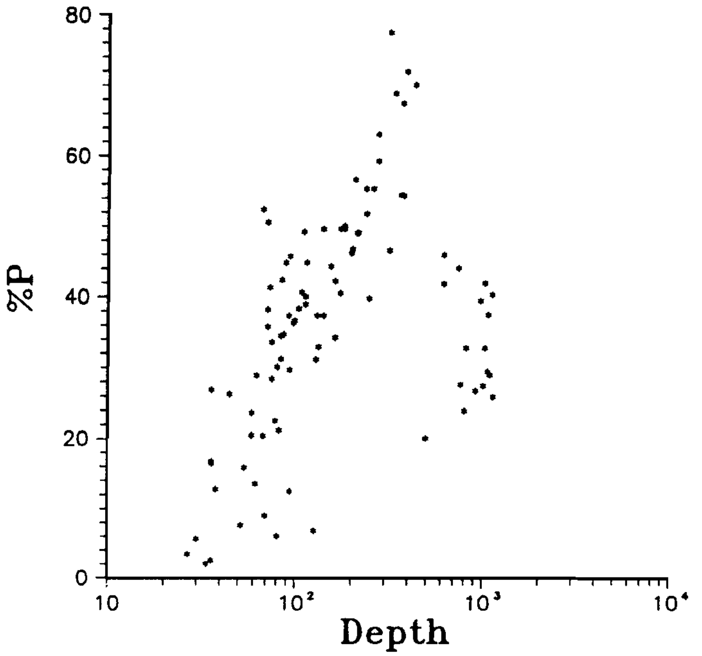


Fig. 2.11. Data of Fig. 2.10, %*P*-values recalculated disregarding infaunal taxa.

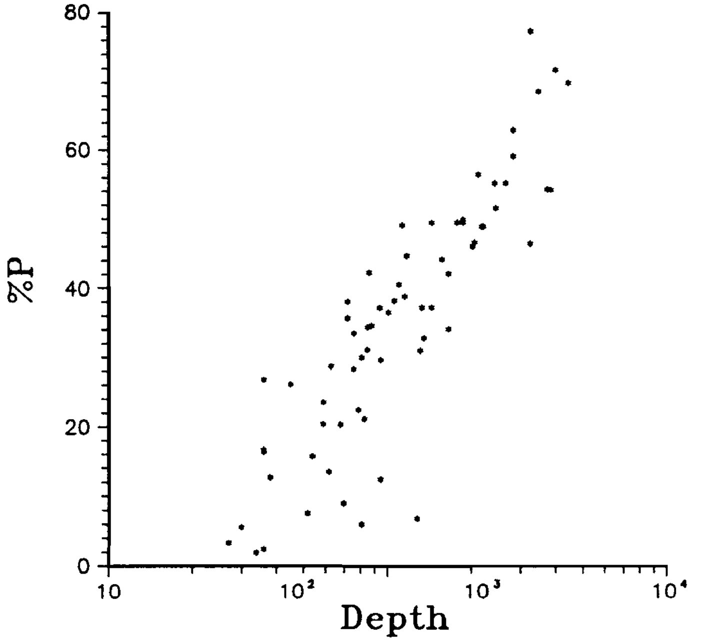


Fig. 2.12. Data of Fig. 2.11, samples from deep basins deleted (see text for explanation).

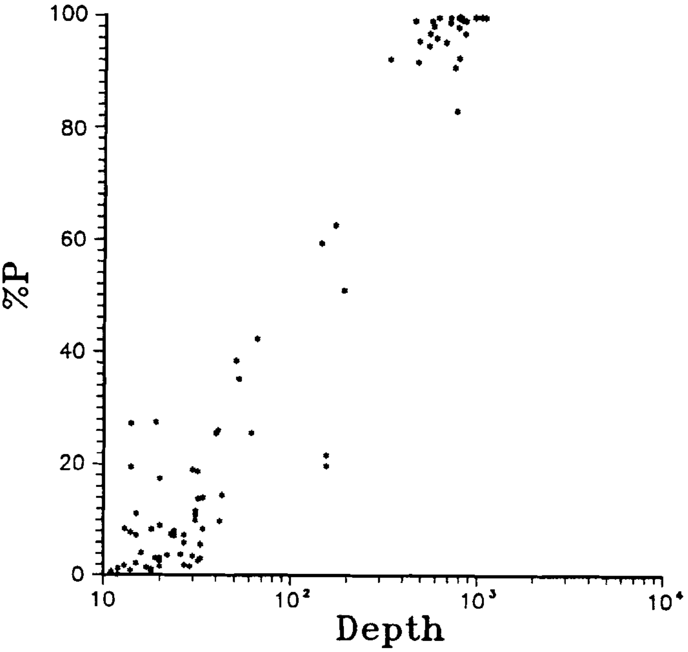


Fig. 2.13. Raw data of %P-values versus depth from the southeastern coast of the USA (Wilcoxon, 1964; n = 85).

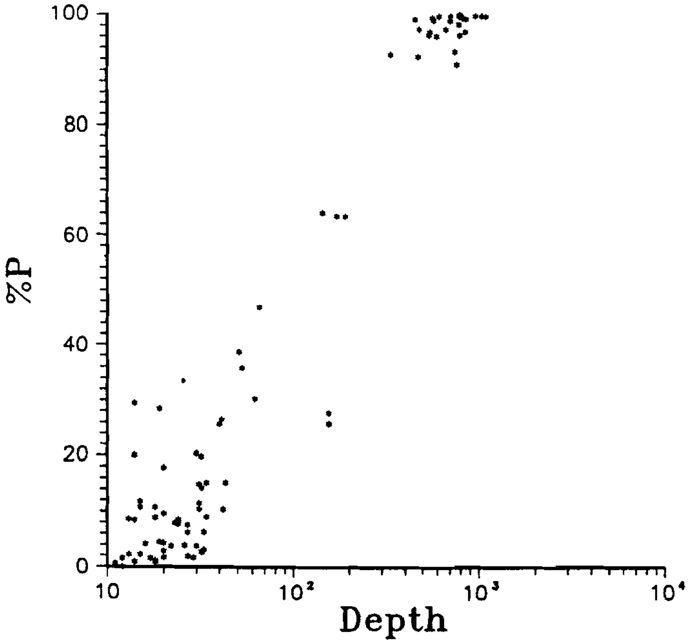


Fig. 2.14. Data of Fig. 2.13, %P-values recalculated disregarding infaunal taxa.

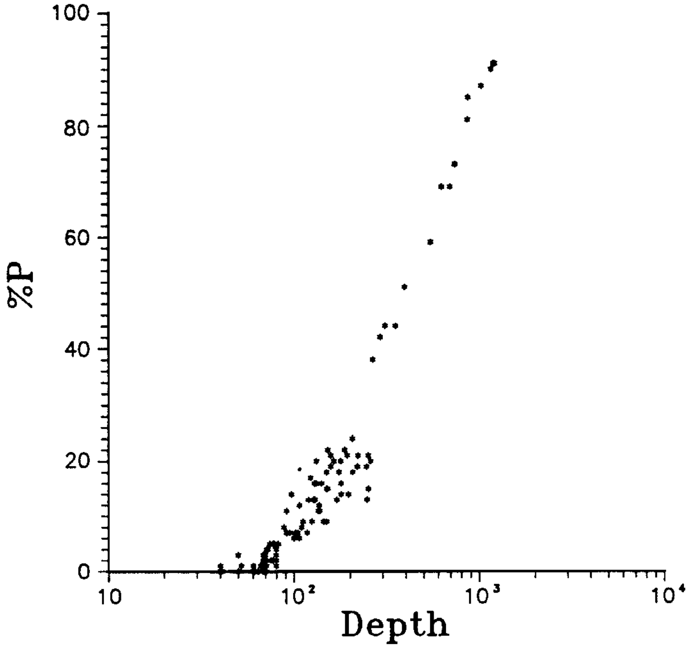


Fig. 2.15. Raw data of %*P*-values versus depth from the Adriatic Sea (Jorissen, 1988; *n* = 111).

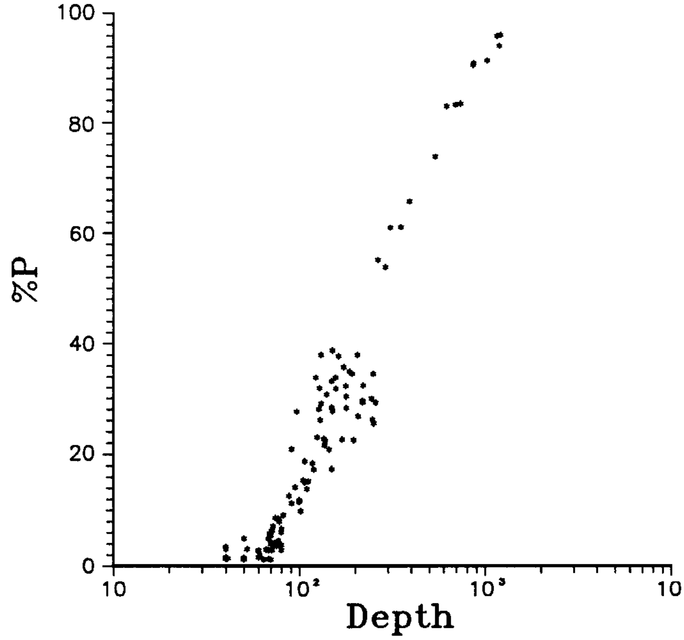


Fig. 2.16. Data of Fig. 2.15, %*P*-values recalculated disregarding infaunal taxa.

In the remaining three areas (i.e. Gulf of Mexico, Gulf of California and the Adriatic Sea), we find surprisingly similar functions of %P^* versus Ln(D); in this context it is noteworthy that the regression function based on the Adriatic Sea material is the most deviating one, especially in shallower water. However, the functions remain near-identical; therefore we grouped all the data together (Fig. 2.17) and calculated one function with the form:

$$Ln(D) = a + b\,\%P^* \qquad (2.4)$$

or

$$D = e^{(a+b\%P^*)} \qquad (2.5)$$

where we found $a = 3.58718$ and $b = 0.03534$. The correlation of %P^* versus Ln(D) is highly significant ($r = 0.93$, $n = 583$; $p < 0.001$). The values of a and b imply that a value of $P = 100$ would result in a depth estimate of about 1250 m, whereas $P = 0$ would give 36 m. This means that according to this relationship the model would be useful in the bathymetrical range 36-1250 m.

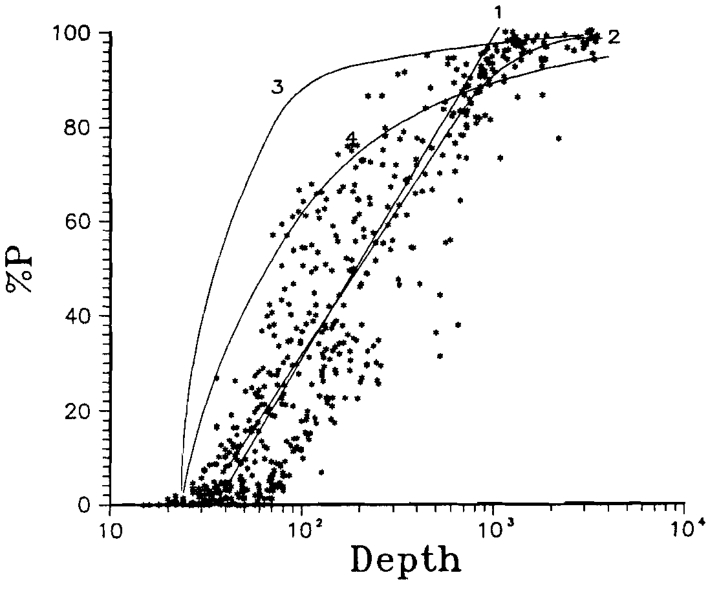


Fig. 2.17. Plot of %P versus depth from the Gulf of Mexico, the Gulf of California and the Adriatic Sea. In this plot %P versus depth regressions are indicated according to the following criteria:
(1) $D = e^{(3.58718 + (0.3534\ \%P))}$; (2) $J(d)$ equation, $k = 0.4$, $E = 4$; (3) %P according to Betzer et al. (1984); (4) %P according to Betzer et al. (1984), but using E= 4. For further explanation, see text.

Confidence limits and palaeobathymetry

In Fig. 2.18 the result of the application of the regression function of Ln(*D*) versus *%P** is depicted. It can be seen that although most of the predicted depth values are reasonably correct, still a relatively large number of predicted values deviate rather far from real values. In our view this is very likely attributable to irregularities such as resedimentation, which are still not completely eliminated. On the basis of these data we calculated the confidence limits of the palaeobathymetrical estimates according to a modification of the basic form:

$$T_\alpha \; S_e \sqrt{\frac{1}{N} + \frac{(\%P^*)^2}{(N-1)\;S_v}} \qquad (2.6)$$

where S_e = standard error, S_v = variance of *%P** and T_α = student-t statistic.

According to this model, a depth estimate of 1200 m (corresponding to about 99% *P*) would have 90% confidence limits of 860 and 1650 m. An estimate of 430m (corresponding to 50% *P*) would result in lower and upper confidence limits of 310 and 590 m respectively. The data set from the Adriatic Sea, which exhibits an extremely tight regression, demonstrates that these outcomes can be improved considerably by using well-screened material.

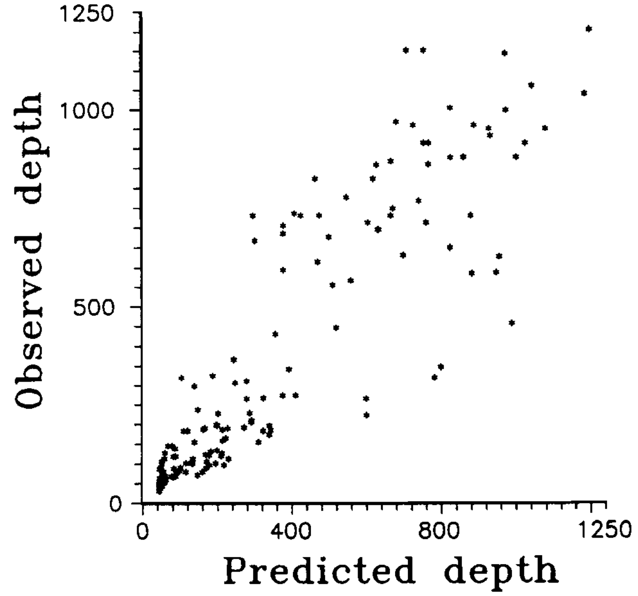


Fig. 2.18. Plot of predicted and observed depth values in the Gulf of Mexico, based on: $D = e^{(3.58718 + (0.3534 \%P))}$. Only values below 1250 m (the maximum depth estimate possible with the regression) were considered.

We chose a number of cores from the Adriatic Sea to assess the value of the present model under fossil conditions. Most of the cores penetrate the Holocene and the uppermost part of the Pleistocene; the modern water depths from which the cores were taken vary between 68 and 1234 m. Therefore, we cover a wide environmental and bathymetrical range with these cores. In Fig. 2.19 the samples are calibrated to the numerical time scale, using carbon dating as discussed by Jorissen et al. (1993). In this paper we restrict ourselves to the palaeobathymetry of the cores; biostratigraphy, lithostratigraphy and faunal contents will be discussed by Jorissen et al. (1993). In the cores a number of clearly turbiditic sediments occur; samples from these intervals were excluded from the analysis. Further, a number of sapropel levels, i.e. laminated and anoxic deposits, are present. Samples from these intervals were also excluded. All other samples were processed, although in some of them signs of possible downslope displacement or resedimentation could be observed. In Fig. 2.19 we have plotted the palaeobathymetrical estimates, together with the

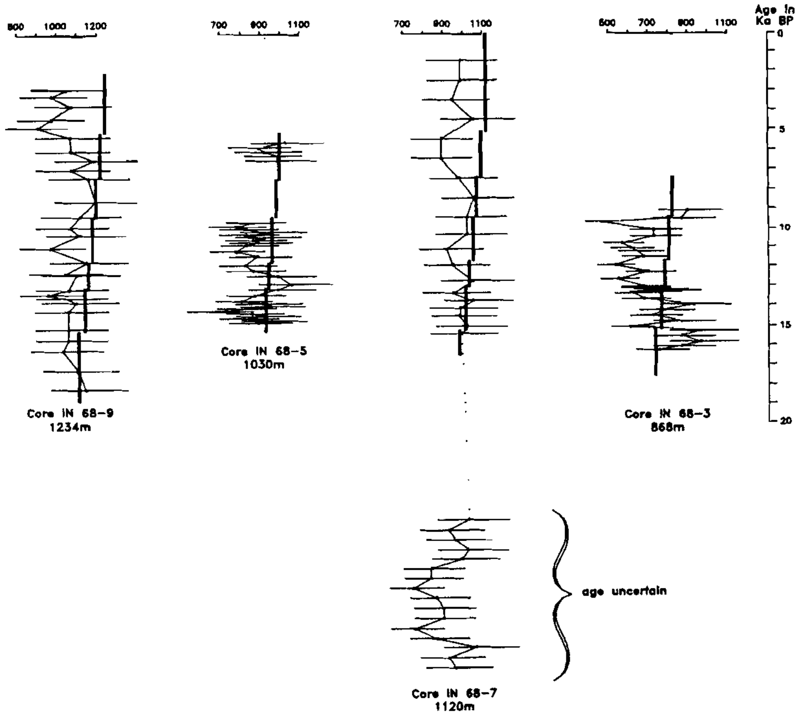
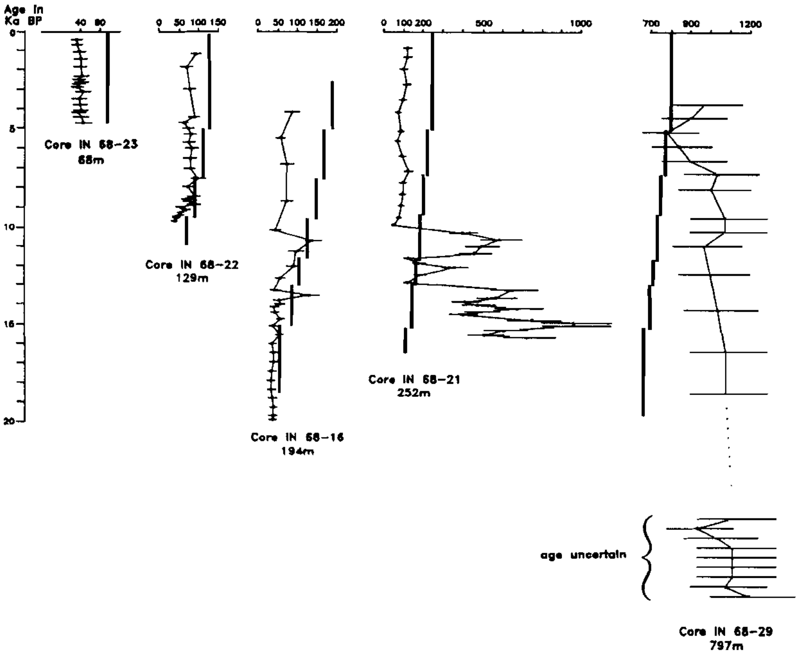


Fig. 2.19. Palaeobathymetrical estimates of samples in Adriatic Sea cores, plotted with 80% confidence limit (horizontal bar). Heavy line indicates theoretical palaeobathymetry based on modern depth minus assumed sea level lowerings due to glaciation. Ages from Jorissen et al. (1993).

confidence limits using a 80% confidence interval. We have also indicated a theoretical palaeobathymetrical estimate, based on modern water depth minus the sea level drop that presumably took place during the various stages of glaciation and deglaciation. A number of cores show good to very good palaeobathymetrical reconstructions. This is true for the whole palaeobathymetric range from 68 to 1234m. A number of intervals, however, show rather considerable deviations and a fluctuating palaeobathymetric pattern. This is true for cores 68-21 and 68-29. Judging from the ^{14}C record extensive resedimentation took place, especially in core 68-29 and in the lower part of core 68-7. Jorissen et al. (1993) concluded that the sedimentation record older than 15 ka is strongly influenced by redepositional processes. The data further suggest that cores derived from the steep margins of the southern Adriatic basin were considerably more prone to resedimentation than those from the basin floor. The resedimentation is not easily discernible from the faunal associations. Preservation is near perfect and the resedimentation did not lead to



mixing of very shallow water associations with deep water ones. This suggests that the sediment displacement took place within narrow bathymetrical limits. In core 68-21, resedimentation is probably not the cause of the deviating palaeobathymetric estimates. Here, the depth estimates are far too high in sediments older than 10 ka; yet, the ^{14}C record does not reveal extensive resedimentation. The extreme dominance of miliolids in this part of the core suggests that bottom life was impoverished, probably due to anomalous salinities in this isolated basin during the glacial lowstands.

Constraints on the model

From our data it is clear that the use of the $\%P^*$ versus depth regression is potentially useful for making palaeodepth estimates between 30 and 1250 m. In general, the regression seems to correspond to the prediction of the $J(d)$ flux model, which explains the $\%P^*$ patterns theoretically. A certain amount of our data scatter is possibly attributable to variation in k induced by variation in PP. We have seen, however, that this effect is quite limited. In general, in waters below the mixed layer, our data confirm the $J(d)$ relationship, predicting decay of organic matter inversely proportional to depth. In fact, our data conflict with the model of Betzer et al. (1984), even if higher benthos efficiencies are considered (Fig. 2.17). Our equation:

$$D = e^{(3.58718+(0.03534P^*))} \tag{2.7}$$

corresponds well to:

$$J(d) = 0.4\ PP/(D/100) \tag{2.8}$$

and a benthos efficiency factor of 4. Both the efficiency factor and k are larger than mentioned by Berger and Diester-Haass (1988). If we use $k = 0.2$, which is probably an acceptable average value, we need an efficiency factor of about 10 to approach eqn. (7) in the bathymetrical range 100-400 m (Fig. 2.17). At about 1000m deep the value $k = 0.2$ and an efficiency factor of 3 (the values estimated by Berger and Diester-Haass) seem to provide good approximations of our equation. This would suggest that the benthos efficiency decreases drastically with depth, for instance due to the gradual displacement of highly opportunistic species with a large progeny by equilibrium species with a small progeny.

The upper limit of 1200 m in our model is artificial and not predicted by the $J(d)$ flux model; this model predicts a "tail" (Fig. 2.17) which is extremely dependent on D but scarcely at all dependent on $\%P^*$. This implies that small changes in $\%P^*$, due to counting artefacts or preservation (dissolution), weigh heavily and lead to highly divergent depth estimates. Therefore, any attempt to apply the model in deeper environments would seem to be fruitless.

High abundances of infaunal elements coincide with relatively low *%P* values. That these low values are caused by relatively high standing stocks of benthic forminifera and not by dissolution is proved by the fact that in these samples the planktonic foraminiferal numbers are not significantly lower than in other samples. In this context it is worth mentioning that in anoxic or dysoxic basins often high benthic foraminiferal standing stocks are reported which are dominated by infauna (cf. Douglas and Woodruff, 1981; Phleger and Soutar, 1973; Lutze and Coulbourn, 1984; Lutze et al., 1986). Verhallen (1987) and Jorissen (1988) speculated on this matter and assumed that decreasing oxygen resulted in increasing organic matter contents and the subsequent initial increase of, in particular, the inbenthic standing stocks. This increase in standing stock is probably also related to the decrease in predation pressure. The increase continues until oxygen becomes a limiting factor, upon which the standing stock decreases dramatically. Clearly we can correct the *%P* for the initial stage, the increase in standing stock, by disregarding the infaunal elements. The second stage, where the total benthic standing stocks decrease, is far more difficult to correct for and at the moment we have no means of doing so. This would depend on detailed and precise knowledge of the relationship between standing stock and oxygen below certain critical limits. Therefore, one should avoid at this stage palaeobathymetrical estimates in anoxic or strongly dysoxic environments, which are recognizable by the accumulation of organic matter and the disappearance of burrowing organisms, and by the very typical low diversity benthic associations.

A major source of error is formed by redeposition and downslope contamination. At first sight this seems to be fairly easy to deal with. The general contention is that this contamination is readily recognizable by the occurrence of mixed associations, i.e. from shallower and deeper water, or by preservation. The sample analysis of the Adriatic Sea cores, however, proves that resedimentation is extremely difficult to trace if it occurs within a narrow bathymetrical range and if fine-grained sediments are resedimented. Only by using carbon dating, were Jorrisen et al. (1990) able to prove the enormous extent of redeposition. The effects of this redeposition on the *P*-values are not consistent: in a number of cases it causes lower *P*-values than expected at a particular depth. In core 68-29, however, a considerably higher than expected *P*-value was found.

The last source of error, for which we know of no method to correct for, is formed by differential dissolution processes. In many sediments, especially organic-rich ones, dissolution may play an important role by selective dissolution of, in particular, the juvenile planktonic foraminifera. The last forms affected by dissolution will be the benthic foraminifera, thus leading to *P*-values which are relatively too low. This probably plays a role in the Gulf of Mexico and in the Gulf of California.

Concerning the constants of the equation, there is a discrepancy between the values as found by us, by Wright (1977) and Van Marle et al. (1986). The differences between our equation and that of Wright are very small. The equation of Van Marle et al., however, is considerably different; they correctly state that oxygen could have been a limiting factor on their benthic populations, which could thus have influenced their %*P*-values. We believe that this is the case. In our study we found no reason whatsoever why the equations should be considerably different under various climatological and oceanographical regimes. In fact, our study on the Adriatic Sea cores seems to indicate that the relationship is valid provided that great care is taken in selecting the samples, i.e. by avoiding strongly oxygen-deficient areas and areas where active redeposition takes place. Our study certainly shows that these effects are probably far more important than variation in the export factor *k* coupled with variation in the primary productivity.

Conclusions

Our data indicate that ratios between planktonic and benthic foraminifera can be well described by using organic flux equations, as has already been indicated by Berger and Diester-Haass (1988). The fact that organic fluxes are inversely proportional to depth, explains why *P/B* ratios also co-vary with depth. Our material proves that disregarding infaunal living benthic foraminifera in calculating the *P/B* ratios improves the regression between *P/B* ratio and depth considerably. More importantly, however, the regressions between *P/B* ratio and depth from various areas (Gulf of Mexico, Gulf of California, west coast of the USA and the Adriatic Sea) become very similar after correction of the *P/B* ratios for inbenthic living foraminifera. The general relationship between depth and %*P* can be described according to:

$$Depth = e^{(3.58718+(0.035341\,\%P))}$$

Statistical analysis shows that the 80% confidence limits are still quite large, but can be reduced if better screened material is employed to base the regression on.

Study of material from recent environments, as well as material from piston cores from the Adriatic Sea, shows that variations in productivity and the export factor *k* have no profound effect on the relationship between depth and %*P*. The same holds for variation in temperature regime. Palaeodepth reconstructions are vulnerable, however, to variations in preservation (e.g. by dissolution) of the material. Although easily recognizable, it is not easy to correct for this in a quantitative way. The best procedure seems to neglect all samples which show signs of dissolution. The effects of redeposition, especially of fine-grained sediments, proved to be the most damaging in palaeobathymetric reconstructions, and by far the most difficult to detect.

Acknowledgements

We thank Tom van Hinte for drawing the figures and two anonymous reviewers for suggestions for improving the manuscript. This research was partly supported by grant 751.356.021 from The Netherlands Organization for Scientific Research (NWO).

CHAPTER 3

Bathymetric distribution and microhabitat partitioning of live (Rose Bengal stained) benthic foraminifera along a shelf to deep sea transect in the southern Adriatic Sea*

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Abstract Rose Bengal stained foraminifera from box cores, collected in the southern Adriatic Sea over a depth transect ranging from 146 to 1200 m water depth, have been studied. Total numbers of supposedly deposit-feeding foraminifera decrease in a fairly regular manner with increasing water depth and distance from land, probably as a consequence of a decreasing flux of organic matter. Suspension-feeding Astrorhizid taxa have an irregular distribution, apparently not related to water depth. Highest numbers of stained foraminifera are invariably found at the sediment surface, whereas numbers decrease exponentially deeper in the sediment. Most species have maximum densities near the sediment surface, but a few of the rarer species are concentrated around a level deeper in the sediment. The vertical distribution patterns of a number of common species are observed to be variable with depth along the transect, apparently determined by several different environmental parameters.

INTRODUCTION

General introduction and objectives

Fossil benthic foraminiferal assemblages in deep-sea sediment cores are widely employed to reconstruct past environmental conditions in the world's oceans. Traditionally, the bathymetric distribution of modern benthic foraminiferal species received much attention (e.g. Phleger, 1951; Parker, 1954), and the results of these studies are used for estimation of the depositional depth and environment of ancient

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* *submitted to Marine Micropaleontology*

marine sediments. More recently, these protozoan microfossils find their application also in regional and global paleoceanographic studies. The use of benthic foraminifera is especially promising in the reconstruction of paleofluxes of organic carbon in the ocean (Altenbach and Sarnthein, 1989; Herguera and Berger, 1991; Herguera, 1992), and may yield better results than paleoflux reconstructions based on the buried organic carbon content of sediments. Foraminiferal assemblages may also provide valuable information on the oxygen content of ocean bottom water masses and sediment pore water (e.g. Sen Gupta and Machain-Castillo, 1993; Loubere, 1994).

Studies on the distribution of living (Rose Bengal stained) benthic foraminifera in sediments of shallow and deep-marine environments have provided much valuable information on the ecology of this group, which is essential for the proper interpretation of fossil foraminiferal data. The observation by Corliss (1985) and many others afterwards, that benthic foraminifera occupy vertically differentiated microhabitats, has opened new perspectives to the understanding of foraminiferal ecology. The distribution of foraminiferal species with respect to potential resources, pore-water oxygen gradients, and relative to other foraminiferal species as well as other benthic biota inhabiting the sediment, provides a key to understanding the ecological characteristics of foraminiferal species.

Pore-water oxygen content probably plays an important role in determining the distribution of foraminifera in sediments of the shelf and continental slope (Corliss and Emerson, 1990; Jorissen et al, 1995). Some characteristic taxa like *Globobulimina* and *Chilostomella* are common in surface sediments of recent low-oxygen basins (e.g. Phleger and Soutar, 1973; Douglas and Heitman, 1979; Bernhard and Reimers, 1991; Sen Gupta and Machain-Castillo, 1993) but live at several centimetres depth in the oxygen depleted subsurface layer in open oceanic environments (Corliss, 1985; Corliss, 1991; Rathburn and Corliss, 1994), indicating the close association of these taxa with low oxygen (micro)environments. Barmawidjaja et al. (1992) observed seasonal changes in the vertical distribution of foraminifera in sediments from the northern Adriatic Sea, associated with seasonally varying bottom-water oxygenation. Vertical migration of benthic foraminifera in response to bottom water and pore-water oxygen variation has been experimentally confirmed by Alve and Bernhard (1995).

Food availability is probably a limiting factor on the vertical distribution of foraminifera in lower slope and abyssal plain environments (Gooday, 1986; Corliss and Emerson, 1991; Jorissen et al., 1995). Organic detritus and associated bacteria are thought to be important food types of deep-sea foraminifera (Lipps, 1983); evidence for ingestion of such material has been reported by Goldstein and Corliss, 1994. Seasonal falls of phytodetritus have been recognized as an important food source for opportunistic epifaunal foraminifera in the deep sea, such as *Epistominella exigua* (Gooday, 1988; Gooday, 1993). Other deep-sea species have been found clinging to elevated objects on top of the sediment, and are supposed to be suspension feeders (Altenbach and Sarnthein, 1989; Linke and Lutze, 1993). Some arenaceous taxa gain access to suspended food sources above the sediment water interface by constructing large tubular and arborescent tests extending above the sediment surface (DeLaca et al, 1981; Jones and Charnock, 1985). Further, the abundance of infaunal foraminifera relative to epifaunal forms has been suggested to be strongly linked with the organic carbon flux to the seafloor, and the availability of nutritive organic matter below the sediment surface (Corliss and Chen, 1988). Biotic interactions, such as active predation or passive ingestion of foraminifera by macro- and meiofaunal organisms, and competition for food between foraminifera and other organisms, or between different species of foraminifera, are thought to play an important role as well in determining microhabitat differentiation (Gooday, 1986).

The discovery of microhabitat partitioning among deep-sea foraminifera has been important in the interpretation of carbon stable isotope records in benthic foraminifera. Whereas the tests of epifaunal species like *Cibicidoides wuellerstorfi* are found to be in near $\delta^{13}C$ equilibrium with the Σ CO_2 of the ambient bottom-water mass (Woodruff et al., 1980), much 'lighter', deviating $\delta^{13}C$ values observed in infaunal species like *Uvigerina peregrina*, *Melonis barleeanum* and *Globobulimina affinis* are thought to reflect the isotopic composition of the sediment pore-water, which is enriched in ^{12}C by decomposition of isotopically light organic matter (Grossman, 1984b; Berger and Vincent, 1986; McCorkle et al., 1990).

In this study we will examine the living (Rose Bengal stained) benthic foraminiferal fauna present in 8 box cores collected along a bathymetric transect in the southern Adriatic Sea. The objectives of this study are to determine total standing stocks of foraminifera, composition of foraminiferal assemblages, vertical distribution of foraminiferal populations within the sediment, and microhabitat characteristics of common foraminiferal species, and to describe their variation along the transect, in relation to environmental gradients present along the transect. The resulting data on the present-day distribution and ecological characteristics of some common Mediterranean species are in the first place valuable for a better interpretation of fossil foraminiferal records from the Mediterranean area, but will hopefully also add to the knowledge of the ecology of benthic foraminifera in general. Some of the data on the distribution of total foraminiferal populations in the sediment were discussed earlier by Jorissen et al. (1995).

Study area

The Adriatic Sea is a land-locked marginal basin of the Eastern Mediterranean Sea, projecting in NW to SE direction between the landmasses of Italy and the Balkan states. The northern part of the Adriatic Sea is relatively shallow, gradually deepening southward till about 100 m, then deepening more abruptly till a maximum of 280 m, then shallowing again over the Palagruža Sill, which separates the northern from the southern part. The southern Adriatic Sea has at its centre a deep basin of more than 1200 m depth, bounded by steep slopes and relatively broad shelves. The bottom of the southern basin rises to 780 m in the Otranto Strait, where the Adriatic opens to the Ionian Sea.

The Adriatic Sea has since long received attention for its role in the formation of Eastern Mediterranean Deep Water (e.g. Pollak, 1951; Zore-Armanda, 1963). More recent studies on the circulation in the Adriatic Sea have been published by Sturm et al. (1992), Orlić et al. (1992), Artegiani et al. (1993). The North Adriatic is strongly influenced by the inflow of fresh water, of which the Po river is the major source. During periods of high runoff and stratification of the water column in summer, low-saline water derived from the Po discharge area may spread out over the entire Adriatic Sea. In winter, the low-saline water is flowing southward in a narrow band mostly confined to the Italian coast. Episodic cold winds blowing in winter from a northeasterly direction over the shallow northern Adriatic Sea cause cooling of the surface water, with formation of dense North Adriatic Water (NAW, Temperature 11°C, Salinity 38.5‰). This NAW flows southward along the Italian shelf. Part of the NAW is thought to mix with Mediterranean water masses present at surface and intermediate depth in the southern Adriatic basin, producing South Adriatic Water (SAW, Temperature 13°C, Salinity 38.6‰). SAW may also be formed by strong cooling in the centre of the Southern Adriatic Sea during winter. SAW fills the bottom of the deep southern Adriatic basin, and flows out along the southwestern basin slope and via Otranto Strait into the Ionian Basin. SAW is thought to be the main contributor to Eastern Mediterranean Bottom Water. Mediterranean water masses flow into the southern Adriatic basin along the northeastern side of the Otranto Strait. Because of the strong vertical buoyancy fluxes in the Adriatic Sea, the vertical differences in temperature and salinity below the pycno-cline are relatively low, maximally about 1°C and 0.5‰, respectively.

The southern Adriatic Basin is well-ventilated, with high concentrations of dissolved oxygen over the entire water column (Orlić et al., 1992). Pollak (1951) reported values of around 5 ml l^{-1} in the Otranto Strait, with minima of slightly less than 4 ml l^{-1} at 200 m depth. The northern Adriatic Sea, by contrast, is affected by strong seasonal dysoxia in the bottom water, caused by the rapid accumulation of organic detritus following seasonal algal blooms, in combination with restricted bottom-water ventilation during the summer months (Justić, 1987; Barmawidjaja et al., 1992).

The Eastern Mediterranean in general is characterized by extremely low surface water primary productivity. The value of 20.3 g C m^{-2} yr^{-1} given by Dugdale and Wilkerson (1988) is even lower than the 25-30 g C m^{-2} yr^{-1} found in the oligotrophic centres of open oceanic gyres (Berger et al., 1987). In the northern Adriatic Sea, primary production has been observed to range from 55 g C m^{-2} yr^{-1} in the eastern part of the basin, up to 120 g C m^{-2} yr^{-1} in the western part near the Po delta (Kveder et al., 1971; reference in Justić, 1987). Primary production in the southern Adriatic Sea is probably lower than in the northern Adriatic Sea, but higher than in the eastern Mediterranean Sea, implying a range of about 20-50 g C m^{-2} yr^{-1} . The northern Adriatic Sea has a particularly high productivity, mainly fed by nutrients supplied by discharge from the Po river. The increasing load of anthropogenic nutrients originating in the densely populated lower course of the Po river has resulted in an increasing coastal eutrophication in the Po delta area and beyond (Revelante and Gilmartin, 1976; Degobbis et al., 1979; Justić, 1987). An anticlockwise circulation transports nutrient-rich surface waters from the Po river discharge area further southeastward along the Italian coast. As a result a fertility gradient exists in the Adriatic Sea, with fertility decreasing in a north-south direction, but also decreasing from the Italian coast offshore towards the central and eastern side of the basin (Revelante and Gilmartin, 1977). Such a gradient becomes also apparent from satellite images of surface-water chlorophyll concentrations (Sturm et al., 1992).

Benthic foraminiferal assemblages (>150 μm) in surface sediments of the Adriatic Sea have been described by Jorissen (1988). This author found a closely spaced succession of bathymetric assemblages in the shallow coastal waters of the Italian shelf, and a more uniform assemblage in deeper water of the southern Adriatic Sea. Bathymetric variation in planktonic/benthic foraminiferal ratios in the Adriatic Sea was investigated by Van der Zwaan et al. (1990). Barmawidjaja (1991), Barmawidjaja et al. (1992) and Jorissen et al. (1992) studied the distribution of Rose Bengal stained foraminifera in sediments of the northern Adriatic Sea, in relation to the seasonal cycle in productivity and bottom-water oxygenation. As mentioned earlier, seasonal changes in the vertical distribution of foraminifera were observed, in response to the seasonally varying bottom-water oxygenation.

MATERIALS AND METHODS

In March 1991 piston cores and box cores were collected of sediments from the shelf, slope and deep basin of the southern Adriatic Sea, by a research team of the University of Bologna and the Marine Geological Institute of the Italian National Research Council of Bologna, on board of the R.V. "Minerva" (Biasini et al., 1990). The present investigation is based on material from 8 box cores, recovered during this cruise along a bathymetric transect in the southern Adriatic Sea (Fig. 3.1, Table 3.1). Box core AD91/32 was collected from the shelf at approximately 40 km distance from the Italian coast, at a waterdepth of 146 m. Cores AD91/30, 29, 28, 27, 26, 25, in order of increasing depth and distance to shore, were recovered from the basin slope. Box core AD91/01 was recovered from the centre of the southern Adriatic basin, at 1200 m depth and a minimum distance to shore of approximately 110 km. The average bottom inclination along the transect is less than 0.5° both on the shelf and in the central basin, and 1° and locally up to 3° on the slope.

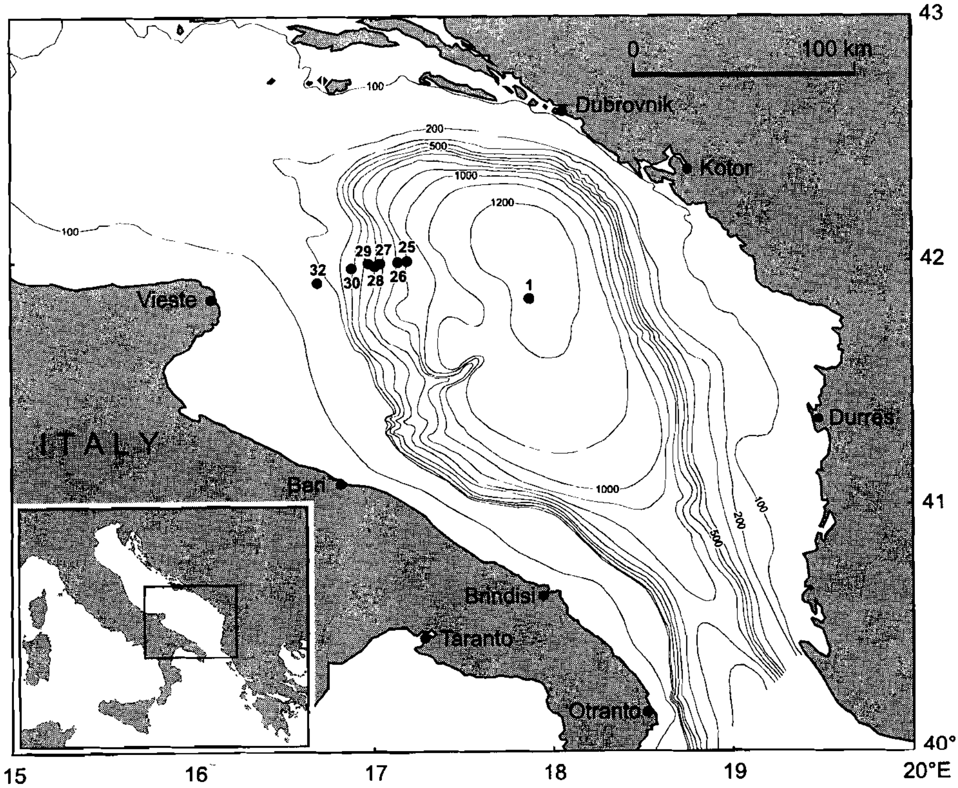


Fig. 3.1. Bathymetric map of the South Adriatic Basin, with location of box core stations.

The top of the sediment seemed intact in all box cores, but a semi-fluid layer of suspended material on top of the sediment was lost when the box core casing was removed. The sediments consist of vaguely stratified silty clay, at station 32 on the shelf admixed with sand and shell-debris. The upper centimetres of the sediment are oxidized and have a brown to yellowish-brown colour, grading into grayish or brownish olive, reduced sediments deeper down. Based on a rather arbitrary appreciation of sediment colour, the thickness of the oxidized layer seems to increase with increasing waterdepth, from 4 cm on the shelf, to about 20 cm in the deep part of the basin.

For the study of living benthic foraminifera, subsamples were collected from the uppermost 5 to 10 cm of the box cores, at vertical intervals of 0.5 or 1.0 cm. The surface area of the samples varied between 20 and 42 cm^2. The subsamples were stored in plastic vials and ethanol with Rose Bengal (1 to 2 gr/l) was added.

Table 3.1. Geographical position and water depth of the box core stations, sediment characteristics, and surface area and vertical interval of subsamples.

core	latitude (N)	longitude (E)	depth (m)	sediment type	subsample area (cm2)	subsample interval (cm)
AD91-32	41°54.80	16°41.75	146	sandy mud	32	0-0.5, 0.5-1, 1-1.5, 1.5-2, 2-3, 3-4, 4-5, 5-6
-30	41°59.00	16°55.50	398	silty clay	20	0-0.5, 0.5-1, 1-2, 2-3, 3-4, 4-5
-29	41°59.50	16°58.75	487	silty clay	28	0-0.5, 0.5-1, 1-1.5, 1.5-2, 2-3, 3-4, 4-5, 5-6, 6-7, 7-8, 8-9, 9-10
-28	41°59.00	17°01.00	578	silty clay	30	0-1, 1-2, 2-3, 3-4, 4-5, 5-6
-27	41°59.50	17°02.75	664	silty clay	42	0-0.5, 0.5-1, 1-1.5, 1.5-2 2-3, 3-4, 4-5, 5-6, 6-7, 7-8, 8-9, 9-10
-26	41°59.80	17°08.70	794	silty clay	25	0-1, 1-2, 2-3, 3-4, 4-5, 5-6
-25	42°00.00	17°11.75	898	silty clay	33	0-0.5, 0.5-1, 1-1.5, 1.5-2, 2-3, 3-4, 4-5, 5-6, 6-7, 7-8, 8-9, 9-10
-01	41°50.84	17°52.48	1200	silty clay	20	0-0.5, 0.5-1, 1-1.5, 1.5-2 2-3, 3-4, 4-5, 5-6, 6-7, 7-8, 8-9, 9-10

In the laboratory the sediment was freeze-dried, weighed dry, and subsequently sieved over 63 μm, 150 μm and 595 μm sieves. Stained foraminifera were wet-picked from a gridded tray from the 63-150 μm and 150-595 μm fractions, and sorted in micropaleontological slides. The original counting lists are included in Appendix A. Unless stated otherwise, all observations refer to the total 63-595 μm fraction. All specimens containing distinct clots of stain were sorted out, but only the well-stained specimens were subsequently counted, whereas unconvincingly stained specimens were neglected. Specimens were considered well-stained if more than half of the chambers, usually starting from the earliest chambers of the test, were filled with bright red to violet stain. Specimens with only a superficial pink hue, or with red specks on the outside, or with only a few chambers filled with dark red clots, or those which were obviously inhabited by nematode worms and commonly displaying bore holes, were not counted.

Foraminifera with an opaque agglutinated or imperforate calcitic test wall were occasionally broken with a dissection needle, if there was doubt whether the interior contained stained protoplasm.

Stained planktonic foraminifera were commonly found in the upper 1 or 2 cm in most box cores, usually displaying one or more bore holes, sometimes with agglutinated tubes extruding from these holes. We think that the stained material in these planktonic foraminiferal tests does not represent the original planktonic organism, but an intruding benthic organism, possibly similar to the *Globigerina*-inhabiting foraminifera described from the northeast Atlantic by Gooday (1986). We did not systematically quantify these forms, or soft-walled or tunneling Allogromiids encountered in some samples, since reliable quantification was not feasible.

Fragments of Astrorhizidae were common in the surface samples of most box cores. These delicate, arborescent foraminifera were fragmented during washing and sieving of the material. As the numerous fragments may represent only a small number of intact individuals, we treated Astrorhizidae separately from the other foraminiferal groups. However, the number of fragments can give a rough impression of the biomass proportion of Astrorhizidae versus that of other foraminifera.

RESULTS

Bathymetric distribution: standing stocks and species zonation

The total abundance of stained benthic foraminifera per sediment area, excluding Astrorhizid fragments, decreases sharply with increasing waterdepth, from nearly 80 individuals per cm^2 on the shelf, to less than 3 per cm^2 in the deep basin (Fig. 3.2). The low number of stained foraminifera found in core 27 deviates from this regular pattern.

The distribution of Astrorhizid fragments (Fig. 3.2) is highly irregular, contrasting with the pattern observed for the other foraminifera. The abundance of fragments is low on the shelf (core 32), then increases to reach a maximum on the basin slope, then decreases again towards the centre of the basin. Also for this group, the abundance is conspicuously low in core 27.

Along the transect no large variation is found in the relative abundance of arenaceous, calcareous perforate and calcareous imperforate foraminifera (excluding Astrorhizids, see Fig. 3.2). The first two groups make up more than 90% of the faunas, with calcareous perforate foraminifera being slightly more abundant in the cores from the shelf and from the basin centre, and arenaceous foraminifera being more abundant in the cores from the slope. Imperforates constitute only a minor part of the stained faunas.

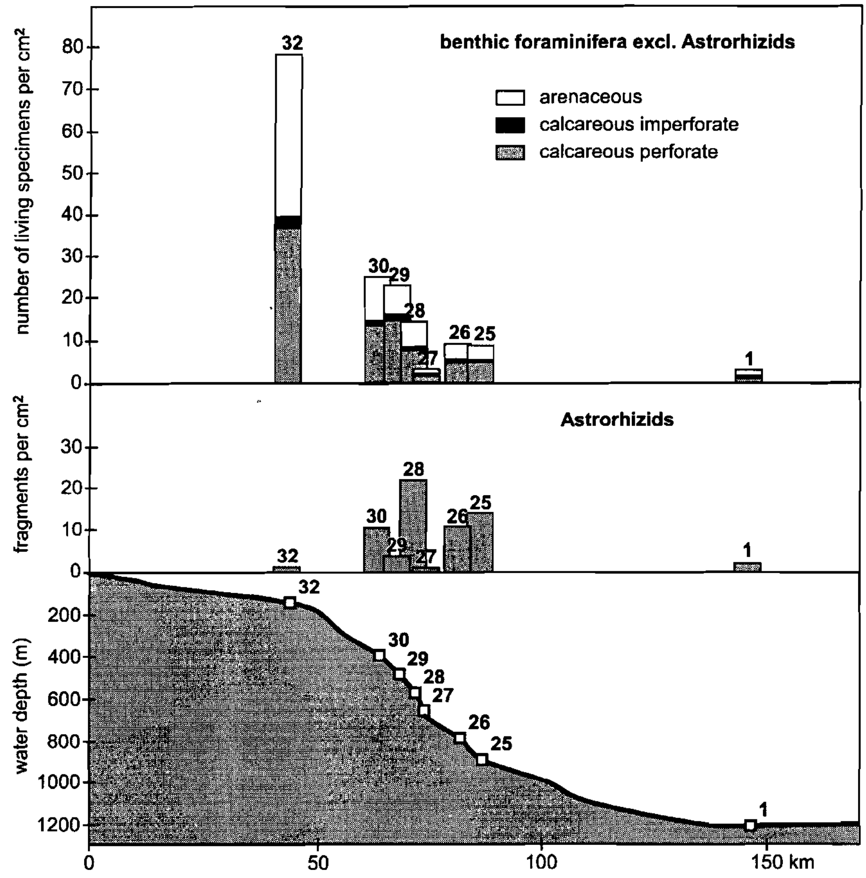


Fig. 3.2. Standing stocks of benthic foraminifera along the studied transect, Astrorhizids not included (upper panel), and abundance of stained Astrorhizid fragments (middle panel). The lower panel shows the position of the box-core stations along the bathymetric gradient.

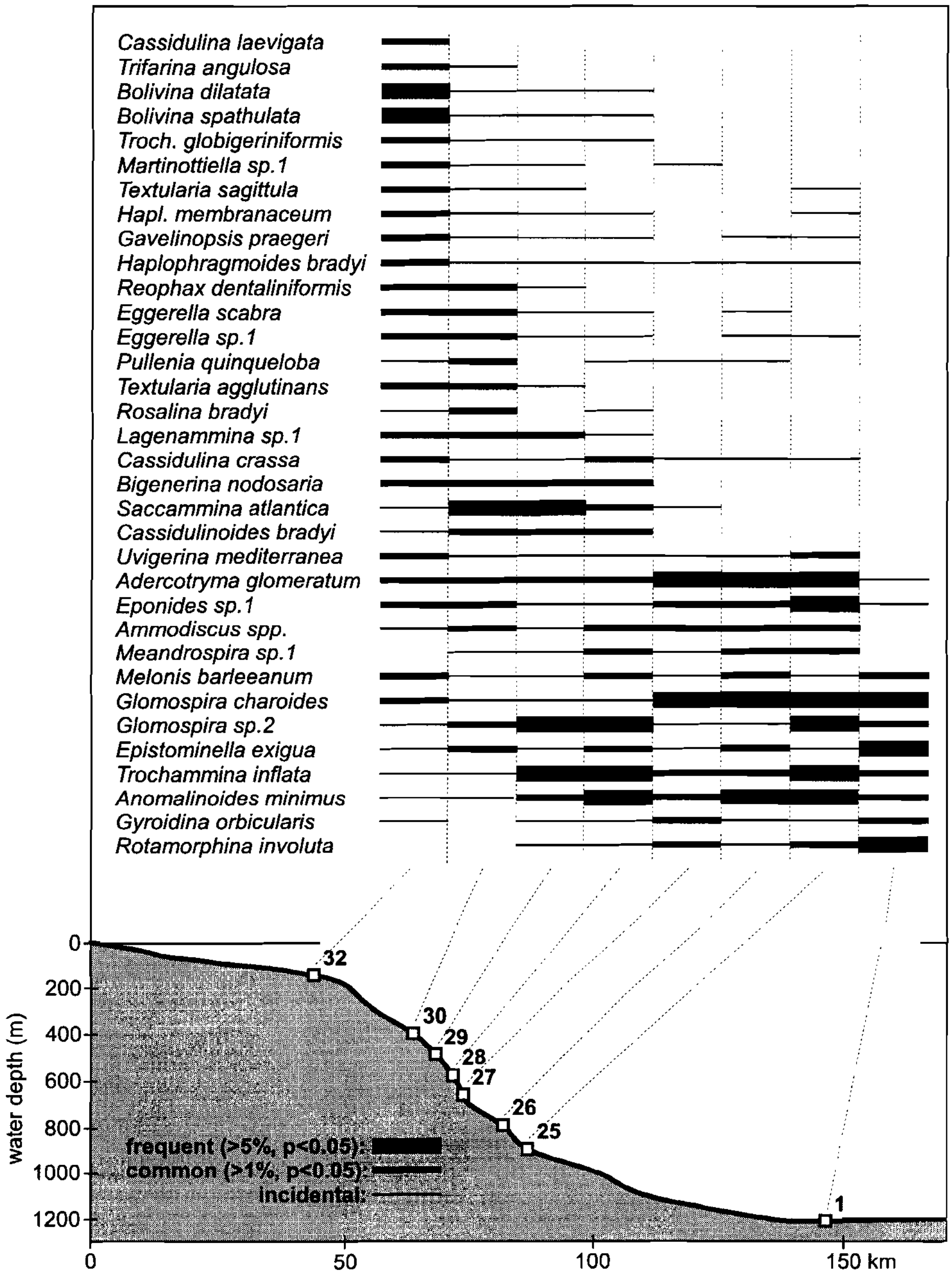


Fig. 3.3. Bathymetric distribution of common species of benthic foraminifera.

The average size of foraminifera is larger in the shelf and upper slope cores than in cores from the lower shelf and central basin. Foraminifera in the 150-595 µm sieve fraction constitute between 20 and 25% of the total (63-595 µm) population in cores 32, 30 and 29, and between 10 and 15% in all deeper cores.

From the over 150 different species encountered in the box cores, only 34 are significantly more abundant than 1% in one or more of the box cores. The bathymetric distribution of these common species is summarized in Fig. 3.3. Illustrations of common species are given in Plates 3.1 to 3.3. Due to the large difference in total numbers of foraminifera encountered in the various stations, ranging one order of magnitude from the shallowest to the deepest station, the number of common species is much larger for the shallower than for the deep stations. However, part of the observed decrease in the number of common species seems to be real, and is due to the successive disappearance of species with increasing depth, with only a few widely distributed species remaining, and few new species being added.

Characteristic shelf species are, in order of decreasing frequency, *Bolivina spathulata*, *Bolivina dilatata*, *Haplophragmoides membranaceum*, *Trochammina globigeriniformis*, *Textularia sagittula*, *Haplophragmoides bradyi*, *Cassidulina laevigata*, *Martinottiella* sp.1., *Gavelinopsis praegeri* and *Trifarina angulosa*. These species are common only in core 32, although most of them are found in low numbers in deeper water as well. *Textularia agglutinans*, *Eggerella scabra*, *Reophax dentaliniformis* and *Eggerella* sp.1 are common in cores 32 and 30 from the shelf and the uppermost slope, whereas *Rosalina bradyi* and *Pullenia quinqueloba* are typical for the uppermost slope only. The species *Saccammina atlantica*, *Bigenerina nodosaria*, *Cassidulinoides bradyi* and *Lagenammina* sp.1 have a bathymetric range from shelf/upper slope to middle slope depth. Remarkably broad bathymetric ranges, spanning most of the studied bathymetric interval, are observed in the species *Adercotryma glomeratum*, *Glomospira charoides*, *Melonis barleeanum*, *Glomospira* sp.2, *Eponides* sp.1, *Uvigerina mediterranea*, *Epistominella exigua* and *Ammodiscus* spp.. Characteristic species of deeper water are *Anomalinoides minimus* and *Trochammina inflata*, which are common from station 29 downward, *Meandrospira* sp.1, from station 28 downward, and *Rotamorphina involuta* and *Gyroidina orbicularis*, which are common on the lower slope and the basin centre.

Plates 3.1, 3.2, 3.3 >>> See captions on page 53.

PLATE 3.1

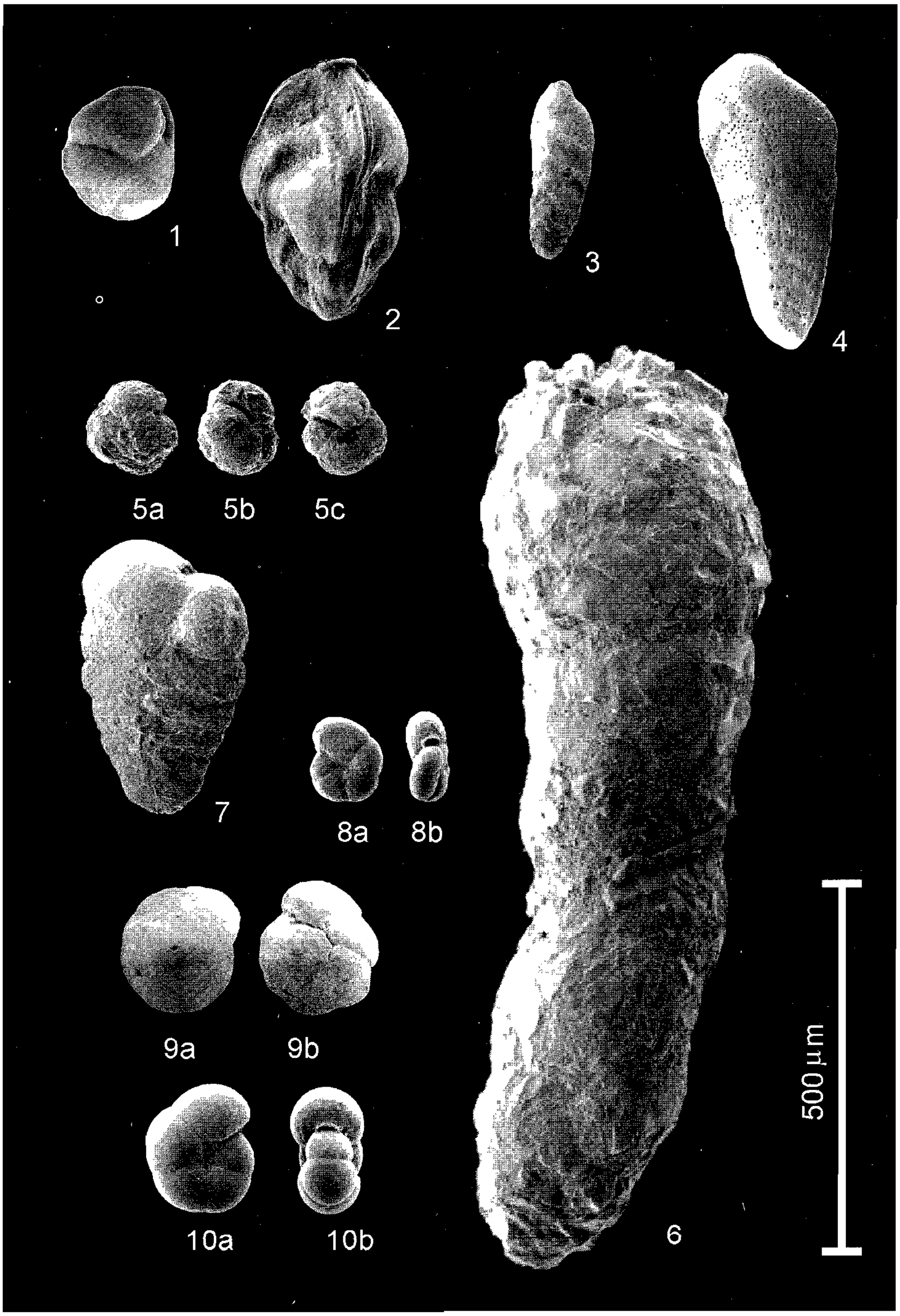


PLATE 3.2

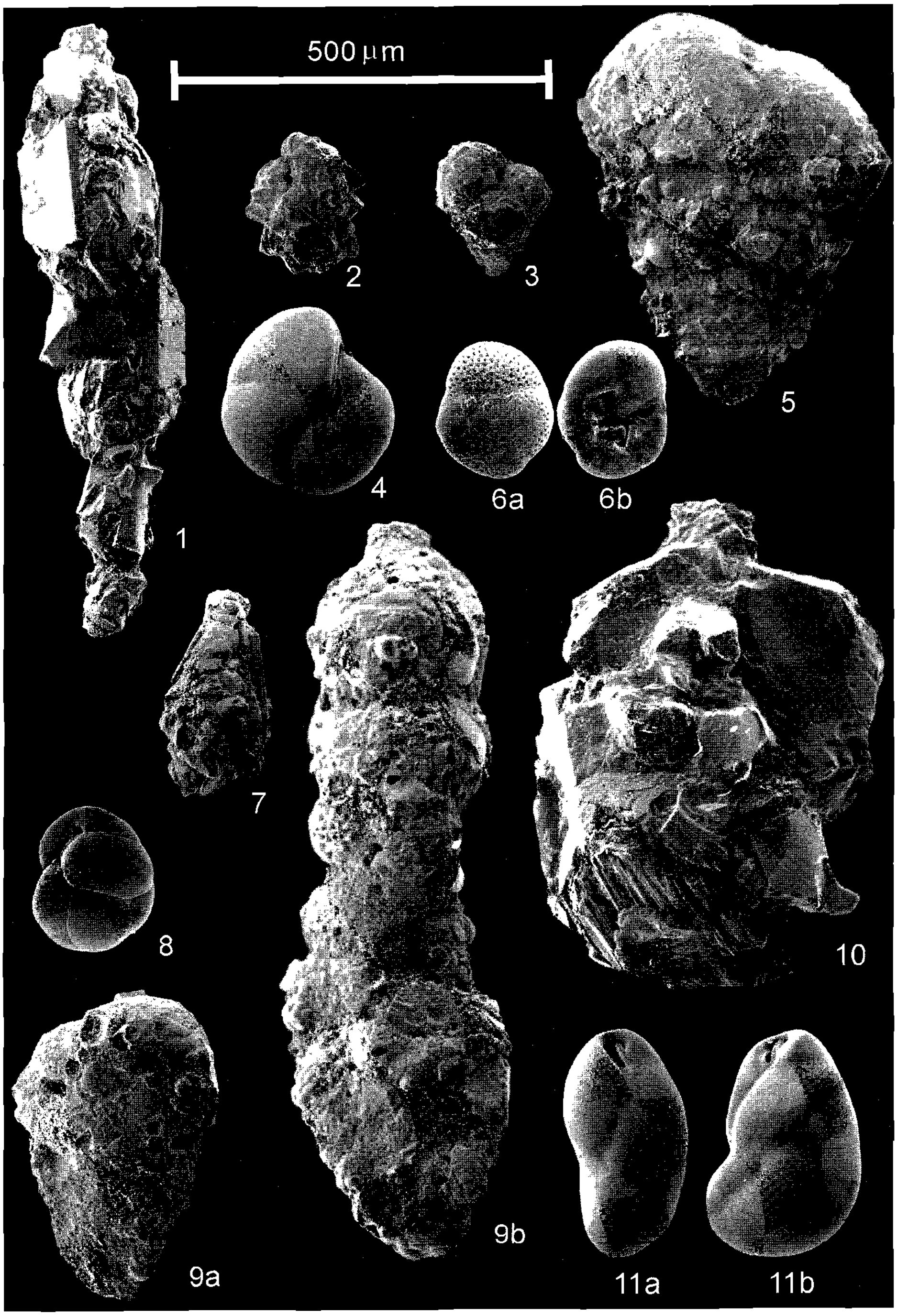
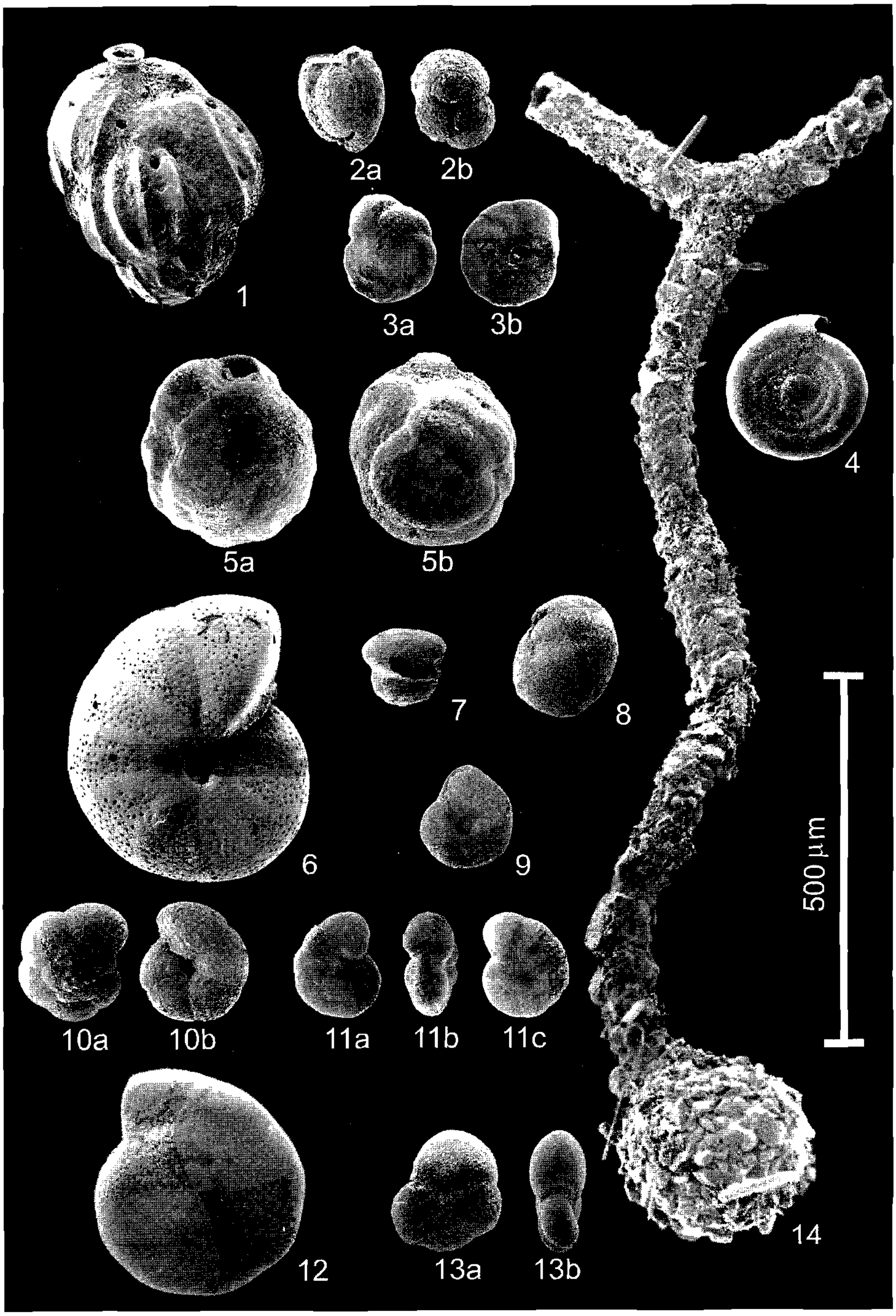


PLATE 3.3



Plates 3.1, 3.2, 3.3
SEM micrographs of common benthic foraminifera of the southern Adriatic Sea. The depicted specimens were collected from the surface layer (0-0.5 cm) of box core AD91-32, unless otherwise stated. All specimens are depicted at 100x natural size, see also scale bar.

<<< Plate 3.1
Shelf species. 1: *Cassidulina laevigata*, side view; 2: *Trifarina angulosa*, side view; 3: *Bolivina dilatata*, side view; 4: *Bolivina spathulata*, side view; 5: *Trochammina globigeriniformis*, a: dorsal, b: apertural view, c: ventral; 6: *Martinottiella* sp.1., side view; 7: *Textularia sagittula*, side view; 8: *Haplophragmoides membranaceum*, a: side view, b: apertural view; 9: *Gavelinopsis praegeri*, a: dorsal, b: ventral (core 29, 0-0.5 cm); 10: *Haplophragmoides bradyi*, a: side view, b: apertural view.

<< Plate 3.2
Shelf and upper slope species. 1: *Reophax dentaliniformis*, side view; 2: *Eggerella scabra*, side view (core 29, 0-0.5 cm); 3: *Eggerella* sp.1, side view; 4: *Pullenia quinqueloba*, side view; 5: *Textularia agglutinans*, side view; 6: *Rosalina bradyi*, a: dorsal, b: ventral; 7: *Lagenammina fusiformis*, side view; 8: *Cassidulina crassa*, side view; 9: *Bigenerina nodosaria*, a: biserial stage, b: full-grown specimen; 10: *Saccammina atlantica*, side view; 11: *Cassidulinoides bradyi*, a: apertural view, b: ventral (core 29, 3-4 cm).

< Plate 3.3
Shelf and slope species. 1: *Uvigerina mediterranea*, side view; 2: *Adercotryma glomeratum*, a: apertural view, b: side view; 3: *Eponides* sp.1, a: dorsal, b: ventral (core 25, 0-0.5 cm); 4: *Ammodiscus* sp., side view (core 29, 0-0.5 cm); 5: *Meandrospira* sp.1, a: apertural view, b: dorsal (core 29, 0-0.5 cm); 6: *Melonis barleeanum*, side view; 7: *Glomospira charoides*, side view; 8: *Glomospira* sp.2, side view; 9: *Epistominella exigua*, ventral (core 25, 0-0.5 cm); 10: *Trochammina inflata*, a: dorsal, b: ventral (core 29, 0-0.5 cm); 11: *Anomalinoides minimus*, a: dorsal, b: apertural view, c: ventral (core 25, 0-0.5 cm); 12: *Gyroidina orbicularis*, dorsal (core 29, 0-0.5 cm); 13: *Rotamorphina involuta*, a: side view, b: apertural view (core 25, 0-0.5 cm); 14: Astrorhizid foraminifer: *Saccorhiza ramosa*, side view (core 25, 0-0.5 cm).

Vertical distribution in the sediment:
standing stocks and microhabitat characteristics of species

In all cores, the majority of stained foraminifera is found in the upper few centimetres of the sediment, and numbers decline exponentially deeper into the sediment (Fig. 3.4). Only a small proportion of the population is found below 5 cm depth in the more extensively subsampled box cores: 0% in core 1, less than 5% in cores 32, 29, 27, but possibly more than 10% in core 25. Data from the upper 5 cm are used here to illustrate the variation along the transect in the vertical distribution of stained foraminifera. More than half of the total foraminiferal population of the 0-5 cm interval inhabit the upper 1 cm of the sediment (Fig. 3.5). The percentage of fauna inhabiting the top centimetre is highest at the two extremes of the transect: 64% in core 32 and 76% in core 1. The lowest percentage is found at mid-slope depth: 56% in core 28. The latter core is marked by the highest relative abundance of fauna in the 4-5 cm interval: 7%, compared to an average of 3% in the other cores. Cores 25 and 1 present the greatest contrast between adjacent stations in vertical distribution of fauna; whereas in core 25 about 5% of the 0-5 cm population is found below 4 cm, and possibly more than 10% (relative to the 0-5 cm fauna) below 5 cm, no living foraminifera were found below 4 cm in core 1.

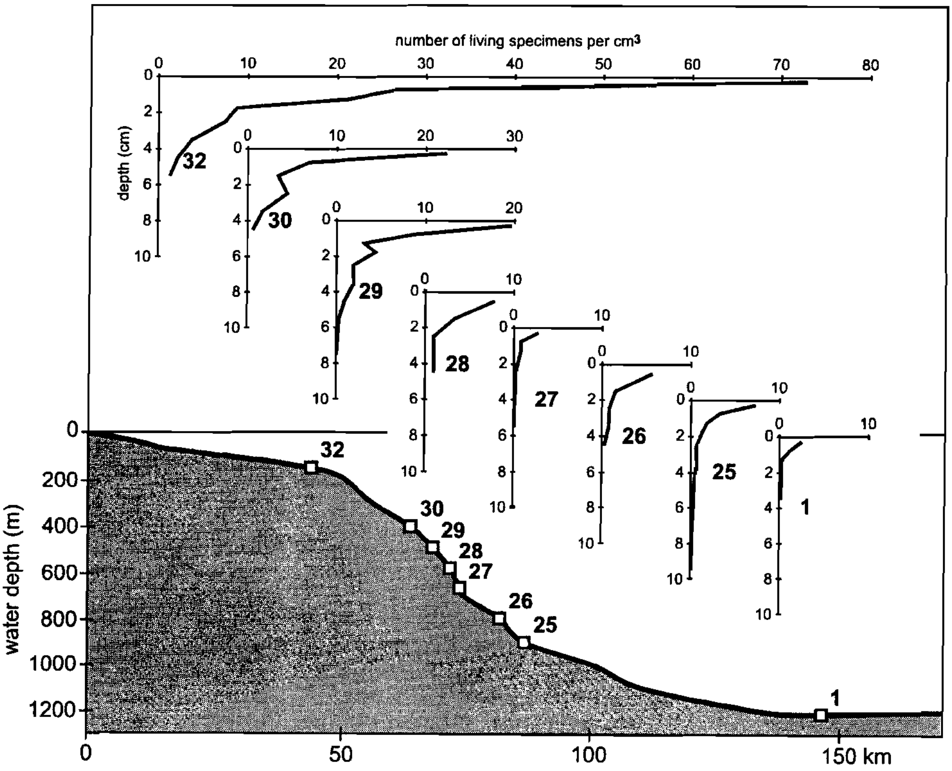


Fig. 3.4. Vertical distribution of stained foraminifera in the sediment. Astrorhizids not included.

The distribution in the sediment of common species listed in Fig. 3.3 is illustrated in Fig. 3.6. For completeness, incidental occurrences are also included in this Figure. Whereas total numbers decrease more or less regularly down into the sediment, individual species may have a very different distributional pattern. Most of the common species are maximally abundant at the top of the sediment, decreasing rapidly (e.g. *Trochammina globigeriniformis*, *Cassidulina laevigata*, and *Uvigerina mediterranea*) or more gradually (e.g. *Bolivina spathulata*, *Bolivina dilatata*, *Bigenerina nodosaria*, *Textularia agglutinans*) in abundance downcore. None of these species, however, fulfills the criterion to be considered as epifauna in a strict sense, i.e. that no live specimens are found below the uppermost sediment layer (Jorissen et al., 1995). A number of species have maximum numbers in both the uppermost sampling interval and the interval below this (e.g. in core 32 *Haplophragmoides bradyi*, *H. membranaceum* and *Reophax dentaliniformis*. This pattern probably reflects a very shallow infaunal microhabitat near the base of the topmost interval

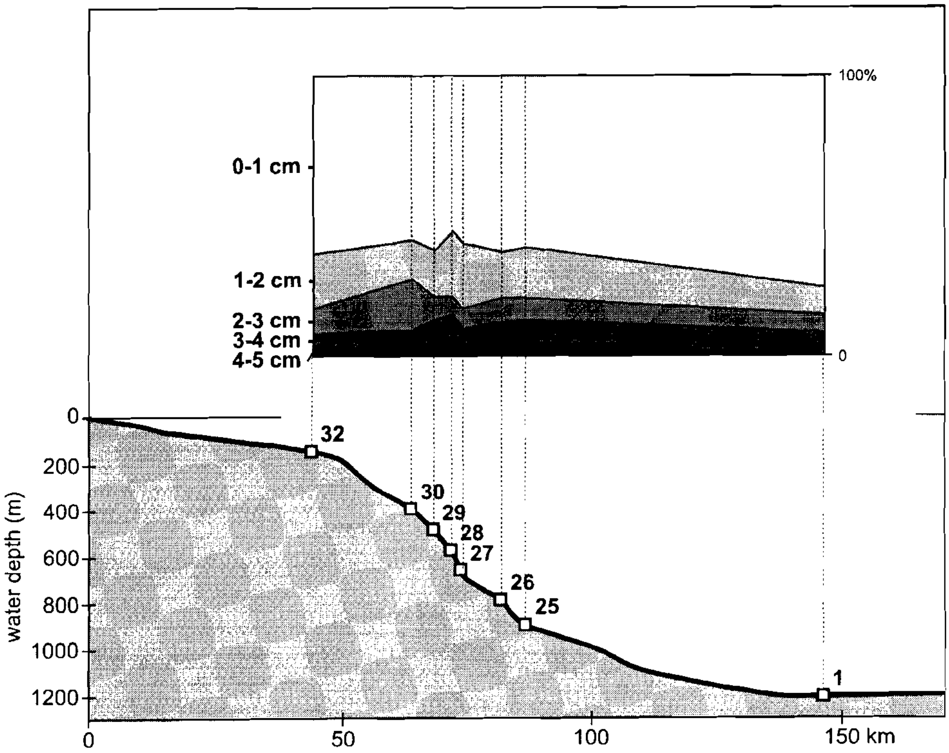


Fig. 3.5. Variation along the transect in the relative abundance of foraminifera inhabiting successive depth intervals in the sediment.

(0.5 cm). Some other species, on the other hand, show a distinct maximum below the surface sediment layer, and can be counted as true infauna. Although there is a large overlap in the distribution of these infaunal taxa, their respective abundance maxima apparently occur at different horizons in the sediment (e.g. in station 32 *Adercotryma glomeratum*: 0.5-1 cm; *Melonis barleeanum*: around 1 cm; *Glomospira charoides*: 1-1.5 cm; *Martinottiella* sp.: around 2 cm; *Cassidulinoides bradyi*: 1-4 cm).

Whereas common species like *Epistominella exigua* and *Trochammina inflata* occupy essentially a similar near-surface microhabitat in all cores, specific distribution patterns seem to change along the transect for some other species. For example the infaunal species *Cassidulinoides bradyi* shifts from a shallow to a deeper infaunal position with increasing water depth. A similar increasing microhabitat is found for *Bigenerina nodosaria* and *Eponides* sp.1, which on the shelf and upper slope (cores 32 and 30), occur in greatest abundance at the sediment surface, but which in deeper waters of the middle and lower slope and in the deep central basin tend to occupy a

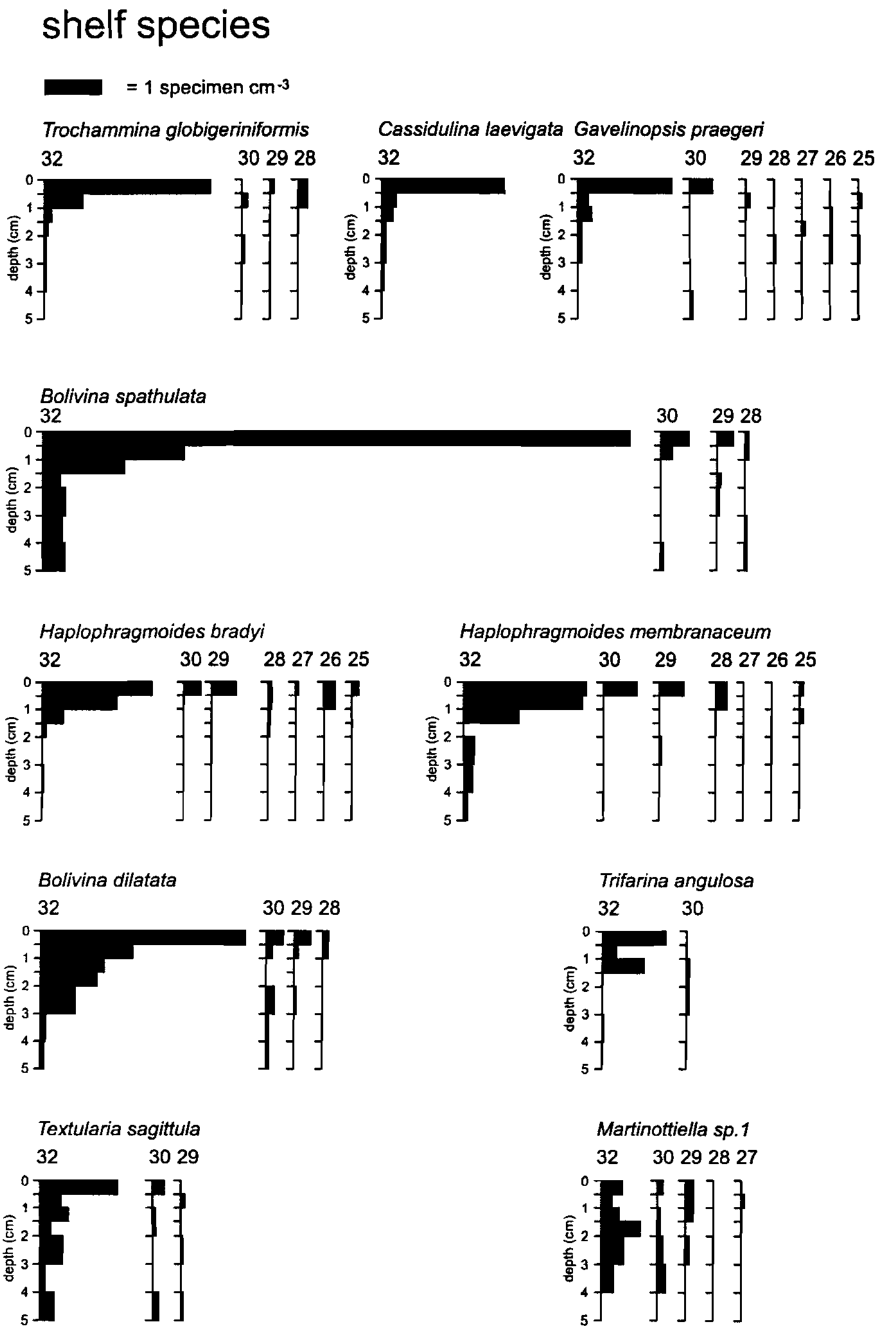


Fig. 3.6. Vertical distribution of common species in the sediment.

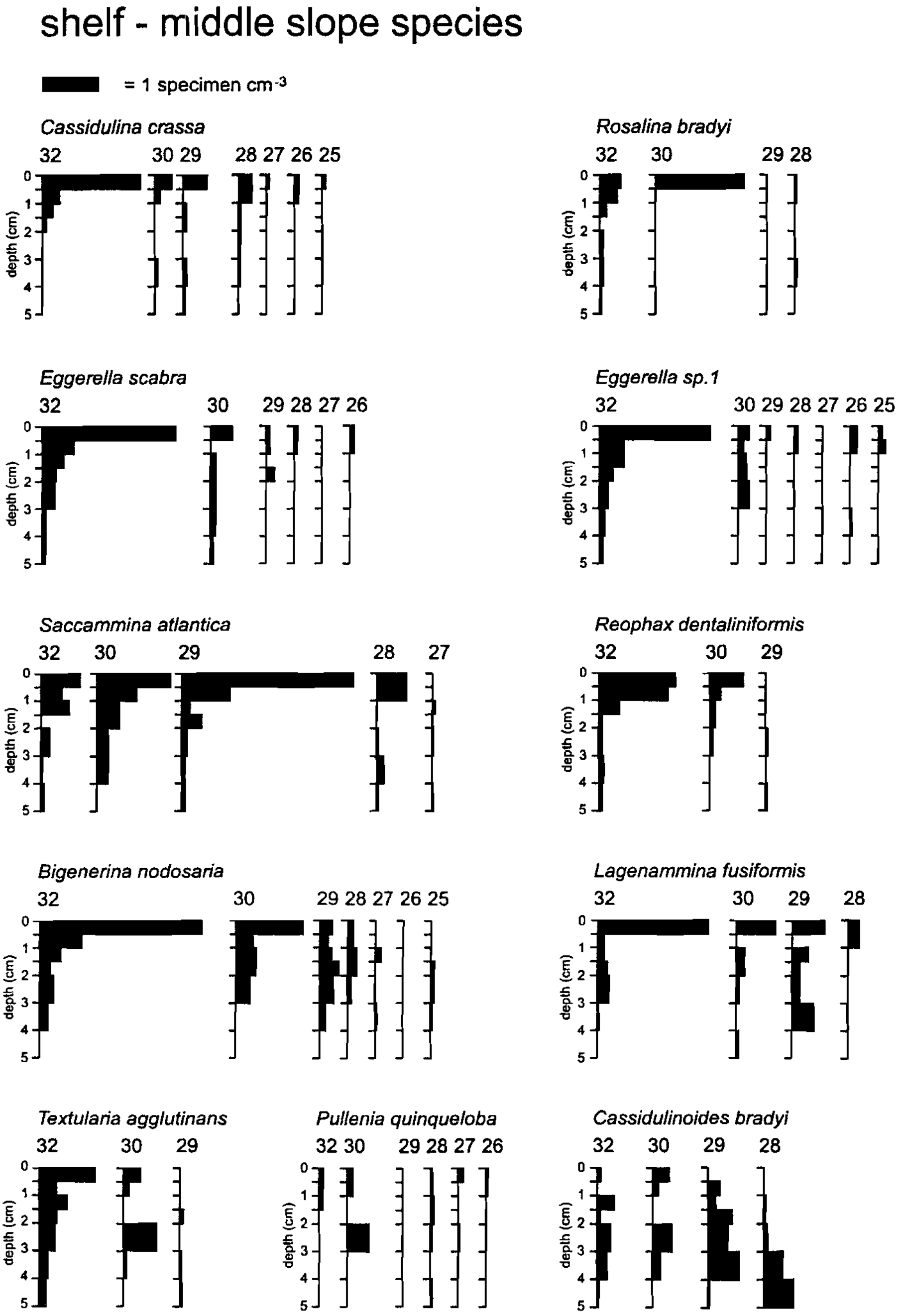
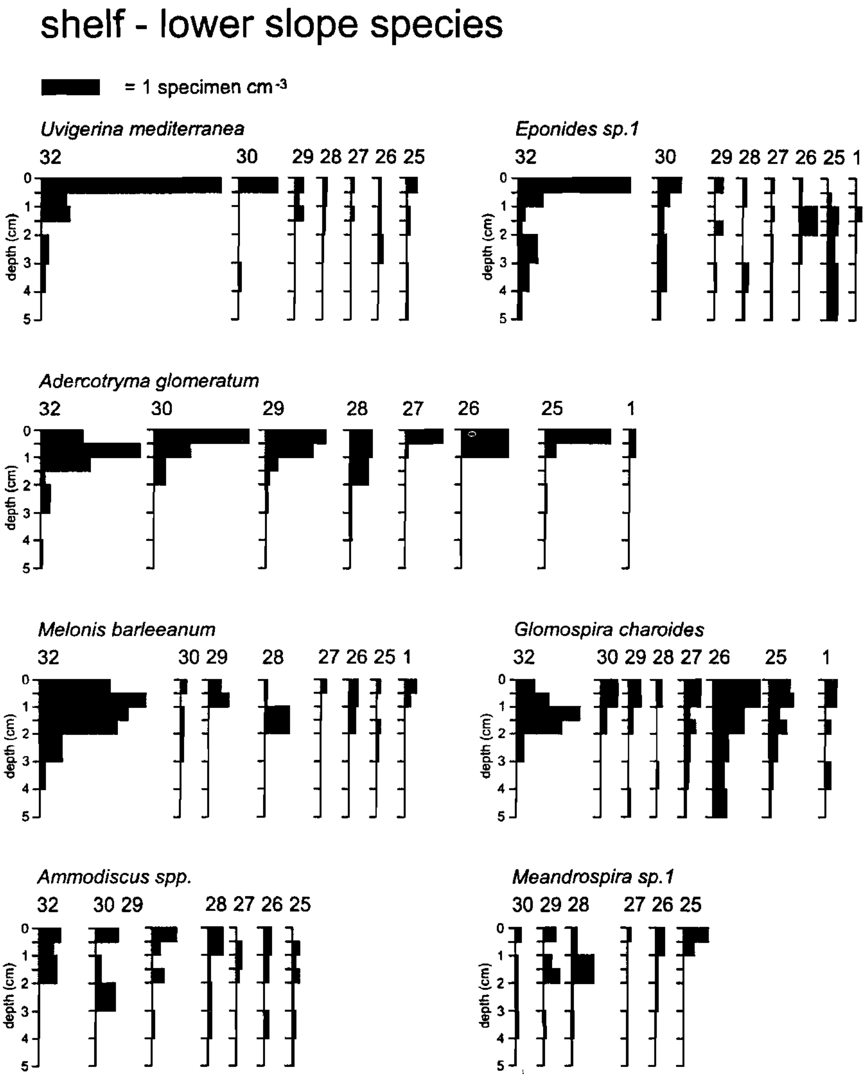


Fig. 3.6 continued



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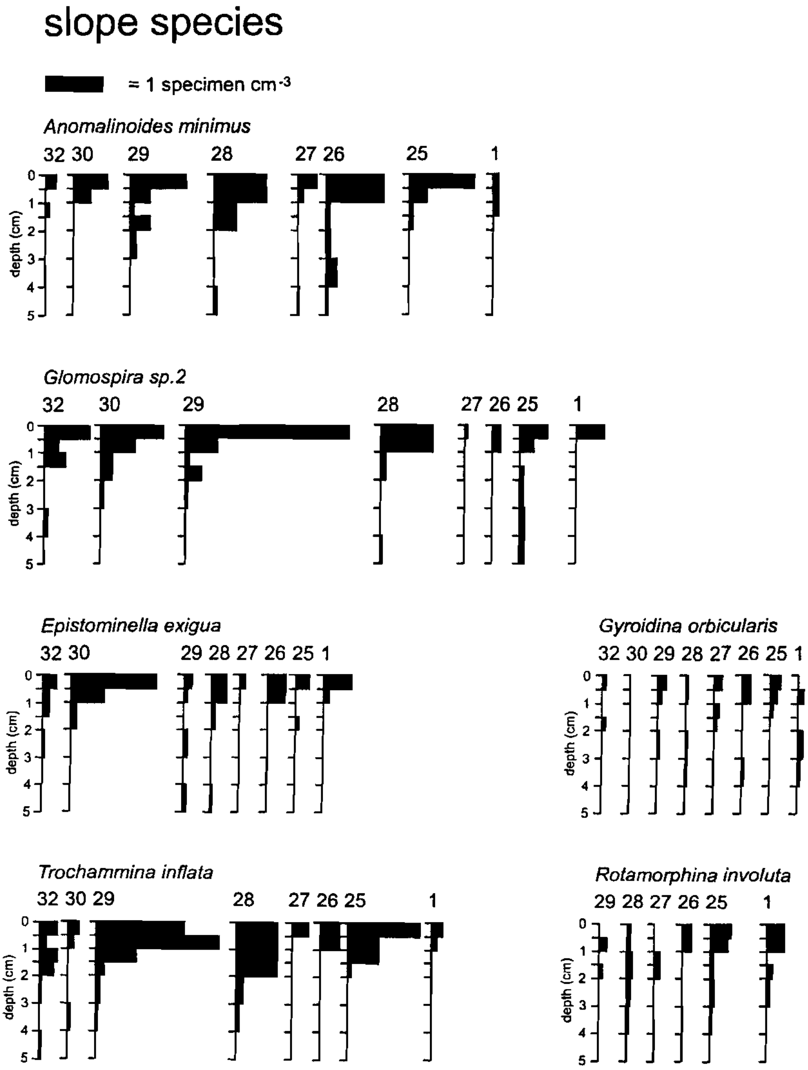

Fig. 3.6 continued

microhabitat deeper in the sediment. In these deep waters the surface habitat is occupied by species like *Adercotryma glomeratum*, *Anomalinoides minimus* and *Rotamorphina involuta*. The arenaceous taxa *Glomospira charoides* and *Adercotryma glomeratum* apparently display a microhabitat change in the opposite direction. These species belong to the shallow infauna in core 32, but have surface abundance maxima in most of the deeper cores.

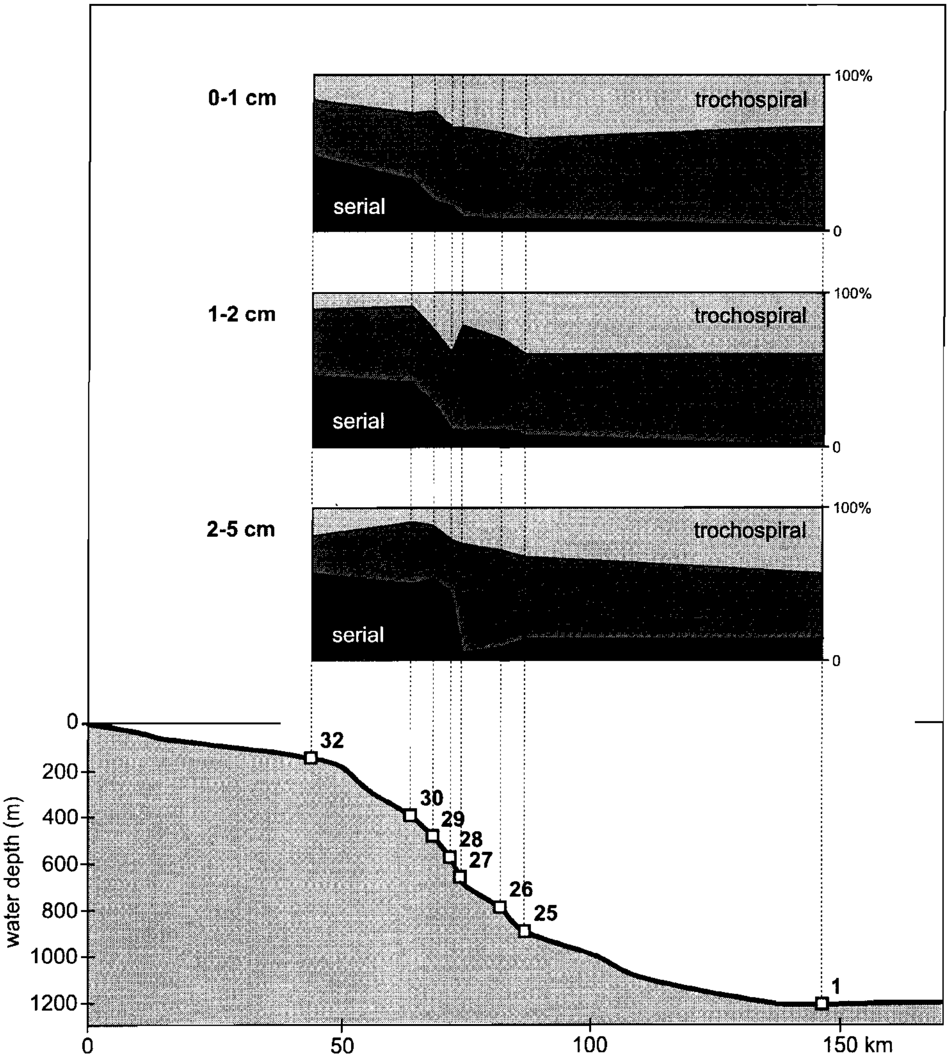

Fig. 3.7. Variation along the transect in the relative abundance of trochospiral and serial morphotypes, given for 3 successive depth-intervals.

A number of studies have pointed to the possible functional relationshipbetween test morphology of benthic foraminifera and the microhabitat which they occupy (Corliss, 1985; Jones and Charnock, 1985; Corliss and Chen, 1988; Corliss, 1991). In general, trochospiral test morphologies are viewed as typical of epifaunal foraminifera, whereas elongated test morphologies, usually with a uni-, bi- or triserial arrangement of chambers, are thought to be typical of infaunal foraminifera. Opinions differ on a number of other morphotypes. In the Adriatic cores, trochospiral morphotypes tend to decrease in relative abundance with depth into the sediment, and elongated serial morphotypes increase somewhat downcore (Fig. 3.7). The two morphotypes are, however, not restricted to exclusively a surface or a subsurface microhabitat, but are well represented at all core levels. A very clear decrease in serial morphotypes, and an increase in trochospiral morphotypes, is observed along the transect from shallow to deep water.

DISCUSSION

Bathymetric distribution

Keeping in mind the limited number of our observations, and the possible uncertainties about the reliability of the Rose Bengal method, it is remarkable that we find such a clear relationship between live benthic foraminiferal abundance and waterdepth. Assuming that the size of benthic foraminiferal populations is controlled by the supply of organic matter to the seafloor (e.g. Altenbach and Sarnthein, 1989), the observed abundance pattern is in good agreement with the expected decrease of organic flux with increasing waterdepth. As proposed by Suess (1980), the flux of particulate organic matter in the deep sea $C_{flux}(z)$ is proportional to surface water productivity C_{prod} and inversely proportional to waterdepth z:

$$C_{flux}(z) = \frac{C_{prod}}{0.0238\,z + 0.212} \qquad (3.1)$$

Assuming that C_{prod} is about 35 g C m^{-2} yr^{-1} (average between 20 and 50 g C m^{-2} yr^{-1}), the flux of organic carbon to the seafloor can be estimated to decrease from 9.5 g C m^{-2} yr^{-1} at shelf station 32 to 1.2 g C m^{-2} yr^{-1} at station 1 in the centre of the South Adriatic Basin. Linear regression of the observed foraminiferal abundance N (expressed as # cm^{-2}) versus estimated organic carbon flux $C_{flux}(z)$ (expressed as mg C cm^{-2} yr^{-1}), assuming that $N = 0$ for $C_{flux}(z) = 0$, gives the following relationship:

$$N(C_{flux}) = 74\,C_{flux}(z) \qquad (3.2)$$

for foraminifera >63 μm (see Fig. 3.8), and

$$N(C_{flux}) = 15\,C_{flux}(z) \qquad (3.3)$$

for foraminifera >150 μm (Fig. 3.8). It is observed, however, that numbers of live foraminifera decrease more rapidly with increasing water depth than expected on the basis of Suess' organic flux equation. A possible explanation for this deviation is that surface water productivity, from which the organic carbon flux was estimated, is not constant along the transect, but decreases in an offshore direction (e.g. Revelante and Gilmartin, 1977; Sturm et al, 1992). Alternatively, the shelf and upper slope sediments may receive a higher input of organic carbon by export and lateral near-bottom transport of organic detritus from the adjacent shelf areas. According to Walsh (1991; 1992), significant redistribution of organic carbon occurs especially on the upper continental slope by resuspension and lateral transport of organic detritus in bottom nepheloid layers. The low number of live foraminifera in station 27 may be due to a local disturbance, possibly by recent erosion, or by reworking of the sediment by macrofauna.

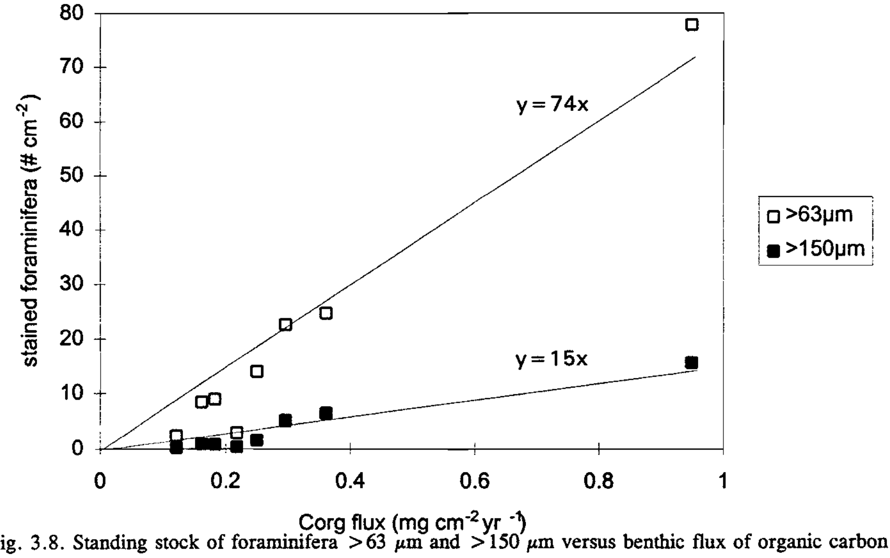

Fig. 3.8. Standing stock of foraminifera >63 μm and >150 μm versus benthic flux of organic carbon, as estimated from the flux equation given by Suess (1980).

Compared to standing stocks reported from other areas of the world ocean (eastern boundary current upwelling areas not included), the standing stocks observed in the southern Adriatic Sea appear extremely low, especially those of the lower slope and basin plain (Fig. 3.9). Some of the observed difference may be due to differences in methodology, notably with respect to criteria to discriminate living (stained) from dead (non-stained) foraminifera, and inclusion of Astrorhizids and various soft-bodied taxa in some studies. More importantly, however, the low standing stocks in the southern Adriatic Sea are likely to reflect the generally low surface water productivity in that area, compared to the higher productivity in other areas. Also, the relatively high water temperature in the Adriatic Sea may lead to more rapid mineralisation of organic carbon sinking through the water column, and thus a reduced flux of organic carbon reaching the benthos.

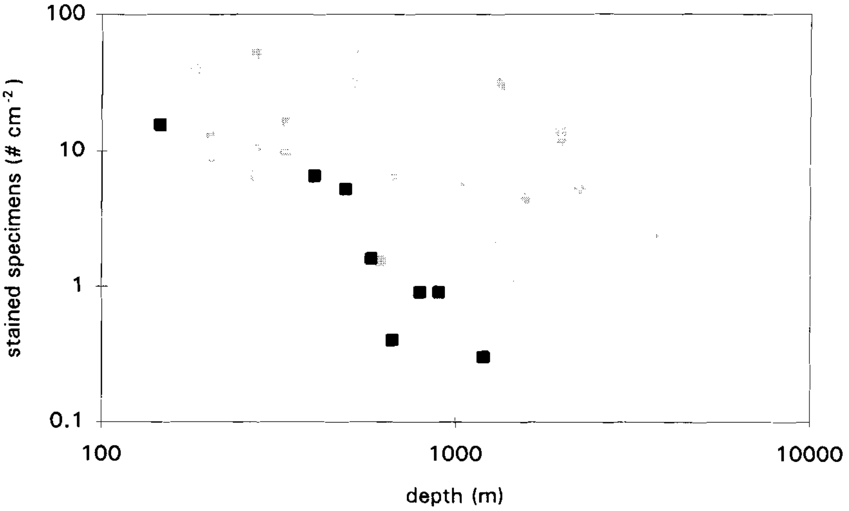

Fig. 3.9. Standing stocks of >150 μm foraminifera in the southern Adriatic Sea (black squares), in comparison with standing stocks reported from other areas (grey squares): NE Atlantic, Gooday (1986); NW Atlantic, Corliss (1991); Skagerrak, Corliss and Van Weering (1993); Canadian Arctic, Hunt and Corliss (1993); Sulu Sea, Rathburn and Corliss (1994); NE Atlantic, unpublished data).

A relationship between benthic foraminiferal shell abundance in marine sediments and water depth has for long been observed (e.g. Parker, 1954), and the abundance of benthic foraminifera relative to planktonic foraminifera can be used as an indicator of depositional depth in fossil marine sediments (Grimsdale and Van Morkhoven, 1955; Gibson, 1989). Van der Zwaan et al. (1990) stressed the relationship between benthic foraminiferal shell production and the depth-dependent organic flux. The present data confirm this relationship, as far as live foraminiferal populations may be compared with taphonomic assemblages. In this context it is relevant to notice that about half of the live population consists of weakly agglutinated non-fossilizing foraminifera, not counting Astrorhizids. Thus, in the case of the Adriatic samples, ususally less than half of the living population will be preserved in the fossil record.

Studies from other areas where total live populations have been studied confirm that poorly-fossilizing foraminifera generally form a significant part of the living population (e.g. Bernstein et al., 1978; Gooday, 1986; Schröder et al., 1988; Alve and Nagy, 1990; Corliss, 1991; Barmawidjaja et al., 1992; Hunt and Corliss, 1993; Rathburn and Corliss, 1994).

The distribution of Astrorhizid fragments along the transect shows no evident relationship with waterdepth. The lack of a relationship could be only a result of the rather small surface area of the samples, and an uneven distribution of these relatively large organisms. Inclusion of only a few large specimens in a sample could yield a rich harvest of fragments after drying and sieving of the samples. Alternatively, it may be significant that many of these arborescent forms are probably suspension feeders (e.g. DeLaca et al., 1981; Jones and Charnock, 1985), depending for their nutrition on the presence of bottom currents, carrying organic particles in suspension. The high numbers of Astrorhizid fragments in cores from the basin slope may then be related with the outflow of Southern Adriatic Water, which follows the western slope of the Southern Adriatic Basin, leaving the basin via Otranto Strait (e.g. Orlić et al., 1992). On the bottom of Otranto Strait similarly high numbers of Astrorhizid fragments were observed (Jorissen et al., 1995). The common occurrence of suspension-feeding foraminifera stresses the importance of lateral transport of organic matter in the southern Adriatic Basin.

Vertical distribution in the sediment

Despite the great variation in standing stock and species composition observed along the transect, the vertical distribution of foraminifera, in terms of average living depth and the proportions of the population inhabiting successive sediment layers, does not vary that much. There seems to be, however, a trend of increasing endobenthic habitation from the shelf toward the mid-slope station 28, and a reverse trend of increasing epibenthic habitation, from station 28 toward the basin centre.

Foraminifera may inhabit subsurface layers of the sediment for various reasons (e.g. Gooday, 1986): to avoid predation by meio- or macrofaunal organisms and passive ingestion by surface deposit-feeding macrofauna; to avoid food-competition by foraminifera or other fauna; to search for specific food-types available in the deeper sediment layers. Scarcity of food and a lack of dissolved free oxygen at deeper levels in the sediment are probably the most important factors limiting the downward expansion of foraminiferal habitation (Corliss and Emerson, 1990). In box cores from the northwest Atlantic Ocean, Corliss and Emerson (1990) observed an increase of the habitat depth (depth above which 95% of the population is living; Shirayama, 1984b) from 3 cm at 202 m water depth to 13 cm at 2225 m, and again a shallow habitat depth of 4 cm at 4800 m. They related the increasing habitat depth to an increasing depth of oxygen penetration in the sediment, which in turn is related to a decrease of the organic flux. At great depth, however, scarcity of food would prevent foraminifera to live deep in the sediment.

The trends we noticed in the downward expansion of foraminiferal populations in the Adriatic Sea are strongly reminiscent of those described by Corliss and Emerson (1990) for the NW Atlantic. Although we lack direct measurements of sediment pore-water oxygen contents, the increasing thickness of the oxidized sediment layer from the shelf to the deep central basin is suggestive of an increasingly deep oxygen penetration into the sediment towards the deeper stations. Decreasing standing stocks reflect the decreasing flux of organic matter. Thus, the increasing relative abundance of subsurface-dwelling foraminifera, as well as the increasing average living depth, going from the shelf (core 32) to mid-slope depth (core 28), may well be related to an increasing thickness of the oxic sediment layer. At greater depths, the abundance of subsurface dwellers, and the average living depth, decrease again as a consequence of food limitation. If indeed low food supply plays a role in limiting the living depth at the deeper stations, it is interesting that this occurs at such a moderate water depth, whereas in the more eutrophic northwest Atlantic Corliss and Emerson (1990) observe this phenomenon at the much greater depth of 4800 m. The control of food and oxygen availability on benthic foraminiferal living depth is discussed in more detail by Jorissen et al. (1995).

The limiting role of oxygen on the living depth of foraminifera has been disputed more recently (e.g. Rathburn and Corliss, 1994). There is ample evidence for the ability of benthic foraminifera to survive under dysoxic or even totally anoxic conditions (Bernhard, 1989; Corliss and Emerson, 1990; Bernhard and Reimers, 1991; Moodley and Hess, 1992; Corliss and Rathburn, 1994). Test-morphological as well as cell-physiological adaptations may enhance respiration under low-oxygen conditions (Leutenegger and Hansen, 1979; Corliss, 1985; Bernhard, 1986; Moodley and Hess, 1992), whereas alternative respiratory mechanisms may be involved in foraminiferal survival under anoxic conditions (Bernhard and Reimers, 1991). Yet, it seems that such adaptations are only helpful to bridge anoxic periods of limited extent. Benthic foraminifera appear unable to survive prolonged anoxia (Bernhard and Reimers, 1991), and they are absent under constant, totally anoxic conditions (Murray, 1991). It seems therefore reasonable to assume that the presence of permanently anoxic sediments below the oxidized sediment layer imposes a limit on the downward extension of benthic foraminiferal populations.

Competitional pressure and predation may play a role in forcing foraminifera to inhabit subsurface habitats where food and oxygen are scarce, but apparently the lower depth limit on the downward distribution of foraminifera is more strongly controlled by oxygen limitation. This may be concluded from the fact that foraminifera have a relatively shallow living depth on the shelf, although biological activity, including predation and competition, may be expected to be most intense at relatively shallow water depth. However, if the available living space of foraminifera may be primarily determined by the limiting factors oxygen and food, biological interrelationships may be important in the partitioning of the available living space into different microhabitats. Additionally, differentiated feeding behaviour may play an important role as well. As apparent from our (limited) data, microhabitat patterns of foraminiferal species may change in different ways along the studied transect, demonstrating the complex control by different environmental parameters.

Trochammina globigeriniformis, *Cassidulina laevigata* and *Uvigerina mediterranea* are typical near-surface dwelling species of core 32. They apparently are superior competitors in food and oxygen-rich surface microhabitats, resistant to a relatively high level of disturbance by macrofaunal predators and deposit-feeders. Downcore, however, these species rapidly lose their dominance, in favour of species which have a higher tolerance to reduced concentrations of food and oxygen, or which have a more generalistic feeding behaviour. Also with increasing water depth and consequently with decreasing food flux, these species rapidly decrease in significance, demonstrating their dependence on a relatively high food flux.

Bolivina spathulata and *Bolivina dilatata*, the two most common species in core 32, and *Eggerella scabra* and *Eggerella* sp.1, are also mainly restricted to the shallower waters, but they penetrate deeper into the sediment. They apparently are more resistant to low concentrations of oxygen, and are able to efficiently exploit subsurface food resources.

Near-surface dwelling species at deeper stations generally have less pronounced surface maxima, and decrease more gradually downcore (e.g. *Saccammina atlantica* and *Glomospira* sp.2 on the upper slope, on the lower slope *Adercotryma glomeratum*, *Anomalinoides minimus* and *Trochammina inflata*, and *Epistominella exigua* in the core from the basin centre). This may be due to the more gradual downcore oxygen gradient and a generalistic deposit-feeding behaviour.

The vertical distribution pattern of *Eponides* sp.1 and *Bigenerina nodosaria* in core 32, comparable to that of the previously mentioned species of *Bolivina* and *Eggerella*, indicates their tolerance for reduced oxygen levels, and non-specific feeding behaviour. The shift of these species to the subsurface layer as observed in cores from the slope may be caused by competitional pressure exerted by surface-dwelling species present on the slope.

By contrast, *Adercotryma glomeratum* changes from a well-defined subsurface microhabitat on the shelf (core 32) to a more superficial microhabitat on the slope. It seems to be attracted to the sediment surface, possibly by specific food resources which are concentrated there. On the shelf, however, this species is apparently forced to occupy a less favourable subsurface position, which may be due to the presence of more competitive shelf-dominating species in the surface layer. In deeper water, where the dominance of the shelf species declines, it may take over the near-surface habitat.

For similar reasons, *Glomospira charoides* may expand its microhabitat range toward the sediment surface in deeper water, but it apparently expands its range in downcore direction as well. The increased downward distribution of this species may be related with the deeper penetration of oxygen with increasing water depth, and the apparently undifferentiated feeding depth of this species.

Finally, it has been suggested that typical deep-infaunal species like *Cassidulinoides bradyi*, which move toward deeper microhabitats with increasing waterdepth, may feed on bacterial floras present around the oxic-anoxic boundary (Jorissen et al, 1995). Alternatively, these species may only resist competition by shallower-dwelling species by inhabiting the oxygen-depleted sediment layer near the oxic-anoxic boundary. In both cases, these species are forced to live deeper in the sediment as the oxic layer increases in thickness. Food scarcity deeper in the sediment is eventually limiting the further downward migration of these species. This may explain the absence of these deep-infaunal species beyond middle slope depth.

The proposed association of trochospiral test morphologies with epifaunal microhabitats, and elongated serial test morphologies with infaunal microhabitats (Corliss, 1985; Jones and Charnock, 1985; Corliss and Chen, 1988; Corliss, 1991), seems to be confirmed in a general sense by our data. It must be noticed, however, that so-called epifaunal morphotypes may also be common in subsurface microhabitats (e.g. *Eponides* sp.1) and infaunal morphotypes may likewise be common in surface microhabitats (e.g. *Uvigerina mediterranea*, *Bolivina spathulata*). Similar observations can be made for different morphotypes as well, and it seems therefore justified to warn against too simple interpretations on the basis of morphotype alone. Our data show that microhabitats of benthic foraminiferal species are not static, but may be highly variable from place to place, as determined by local environmental conditions.

CONCLUSIONS

In the investigated box core samples from the southern Adriatic Sea, the total abundance of live (stained) benthic foraminifera (Astrorhizids excluded) decreases with increasing water depth, reflecting the expected decrease in particulate organic matter flux with increasing depth to the seafloor. Comparison of the observed abundance pattern with the pattern expected on the basis of Suess' (1980) organic carbon flux equation reveals that a decrease in surface water production in offshore direction, or alternatively an enrichment of the shelf and upper slope sediments by lateral transport of organic carbon, may play a role as well.

Standing stocks of stained foraminifera appear low, when compared to standing stocks observed in other areas of the world ocean. This probably reflects the low productivity of the southern Adriatic Sea.

The distribution of arborescent Astrorhizid foraminifera may be controlled primarily by the presence of bottom-water currents along the basin slope, supplying these presumably suspension-feeding foraminifera with suspended particulate organic matter.

A distinct bathymetric zonation of species is observed. Dominant shelf species are mainly restricted to the shelf, whereas dominant species of the basin slope have broader bathymetric ranges. With increasing depth, most of the common species of shallower water disappear, and only a few deep-water species are added.

The downward expansion of foraminiferal populations into the sediment seems primarily limited by oxygen depletion deeper in the sediment on the shelf and upper slope, and by food scarcity in deeper sediment on the lower slope and notably in the basin centre.

Microhabitats occupied by foraminiferal species may be highly variable from place to place, determined by the concentration of dissolved oxygen in sediment pore waters, availability of organic matter in general or the presence of more specific food types, and biological interactions like competition and predation. Assumptions regarding the microhabitat characteristics of fossil foraminiferal species, based on general morphological characteristics, should be used with circumspection.

ACKNOWLEDGEMENTS

We thank Prof. A.M. Borsetti for providing us with the opportunity to participate in the AD91 cruise. This research was partly funded by the Netherlands Organization for Scientific Research (NWO), grant number 751.356.021.

CHAPTER 4

A conceptual model explaining benthic foraminiferal microhabitats*

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Abstract We present a conceptual model which explains benthic foraminiferal microhabitat preferences in terms of differences in the downward organic flux. We argue that under oligotrophic conditions the microhabitat depth is controlled by the availability of metabolizable food particles in the sediment. Under more eutrophic conditions, the ecosystem is no longer food-controlled, but instead, a critical oxygen level determines down to what depth we find a living fauna. Under food-limited conditions, anaerobic degradation of organic matter may provide an additional food source around the redox front, which could explain deep infaunal maxima reported in the literature. In a sample transect through the Adriatic Sea, both microhabitat controls (food-limited and oxygen-limited) are present. On the shelf and the upper part of the slope, the rather shallow microhabitat depth is controlled by a critical oxygen level. In the 1250 m deep southern basin and on the lower part of the slope, on the contrary, the availability of metabolizable organic matter, and not a critical oxygen level, determines down to what depth living foraminifera are found.

1. Introduction

Recent years have seen a flood of papers on the microhabitats of benthic foraminifera, which emphasized the position of the living benthic foraminifer with respect to the sediment-water interface. There are several reasons for this interest:

(1) the observed interspecific differences in vertical distribution in the sediment have been welcomed as a factor that could be added to the rather limited array of parameters available to interpret present and past foraminiferal distributions. Corliss and Chen (1988), for example, suggested a close relationship between the percentage of infauna and the organic flux.

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(2) infaunal taxa may be largely underrepresented in surface sediments; Loubere (1989) showed that this is true both for the living and for the fossil fauna. Hence, the common practice of using a sample of the top 1 or 2 cm for the determination of the composition and density of the foraminiferal fauna is incorrect.

(3) microhabitat differences are supposed to have a bearing on the $\delta^{13}C$ of the foraminiferal test. Epifaunal species reflect bottom water conditions, whereas infaunal species should be indicative of the isotopic composition of the interstitial waters. The $\delta^{13}C$ between epifaunal and infaunal taxa has been supposed to vary as a function of the organic carbon accumulation rate and bottom water oxygen concentrations (McCorkle et al., 1990).

Since the first observations in the sixties, most authors have become convinced of the presence of living foraminifera deep in the sediment. If we have a closer look at the published observations of foraminiferal microhabitats, a picture arises of a well-developed species zonation within the sediment in deep water environments (e.g. Corliss, 1985; 1991; Gooday, 1986; Mackensen and Douglas, 1989) versus a much more heterogeneous distribution in shallow water environments (e.g. Buzas, 1974; 1977; Moodley, 1990; Corliss and Van Weering, 1993). This difference is generally explained by the higher energy and increased bioturbation in shallow water environments (Buzas et al., 1993).

Most authors agree that the most important factors controlling the foraminiferal microhabitat are oxygen and food (e.g. Gooday, 1986; Corliss and Emerson, 1990). Some authors, however (e.g. Corliss and Chen, 1988; Rosoff and Corliss, 1992; Rathburn and Corliss, 1994), attribute more importance to nutritional conditions (organic flux) than to oxygen levels, whereas others (e.g. Mackensen and Douglas, 1989; Barmawidjaja et al., 1992; Jorissen et al., 1992) consider the oxygenation of the bottom and interstitial waters as the primary factor controlling the sediment penetration depth of the faunas.

In this paper, we focus on the respective importance of each of these two factors. We present a conceptual model, which follows explications of the vertical distribution of total meiobenthos and benthic foraminifera, proposed respectively by Shirayama (1984b) and Corliss and Emerson (1990). This model shows why the vertical distribution of benthic foraminifera is sometimes controlled by oxygen concentration, and on other occasions by the nutritional conditions. We illustrate this model by reference to a sample transect through the Adriatic Sea.

2. Defining the foraminiferal microhabitat

A property that many of the published papers considering vertical distribution of foraminifera have in common is their tendency to classify; to order the available species in a number of microhabitat categories. Many terms have been proposed for classification, varying from very general to highly specific: infaunal, epifaunal, inbenthic, epibenthic, shallow infaunal, deep infaunal, potentially infaunal, predominantly infaunal, epiphytic, etc, etc. Unfortunately most of these terms have been used as interpretative, rather than descriptive denominators.

The main distinction in microhabitat characteristics is that between epifaunal and infaunal organisms. Biologists generally reserve the term epifaunal for organisms living on top of the sediment. In the case of smaller foraminifera, it is nearly impossible to establish whether they are truely epifaunal. Usually, the most accurate statement we can make is that a species lives in the topmost 0.5 cm of the sediment. Especially when soft bottom substrates are considered, one can argue (as was done by Buzas at al., 1993) that a real substrate does not exist, and that all mud-dwelling foraminifera are thus infaunal. If this is true, then what currently is meant by the terms epifaunal and infaunal could much better be described by the terms shallow and deep infaunal. Only those taxa which have been described as having an "elevated microhabitat" (Lutze and Thiel, 1989) should be considered as real epifaunal taxa. However, the term "infaunal" also poses problems; one of them being the fact that only very few species living exclusively deep in the sediment have been reported so far. In the literature, authors commonly use the term infaunal to describe species which show a subsurface maximum, but in several papers, such species were not found, and the term infaunal is used for all taxa which do not show a clear preference for a life position close to the sediment surface.

Recent studies have shown that even the microhabitat of a single species may show important geographical and/or temporal changes. In the light of this finding, Linke and Lutze (1993) have argued that foraminiferal microhabitats should not be classified according to a static concept, but should instead be regarded as the expression of a dynamic adaptation to optimize food acquisition. Although we realize that isotopists and other people using microhabitat characteristics like to have simple labels such as infaunal or epifaunal, we agree with Linke and Lutze (1993), and think that workers on foraminifera should refrain from providing lists with simplified microhabitat labels for their species.

In order to cope with these problems, we think that it is preferable to describe species distribution patterns in quantitative rather than qualitative terms. Since both parameters defined by Shirayama (1984b); the 95%-level (habitat depth) and 50%-level (mode) fail to show the quantitative importance of the infaunal component, we have chosen to use another parameter in this paper, the average living depth (ALD), which is defined as follows:

$$ALD_x=\sum_{i=1,x}(n_i\ D_i)/N \qquad (4.1)$$

in which x is the lower boundary of the deepest sample included in the calculation; n_i is the number of specimens in interval i; D_i is the midpoint of sample interval i, and N is the total number of individuals for all levels.

In case of a strictly epifaunal taxon, the ALD should be one half of the thickness of the topmost level. Higher values are indicative of more infaunal patterns.

2.1. The nature of the microhabitat record; the Rose Bengal "problem"

Unfortunately, live foraminiferal faunas are difficult to quantify, because a direct observation of coloured protoplasm, or of active life-processes is in most cases not possible (compare Vénec-Peyré and Le Calvez, 1986). A routinely use of the apparently accurate ATP-assays (Bernhard, 1988) for the quantification of foraminiferal standing stocks is hampered by their too time-consuming character. This means that most of our distributional data on live foraminifera are not based on ATP-assays, but on samples stained by Rose Bengal.

Several authors (e.g. Douglas et al., 1978, 1980; Bernhard, 1988; 1989) have questioned the adequateness of the Rose Bengal staining method. Douglas et al. (1980) found that 30% of the stained specimens from anoxic sediments sampled in Santa Monica Basin showed signs of protoplasm decay, and were probably dead at the time of collection. Bernard (1988) showed that heat-killed foraminifera (which were stored at - 1°C) still stained four months after their death. Corliss and Emerson (1990), who present a model for protoplasm degradation incorporating bioturbation rates, estimated (half-life) degradation times to be 0.07 - 2 years at the sediment surface, and 2 - 80 years deeper in the sediment. For this reason, they followed a conservative approach, and assumed that stained specimens were alive either at the time of collection, or in the "recent" past. They argued that the best proof of the reliability of the staining procedure was the nature of the observed patterns, which showed that some species were restricted to the sediment surface, while others clearly showed subsurface maxima.

We agree that it is feasible that the proces of protoplasm decay is faster at the well-oxidized, heavily bioturbated sediment surface, than in the anoxic layers of the sediment, where macrofaunal bioturbation, which can induce downward transport (renewal) of oxidants, is often nearly absent. However, this difference in protoplasm degradation time may have a serious bearing on the presence of stained foraminifera. A difference in protoplasma degradation time by a factor ten, would mean that foraminifera remain stainable ten times longer in the anoxic zone than at the sediment surface. If this time interval exceeds the average foraminiferal lifespan, than the stained fauna could possibly contain representatives of several successive generations. Therefore, we suspect that Rose Bengal stained foraminifer countings can result in significant overestimations of the actual infaunal standing stocks.

This effect may be reinforced by a second factor; on the basis of lower ATP concentrations, Bernhard (1992) suggested that specimens inhabiting anoxic sediments may have the ability to lower their metabolism. If this is true, then the anoxic sediment may act as a foraminifer trap; foraminifera caught in the anoxic zone may be incapable to escape, and may remain in a state of more or less inactivity for considerable periods of time. Together, these two factors, slow protoplasm degradation rates and foraminiferal trapping, may lead to substantially raised numbers of stained forams below the zero-oxygen level. This could mean that some of the clear infaunal maxima described in the literature may not altogether represent the living fauna. These infaunal maxima, however, certainly represent taxa with a special kind of behaviour (e.g. more actively or deeper burrowing), not found in other taxa.

Despite these pitfalls, the Rose Bengal method remains the most practical way to quantify life foraminiferal faunas. Lutze and Altenbach (1991) esteem the method, and believe that it leads to 96% correct identifications when it is carefully employed. In our work, only perfectly stained specimens have been counted. For deep infaunal species, well-coloured specimens found at a relatively shallow depth have been used as a standard.

2.2. Factors controlling the microhabitat

Many factors have been proposed to explain the benthic foraminiferal microhabitat, the most important ones being food availability, oxygen concentration, ecosystem stability, bioturbation, competition and predation.

Unfortunately, all of the above-mentioned factors are closely interrelated. The underlying, basic controlling factor seems to be the organic flux, the transport of organic matter from surface waters to the sea-bottom. At the one hand this flux provides food to the benthic ecosystem, but on the other hand the remineralization of the organic matter on the sea-bottom consumes oxygen, and so influences the oxygen concentrations of bottom and pore waters. Food availability, which can thus be considered as a function of the downward flux of organic matter, has a quantitative as well as a qualitative aspect:

- a strong correlation between the organic flux and the foraminiferal density has been suggested by Altenbach and Sarnthein (1989), Herguera and Berger (1991) and Herguera (1992), and
- some foraminifera species have a preference for very fresh, easily metabolizable

food particles, whereas others tolerate more refractory organic matter (e.g. Caralp, 1989a; Gooday et al., 1992; Gooday, 1993). Labile organic matter is concentrated at the sediment surface, whereas deeper in the sediment, the organic matter will become increasingly refractory. For this reason, interspecific differences in vertical distribution may also reflect differences in nutritive behaviour. The importance of oxygen as a limiting factor is under dispute. Several studies have shown substantial numbers of living foraminifera in what appear to be completely anoxic environments (Corliss and Emerson, 1990; Bernhard, 1992). As a consequence of such observations, it has been suggested that foraminifera may be facultative anaerobes (Bernhard, 1989, 1993; Bernhard and Reimers, 1991; Sen Gupta and Machain-Castillo, 1993). Even the most resistant foraminifera, however, tend to disappear after prolonged anoxia (Bernhard and Reimers, 1991), an observation which is confirmed by the successions found in sapropels, where oxygen depletion of the bottom waters ultimately resulted in sediments devoid of benthic microfossils (e.g. Verhallen, 1990).

Ecosystem stability interferes strongly with the first two factors controlling microhabitat preference. Periodic anoxia result in ecosystems which never go beyond an early stage of colonization, characterized by a strong dominance of opportunistic epifaunal species, which are able to proliferate between the anoxic intervals. Colonization of an empty ecosystem (after an anoxic event) probably starts at the sediment surface; deeper layers will only be invaded in a second stage (Barmawidjaja et al., 1992; Jorissen et al., 1992). Several species appear even to be capable of tracking seasonal movements of a critical oxygen level (Barmawidjaja et al., 1992; Ohga and Kitazato, 1994; Alve and Bernhard, 1995); a behaviour which is reflected by their variable microhabitat. A pulselike input of food (phytodetritus deposits) can also affect microhabitat characteristics, since it advantages a group of opportunistic epifaunal taxa, which profit from the abundancy of high quality food by a rapid multiplication, and in this way cause a fauna with a strong dominance of epifauna (Gooday, 1993).

Macrofaunal bioturbation may also influence the microhabitat characteristics, by bringing food and oxygen down to deeper sediment layers. Thereby, well-oxygenated micro-environments with metabolizable organic matter can be created in the anoxic zone (Meyers et al., 1988).

The influence of other biological parameters, such as competition and predation, is difficult to assess. For some meiofaunal and macrofaunal organisms is has been claimed that species interactions rather than physical/chemical parameters maintain a vertical separation (e.g. Branch, 1984; Fleeger and Gee, 1986). In the case of foraminifera this suggestion has also been made (e.g. Gooday, 1986). Although we realise that it may be an over-simplification not to include biological parameters in the present model, we are more or less forced to do so because at present we are not able to tell whether foraminifera can actively adjust their living position in order to find less competitive and/or less predated environments. Not including these parameters is at least partly justified by the fact that also the vertical distribution of the competing and predating organisms is also strongly influenced by food and oxygen, the very factors considered in this paper.

3. The *TROX*-model: the microhabitat explained in terms of *TR*ophic conditions and *OX*ygen concentrations

In Figure 4.1, we present a conceptual model, in which the penetration depth of benthic foraminiferal faunas (or microhabitat depth) is explained as a function of the basically negative interplay between oxygen and food availability. The model follows the assumption of Shirayama (1984b) that the depth in the sediment down to which organisms can live is determined by oxygen availability, and, that in the presence of oxygen, the vertical distribution of organisms is controlled by food availability. We suggest that foraminiferal species have both a certain critical oxygen requirement and certain food requirements (in terms of quality and quantity of food items). Of course, both parameters will vary considerably amongst the various species. In the model, the microhabitat depth is determined by a critical food level in oligotrophic environments, whereas it is limited by a critical oxygen level in eutrophic areas. The same interpretation was proposed by Corliss and Emerson (1990) for differences in foraminiferal habitat depth in the northwest Atlantic Ocean.

Figure 4.1 shows how the maximal microhabitat depth (indicated by the black shading) changes as a function of the downward organic flux. In very oligotrophic areas (the left side in Figure 4.1), all metabolizable food particles will be consumed at the sediment surface; the underlying sediment will contain only small quantities of (refractory) organic matter, and for that reason, infaunal species will be absent. When moving to the more eutrophic areas (to the right in Figure 4.1), we see that the microhabitat deepens. This is the result of the fact that metabolizable organic matter is no longer restricted to the sediment surface, but is partially transported (by bioturbation) to deeper sediment layers, where it provides the nutritional conditions required to sustain infaunal taxa. When we go to the fully eutrophic environments at the far right side of Figure 4.1, it is no longer the critical food level, but a critical oxygen level which determines the penetration depth of the infauna. In these environments, the degradation of the organic matter within the sediment consumes more oxygen than can be provided by bioturbation and diffusion from above. This results in a situation with an excess of food in the sediment. A further increase of the organic flux leads to an increased consumption of oxygen in the benthic environment,

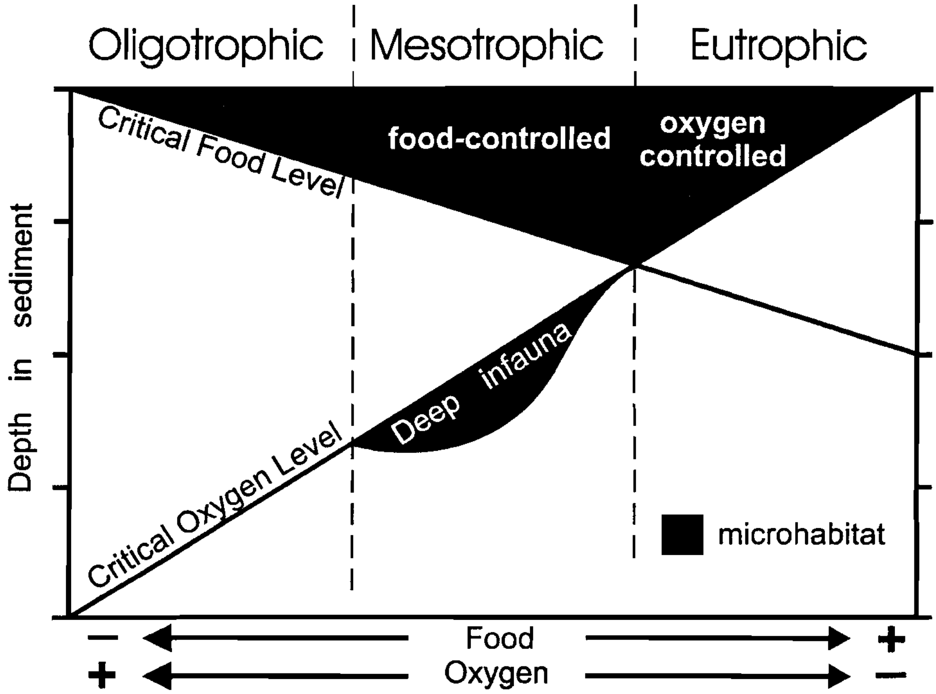

Fig. 4.1. Conceptual model explaining the benthic foraminiferal living depth (black area) in terms of food availability and oxygen concentration. See text for further explanation.

and to a shallowing of the oxygenated sediment-layer. In extreme situations all oxygen will be consumed at the sediment surface, deeper sediment layers will be anoxic, and, as under extremely oligotrophic conditions, all benthic foraminifera will be found exclusively at the sediment-water interface.

A possible complication of this scheme is indicated by the presence of a subsurface maximum of foraminifera, around and even below the redox front (Corliss and Emerson, 1990; Corliss, 1991; Linke and Lutze, 1993). Based on the presence of substantial numbers of foraminifera in apparently completely anoxic sediments, it has been suggested that some species may be facultative anaerobes, which feed on a specific food source related to the redox front (e.g. Bernhard, 1993; Rathburn and Corliss, 1994). In our opinion, such behaviour can only be profitable in food-limited environments. For that reason, and also because we do not find this type of behaviour in very oligotrophic settings, we suggest that this deep, redox-front bound infauna is typical of relatively mesotrophic conditions. We suspect that in more oligotrophic areas, the distance to the redox front may simply become to large to allow this type of feeding behaviour.

4. An illustration of the TROX-model: a sample transect through the Adriatic Sea.

In order to illustrate the validity of our model, we present the general microhabitat characteristics for 15 stations along a sample transect through the Adriatic Sea (Fig. 4.2). Data on individual species distributions will be presented elsewhere (De Stigter et al., this thesis, Chapter 3). All stations were sampled in March 1991 with a conventional box-corer; muddy sediments were found at all stations, and all sediment surfaces were apparently undisturbed (Biasini et al., 1990). The box was opened on one side, all of the sediment (a 2 cm thick vertical slice) previously touching the side walls was removed, and a (measured) surface of 20 - 40 cm^2 was selected for sampling. The superficial unconsolidated muds were taken off with a spoon (every 0.5 or 1.0 cm) and for all deeper, consolidated sediment 1 cm thick slices were taken from the side of the box with a trowel. All samples were stored in a 1 g/l solution of Rose Bengal in ethanol. Stained foraminifera were collected wet from the 63-150 and 150-595 µm sieve fractions. During sorting of stained foraminifera, a very conservative approach was adopted, and specimens were only considered stained, if a bright red colour was detected in several chambers. In case of doubt, specimens were broken in order to study their contents. We feel confident that the big majority of the stained foraminifera were alive at the time of collection. In the Adriatic Sea, where the temperature of the bottom waters is about 13-14°C (Buljan and Zore-Armanda, 1976), protoplasma degradation is probably a much faster process than in cold (1-2°C) open ocean bottom waters.

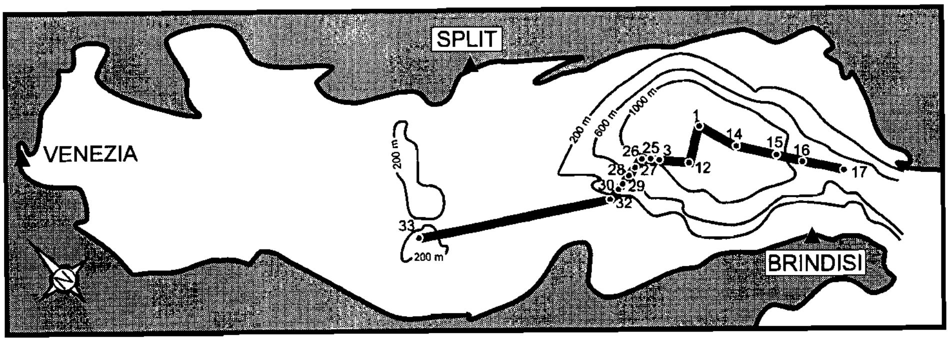

Fig. 4.2. Location of the studied sample transect through the Adriatic Sea, with the 15 stations studied, and their bathymetry.

In general, the deeper parts of the Adriatic Sea can, like the entire Mediterranean Sea, be considered as oligotrophic. However, part of the large shelf area is strongly influenced by the outflow of the Po river, which is one of the largest rivers in the Mediterranean (average annual discharge volume: 50 km^3). The runoff products cause eutrophicated conditions in the whole northern part of the Adriatic Sea, which is one of the most productive areas of the Mediterranean (Sournia, 1973; Degobbis et al., 1979). A counter-clockwise surface current system transports land-derived organic matter and marine phytoplankton detritus in southward direction along the Italian coast. Our 15 sample stations (Fig. 4.2) were positioned in the 1250 m deep southern basin, on the rather steep slope, in the 250 m deep central basin, and on the outer shelf. Following Suess (1980), we assume that the amount of organic matter transported to the benthic ecosystem is controlled by production in the surface waters and by the water depth. Thus, along our sample transect, the deep southern basin can be considered as the oligotrophic extreme, and the upper shelf station as the (relative) eutrophic extreme. Of course the shallow shelf areas in the vicinity of the Po outlets are far more productive than our upper shelf station. The central Adriatic basin is probably somewhat food-enriched by density currents branching off from the nutrient-rich waters which are transported southward across the shelf (Franco et al., 1982).

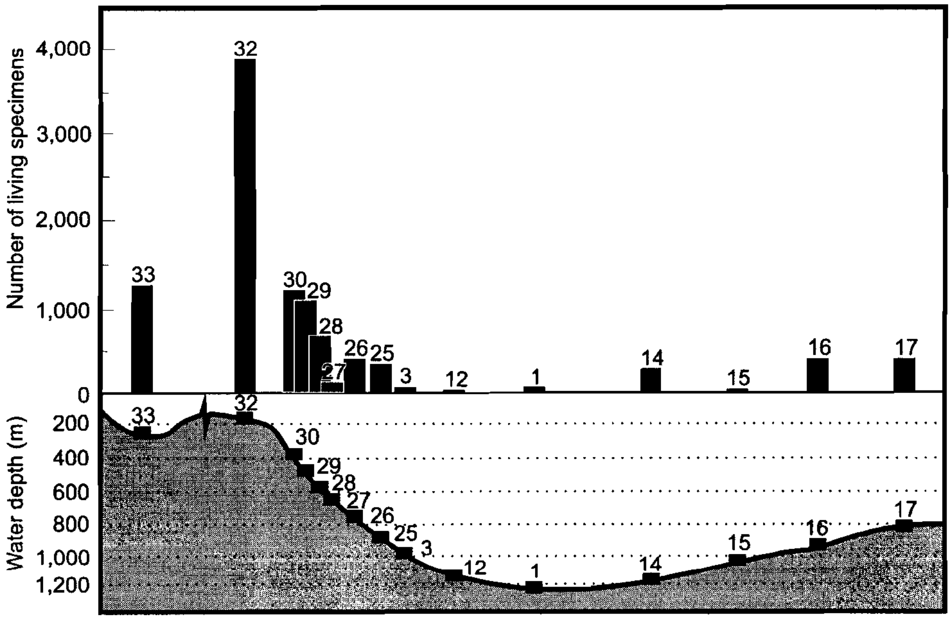

Fig. 4.3. Total numbers of stained foraminifera for a 5 cm deep sediment column, standardized for a

This general trend of organic matter input to the benthic ecosystem is clearly reflected by the total numbers of stained benthic foraminifera in the top 5 cm of the sediment (Fig. 4.3, all values standardized to a surface of 50 cm^2). We see minimum numbers of about 100 stained foraminifera in the deep basin and on the lower slope, intermediate values (300-700) on the middle slope, relatively high values (1000-1500) on the upper slope and in the 250 m deep central basin, and a maximum of 4000 stained foraminifera per 50 cm^2 on the outer shelf. An exception to this trend is the very low foraminifer density in station 27. We explain this by the position of the station on a steep part of the slope, where the organic matter input is possibly lowered by downslope currents.

A comparison with literature data (summary in Douglas and Woodruff, 1981) shows that the values for the deep basin are very low in comparison with data from similar water depths, confirming the oligotrophic character of the Adriatic Sea. In relative terms (with respect to the variation observed in the Adriatic Sea), we will consider the middle slope as mesotrophic, and all shallower environments as eutrophic.

In the counts of the total number of foraminifera (Fig. 4.3), we did not include tubular fragments of *Hyperammina*, *Rhizammina* and similar genera, which are strongly concentrated in the topmost level; their density is depicted in Figure 4.4. We

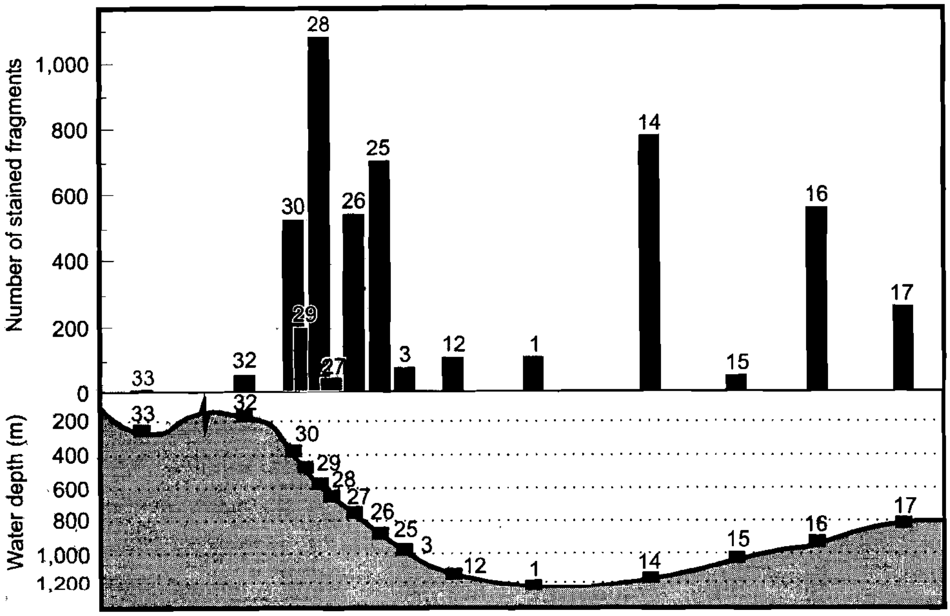

Fig. 4.4. Total numbers of stained fragments of *Hyperammina* and *Rhizammina* in the 15 stations.

see maximum numbers on the middle and upper slope, and minimum numbers in the deep basin. It has been suggested that the abundance of these supposed suspension feeding foraminifera is related to current activity (Linke and Lutze, 1993). Therefore the pattern in Fig. 4.4 could indicate increased current velocities at our slope stations. The fact that we find high numbers of these deep sea taxa (compare Jones and Charnock, 1985; maximum in the Atlantic Ocean between 1650 and 2250 m depth) at a relatively shallow depth (400-900 m) confirms the oligotrophic character of the Adriatic Sea.

For our general description of microhabitat patterns, we considered only perforate calcareous taxa. We have two reasons for this:

(1) almost all arenaceous taxa (and miliolid taxa, which are very poorly represented) have a strong epifaunal tendency. Many of them may be suspension feeders, and their vertical distribution will not vary. Especially in the (middle slope) stations where they are frequent, the behaviour of infaunal taxa would be obscured by their inclusion, and

(2) most of the arenaceous taxa do not fossilize, which would diminish the applicability of our data for the reconstruction of paleoenvironments.

In Figure 4.5, we show the average living depth (ALD_x) for the perforate component of the fauna. Because not all stations were sampled down to the same depth, we considered only stained foraminifera found in the top 5 cm (ALD_5). Figure 4.5 shows a very clear trend; we see a relatively shallow ALD, of about 1 cm, in the central basin and on the lower part of the slope. Most foraminifera live close to the sediment-water interface there. When moving upslope, we see a gradual increase of the microhabitat depth, until a maximum value of 1.81 cm at 578 m depth. In still shallower stations, we see a shallowing of the microhabitat depth, culminating in very low values on the upper shelf and in the central basin. This time, not only station 27, but also station 26 (which is also situated on the steepest part of the slope), shows an anomalous value, which is possibly the result of downslope transport, resulting in trophic conditions which are too poor for this water depth. When considering these data, one should keep in mind that we only considered the top 5 cm of the sediment. If we would have included deeper sediment layers, then the ALD would have increased in the stations which have already a deep ALD, because in these stations we still found significant numbers of stained foraminifera at the deepest sampling level. The ALD of the stations with a shallow microhabitat would not have changed, because in these stations the lowermost levels hardly contained any stained foraminifera.

Figure 4.6, in which the ALD's have been plotted against the foraminiferal density (used as a measure of organic input to the benthic ecosystem), confirms the

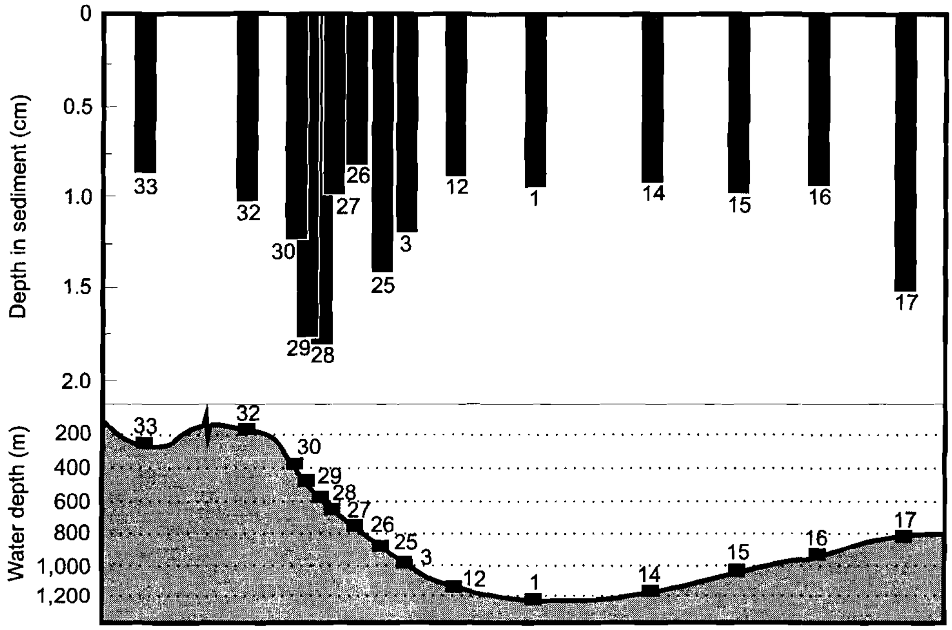

Fig. 4.5. Average living depth in the top 5 cm (ALD_5, see text for definition) of the perforate component of the stained fauna in our 15 stations.

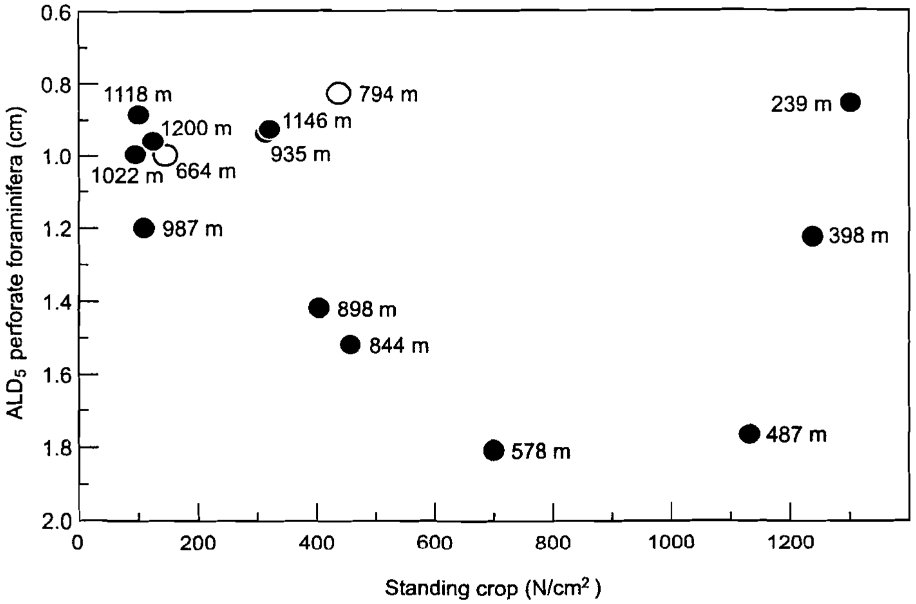

Fig. 4.6. ALD_5 (see Figure 4.5) plotted against the total number of stained foraminifera; the open dots indicate stations where we suspect relatively impoverished nutritive conditions due to downslope transport.

gross relation between microhabitat and trophic level. In the deep southern basin, where we expect the most oligotrophic conditions, we see a very superficial microhabitat. If we move upslope, increasing foraminiferal densities (indicative of a higher organic input) are accompanied by a deepening of the microhabitat depth. In terms of our model (Fig. 4.1), this would mean that in this part of the Adriatic Sea, the microhabitat depth is food-controlled. In the deep basin, the majority of the food particles are consumed at the surface, and within the sediment there is not enough food to sustain an important infauna. Upslope, the organic input will increase, and consequently, the deeper sediment layers will contain more food particles, as well as foraminifera feeding on this subsurface resource. Maximum microhabitat values are found between 600 and 450 m, in an environment which can be considered as mesotrophic. If we go to still shallower environments, we see a rather abrupt drop in the ALD. It is clear that in this part of the Adriatic Sea, an increase in trophic level does no longer lead to an increase in microhabitat depth. Unfortunately we do not have oxygen measurement for the present data set. However, Jorissen et al. (1992) showed a positive relationship between the density of infaunal specimens and the oxygen concentration of the bottom water in the extremely eutrophic shelf environments of the northern Adriatic Sea. Furthermore, Barmawidjaja et al. (1992) found strong indications that the benthic foraminiferal microhabitat fluctuated as a function of seasonal variations of the depth of the redox front. These data show that in the strongly eutrophicated upper shelf environments, the microhabitat depth is oxygen-controlled. On the basis of the present data, we think that this is also the case for the central basin and on the upper slope, and that the turnover point from an oxygen-controlled microhabitat depth to a food-controlled microhabitat depth is situated at a water depth of about 400 m.

Four species show in several stations a maximum frequency at some depth in the sediment: *Cassidulinoides bradyi*, *Chilostomella czizeki*, *Fursenkoina tenuis* and *Globobulimina pyrula*. In Figure 4.7 their cumulative densities (standardized for a 50 cm^2 sample surface) have been plotted for six stations. It should be noted that even when taken together, these four species are infrequent in comparison with the numbers of foraminifera found at the sediment surface. If we use the average living depth (ALD_5) as a measure, we see that the habitat depth of this group of species gradually deepens from shelf/upper slope to middle slope. A maximum is reached in station 28 (578 m depth). In station 27 (664 m depth) and in all deeper stations, these species are no longer found. As explained previously, we suggest that at depths shallower than 400 m, food is not a limiting parameter, and that the habitat depth is related to a critical oxygen level. Below 400 m, the system apparently becomes food-controlled. The high values for the ALD_5 found in stations 29 and 28 could be the result of species burrowing down to additional food sources associated with the redox front (as suggested by Corliss and Emerson, 1990; Corliss, 1991; and Bernhard, 1992). It should be noted that in these stations, there are still numerous stained specimens present in the 4-5 cm level; if we had sampled to a greater depth, the ALD would probably have been still larger! Unfortunately, oxygen data, which should have enabled us to check that these taxa are indeed living around the redox front, were not available. The complete disappearance of these deep infaunal species below 600 m probably indicates that the increasing distance to the redox front, and the increasing compaction of deeper sediment layers, virtually impede foraminifera to dig to this additional food source, or even, that in these increasingly oligotrophic environments metabolizable organic matter is no longer present around the redox front.

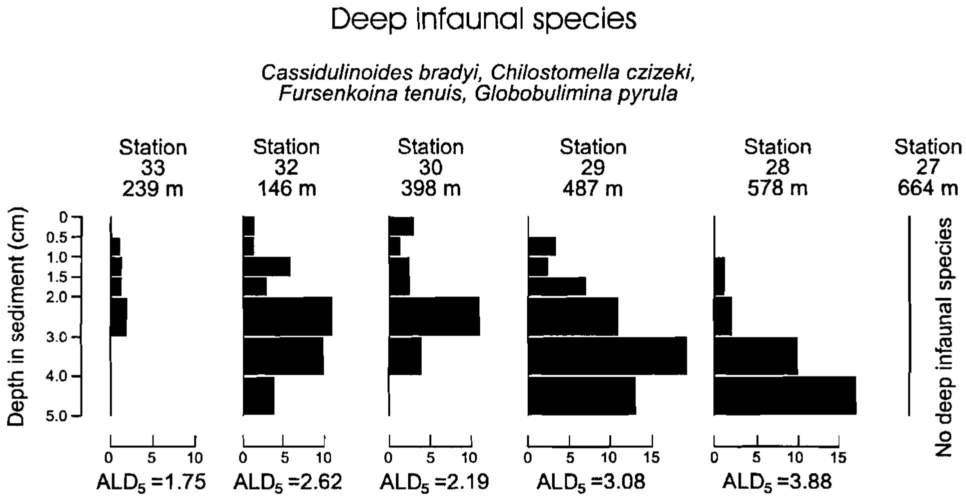

Fig. 4.7. Total number of "deep infaunal species" in the top 5 cm of 6 successive stations between 239 and 664 m depth.

5. Discussion and conclusions

The present model, in which benthic foraminiferal microhabitats vary as a function of the interplay between food availability and oxygen concentration, explains many of the apparently contradictory observations published in the literature. It shows why in some (relatively oligotrophic) areas there exists a positive relationship between the organic flux and the microhabitat depth, whereas in other (more eutrophic) areas this relationship is negative.

Although the model shows that the relationship between the organic flux and the microhabitat depth is not a unidirectional, linear one, it does not deny the supposed relationship between the organic flux and the *percentage* of infauna (Corliss and Chen, 1988). If we go from oligotrophic towards more eutrophic environments, the depth of the microhabitat deepens, and probably the size of the infaunal niche becomes bigger. This will logically lead to an increase of the percentage of infauna. In the eutrophic, oxygen-controlled environment, the microhabitat depth becomes shallower, and the infaunal niche will thus become smaller. However, the increasing oxygen-stress will preferentially remove the less resistant epifaunal taxa, so that the net result will be a further increase of the percentage of infaunal taxa, until approximately 100% in strongly dysoxic environments like sapropels (e.g; Verhallen, 1990). It is important to realize that under strongly dysoxic conditions these usually infaunal taxa will probably live at the sediment surface. Unstable ecosystems, however, may provide exceptions to this scheme; Several papers (e.g; Barmawidjaja et al., 1992; Gooday, 1993) suggest that certain opportunistic epifaunal species are very successful in the colonization of empty niches. In the case of seasonal re-oxygenation of anoxic environments, where the bulk of the foraminiferal production will be concentrated in a short period, the resulting fauna may very well be dominated by these opportunistic epifaunal pioneer species. This last example illustrates very well the problems with the paleoecological applicability of microhabitat characteristics. General rules, like an increasing percentage of infauna with an increasing organic flux, may yield important information, and can sometimes even allow quantification of a number of parameters, but can only be used if the functioning of the ecosystem under consideration is well understood.

The Adriatic Sea sample transect provides a good illustration of our TROX model. The foraminiferal density, which we use as indicator for the input of organic matter in the benthic ecosystem, shows a very logical pattern. Both the oligotrophic deep basin and the relatively eutrophic upper slope and shelf environments show faunas with rather superficial microhabitats. In the first case the microhabitat is food-controlled, in the second case oxygen appears to be the limiting factor. The deepest microhabitats are found between 400 and 600 m depth. It is here, in an essentially food-controlled, relatively mesotrophic, environment, that we find deep infaunal taxa, which probably forage for metabolizable organic matter around the redox front.

For the near future, we envisage a quantification of the model; it is important to find when exactly (at what organic flux level) a benthic system shifts from food-controlled to oxygen-controlled, and to quantify the relationship between the microhabitat depth, the availability of metabolizable organic matter, and the oxygen concentration of bottom and pore waters. However, many complicating factors (e.g.

sediment porosity, bioturbation, lateral oxygen advection by bottom currents) are interfering with the basic controlling parameters, and will render the quantification of the present model a difficult task.

Acknowledgements

The model presented in this paper is based on many ideas previously published in the literature; especially the work of Y. Shirayama and B.H. Corliss should be mentioned. It also benefitted greatly from discussions with many colleagues. We are especially grateful to G.J. Van der Zwaan and M.A. Buzas, who with their constructive criticism significantly contributed to the materialization of the model. The reviews of A.J. Gooday and M. Langer resulted in some final ameliorations. We thank A.M. Borsetti for her invitation to participate in cruise AD91, and her permission to use the Adriatic Sea material. Henko de Stigter acknowledges financial support from the Netherlands Organization for Scientific Research (NWO), grant no. 751-356-021. Joen Widmark is grateful to the Swedish Natural Science Research Council (NFR) for financial support, including a travel grant (no. R-RA 08810-307).

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CHAPTER 5

Differential rates of benthic foraminiferal test production in surface and subsurface sediment habitats in the southern Adriatic Sea*

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Abstract Live communities and corresponding dead assemblages of benthic foraminifera recovered in box cores from the southern Adriatic Sea differ significantly with respect to the relative abundances of groups and species of foraminifera. Taphonomic destruction of disintegration-prone arenaceous species is held responsible for the observed strong reduction in relative abundance of arenaceous foraminifera in the dead assemblage. Systematic differences in live and dead relative abundances of calcareous and calcite-cemented arenaceous species may not be due to selective taphonomic destruction, but rather to differential rates of test production. We observed that shallow-dwelling foraminifera are often overrepresented in the dead assemblage, compared to their relative number in the live community, whereas deeper-dwelling species tend to be underrepresented. On this basis we hypothesize that test production rate of benthic foraminiferal species may be related to their living depth.

INTRODUCTION

It has for long been recognized that precious information about past environmental conditions may be gained from the study of foraminifera present in fossil marine sediments. Much of the basis for paleoenvironmental interpretation is provided by the study of dead assemblages of foraminifera present in Recent seafloor sediments in relation to known gradients of a.o. water depth, temperature, salinity, oxygen content and organic carbon flux. More detailed and fundamental understanding of the mechanisms controlling foraminiferal distribution is gained from observation of living communities of foraminifera in their natural environment and in laboratory culture.

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submitted to Marine Micropalentology

Such studies have the advantage over dead assemblage studies that they provide direct evidence of foraminiferal behaviour with respect to known environmental parameters. By contrast, dead and fossil foraminiferal assemblages usually contain a time-averaged blend of foraminiferal shells produced over periods of years up to hundreds of years, under different seasonal conditions and in various sedimentary microenvironments, and modified by taphonomic processes. For a meaningful integration of live and dead foraminiferal data, a good understanding is required of the processes transforming a living foraminiferal community into a dead and subsequently into a fossil assemblage.

In this contribution we focus on benthic foraminifera from unconsolidated marine sediments. Figure 5.1 outlines the most important processes which control the generation of fossil benthic foraminiferal assemblages. The living community of foraminifera which produces the foraminiferal shells eventually incorporated in the fossil assemblage, is usually concentrated in the upper few centimetres of the sediment, with maximum densities of individuals occurring near the sediment-water interface. Living foraminifera may be found well below 10 cm depth in the sediment (e.g. Corliss, 1985), but these usually compose a minor part of the total community. The living community may be considered to approach a state of dynamic equilibrium with the surrounding environment. The community size is under normal circumstances determined by the availability of metabolizable food (e.g. Altenbach and Sarnthein, 1989). Seasonal peaks in primary production and organic carbon flux to the benthic environment have been observed to trigger rapid growth of benthic foraminiferal populations (Boltovskoy and Wright, 1976; Murray, 1983; Gooday, 1988; Altenbach, 1992). The taxonomic composition of foraminiferal communities is controlled by limiting physical and chemical parameters, and by complex biological interactions. The sediment layer inhabited by foraminifera is often vertically differentiated with respect to pore-water oxygen concentration, availability of metabolizable organic carbon, and related to this, biological activity. The vertical differentiation of the sediment is often reflected by distinct successions of epifaunal, shallow infaunal and deep infaunal species of foraminifera (e.g. Corliss, 1985; Gooday, 1986). Physical and biological disturbances further create lateral inhomogeneity, resulting in patchy distribution of foraminifera on the seafloor (e.g. Bernstein et al., 1978). Individuals are added to the live community by reproduction, or by import by bottom currents or other transporting agents. Individuals are lost to the live community, yielding empty tests, by death of the organism as a consequence of non-destructive predation or passive ingestion by other organisms, reproduction, cell senescence or disease. Individuals are lost without leaving fossil remains by ingestion and destructi-

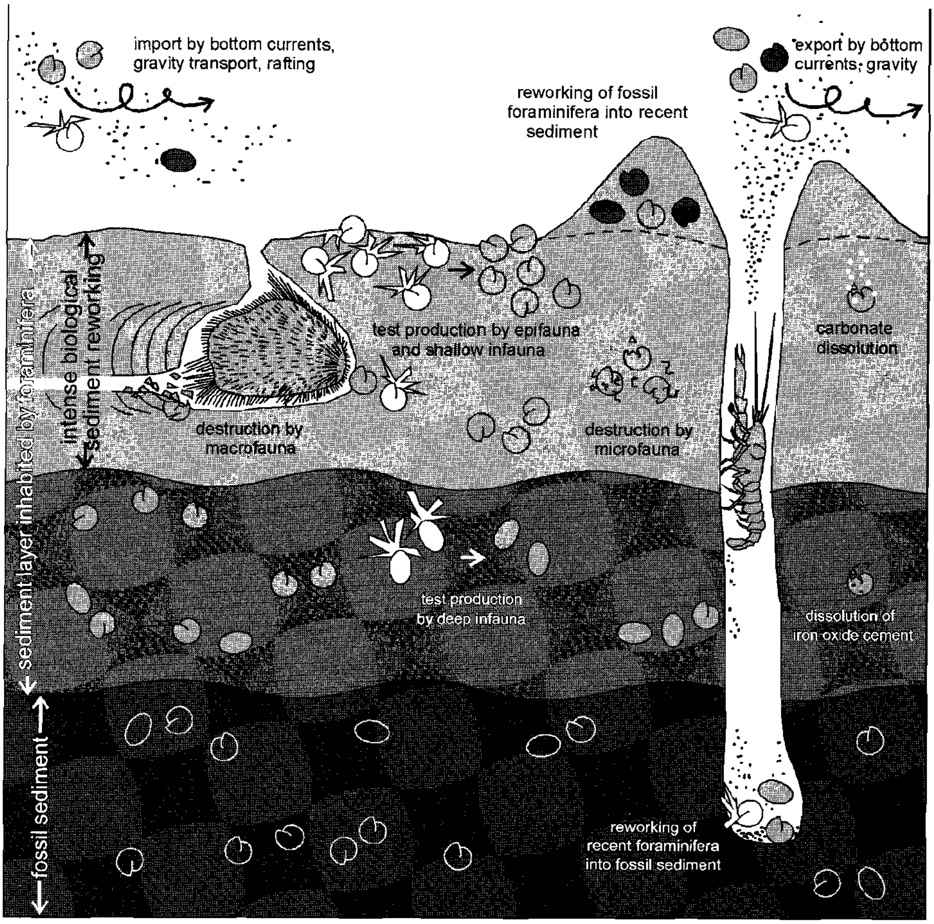

Fig. 5.1. Overview of processes affecting the generation of the benthic foraminiferal assemblage.

on by macrofauna, physical destruction, or by removal by eroding currents.

The dead assemblage forms within the biologically active sediment layer by accumulation of empty foraminiferal shells produced in situ by the living community. Vertical zonation of the living community may initially be reflected in the dead assemblage, but usually zonation is partially or completely obliterated by biological sediment mixing. Bottom currents and gravitational sediment transport may introduce allochthonous foraminifera of Recent age or older to the dead assemblage (e.g. Murray et al., 1982; Gibson, 1989), and where ancient sediments underlying the Recent cover are within the reach of deep-burrowing macrofauna, the dead assemblage may be contaminated with much older material. In extreme cases where no Recent sedimentation occurs, residual sediments may be found containing a fossil fauna totally unrelated to the present-day living community. Foraminifera may locally be removed from the dead assemblage by sediment erosion, but of more importance to the evolution of the dead assemblage are processes of selective destruction. Calcitic and aragonitic tests are destroyed by dissolution in carbonate-undersaturated deep-sea waters, and in acidified pore-waters of organic carbon-enriched sediments (e.g. Douglas and Woodruff, 1981). Many arenaceous foraminifera disintegrate completely after death of the organism. Some tests are only weakly cemented with easily degradable organic cement. Other species use iron-oxide compounds in their cement, which become instable in the reducing environment below the oxidized surface sediment layer (Schröder, 1988). Partially corroded and weakened arenaceous tests become vulnerable to mechanical destruction by burrowing organisms and later by compaction of the sediment. Biological activity is an important additional cause of destruction of foraminiferal tests. Etching and boring by bacteria, protozoans and metazoan meiofauna, and passive ingestion by deposit-feeding macrofauna and passage through their digestive tracts, leads to weakening or complete destruction of tests (Mageau and Walker, 1975; Lipps, 1983). Chemical and biological destruction is most intense in the upper layer of the sediment, which is continuously reworked by benthic fauna. Here the greatest changes in composition of the dead assemblage usually occur, with fragile species decreasing downwards in abundance, and destruction-resistant species becoming relatively enriched (Denne and Sen Gupta, 1989; Mackensen and Douglas, 1989). The tests of deep infaunal species, produced below the zone of most intense test destruction, may suffer less destruction (Loubere et al., 1993).

The fossil assemblage is established by burial of the mixed and modified dead assemblage below the zone of biological activity. The boundary between biologically active surface sediment and fossil sediment is usually a very gradual one. Arbitrarily the boundary can be taken as the lower limit of diffuse biological mixing, which in slowly accumulating sediments may be located on the basis of the vertical distribution of the short-lived radionuclide ^{210}Pb (halflife 22 years). Large burrowing animals may incidentally burrow much deeper, however, reworking fossil foraminifera into the Recent sediment layer, and Recent foraminifera into the fossil layer. Diagenetic processes may affect the fossil assemblage well below the surfacial sediment layer (Douglas and Woodruff, 1981). The abundance of foraminiferal shells in the fossil sediment is determined by the autochthonous production and allochthonous input of foraminifera, minus the loss by taphonomic destruction and erosion, and by dilution with sediment. The taxonomic composition of the fossil assemblage reflects the composition of the original live community, with addition of allochthonous species and subtraction of non-fossilizing species. The relative proportions of species in the fossil assemblage differ from those in the live assemblage, depending on differences in the rate of test production and the rate of test destruction in different species, averaged over time spans of many years up to hundreds of years.

A number of studies have described the effects of taphonomic processes on benthic foraminiferal assemblages (e.g. Wefer and Lutze, 1978; Smith, 1987; Denne and Sen Gupta, 1989; Mackensen and Douglas, 1989; Rathburn and Miao, 1995). Loubere and Gary (1990) and Loubere et al., (1993) related the processes of foraminiferal test production and taphonomic destruction to sediment geochemistry and the organic carbon flux to the sediment. Rates of foraminiferal test production in natural environments appear difficult to assess, and little information has been gathered in the literature on this point. Ratios of benthic foraminiferal production rate to standing stock compiled by Murray (1983) vary between 1:1 and 12:1, suggesting large differences in foraminiferal production rates. Loubere et al. (1993) assumed in their fossil assemblage generation model that benthic foraminiferal test production rate is proportional to available pore water oxygen, which decreases with depth in the sediment.

The aim of the present study is to investigate rates of test production in benthic foraminifera from the southern Adriatic Sea. We do this by comparing live foraminiferal abundances in box cores with dead foraminiferal accumulation rates. The relative importance of different species as contributors to the dead assemblage is assessed qualitatively by comparing the relative abundances of species in live and dead assemblages. The land-enclosed southern Adriatic basin, which has a maximum depth of more than 1200 m, seems a good site to perform such a study. The presence of a Holocene sediment cover in the studied area, with estimated sediment accumulation rates varying between 2 and 20 cm ka^{-1}, suggests that the foraminiferal assemblage present in the surface sediment is reasonably complete and representative for present environmental conditions. Carbonate preservation is good in the relatively warm (12.4-13.8°C: Guibout, 1987; Orlić et al., 1992) and carbonate-saturated bottom water and in the organic carbon-poor sediments, as testified by the good preservation of calcitic and aragonitic pteropod fossil material. Foraminiferal preservation is also favoured by low productivity (e.g. Revelante and Gilmartin, 1977; Dugdale and Wilkerson, 1988) of southern Adriatic surface waters and the consequently low biological activity on the seafloor. Finally, the absence of sharp temperature contrasts below the thermocline (e.g. Guibout, 1987; Orlić et al, 1992) precludes the possibility of temperature-dependent differences in foraminiferal productivity.

A more detailed account of the bathymetric distribution of live benthic foraminifera along the studied transect in the southern Adriatic Sea, and their vertical distribution in the sediment, is presented in two other papers (Jorissen et al., 1995; De Stigter et al., this thesis, Chapter 3). Some of these data which are relevant for the present study are summarized here.

MATERIALS AND METHODS

Live and dead benthic foraminiferal assemblages investigated in the present study were collected from a series of 8 box cores, raised from the bottom of the southern Adriatic Sea in March 1991, by a team of the University of Bologna, Italy, and the Institute of Marine Geology of Bologna, aboard the R.V. Minerva. The selected box cores cover a bathymetric transect descending from 146 m waterdepth on the shelf off Vieste, Italy, down the basin slope to 1200 m depth in the centre of the South Adriatic Basin (Fig. 5.2). Position and depth of the box core stations, and a summary of sediment characteristics, are listed in Table 5.1.

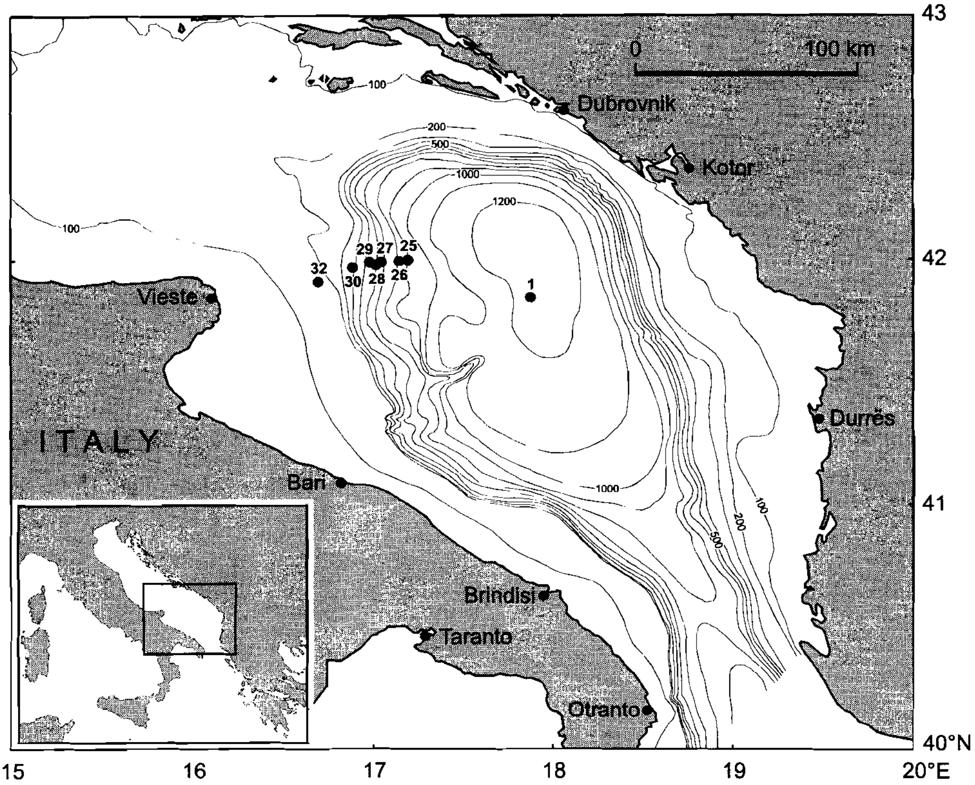

Fig. 5.2. Bathymetric map of the South Adriatic Basin, with location of the box core stations.

Sandy mud was encountered in the shallowest station, whereas sediments in all other stations consist of silty clay. In a number of cores a gradual transition from yellowish brown oxidized surface sediment to grey or greyish brown reduced sediment deeper downcore was noticed. Based on the rather subjective appreciation of sediment colour, the oxidized sediment layer appears to increase in thickness from 4 cm on the shelf to about 19 cm in the deepest part of the basin.

Table 5.1 Geographical position and water depth of the box core stations, sediment characteristics, and surface area and vertical interval of subsamples.

core	latitude (N)	longitude (E)	depth (m)	sediment type	subsample area (cm2)	subsample interval (cm)
AD91-32	41°54.80	16°41.75	146	sandy mud	32	0-0.5, 0.5-1, 1-1.5, 1.5-2, 2-3, 3-4, 4-5, 5-6
-30	41°59.00	16°55.50	398	silty clay	20	0-0.5, 0.5-1, 1-2, 2-3, 3-4, 4-5
-29	41°59.50	16°58.75	487	silty clay	28	0-0.5, 0.5-1, 1-1.5, 1.5-2, 2-3, 3-4, 4-5, 5-6, 6-7, 7-8, 8-9, 9-10
-28	41°59.00	17°01.00	578	silty clay	30	0-1, 1-2, 2-3, 3-4, 4-5, 5-6
-27	41°59.50	17°02.75	664	silty clay	42	0-0.5, 0.5-1, 1-1.5, 1.5-2 2-3, 3-4, 4-5, 5-6, 6-7, 7-8, 8-9, 9-10
-26	41°59.80	17°08.70	794	silty clay	25	0-1, 1-2, 2-3, 3-4, 4-5, 5-6
-25	42°00.00	17°11.75	898	silty clay	33	0-0.5, 0.5-1, 1-1.5, 1.5-2, 2-3, 3-4, 4-5, 5-6, 6-7, 7-8, 8-9, 9-10
-01	41°50.84	17°52.48	1200	silty clay	20	0-0.5, 0.5-1, 1-1.5, 1.5-2 2-3, 3-4, 4-5, 5-6, 6-7, 7-8, 8-9, 9-10

For benthic foraminiferal microhabitat studies, sediment subsamples were carefully taken off with a spoon from an area of box core of between 20 and 42 cm^2, at vertical intervals of 0.5 or 1 cm till 2 cm depth, and at 1 cm intervals till 5 or 10 cm depth. Subsamples were immersed in a Rose Bengal in ethanol solution (1 g l^{-1}) and gently shaken to disperse the sediment. In the laboratory, the samples were freeze-dried, and washed with tap-water over sieves of 63, 150 and 595 μm mesh-width. Live (Rose Bengal stained) foraminifera were collected wet from transparent gridded trays from the complete 63-150 μm and 150-595 μm fractions, and stored in micropaleontological slides. This was done for all samples between 0 and 5 cm, and also for a number of samples between 5 and 10 cm. For comparison with the dead assemblage, counts from the 63-150 and 150-595 µm fractions were combined. Only specimens containing dense, brightly red stained protoplasm were counted as alive. Counting lists of stained foraminifera are included in Appendix A. Foraminifera with only diffuse or superficial stain were neglected. Arenaceous and calcitic foraminifera were collected systematically, as well as fragments of Astrorhizid foraminifera, which were very abundant in samples from the basin slope. *Globigerina*-inhabiting foraminifera, however, and soft-walled and tunnelling Allogromiids, were not systematically collected.

After the stained foraminifera had been removed from the samples, dead (unstained) foraminifera were collected from the remaining residues of the 0-0.5 or 0-1 cm (for brevity indicated as the 0-1 cm interval in the following) and 4-5 cm subsamples of all box cores. An Otto microsplitter was used to obtain manageable quantities (between 200 and 300 specimens per sample per size fraction) of dead foraminifera. Counts of the 63-150 and 150-595 µm fractions were combined. Original counting lists of dead foraminifera are included in Appendix B.

The classical study of Eastern Mediterranean foraminifers of Parker (1958) served as a guide for the identification of many of the common species. The revision of Brady's (1884) work on Atlantic foraminifera by Barker (1960) proved helpful for the identification of especially arenaceous foraminifera. Additional sources include studies of Adriatic foraminifera by Jorissen (1988) and Barmawidjaja et al. (1992). Infrequent and taxonomically diverse groups, including all imperforates, were identified only to generic or even higher taxonomic level, with reference to Loeblich and Tappan (1987a, 1987b).

In 5 of the 8 selected box cores the downcore distribution of ^{210}Pb was determined by gamma spectrometry, to assess the vertical extent of diffuse biological sediment mixing (Fig. 5.3). The presence of ^{210}Pb activity in excess of background activity is indicative of relatively recent deposition of the sediment, or mixing of older sediment with recently deposited material. Excess ^{210}Pb activity is reduced to less than 1% of the initial activity within 150 years (or roughly 7x the halflife of 22 years). In all cores where ^{210}Pb was measured, excess ^{210}Pb was found to several centimetres depth in the sediment, much deeper than can be accounted for by the sediment accumulation rate of 2 to 20 cm ka^{-1}. The observed ^{210}Pb profiles are therefore more likely to reflect biological sediment mixing.

Sediment accumulation rates (*SAR*) could not be determined directly for the box cores, as reliable horizons for stratigraphic correlation were lacking in the cores. We therefore used biochronostratigraphic data from a number of piston cores recovered in the same area, partially published in Jorissen et al. (1993). Sediment thickness above the Holocene-Pleistocene boundary in these piston cores, divided by the ^{14}C AMS age of this boundary of 9.6 ka BP (see Jorissen et al., 1993), yields sedimentation rate values for the Holocene varying between 3.3 and 24 cm ka^{-1}. The values of *SAR* generally increase with water depth (Fig. 5.4), which may be explained by winnowing of fine-grained sediment on the shelf edge and upper slope, and preferential deposition of fines in the deeper part of the basin. A simple mathematical function obtained by linear regression of the data plotted in Figure 5.4 was subsequently used to estimate *SAR* values for the studied box cores. Benthic foram accumulation rates (*BFAR*) were obtained by multiplying benthic foraminiferal abundance per sediment volume with *SAR*.

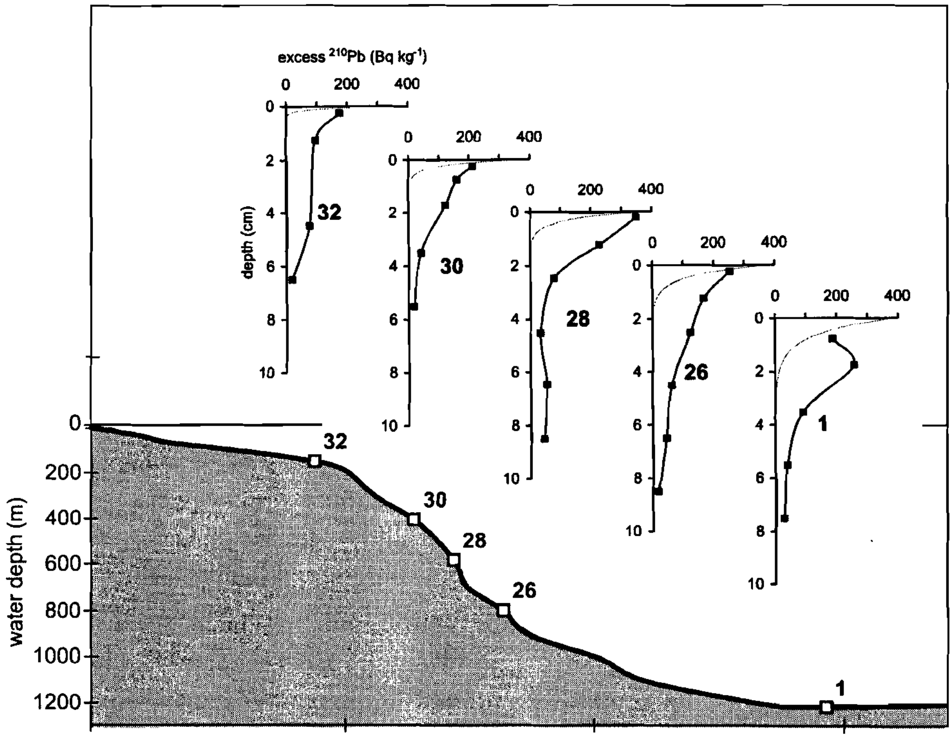

Fig. 5.3. Downcore distribution of excess ^{210}Pb activity, as estimated by gamma-spectrometry from ^{214}Pb activity. The theoretical distribution of excess ^{210}Pb, assuming no vertical mixing, sediment accumulation rates as derived from Fig. 5.4, and constant ^{210}Pb flux, is indicated by the thinner line. The position of the box cores along the bathymetric gradient is indicated in the lower part of the Figure.

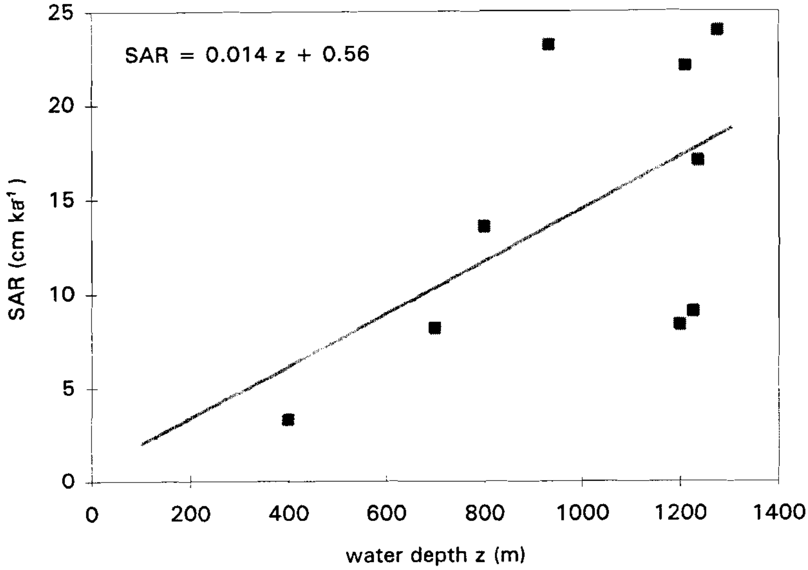

Fig. 5.4. Plot of sediment accumulation rates (*SAR*) in southern Adriatic piston cores vs. waterdepth (*z*). Data partially derived from Jorissen et al. (1993).

RESULTS

General characteristics of live communities and dead assemblages

The abundance of live (stained) benthic foraminifera (Astrorhizids excluded) in the combined 63-595 μm fraction decreases rapidly with increasing water depth, from 78 individuals per square centimetre of sediment in core 32 to less than 3 cm^{-2} in core 1 (Fig. 5.5). Astrorhizid fragments are irregularly distributed, with maximum abundances on the basin slope (Fig. 5.5). In all cores, the highest density of stained foraminifera is found near the sediment-water interface, and numbers decline exponentially deeper into the sediment (Fig. 5.6). More than half of the population is living shallower than 1 cm in the sediment, whereas only a small proportion is found deeper than 5 cm in the more extensively subsampled box cores: less than 5% in cores 32, 29 and 27, 0% in core 1, but possibly more than 10% in core 25.

Dead foraminifera (Astrorhidzids excluded) are far more abundant than live ones, their density per cubic centimetre of sediment varying between 10.10^3 to 39.10^3 for, respectively, the 0-0.5 and the 4-5 cm intervals of core 32, and between 135 and 146 for the 0-0.5 and 4-5 cm intervals of core 1 (Fig. 5.7). Foraminiferal density is often higher in the 4-5 cm interval than at the surface.

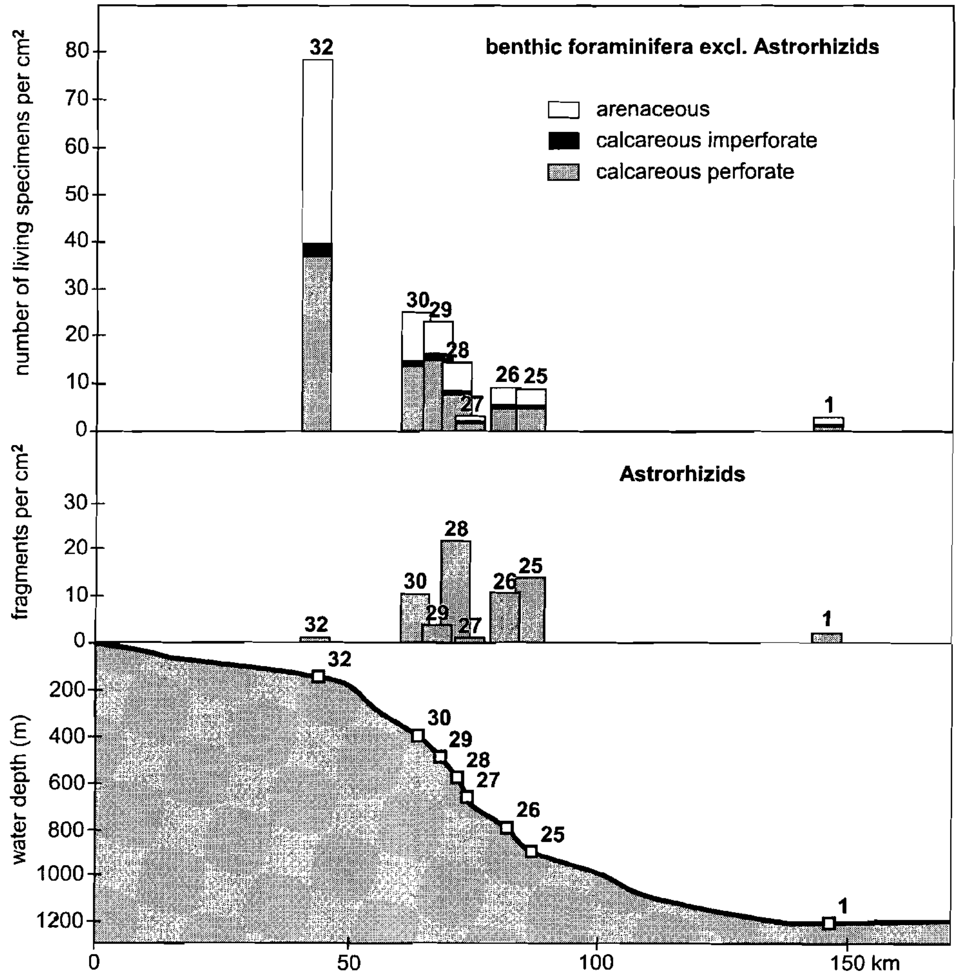

Fig. 5.5. Standing stocks of stained benthic foraminifera (Astrorhizids excluded) in southern Adriatic box cores (upper panel), and abundance of stained Astrorhizid fragments (middle panel).

In all cores, the dead assemblages are very different from the corresponding live assemblages with respect to the relative abundances of arenaceous and calcareous foraminifera (Fig. 5.8, Table 5.2). Excluding Astrorhizidae, arenaceous foraminifera constitute between 37 and 66% of live communities, but only between 6 and 18% of the dead assemblage of surface (0-1cm) samples, and consistently less, between 3 and 16%, in the 4-5 cm samples. For comparison, calcareous perforates constitute between 30 to 61% of live communities, between 68 and 86% of surface dead assemblages, and between 64 and 87% of the deeper dead assemblages. Accounting

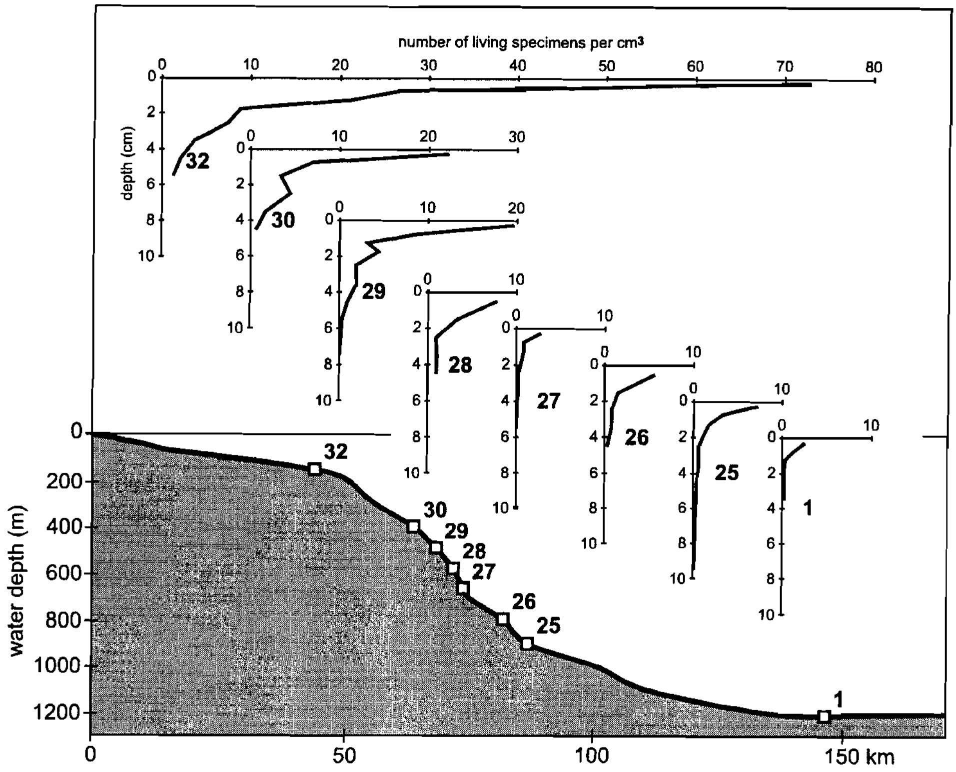

Fig. 5.6. Vertical distribution of stained benthic foraminifera (Astrorhizids excluded) in the studied box cores.

for only 6% at most, calcareous imperforates are least represented in the live assemblages, but significantly higher abundances, up to 15%, are observed in the dead assemblages. Arenaceous foraminifera are not only less abundant in the dead assemblages by relative number of specimens, compared to the live community, but also by number of common species: the number of arenaceous species or species groups represented by 10 or more specimens is 32 for a total number of 4711 collected live foraminifera (excluding Astrorhizids), but only 12 for 4419 dead specimens of the 0-1 cm interval, and 12 for 4739 dead specimens of the 4-5 cm interval. For calcareous perforates the numbers of common species or species groups are 43 for the total live community, and 46 and 47 for, respectively, the dead assemblage of the 0-1 and 4-5 cm intervals.

Astrorhizid fragments are more numerous than all other live foraminifera together in some of the stations on the slope of the southern Adriatic basin. In the dead

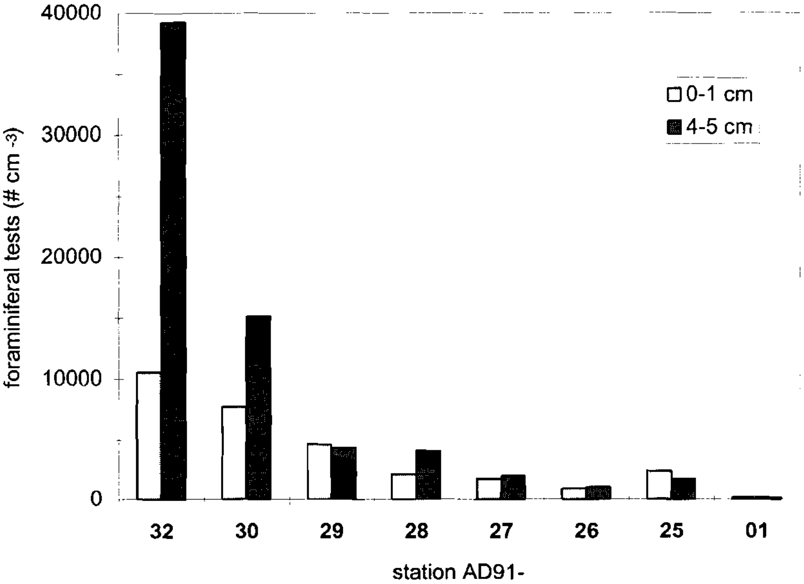

Fig. 5.7. Abundance of dead benthic foraminifera, standardized per cubic centimetre of sediment, in the 0-1 cm (light-grey bars) and the 4-5 cm (dark-grey bars) intervals of box cores.

Table 5.2. Relative abundances (%) of major groups of benthic foraminifera in live communities and dead assemblages of southern Adriatic box cores. The abundance of Astrorhizids is given as percentage relative to the total of non-Astrorhizid groups.

station:	**32**			**30**			**29**			**28**		
live/dead:	live	dead		live	dead		live	dead		live	dead	
interval (cm):	0-5	0-0.5	4-5	0-5	0-0.5	4-5	0-5	0-0.5	4-5	0-5	0-1	4-5
calcareous perforate	49.9	82.4	84.3	41.9	86.3	84.5	30.2	82.0	83.5	43.2	81.9	85.4
calcareous imperforate	2.8	7.3	8.2	2.8	5.2	10.9	4.3	8.4	8.3	2.6	9.8	6.8
arenaceous	47.4	10.4	7.5	55.3	8.4	4.6	65.6	9.6	8.3	54.2	8.3	7.9
Astrorhizid fragments	*1.45*	*0.0*	*0*	*42.5*	*1.3*	*0.38*	*17.2*	*2.9*	*0.14*	*155*	*5.1*	*0.46*

station:	**27**			**26**			**25**			**01**		
live/dead:	live	dead		live	dead		live	dead		live	dead	
interval (cm):	0-5	0-0.5	4-5	0-5	0-1	4-5	0-5	0-0.5	4-5	0-5	0-0.5	4-5
calcareous perforate	40.8	87.5	86.3	42.4	80.4	88.1	40.1	79.0	84.3	61.2	69.8	70.4
calcareous imperforate	5.6	6.7	9.1	3.1	12.6	8.8	2.2	12.8	10.7	2.0	12.3	14.6
arenaceous	53.6	5.9	4.5	54.5	7.0	3.1	57.7	8.2	5.0	36.7	17.9	15.0
Astrorhizid fragments	*33.6*	*0.8*	*0*	*121*	*9.1*	*0.63*	*167*	*16.1*	*4.13*	*89.8*	*38.2*	*22.7*

assemblages, however, much lower numbers are found, diminishing downcore.

The low preservation potential of many arenaceous species is the most likely explanation for the relative scarcity of arenaceous foraminifera in the dead assemblage. The downcore decrease in abundance of arenaceous foraminifera, also apparent in the Astrorhizid group, gives evidence for the progressive taphonomic destruction of arenaceous foraminiferal tests. Further evidence is given by the often abraded appearance of empty tests, and bleaching of the initially orange-brown iron oxide cement of some species (e.g. *Adercotryma glomeratum*, *Eggerella scabra*, *Trochammina inflata*, *Saccorhiza ramosa*, etc.), indicating dissolution of the iron oxide component of the cement. Arenaceous species which are well-preserved in the dead assemblage are those which have a calcite cement: a number of Textularid species

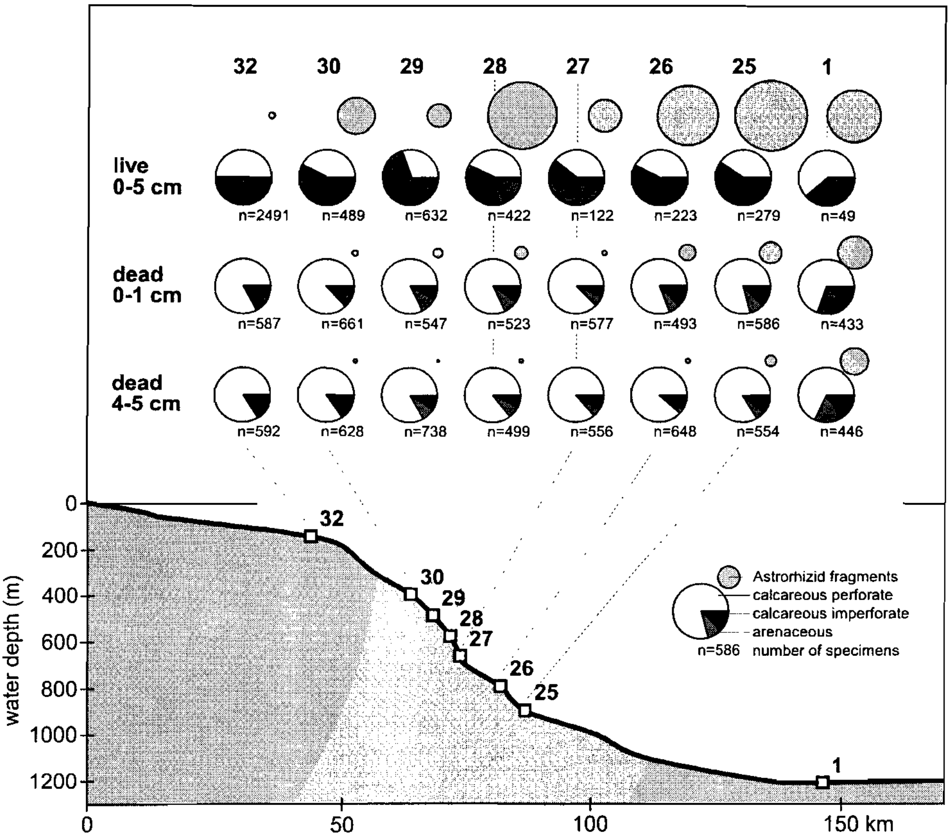

Fig. 5.8. Relative abundance of major groups of benthic foraminifera in live communities, and in dead assemblages of the 0-1 cm and 4-5 cm intervals. The proportion of Astrorhizid fragments (shaded circle) relative to the total of non-Astrorhizid groups is indicated by the area of the circle. Note the strong reduction in abundance of arenaceous foraminifera and Astrorhizids in the dead assemblages, as compared

and *Pseudoclavulina crustata*. Calcareous perforates and imperforates are well-preserved in the studied cores. Calcite dissolution apparently plays an insignificant role in the taphonomic modification of the dead assemblage. Due to the elimination of a large portion of the arenaceous component, calcareous foraminifera become relatively enriched in the dead assemblage. For further quantitative comparison of live and dead assemblages, we will now focus on the fossilizing, that is the calcareous and calcite-cemented arenaceous foraminifera, excluding all organic-cemented arenaceous foraminifera.

In Figure 5.9 estimated accumulation rates of fossilizing dead benthic foraminifera are plotted against standing stocks of fossilizing live foraminifera. For estimation of benthic foram accumulation rate we averaged the dead foraminiferal density of the 0-1 and 4-5 cm interval of the box cores. For each living individual, between 1 and 11 (average 4.6) dead foraminifera are added each year to the sediment.

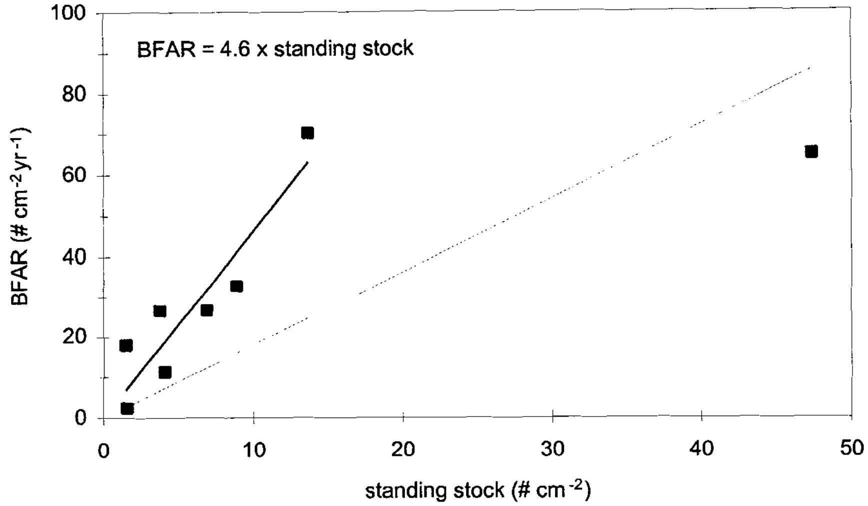

Fig. 5.9. Plot of benthic foraminiferal accumulation rate (*BFAR*) vs. standing stock of fossilizing (calcareous and calcite-cemented arenaceous) foraminifera. The outlying data point represents core 32. Linear regression (with 0 intercept) was calculated from all data (thin line), and from all data minus the outlying point (bold line). A regression equation is only given for the bold line.

The dead assemblages of surface and deeper samples

The relative abundance of species in the dead assemblage of 0-1 and 4-5 cm intervals of the box cores, calculated as a percentage of the total of fossilizing foraminifera, is listed in Table 5.3. Five species are significantly more abundant

Table 5.3. Relative abundance of common calcareous and calcite-cemented arenaceous taxa in 0-1 and 4-5 cm dead assemblages (calculated as % of total calcareous and calcite-cemented assemblage). Significantly ($P<0.05$) differing percentages are marked by shading. Columns on the right give the total numbers of specimens counted per species, average living depth (ALD), difference ratio R, and preservational rank (1: robust species, 2: medium species, 3: fragile species). No ALD was calculated for species represented by less than 10 dead specimens in both the 0-1 cm and 4-5 cm interval.

core: interval:	**32** 0-0.5	 4-5	**30** 0-0.5	 4-5	**29** 0-0.5	 4-5	**28** 0-1	 4-5
calcareous perforates	*82.7*	*84.7*	*87.9*	*85.3*	*85.0*	*85.4*	*84.5*	*87.7*
Alliatina primitiva	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.3
Amphicoryna scalaris	0.2	0.2	0.3	0.5	0.7	1.1	0.7	0.3
Anomalina sp.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Anomalinoides minimus	0.0	0.0	0.5	0.3	1.0	1.9	2.0	0.7
Anomalinoides sp.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Asterigerinata spp.	2.1	3.5	1.1	1.1	0.3	0.3	0.7	0.3
Asterononion sp.1	0.3	0.0	0.9	0.3	0.3	0.5	0.1	0.7
Bolivina albatrossi	0.0	0.5	0.3	1.7	0.6	0.2	1.3	0.3
Bolivina dilatata	0.6	0.1	0.0	0.3	1.0	0.3	0.3	0.7
Bolivina spathulata	9.6	11.0	10.5	9.2	6.1	6.8	8.4	6.5
Bolivina subspinescens.	0.3	0.3	0.0	1.0	0.3	1.0	0.3	0.3
Bulimina aculeata	4.3	3.1	0.9	1.5	1.3	1.5	0.7	1.9
Bulimina costata	1.0	0.2	5.5	3.1	2.9	3.5	5.3	2.3
Bulimina marginata	4.6	3.7	4.7	4.7	4.1	5.0	3.9	4.9
Cassidulina crassa	7.1	9.2	13.9	10.7	17.5	14.0	8.0	12.4
Cassidulina laevigata	9.1	7.1	13.8	7.8	8.4	9.8	11.0	9.6
Cassidulina oblonga	3.0	1.8	1.6	1.2	2.8	0.5	0.7	0.4
Cassidulinoides bradyi	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cibicides pachydermus	0.2	0.3	0.3	0.1	0.7	0.2	0.3	0.1
Cibicides spp.	4.1	3.7	2.4	1.1	2.2	2.2	1.9	2.4
Dentalina spp.	0.1	0.0	0.3	0.3	0.5	0.2	0.0	0.1
Elphidium spp.	9.9	10.3	1.0	1.7	0.5	0.9	1.0	1.1
Epistominella exigua	0.0	0.3	0.3	1.4	1.0	0.2	0.7	0.3
Epistominella vitrea	0.6	3.4	1.3	2.0	1.0	1.5	1.3	2.3
Eponides sp.1	0.9	2.3	1.3	0.7	1.0	1.2	0.7	3.4
Eponides sp.2	0.0	0.0	0.0	0.0	0.3	0.3	0.0	0.0
Fissurina spp.	0.3	0.0	0.4	0.5	0.6	0.9	0.7	1.0
Fursenkoina tenuis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gavelinopsis praegeri	4.1	3.0	4.6	6.6	4.5	4.5	3.7	3.9
Globobulimina pyrula	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0
Globocassidulina subglobosa	1.2	4.4	4.0	5.8	7.2	7.6	9.3	8.4
Gyroidina altiformis	0.2	0.1	0.1	0.0	0.6	0.2	0.5	0.5
Gyroidina orbicularis	0.1	0.3	0.2	0.1	0.6	1.0	0.5	0.4
Gyroidina umbonata	0.8	0.4	1.6	1.6	2.3	1.2	1.7	0.6
Gyroidinoides sp.1	0.0	0.0	0.3	0.7	2.2	1.7	1.3	1.7
Hanzawaia boueana	0.8	1.0	0.6	1.1	0.3	0.8	0.5	0.5

27		**26**		**25**		**1**		**specimens**		**ALD**	**R**	**type**
0-0.5	4-5	0-1	4-5	0-0.5	4-5	0-0.5	4-5	0-1	4-5			
90.2	*87.5*	*85.8*	*89.9*	*84.5*	*88.1*	*84.2*	*82.4*	*3445*	*3795*	*1.2*	*0.0*	
0.3	0.4	0.4	0.3	0.3	0.4	3.2	0.5	11	6	1.3	0.3	3
0.3	0.5	0.4	0.3	0.0	0.4	0.0	0.0	27	42	0.7	-0.2	2
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0	0	0.9		2
1.7	2.5	2.3	6.0	2.7	1.9	6.0	9.8	46	63	0.9	-0.2	2
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0	0	2.2		2
0.3	0.4	0.0	0.0	0.7	0.0	0.0	0.0	20	23		-0.1	1
0.3	0.8	0.0	0.3	0.7	0.0	0.0	0.0	12	9		0.0	2
0.9	0.8	1.9	0.7	1.3	1.5	0.4	0.5	20	18	1.1	0.0	2
0.6	0.4	0.4	0.3	0.0	0.4	0.0	0.5	9	10	1.1	0.1	2
5.0	8.4	1.5	2.4	2.4	3.4	0.8	1.5	180	211	0.9	0.0	2
0.3	0.4	0.0	0.3	1.0	0.4	0.0	0.0	7	14	1.0	-0.3	2
0.3	1.3	0.0	0.7	0.3	0.4	0.0	0.0	53	63		-0.1	1
2.8	1.5	0.0	1.0	2.0	0.4	0.0	0.0	141	121	0.4	0.2	2
2.3	2.5	1.9	2.1	1.0	2.7	0.0	0.5	179	208	1.0	-0.1	2
19.7	15.1	23.1	21.2	17.9	17.9	19.5	17.3	422	410	0.7	0.0	2
7.7	8.9	3.4	3.7	4.0	5.7	0.8	1.0	270	276	0.6	0.1	2
0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	42	31	1.1	0.3	1
0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1	0	2.9		3
0.4	0.1	0.0	0.0	0.0	0.0	0.1	0.0	22	18	0.8	0.4	1
0.4	0.5	1.2	1.0	1.4	1.2	2.5	1.7	105	86		0.1	1
0.3	0.0	0.8	0.7	0.0	0.0	1.4	0.0	18	7	1.6	0.4	1
0.9	0.4	0.0	0.7	0.0	0.0	0.0	0.0	81	94		-0.1	1
1.4	0.8	5.7	3.4	7.1	3.0	3.2	4.9	55	37	0.7	0.2	3
4.9	6.7	4.9	5.7	4.4	7.4	1.2	5.4	60	99		-0.3	3
2.0	2.5	3.8	6.0	2.7	4.1	0.8	2.9	40	69	1.8	-0.3	3
0.6	0.8	0.8	0.0	0.0	0.4	0.0	0.0	5	5			2
1.5	0.5	0.0	1.0	3.0	0.8	1.3	4.0	34	42	1.1	0.0	2
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0	0	3.3		3
4.3	2.7	0.4	3.4	2.7	2.6	0.8	1.0	105	140	0.8	0.0	2
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0	3	3.3		3
10.9	6.4	10.4	7.5	8.8	11.3	5.8	3.1	223	217	1.5	0.0	1
0.1	0.0	0.5	0.9	0.1	0.8	5.2	1.5	78	56		0.1	1
0.1	0.5	0.0	0.1	0.0	0.0	1.7	0.4	34	53	1.1	-0.1	1
3.2	1.8	2.3	6.0	2.7	3.4	4.9	2.9	82	68	0.6	0.1	2
0.9	1.2	3.4	2.0	2.7	3.3	2.0	1.0	37	37	1.5	0.0	2
0.6	0.9	0.8	0.0	0.7	0.4	0.0	0.0	29	40	1.3	-0.2	2

Table 5.3 continued

Hanzawaia rhodiense	0.2	0.0	0.1	0.4	0.0	0.0	0.0	0.1
Hyalinea balthica	1.3	1.0	2.1	1.9	1.2	0.8	2.3	2.2
Lagena spp.	0.5	0.0	0.2	0.4	0.7	0.0	0.3	0.1
Lenticulina spp.	0.0	0.4	0.2	0.6	1.0	0.2	0.9	0.9
Melonis barleeanum	1.6	0.8	0.2	0.9	0.2	0.8	0.2	1.1
Nonionella sp.1	0.0	0.0	0.5	1.4	0.6	0.3	0.7	1.0
Nonionella sp.2	0.3	0.3	0.0	0.3	1.0	0.5	0.0	0.3
Planulina ariminensis	0.0	0.0	0.1	0.9	1.2	1.0	0.6	0.8
Pullenia quinqueloba	0.1	0.2	0.1	0.4	0.1	0.2	0.0	0.1
Robertina translucens	0.0	0.1	0.3	0.3	0.0	0.4	0.7	0.0
Rosalina bradyi	0.8	1.3	1.0	0.5	0.3	1.2	0.3	0.7
Rosalina globularis	0.0	0.0	0.6	0.8	0.4	0.1	0.7	0.3
Rosalina spp.	0.0	0.2	0.1	0.3	0.0	0.9	0.5	0.3
Rotamorphina involuta	0.4	0.3	0.0	0.4	0.4	0.2	0.0	0.4
Seabrookia earlandi	0.0	0.0	0.5	0.0	0.0	0.5	0.3	1.0
Siphonina reticulata	0.0	0.0	0.0	0.0	0.4	0.1	0.0	0.3
Sphaeroidina bulloides	0.5	0.3	0.5	0.5	0.1	0.1	0.7	0.2
Spirillina spp.	0.0	0.3	0.0	0.3	0.0	0.0	0.1	0.1
Svratkina tuberculata	0.0	0.3	0.5	0.0	0.3	0.3	0.0	0.0
Trifarina angulosa	0.9	1.0	2.7	2.8	1.4	1.2	2.0	1.9
Trifarina pauperata	1.2	0.5	0.5	0.0	0.0	0.9	0.7	1.3
Uvigerina mediterranea	2.9	3.2	1.7	1.4	1.1	2.1	2.1	2.0
Uvigerina peregrina	2.7	2.5	2.2	1.8	0.9	0.9	2.1	1.3
Uvigerina proboscidea.	0.0	0.1	0.2	0.0	0.1	0.1	0.2	0.1
calcareous imperforates	*7.3*	*8.2*	*5.3*	*11.0*	*8.7*	*8.4*	*10.2*	*7.0*
fossilizing arenaceous	*10.0*	*7.1*	*6.7*	*3.7*	*6.3*	*6.2*	*5.3*	*5.4*
Bigenerina nodosaria	2.3	2.1	1.7	0.6	2.1	1.0	1.3	0.5
Pseudoclavulina crustata	0.4	0.1	0.1	0.0	0.2	0.2	0.3	0.3
Siphotextularia concava	0.8	0.4	0.4	1.0	0.8	1.4	0.1	0.3
Textularia agglutinans	4.8	2.8	3.2	0.6	1.5	1.7	2.4	1.7
Textularia conica	0.2	0.7	0.4	0.2	0.7	0.4	0.9	1.8
Textularia sagittula	1.5	1.0	0.9	1.3	1.0	1.5	0.4	0.7
total fossilizing	*100*	*100*	*100*	*100*	*100*	*100*	*100*	*100*
robust species	*37.6*	*38.8*	*23.1*	*23.6*	*24.8*	*23.3*	*25.9*	*27.0*
medium	*59.6*	*53.8*	*72.6*	*69.4*	*70.7*	*71.4*	*69.5*	*63.4*
fragile species	*2.8*	*7.5*	*4.3*	*7.0*	*4.4*	*5.3*	*4.6*	*9.5*

(P<0.05) in the 4-5 cm interval than in the 0-1 cm interval in one of the 8 cores, nine species are significantly less abundant in the 4-5 cm interval in one of the cores, but in all cases opposing trends are found in one or more of the other cores. Significant but opposing trends are observed in 2 of the cores for *Epistominella vitrea* and *Globocassidulina subglobosa*. In core 30 imperforate foraminifera are significantly

0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3	3	1.0		3
0.6	1.7	1.9	0.3	1.4	0.4	0.0	0.0	61	54		0.1	1
0.9	0.0	0.4	1.0	0.7	0.0	1.7	2.0	36	20	1.1	0.4	2
0.3	0.9	0.8	0.4	0.0	0.0	0.5	0.2	32	32		0.1	1
0.3	0.1	0.0	0.7	0.0	0.0	0.2	0.1	26	40	1.2	-0.3	1
0.9	1.2	1.1	2.4	2.0	1.1	3.6	3.4	27	29		-0.1	2
0.6	0.4	1.9	1.3	1.0	1.5	0.0	1.5	14	18	0.9	-0.1	3
0.4	0.7	0.0	0.1	0.0	0.0	0.6	0.1	31	52	1.6	-0.2	1
1.2	0.9	0.0	0.0	0.4	0.4	0.0	0.0	15	16	1.7	-0.1	2
0.3	0.0	0.0	0.7	0.4	0.0	0.4	1.0	14	15		0.2	3
0.3	0.5	0.8	0.3	0.7	1.5	0.0	0.0	21	34	0.9	-0.2	1
0.6	0.5	0.0	0.0	0.0	0.4	0.0	0.0	14	21		0.1	2
1.2	1.7	0.4	0.3	1.0	0.4	0.8	0.0	14	20		-0.2	2
0.9	0.0	0.8	0.7	2.0	1.5	9.3	2.0	43	22	1.1	0.4	3
0.3	0.4	0.0	0.0	0.7	0.7	0.0	0.5	6	10	0.7	-0.3	3
0.0	0.0	0.4	0.0	0.0	0.4	0.0	0.0	5	5	1.5		1
0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	21	13		0.2	3
0.0	0.5	0.0	0.0	0.3	0.8	0.0	0.5	5	12		-0.5	3
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3	3	1.5		1
0.4	1.0	0.0	0.0	0.0	0.8	0.0	0.0	63	80	0.8	-0.1	1
0.6	0.0	0.8	0.0	1.0	0.7	0.0	0.5	15	14	2.4	0.0	2
1.2	1.6	0.3	0.8	0.1	1.1	2.6	3.8	210	411	0.8	-0.2	1
2.3	2.9	1.7	1.9	0.8	0.6	1.5	1.5	234	224	1.1	0.0	1
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	8	4			2
6.9	*9.3*	*13.4*	*9.0*	*13.7*	*11.1*	*14.8*	*17.1*	*428*	*466*	*1.0*	*0.0*	*2*
3.0	*3.2*	*0.8*	*1.1*	*1.7*	*0.8*	*1.0*	*0.5*	*275*	*227*	*1.4*	*0.1*	
0.7	0.9	0.0	0.4	0.3	0.4	0.0	0.0	75	50	1.2	0.1	2
0.1	0.0	0.0	0.0	0.0	0.0	0.1	0.0	24	11	0.9	0.4	2
0.4	0.9	0.4	0.3	0.7	0.0	0.0	0.0	27	38		-0.1	2
1.2	0.5	0.4	0.3	0.0	0.4	0.8	0.0	97	68	1.8	0.3	2
0.3	0.0	0.0	0.0	0.0	0.0	0.1	0.0	22	24		0.0	2
0.3	0.9	0.0	0.0	0.7	0.0	0.0	0.5	30	36	1.7	-0.1	2
100	*100*	*100*	*100*	*100*	*100*	*100*	*100*	*4148*	*4488*	*1.2*	*0.0*	
19.4	*19.2*	*18.7*	*16.3*	*14.3*	*18.4*	*22.2*	*12.5*	*1384*	*1591*		*0.0*	*1*
69.5	*68.6*	*63.1*	*65.5*	*66.8*	*62.2*	*59.6*	*67.3*	*2487*	*2576*		*0.0*	*2*
11.0	*12.2*	*18.1*	*18.2*	*18.9*	*19.4*	*18.1*	*20.2*	*277*	*321*		*-0.1*	*3*

more abundant in the 4-5 cm interval, and in the same core fossilizing arenaceous foraminifera apparently decrease downcore, but again opposing trends are present in some other cores.

To investigate the possible influence of differential preservation on the downcore distribution of foraminifera, we somewhat arbitrarily assigned species to three groups of dissolution and fragmentation-resistant *'robust'*, moderately resistant *'medium'* and poorly resistant *'fragile'* species. Robust, thick-walled, non-transparent species, such as *Cibicides pachydermus*, *Globocassidulina subglobosa*, *Gyroidina altiformis*, *Melonis barleeanum*, *Planulina ariminensis*, *Uvigerina mediterranea* were assigned to the first group, a number of moderately resistant species, including imperforates and fossilizing arenaceous foraminifera, were included in the second group, whereas fragile, transparent-looking species, for example *Cassidulinoides bradyi*, *Alliatina primitiva*, *Epistominella exigua*, *Epistominella vitrea*, *Globobulimina affinis*, *Robertina translucens* and *Rotamorphina involuta* were assigned to the third. The relative abundances of these groups, listed also in Table 5.3, are significantly different between 0-1 cm and 4-5 cm samples in a number of cases, but systematic trends are not observed. More in general, we conclude that although the relative abundance of individual species and groups may differ significantly for the 0-1 cm and 4-5 cm intervals in a number of cases, no systematic downcore trends become apparent.

To quantify the relative difference in species abundance in 0-1 cm and 4-5 cm dead assemblages, we calculated for each core for the common species (represented by 10 or more specimens in the total dead fauna of either or both the 0-1 and 4-5 cm intervals) a 'difference ratio' R_i as follows:

$$R_i = \frac{(d_{(0\text{-}1cm),i} - d_{(4\text{-}5cm),i})}{(d_{(0\text{-}1cm),i} + d_{(4\text{-}5cm),i})} \qquad (5.1)$$

where $d_{(0\text{-}1cm),i}$ and $d_{(4\text{-}5cm),i}$ are, respectively, the relative abundance of a species in the dead assemblage of the 0-1 cm and 4-5 cm interval of core i. For species which are exclusively found in the 0-1 cm interval R_i is +1, species which are equally abundant in the 0-1 and 4-5 cm interval have a neutral R_i value of 0, and for species which are exclusively found in the 4-5 cm interval R_i is -1. A generalized difference ratio R was then obtained as follows:

$$R = \frac{1}{N}\,\Sigma_i\, n_i\, R_i \quad \text{or:} \quad R = \frac{1}{N}\,\Sigma_i\, n_i\, \frac{(d_{(0\text{-}1cm),i} - d_{(4\text{-}5cm),i})}{(d_{(0\text{-}1cm),i} + d_{(4\text{-}5cm),i})} \qquad (5.2)$$

where N is the total number of dead specimens of a species counted and n_i is the total number of specimens counted in core i. R_i's were not simply averaged, because this would give R_i's based on a large number of specimens the same weight as R_i's based on only one or no specimen at all. The resulting ratios for the dead assemblages are listed in Table 5.3.

The difference ratio was plotted against a scale of relative robustness/fragility of species (Fig. 5.10a), and against average living depth (*ALD*) of species in the 0-5 cm interval (Fig. 5.10b) to test whether the vertical distribution of foraminifera in the dead assemblages may be affected by differences in preservation, or reflects their original living depth. Average living depth (*ALD*), generalized for 8 stations, was calculated for common species (10 or more stained specimens in the total live population) as follows:

$$ALD = \frac{1}{N} \Sigma_{ij}\, n_{ij}\, z_{ij} \qquad (5.3)$$

where N is the total number of live specimens of a species counted, n_{ij} is the number of specimens of a species encountered at depth interval j of core i, and z_{ij} is the midpoint depth of depth interval j of core i. The few observations of stained foraminifera below 5 cm depth were not included here. The resulting *ALD*'s are listed in Table 5.3.

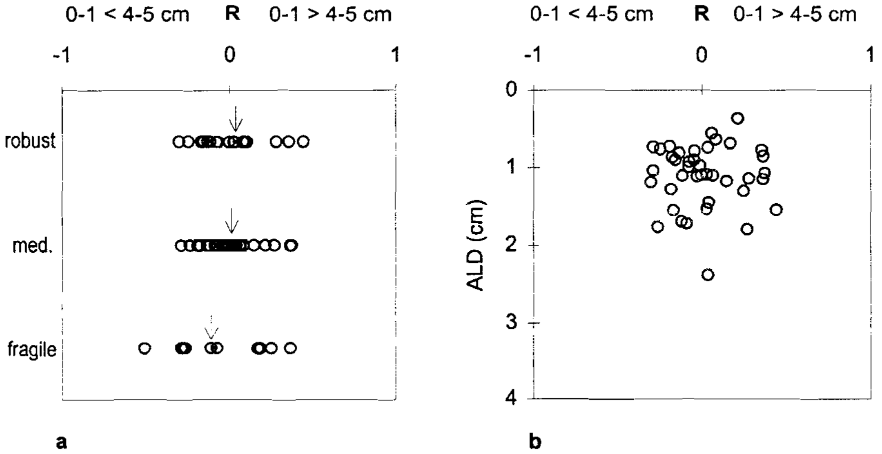

Fig. 5.10. (a) Plot of the 0-1 cm and 4-5 cm dead assemblage difference ratio vs. preservational characteristics of species. Arrows indicate the values for the total robust, medium and fragile group; (b) Plot of the 0-1 cm and 4-5 cm dead assemblage difference ratio vs. average living depth (ALD) of species.

As apparent from Figure 5.10a, the range of R values of individual species does not differ much for robust, medium or fragile species, and the difference ratio calculated for, respectively, all robust and medium foraminifera together is almost 0, suggesting a homogeneous vertical distribution of moderately resistant foraminifera. The difference ratio calculated for all fragile foraminifera together is slightly negative, however, indicating a slight enrichment of fragile foraminifera in the 4-5 cm interval.

The plot in Figure 5.10b shows that R values of species with different average living depth cluster symmetrically around 0, suggesting that original living depth of foraminifera does not result in systematic variation in their vertical distribution.

From the comparison of the 0-1 cm and 4-5 cm dead assemblages we conclude that the vertical distribution of species in the upper 5 cm of sediment is largely homogeneous, although fragile species may be slightly enriched at deeper levels. To obtain a larger sample size for comparison with the live communities, the counts from the 0-1 cm and 4-5 cm intervals of each station were summed, producing composite dead assemblages which we consider representative for the 0-5 cm interval.

Comparison of the live and dead assemblages

Comparing the live and the composite dead assemblages (Table 5.4), we found a large number of significant differences in species relative abundance. For 43 different taxa, more than 100 significant ($P<0.05$) differences were found between the relative abundance in the live communities and corresponding dead assemblages. A significant increase in abundance in the dead assemblage was observed in more than one core in the species *Bulimina costata* (3 cores), *Bulimina marginata* (3 cores), *Cassidulina crassa* (all 8 cores), *Cassidulina laevigata* (6x), *Epistominella vitrea* (3x), *Gavelinopsis praegeri* (3x), *Globocassidulina subglobosa* (6x), *Hyalinea balthica* (3x). Only for *B. costata* opposing but statistically insignificant trends were found in 2 of the remaining cores. In all other cases the remaining data support the observed trend, or are neutral. A decrease in abundance in more than one core was observed in the species *Anomalinoides minimus* (6 cores), *Bolivina dilatata* (2x), *Cassidulinoides bradyi* (4x), *Alliatina primitiva* (3x), *Epistominella exigua* (3x), *Eponides* sp.1 (3x), *Fursenkoina tenuis* (2x), *Gyroidina orbicularis* (4x), *Melonis barleeanum* (7x), *Pullenia quinqueloba* (2x), *Rotamorphina involuta* (4x), *Seabrookia earlandi* (2x), *Siphonina reticulata* (4x), *Uvigerina mediterranea* (2x), *Bigenerina nodosaria* (5x). For some of the mentioned species, opposing trends were found in a few of the remaining cores, but this was mostly due to the occurrence of single specimens, thus having little significance. *Bolivina spathulata* was more abundant alive than dead in station 32, but consistently less abundant in all other stations. Opposing trends were also found in *Uvigerina peregrina*. A number of typically shallow-water taxa (*Asterigerinata mamilla* and *Elphidium* spp.) were present in significant numbers in the dead assemblage on the shelf (core 32), but were not found alive. These probably represent allochthonous or Pleistocene relict faunas, mixed into the Recent sediments. A different colour and a more abraded and polished appearance gives further evidence for the reworked nature of these elements.

As a measure of the relative difference in live and dead abundance of common species, a difference ratio *R* was calculated in a similar manner as the ratio used before to quantify the difference between surface and deeper dead assemblages:

$$R = \frac{1}{N} \Sigma_i \, n_i \, \frac{(l_i - d_i)}{(l_i + d_i)} \tag{5.4}$$

where N is the total number of live specimens of a species, n_i is the number of live specimens in core i, and l_i and d_i are, respectively, the relative abundances of a species in the live community and dead assemblage in core i. For species which are exclusively found in the live community R has a value of +1, species which are equally abundant in the live community and dead assemblage have a neutral R value of 0, and for species which are exclusively found in the dead assemblage R is -1. R was only calculated for species represented by 10 or more live and/or dead specimens. The resulting ratios, listed in Table 5.4, are homogeneously distributed between the extremes of -1 and +1.

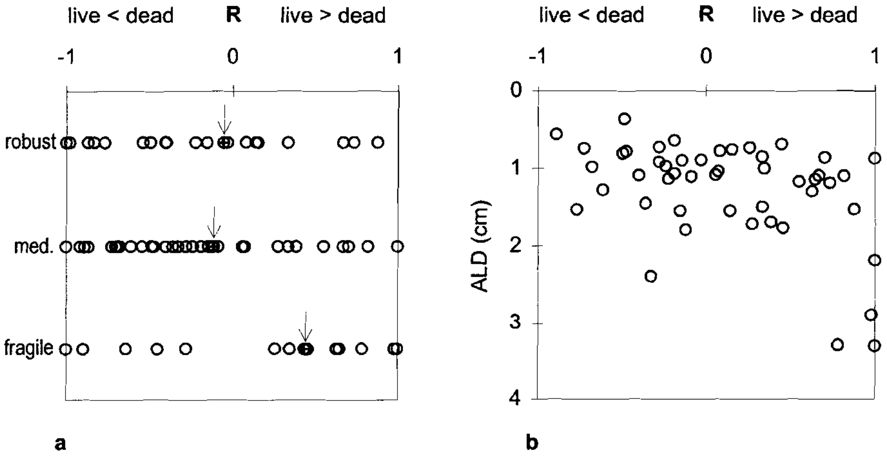

Fig. 5.11. (a) Plot of live-dead difference ratio vs. preservational characteristic of species. Arrows give the value for the total robust, medium and fragile group; (b) Plot of live-dead difference ratio vs. average living depth of species.

The live-dead difference ratios of species plotted against a scale of preservational potential (Fig. 5.11a) show similar ranges between -1 and +1 for robust, medium and fragile species. The values of R calculated for, respectively, all robust and all medium foraminifera together are slightly negative, indicating a slight enrichment of these groups in the dead assemblage. For the fragile group R is well above 0, indicating that fragile foraminifera are underrepresented in the dead assemblage, compared to the corresponding live community. When the live-dead difference ratio is plotted against average living depth of the species (Fig. 5.11b), it appears that R values are asymmetrically distributed around 0 for species with different *ALD*. Of the species

Table 5.4. Relative abundances of common calcareous and calcite-cemented arenaceous taxa in live communities and composite dead assemblages (calculated as percentage of the total calcareous and calcite-cemented assemblage). Significantly ($P<0.05$) differing percentages are marked by shading. Columns on the right give the total numbers of live and dead specimens counted per species, average living depth (*ALD*), difference ratio *R*, and preservational rank (1: robust species; 2: medium species; 3: fragile species). No *ALD* was calculated for species represented by less than 10 live specimens, and no *R* was calculated for species represented by less than 10 specimens in both the live and dead assemblages.

core:	**32**		**30**		**29**		**28**	
live/dead:	live	dead	live	dead	live	dead	live	dead
calcareous perforates	*81.9*	*83.7*	*75.8*	*86.6*	*77.0*	*85.2*	*88.3*	*86.1*
Alliatina primitiva	1.1	0.0	1.5	0.0	0.8	0.1	2.9	0.2
Amphicoryna scalaris	0.5	0.2	0.7	0.4	0.0	1.0	1.0	0.5
Anomalina sp.1	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Anomalinoides minimus	0.3	0.0	3.3	0.4	11.3	1.5	20.4	1.3
Anomalinoides sp.1	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Asterigerinata spp.	0.0	2.8	0.0	1.1	0.0	0.3	0.0	0.5
Asterononion sp.1	0.0	0.1	0.0	0.6	0.0	0.4	0.0	0.4
Bolivina albatrossi	1.3	0.3	1.8	1.0	1.6	0.4	0.5	0.8
Bolivina dilatata	9.4	0.3	3.3	0.2	2.4	0.6	1.5	0.5
Bolivina spathulata	17.9	10.3	2.9	9.8	2.4	6.5	1.9	7.5
Bolivina subspinescens.	1.2	0.3	0.0	0.5	0.8	0.7	0.0	0.3
Bulimina aculeata	0.5	3.7	0.0	1.2	0.0	1.5	0.0	1.3
Bulimina costata	0.6	0.6	1.1	4.3	0.4	3.3	0.5	3.8
Bulimina marginata	1.2	4.2	2.6	4.7	0.8	4.6	0.0	4.4
Cassidulina crassa	2.4	8.2	1.8	12.3	4.4	15.5	4.9	10.2
Cassidulina laevigata	3.0	8.1	0.0	10.8	0.0	9.2	0.0	10.3
Cassidulina oblonga	0.6	2.4	2.2	1.4	0.8	1.5	1.5	0.5
Cassidulinoides bradyi	1.5	0.0	5.1	0.0	15.3	0.0	14.1	0.0
Cibicides pachydermus	1.6	0.3	1.1	0.2	0.0	0.4	0.0	0.2
Cibicides spp.	0.1	3.9	0.7	1.8	0.4	2.2	0.0	2.1
Dentalina spp.	0.5	0.0	0.7	0.3	1.6	0.3	0.5	0.0
Elphidium spp.	0.0	10.1	0.0	1.3	0.0	0.7	0.0	1.0
Epistominella exigua	0.6	0.1	8.4	0.8	2.0	0.5	5.3	0.5
Epistominella vitrea	0.4	2.0	0.4	1.7	0.4	1.3	0.0	1.8
Eponides sp.1	4.0	1.6	5.5	1.0	2.0	1.1	2.9	2.0
Eponides sp.2	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0
Fissurina spp.	1.0	0.1	0.0	0.5	0.0	0.8	0.0	0.9
Fursenkoina tenuis	0.5	0.0	1.8	0.0	3.2	0.0	0.0	0.0
Gavelinopsis praegeri	2.4	3.5	1.8	5.6	0.4	4.5	0.5	3.8
Globobulimina pyrula	0.5	0.0	0.7	0.0	3.6	0.1	0.0	0.0
Globocassidulina subglobosa	0.7	2.8	3.3	4.8	1.2	7.4	0.0	8.9
Gyroidina altiformis	0.0	0.1	0.0	0.0	0.0	0.3	1.5	0.5
Gyroidina orbicularis	0.1	0.2	0.0	0.1	1.6	0.8	1.9	0.5
Gyroidina umbonata	1.3	0.6	0.4	1.6	2.0	1.6	1.0	1.2
Gyroidinoides sp.1	0.3	0.0	1.1	0.5	2.0	1.9	0.0	1.5
Hanzawaia boueana	0.6	0.9	0.4	0.8	0.0	0.6	0.0	0.5

27		**26**		**25**		**01**		**specimens**		**ALD**	**R**	**type**
live	dead	live	dead	live	dead	live	dead	live	dead			
82.3	*88.8*	*93.1*	*88.1*	*90.2*	*86.3*	*96.8*	*83.3*	*2108*	*7240*	*1.2*	*0.0*	
0.0	0.4	2.0	0.4	0.0	0.4	3.2	1.8	31	17	1.3	0.6	3
0.0	0.4	0.0	0.4	0.0	0.2	0.0	0.0	11	69	0.7	-0.3	2
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	10	0	0.9	1.0	2
16.1	2.1	35.3	4.4	21.3	2.3	9.7	8.0	158	109	0.9	0.7	2
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	15	0	2.2	1.0	2
0.0	0.4	0.0	0.0	0.0	0.3	0.0	0.0		43		-1.0	1
0.0	0.6	0.0	0.2	0.0	0.3	0.0	0.0		21		-1.0	2
0.0	0.8	1.0	1.2	0.0	1.4	0.0	0.4	30	38	1.1	0.1	2
0.0	0.5	0.0	0.4	0.0	0.2	0.0	0.3	161	19	1.1	0.8	2
0.0	6.7	0.0	2.0	0.0	2.9	0.0	1.2	290	391	0.9	-0.1	2
0.0	0.4	1.0	0.2	0.0	0.7	0.0	0.0	21	21	1.0	0.1	2
0.0	0.8	0.0	0.4	0.0	0.4	0.0	0.0	8	116		-0.9	1
3.2	2.2	1.0	0.6	0.8	1.2	0.0	0.0	18	262	0.4	-0.5	2
0.0	2.4	1.0	2.0	0.0	1.9	0.0	0.3	28	387	1.0	-0.7	2
1.6	17.4	2.0	22.1	0.8	17.9	0.0	18.3	67	832	0.7	-0.7	2
0.0	8.3	0.0	3.6	0.0	4.9	0.0	0.9	46	546	0.6	-0.9	2
0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	20	73	1.1	-0.2	1
0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	103	1	2.9	1.0	3
0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.1	27	40	0.8	0.1	1
0.0	0.4	0.0	1.1	0.0	1.3	0.0	2.1	5	191		-0.8	1
0.0	0.2	0.0	0.7	0.8	0.0	0.0	0.7	15	25	1.6	0.1	1
0.0	0.6	0.0	0.4	0.0	0.0	0.0	0.0		175		-1.0	1
3.2	1.1	7.8	4.4	4.1	5.0	19.4	4.1	69	92	0.7	0.4	3
0.0	5.8	0.0	5.4	0.0	5.9	0.0	3.4	8	159		-0.9	3
8.1	2.3	9.8	5.1	18.9	3.4	3.2	1.9	126	109	1.8	0.5	3
0.0	0.7	0.0	0.3	0.0	0.2	0.0	0.0		10		-1.0	2
4.8	1.0	0.0	0.6	1.6	1.9	3.2	2.7	21	76	1.1	-0.1	2
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	20	0	3.3	1.0	3
1.6	3.5	2.0	2.1	1.6	2.7	0.0	0.9	49	245	0.8	-0.5	2
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	18	3	3.3	0.8	3
0.0	8.7	1.0	8.8	0.0	10.0	3.2	4.4	24	440	1.5	-0.8	1
0.0	0.1	1.0	0.7	0.0	0.4	0.0	3.3	4	134		-0.5	1
9.7	0.3	4.9	0.1	4.9	0.0	12.9	1.0	31	87	1.1	0.7	1
3.2	2.5	3.9	4.4	0.8	3.0	0.0	3.9	34	150	0.6	-0.2	2
1.6	1.1	0.0	2.6	0.8	3.0	0.0	1.5	15	74	1.5	-0.4	2
0.0	0.8	0.0	0.3	0.0	0.5	0.0	0.0	10	69	1.3	-0.6	2

Table 5.4 continued

Hanzawaia rhodiense	0.7	0.1	0.0	0.2	0.0	0.0	0.0	0.0
Hyalinea balthica	0.1	1.1	0.0	2.0	0.0	1.0	0.0	2.3
Lagena spp.	0.3	0.2	0.0	0.3	0.4	0.3	0.0	0.2
Lenticulina spp.	0.3	0.2	0.7	0.4	0.4	0.5	0.0	0.9
Melonis barleeanum	7.5	1.2	1.1	0.6	3.2	0.6	6.8	0.7
Nonionella sp.1	0.1	0.0	0.4	0.9	0.0	0.5	0.0	0.8
Nonionella sp.2	1.4	0.3	0.0	0.2	0.0	0.7	0.0	0.2
Planulina ariminensis	0.4	0.0	1.1	0.5	0.8	1.1	0.5	0.7
Pullenia quinqueloba	0.2	0.1	3.7	0.2	0.0	0.2	2.4	0.0
Robertina translucens	0.1	0.0	0.4	0.3	0.0	0.2	0.0	0.4
Rosalina bradyi	1.2	1.0	5.9	0.8	0.0	0.8	1.0	0.5
Rosalina globularis	0.0	0.0	0.0	0.7	0.0	0.2	0.0	0.5
Rosalina spp.	0.3	0.1	0.0	0.2	0.0	0.5	0.0	0.4
Rotamorphina involuta	0.0	0.3	0.0	0.2	1.2	0.3	3.9	0.2
Seabrookia earlandi	0.5	0.0	0.7	0.3	2.4	0.3	0.0	0.7
Siphonina reticulata	0.4	0.0	2.2	0.0	2.4	0.2	3.9	0.2
Sphaeroidina bulloides	0.0	0.4	0.4	0.5	0.0	0.1	0.5	0.5
Spirillina spp.	0.0	0.1	0.0	0.2	0.0	0.0	0.0	0.1
Svratkina tuberculata	0.7	0.1	0.0	0.3	0.4	0.3	0.0	0.0
Trifarina angulosa	2.3	1.0	0.7	2.8	0.0	1.3	0.0	1.9
Trifarina pauperata	1.3	0.9	0.4	0.3	0.0	0.5	0.0	1.0
Uvigerina mediterranea	4.7	3.1	2.9	1.5	2.0	1.7	1.5	2.1
Uvigerina peregrina	0.9	2.6	0.4	2.0	0.8	0.9	1.5	1.7
Uvigerina proboscidea.	0.0	0.0	0.0	0.1	0.0	0.1	0.5	0.1
calcareous imperforates	*4.6*	*7.8*	*5.1*	*8.1*	*10.9*	*8.6*	*5.3*	*8.6*
fossilizing arenaceous	*13.5*	*8.5*	*19.0*	*5.3*	*12.1*	*6.2*	*6.3*	*5.3*
Bigenerina nodosaria	5.3	2.2	9.9	1.2	9.3	1.5	4.9	0.9
Pseudoclavulina crustata	0.1	0.2	1.1	0.0	0.4	0.2	1.0	0.3
Siphotextularia concava	0.4	0.6	0.0	0.7	0.0	1.1	0.5	0.2
Textularia agglutinans	3.4	3.8	6.2	2.0	1.2	1.6	0.0	2.0
Textularia conica	0.1	0.5	0.0	0.3	0.0	0.5	0.0	1.3
Textularia sagittula	4.2	1.3	1.8	1.1	1.2	1.3	0.0	0.6
total fossilizing	*100*	*100*	*100*	*100*	*100*	*100*	*100*	*100*
robust species	*22.8*	*38.2*	*23.1*	*23.4*	*15.7*	*23.9*	*20.4*	*26.5*
medium	*65.8*	*56.7*	*50.2*	*71.0*	*52.8*	*71.1*	*48.1*	*66.5*
fragile species	*11.5*	*5.2*	*26.7*	*5.6*	*31.5*	*5.0*	*31.6*	*7.0*

with *ALD* less than 1 cm, 11 have negative *R* values, against 7 with a positive *R*. The balance is shifted for species with *ALD* of 1 cm or more: 10 species have a negative *R*, against 19 with a positive *R*. Relatively shallow-dwelling species (*ALD*<1) are thus often overrepresented (*R*<0) in the dead assemblage (examples in favour: *Bolivina spathulata*, *Bulimina costata*, *B. marginata*, *Cassidulina crassa*, *C.*

0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	10	6	1.0	0.3	3
0.0	1.2	0.0	1.0	0.0	0.9	0.0	0.0	1	115		-1.0	1
3.2	0.5	0.0	0.7	2.5	0.4	0.0	1.9	11	56	1.1	-0.2	2
0.0	0.6	0.0	0.6	0.8	0.0	0.0	0.3	8	64		-0.4	1
3.2	0.2	6.9	0.4	2.5	0.0	9.7	0.1	153	66	1.2	0.7	1
0.0	1.1	0.0	1.8	0.0	1.6	0.0	3.5	3	56		-0.9	2
0.0	0.5	0.0	1.6	0.0	1.2	0.0	0.8	21	32	0.9	-0.3	3
0.0	0.6	1.0	0.0	0.8	0.0	0.0	0.3	14	83	1.6	-0.2	1
4.8	1.0	1.0	0.0	0.0	0.4	0.0	0.0	22	31	1.7	0.4	2
0.0	0.2	1.0	0.4	0.0	0.2	0.0	0.7	3	29		-0.6	3
0.0	0.4	0.0	0.5	0.0	1.1	0.0	0.0	36	55	0.9	0.0	1
1.6	0.6	1.0	0.0	0.0	0.2	0.0	0.0	2	35		-0.5	2
0.0	1.4	0.0	0.4	0.0	0.7	0.0	0.4	5	34		-0.7	2
6.5	0.5	3.9	0.7	13.1	1.8	25.8	5.5	43	65	1.1	0.6	3
0.0	0.4	0.0	0.0	0.0	0.7	3.2	0.3	17	16	0.7	0.3	3
4.8	0.0	0.0	0.2	1.6	0.2	0.0	0.0	31	10	1.5	0.9	1
0.0	0.2	1.0	0.0	0.0	0.0	0.0	0.0	3	34		-0.5	3
0.0	0.2	0.0	0.0	0.0	0.6	0.0	0.3		17		-1.0	3
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	11	6	1.5	0.3	1
0.0	0.7	0.0	0.0	0.0	0.4	0.0	0.0	37	143	0.8	-0.5	1
0.0	0.3	0.0	0.3	0.0	0.9	0.0	0.3	20	29	2.4	-0.3	2
3.2	1.4	3.9	0.6	5.7	0.6	0.0	3.2	101	621	0.8	0.2	1
1.6	2.6	0.0	1.8	4.1	0.7	0.0	1.5	25	458	1.1	-0.4	1
0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1	12		-0.4	2
11.3	*8.1*	*6.9*	*10.9*	*4.9*	*12.4*	*3.2*	*16.0*	*142*	*894*	*1.0*	*-0.2*	*2*
6.5	*3.1*	*0.0*	*1.0*	*4.9*	*1.3*	*0.0*	*0.7*	*310*	*502*	*1.4*	*0.3*	
4.8	0.8	0.0	0.2	3.3	0.4	0.0	0.0	147	125	1.2	0.6	2
1.6	0.1	0.0	0.0	0.8	0.0	0.0	0.0	10	35	0.9	0.3	2
0.0	0.7	0.0	0.4	0.0	0.3	0.0	0.0	7	65		-0.7	2
0.0	0.8	0.0	0.4	0.0	0.2	0.0	0.4	72	165	1.8	-0.1	2
0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	2	46		-0.9	2
0.0	0.6	0.0	0.0	0.8	0.3	0.0	0.3	72	66	1.7	0.3	2
100	*100*	*100*	*100*	*100*	*100*	*100*	*100*	*2560*	*8636*	*1.2*	*0.0*	
22.6	*19.3*	*18.6*	*17.4*	*21.3*	*16.4*	*25.8*	*17.1*	*556*	*2975*	*1.1*	*-0.1*	*1*
59.7	*69.1*	*55.9*	*64.4*	*42.6*	*64.5*	*19.4*	*63.7*	*1516*	*5063*	*1.1*	*-0.1*	*2*
17.7	*11.6*	*25.5*	*18.2*	*36.1*	*19.2*	*54.8*	*19.2*	*488*	*598*	*1.8*	*0.4*	*3*

laevigata, *Gavelinopsis praegeri*, *Nonionella iridea*, *Rosalina bradyi*, *Trifarina angulosa*; examples contra: *Anomalina* sp.1, *Anomalinoides minimus*, *Cibicides pachydermus*, *Epistominella exigua*, *Seabrookia earlandi*, *Uvigerina mediterranea*, *Pseudoclavulina crustata*), whereas deeper dwelling species tend to be underrepresented (*R*>0) in the dead assemblage (examples in favour: *Anomalinoides* sp.1, *Bolivina* *albatrossi*, *B. dilatata*, *B. subspinescens*, *Cassidulinoides bradyi*, *Ceratobulimina arctica*, *Eponides* sp.1, *Fursenkoina tenuis*, *Globobulimina pyrula*, *Gyroidina orbicularis*, *Melonis barleeanum*, *Pullenia quinqueloba*, *Rotamorphina involuta*, *Siphonina reticulata*, *Bigenerina nodosaria*, *Textularia sagittula*; examples contra: *Cassidulina oblonga*, *Fissurina* spp., *Globocassidulina subglobosa*, *Uvigerina peregrina*, *Textularia agglutinans*.

In Figure 5.12 the average living depth of species is plotted against their relative preservational potential. The greatest variation in *ALD* is found in the fragile group, and also species with the deepest average living depth are found in this group.

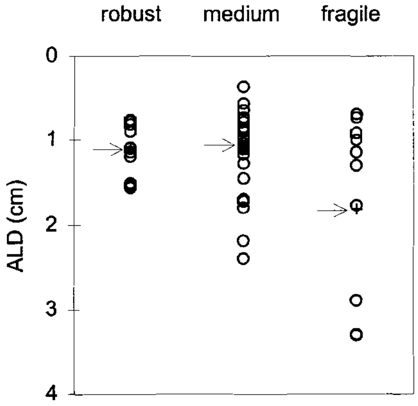

Fig. 5.12. Average living depth of species with different preservation potential. Arrows give the value for the total robust, medium and fragile groeps.

DISCUSSION

To extract meaningful information from the comparison of live and dead foraminiferal assemblages, it is essential that we can assume with some certainty that the dead assemblage was produced by a community of living foraminifera not very different from the one found at present. Biochronostratigraphic data from Jorissen et al. (1993) indicate that a Holocene cover is present in the area where we obtained our box core samples. Based on estimated sediment accumulation rates, the upper 5 cm of sediment from which the dead foraminiferal assemblage is derived represents the last 0.3 to 2.5 ka, not counting the effect of mixing with older sediment. On the shelf and shelf edge, Pleistocene relict sediments may be present below a thin layer of

Recent sediments. This may explain the presence of reworked shallow-water fauna in core 32. Shallow-water *Elphidium* and *Asterigerinata* also occur in low numbers in cores from the basin slope, indicating downslope transport of foraminifera. The low frequencies of typically shallow-water elements in deeper water sediments, and the existence of a distinct bathymetric zonation of species in the dead assemblage, preclude extensive allochthonous input in the dead assemblage.

Based on the distribution of excess ^{210}Pb activity in cores from the shelf, slope and deep basin, the zone of diffuse biological sediment mixing generally extends to slightly below the upper 5 cm investigated in the present study. Additional evidence for biological activity below 5 cm is given by the presence of (rare) stained foraminifera below this depth in a number of cores. Foraminifera together with nematodes typically penetrate to greater depth in the sediment than other meiofauna or macrofauna (e.g. Coull et al., 1977; Gerlach et al., 1985), and the vertical distribution of these groups may thus provide additional information on the downcore extent of biological activity. The investigated assemblages of empty foraminiferal shells must therefore be considered as dead rather than fossil assemblages, as they are still in a zone of active biological transformation.

Contrary to what has been reported from other areas (Denne and Sen Gupta, 1989; Mackensen and Douglas, 1989) we find no evidence of sharp gradients in species relative abundance in the upper centimetres of sediment. The difference is partly due to the fact that in other studies disintegration-prone arenaceous foraminifera were included in the analysis of downcore trends in relative abundance of species. Yet, even taking the preservational bias introduced by including poorly-fossilizing arenaceous taxa into account, significant vertical trends remain present in the calcareous assemblage, in their data. These trends are produced by habitat differentiation of species and selective dissolution of fragile calcareous tests. According to Loubere et al. (1993), vertical trends are most likely to develop in areas of high organic carbon flux or low bottom water oxygen content, in which significant benthic foraminiferal test production occurs below the zone of intense biological sediment reworking. In areas of low C_{org} flux and high bottom water O_2, test production occurs within the zone of active sediment reworking, and both tests produced at the sediment surface, as well as those produced deeper in the sediment, will pass through the same taphonomic filter. This situation seems to apply well for the oligotrophic and well-oxygenated southern Adriatic Sea. We may add to this that the low rate of sediment accumulation, resulting in long residence times of dead foraminifera within the zone of active mixing, and a very limited new production of tests, also favour the development of a homogeneous dead assemblage. The downcore decrease in abundance of disintegration-prone arenaceous foraminifera (including Astrorhizids), and also of ^{210}Pb, indicates that sediment mixing is insufficient to homogenise more short-lived elements.

To what extent calcareous and calcite-cemented foraminifera are affected by taphonomic destruction is difficult to assess. Calcite dissolution seems to play an insignificant role in the organic carbon-poor sediment, as indicated by the good preservation of calcitic and aragonitic fossil material. Biological activity may be a more important factor of taphonomic destruction in the area. In the studied material, borings and extensive tunnel systems in foraminiferal tests walls were commonly observed. The ratio of benthic foraminiferal accumulation rate to standing stock may give some indication of the extent of test destruction. There are many arguments to cast doubt upon the representativeness of the observed standing stocks. For example, Rose Bengal staining may overestimate the number of living foraminifera (Bernhard, 1988, 1989; Corliss and Emerson, 1990), benthic foraminiferal population size may be highly variable over a yearly cycle (Boltovskoy and Wright, 1976; Murray, 1983; 1991) the surface area of sediment samples may be too small to be representative of patchily distributed foraminifera. Furthermore, estimated sediment accumulation rates may not be correct, leading to errors in the calculation of *BFAR*. Notwithstanding all the reservations with which we must consider our results, it is remarkable that a reasonably good correlation was found between *BFAR* and standing stock (Fig. 5.9). Assuming steady state, the average 4.6:1 ratio of *BFAR* (per year) to standing stock implies that the average turnover time of live foraminifera is less than one quarter of a year, or about 2.5 months. This is well within the range of natural generation lengths mentioned in the literature, varying between a couple of weeks for shallow-water species under favourable conditions, up to a year or more for deeper marine species (Boltovskoy and Wright, 1976; Murray, 1983, 1991). In the strongly nutrient-limited bottom environment of the southern Adriatic, foraminiferal generation lengths may be expected to be in the order of months, rather than weeks, and the estimated rates of test accumulation in the sediment may not be too far off from the original rates of test production.

If the above is true, it is tempting to interpret the observed differences in live and dead relative abundance of species in terms of differential test production, rather than only differential preservation. The observation that deeper-dwelling foraminifera are more often underrepresented in the dead assemblage than shallow-dwelling foraminifera (Fig. 5.11b) suggests that foraminiferal productivity may be related with living depth. This comes very near to the assumption made by Loubere et al. (1993), that test production rate within the sediment is proportional to available oxygen (which decreases with depth). On theoretical grounds a relationship with habitat depth may be expected, and pore-water oxygen content may indeed play a significant role. A higher rate of test production in near-surface dwelling species may in the first place be due to the larger flux of metabolizable organic carbon through the sediment-water interface, compared to the flux toward deeper levels. Additionally, as high-quality organic carbon often arrives in seasonal pulses, epifaunal species with the opportunistic ability to fast reproduction will have an advantage in the competition for food. This is especially true in food-limited deep-sea environments, where the larger part of the metabolizable organic carbon flux is consumed very close to the sediment-water interface. A rapid response to the deposition of fresh organic detritus has been observed in relatively shallow waters (Altenbach, 1992) as well in the deep-sea (Gooday, 1988; 1993). In the infaunal habitat food is supplied more gradually over the year by sediment mixing, but it is generally of a lower quality after having passed through the epifaunal community. Bacteria may play an important role in making low-quality organic matter available for consumption by deposit-feeding foraminifera. Evidence for the uptake of bacteria, organic detritus as well as large quantities of sediment by deposit-feeding benthic foraminifera was compiled by Goldstein and Corliss (1994). Apart from the ability to handle low-quality organic matter, infaunal foraminifera must be physiologically adapted to live in an environment characterised by low oxygen concentrations. A consequence of the special effort needed to inhabit the subsurface habitat is that relatively little energy is available for the production of offspring. Infaunal species are therefore likely to combine long life-spans with a low rate of reproduction.

In the literature little observational evidence is found supporting the hypothesis of differential reproduction rates in surface and subsurface habitats. However, in the northern Adriatic Sea, seasonal maxima and minima in standing stock of benthic foraminifera recorded by Barmawidjaja et al. (1992) differ by a factor 26 in the superficial 0-1 cm of the sediment, and only a by factor 2.5 in the 1-7 cm interval. Similarly in the southern North Sea, summer and winter standing stocks recorded by Moodley (1990) differ by a factor 3.8 in the surface 0-5 cm layer, and 1.6 in the 5-25 cm interval. Apparently, foraminifera living near the sediment surface can reproduce faster under favourable conditions than those inhabiting an infaunal habitat.

After these speculations it must be stressed that the present data are certainly not sufficient to fully support the hypothesis presented here. The data show that there are many exceptions to the hypothetical rule. Some shallow-dwelling species are equally underrepresented in dead assemblages as are deeper-dwelling species. Also, the data do not rule out the possibility of selective destruction. It was observed that fragile species tend to be underrepresented in dead assemblages, compared to the corresponding live communities (Fig. 5.11a). This would point to selective destruction of fragile species. However, fragile species also tend to have a deeper average living depth than other taxa (Fig. 5.12), and their relative scarcity in the dead assemblage may thus also be explained by low productivity. More extensive observation at different times of the year and at different places would be needed to show whether the exceptions as well as the rule are part of a recurrent pattern.

CONCLUSIONS

Summarizing the above discussion, *we are relatively sure* that dead foraminiferal assemblages which we collected from the surface 5 cm of southern Adriatic sediment cores are representative of relatively recent (last 2.5 ka) environmental conditions in this area, and may be compared with present-day live communities of benthic foraminifera. Living foraminifera occur in vertically differentiated microhabitats, but because the production of tests occurs within the well-mixed sediment zone, the dead assemblage has a vertically homogeneous composition, as far as calcareous and calcite-cemented arenaceous foraminifera are concerned. Taphonomic destruction of disintegration-prone arenaceous foraminifera results in a great reduction in relative abundance and number of species of this group in the dead assemblage. *We suggest* that the dissimilarity observed between live and dead relative abundance of calcareous and calcite-cemented arenaceous taxa is primarily due to differential rates of test production, although we cannot exclude the possibility of selective destruction of delicate species. Based on the observed correlation between average living depth of species and their relative abundance in dead assemblages *we hypothesize* that shallow-dwelling foraminifera tend to have higher rates of test production than deeper-dwelling species. This could be due to the higher flux of metabolizable organic carbon in the surface habitat, the greater reproductive potential of shallow-dwelling species, and the limitation of infaunal production by low oxygen levels.

ACKNOWLEDGEMENTS

We especially thank Prof. A.M. Borsetti (Instituto di Geologia Marina del CNR, Bologna, Italy) and Dr. F.J. Jorissen (Dépt. Géologie et Océanographie, Université Bordeaux I, Bordeaux, France) for kindly providing samples from box cores for the purpose of this study. During the course of this study, the first author was funded by the Netherlands Organisation for Scientific Research (NWO), grant number 751.356.-021.

CHAPTER 6

Evidence for the control of organic carbon flux on the bathymetric zonation of benthic foraminifera.*

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Abstract We compared Recent benthic foraminiferal assemblages from surface sediments of the South Adriatic Basin with assemblages of latest Pleistocene (<18 ka BP) and Holocene age recovered in two piston cores from the same area. Benthic species which at present are dominant in outer shelf and slope assemblages, occupied much deeper habitats during the latest Pleistocene, but retreated to their present shallower position in the course of the Holocene. Present-day deep-water species were nearly absent on the deep basin plain and lower slope during the latest Pleistocene, establishing their present dominance only late in the Holocene. We suggest that decreasing marine productivity and organic carbon flux to the seafloor, as reflected by planktonic and benthic foraminiferal accumulation rates, are the principal cause for the changes in bathymetric distribution of species.

INTRODUCTION

Reconstructions of the depositional depth of marine sediments, essential for example in studies of basin evolution, are often based on fossil faunal evidence. Especially benthic foraminifera are widely used for this purpose, because of the great abundance and diversity of this group in Recent marine environments, and good preservation in fossil sediments. Paleodepth estimates are usually based on a direct comparison of fossil foraminiferal faunas with Recent analogues, under the assumption that foraminiferal taxa have a constant bathymetric range of occurrence. That this assumption is not generally valid was demonstrated by Pflum and Frerichs (1976), who found that the bathymetric ranges of many foraminiferal species change markedly in front of large river deltas. Apparently, factors covarying with water depth, rather than depth itself, determine the bathymetric zonation of benthic foraminifera. The decreasing availability of metabolizable organic carbon with increasing depth in the ocean may be a factor of prime importance, controlling not only the abundance and productivity of benthic fauna (e.g. Tietjen, 1992), but also the formation of biologically and chemically defined benthic microenvironments inhabited by different species (e.g. Corliss and Emerson, 1990; Jorissen et al., 1995). Generally, a good correlation exists between organic carbon flux and benthic foraminiferal abundance (e.g. Altenbach and Sarnthein, 1989; Berger and Diester-Haass, 1988; Van der Zwaan et al., 1990; Herguera and Berger, 1991), and distribution patterns of specific groups of foraminifera may also be controlled by the organic flux (e.g. Lutze et al., 1986; Corliss and Chen, 1988; Van Leeuwen, 1989; Sjoerdsma and Van der Zwaan, 1992; Loubere, 1994). Foraminiferal species requiring abundant food may usually be restricted to relatively shallow depths in the ocean, extending their range to deeper water under conditions of increased surface water productivity and hence increased organic flux to the sea floor. Species tolerant to food scarcity can live in oligotrophic deep-sea environments, but may move to shallower depth under conditions of reduced surface productivity. The hypothesis of changing bathymetric ranges of benthic fauna in response to changes in surface water productivity was formulated earlier by Carney (1989).

We tried to test this hypothesis for benthic foraminifera, by comparing the Recent distribution in the oligotrophic South Adriatic Basin with the distribution under the more productive conditions at the end of the last glacial period.

The Adriatic Sea

The Adriatic Sea is an elongate, 800 km long and 200 km wide, NW-SE extending, marginal basin of the Eastern Mediterranean Sea, almost completely surrounded by landmasses (Fig. 6.1). It has three subbasins: the North Adriatic Basin, which is broad and shallow, generally less than 100 m deep; the Central Adriatic Basin, a depression halfway the length of the Adriatic Sea, with a maximum depth of 280 m; and the South Adriatic Basin, which has a flat basin plain of over 1200 m deep, surrounded by steep slopes and broad shelves. The 75 km wide and 780 m deep Otranto Strait connects the South Adriatic Basin with the much deeper Ionian Basin.

The hydrography of the Adriatic Sea has been reviewed by Buljan and Zore-Armanda (1976) and Orlić et al. (1992). The surface water circulation in the Adriatic Sea essentially consists of a large cyclonic meander with several smaller cells embedded in it. Through Otranto Strait warm and extremely oligotrophic Eastern Mediterranean surface water enters the South Adriatic Basin, spreading over most of

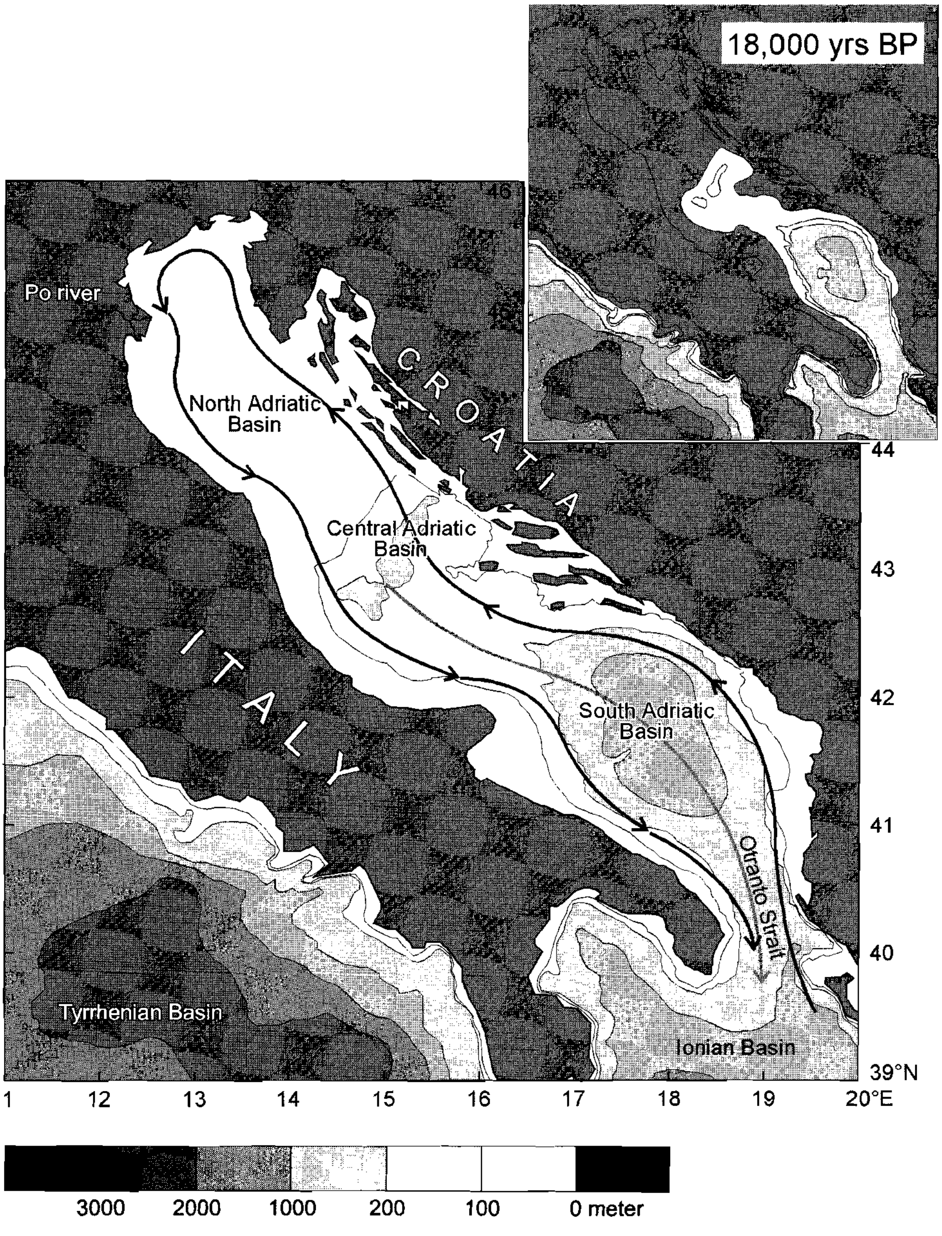

Fig. 6.1. General outlines of the Adriatic Sea. Surface circulation is schematically indicated by black arrows. Grey arrow represents the deep outflow of South Adriatic Water. Inset: reconstruction of the Adriatic Sea 18,000 years BP, with sea level 120 m (Fairbanks, 1989) below present level.

the central and eastern part of the basin, and flowing further in NW direction along the Albanian and Dalmatian coast. From the North Adriatic Basin, which receives considerable freshwater input especially from the Po river, cooler, less saline and nutrient-enriched water is carried in a SE-directed return flow along the Italian coast, leaving the South Adriatic Basin along the SW side of Otranto Strait. Winter cooling and excess evaporation locally increase the density of Adriatic surface water sufficiently to make it sink. By this process South Adriatic Water is formed, which fills the deeper parts of the South Adriatic Basin and, flowing over the sill of Otranto Strait, forms a major component of Eastern Mediterranean Deep Water (Pollak, 1951). As a result of the local sinking of water masses, the South Adriatic Water is rich in dissolved oxygen (>4 ml l^{-1}: Pollak, 1951), and no great temperature or salinity contrasts are found at depths below the thermocline (bottom-water temperature between 12.4 and 13.8°C, and salinity between 38.5 and 38.7‰: Guibout, 1987; Orlić et al., 1992).

Patterns of primary production in the Adriatic Sea clearly reflect the dominant role of north Italian rivers, and in particular the Po river, as sources of nutrients. Away from the Po river delta decreasing gradients of chlorophyll concentration, algal cell density and surface primary productivity are observed, both across the Adriatic Basin from the Italian coast toward the Dalmatian coast, as well as along the length of the basin from NW to SE (e.g. Revelante and Gilmartin, 1976; 1977; Sturm et al., 1992). Primary production in the northern Adriatic Sea was estimated to decrease from a maximum of 120 g C m^{-2} yr^{-1} near the Po delta to 55 g C m^{-2} yr^{-1} further eastward (Kveder et al., 1971; reference in Justić, 1987). Annual productivity rates for the southern Adriatic Sea are probably closer to Eastern Mediterranean values of 20 g C m^{-2} yr^{-1} (Dugdale and Wilkerson, 1988), considering the Eastern Mediterranean origin of most of the South Adriatic surface water and the absence of large rivers discharging into the southern Adriatic Sea.

Relatively high organic carbon contents of 0.8% to >1% are found in mud and sandy mud deposits extending all along the SW (Italian) half of the North and Central Adriatic Basin, as well as along the shelves bordering the South Adriatic Basin (Faganeli et al., 1994). Lower values of 0.7-0.8% are characteristic for the sandy sediments of the NE (Dalmatian) half of the North and Central Basin, whereas the lowest values, 0.5-0.7%, are found in the hemipelagic sediments of the deeper parts of the South Adriatic Basin. In this latter area, the organic carbon is less depleted of ^{13}C compared to shallower parts of the basin, indicating a higher relative contribution of marine organic matter (Faganeli et al., 1994). Taking into account the large difference between sediment accumulation rates estimated for the Italian mudbelt (up to 4.5 mm yr^{-1}: Van Straaten, 1970) and those in the deep southern basin (in the order of 0.1-0.2 mm yr^{-1}: Jorissen et al., 1993), it is clear that actual burial rates of organic carbon are far higher in the Italian mudbelt area than in the deep South Adriatic Basin: from the values mentioned above, and taking a sediment porosity of 60%, it can be calculated that the carbon burial rate in the Italian mudbelt could be as high as 47 g C m^{-2} yr^{-1}, which is more than one third of the estimated annual primary production of that area. For comparison, the average organic carbon burial rate in the deep South Adriatic Basin would be about 1 g C m^{-2} yr^{-1}, or a few percent of surface production.

The high efficiency of organic carbon burial in the Italian mudbelt area must result in a significant trapping of nutrients and organic matter in this area. Additionally, denitrification, which is an important mechanism of nitrogen loss from the marine system (Billen et al., 1991), may be cause of nutrient loss in the northern Adriatic Sea. Denitrification, substituting oxic mineralisation of organic carbon, is favoured by the dysaerobic bottom conditions which typically occur during summer months in that area, and which are due to high rates of organic matter decomposition under stratified waters (Giordani and Angiolini, 1983; Justić, 1991). As a consequence, only a fraction of the riverine nutrient input to the northern Adriatic Sea will eventually reach the South Adriatic Basin.

Productivity change in the Adriatic Sea over the last glacial cycle

The nutrient budget of the Adriatic Sea may have been subject to considerable change over the last glacial-interglacial cycle, having consequences for marine productivity. Melting of Alpine and Apennine glaciers at the end of the last glacial period, with peaks around 14 and 10 ka BP (Maisch, 1983), must have produced large volumes of meltwater, which were poorly retained by the sparse steppe vegetation present during that time in the Adriatic region (e.g. Zonneveld, 1996). Due to the low sea-level stand, streams of sediment- and nutrient-loaded runoff waters debouched directly into the Central Adriatic Basin, far South of the present major discharge areas (e.g. Colantoni et al., 1979). Furthermore, nutrients and organic carbon may have been less effectively retained on the shelf, which as a consequence of the low sea level was much reduced in area compared to present (Fig. 6.1). As a result of the enhanced nutrient input into the southern Adriatic Sea, surface productivity may have been considerably higher than at present.

The nutrient input decreased during the Holocene, due to decreasing meltwater production, the spreading of deciduous oak forest over the region (Zonneveld, 1996), probably limiting continental runoff rates, and the increasing area of shelf separating the South Adriatic Basin from riverine nutrient sources further North. Increased thermal stratification of the water column, limiting the advection of nutrient-enriched deep water to the euphotic zone, may have contributed significantly to further reduce marine productivity. Evidence for increased (seasonal) water column stratification is given by the dominance of the planktonic foraminifer *Globigerinoides ruber* in Holocene foraminiferal assemblages from the Adriatic Sea (Rohling et al., 1993b; in press, b; Jorissen et al., 1993). In the Recent Mediterranean Sea, this species is characteristically found in the nutrient-depleted warm surface layer (e.g. Pujol and Vergnaud Grazzini, 1995).

MATERIALS AND METHODS

Quantitative data on the Recent distribution of benthic foraminifera in the South Adriatic Basin were obtained from Jorissen (1988). We used census data of benthic foraminifera studied in 150-595 μm sieve residues of surface sediments recovered in grabs and sediment core-tops. We selected data from 48 southern Adriatic sample stations where the water depth is 100 m or more. We added faunal data from 8 box-core stations reported by De Stigter et al. (this thesis, Chapter 5). To minimize bias of downslope displacement, we discarded a number of sample stations located near the base of steep basin slopes (nr. 306, 310, 359, 360 and 404 of Jorissen, 1988), where relatively high numbers of inner shelf taxa are present. The location of the remaining sample stations is indicated in Figure 6.2. Twenty-six common taxa (>5% in at least one sample), constituting about 80% of the total benthic assemblage, were grouped by a conventional statistical clustering technique (weighed pair group analysis) into 6 assemblages. The relative frequencies of these assemblages were plotted against depth of the sample stations, reducing variability by applying a 5-point moving average.

The Recent foraminiferal assemblages were compared with fossil assemblages present in two sediment cores from the South Adriatic Basin (see Fig. 6.2 for location): IN68-9 from the basin plain of the South Adriatic Basin (station 362A, lat 41°47.5 N, long 17°54.5 E, present water depth 1234 m) and IN68-33 from the western slope of the same basin (station 415, lat 41°32.5 N, long 17°17.9 E, present water depth 696 m). The cores were recovered in 1968 during a cruise of the Italian research vessel "Bannock". Core descriptions are in Colantoni and Gallignani (1977).

Results of benthic and planktonic foraminiferal analysis of core IN68-9 have been published previously by Jorissen et al. (1993) and Rohling et al. (1993b). The foraminiferal data used in these studies are included in our data set. Additional samples were collected from core IN68-9 at regular 1 cm intervals. Wet weight of the samples was determined, and the sample volume was measured by multiplying length, width and heigth of the rectangular sample slabs. Samples were split in three

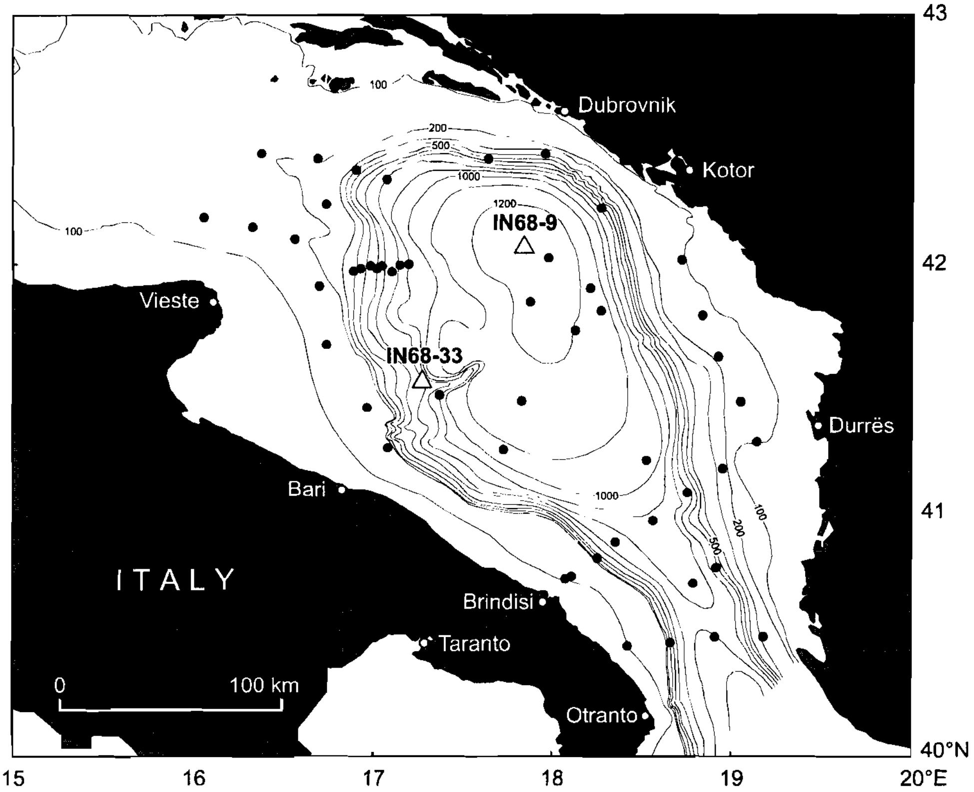

Fig. 6.2. Location of cores IN68-9 and IN68-33 (triangles). Black dots represent sample stations of Jorissen (1988) and De Stigter et al. (this thesis, Chapter 5).

parts for analysis of, respectively, foraminifera, organic carbon content, and palynomorphs. The volumes of the sample splits were calculated from their wet weight fraction relative to the weight of the unsplit sample. Palynological results are published by Zonneveld (1996). Samples from core IN68-33, collected also at 1 cm intervals, were used only for foraminiferal analysis. The volume of these samples was determined by displaced water volume. Samples destined for foraminiferal analysis were oven-dried at 50°C for 24 hours, weighed dry, and subsequently washed over a set of sieves with mesh widths of 63, 150 and 595 μm. For the present study, we counted benthic and planktonic foraminifera of the 150-595 μm fraction in selected samples of core IN68-9, and in all samples of core IN68-33. An Otto microsplitter was used to obtain convenient split fractions containing approximately 250 benthic and 250 planktonic foraminifera. For identification of benthic foraminifera we used similar taxonomic categories as were used by Jorissen (1987, 1988) and Jorissen et al. (1993). Benthic taxa were subsequently grouped in similar clusters as used for the Recent benthic foraminifera. Planktonic species were identified as in Jorissen et al. (1993) and Rohling et al. (1993b), following largely the planktonic foraminiferal taxonomy of Hemleben et al. (1989).

As a proxy of paleocarbon flux, we used benthic foraminiferal accumulation rates (*BFAR*), calculated from benthic foraminiferal abundance in the cores and estimated sediment accumulation rates (*SAR*). *BFAR* has previously been applied for estimation of paleocarbon flux by Herguera and Berger (1991), who found as a rule of thumb that for each milligram of organic carbon arriving at the seabed, one benthic foraminiferal test >150 μm is produced. A number of other studies confirm the good correlation between organic carbon flux and benthic foraminiferal abundance (Altenbach and Sarnthein, 1989; Berger and Diester-Haass, 1988; Van der Zwaan et al., 1990). As far as lateral transport of organic carbon can be neglected, surface water productivity may be estimated from the benthic flux of organic carbon by use of empirical flux equations (e.g. Suess, 1980; Betzer et al., 1984; Berger et al., 1987; Martin et al., 1987). In the present study, however, we use *BFAR* only as a qualitative indicator of organic carbon flux and surface productivity. We also calculated planktonic foraminiferal accumulation rates (*PFAR*), which we tentatively use as an additional proxy of surface productivity.

Stratigraphic correlation of cores IN68-9 and IN68-33 is possible by use of a number of lithological and planktonic foraminiferal marker horizons. Van Straaten (1967; 1970) demonstrated the continuity of turbidites and volcanic ash layers in sediment cores from the South Adriatic Basin. In the present study we adopt Van Straaten's number codes of turbidite layers T1-T8 and volcanic ash layers V1-V8. Lateral continuity of foraminiferal marker horizons was demonstrated by Jorissen et al. (1993). In the latter study, numerical ages of lithological and foraminiferal horizons were estimated by interpolation between six ^{14}C AMS-dated reference horizons in core IN68-9. We used the same ^{14}C AMS dates in the present study for estimation of sample ages and sediment accumulation rates. We did not apply linear inter- and extrapolation between ^{14}C-dated horizons, because this induces abrupt and unrealistic changes in reconstructed accumulation rates. Instead, we constructed a sediment accumulation diagram with gradual changes in the rate of sediment accumulation, by plotting the cumulative thickness of hemipelagic sediment against ^{14}C-time (leaving out turbidites and ash layers), and fitting this with a suitable cubic spline function. Sample ages and sediment accumulation rates (in cm ka^{-1}) in core IN68-9 were subsequently derived from this diagram. Core IN68-33 was correlated to the time-stratigraphic framework constructed for core IN68-9, by use of lithological and planktonic foraminiferal marker horizons. Sample ages and sediment accumulation rates of core IN68-33 were derived from a sediment accumulation diagram constructed as described above.

Additionally, a number of samples of core IN68-9 were analysed for particulate organic carbon content, $^{12}C/^{13}C$ isotopic ratio of organic carbon, and $^{16}O/^{18}O$ isotopic ratio of planktonic foraminiferal carbonate. Particulate organic carbon content (expressed as % of dry sediment weight) was determined for 38 samples by measurement of CO_2 released at combustion of decarbonated samples at 900°C. The CO_2 gas was subsequently led through a VG SIRA 24 mass spectrometer for measurement of δ^{13}Corg. Burial rates of organic carbon (expressed as g C cm^{-2} ka^{-1}) were calculated by multiplying the C_{org} content per sample volume with the sediment accumulation rate. Oxygen isotope measurements previously reported for core IN68-9 (Jorissen et al., 1993), were duplicated, this time with more specimens of *Globigerina bulloides* per measurement (usually more than 100 specimens, or equivalent to 1 mg $CaCO_3$), and using a VG SIRA 24 mass spectrometer. The number of samples was extended to 60 (with 30 duplicates). To ensure data consistency, we did not include the previous data set in the present study. $\delta^{18}O$ values are reported as per mil deviations from the PDB-1 standard (Epstein et al., 1953).

Part of the data used in the present study appear also in a study by Rohling et al. (in press, b).

RESULTS

1. Recent bathymetric zonation of southern Adriatic benthic foraminifera

In terms of presence/absence, the most narrow bathymetric range observed among the common species in the combined data set of Jorissen (1988) and De Stigter et al. (this thesis, Chapter 5), applying to three species only, is from 100 to 900 m water depth. The majority of common species is present over the entire depth range of 100 to 1200 m. Yet, the relative abundance of most taxa varies systematically with water depth. Taxa with similar distribution patterns were grouped by statistical clustering into six clusters (Fig. 6.3). Cluster 1, composed of *Textularia agglutinans*, *Bigenerina nodosaria*, *Hanzawaia boueana*, *Textularia sagittula*, *Cassidulina oblonga*, and a number of characteristic inner-shelf taxa such as *Ammonia* spp., *Elphidium* spp., *Cibicides lobatulus*, *Asterigerinata* spp. and *Neoconorbina terquemi*, decreases with water depth, from a maximum frequency of more than 50% at 100 m till less than 5% at 1200 m. Cluster 2, composed of *Amphicoryna scalaris*, *Bulimina marginata/aculeata* and *Sphaeroidina bulloides*, and cluster 3, composed of *Bolivina spathulata*, *Trifarina angulosa*, *Hyalinea balthica* and *Cassidulina laevigata*, show very similar patterns, increasing sharply between 100 and 200 m, then decreasing gradually to almost 0% at 1200 m. Cluster 4, comprising the species *Gavelinopsis praegeri*, *Melonis barleeanum* and undifferentiated imperforates, is more evenly distributed but with somewhat higher frequencies at mid-slope depth. Cluster 5, with the species *Pseudoclavulina crustata*, *Planulina ariminensis*, *Bulimina costata*, *Cibicides pachydermus* and *Hoeglundina elegans*, increases gradually from almost 0% at 100 m till about 15% at 400 m, then fluctuates between 10 and 20% between 400 and 900 m, and then decreases till 5% at 1200 m. Cluster 6, composed of the species *Uvigerina mediterranea*, *Gyroidina altiformis*, *Gyroidina orbicularis*, *Uvigerina peregrina* and *Cassidulina crassa*, increases with water depth from a minimum of less than 5% at 100 m till about 70% at 1200 m. The group 'others', containing the less common species, shows no distinct bathymetric trend. Thus, the common Recent benthic species can be assigned to three major bathymetric groups: a shelf and upper slope group (clusters 1, 2 and 3), a slope group (clusters 4 and 5), and a lower slope and basin plain group (cluster 6).

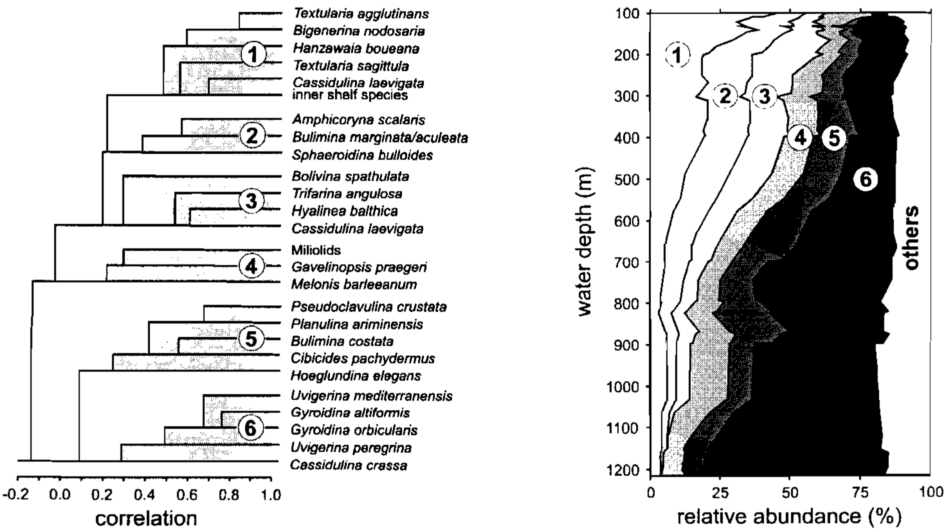

Fig.6.3. Cluster diagram of common benthic foraminiferal taxa from southern Adriatic surface sediments (left), and variation in the relative abundance of clusters with water depth (right).

2. Time-correlation of IN68-9 and IN68-33: lithology and planktonic foraminiferal content

An overview of the lithological succession and planktonic foraminiferal abundance patterns of IN68-9 and IN68-33 is presented in Figures 6.4 and 6.5, respectively. Core IN68-9 has a total length of 613 cm. It consists of greenish-grey hemipelagic

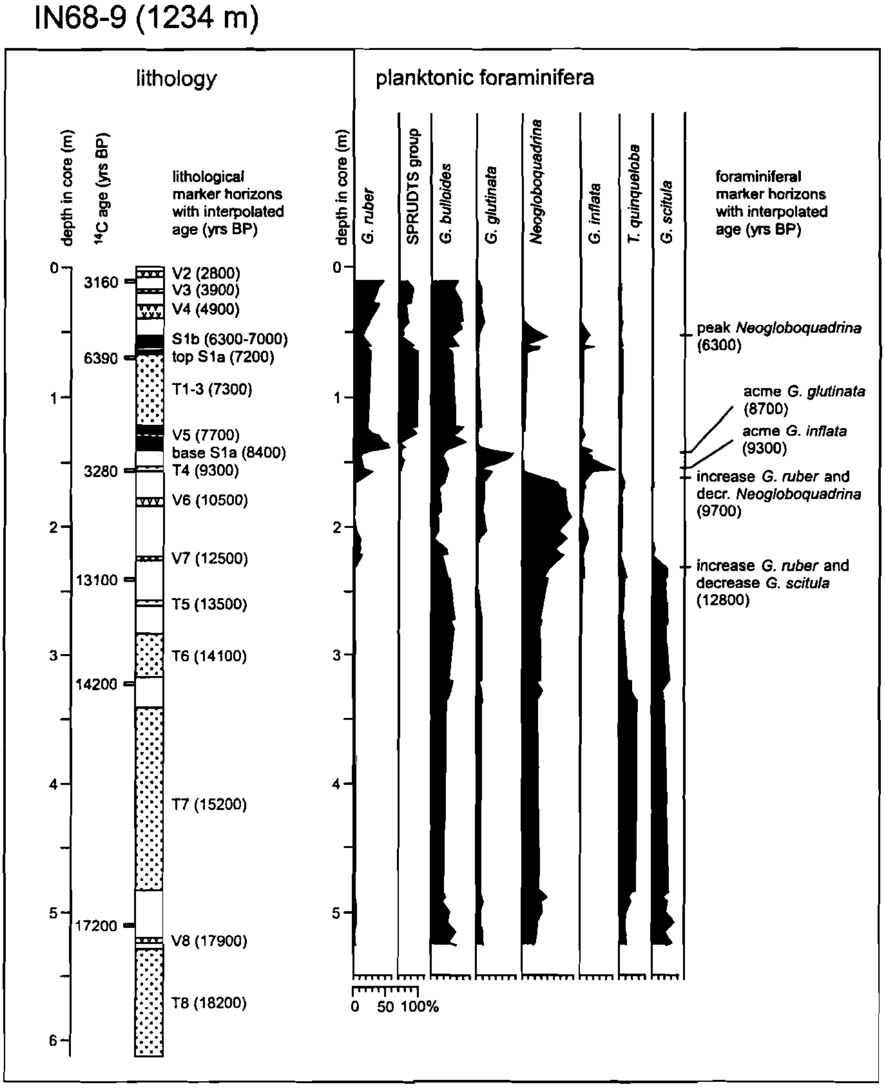

Fig. 6.4. Lithology and planktonic foraminiferal record of core IN68-9, with measured ^{14}C AMS ages, and interpolated ages of marker horizons. T: turbidites; V: volcanic ash layers; S: sapropel. Part of the planktonic foraminiferal data appeared in Jorissen et al. (1993) and Rohling et al. (1993b).

muds with 8 intercalated, mostly fine-grained, turbidites (T1-T8), ranging in thickness from 3 to 142 cm, and 7 volcanic ash layers (V2-V8), which are between 2 and 10 cm thick. Of particular interest is the presence of darker-coloured laminated mud between 54 and 140 cm depth in the core. This interval, which is widely recognized in deep-sea sediments of the Eastern Mediterranean Basin, is known as sapropel S1 (e.g. Kidd et al., 1978). The characteristic fine sedimentary lamination in this interval, indicating absence of bioturbation, and the general absence of benthic fossil remains, testifies to anoxic bottom conditions during deposition of this sediment. A homogeneous interval at 62-65 cm depth divides S1 in a lower and upper part, respectively S1a and S1b (Rohling et al., in press, b).

Core IN68-33 has a length of 128 cm. It consists for the larger part of greenish-grey muds, in which two volcanic layers of 5 and 2 cm thickness are intercalated (V5 and V6). Turbidites are not present, suggesting that the slope site from which IN68-33 was recovered was bypassed by turbidity currents. A laminated interval, identified as sapropel S1, is present between 3 and 51 cm depth in the core. We assume that the reappearance of benthic foraminifera in good numbers in the upper few centimetres of the core marks the top of S1. A homogeneous interval separating S1a and S1b comparable to the one occurring in IN68-9 was not observed.

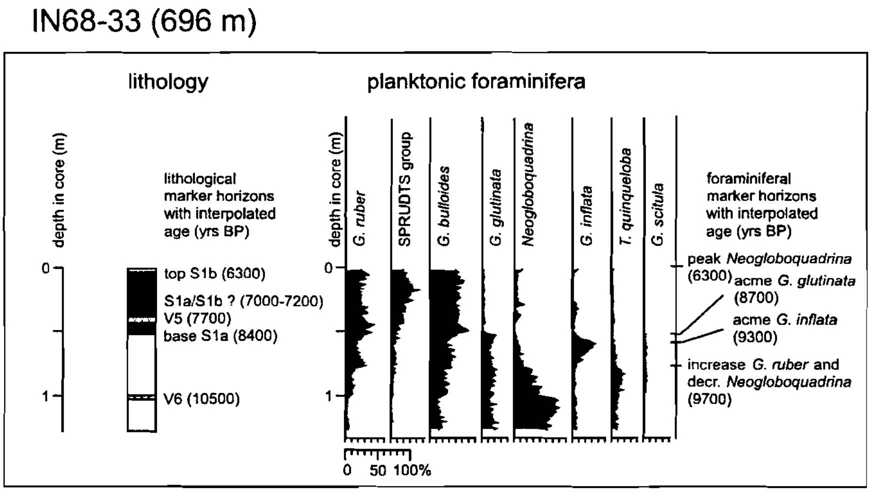

Fig. 6.5. Lithology and planktonic foraminiferal record of core IN68-33, with interpolated ages of marker horizons. V: volcanic ash layers; S: sapropel.

Further correlation of core IN68-33 to the age-calibrated reference core IN68-9 was possible by comparison of planktonic foraminiferal abundance patterns (Fig. 6.4 and 6.5). We tentatively dated the base of IN68-33 at 11.5 ka BP based on the slightly elevated frequency of *Globigerinoides ruber* around that age, followed by a minimum around 11 ka BP. More pronounced foraminiferal patterns which the two cores have in common include the frequency decrease in *Neogloboquadrina* and *Turborotalita quinqueloba* (9.7 ka BP), coinciding with an increase in *G. ruber* and *Globigerina bulloides*; a frequency peak in *G. inflata* (9.3 ka BP); a peak in *Globige-*

rinita glutinata (8.7 ka BP); and maximum frequencies of a cluster of warm water species including *Globigerinoides sacculifer*, *Hastigerina pelagica*, *Globoturborotalita rubescens*, *Orbulina universa*, *Globogerinella digitata*, *Globoturborotalita tenella*, *Globigerinella siphonifera* (in Figs. 6.4 to 6.7 indicated as 'SPRUDTS group') occurring from ash layer V5 up to the top of S1.

2. Productivity record in core IN68-9

In core IN68-9, considerable variation is observed in planktonic and benthic foraminiferal accumulation rates (*PFAR* and *BFAR*, respectively; Fig. 6.6), which in our view reflects the variation through time in surface water productivity and benthic flux of organic carbon. Moderately high values of *PFAR* and *BFAR* characterize the interval between 18 and 15 ka BP. No change is observed during this interval in oxygen isotopic values, or in the composition of planktonic foraminiferal assemblages (Fig. 6.6), indicating that full glacial conditions continued till 15 ka BP. *PFAR* and *BFAR* reach maximum values between 15 and 13 ka BP. This maximum coincides with a shift in the oxygen isotope curve toward lighter values, which probably corresponds to the first major deglaciation phase, Termination Ia (e.g. Ruddiman and Duplessy, 1985). Maximum rates of sediment accumulation and organic carbon burial occur in the same interval. Minimum values of organic $\delta^{13}C$, possibly indicating a relatively high contribution of land-derived organic matter, just precedes the maximum in organic carbon burial at 14 ka BP. After 13 ka BP, *PFAR* and *BFAR*, as well as SAR, decrease rapidly, while the C_{org} burial rate decreases more gradually. The planktonic foraminiferal assemblage changes markedly at 13 ka BP; *G. scitula*, characteristic of the glacial assemblages, nearly disappears, while *G. ruber*, indicative of warmer surface waters, increases slightly. *PFAR* and *BFAR* remain relatively low between 13 and 11 ka BP, but reach a second maximum between 11 and 10 ka BP. In the same interval, oxygen isotope values, *SAR*, C_{org} burial rate and $\delta^{13}C_{org}$ remain relatively stable. However, minima in *PFAR* and *BFAR* around 12 ka BP apparently coincide with increased abundances of *G. ruber* and *G. inflata*, while these species become less frequent during the subsequent maxima in *PFAR* and *BFAR*. *PFAR* and especially *BFAR* decrease rapidly after 10.5 ka BP, to remain relatively low during most of the Holocene. In the oxygen isotope curve, a shift toward lighter values corresponding to the second major phase of deglaciation (Termination Ib), occurs between 10 and 9 ka BP. At the same time, a major change occurs in the planktonic foraminiferal assemblage; *Neogloboquadrina*, dominant during the late glacial, nearly disappears, while *G. ruber* increases strongly in relative abundance. The continuously high relative abundance of *G. ruber* after 9 ka BP is indicative of warm surface

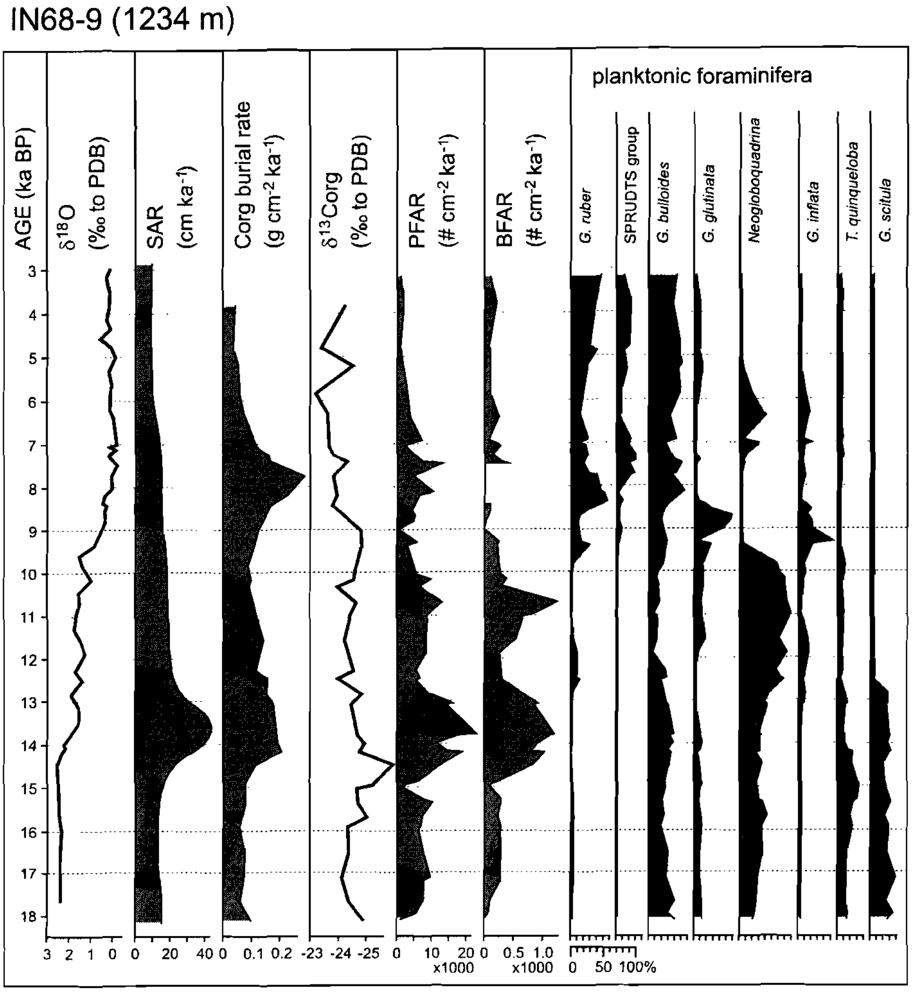

Fig. 6.6. Variation with time of $\delta^{18}O$ in *G. bulloides*, sediment accumulation rate (*SAR*), C_{org} burial rate, $\delta^{13}C$ of sediment organic carbon, planktonic and benthic foraminiferal accumulation rate (*PFAR* and *BFAR*, resp.), and relative abundance of planktonic species, as observed in core IN68-9. Part of the planktonic foraminiferal data appeared in Jorissen et al. (1993) and Rohling et al. (1993b).

waters. Organic $\delta^{13}C$ values become less negative after 9 ka BP than in the preceding period, which may indicate a lower contribution of land-derived organic matter. A temporary increase in *PFAR* during the Holocene, with maxima between roughly 8.5 and 6.5 ka BP, corresponds to deposition of sapropel S1. In the same interval, *BFAR* is reduced to zero around 8 ka BP, but reaches relatively high values, higher than in the later Holocene, around 7.5 ka BP.

3. Productivity record in core IN68-33

Patterns of *PFAR* and *BFAR* variation in core IN68-33 (Fig. 6.7) resemble to some extent those observed in IN68-9 (Fig. 6.6), although the timing of minima and maxima in IN68-33 may be up to 1000 years later than in the other core. *PFAR* increases from 11.5 ka BP, reaching maximum values between 11 and 9 ka BP; *BFAR* maxima occur between 10 and 9 ka BP, corresponding with a conspicuous maximum in SAR, which was not observed in IN68-9. Low values of *PFAR* and *BFAR* characterize the interval between 9 and 8 ka BP. After this, *PFAR* increases again, reaching maximum values around 7 and 6 ka BP. *BFAR* remains low in this interval, with the exception of a sharp peak near 6 ka BP, marking the end of sapropel deposition. It is worth mentioning that the values of *PFAR* maxima and minima in core IN68-33 are of comparable magnitude to those in IN68-9; respectively 8.10^3 and 13.10^3 specimens cm^{-2} ka^{-1} around the Pleistocene-Holocene transition, 2.10^3 specimens cm^{-2} ka^{-1} in both cores around 9 ka BP, and, respectively, 7.10^3 and 13.10^3 specimens cm^{-2} ka^{-1} for the interval corresponding to S1.

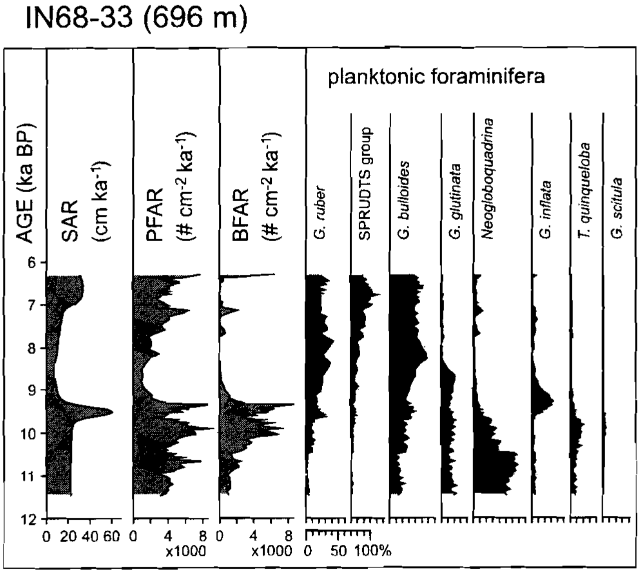

Fig. 6.7. Variation with time of *SAR*, *PFAR* and *BFAR*, and relative abundance of planktonic foraminiferal species, for core IN68-33.

4. Productivity variation and changes in the benthic assemblage

Variation in the relative abundance of the main bathymetric groups of benthic foraminifera through time is shown in Figure 6.8, together with the variation in *PFAR* and *BFAR*. On the basin plain (core IN68-9), benthic foraminifera of the Recent lower slope and basin plain group (cluster 6) become dominant in the benthic assemblage only late in the Holocene, after about 7.5 ka BP. Earlier in the Holocene and during the latest Pleistocene, this deep-water group is much less abundant, with minimum frequencies corresponding with *PFAR* and *BFAR* maxima. The slope group (clusters 4 and 5) is clearly dominant in this interval, and also the shelf and upper slope group (clusters 1,2 and 3) are relatively well-represented. The remaining

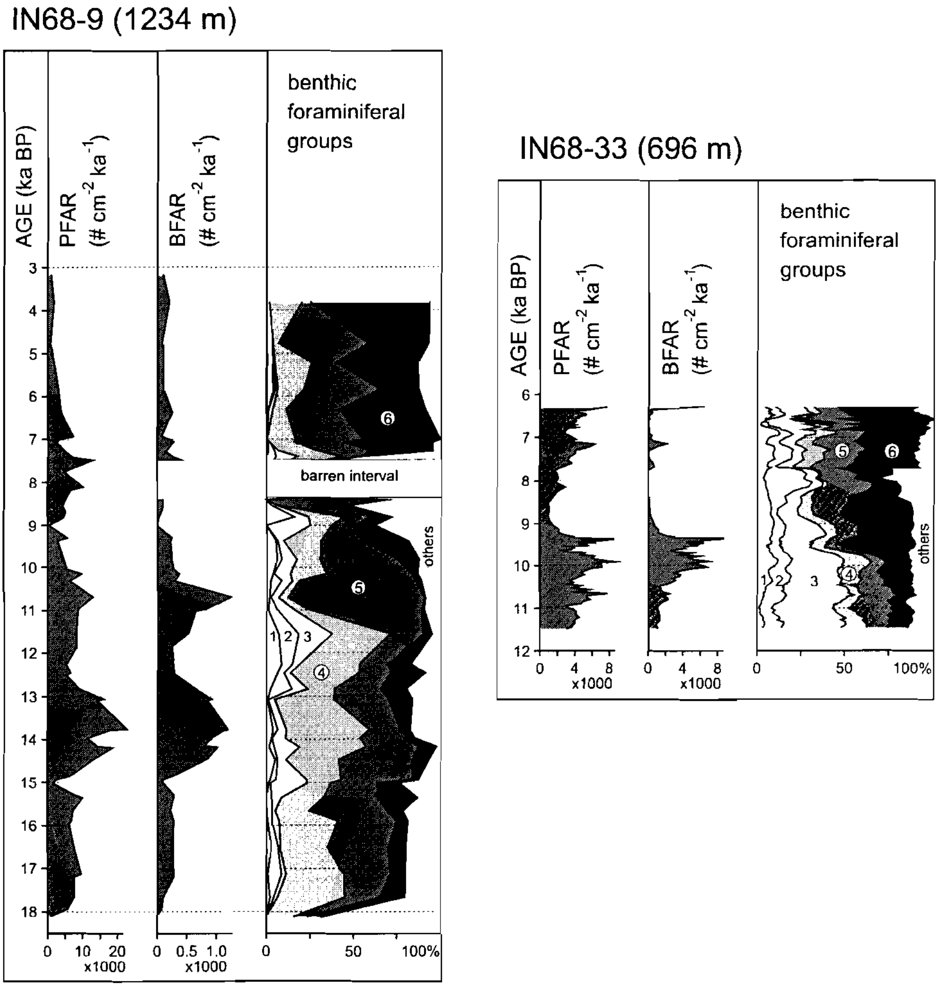

Fig. 6.8. Variation with time of *PFAR* and *BFAR*, and relative abundance of benthic foraminiferal groups, for cores IN68-9 and IN68-33. Benthic foraminiferal abundance patterns for core IN68-33 were smoothed by applying a 5-point moving average.

species which do not belong to one of the three major bathymetric groups, compose a relatively small part of the foraminiferal assemblages in the late Holocene (after 7 ka BP). In the Pleistocene, the common occurrence of *Karreriella bradyi* leads to an increase in the relative abundance of the 'others' group. Similarly, the increasing relative abundance of otherwise rare species like *Globobulimina pyrula*, *Chilostomella mediterranensis*, and *Bulimina costata* in the period preceding and during deposition of S1a (from about 9.5 till 7 ka BP), results in an anomalously high contribution of the 'others' group in this interval. The fauna present during deposition of S1b, from 7 to 6.3 ka BP, is not very different from that occurring after 6.3 ka BP.

Benthic foraminiferal assemblages from mid-slope depth (core IN68-33), differ from the basin plain assemblages by their much higher proportion of shallow-water elements. Yet, the overall faunal pattern in core IN68-33 is basically similar to that observed in IN68-9. The faunal assemblage present in the upper part of core IN68-33 is comparable to the Recent mid-slope assemblage. In the latest Pleistocene, however, between 11.5 and 10 ka BP, shelf and upper slope species are relatively abundant. Between 10 and 9 ka, the shelf and upper slope group decreases in importance relative to the deeper-water groups. In the same interval, *PFAR* and *BFAR* decrease dramatically. Comparably to the pattern observed in IN68-9, the 'others' group is relatively unimportant, except in the interval corresponding to S1a.

DISCUSSION

1. Recent bathymetric zonation of foraminiferal assemblages

Previous studies on the distribution of Recent benthic foraminifera in the Adriatic Sea (Jorissen, 1987; 1988; Van der Zwaan and Jorissen, 1991; Jorissen et al., 1992) demonstrate the succession of taxonomically distinct faunal assemblages along gradients of bathymetry, salinity, bottom-water oxygen content, sediment organic carbon content and sediment substrate. The greatest faunal contrasts are observed in the inner shelf area along the Italian coast, where environmental gradients appear most pronounced. In the deeper parts of the Central and South Adriatic Basin, Jorissen (1987) distinguishes only one biofacial unit, composed, however, of many different species. These observations are corroborated by observations on benthic mollusc faunas by Van Straaten (1970; 1985), which also show more areal contrast on the inner shelf area versus uniformity in the deeper waters. The relative faunal uniformity probably is due to the absence of sharp environmental gradients in deeper water. Indeed, below the thermocline the deep water of the South Adriatic Basin is relatively homogeneous with respect to its temperature, salinity, and oxygen content (see e.g. Pollak, 1951; Guibout, 1987; Orlić et al., 1992), and the seafloor beyond the shelf edge is uniformly covered with slowly accumulating hemipelagic mud (Van Straaten, 1970). In terms of common species inventory, benthic assemblages from beyond the shelf edge may indeed appear uniform, due to the fact that the majority of common deep-water species occur from shelf to basin plain depth. The relative abundance of species, however, changes very clearly, although gradually, with water depth (see e.g. Fig. 6.4). Additionally, it is observed that the density of live benthic foraminifera in the South Adriatic Basin decreases exponentially from the shelf edge to the basin plain (Jorissen et al., 1995; De Stigter et al., this thesis, Chapter 3). In our opinion, the only depth-related factor constituting a biologically significant gradient in the deep southern Adriatic, which could reasonably explain the observed faunal gradients, is the sinking flux of organic carbon. That is, assuming that the inverse relationship between water depth and C_{org} flux observed in other areas of the ocean (Suess, 1980) holds for this area as well. To which extent redistribution of deposited organic matter by bottom currents or gravitational sediment transport occurs in this area is uncertain. Evidence for lateral transport of suspended organic matter may be provided by the occurrance of relatively high numbers of presumably suspension-feeding Astrorhizid foraminifera on the basin slope and on the bottom of Otranto Strait (Jorissen et al., 1995; De Stigter et al., this thesis, Chapter 3). Redistribution of organic matter may explain some of the irregularities in the bathymetric zonation, but apparently does not obliterate the overall bathymetric zonation. The existence of a bathymetric zonation also precludes the likeliness of extensive downslope transport of benthic foraminiferal tests.

2. Variation of organic carbon flux through the latest Pleistocene and Holocene

Measuring the sinking flux of organic carbon in the present-day ocean is a highly complex task, hindered by high costs of sediment trap deployments and numerous technical difficulties (e.g. U.S. Global Ocean Flux Study, 1989). Estimation of paleocarbon fluxes is complicated by the fact that most, in the order of 99% (see e.g. Khripounoff and Rowe, 1985; Pfannkuche, 1992), of the organic carbon arriving at the seabed is relatively rapidly remineralized or recycled as benthic biomass, and does not appear in the sedimentary record. The remainder that becomes permanently buried may have been protected from remineralization by association with mineral surfaces, as suggested by Mayer (1993) and Keil et al. (1994). The burial rate of organic carbon is therefore closely coupled to the accumulation rate of sediment, as observed in core IN68-9. The enhanced C_{org} burial rate in sapropel S1 may indicate conditions of enhanced preservation.

The organic carbon flux to the benthos may be better estimated from the abundance of benthic organisms, which are the consumers of this carbon. Unfortunately, most benthic organisms leave little or no trace in the sedimentary record, with the fortunate exception of (part of) benthic foraminifera. The potential of benthic foraminiferal accumulation rate (*BFAR*) as a quantitative indicator of benthic flux of organic carbon has been demonstrated by Herguera and Berger (1991). Applying the same *BFAR* to C_{org} conversion factor as proposed by these authors (1 mg C_{org} for each benthic foraminiferal test >150 µm) to the late Holocene *BFAR* values of core IN68-9 (average *BFAR* between 7 and 3.2 ka: 120 specimens cm^{-2} ka^{-1}), gives a benthic flux of 120 mg C cm^{-2} ka^{-1} or 1.2 g C m^{-2} yr^{-1}. Surface primary production may be estimated on the basis of the benthic flux of organic carbon by applying Suess' (1980) organic flux equation:

$$C_{flux}(z) = \frac{C_{prod}}{0.0238\,z + 0.212} \qquad (6.1)$$

where $C_{flux}(z)$ is the organic carbon flux at depth z (g C m^{-2} yr_{-1}), C_{prod} is primary production (g C m^{-2} yr^{-1}) and z is water depth (m). Taking the organic flux as 1.2 g C m^{-2} yr^{-1} and water depth as 1234 m, yields an estimated primary production of 35 g C m^{-2} yr^{-1}. This seems a realistic value for the southern Adriatic Sea, being between observed primary production rates of 20 g C m^{-2} yr^{-1} for the Eastern Mediterranean and 55 g C m^{-2} yr^{-1} for the eastern North Adriatic. However, by similar calculation, and taking sealevel change into account, *BFAR* maxima occurring around the Pleistocene-Holocene transition (1200 and 8000 specimens cm^{-2} ka^{-1} in core IN68-9 and IN68-33, respectively) would imply primary production values of, respectively, 350 and 1250 g C m^{-2} yr^{-1}. While the first value is comparable to values of primary production in upwelling areas, the latter value seems absurdly high. The obvious overestimation of primary production for high values of *BFAR* may indicate that the assumed linear relationship between organic carbon flux and primary production, implicit in the flux equation of Suess (1980), is not valid here. Rather, the export of organic carbon may increase exponentially with increasing surface productivity (Betzer et al., 1984; Berger and Wefer, 1990). Surface productivity may also be overestimated if lateral transport of organic matter contributes significantly to the benthic carbon flux. It may be argued, however, that *BFAR* could also be affected by other factors than organic carbon flux. A good example is given by the extremely low or zero values of *BFAR* observed in both cores in parts of sapropel S1, which probably result from extreme oxygen deficiency. Variation in the intensity of destructive taphonomic processes, partly related to the organic flux (e.g. Loubere et al., 1993), as well as variation in the supply of allochtonous foraminifera, may also result in variation in *BFAR*. In the Adriatic Sea, taphonomic loss of foraminiferal tests by calcite dissolution seems unimportant in view of the water depth well above the calcite lysocline, low organic carbon content of the sediment and moderately high calcium carbonate content. Loss by biological processes is difficult to assess. Transported foraminifera of inner shelf origin account for approximately 1% of both Pleistocene and Holocene assemblages in core IN68-9 (turbidites not taken into consideration). In IN68-33 this percentage is higher, around 5%, with exceptional cases of up to 15% in the Pleistocene-Holocene transitional interval. If these shallow-water foraminifera were transported as bedload by cross-shelf and downslope bottom currents, it is very likely that foraminifera from outer shelf and slope habitats have been equally affected by transport. Inner shelf foraminifera may also have been transported, however, attached to floating plant litter or by strong surface currents.

Although the reliability of *PFAR* and *BFAR* as quantitative indicators of surface productivity and benthic organic carbon flux may be uncertain, the observed patterns of *PFAR* and *BFAR* generally seem to correspond well with the expected variation in productivity: maxima in periods of rapid glacial melting or when the water column is weak stratified, and minima in periods of reduced meltwater production or of enhanced thermal stratification of the water column.

3. The effect of varying organic flux on the benthic foraminiferal assemblage

The composition of benthic foraminiferal assemblages has unmistakably varied over the stratigraphic interval studied. To what extent the bathymetric zonation of species has changed with time, and if these changes can be attributed to a varying flux of organic carbon to the seafloor, remains to be discussed. Comparison of the foraminiferal record of the basin plain (IN68-9) with that of the middle slope (IN68-33) shows that the depth at which the various bathymetric groups reach their maximum relative abundance must have changed with time. During the Pleistocene, the Recent lower-slope and basin-plain group was poorly represented both on the basin plain and on the middle slope. The slope group dominated the basin-plain assemblage, but it was relatively less abundant in faunal assemblages of the middle slope. The shelf and upper-slope group, especially represented by taxa of cluster 3, was dominant on the middle slope, and common on the basin plain. In the course of the Holocene, the various bathymetric groups apparently retreated to their present-day bathymetric position. The shelf and upper-slope group decreased in relative abundance in the faunal assemblages of both the middle slope and of the basin plain. The slope group increased slightly in abundance on the middle slope, while losing its dominance on the basin plain. At the same time, the lower-slope and basin-plain group became dominant on the basin plain and on the middle slope. In our opinion, these changes in the bathymetric distribution of benthic foraminifera are insufficiently explained by simple eustatic sealevel variation (120 m difference at most), and must be due to changes in the organic carbon flux. However, other biologically significant factors like temperature and oxygen content of the bottom water, which in the present South Adriatic Basin vary little with depth below the thermocline, as well as the composition of organic matter sinking to the bottom, may have varied considerably through the studied time interval, and may have interfered with the organic-flux signal. The effect of varying bottom-water oxygen content is clearly demonstrated in the appearance around sapropel S1 of an anomalous benthic foraminiferal fauna, dominated by low-oxygen tolerant species like *Globobulimina pyrula*, *Chilostomella mediterranea*, and *Bulimina costata*. Although actual deposition of sapropel sediment occurred not earlier than 8.4 ka in the centre of the South Adriatic Basin, the first indications for an increasingly anomalous benthic fauna can be observed almost one thousand years earlier (see Rohling et al., in press, b).

We realize that the positive correlation between high *PFAR* and *BFAR*, and high relative abundance of shallow-water species, could also be explained by a periodic increase in downslope transport. It seems improbable, however, that by this process such regular patterns could be produced as observed in the two cores studied.

CONCLUSIONS

Recent benthic foraminifera in the South Adriatic Basin show a distinct bathymetric zonation, which is expressed in changes in the relative abundance of species, rather than in well-defined upper and lower depth limits of species. The water depth at which various bathymetric groups of species reach their maximum relative abundance has been variable over the past 18 thousand years. Species which at present have their optimum depth on the shelf and upper slope, were dominant at mid-slope depth during the latest Pleistocene (18-10 ka), under a regime of relatively high organic carbon flux to the seafloor. They retreated to their present-day position in the course of the Holocene when the organic carbon flux decreased. Likewise, species which at present are most abundant on the slope of the South Adriatic Basin, occupied the basin plain during the latest Pleistocene. Our observations suggest that the shifts in the bathymetric position of benthic foraminifera were related to increases and decreases in organic carbon flux. This would support the hypothesis that the bathymetric zonation of deep-sea benthic species is principally produced by bathymetric variation in organic carbon flux.

ACKNOWLEDGEMENTS

We thank Prof. A.M. Borsetti of the Institute of Marine Geology in Bologna, Italy, for kindly providing us with sample material of core IN68-9. The first author was funded by the Netherlands Organisation for Scientific Research (NWO), grant nr. 751-356-021.

CHAPTER 7

200 YEAR INTERRUPTION OF HOLOCENE SAPROPEL FORMATION IN THE ADRIATIC SEA*

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Abstract An interruption of Holocene sapropel S_1 is found in cores from various subbasins of the eastern Mediterranean. In core IN68-9 from the Adriatic Sea, sapropel S_1 is dated between 8300 and 6340 BP, interrupted between 7100 and 6900 BP (^{14}C years uncorrected for reservoir age). Lithology and variations in the foraminiferal faunas suggest that the interruption is genuine, and not the result of resedimentation. The results indicate that S_1 was deposited within a period of enhanced levels of productivity (resulting from increased seasonal contrasts) which started around 9300 BP and ended around 5200 BP. The onset, interruption, and final ending of S_1 deposition in the Adriatic Sea, however, appear to have been triggered by changes in ventilation of the basin related to changes in sea surface temperature (SST). Although the rough estimates of SST change are relatively small (<2°C), they still are significant when compared with the relative SST changes considered necessary to upset convection in the Adriatic. Moreover, recent studies show that the influence of the inferred temperature changes should be viewed in combination with that of reduced salinities due to 1) the deglaciation, and 2) increased humidity in the eastern Mediterranean area during the deposition of S_1. The lithological and benthic foraminiferal evidence that sapropel formation ended around 6340 BP contradicts a recent conclusion from a geochemical study that sapropel formation would have ended as late as 5000 BP. More significantly, the results of the present study combined with other reports on sapropel interruptions suggest that the process of sapropel formation is not a very stable mode in the basin, but that it may be relatively easily interrupted in response to subtle rearrangements in the balance between productivity and, especially, deep water ventilation.

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*Journal of Foramimiferal Research, in press

1. INTRODUCTION

In the eastern Mediterranean, organic carbon rich, often laminated, intervals (sapropels) have been deposited since at least early Pliocene times (Cita and Grignani, 1982. Thunell et al., 1984; Hilgen, 1991). Sapropel formation has been shown to be astronomically timed, occurring around minima in the precession cycle (Rossignol-Strick, 1985; Hilgen, 1991). The most recent sapropel, S_1, was deposited in the early Holocene. AMS^{14}C dates for S_1 range from: 8700 - 6000 BP (Troelstra et al., 1991; Lander Rasmussen, 1991). 8300 - 6340 BP (Jorissen et al., 1993) and 9200 -6400 BP (Perissoratis and Piper, 1992), which agree with earlier ^{14}C based estimates (Stanley and Maldonado, 1979; Vergnaud-Grazzini, 1985). Higgs et al. (1994) proposed that the formation of S_1 ended much later, around 5000 BP, and that postdepositional downward oxidation of the sapropel created an apparent sapropel-top with an older age than the original top. They suggested that the original top resided close to the level of their upper Mn peak (about 5000 BP), but also suggest that this should be verified with benthic foraminiferal faunas.

A pale-coloured horizon interrupts the dark-coloured appearance of S_1 in several cases from various subbasins of the central and eastern Mediterranean (Table 7.1). Sapropels S_6 and S_8 are also composite (e.g. Cita et al., 1977; Vergnaud-Grazzini et al., 1977; Blechschmidt et al., 1982; Cita and Grignani, 1982; Cita et al., 1984; Vergnaud-Grazzini, 1985). Since these older sapropels are only encountered in long cores, usually from areas with low sedimentation rates, it is hard to study them in sufficient detail to pay special attention to the interruptions. High sedimentation rate cores allow greater resolution, which should enable us to discern whether the interruptions are a sedimentological feature (as suggested by Stanley et al., 1978) or a genuine interruption of the process of sapropel formation.

Although several such cores containing S_1 have been discussed, almost none of the studies discussed its two-layered appearance. The thin homogenized interruption interval within S_1 is only obvious (and can only be sampled for faunal analysis) in cores from exceptional settings with high sedimentation rates, such as the Adriatic Sea. Within this context, we focus on the nature of the S_1 interruption in piston-core IN69-9 from the southern Adriatic Basin (Fig. 7.1), where S_1 was found to be distinctly two-layered at most sites deeper than 800 m (Table 7.1). The inferred implications for productivity and deep water ventilation in the Adriatic Sea may well be relevant to the entire eastern Mediterranean, since the Adriatic Sea plays a crucial role in the oxygenation of bottom waters in that basin (Pollak, 1951; Wüst, 1961; Mangini and Schlosser, 1986; Malanotte-Rizzoli and Hecht, 1998).

Table 7.1. Reported occurrence of interruption within Holocene sapropel S_1. Sources: 1. Bottema and Van Straaten (1966); 2. Van Straaten (1966); 3. Van Straaten (1970); 4. Van Straaten (1972); 5. Van Straaten (1985); 6. Jorissen et al. (1993). 7. Perissoratis and Piper (1992); 8. Thunell et al. (1977); 9. Stanley et al. (1978); 10. Rossignol-Strick et al. (1982); 11. Cita et al. (1984); 12. Vismara-Schilling (1984).

Location	Depth-range	Sources
Adriatic Sea	700-1250 m	1,2,3,4,5,6
Northern Aegean Sea	260-425 m	7
Core T171-24 NE off Lybia	2380 m	8
Cores T36 and M18, western Hellenic Trench	1500-2000 m	9
Core Medor 75 KS52, northern Levantine Basin, Strabo Trench, SE of Crete	3118 m	10
Core PC10, central Herodotus Abyssal Plain, off NW Egypt	3198 m	11
Core 10, Cobblestone Area 4 Mediterranean Ridge, N. Ionian Basin	3832 m	12

First, the overall changes in the planktic and benthic foraminiferal faunas (Figs. 7.3, 7.4) are integrated with lithological variations in the upper 310 cm of IN68-9 (about 14,000 to 3000 BP), Then, a synthesis of key indicator species for 1) sea surface temperature (SST), 2) productivity of the benthic ecosystem, and 3) sea floor oxygenation (Figs. 7.3, 7.4, 7.5), is used to reconstruct the processes that caused the onset, interruption and ending of S_1 formation.

2. CORE IN68-9

2.1. General Description

Core IN69-9 from the southern Adriatic Sea (41°47'5 N, 17°54'5 E; 1234 m waterdepth) is used as the standard core in a recently proposed biochronology for the central Mediterranean, its chronology being constrained by 6 AMS^{14}C datings (Jorissen et al., 1993). Previous studies on IN68-9 concerned benthic and pelagic

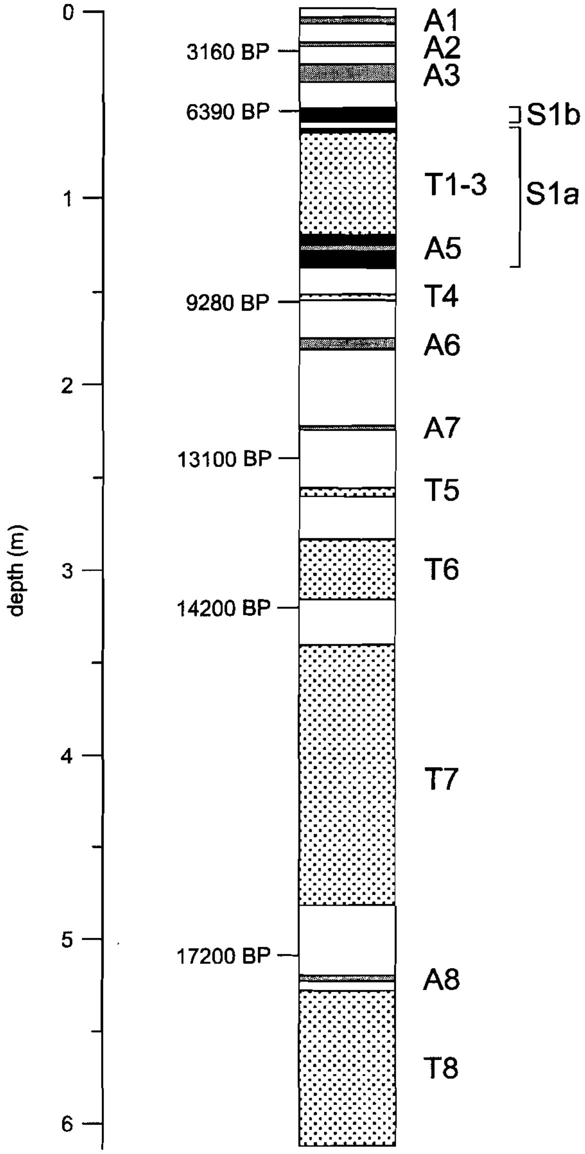

Figure 7.1. Lithology of core IN68-9. Ages displayed to the left of the core are AMS^{14}C datings (after Jorissen et al., 1993). To the right of the core, A indicates ash-layers and T turbidites. Interpolated ages of the various horizons, including the two S_1 subunits, are given in Table 7.2. The original lithological description was made by Van Straaten (1970; also unpubl. data).

molluscs (Van Straaten, 1970: his core 362A) and - on a much coarser scale - planktic and benthic foraminifera for biostratigraphic and longer-term paleoceanographic purposes (Jorissen et al., 1993; Rohling et al., 1993b).

For the present study, we strongly increased the detail of the foraminiferal records in the late glacial to Holocene interval (310-0 cm)(Figs. 7.3, 7.4, 7.5). The record through sapropel S_1 now averages about one sample per 100 to 200 years (Table 7.2). IN68-9 mainly consists of hemipelagic muds, including a dark-coloured laminated sapropel, alternating with several ash-layers and turbidites (Fig. 7.1). The hemipelagic muds typically contain about 0.5% organic carbon, while values in the sapropel fluctuate between 0.9 and 2.1% (Fig. 7.5). Sapropel S_1 is found between 140 and 54 cm. Within S_1, an ash-layer is present between 130 and 128 cm, and a turbiditic interval between 122 and 67 cm. In addition, the sapropel was found to be interrupted by a distinct, lighter

coloured and apparently homogeneous interval between 65 and 62 cm. Two samples were taken from this narrow interval, while immediately past its base and top a sample was taken from the adjacent sapropelic sediments (Table 7.2). Carbonate preservation was observed to be excellent throughout the core, as witnessed also by the continuous presence of aragonitic pteropod shells.

2.2. Age Model

Table 7.2 lists the AMS^{14}C dating results (see Jorissen et al., 1993) and interpolated ages for the various stratigraphic horizons and investigated samples in core IN68-9. After correction of the uncorrected ($^{14}C_{nc}$) ages for a reservoir age of about 4OO years, giving corrected ($^{14}C_c$) ages, the datings could be converted to calendar years (Stuiver et al., 1991). Since the present study concentrates on the formation of S_1 and processes shortly before and after that, and since sample resolution is not much finer than 1 sample per century, the relatively minor Holocene ^{14}C platforms (Stuiver et al., 1991) do not appreciably affect the results. The main platforms influencing $^{14}C_c$ dates occur earlier, around 9600 (calendar-age range 10,400-10,800 BP) and 10,000 BP (calendar-age range 11,000- 11,200 BP)(Stuiver et al., 1991), intervals we do not particularly concentrate on and where, consequently, sample resolution is much lower anyway (1 per 200 to 300 years; Table 7.2). Figure 7.2 shows the age versus depth plots for core IN68-9, in two forms: (1) with turbidites and ash-layers included, assuming quasi-instantaneous deposition for those intervals (cf. Jorissen et al., 1993), and (2) excluding the turbidites and ash-layers. Especially the plot versus calendar years shows an almost straight line since about 15,000 BP, suggesting absence of any major non-linearity that might upset the (interpolated) time-relations inferred in this paper (cf. Table 7.2).

Table 7.2. Left hand side: Stratigraphic horizons in core IN68-9. A = Ash; T = Turbidite; II/III and I/II = Faunal Zones II/III and I/II boundaries (Jorissen et al., 1993). Bold: AMS^{14}C dated levels (Jorissen et al., 1993). Italics: inter/extrapolated from dated levels. $^{14}C_{nc}$ = ages uncorrected for reservoir age, $^{14}C_{c}$ = corrected for reservoir age of 400 years (Bard, 1988; Broecker et al., 1988a; Bard et al., 1990). Cal.= calendar years BP, according to Stuiver et al. (1991) (* indicates calendar age from linear extrapolation in their graph, which stops around 6000 BP). Calendar age inter/extrapolations are redone using calendar-ages of dated levels. Right hand side: Investigated samples, $^{14}C_{nc}$ ages and calendar ages. Bold = samples corresponding to AMS^{14}C dated levels. Italics = inter-/extrapolated ages.

Horizon	Depth cm	**14Cnc** *interp.* yrs BP	**14Cc** *interp.* yrs BP	**cal.** *interp.* yrs BP	Sample cm	14Cnc yrs BP	cal. yrs BP	Sample cm	14Cnc yrs BP	cal. yrs BP
A2	4-5	2800	2400	3130	**11.5**	**3160**	**3500**	149.5	8960	9600
Dating	**11.5**	**3160**	**2760**	**3500***	17.5	3790	4250	155.5	9280	9930
A3	18-20	3840	3440	4190	28.5	4720	5150	158.5	9340	10030
A4	30-40	4880	4480	5260	29.5	4830	5200	166.5	9740	10570
Top S1b	54	6340	6340	6750	42.5	5140	5580	170.5	9970	10840
Dating	**54.5**	**6390**	**6000**	**6800**	43.5	5240	5630	172.5	10040	10970
Base S1b	62	6900	6500	7360	48.5	5770	6160	175.5	10200	11170
Top S1a	65	7100	6700	7580	53.5	6290	6690	179	10340	11340
T1-3	67-122	7230	6830	7730	**54.5**	**6390**	**6800**	188.5	10560	11640
A5	128-130	7630	7230	8160	61.5	6860	7320	193.5	10810	11970
Base S1a	140	8300	7900	8900	62.75	6950	7410	194.5	10860	12040
T4	154-157	9260	8860	9930	63.5	7000	7460	204.5	11360	12710
Dating	**157.25**	**9280**	**8900**	**9950**	66.5	7200	7680	210.5	11660	13110
I/II	163.5	9600	9200	10370	69	7240	7730	218.5	12060	13650
A6	178-184	10330	9930	11340	123.5	7340	7830	222.5	12260	13910
A7	224-226	12340	11940	14010	124.5	7410	7910	223.5	12310	13980
II/III	233	12700	12300	14480	129	7640	8160	233.5	12710	14510
Dating	**241.5**	**13100**	**12700**	**15050**	130.5	7670	8200	240.5	13060	14980
T5	258-262	13510	13110	15560	136	8050	8610	**241.5**	**13100**	**15050**
T6	285-318	14090	13690	16260	137	8110	8680	259.5	13510	15560
Dating	**322.5**	**14200**	**13800**	**16400**	139.5	8280	8860	274.5	13830	15940
T7	342-484	15470	15070	17760	140.5	8350	8940	306.5	14090	16260
Dating	**510.5**	**17200**	**16800**	**19600**	142.5	8490	9080	405.5	15470	17760
A8	521-525	17880	17480	20330	144.5	8620	9230	485.5	15570	17860
T8	530-613	18210	17810	20680	146.5	8790	9380	526	17950	20400

Since the offsets between the time-scales of changes expressed in ^{14}C and calendar-ages (Table 7.2, Figure 7.2) are relatively minor in the early Holocene interval that we concentrate on, we opt for using the primary dating results. We plot and discuss our results in terms of uncorrected ^{14}C years ($^{14}C_{nc}$), instead of correcting them for reservoir age in the Mediterranean, since this reservoir age might be subject to future adjustments from the approximated 400 years.

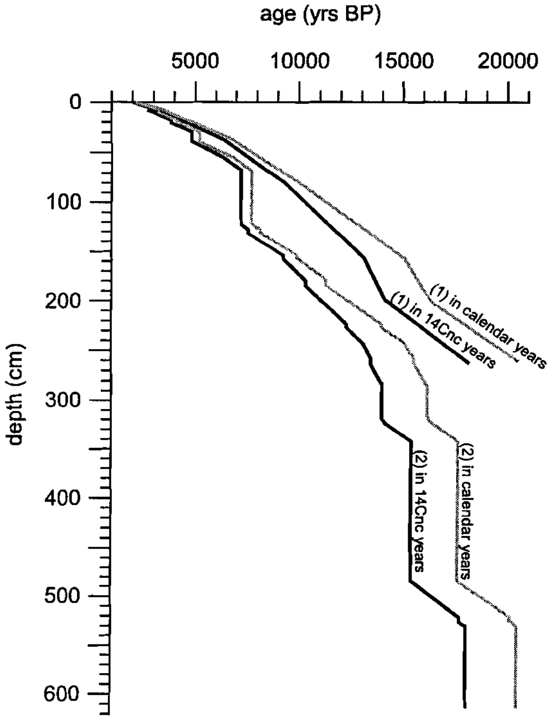

Figure 7.2. Age versus depth plots for core IN68-9. (1) Turbidites and ash-layers included, assuming quasi-instantaneous deposition for those intervals (cf. Jorissen et al., 1993). (2) Excluding the turbidites and ash-layers. Solid lines are plotted versus uncorrected ^{14}C ages, grey lines versus calendar years (see conversion of ages in Table 7.2).

3. FORAMINIFERA

3.1. Planktic Foraminifera

3.1.1. Individual Species: Records and Interpretation

Planktic foraminifera (150-595 μm fraction; cf Jorissen et al., 1993) are present throughout core IN68-9, except within the turbidites. In the upper 310 cm, several large changes occur in the composition (Figure 7.3). A minimum of 200 specimens

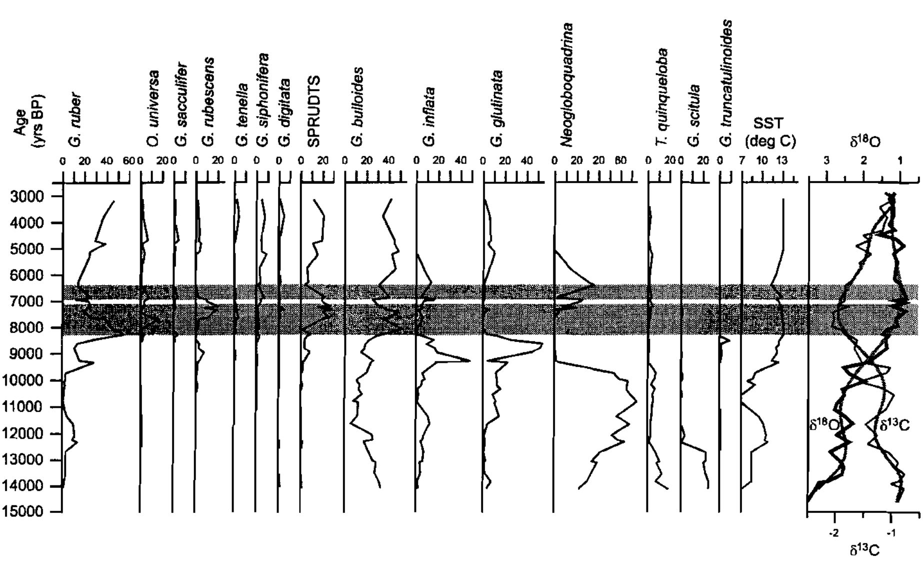

Figure 7.3. Percentages of planktic foraminiferal species versus age in core IN68-9 for the past 14,500 years. Shaded intervals represent the two S_1 subunits. Heavy line in the stable isotope column is $\delta^{18}O$, normal line $\delta^{13}C$. The shaded curves are polynomial smoothings to show the general trends. SPRUDTS is a faunal cluster explained in section *3.1.1.* and Table 7.3; the main species of this cluster are also displayed individually. SST is a Sea Surface Temperature proxy-record constructed and calibrated as discussed in section *3.1.2.* Note that the isotopic records are not those presented earlier by Jorissen et al. (1993), but completely new ones with a resolution similar to that of the faunal analyses. Rather than adding more samples to the Jorissen et al. (1993) record (which actually consisted of two combined sets of analyses already), we chose

was counted for every sample. The relevant habitat characteristics for the species involved are summarized in Table 7.3, with references for further information.

Although *Neogloboquadrina pachyderma* (dextral) dominates the pre-12,700 BP interval, *Globorotalia scitula* - a cool to cold water species that occurs to great depth - also is abundant. *Turborotalita quinqueloba*, a species that thrives in cool surface waters, is common in the glacial interval as well, but, unlike *G. scitula*, it continues until about 9600 BP. *Globigerinoides ruber*, a warm oligotrophic mixed-layer dweller, is common after 12,700 BP, although it displays a brief decrease between 11,000 and 9600 BP. After 9600 BP, a marked increase occurs in the SPRUDTS-group (*Globigerinoides sacculifer, Hastigerina pelagica, Globoturborotalita rubescens, Orbulina universa, Globigerinella digitata, Globoturborotalita tenella*, and *Globigerinella siphonifera*). These individually low frequency species are grouped because of their tendency to do so in cluster analyses (Rohling et al., 1993b) and form a useful warm, subtropical water indicator, especially when considered in combination with *G.*

Table 7.3. Summary of main habitat characteristics of the plank-tonic foraminiferal taxa discussed in this paper (modified after review in Rohling et al., 1993b). Sources: 1. Tolderlund and Bé (1971); 2. Fairbanks et al. (1982); 3. Hemleben and Spindler (1983); 4. Almogi-Labin (1984); 5. Thunell and Reynolds (1984); 6. Bé et al. (1985); 7. Vergnaud-Grazzini et al. (1986); 8. Hemleben et al. (1989); 9. Pujol and Vergnaud-Grazzini (1989); 10. Van Leeuwen (1989); 11. Hutson (1977); 12. Reynolds and Thunell (1989); 13. Fairbanks et al. (1980); 14. Rohling et al. (in press, a); 15. Fairbanks and Wiebe (1982); 16. Bé (1969); 17. Kipp (1976); 18. Coulbourn et al. (1980); 19. Duplessy et al. (1981); 20. Thiede (1983); 21. Zhang (1985); 22. Overpeck et al. (1989); 23. Barmawidjaja et al. (1989).

Species	Habitat	Sources
G. ruber	Shallow dweller in warm, oligotrophic mixed layer.	1,2,3,4,5,6,7,8, 9,10
SPRUDTS-*group* = *G. sacculifer, H. pelagica, G. rubescens, O. universa, G. digitata, G. tenella, G. siphonifera*	As a group applicable as warm (subtropical) water indicator, especially when considered in combination with *G. ruber*. Group name based on first letters of species names (Rohling et al., 1993a).	1,2,3,4,5,6,7,8, 9,10,11,12
G. inflata	Well-mixed, cool environment with intermediate to high nutrient levels. Dominates in frontal systems.	1,9,10,11,13,14
G. glutinata	Both in mixed layer and deeper waters. Wide T and S ranges. Cosmopolitan.	1,2,4,5,6,8,12
T. quinqueloba	Tolerant to fairly low S and indicative of low T and/ or enhanced fertility in surficial waters.	1,7,8,9,10,11,12
Neogloboquadrina	Important part of life-cycle in deeper, eutrophic waters, in Deep Chlorophyll Maximum (DCM). Therefore: indicative of stratification in mixed layer. The type discussed in the present paper, *N. pachyderma* (dextral) is by far the dominant type in eastern Mediterranean records. Typical *N. dutertrei* types may be found in previous interglacial intervals (esp. stage 5). No substantial numbers of *N. pachyderma* (sinistral) have ever been found in Quaternary eastern Mediterranean records.	2,3,5,6,8,9,10, 12,13,13,15
G. scitula	Down to great depths in cool to cold waters.	5,8,16
G. bulloides	No depth or temperature preference, but highly dependent on enhanced food levels, e.g. by upwelling, strong seasonal mixing, or river input.	1,4,6,8,9,10,12, 16,17,18,19,20, 21,22,23

ruber (Table 7.3). Note that abundances are probably not directly controlled by temperature, but rather by the degree of development of a persistent seasonal thermocline, separating a warm oligotrophic mixed layer (habitat of "warm" species) from cooler and more eutrophic waters below.

The faunal changes in the Adriatic Sea described above suggest ending of truly glacial conditions around 12,700 BP, a poorly developed return to cooler conditions between 11,000 and 9600 BP (corresponding to the Younger Dryas), and a final ending of the glacial period around 9600 BP.

Around 9600 BP, *Globorotalia inflata* shows a sudden increase in dominance following a total decline of *Neogloboquadrina pachyderma* (d). Around 9000 BP, the high abundance of *G. inflata* is rapidly followed by high abundance of *Globigerinita glutinata*.

Since *Neogloboquadrina pachyderma* (d) thrives in eutrophic waters, and is mostly found in association with a deep chlorophyll maximum at the base of the euphotic layer fueled by upward mixing of nutrients from deeper waters (Table 7.3), its high abundances strongly suggest (seasonally?) stratified conditions within the euphotic layer. *G. inflata* proliferates in well-mixed, cool environments with relatively high nutrient levels and shows peak abundances associated with strong vertical mixing and distinct frontal systems (Table 7.3). Hence, the abrupt decline of *Neogloboquadrina pachyderma* (d) in favour of *G. inflata* probably reflects disappearance of a more stably stratified habitat, and increased dominance of strong vertical mixing and/or frontal systems in relatively eutrophic waters. The subsequent change to *G. glutinata* dominance is hard to understand because of its cosmopolitan character (Table 7.3). Tentatively, we propose that it reflects the next phase in the decline of nutrient availability, to a system with only occasional input of nutrients from deeper waters. According to this interpretation, *Neogloboquadrina pachyderma* (d), *G. inflata*, and *G. glutinata* should have an increasing reproduction-potential, respectively. The inferred highest reproduction-potential of *G. glutinata* would enable it to numerically overwhelm the other species in response to very short-lived eutrophication events, which might also (partly) explain its observed cosmopolitan character. This proposal needs to be substantiated by further research on the modern characteristics of the species involved.

Globigerina bulloides is abundant throughout the record, but shows a maximum in the sapropel. In the interruption between the two sapropelic subunits, *G. bulloides* abundances drop to a temporary low. Although the percentages of *G. bulloides* above S_1 show a brief low, they subsequently return to values that are rather similar to those within S_1.

G.bulloides is an opportunistic species thriving in any eutrophic setting (Table 7.3). Plankton towing showed maximum abundance of *G. bulloides* in winter in the Tyrrhenian Sea (Vergnaud-Grazzini et al., 1986) and in late spring in other western Mediterranean basins (Vergnaud-Grazzini, 1973; Cifelli, 1974; Devaux, 1985). Its peak abundance in especially the lower S_1 subunit suggests that sapropel formation coincided with surface water eutrophication. Previously, part of this eutrophication has been ascribed to increased (Po) river discharge (Rohling et al., 1993b), but our new isotopic results (section 4) are not in support of such inferred direct Po river influence on *G. bulloides* abundances.

3.1.2. Sea Surface Temperature Record

To estimate sea surface temperature (SST) variations, cumulative frequencies of the warm water indicators *G. ruber* and the SPRUDTS-group are calculated versus the cooler/cold water species *T. quinqueloba*, *G. scitula*, *G. inflata*, and *Neogloboquadrina pachyderma* (d). *A-priori* grouping is easily performed and gives results comparable to those from more elaborate statistical methods (cf. Cita et al., 1977; Thunell et al., 1977; Rohling and Gieskes, 1989; Rohling et al., 1993b). Note that our record, as all other fauna-based SST records, will be biassed to some extent due to the additional dependence on nutrient availability of especially the species on the "cool" side (e.g. *Neogloboquadrina pachyderma* (d) and *G. inflata*). In spite of the enhanced detail, the down-core pattern of our *a-priori* grouping strongly resembles that derived previously using Principal Components Analysis, providing an essentially semi-quantitative indicator of 'cooling' and 'warming' trends (Rohling et al., 1993b). For a better understanding of the order of magnitude of the SST-changes involved, however, we now calibrate the percentage-vadations in the *a-priori* grouping to changes in °C as follows:

(i) Fossil evidence suggests that last glacial maximum (LGM) winter SST in the Adriatic was about 6°C lower than today (1-3°C less difference in summer) (Bigg, 1994), which is supported by a recent U^k_{37} SST record suggesting about 8°C change in the Alboran Sea (western Mediterranean) (Cacho et al., 1994), and foraminiferal transfer function results suggesting about 5°C change in the Aegean Sea (Thunell, 1979). **(ii)** Modern winter SST in the Adriatic Sea is about 13°C (Levitus, 1982), so that the range of about 100% change in our percentage-plot for SST should correspond to a temperature-range between about 7 and 13°C (winter SST is considered since it is important for deep convection in the Adriatic). **(iii)** Next, the rate of change in the percentage-plot needs to be calibrated to the rate of change in °C. It is unrealistic to use a simple linear relation, since it would imply a 1:4 ratio for the relative proportions of the 14-12 and 10-8 kyr BP winter SST increases, whereas vegetation-based records of winter temperature in southern France (Guiot, 1987) and the U^{k}_{37} SST record for the Alboran Sea (Cacho et al., 1994) suggest a ratio of about 1:2. We find such an approximate 1:2 ratio when calibrating our percentage-record to °C using a logarithmic relationship. **(iv)** The resultant SST-proxy record is plotted versus age along with the other results (Figs. 7.3, 7.5).

3.2. Benthic Foraminifera

3.2.1. Individual Species: Records and Interpretation

The discussion of benthic foraminifera concentrates on the changes directly associated with, and for some distance below and above S_1. Hence, the benthic record shown extends from about 200 cm (11,000 BP) to the very top of the core (Fig. 7.4). Benthic foraminifera (150-595 μm fraction; cf. Jorissen et al., 1993) are present up to the very base of S_1 (8300 BP). Thereafter, benthics are absent until 7200 BP, with the exception of the interval between 7400 to 7240 BP, just below the turbidite within the lower S_1 subunit. After the lower subunit, benthic foraminifera are present throughout. At least 200 specimens were counted for every sample.

Around 9600 BP, a rather diverse fauna is found with dominant *Gyroidina altiformis* and *Uvigerina mediterranea*. This fauna is very similar to that after 5200

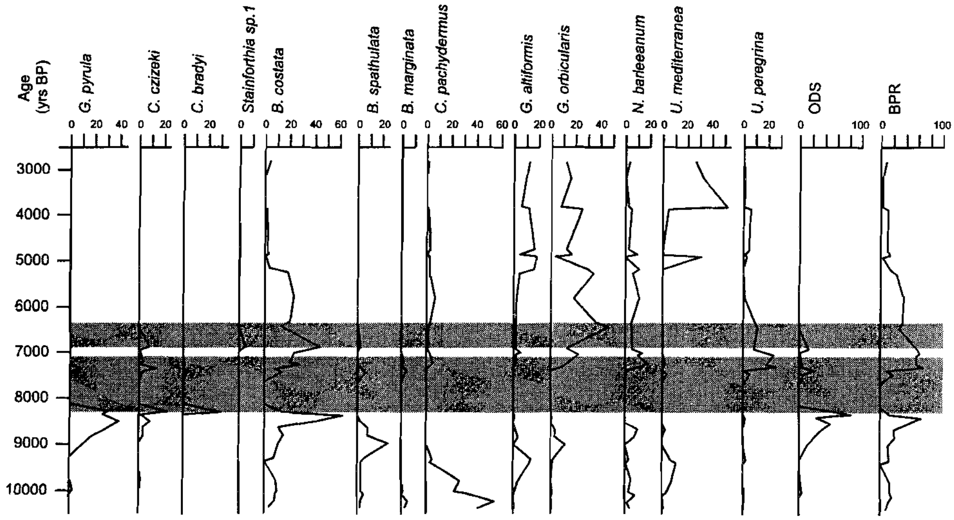

Figure 7.4. Percentages of benthic foraminiferal species versus age in core IN68-9 for the past 10,500 years. ODS is Oxygen Deficiency Stress group explained in section *3.2.2.* BPR is Benthic Productivity group explained in section *3.2.2.*

BP, which characterizes the relatively oligotrophic conditions of the modern Mediterranean. At about 9300 BP, *G. altiformis* and *U. mediterranea* largely disappear, while *Gyroidina orbicularis* and *Bolivina spathulata* increase in frequency, as does, somewhat later, *Bulimina costata*. After 8600 BP, faunal diversity becomes very low and progressively more dominated by *Nonion barleeanum*, *Globobulimina pyrula*, *Chilostomella czizeki* and *Cassidulinoides bradyi*, while *B. costata* shows a change in morphology from rather short (*inflata*) morphotypes with discontinuous costae to elongated (*costata*) types with continuous costae along the entire test.

The described faunal succession coincides with a significant increase in the organic carbon content after about 9500-9000 BP (Fig. 7.5), and culminates in complete absence of benthic fauna and preservation of laminae after 8300 BP (base S_1), indicating persistent anoxia (Josefson and Widbom, 1988; Bernhard and Reimers, 1991). Combined, these patterns lead us to suggest that the faunal succession resulted from increasing fertility and decreasing oxygenation of the benthic environment. In this scenario, 1) *G. orbicularis* and *B. spathulata* would reflect the first stage of ecosystem enrichment; 2) *B. costata* and *N. barleeanum* would become dominant through increasing low-oxygen stress while benthic fauna can still profit from high food availability; and 3) *G. pyrula*, *C. czizeki* and *C. bradyi* would reflect very strong dysoxia, possibly even intermittent anoxia. These inferences based on core IN68-9 are supported by previous studies characterizing most of the involved species as indicative of ecosystem enrichment and oxygen depletion (Table 7.4). Specifically relevant to our proposed scenario for the observed benthic faunal succession is the common dominance of *Bulimina costata*, *Globobulimina*, *Chilostomella*, and *Stainforthia* in oxygen minimum zones around the world (Sen Gupta and Machain-Castillo, 1993). Moreover, under well-oxygenated conditions, *G. pyrula*, *C. czizeki* and *C. bradyi* occupy deep infaunal habitats near the redox-front, tolerating strongly dysoxic conditions, whereas *N. barleeanum* occupies a shallower position, suggesting less tolerance to dysoxia (e.g. Corliss, 1985; Corliss and Emerson, 1990; Jorissen et al., 1995). Nolet and Corliss (1990) also found dominance of *Globobulimina* and *Chilostomella* directly at the base or within a number of late Quaternary sapropels, which they ascribe to strong low-oxygen tolerance of these taxa. As do other (potentially) infaunal species in the recent Adriatic (Barmawidjaja et al., 1992), these taxa likely follow taxon-specific critical oxygen levels that migrate towards the sediment-water interface when oxygenation deteriorates (e.g. Mackensen and Douglas, 1989), ultimately causing species with the highest tolerance of dysoxia/intermittent anoxia to dominate the fauna, persisting at the sediment surface.

Immediately above the turbidite of 7230 BP, the benthic fauna in the lower S_1

After the sterile base-interval of S_1, the first return of benthic foraminifera is found at

Table 7.4. Benthic foraminiferal taxa proposed as indicators of ecosystem enrichment and/or oxygen depletion. The cited sources sometimes described the taxa under different names. Sources: 1. Jorissen (1987); 2. Sen Gupta and Machain-Castillo (1993); 3. Lutze and Coulbourn (1984); 4. Lutze (1986); 5. Altenbach and Sarnthein (1989); 6. Mackensen et al. (1985); 7. Caralp (1989b); 8. Loubere, 1994; 9. Miller and Lohmann (1982); 10. Bernhard and Reimers (1991); 11. Alve, 1990.

Taxon	Sources
Bulimina costata	1,2
Uvigerina peregrina	3,4,5
Nonion barleeanum	1,6,7,8
Globobulimina / Chilostomella	2,8,9,10
Stainforthia	11

7400 to 7300 BP, just below the turbidite. The fauna is very diverse in that interval, containing substantial numbers of *Cassidulina carinata*, *Trifarina angulosa*, and *Bulimina marginata*. These species, virtually absent in the other samples, have a lower depth limit of 800 m in the present-day Adriatic Sea (Jorissen, 1988), so that the 7400-7240 BP fauna seems to reflect downslope transport into a still anoxic environment. The high percentages of *C. czizeki* and *G. pyrula* suggest admixture of dysoxic lower slope (500-800m) faunas with better oxygenated upper slope (200--500m) faunas.

subunit is dominated by *B. costata*, *Uvigerina peregrina* and *N. barleeanum*. The interruption of S_1 shows an increase of *G. orbicularis*, and total disappearance of *G. pyrula*, *C. czizeki*, *C. bradyi*. Interpreted in terms of the above explanation for benthic change prior to S_1, the fauna after 7200 BP reflects slight reoxygenation of the bottom waters, in a still eutrophic benthic environment. The changes associated with the S_1 interruption (7100 - 6900 BP) suggest substantially improved bottom water oxygenation, while fertility in the benthic ecosystem decreased to levels comparable to those reflected in the last 500 years prior to the onset of sapropel formation.

The onset of the second S_1 subunit (6900 BP) corresponds with a return of *C. czizeki*, and a maximum of *B. costata* (elongated *costata* morphotypes), suggesting a return to distinct dysoxia after the reoxygenation represented by the S_1 interruption.

G. orbicularis and *inflata* morphotypes of *B. costata* (encountered also below S_1) dominate between 6900 and 6340 BP (second S_1 subunit), continuing until 5200 BP. The ensuing frequency drop around 5200 BP suggests that oxygenation and productivity became comparable to the present relatively oligotrophic situation. This date differs completely from that of Fontugne et al. (1989), who argued on the basis of sedimentological evidence that, since the formation of S_1, fully oxygenated conditions would only have returned around 1650 BP.

3.2.2.Summary of Benthic Productivity and Oxygen Deficiency Stress Records

To summarize the benthic faunal changes, we use the successions observed in IN68-9 to propose a clustering of species that - individually - were previously proposed to indicate ecosystem enrichment and/or oxygen depletion (Table 7.4). The first group consists of *Bulimina costata*, *Uvigerina peregrina* and *Nonion barleeanum*, characterizing a relatively advanced stage of ecosystem enrichment, where only species with a certain tolerance for low oxygen conditions can profit from the abundance of food ("Benthic Productivity" (BPR) group; Figs. 7.4, 7.5). The second group consists of *Globobulimina pyrula*, *Chilostomella czizeki*, *Cassidulinoides bradyi* and *Stainforthia* sp., characterizing the ultimate stage before totally azoic conditions,

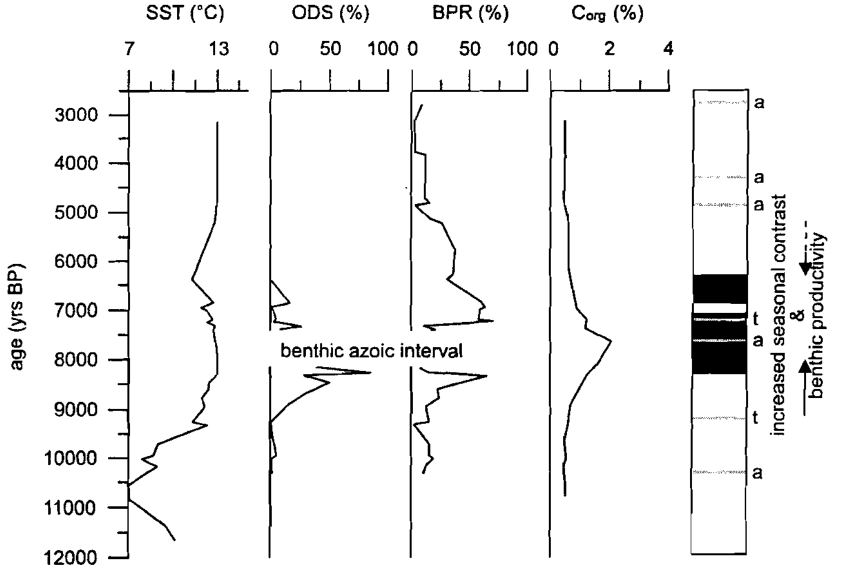

Figure 7.5. Summarizing diagram of Sea Surface Temperature (SST; section *3.1.2.*), sea floor Oxygen Deficiency Stress (ODS; section *3.2.2.*), Benthic Productivity (BPR; section *3.2.2.*), Organic Carbon content (C_{org} in %), versus age (yrs BP) in core IN68-9. In the lithological column, both S_1 subunits are indicated in black, and the chronostratigraphic positions of ash layers (a) and turbidites (t) are indicated with a shaded line.

tolerating severe low-oxygen stress ("Oxygen Deficiency Stress" (ODS) group; Figs. 7.4, 4). As yet, it is impossible to fully quantify the ODS and BPR proxies. Concerning the ODS-curve, however, we suggest that the taxa only become present in substantial numbers (ODS score >10%) when bottom water oxygen concentrations become lower than 1.0 ml l^{-1} (e.g., Sen-Gupta and Machain-Castillo, 1993), while dominance (ODS score > 50%) likely reflects virtually anoxic conditions.

The increasing BPR values between 9300 and 8500 BP are followed by an abrupt drop immediately below the sapropel. This sudden decrease likely is an artifact, resulting from an overriding effect of severe low-oxygen stress (ODS peak). Even though the species combined in the BPR record must be fairly tolerant to low oxygen conditions, the progressively increasing oxygen deficiency presumably passed their tolerance limit around 8500 BP, so that only species tolerant of extreme low-oxygen conditions remained. This interpretation is supported by the azoic conditions (persistent anoxia) found only 200 years later (onset of S_1; 8300 BP).

4. STABLE ISOTOPES

Analyses of $\delta^{18}O$ and $\delta^{13}C$ have been performed using the planktic foraminiferal species *G. bulloides* (Fig. 7.3) instead of the more commonly used *G. ruber*, because only *G. bulloides* was found in sufficient numbers throughout the core. Unlike *G. ruber*, *G. bulloides* is not a shallow dwelling summer mixed-layer species. Today, it thrives in the western Mediterranean in winter and/or (late) spring (Vergnaud-Grazzini, 1973; Cifelli, 1974. Devaux, 1985. Vergnaud-Grazzini et al., 1986). Therefore, and since the analysing equipment required >40 specimens per sample, the $\delta^{18}O_{bulloides}$ measurements are crude 'averages' only, influenced by lateral/vertical advection in the watercolumn and by the combination of specimens from various seasons and various years within one measurement. Similar arguments hold for $\delta^{13}C_{bulloides}$, since the opportunistic feeding behaviour of *G. bulloides* creates an uncontrollable level of 'noise' in the record. For both the $\delta^{18}O$ and $\delta^{13}C$ records, polynomial smoothing is applied to highlight the major trends, which we do consider to be relatively robust and reliable (Fig. 7.3).

The smoothed $\delta^{18}O$ record (Fig. 7.3) shows a basically two-step deglaciation. The first step, at the base of the studied section of IN68-9, ends around 12,700 BP (Termination Ia: Mix and Ruddiman, 1985; Bard et al., 1987). Thereafter, the curve levels out until about 10,700 BP, followed by a second trend of depletion until about 7000 BP. The actual measurements show that 60% of this second trend of depletion took place between about 9800 and 9000 BP (Termination Ib: Duplessy et al., 1981; Mix and Ruddiman, 1985; Broecker et al., 1988b). After 7000 BP, the smoothed record shows a very gradual trend of minor enrichment.

Rossignol-Strick et al. (1992) show $\delta^{18}O$ and pollen records for core KET8216 (southern Adriatic). Although their isotope record (based on *G. ruber*) is as indiscriminate concerning the Younger Dryas as ours, these authors argue that a distinct Younger Dryas is visible in their (marine) pollen record, as is usually the case in (continental) pollen sequences from circum-Mediterranean countries (e.g., Guiot, 1987; Magaritz and Goodfriend, 1987; Pons et al., 1987; Rognon, 1987; Lowe, 1992). As yet, we cannot explain this discrepancy between the distinct Younger Dryas expression in pollen records, and its poor expression in Adriatic records of $\delta^{18}O_{bulloides}$ and $\delta^{18}O_{ruber}$.

The (smoothed) record of $\delta^{13}C$ shows a remarkable correlation with that of $\delta^{18}O$, except after 7500 BP, when the relative rate of change in the $\delta^{13}C$ record is considerably larger than that in the $\delta^{18}O$ record. The $\delta^{13}C$ record shows notable depletion within S_1 (mainly the lower subunit), and a gradual, but distinct enrichment after about 7300 BP.

In the Adriatic Sea, it seems likely that particulate organic matter discharged by the nearby Po river contributed to the diet of *G. bulloides*, and the isotopes provide a means to evaluate whether the species was extra abundant during periods of increased river discharge. If such a simple relation between high abundances and increased river discharge would exist (e.g., for the lower S_1 subunit), not only low $\delta^{13}C$ values (input of ^{13}C depleted continental organic matter) should be found, but also low $\delta^{18}O$ values (input of low $\delta^{18}O$ freshwater). No notable depletion of $\delta^{18}O$ values is found in the lower S_1 subunit, however, proving the assumption of primary river discharge control on Adriatic *G. bulloides* abundance to be largely incorrect.

5. DISCUSSION AND CONCLUSIONS

5.1. Relation Between Changes in the Planktic and Benthic Environments

This section focuses mainly on the relation between the proxy-records of Sea Surface Temperature (SST; Figs. 7.3, 7.5), Benthic Productivity (BPR; Figs. 7.4, 7.5) and sea floor Oxygen Deficiency Stress (ODS; Fig. 7.4, 7.5). These records represent changes in long-term average conditions in the basin, even when words like "abrupt" and "rapid" are used, since the average sample resolution - relatively high as it may be - is not sufficient to address changes on time-scales smaller than about a century.

The winter SST record (Figs. 7.3, 7.5) suggests glacial values around 7°C in the southern Adriatic until a first substantial warming around 12,700 BP, followed by a return to near-glacial winter SST conditions between 11,000 and 10,000 BP (Younger Dryas). Thereafter, a second major warming takes place until about 9500 BP, followed by a more gradual increase culminating between 8300 to 8000 BP with near-modern temperatures (13°C). The suggestion that maximum temperatures were reached around 8000 BP is consistent with the vegetation-based paleotemperature reonstructions for southern France (Guiot, 1987).

The high SST conditions reached around 9300 BP suggest prevalence of a season with a relatively warm and oligotrophic mixed layer in the basin. In addition, the abundance of *G. inflata* in this interval suggests a well developed rather eutrophic, well-mixed season, while the high abundances of *G. glutinata* may also be related to a process of eutrophication (section *3.1.1*). Moreover, although still rather low, *G. bulloides* abundances start to increase after 9300 BP, suggesting increasingly favourable (eutrophic) conditions, possibly in the form of seasonal blooms.

The planktic record, therefore, suggests enhanced seasonal contrasts in temperature and productivity after about 9300 BP, so that the organic flux to the sea floor (export production) must have become increasingly seasonal. Even without a change in the total annual export production, a change from a rather constant flux to a pulsed, seasonal flux would influence benthic life and increase the potential for organic matter burial in the sediment (Berger and Wefer, 1990). Hence, the increases in the C_{org} content and the BPR record, indicating enrichment of the benthic environment, support the inferred enhanced seasonal contrasts after 9300 BP (Fig. 7.5). Additional support comes from the general decrease in 'annual stability' around the Pleistocene/ Holocene boundary inferred from planktic foraminiferal faunas in a wider eastern Mediterranean context (Rohling et al., 1993b).

Around 8500 BP, the final increase of winter SST increase towards the maximum values of 8300-8000 BP coincides with an increase of low-oxygen stress in the benthic community (ODS; Figs. 7.4, 7.5), which also culminates around 8300 BP - the onset of S_1 - in complete and persistent anoxia causing azoic conditions at the sea floor until about 7200 BP. During deposition of sapropel S_1 a gradual cooling is suggested, with some minor lows associated with the 7100-6900 BP interruption of S_1. The benthic fauna reflects some improvement of the oxygenation in a still eutrophic enviromnent around 7200 BP, and substantially increased oxygenation between 7100 and 6900 BP. Slight warming at the base of the second sapropelic subunit (6900 BP) coincides with the return of very poorly oxygenated conditions at the sea floor. Continued gradual cooling towards the top of S_1 is accompanied by a change in the benthic fauna reflecting progressive decrease of the stress from oxygen deficiency. Finally, winter SST rises from 6340 to 4500 BP, when modern conditions were established, while around 5200 BP, benthic productivity and oxygenation arrive at present-day levels.

5.2. Ventilation Versus Productivity

The BPR record suggests (well) eutrophicated conditions starting to build up about 9300 BP (1000 years before the onset of S_1), and reaching a likely maximum between 8300 and 7400 BP (considering the high values bordering the azoic interval, it seems likely that highly/highest eutrophicated conditions prevailed during deposition of that interval). Then, a rapid decline is suggested between about 6900 BP and 5200 BP, followed by relatively stable oligotrophic conditions. The generally enhanced seasonal contrasts in productivity inferred since about 9300 BP (with a possible end reached around about 5500 BP) also suggests increased organic flux to the sea floor. This coincidence of increased (seasonality of) productivity with sapropel formation would seem to support a recent conclusion that productivity forms the primary control on enrichment of organic carbon in sediments, which was based on recent sapropel formation in the Black Sea (Pedersen and Calvert, 1990; see review in Rohling, 1994).

However, in IN68-9, neither the record of benthic productivity, nor that of the main planktic productivity markers *G. bulloides*, *Neogloboquadrina pachyderma* (d), and *G. inflata*, show patterns suggestive of a causal link between short-term productivity variations and the depositional sequence of two S_1 subunits interrupted by a lighter-coloured homogeneous interval, apart from the overall correspondence of the sapropel to an interval of enhanced productivity. On the contrary, the ODS and SST records do suggest such a direct link with the depositional sequence. Enhanced SST values at the base of both S_1 subunits likely caused lowering of surface water densities, helping to install stable stratification and consequently poor or blocked deep water ventilation in the Adriatic Sea. Subsequent temperature decrease during the deposition of either sapropelic interval would have favoured some improvement of deep water ventilation, allowing benthics with sufficient low-oxygen tolerance to repopulate, while the culminated cooling at the end of sapropel deposition caused re-installment of good deep water ventilation and proper sea floor oxygenation.

Summarizing, the data from Adriatic core IN68-9 suggest that within a relatively eutrophic setting - caused by increased seasonal contrasts (and perhaps partly enhanced by nutrient-input via river discharge) - the onset, interruption, and final ending of S_1 deposition in the Adriatic Sea were triggered by changes in ventilation of the basin. The coincidence of SST variations with these changes in ventilation suggests a causal relationship. Although the SST changes are of a relatively small magnitude (<2°C), and granted that they may not be very accurately estimated with our simple SST calibration, they still seem significant in terms of the sensitivity of Adriatic Sea ventilation to changes in its density-structure, since even relative temperature increases of the order of only 0.7°C might suffice to upset the basin's vertical circulation, causing onset of sapropel formation (Mangini and Schlosser, 1986). Moreover, the density variations resulting from the inferred temperature changes should be viewed in combination with the underlying influence of 1) a strong salinity decrease in the eastern Mediterranean associated with the deglaciation (Thunell et al., 1987; Thunell and Williams, 1989; Rohling, 1994); 2) increased humidity in the eastern Mediterranean area coinciding with the deposition of S_1 (see review in Rohling and Hilgen, 1991). Our conclusions are similar to those based on benthic foraminiferal evidence in S_5, which identified anoxia resulting from reduced ventilation of deep waters as the critical factor in its deposition, although a surface productivity increase may have occurred immediately preceding and during the deposition of S_5 (Nolet and Corliss, 1990).

5.3. Age of the Original Top of S_1

Although the benthic fauna records relatively eutrophic conditions at the sea floor until 5200 BP, it also indicates a return to well oxygenated conditions (also reflected by the disappearance of lamination), i.e. ending of sapropel formation, around 6340 BP. This contradicts the conclusion of Higgs et al. (1994) that sapropel formation ended as late as 5000 BP, while the presently visible top of the sapropel would 1) represent a geochemical front caused by downward oxidation after the re-installment of oxygenated bottom water conditions and, therefore, 2) appear older than the original top. Similar inferences were made earlier, but, as did Higgs et al. (1994), always using cores with sedimentation rates as low as 2 to 4 cm kyr^{-1} (De Lange et al., 1989; Lander-Rasmussen, 1991; Rohling et al., 1993b; Pruysers et al., 1991; 1993). The sedimentation rate in the S_1 interval of core IN68-9 is ~15 cm kyr^{-1}, so that post-depositional re-oxidation would not likely be of much importance. This expectation is confirmed by the observed match between the faunal and lithological boundaries of S_1. The 6340 BP age for the very top of S_1 in IN68-9 suggests that it would be the lower, rather than the upper, Mn peak in the records of Higgs et al. (1994) that approximately matches the original top of S_1. This supports the conclusion of a study similar to that of Higgs et al. (1994), in which Pruysers et al. (1993; their core 9G1, SE of Crete) matched the original sapropel-top with the lower Mn peak, explaining the upper peak in terms of non-steady state formation of double peaks in response to increased organic carbon accumulation between 1900 and 1350 BP, causing retreat of the oxidation front.

5.4. Sapropel Interruption: Common or Rare?

The correspondence between changes in lithology and benthic foraminiferal fauna suggests that both the sapropel interruption, and the second sapropelic subunit in core

IN68-9 are genuine, and not the result of resedimentation. Van Straaten (1966, 1972) arrived at the same conclusion on the basis of bentific mollusc studies that relate the sapropel interruption to a period of relatively intensified winter cooling and consequently improved deep water formation.

In the northern Aegean Sea, S_1 is interrupted in cores from sites deeper than 250 m (Perissoratis and Piper, 1992). These authors dated the top of S_1 at 6400 BP, and the base at 9200 BP. By interpolation, the Aegean S_1 interruption can roughly be placed between 7000 and 6700 BP. Given the inaccuracy involved in the interpolation of the AMS^{14}C-dates, the match with the age-range of the Adriatic S_1 interruption (7100 to 6900 BP) is striking. This could indicate that the reoxygenation was not only significant in the Adriatic Sea, but that improved deep water formation in that basin caused increased oxygen advection to the entire deep eastern Mediterranean. Since the upper depth limit of S_1 in the northern Aegean Sea was much shallower than 250 m (Perissoratis and Piper, 1992), it seems unlikely that the Aegean Sea itself produced deep water, as it may do today. Instead, the Aegean S_1 interruption may be primarily related to improved deep water formation in the Adriatic Sea, which potentially caused an eastern Mediterranean wide reoxygenation event. In that case, future research on other high sedimentation-rate cores throughout the basin should show interruption of S_1.

Interruptions have not only been found in Quaternary, but also in Pliocene sapropels. High-resolution study of Upper Pliocene sapropel C2 (Singa section, S. Italy), showed an (~900 years) interval containing high abundances of the low-oxygen tolerant benthic foraminiferal species *Bulimina marginata* inbetween benthic azoic intervals (Rohling et al., 1993a). Planktic foraminiferal abundance variations and stable isotopes suggest that this interval of temporarily improved sea floor oxygenation was preceded by surface water cooling, while the return to persistently anoxic (i.e., azoic) conditions was related to warming. The low diversity benthic fauna in the repopulated interval of C2 indicates continuing low-oxygen stress, whereas the higher diversity fauna in the Adriatic S_1 interruption suggests a far more advanced state of reoxygenation. In Pliocene sapropel C2, therefore, the sapropel interruption appears to be caused by a short period of reoxygenation in a relatively stable, anoxic context, whereas the Adriatic record of S_1 reflects a long-term trend of progressively improving oxygenation, interrupted by a short relapse that caused the formation of the second S_1 subunit. Although the faunal expressions are not exactly alike in the studies of C2 and S_1, both suggest a high sensitivity of the process of sapropel formation to short periods of improved deep water formation.

ACKNOWLEDGEMENTS

We thank W.J. Zachariasse, R.C. Thunell, A.E.S. Kemp, and an anonymous reviewer for stimulating discussions and critical reviews. A.M. Borsetti enabled us to work with the material of core IN68-9. W. Renema and J. Cleveringa helped pick foraminifera.

CHAPTER 8

Temporary repopulation by low-oxygen tolerant benthic foraminifera within an Upper Pliocene sapropel: Evidence for the role of oxygen depletion in the formation of sapropels*

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Abstract Foraminiferal study of a continuous set of samples across the Upper Pliocene C2 sapropel (Singa section, southern Italy) revealed an interval containing substantial numbers of benthic foraminifera, bound by sediments in which benthic foraminifera are absent. The absence of benthic foraminifera is indicative of anoxic conditions. The interval with benthic foraminifera contains an association that is strongly dominated by the species *Bulimina marginata*, which is tolerant to low oxygen concentrations. The bottom water oxygenation did not improve sufficiently to allow development of a more diverse benthic foraminiferal fauna, or the return of intensively burrowing organisms. Variations in the planktic foraminiferal fauna and in the stable isotope records suggest that a surface water cooling preceded the benthic repopulation. A warming seems to have coincided with the return to bottom anoxia. The planktic productivity markers *Globigerina bulloides* and *Neogloboquadrina* show minor variations across the repopulated interval. The benthic repopulation, which reflects improved bottom water oxygenation, was probably favored by enhanced dense water formation in response to general cooling of the surface waters.

INTRODUCTION

Miocene to Recent eastern Mediterranean sequences of marine sediments contain numerous sapropels (e.g. Cita and Grignani, 1982; Thunell et al., 1984; Thunell, 1986; Hilgen, 1987, 1990; Rohling and Gieskes, 1989). Often, these sapropels display a distinctly laminated structure (a.o. Van Straaten, 1970, 1972; Mullineaux and

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* *Marine Micropaleontology, 22 (1993) 207-219*

Lohmann, 1981; Cita and Grignani, 1982; Shaw and Evans, 1984; Mangini and Schlosser, 1986; Thunell, 1986; Gudjonsson, 1987; Howell et al., 1988). Preservation of laminae is indicative of an anoxic bottom environment, hostile to burrowing benthic organisms which otherwise tend to homogenize the sediment.

Benthic foraminifera appear more tolerant to low-oxygen conditions than most other metazoan meio- and macrofauna (Josefson and Widbom, 1988). Populations of benthic foraminifera may be extremely numerous in dysoxic environments (Sen Gupta and Machain-Castillo, 1993), and several species have been observed to survive even under completely anoxic conditions (Bernhard and Reimers, 1991; Moodley and Hess, 1992). Prolonged anoxia, however, appear lethal to benthic foraminifera (Bernhard and Reimers, 1991). Absence of benthic foraminifera, therefore, is indicative of persistently anoxic conditions.

Intervals devoid of benthic foraminifera are common within Upper Pliocene to Holocene eastern Mediterranean sapropels (Van Straaten, 1972; Nolet and Corliss, 1990; Verhallen, 1991). Additional evidence for anoxic bottom water conditions at times of sapropel formation comes from the relatively high contents of organic matter, and the common abundance of pyritized foraminiferal tests and burrows (Van Straaten, 1972; Stanley, 1983; Thunell et al., 1984). These findings resulted in models of sapropel formation in basins with stagnant and consequently anoxic waters below the upper depth limit of sapropel distribution (a.o. Van Straaten, 1972; Mullineaux and Lohmann, 1981; Cita and Grignani, 1982; Ross and Kennett, 1984). Nolet and Corliss (1990) recently presented data from six eastern Mediterranean cores containing Quaternary sediments. Focusing on variations in the benthic foraminiferal records across sapropel S_5 (deposited about 120,000 yrs B.P.) they persuasively argued that reduced deep water ventilation and consequent deep water anoxia was the critical factor in the deposition of S_5. However, Nolet and Corliss (1990) also showed increased benthic foraminiferal numbers several centimeters below the sapropel, preceding the increase in organic carbon content. This could be interpreted as an increase in the organic carbon flux, which started before the actual sapropel developed.

Alternatively, Pedersen and Calvert (1990) proposed that high primary production, rather than water-column anoxia, provides the first-order control on sapropel formation. That conclusion was also reached by Calvert (1983), who argued that stagnation alone could never have sufficed to account for sometimes very high ($>$ 15%) C_{org} contents, and by De Lange and Ten Haven (1983) and Boyle and Lea (1989), who reported increased C_{org} fluxes and Cd/Ca based evidence for increased productivity during the deposition of Quaternary sapropels, respectively.

Summarizing, it appears that the formation of sapropels resulted from some combination of decreased oxygen advection to deep waters and increased organic production in the euphotic layer, although the relative importance of either process remains debated. In the present paper, we contribute to that discussion with the results from a detailed investigation of a Pliocene sapropel from southern Italy.

The environmental changes that have initiated and maintained the formation of sapropels may best be studied in detailed sets of samples across sapropels characterized by a high sedimentation rate. Such a set was taken across the Upper Pliocene C2 sapropel in the Singa section (Calabria, southern Italy; see Verhallen, 1987). Within that sapropel, we noticed an interval containing benthic foraminifera, bound by barren intervals. In the present paper, we evaluate the possible environmental changes that could have induced this temporary repopulation. In addition, changes in the planktic foraminiferal and stable isotope records across the repopulated interval are used to discuss the relative importance of primary productivity and deep water formation rates with respect to the process of sapropel formation.

MATERIAL AND METHODS

Sapropel C2 has an approximate age of 1.92 Ma (Hilgen, 1991). In the Singa IV section (cf. Verhallen, 1987, 1991), the Upper Pliocene C2 sapropel has a thickness of 51 cm, and it contains a well developed internal lamination. This lamination is most prominent in the top 26.5 cm, and less so in the lower 24.5 cm. The top of C2 passes abruptly into homogeneous clay. Directly below the C2 sapropel, we found homogeneous sediments with grain size in the fine silt fraction. As can be seen in Fig. 8.1, these fine silts are extremely rich in foraminifera; they may be classified as foraminiferal packstones (sensu Dunham, 1962) and may be of turbiditic origin. The occurrence of foraminiferal packstones below sapropels is a rather common feature in the C-group sapropels of the Singa Section (Verhallen, 1991).

It is hard to exactly determine the amount of time involved in the formation of Pliocene sapropels, such as C2, but some constraints can be made. Firstly, sapropel formation also occurred in the early Holocene, and ^{14}C dating has shown that the early Holocene sapropel formed during a period of 2000 to 3000 years (a.o. Stanley and Maldonado, 1979; Vergnaud-Grazzini, 1985; Rasmussen, 1991; Jorissen et al., 1993). Secondly, Hilgen (1991) and Lourens et al. (1992) discussed the astronomically induced sedimentary cycles containing the Pliocene sapropels, and from these studies the average duration of sapropel formation may be estimated at about 3000 years. Tentatively, the lamination might be regarded as varves, with a dark-light couplet for every year (P.J.J.M. Verhallen, pers. comm., 1991).

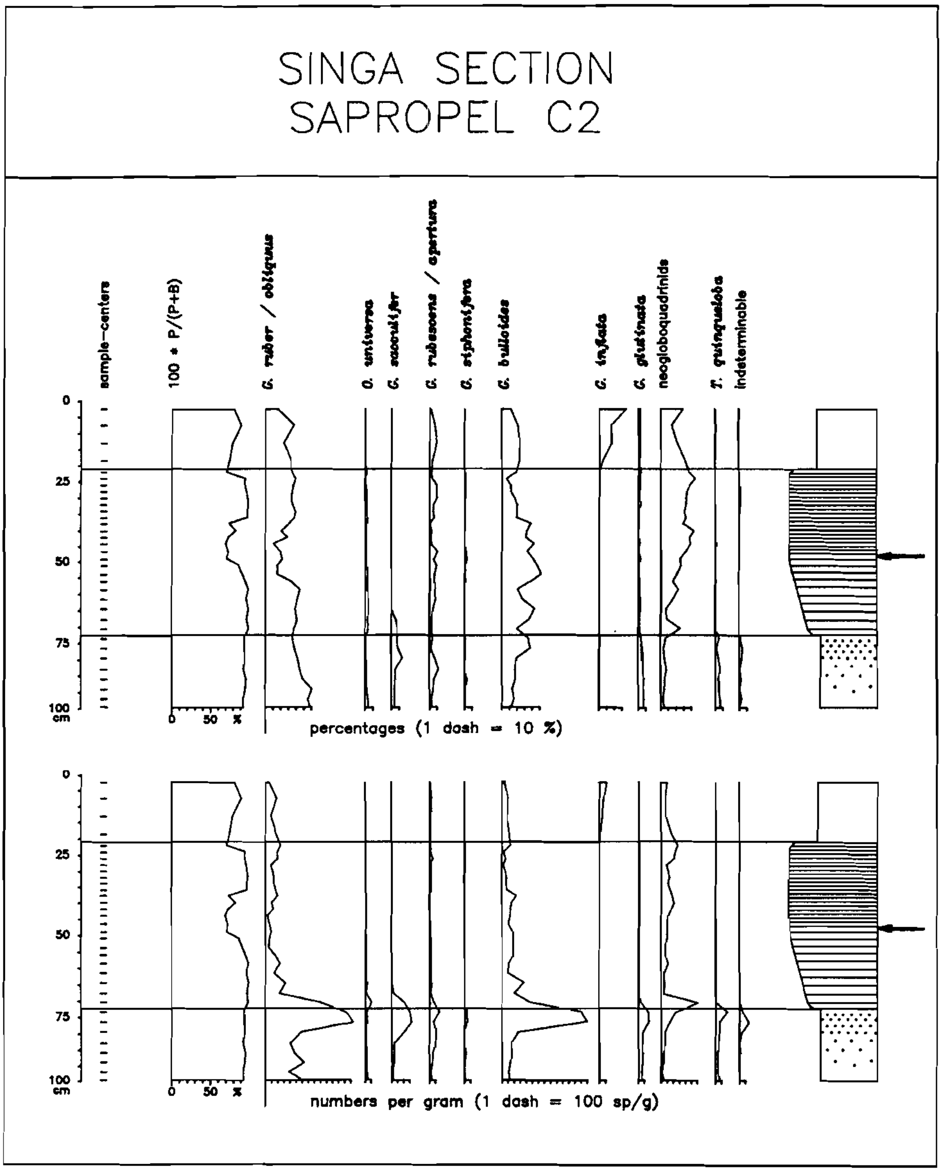

Fig. 8.1. Abundance distribution of planktic foraminiferal species in the Upper Pliocene sapropel C2 (Singa section, southern Italy). Upper diagram shows percentages, lower diagram shows numbers per gram dryweight. *100*P/(P+B)* indicates the percentage plankton per total foraminifera. The representation of lithology is schematic, and the indicated laminae are not to scale. A prominent change in the thickness of the laminae occurs at 26.5 cm below the top of the sapropel (arrow). The dotted interval consists of silty clay to sandy silt sized material. This level may be classified as a foraminiferal packstone (sensu Dunham, 1962).

Table 8.1. Percentages of the planktic foraminifera in the continuous set of samples from 21 cm above to 23.5 cm below the sapropel C2. The column "depth" gives the sample-midpoints, p/(p+b) the plankton percentage, which actually is calculated according to [100xP/(P+B)]. Ruber = *G. ruber*, univ = *0. universa*; sacc = *G. sacculifer*; rubesc = *G. rubescens/apertura*; sipho = *G. siphonifera*; bull = G. *bulloides*; infl = *G. inflata*; glut = *G. glutinata*; neogl = *Neogloboquadrina*; quinq = *T. quinqueloba*; indet = indeterminable.

depth	p/p+b	ruber	univ	sacc	rubesc	siphon	bull	infl	glut	neogl	quinq	indet	δ18O	δ13C
2.50	81.50	16.31	0.71	0.00	2.13	0.00	12.06	35.46	2.84	29.08	0.71	0.71	0.06	-0.60
7.50	90.83	37.16	1.38	0.00	6.88	0.92	20.64	16.06	2.29	13.76	0.92	0.00	1.06	-0.59
13.00	79.17	23.68	0.00	0.00	9.87	0.00	23.68	16.45	2.63	21.05	1.97	0.66	0.92	-0.52
18.50	74.89	33.53	0.60	0.00	4.19	0.60	22.75	4.79	1.20	31.74	0.60	0.00	0.03	-0.56
22.00	70.88	34.16	1.98	0.00	2.97	0.50	18.81	0.50	3.47	37.13	0.50	0.00	-1.28	1.09
24.00	95.78	38.77	0.88	0.00	3.52	2.20	5.73	0.44	2.64	45.37	0.00	0.44	-1.10	1.00
26.00	95.38	36.56	1.08	0.00	9.68	1.08	11.29	0.00	1.61	38.17	0.54	0.00	-1.00	1.22
28.00	97.34	34.43	2.73	0.00	9.84	2.19	11.48	0.00	2.73	33.88	0.55	2.19	-1.18	1.03
30.00	98.65	33.18	2.27	0.00	10.00	0.45	16.36	0.00	2.27	32.73	0.91	1.82	-1.49	0.94
32.00	99.65	34.52	3.20	0.00	5.34	0.00	19.57	0.00	3.91	32.38	0.36	0.71	-1.81	0.80
34.00	97.99	38.36	2.74	0.00	4.79	2.05	19.18	0.68	0.68	30.14	0.00	1.37	-1.64	0.96
36.00	98.26	37.46	3.54	0.00	6.19	0.29	18.88	0.00	1.47	32.15	0.00	0.00	-1.82	0.69
37.75	73.91	31.09	2.52	0.00	0.00	0.00	37.82	0.00	0.00	28.57	0.00	0.00	-1.63	0.56
40.00	82.96	20.54	0.89	0.00	2.68	0.00	32.14	0.00	0.00	43.30	0.45	0.00		
42.00	73.04	28.67	2.15	0.00	1.43	0.00	30.47	0.00	0.72	36.56	0.00	0.00	-1.40	0.92
44.00	69.40	10.26	2.05	0.51	2.05	0.00	42.05	0.00	2.05	38.46	1.54	1.03	-1.03	1.40
46.50	72.38	19.08	2.63	0.00	10.53	1.97	32.89	0.00	0.00	32.24	0.00	0.66	-1.14	1.25
49.00	71.80	21.99	1.05	0.00	5.24	3.14	40.84	0.00	3.14	24.08	0.52	0.00		
51.00	86.84	15.45	2.42	0.00	9.09	0.61	46.06	0.00	0.61	25.76	0.00	0.00	-1.15	1.34
53.75	91.74	15.17	3.79	0.00	6.64	1.42	51.66	0.00	0.95	20.38	0.00	0.00	-0.81	1.35
56.00	95.65	33.12	3.25	0.00	5.84	1.95	38.31	0.00	1.30	14.94	0.65	0.65	-1.63	0.78
58.50	99.66	44.71	3.07	0.00	7.51	0.34	20.48	0.00	1.71	22.18	0.00	0.00	-1.68	1.01
61.50	96.92	41.36	4.55	0.00	8.18	1.36	26.36	0.00	3.18	15.00	0.00	0.00	-1.73	0.77
64.50	99.65	38.30	4.26	0.00	4.96	1.06	42.55	0.00	2.48	6.03	0.35	0.00	-1.69	1.13
67.75	97.62	40.85	3.05	6.10	3.05	1.22	35.37	0.00	0.61	7.93	1.22	0.61	-1.05	1.22
70.50	99.69	36.76	4.36	8.72	2.80	0.31	19.00	0.31	1.87	25.23	0.31	0.31	-1.70	0.87
73.50	94.24	34.89	0.72	7.91	4.32	1.08	34.17	0.00	4.32	6.12	5.04	1.44	0.69	-0.24
76.50	95.31	37.30	0.82	8.61	1.64	1.23	36.48	0.00	4.51	3.69	1.64	4.10	1.06	-0.14
79.50	95.03	41.28	0.58	14.53	6.98	0.58	18.60	0.00	5.23	4.65	4.07	3.49	1.05	-0.18
83.00	92.89	44.90	1.53	5.10	11.73	0.00	16.33	0.00	6.12	7.14	6.63	0.51	1.29	-0.11
86.00	96.14	48.59	1.20	4.82	6.02	3.61	16.87	0.00	7.63	4.82	4.02	2.41	1.19	-0.15
89.00	95.28	60.33	2.07	3.72	4.96	0.83	12.81	0.00	6.20	4.13	4.55	0.41	0.95	-0.23
92.00	92.70	55.15	3.64	3.64	2.42	0.61	15.76	0.00	7.27	2.42	6.06	3.03	0.96	-0.23
94.50	92.90	57.65	4.12	4.12	3.24	1.47	11.47	0.00	6.76	4.41	6.76	0.00	1.09	-0.20

We sampled a continuous record across the C2 sapropel, from 21 cm above the top to 23.5 cm below the base. The 21 cm of homogeneous clay above C2 is covered by 4 samples, the 51 cm thick sapropel itself by 22 samples, and the 23.5 cm below C2 by 8 samples. The samples were dried and subsequently weighed. Thereafter, the samples were washed over a set of sieves with meshwidths of 63, 150, and 595 µm.

Table 8.2. Numbers of specimens per gram dry weight, except for column p/(p+b) which gives the plankton percentage (100*P/{P+B}). For column-titles, see caption of Table 8.1. Also shown are the numbers of planktic and benthic foraminifera per gram.

depth	p/ p+b	ruber/ g	univ/ g	sacc/ g	rubesc g	siphon g	bull/ g	inf/ g	glut/ g	neo/ g	quin/ g	indet/ g	plank./ g	benth./ g
2.5	81.5	57.9	2.5	0.0	7.6	0.0	42.8	126.0	10.1	103.3	2.5	2.5	439.2	99.7
7.5	90.8	180.9	6.7	0.0	33.5	4.5	100.5	78.2	11.2	67.0	4.5	0.0	585.4	59.1
13.0	79.2	87.3	0.0	0.0	36.4	0.0	87.4	60.7	9.7	77.7	7.3	2.4	461.2	121.4
18.5	74.9	176.9	3.2	0.0	22.1	3.2	120.1	25.3	6.3	167.5	3.2	0.0	621.2	208.3
22.0	70.9	255.6	14.8	0.0	22.2	3.7	140.8	3.7	25.9	277.9	3.7	0.0	841.3	345.7
24.0	95.8	198.9	4.5	0.0	18.1	11.3	29.4	2.3	13.6	232.8	0.0	2.3	632.9	27.9
26.0	95.4	205.2	6.0	0.0	54.3	6.0	63.4	0.0	9.1	214.2	3.0	0.0	682.5	33.0
28.0	97.3	86.9	6.9	0.0	24.8	5.5	29.0	0.0	6.9	85.5	1.4	5.5	377.8	10.3
30.0	98.7	118.0	8.1	0.0	35.6	1.6	58.2	0.0	8.1	116.4	3.2	6.5	484.4	6.6
32.0	99.7	140.6	13.0	0.0	21.7	0.0	79.7	0.0	15.9	131.9	1.5	2.9	538.9	1.9
34.0	98.0	139.5	10.0	0.0	17.4	7.5	69.7	2.5	2.5	109.6	0.0	5.0	495.6	10.2
36.0	98.3	166.9	15.8	0.0	27.6	1.3	84.1	0.0	6.6	143.2	0.0	0.0	579.6	10.3
37.8	73.9	194.8	15.8	0.0	0.0	0.0	236.9	0.0	0.0	179.0	0.0	0.0	738.2	260.6
40.0	83.0	100.7	4.4	0.0	13.1	0.0	157.6	0.0	0.0	212.3	2.2	0.0	613.3	126.0
42.0	73.0	128.3	9.6	0.0	6.4	0.0	136.3	0.0	3.2	163.6	0.0	0.0	562.4	207.6
44.0	69.4	32.6	6.5	1.6	6.5	0.0	133.5	0.0	6.5	122.1	4.9	3.3	430.8	190.0
46.5	72.4	60.4	8.3	0.0	33.3	6.3	104.2	0.0	0.0	102.1	0.0	2.1	435.6	166.2
49.0	71.8	92.9	4.4	0.0	22.1	13.3	172.5	0.0	13.3	101.7	2.2	0.0	543.2	213.3
51.0	86.8	61.0	9.6	0.0	35.9	2.4	181.8	0.0	2.4	101.7	0.0	0.0	532.5	80.7
53.8	91.7	50.2	12.5	0.0	21.9	4.7	170.9	0.0	3.1	67.4	0.0	0.0	476.2	42.9
56.0	95.7	160.0	15.7	0.0	28.2	9.4	185.1	0.0	6.3	72.1	3.1	3.1	634.7	28.9
58.5	99.7	238.2	16.4	0.0	40.0	1.8	109.1	0.0	9.1	118.2	0.0	0.0	690.9	2.4
61.5	96.9	141.3	15.5	0.0	28.0	4.7	90.1	0.0	10.9	51.3	0.0	0.0	500.1	15.9
64.5	99.7	330.5	36.7	0.0	42.9	9.2	367.3	0.0	21.4	52.0	3.1	0.0	1027	3.6
67.8	97.6	230.7	17.2	34.4	17.2	6.9	199.7	0.0	3.4	44.8	6.9	3.4	730.2	17.8
70.5	99.7	889.4	105.5	211.0	67.8	7.5	459.8	7.5	45.2	610.5	7.5	7.5	2590	8.1
73.5	94.2	1335	27.5	302.8	165.2	41.3	1308	0.0	165.2	234.0	192.7	55.1	3994	244.2
76.5	95.3	1444	31.7	333.3	63.5	47.6	1412	0.0	174.6	142.8	63.5	158.7	4044	198.9
79.5	95.0	595.8	8.4	209.8	100.7	8.4	268.5	0.0	75.5	67.1	58.7	50.4	1618	84.7
83.0	92.9	411.4	14.0	46.8	107.5	0.0	149.6	0.0	56.1	65.5	60.8	4.7	1092	83.6
86.0	96.1	478.9	11.9	47.5	59.4	35.6	166.2	0.0	75.2	47.5	39.6	23.8	1168	46.9
89.0	95.3	635.6	21.8	39.2	52.2	8.7	135.0	0.0	65.3	43.5	47.9	4.4	1238	61.4
92.0	92.7	387.8	25.6	25.6	17.1	4.3	110.8	0.0	51.1	17.1	42.6	21.3	887.9	70.0
94.5	92.9	608.1	43.4	43.4	34.1	15.5	121.0	0.0	71.4	46.5	71.4	0.0	1242	95.0

Planktic foraminiferal counts were made in the 150 to 595 μm fraction of all 34 samples. An Otto microsplitter was used to reduce residues into suitable aliquots of at least 200 specimens. The results are presented both as percentages per total planktic foraminiferal count, and as numbers per gram dry weight (Tables 8.1 and 8.2; Fig. 8.1). Also shown is the percentage plankton with respect to the total of foraminifera in each aliquot [100xP/(P+B)]. In addition, Table 8.2 and Fig. 8.2 show the numbers of benthic and planktic foraminifera per gram.

Furthermore, stable isotope ratios of the planktic foraminiferal species *Globigerinoides ruber* have been determined. Standard laboratory procedures, as described by Shackleton and Opdyke (1973), were followed, and analyses were performed on a Sira-9 mass-spectrometer. The results are reported as ppm-deviations from the PDB-1 standard. In the Mediterranean, *G. ruber* is far more abundant in summer than in winter, inhabiting the warm mixed layer above the seasonal thermocline (Vergnaud-Grazzini et al., 1986). Besides salinity, the $\delta^{18}O$ values of *G. ruber* reflects sea surface temperatures in the mixed layer (Ganssen, 1983; Deuser, 1987; Hemleben et al., 1989), while its $\delta^{13}C$ values are close to those of surface δCO_2 (Pujol and Vergnaud-Grazzini, 1989).

RESULTS AND DISCUSSION

Sapropel C2 is generally devoid of benthic foraminifera, except for an approximately 15 cm thick interval in which benthics are abundant. In Figs. 8.1 and 8.3, and Tables 8.1 and 8.2, this interval within C2 shows up by reduced values of the plankton percentage [100xP/(P+B)], and in Table 8.2 and Fig. 8.2 it is very obvious in the number of benthics per gram. The amount of time captured in this repopulated interval may be roughly estimated at about 900 years, assuming that the entire sapropel took about 3000 years to develop (see Introduction).

Preservation of all foraminifera is good troughout sapropel C2, indicating that dissolution effects may not explain the observed faunal patterns. In view of the study of Hutson (1977), dissolution -if relevant- should result in substantial relative enrichment of *Neogloboquadrina* and *Globorotalia inflata*, at the expense of *Globigerinoides ruber*, *Globigerinita glutinata*, and *Globigerina bulloides*. In the repopulated interval, however, *G. ruber* and *G. bulloides* display opposite abundance variations, instead of being both reduced, whereas *Neogloboquadrina* does not seem to display anything but a gradual increase throughout sapropel C2. Moreover, the preservation of pteropod remains throughout C2 also excludes an important role of dissolution.

The temporary invasion of benthic foraminifera within the C2 sapropel is strongly dominated by the species *Bulimina marginata*, which has previously been interpreted as tolerant of low-oxygen conditions with high food concentrations (Seiglie, 1968; Verhallen, 1986, 1987; Jorissen, 1987, 1988). Two other taxa, *Plectofrondicularia* spp. and *Bolivina alata*, are present in much smaller numbers. The perfect preservation of thinwalled *B. marginata* in the repopulated interval again argues against any dissolution of significance.

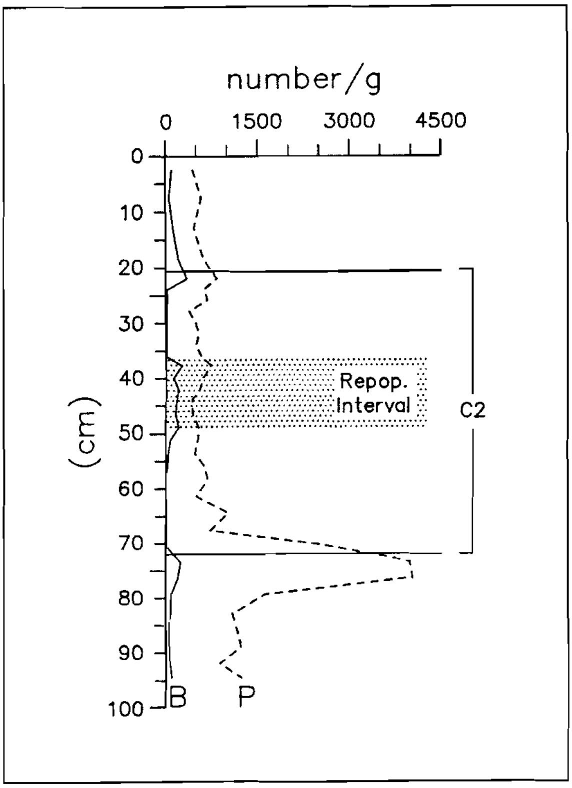

Fig. 8.2. The absolute numbers of planktic and benthic foraminifera per gram dry weight. Solid line (marked *B*) indicates the benthic number. Dashed line (marked *P*) indicates the planktic number.

B. marginata is a common species in the Adriatic Sea, in an area extending south of the Po river delta marked by coastal eutrophication (Jorissen, 1988). A study of living benthic foraminifera in the Adriatic Sea characterized *B. marginata* as a potentially infaunal species (Barmawidjaja et al., 1992). During periods of dysoxic bottom waters in summer and autumn, following algal blooms in the surface waters, this species was found concentrated near the sediment surface. In winter, however, when oxygen concentrations in the bottom water returned to normal values, *B. marginata* invaded deeper levels of the sediment, whereas most other species remained at the sediment surface. The apparent preference of *B. marginata* for an infaunal microhabitat indicates its relative tolerance to low-oxygen conditions. Its characteristic tapered-cylindrical test morphology and numerous pores evenly distributed over the entire test surface, may constitute adaptations for survival in an oxygen-poor environment (Corliss, 1985).

We think that throughout the repopulated interval within C2 dysoxic conditions prevailed, possibly alternating with anoxia on a seasonal time scale. Such conditions would permit a specialized low-oxygen resistant fauna to maintain a sizable population in this interval. Oxygen concentrations, however, remained sufficiently low to prevent the development of a diverse benthic foraminiferal fauna. Lamination is not disturbed in the repopulated interval, suggesting that sediment pore-waters remained completely anoxic, preventing benthic foraminifera to live below the sediment surface. A modern analogue of such conditions may be found in the dysoxic Santa Barbara Basin in the Californian Pacific margin, from which living foraminiferal faunas have been described by Phleger and Soutar (1973) and Bernhard and Reimers (1991). These faunas are extremely rich in individuals, but little diverse and dominated by presumably infaunal taxa.

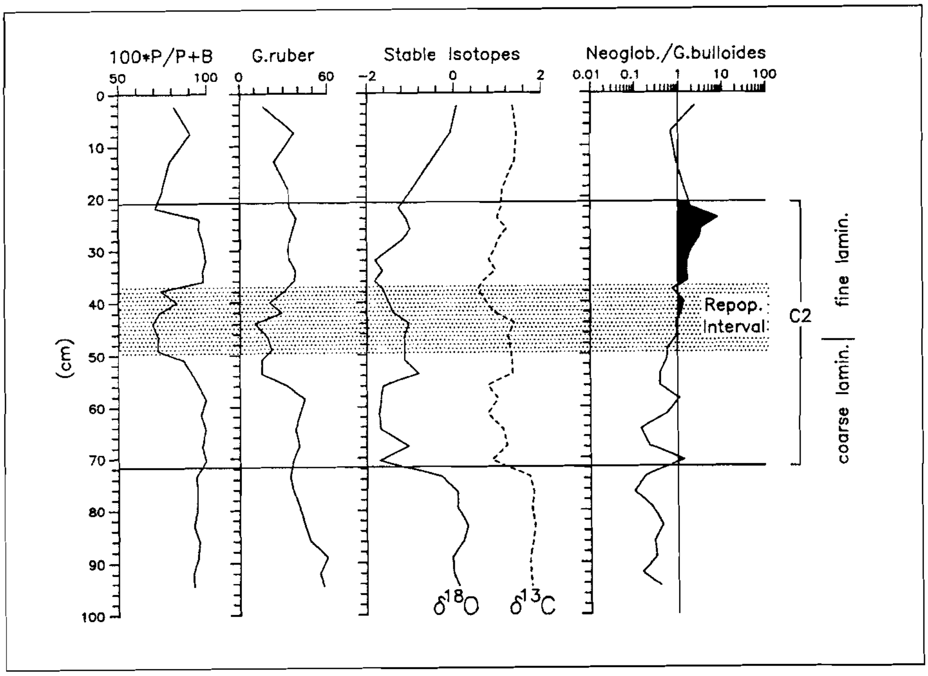

Fig. 8.3. The records of plankton percentage [100xP/(P+B)], *G. ruber*, $\delta^{18}O$ and ^{13}C, and the ratio of *Neogloboquadrina* over *G. bulloides*, across the Upper Pliocene sapropel C2. Also indicated is the level of transition from less distinct coarse lamination in the lower half of C2, to very distinct fine lamination in the upper half. Note the close correspondence between the level marking the onset of (temporary) enrichment in the stable isotope records, and that marking the onset of (temporary) *G. ruber* abundance decrease; both lie well below the onset of temporary benthic repopulation (shown by the record of plankton percentage). The change in dominance between *G. bulloides* and *Neogloboquadrina* approximately matches the change in lamination characteristics.

The association of persistently low diversity in the repopulated interval within C2 contrasts with the rapidly diversifying benthic association which occurs above that sapropel. The initial benthic foraminiferal assemblage in the uppermost sample of C2 is again dominated by *B. marginata,* but is rapidly replaced by very diverse faunas in the homogeneous clay on top of C2.

The temporary repopulation of benthic foraminifera within C2 coincides with a relevant decrease in the percentages of the planktic species *Globigerinoides ruber* (Fig. 8.1). This decrease is genuine, and not the result of a closed-sum effect, since the number of *G. ruber* per gram dry weight also shows a decrease (by about a factor 3). In general, *G. ruber* seem to live at the very surface during its entire life cycle (upper 30 m; Hemleben and Spindler, 1983), in the relatively warm mixed layer waters (e.g. Tolderlund and Bé, 1971; Fairbanks et al., 1982; Bé et al., 1985). It is an omnivorous species that bears dinoflagellate symbionts (Bé, 1982; Hemleben et al., 1989 and references therein). Bé (1982) argued that, since secondary producers such as copepods predominate oligotrophic waters, this might explain the predominance of (partly) spinose carnivorous foraminifera (such as *G. ruber)* in those settings.

Since *G. ruber* is especially abundant in the Mediterranean in the summer season (Vergnaud-Grazzini et al., 1986), characterized by a distinct (seasonal) thermocline below a warm and relatively oligotrophic mixed layer, its temporary decrease in abundance within C2 presumably reflects shortening of the "stratified" summer season. Roughly, this would imply that surface waters were cooler as averaged over a year, compared to times when *G. ruber* accumulated in larger numbers in the sediments. The onset of this "cooling" appears to have preceded the beginning of benthic repopulation, while the subsequent increase of *G. ruber* ("warming") corresponds to the end of the temporary repopulation. This interpretation in terms of sea surface temperature (SST) fluctuations seems to be supported by the record of $\delta^{18}O$, which shows depleted values for the whole of C2, except for the interval with reduced abundances of *G. ruber* where heavier $\delta^{18}O$ values are recorded.

Alternatively, the temporary enrichment in $\delta^{18}O$ values within C2 may be explained in terms of a temporary return to rather normal surface water salinities within a period characterized by relatively low salinities. Variations in freshwater input, mainly in the form of runoff, would also explain the observed variations in the $\delta^{13}C$ record across C2. The middle part of C2 would then be deposited under conditions of relatively reduced freshwater input, resulting in a return to higher surface water salinities ($\delta^{18}O$ enriched) as well as decreased input of continental organic matter ($\delta^{13}C$ enriched).

However, as mentioned before, a marked change in thickness of the laminae was observed at 26.5 cm from the top of C2. Above that level, C2 consists of very prominent and thin laminae, whereas less prominent and thicker laminae prevail in the lower half. This suggests that terrigenous input was higher during the formation of the lower half of C2, and relatively reduced during the formation of the upper half. The transition between the coarsely laminated lower half and the finely laminated upper half occurs near the center of the interval characterized by enriched stable isotope values (Fig. 8.3). The variations in freshwater input (runoff) that could be inferred from the stable isotope records, therefore, do not correspond to the variations in terrigeneous input (runoff) inferred from the observed change in lamination.

The planktic foraminiferal indicators for enhanced productivity, *Globigerina bulloides* and *Neogloboquadrina*, display only moderate abundance variations across the repopulated interval. In the vicinity of river mouths, high abundances of *G. bulloides* may result from riverine discharge of particulate organic matter (e.g. Barmawidjaja et al., 1989; Van Leeuwen, 1989). High abundances of *Neogloboquadrina* seem to be related to enhanced levels of primary production in the Deep Chlorophyll Maximum layer in the thermocline, fueled by upward mixing of nutrients from deeper water (e.g. Fairbanks and Wiebe, 1982; Bé et al., 1985; Vergnaud-Grazzini et al., 1986; Rohling and Gieskes, 1989). *G. bulloides* seems to be more abundant in the lower half of C2, whereas *Neogloboquadrina* reaches higher abundances in the upper half. The change in dominance between the two taxa (Fig. 8.3) coincides roughly with the change from the coarsely laminated lower half of C2 to the finely laminated upper half. We think that this change in dominance between *G. bulloides* and *Neogloboquadrina* reflects a change in the main process of eutrophication, namely from higher riverine input of organic matter during the deposition of the lower half of C2, to upward mixing of nutrients from deeper waters into the euphotic layer during deposition of the upper half of the sapropel. This scenario would support the changes in freshwater input we inferred from the change from coarse to fine lamination, rather than that which might be inferred from the combined stable isotope records. Note, in addition, that the abundance fluctuations of *G. ruber* are considerably larger than those of *Neogloboquadrina* and *G. bulloides*, suggesting that total productivity variations were of minor importance relative to the average surface water cooling. Moreover, the isotopic anomalies match the anomaly in *G. ruber* abundance, rather than the transition in dominance between *G. bulloides* and - *Neogloboquadrina*. Combined, these arguments suggest that a main reduction in freshwater input occurred at about halfway the time of deposition of C2, accounting for the onset of fine lamination, and a change from a mainly river-induced process of eutrophication to a more "oceanic" process of eutrophication. This change would have occurred at about the middle of a slightly cooler interval, depicted by markedly decreased abundances of *G. ruber* and enriched $\delta^{18}O$ values.

In this scenario, the variations in the $\delta^{13}C$ record are not easy to understand, but may be attributed to the degree of oligotrophy (and related efficiency of carbon cycling), which is linked to the effectiveness of stratification resulting from the presence of a strong seasonal thermocline. High abundances of *G. ruber* in the lower and upper parts of C2 would reflect strong prevalence of the seasonal thermocline, with consequently low nutrient advection into the mixed layer. In such a configuration, efficient recycling of CO_2 in the mixed layer would effectuate depletions in the $\delta^{13}C$ values. During the interval containing reduced abundances of *G. ruber*, which we interpreted as the result of shortening of the thermally stratified season (average "cooling"), enhanced $\delta^{13}C$ values would have resulted from more pronounced seasonal ventilation of the thermocline.

We now have five keys to understand the environmental changes that induced the benthic repopulation within the C2 sapropel. (1) The repopulation itself indicates that the bottom waters were no longer persistently anoxic. (2) The bottom water did, however, remain poorly oxygenated during the benthic repopulation. (3) A surface water cooling seems to have preceded the benthic repopulation. (4) A surface water warming coincided with the return to persistently anoxic bottom conditions. (5) Primary productivity seems to have remained fairly constant throughout the formation of the C2 sapropel, although the character of nutrient supply may have changed from predominantly riverborne to more "oceanic".

These arguments strongly suggest a causal link between surface water cooling and benthic repopulation. Cooling may have triggered more efficient dense water formation, which would have augmented oxygenation of waters near the sea floor. This, in turn, enabled the repopulation by low-oxygen tolerant benthic foraminifera. However, throughout the roughly estimated 900 years of deposition of the repopulated interval, oxygenation of the waters near the sea floor remained very poor, inhibiting the replacement of the stress tolerant fauna by a more diverse, balanced, fauna. This suggests that the hydrographic changes were not of a very drastic nature.

The onset of cooling seems to have preceded benthic repopulation. The interval between these two events has a thickness of about 5 cm, and with an estimated 3000 years for the total formation period of C2, this offset equals some 300 years. Apparently, such a period of cooler conditions was necessary to restore oxygen concentrations near the sea floor to a sufficiently high level to support the low-oxygen tolerant benthic fauna. The return to warmer surface water conditions acted inversely, and the re-installment of persistently anoxic conditions at the sea floor again resulted in total disappearance of the benthic fauna.

In addition to the above discussion, we speculate that the anoxic conditions that prevailed at the sea floor, at times of sapropel formation, may have been restricted to a 'blanket' at the sea floor, while most of the water-column still contained some oxygen. Such a configuration with a distinct oxygen minimum near the sediment-water interface would result from mineralisation of organic matter that rapidly sinks to the sea floor (pellets). In that case, anoxic conditions could be found at the sea floor, despite of some ongoing dense water formation (cf. Rohling and Gieskes, 1989). The 'blanket' must have been sufficiently thick to prevent colonisation of the sea floor by epibenthic macrofauna extending above the sea floor, or endobenthic macrofauna (e.g. molluscs) capable of extending breathing tubes into the overlying bottom waters. Cramp et al. (1988) suggested that such a restriction of anoxia to a level at or near the sediment-water interface prevailed during the formation of the Holocene sapropel S_1, in the northwestern Aegean Sea. This 'blanket' hypothesis would allow rather subtle improvements in dense water formation to interrupt persistently anoxic conditions near the sea floor. In this respect, the 'blanket' hypothesis contrasts strongly with hypotheses inferring that anoxic conditions prevailed everywhere below the upper depth limit of sapropel formation. In the latter concept, strong oxygen advection to deeper layers (resulting from drastic improvement of dense water formation) would be necessary to accomplish a change from anoxic to dysoxic conditions near the sea floor.

CONCLUDING REMARKS

The faunal, isotopic, and sedimentological changes across the interval repopulated by benthic foraminifera, within the Upper Pliocene C2 sapropel, demonstrate that decreased rates of dense water formation, and subsequently decreased rates of oxygen advection to deep waters, seem to have played a very important role in the process of sapropel formation. In that respect, our findings endorse those of Nolet and Corliss (1990), who studied the Quaternary sapropel S_5.

In the repopulated interval within C2, the benthic fauna is strongly dominated by the species *B. marginata*. Together with the fact that lamination is well preserved, this suggests that conditions at the sea floor did not improve sufficiently to allow further diversification, or invasion of larger burrowing organisms. In other words, conditions at the sea floor were no longer anoxic, but definitely remained strongly dysoxic. A similar pattern shows in the topmost sample of C2, but there it is succeded immediately by homogenize sediments containing a diverse benthic for miniferal association. At that time, oxygenation had apparently improved more drastically, thus determining the end of the formation of sapropel C2.

ACKNOWLEDGEMENTS

We thank N.J. Vouloumanos for assistance in the field, M.J. Urrutiaguer for processing samples for stable isotope analyses, G. van 't Veld and G. Ittman for processing micropaleontological samples, F.J. Jorissen and G.J. van der Zwaan for helpful discussions, and R.C. Thunell and W.J. Zachariasse for critically reviewing earlier versions of the manuscript. E.J. Rohling and H.C. de Stigter were funded by the Netherlands Organisation for Scientific Research (NWO). Stable isotope analyses were supported by the French INSUDBT project, contract number 911903.

CHAPTER 9

Modelling the population dynamics of benthic foraminiferal communities under seasonally fluctuating bottom-water oxygen concentration

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Abstract A mathematically simple model simulation is used to demonstrate that opportunistic species, characterized by a high reproductive success under normal oxic to dysoxic conditions, but with a low reproductive success under food-limited conditions, can succesfully compete with better adapted species in environments marked by periodically occurring severe oxygen stress. Under more stable environmental conditions, species which are better adapted to food-limited conditions replace the opportunists.

Introduction

Dissolved oxygen plays an important role in structuring marine benthic communities. For the majority of marine protozoan and metazoan heterotrophs oxygen is an essential requirement to sustain metabolic activity. Characteristic faunal successions observed along bottom-water oxygen gradients (e.g. Rhoads & Morse, 1970; Wishner et al., 1990) show the sensitivity of benthic organisms to variation in oxygen concentration. The oxygen-dependence is dramatically illustrated by cases of mass mortality of marine fauna following severe oxygen depletion (e.g. Baden et al., 1990; Tyson and Pearson, 1991). Benthic foraminifera appear to be highly tolerant to oxygen deficiency; these protozoans are found thriving under extremely low-oxygen conditions which are prohibitive to most metazoan life (e.g. Josefson and Widbom, 1988; Bernhard and Reimers, 1991). In permanently dysoxic environments (definition of oxygen facies according to Tyson and Pearson, 1991) characteristic foraminiferal communities are found, dominated by low-oxygen tolerant species (Sen Gupta and

Machain-Castillo, 1993). The occurrence of dysoxia-related foraminifera in fossil sediments provides a clue for the reconstruction of low-oxygen conditions in the past ocean. However, in environments where oxygen depletion is a seasonally or interannually occurring phenomenon, different assemblages of foraminifera may be found. Studies of live benthic foraminiferal communities in seasonally oxygen-depleted environments (e.g. Matsushita and Kitazato, 1990; Barmawidjaja et al., 1992) show that maximum foraminiferal production occurs during periods of enhanced oxygenation, and is dominated by a few opportunistic species. Although the success of these species must partly be due to their tolerance to low-oxygen conditions, their potential for rapid population growth, which allows them to outnumber most other competing species, seems more important. In environments where food is abundantly present, but food-competition is low due to frequent devastation of fauna by extreme oxygen depletion, opportunism appears to be a succesful strategy.

Under more constant oxygen concentration, competition between foraminiferal species may be expected to result in a higher degree of specialization, also with respect to oxygen concentration. In the well-oxygenated South Adriatic Sea, foraminifera from shallow microhabitats in the sediment were found to have generally higher test production rates than deeper-dwelling foraminifera (De Stigter et al., this thesis, Chapter 5). The hypothesis put forward in that study is that life in the oxygen- and food-depleted subsurface habitat requires physiological adaptations in infaunal foraminifera which go at the expense of their reproductive capacity. As a consequence, infaunal foraminifera would be unable to compete succesfully with epifaunal foraminifera in well-oxygenated surface habitats. Inversely, epifaunal foraminifera would lack the low-oxygen resistance required to compete with infauna within subsurface habitats.

It is clear that if bottom-water oxygen concentration decreases very gradually over a period of many years, benthic foraminiferal communities will be increasingly dominated by specialized low-oxygen resistant foraminiferal species, which replace species with a preference for higher oxygen concentrations, and vice versa. However, if bottom-water oxygen concentration fluctuates on a shorter seasonal or interannual timescale, the composition of the foraminiferal community may be highly variable, depending on the duration and intensity of successive oxygen minima and maxima, and the population growth rate of different foraminiferal groups under variable environmental conditions. In this paper, the hypothetical dynamic response of foraminiferal communities to fluctuating oxygen concentration is illustrated by means of a simple model simulation, which assumes that foraminiferal production is largely controlled by the availability of food and oxygen.

Food control on benthic foraminiferal production

Despite the selectivity for specific food types observed in many shallow-water species (e.g. Lee, 1980; Lipps, 1983), benthic foraminifera as a group display a variety of feeding mechanisms by which they are able to utilize a wide range of food resources present in the benthic environment (e.g. ?Lee and Anderson, 1993). Below the photic zone, benthic foraminiferal life is fuelled mainly by the supply of organic detritus raining down from the productive surface water. The abundance and productivity of benthic foraminifera in the ocean are generally correlated with the organic carbon flux (e.g. Berger and Diester-Haass, 1989; Altenbach and Sarnthein, 1989; Van der Zwaan et al., 1990; De Stigter et al., this thesis, Chapter 3). In culture experiments, benthic foraminifera are observed to respond to an increase in food supply by increasing their population size (Bradshaw, 1955), as well as by increasing population growth rates (Lipps, 1983). A rapid response to food supply may particularly be found in food-limited deep-sea environments. Observations by Gooday (1988; 1993) suggest that some deep-sea species may be able to rapidly colonize fresh phytodetritus aggregates on the seafloor. Increased reproduction in response to intermittent food pulses enables these foraminifera to compete effectively for the overall scarce food supply. Especially foraminifera in epifaunal habitats may be expected to have the potential to reproduce rapidly, since fresh organic detritus is mainly consumed at the sediment surface. The organic matter which is mixed down into the sediment by bioturbation is generally of a more degraded nature, being stripped of the more readily metabolizable components by the epifaunal community, although some high-quality organic matter may be conveyed from the sediment surface to the subsurface layer by macroinfaunal organisms. Due to the longer persistence of the degraded organic fraction in the sediment, its concentration in the sediment is less variable with time than that of more labile components at the sediment surface. It seems logical to assume that for infaunal foraminifera, as they are feeding on this low-quality organic matter, the energy-costly maintenance of a high reproductive potential is not advantageous.

Under a diminishing supply of food, foraminiferal populations must decrease in size. As foraminifera may respond to adverse environmental conditions by postponing reproduction, thus increasing individual life span (Muller, 1975), the decrease in population size is more likely regulated by a decrease in productivity, rather than by mortality. Experiments by Muller (1975) on benthic foraminifera from salt marshes demonstrated that the generation length of these foraminifera increased from only a few days at optimum conditions of temperature, salinity and pH to more than 100 days under less favourable conditions. Measurements of metabolic activity in deep-sea foraminifera by Linke (1992) indicated that some species may remain active in times of starvation by metabolizing their protoplasm.

Oxygen and benthic foraminiferal survival and reproduction

Although the majority of benthic foraminifera apparently need oxygen for sustaining normal activity, a substantial number of species is known to survive in environments where dissolved oxygen is very scarce or even completely absent (Sen Gupta and Machain-Castillo, 1993). Live foraminifera have been observed in completely anoxic and even H_2S-bearing natural sediments (e.g. Alve, 1990; Corliss and Emerson, 1990; Bernhard and Reimers, 1991; Bernhard, 1993). The resistance of benthic foraminifera to extreme oxygen-deficiency is confirmed by experimental studies, which show that some species may remain active in a completely anoxic environment for periods of 24 h (Moodley and Hess, 1992) and survive for several weeks at least (Bernhard, 1993; Bernhard and Alve, 1996).

The ability of benthic foraminifera to maintain metabolic activity under oxygen-limited conditions has been attributed to a number of physiological and biochemical adaptations. Of prime importance is the fact that benthic foraminifera have small body volumes. Oxygen consumption, being directly correlated with body weight and volume (Vernberg and Vernberg, 1981; Hannah et al., 1994), is therefore low and gives benthic foraminifera an edge over the usually larger benthic metazoans. An elongate or flattened test shape, characteristic of many low-oxygen tolerant taxa, may provide a high ratio of body surface area to body volume, which is favourable for diffusive gas exchange (Corliss, 1985; Bernhard, 1986). Gas exchange may further be increased by a high porosity of the test wall (Corliss, 1985). In culture experiments, *Ammonia beccarii* was observed to develop significantly higher porosity under low-oxygen conditions (Moodley and Hess, 1992). Further enhancement of oxygen uptake may be achieved by clustering of mitochondria below pore-entrances (Leutenegger and Hansen, 1979) or near the aperture of the test (Bernhard and Alve, 1996). Foraminifera living under completely anoxic conditions apparently must be able to accomplish anaerobic respiration by various alternative metabolic pathways, possibly including endosymbiontic bacteria (Bernhard and Reimers, 1991; Bernhard, 1993). Y-et, it has recently been reported by Bernhard and Alve (1996) that some low-oxygen tolerant species kept under completely anoxic conditions have significantly reduced ATP levels compared to conspecifics in aerated controls. This suggests that these species maintain metabolic activity at a reduced level, possibly indicating a state of dormancy.

Despite their remarkable tolerance to severe oxygen depletion, benthic foraminifera seem unable to survive prolonged periods of total anoxia. In the permanently dysoxic environment of the Californian Santa Barbara Basin (bottom-water $[O_2]$ less than 0.5 ml l^{-1}), a thriving population of well-adapted, low-oxygen tolerant benthic foraminifera was found to have disappeared almost completely after the bottom water had remained anoxic for several months (Reimers et al., 1990; Bernhard and Reimers, 1991). The ultimate oxygen dependence of benthic foraminifera is also illustrated by their absence in some fossil anoxic sediments (Mullineaux and Lohmann, 1981; Van der Zwaan, 1982; Katz and Thunell, 1984; Nolet and Corliss, 1990; Verhallen, 1991; Rohling et al, 1993a). However, it is not resolved to what extent the extinction of benthic foraminifera under total anoxia has to be sought in the absence of oxygen, or in the accumulation of noxious H_2S in the sediment and overlying water.

While benthic foraminifera as a group occur from normally oxic to completely anoxic environments, individual species may have more reduced limits of tolerance. This is evident in the first place from the association of characteristic low-diverse assemblages of foraminiferal species with permanent dysoxia. Secondly, the conspicuous vertical zonation of benthic foraminiferal species observed in deep-sea sediments (e.g. Corliss, 1985; Mackensen and Douglas, 1989; Corliss and Emerson, 1990; Rathburn and Corliss, 1994; De Stigter et al., this thesis, Chapter 3) suggests that these species are arranged along some chemical or biological gradient in the sediment. Apart from speculations that this vertical zonation may reflect gradients in food availability, or gradients of competitive pressure, or may result from selective grazing by foraminifera on different bacterial consortia arranged along the redox gradient, the possible relation with the pore-water oxygen gradient has often been mentioned. The deepening of deep-infaunal foraminiferal microhabitats observed with increasing depth of the oxic-anoxic boundary (Corliss and Emerson, 1990; Jorissen et al., 1995; De Stigter et al., this thesis, Chapter 3), as well as observations of vertical migration of benthic foraminifera in response to changes in the oxygen gradient (Barmawidjaja et al., 1992; Alve and Bernhard, 1995), provide supporting evidence for the principal role of oxygen. That oxygen plays an important role as a selective force both on the scale of dysoxic basins as well as in low-oxygen microhabitats below normally oxic surface sediments, is further illustrated by the common occurrence of species of the genera *Globobulimina* and *Chilostomella* in both environments (Phleger and Soutar, 1973; Douglas and Heitman, 1979; Corliss, 1985; 1991; Mackensen and Douglas, 1989). The occurrence of some species over a broad depth range in the sediment, whereas other species in the same location occupy a more restricted microhabitat, may be explained by a greater versatility of some species with respect to different oxygen concentrations. Alternatively, deposit-feeding species which exploit partially degraded organic matter may have a broader distribution in the sediment than species which consume only fresh organic detritus.

The observation that foraminifera from low-oxygen environments, when subjected to complete anoxia, remain active or at least are able to survive for some time (Moodley and Hess, 1992; Bernhard, 1993; Bernhard and Alve, 1996), implies that selection by oxygen concentration is not effectuated by an immediate effect on survival, but may rather be caused by differences in reproductive potential of species under different concentrations of oxygen. Very little is known about foraminiferal reproduction under oxygen-limited conditions. Large standing stocks in permanently dysoxic basins, much larger than in adjacent areas with higher oxygen concentration, suggest that enhanced production of foraminifera may occur under low-oxygen conditions. These high abundances, however, may be primarily due to the almost complete exclusion of benthic macrofauna, resulting in a reduced loss of foraminifera by macrofaunal consumption (see for example Buzas, 1978), and an increased food availability in the absence of macrobenthic competition (e.g. Van der Zwaan, 1982). Furthermore, the large standing stocks do not necessarily imply a high faunal turnover rate. As outlined in the introduction, we suspect that foraminifera in oxygen-depleted habitats have a low population growth capacity compared to foraminifera which inhabit well-oxygenated habitats. A justification for this assumption is that foraminiferal population growth rates apparently are controlled by food availability (e.g. Lipps, 1983), and thus basically by the availability of energy resources, and that anaerobic metabolism of organic carbon yields considerably less energy than aerobic metabolism (e.g. Zehnder and Stumm, 1988). In other words, with a similar amount of food, foraminifera in an anoxic environment can produce a lower amount of energy for maintenance of body mass and for reproduction, than species in an oxic environment. Where molecular oxygen is available in low concentration, physiological adaptations to optimize oxygen uptake seem energetically advantageous. The reason why low-oxygen tolerant species may not compete well under normal oxic conditions is not clear, but possibly the adaptations to low-oxygen conditions are paid for by the loss of other faculties, for example high reproductive potential.

Construction of a population dynamics model

To test the dynamic response of benthic foraminiferal populations to fluctuations in bottom-water oxygen concentration, we constructed a simple model on the basis of the assumption that the dynamics of these population are primarily controlled by the availability of food and oxygen. In this model, three different species, A, B and C, are allowed to compete for a single source of food, which is supplied at a constant rate, while the concentration of oxygen varies with a seasonal cyclicity. Microhabitat partitioning is not considered in the model; all species are present on a single, homogeneous, area of surface sediment. Species A represents foraminifera with a high reproductive potential, a short life cycle, and a low performance under low-oxygen conditions. Species B is the opposite of A, with a low reproductive potential and relatively long life span, and a relatively good performance under low-oxygen. Species C combines the advantageous characteristics of both species: high reproductive potential, short life cycle, and relatively good performance under low oxygen. The advantage is paid for by a lower performance under food-limited conditions.

The basic mechanism by which competition between species is effectuated in the model is illustrated in Figure 9.1. More detailed explanation of the formulation of the model is given later. Figure 9.1a shows how birth rate and mortality of species A and B (expressed per capita per day) vary as a function of food supply (expressed arbitrarily as units of food required for the maintenance of one foraminiferal individual for one day, per capita per day), under high oxygen concentration (5 ml l^{-1}). As shown in the Figure, mortality is constant and independent of food supply, and higher in species A than in species B. The birth rate on the other hand increases inversely-exponentially with increasing food supply, and is generally higher in species A than in species B. In both species, the birth rate is zero if the food supply is below the minimum required for maintenance of the parental foraminifer (1 food unit for species A and B). As soon as the food supply surpasses this minimum, the birth rate increases to values above zero. Initially, the supply of more food results in an increase of the birth rate, but at higher food levels the effect of additional food becomes less due to the physical limitations on both food uptake capacity and the maximum number of offspring. Population growth occurs if the birth rate exceeds mortality, whereas extinction of the population occurs if the birth rate is lower than mortality. A stable population size is maintained at the critical food level where the birth rate equals mortality. Supposing now that a small number of specimens of species A and B are supplied with a comparatively large, constant amount of food, then the populations of species A and B will initially increase rapidly in size, with species A growing more rapidly than species B. However, as the number of individuals in the population increases while the supply of food remains constant, the per capita availability of food logically decreases, which in turn results in a decreased population growth rate in both species. Both populations continue to grow, however, until the per capita food availability is so much reduced that further growth is halted by food scarcity. In the example of Figure 9.1a, the critical level of zero population growth is reached first by species B, while the population of species A continues to grow. As a consequence, food availability is still more reduced, causing extinction of species B. Species A continues to grow until it reaches the critical level of zero growth; from this point onward the population of species A remains stable at its maximum size. Figure 9.1b shows a similar plot of birth rate and mortality versus food supply for species A and B, but now for a low oxygen concentration (1 ml l^{-1}). The mortality of

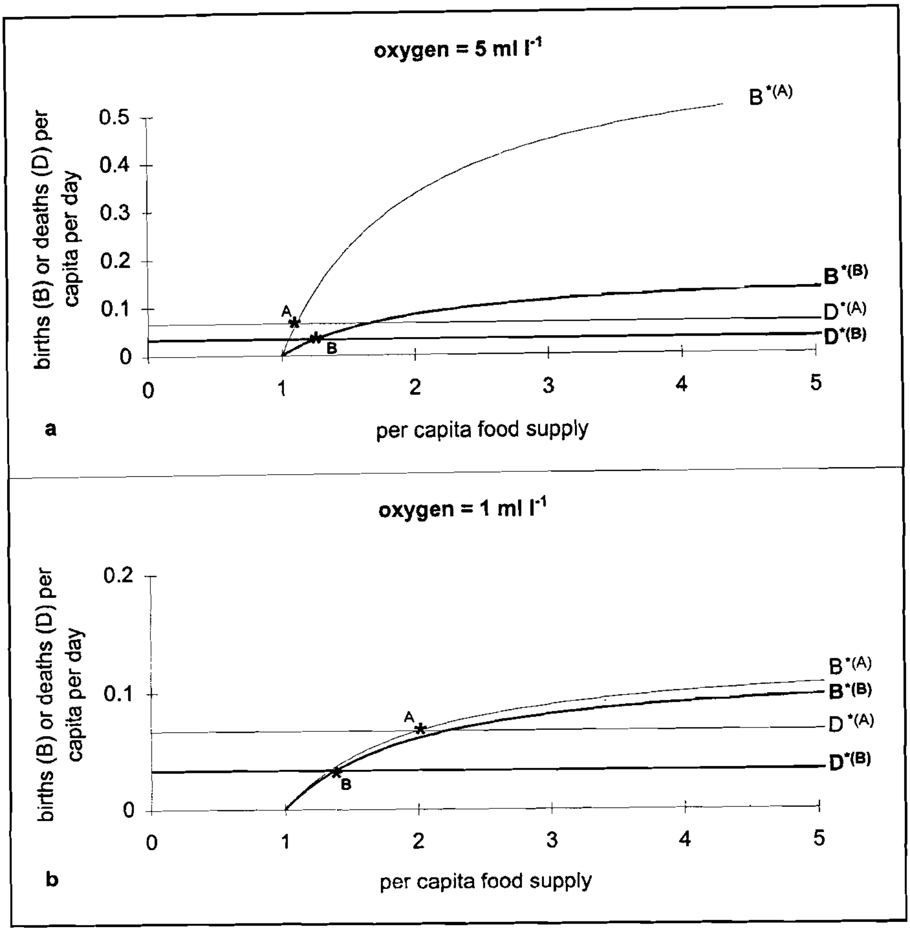

Fig. 9.1. Variation of birth rate (B) and mortality (D) in species A and B (number per capita per day) as a function of food supply (units per capita per day), under (a) 5 ml l^{-1} oxygen, and (b) 1 ml l^{-1} oxygen. The food level for which birth rate and mortality are equal, implying zero population growth, is indicated for each of the two species by an asterisk. Note the different scale of the Y-axis in (a) and (b).

species A and B is similar to that under high oxygen concentration, but the birth rate of species A is much lower, while that of species B is only slightly lower. Supposing again a small starting number of species A and B, and a constant food supply, it is obvious that it is now species A which first reaches the critical level of zero population growth, and becomes extinct, while species B continues growing until reaching maximum population size.

Population dynamics of species A, B and C are modelled by iteration with time steps of one day according to the general equation:

$$N^{(i)}_{t+1} = N^{(i)}_t - D^{(i)}_t + B^{(i)}_t + 0.01 \tag{9.1}$$

where $N^{(i)}_{t+1}$ and $N^{(i)}_t$ are the total numbers of individuals of species i at day t+1 and t, respectively, and $D^{(i)}_t$ and $B^{(i)}_t$ are, respectively, the number of deaths and births of species i on day t. The constant 0.01 was added to prevent extinction of any of the species, and can be seen as an import of juveniles from outside the model space.

Avoiding the complex subject of foraminiferal reproduction cycles (see for this subject e.g. Boltovskoy and Wright, 1976; Lee et al., 1991), we assume a simple relationship between birth and death of foraminifera, in which an individual reproduces only once, and dies in the event. Mortality other than related to reproduction, for example untimely death of juveniles or death caused by predators, is not taken into account in the model. We further assume that every living individual upon death produces an empty shell. The average life span of individuals is held constant, not related to environmental conditions. This implies that changes in population size in response to changes in the environment must be through changes in birth rate, and not through changes in mortality. The maximum life span of the short-lived species A and C in the model is set at 15 days, and of the long-lived species B at 30 days. Successive generations of living foraminifera, born at dayly intervals, are eliminated within 15 or 30 days by skimming off a number of individuals equivalent to 1/15th or 1/30th part of the initial generation each day. The total number of deaths in a species is given by the sum of deaths in each generation, as follows:

$$D^{(i)}_t = \Sigma_{j=1,L^{(i)}} \frac{1}{L^{(i)}} B^{(i)}_{t-j} \tag{9.2}$$

where $D^{(i)}_t$ is the number of deaths of species i at day t, $L^{(i)}$ is the maximum life span of species i, and $B^{(i)}_{t-j}$ is the number of births of the species in the previous 15 or 30 days. $D^{(i)}_t$ represents also the shell flux to the fossil assemblage.

As it is assumed that death of individuals is caused by reproduction, the number of births in species i is given by the number of deaths in species i, multiplied with the number of offspring per parent:

$$B^{(i)}_t = D^{(i)}_t \, B^{*(i)}_t(F_t, O_t) \tag{9.3}$$

where $B^{(i)}_t$ and $D^{(i)}_t$ are, respectively, the number of births and deaths in species i on day t, and $B^{*(i)}_t(F_t,O_t)$ is the food (F) and oxygen (O) dependent number of offspring per parent of species i. The number of offspring per parent varies with food availability and oxygen concentration as follows:

$$B^{*(i)}_t(F_t,O_t) = B^{*(i)}_{\max} \, \frac{F_t - (a^{(i)}N_t - D_t)}{F_t} \, \left(\frac{O_t}{O_{\max}}\right)^{b^{(i)}} \qquad (9.4)$$

where $B^{*(i)}_{\max}$ is the maximum attainable number of offspring per parent of species i, F_t is the total food supply, N_t and D_t are, respectively, the total number of living foraminifera and the total of deaths, O_t and $O_{\max}$ are, respectively, the oxygen concentration and the maximum oxygen concentration, and $a^{(i)}$ and $b^{(i)}$ are species-dependent constants. The setting of the most important model parameters is given in Table 9.1.

Table 9.1. Model parameters

species:		A	B	C
max. life span $L^{(i)}$ (days):		15	30	15
max. offspring per parent $B^{*(i)}_{\max}$:		10	5	10
constant $a^{(i)}$:		1	1	1.5
constant $b^{(i)}$:		1	0.2	0.2
food supply:	100 units day^{-1}			
oxygen concentration:	variable between 0 and 5 ml l^{-1}			

Figure 9.2a shows how according to equations 9.3 and 9.4 the per capita birth rate of the three species is affected by the increase in total number of individuals, at maximum oxygen concentration. In all three species the birth rate decreases with increasing number of individuals. However, in species A and B the birth rate decreases to zero only when the total number of individuals approaches 100 (and hence the per capita food availability is reduced to 1), whereas zero birth rate occurs in species C already when the number of individuals is 67 (and the per capita food availability is reduced to 1.5). In ecological terms this could mean that species A and B are better competitors for food than species C, which turns to the disadvantage of the latter species when food becomes scarce.

Figure 9.2b shows how the per capita birth rate varies with oxygen concentration for the three species, assuming no other control on birth than oxygen. In species A the number of births decreases linearly with decreasing oxygen concentration, whereas in species B and C the decrease is slow at high oxygen concentration, and more rapid when the oxygen concentration approaches 0 ml l^{-1}. As a result of the different combinations of maximum per capita birth rate and oxygen response, species A has a higher number of births than species B at relatively high oxygen concentration, but a lower number of births at low oxygen concentration, whereas species C has higher birth numbers than the two other species over the whole range of oxygen concentrations.

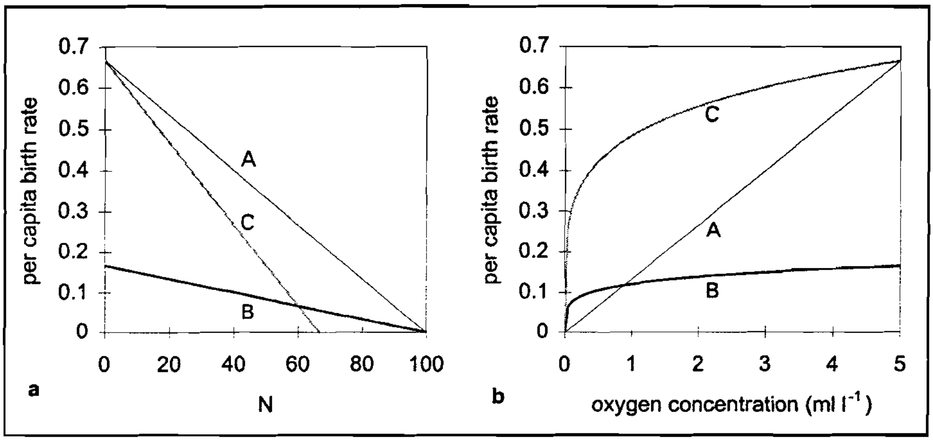

Fig. 9.2. Variation of the per capita birth rate in species A, B and C as a function of (a) the total number of individuals, under 5 ml l^{-1} oxygen concentration, and (b) as a function of oxygen concentration, with a minimum number of individuals.

We simulated culture experiments, in which each species was grown separately and in combination with one or both other species under controlled conditions. The experiments were started with one individual of each species, the food supply was kept constant at 100 units, and oxygen was kept at 5, 4, 3, 2, and 1 ml l^{-1} during the first 100 days in the monoculture experiments, and then turned to 0 ml l^{-1}, whereas in the mixed-culture experiments oxygen was held constant for 150 days. The results are discussed in the following section. Subsequently, we ran the model with a variable oxygen concentration for a much larger number of days, to simulate the population dynamics of natural foraminiferal communities. The starting numbers of each species were set at 0.01, the food supply was kept constant at 100 units per day, and periodic oxygen fluctuations of variable amplitude and relative duration of minima and maxima were applied in the form of a series of modified sinus functions. The general form of the oxygen functions is as follows:

where $O(t)$ is the concentration of oxygen, a and c are constants determining the amplitude and range of the oxygen curve, b is a constant determining the shape of

$$O(t) = a\ 0.5(\sin(\frac{2\pi t}{365}) + \phi)^b + c \qquad (9.5)$$

the curve, and ϕ a phase constant. An annual cycle is produced by dividing t (day-number) by 365. In the experiment, the oxygen concentration was held constant at a maximum value of 5, 3, or 1 ml l^{-1} during the first 365 days, and in 6 subsequent model years the oxygen concentration was periodically depressed to a minimum value of 3, 1, or 0 ml l^{-1} for increasingly long duration, until in the 7th year it was kept at minimum value.

The composition of fossil assemblages was calculated from the model by integration of the shell fluxes $D^{(i)}_t$ over the time-intervals between successive oxygen minima. The results are discussed below.

Model results

Population growth curves obtained from the simulated monoculture experiments display the classical sigmoidal shape well-known from population growth experiments, marked by increasing growth rates at first, then turning to decreasing growth rates until a steady maximum population size is reached (Fig. 9.3). In all species the maximum population size decreases with decreasing oxygen concentration, whereas the time needed to reach this maximum increases with decreasing oxygen. This effect is most pronounced in species A, and least in species C. Turning the oxygen concentration down to zero causes (near) extinction of the population within 15 or 30 days as determined by the maximum life span of the species.

The growth curves obtained for mixed cultures are more diverse in shape. Where one of the species present in the culture grows significantly better than the other(s), the growth curve of the most competent species strongly resembles the curve found in monoculture, with a similar maximum value, although the time needed to reach the maximum may be much longer, due to the co-occurrence with other species in the initial stages of growth. Where one of the species grows significantly less than the other(s), the growth curve of this species assumes an asymmetric bell-shape, increasing initially and sometimes even reaching a high maximum value, but then falling back to zero. This pattern is seen in species A where it competes with B and/or C under low oxygen concentration, and in species B where it competes with A under high oxygen concentration, and in all but one experiment where species C competes with A and/or B. If two species nearly match in population growth rate, as is the case with species A and B at 2 ml l^{-1} oxygen, the outcome of the competition remains undecided within the 150 days of the experiment.

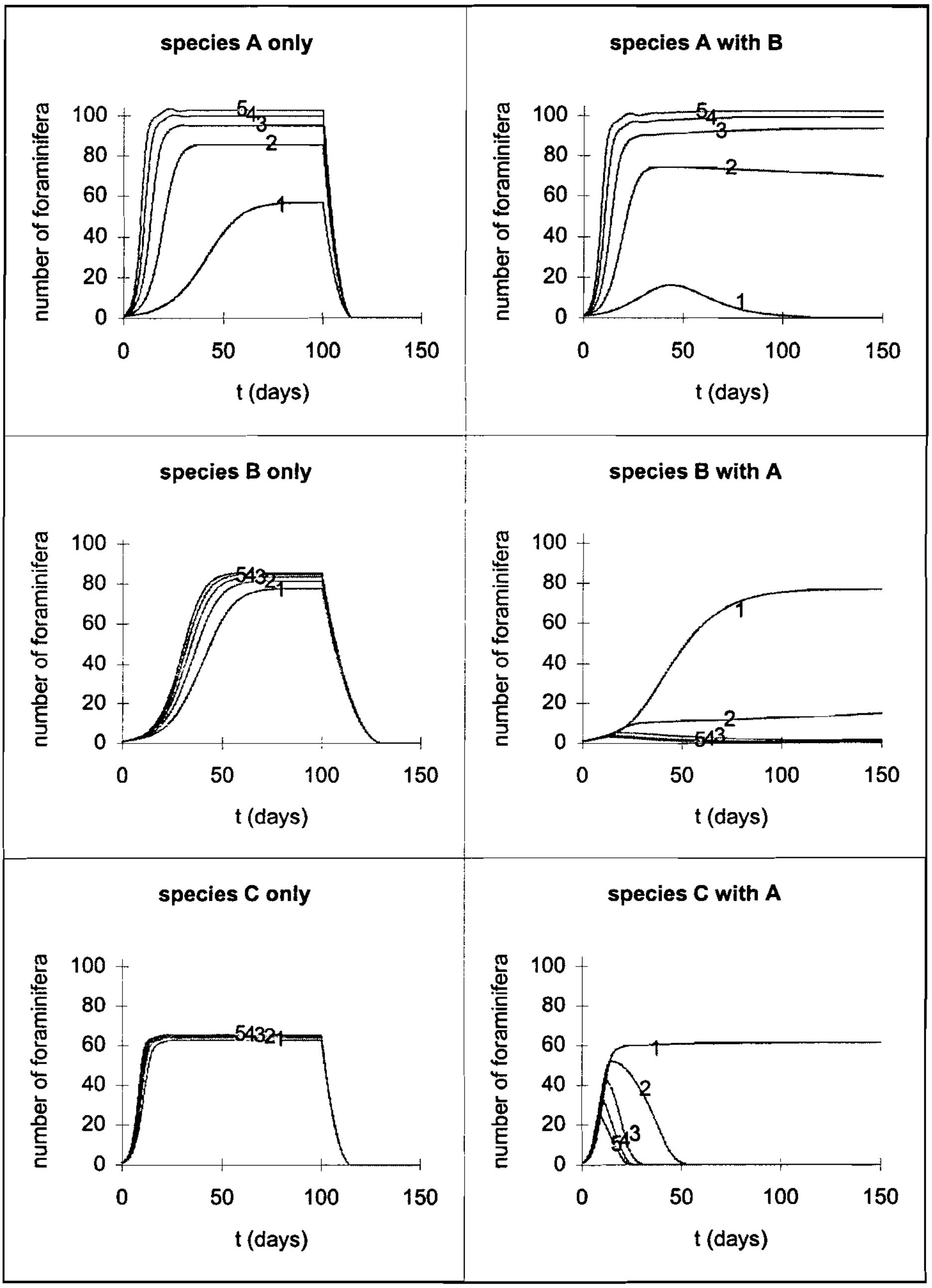

Fig. 9.3. Growth curves of species A, B and C for simulated monoculture and mixed-culture experiments under constant oxygen concentration. The numbers 1 to 5 next to the curves represent the concentration of oxygen in ml l^{-1}. At day 100 the oxygen concentration is turned down to zero. See text for discussion.

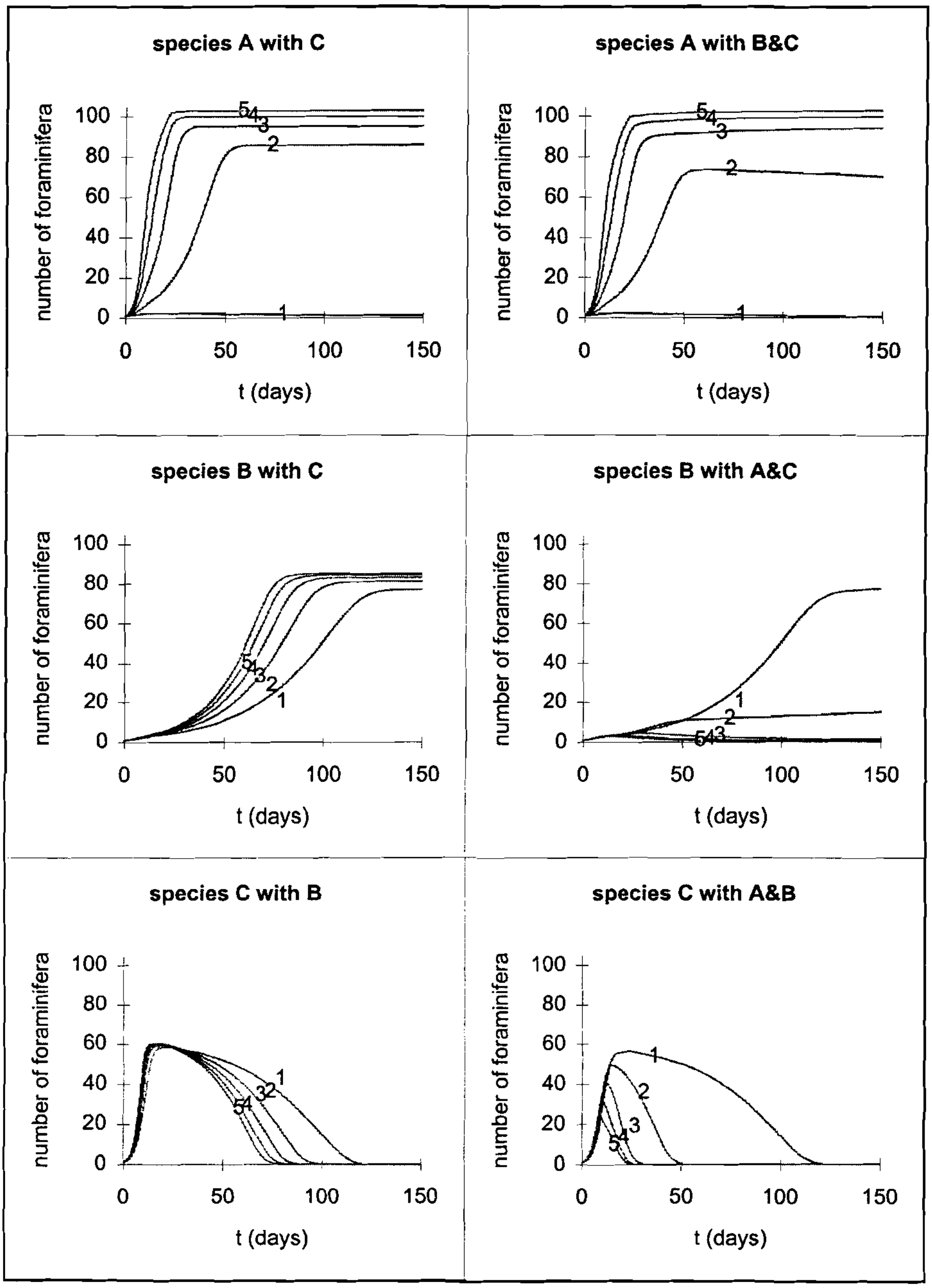

Fig. 9.3. continued

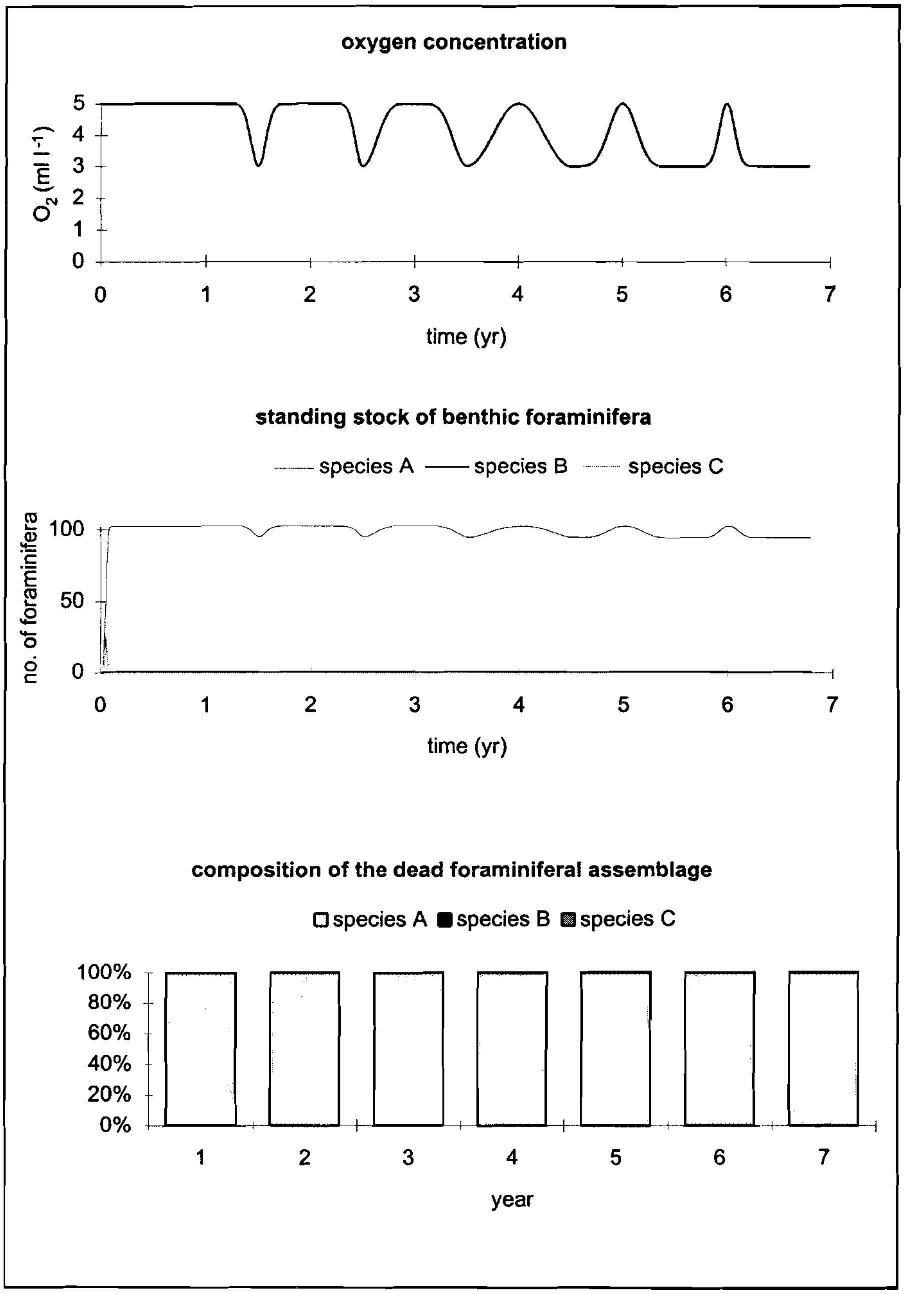

Fig. 9.4a. Simulated variation in population size of species A, B and C under fluctuating bottom-water oxygen concentration, and composition of the corresponding fossil assemblages. See text for discussion.

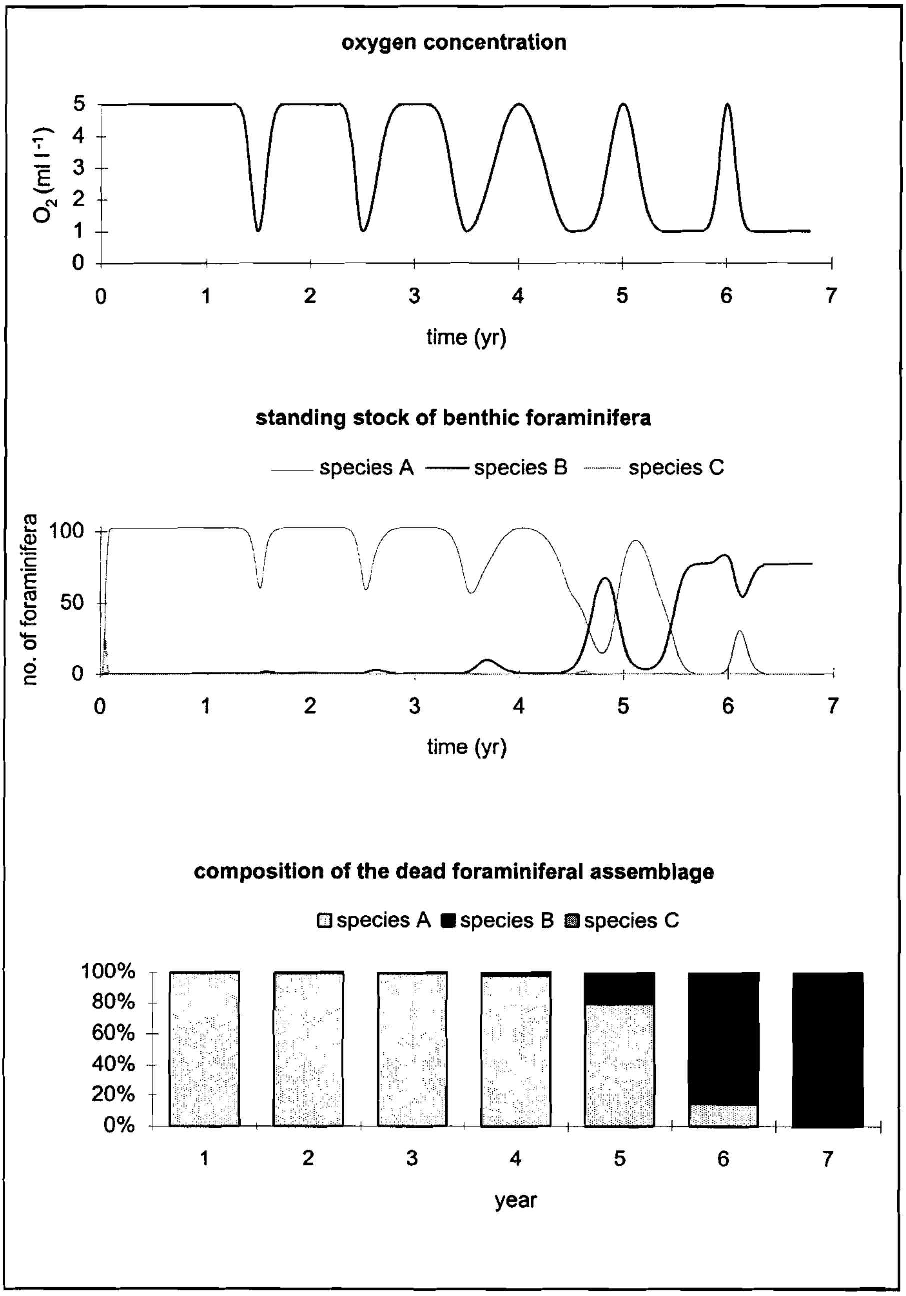

Fig. 9.4b. See text for discussion.

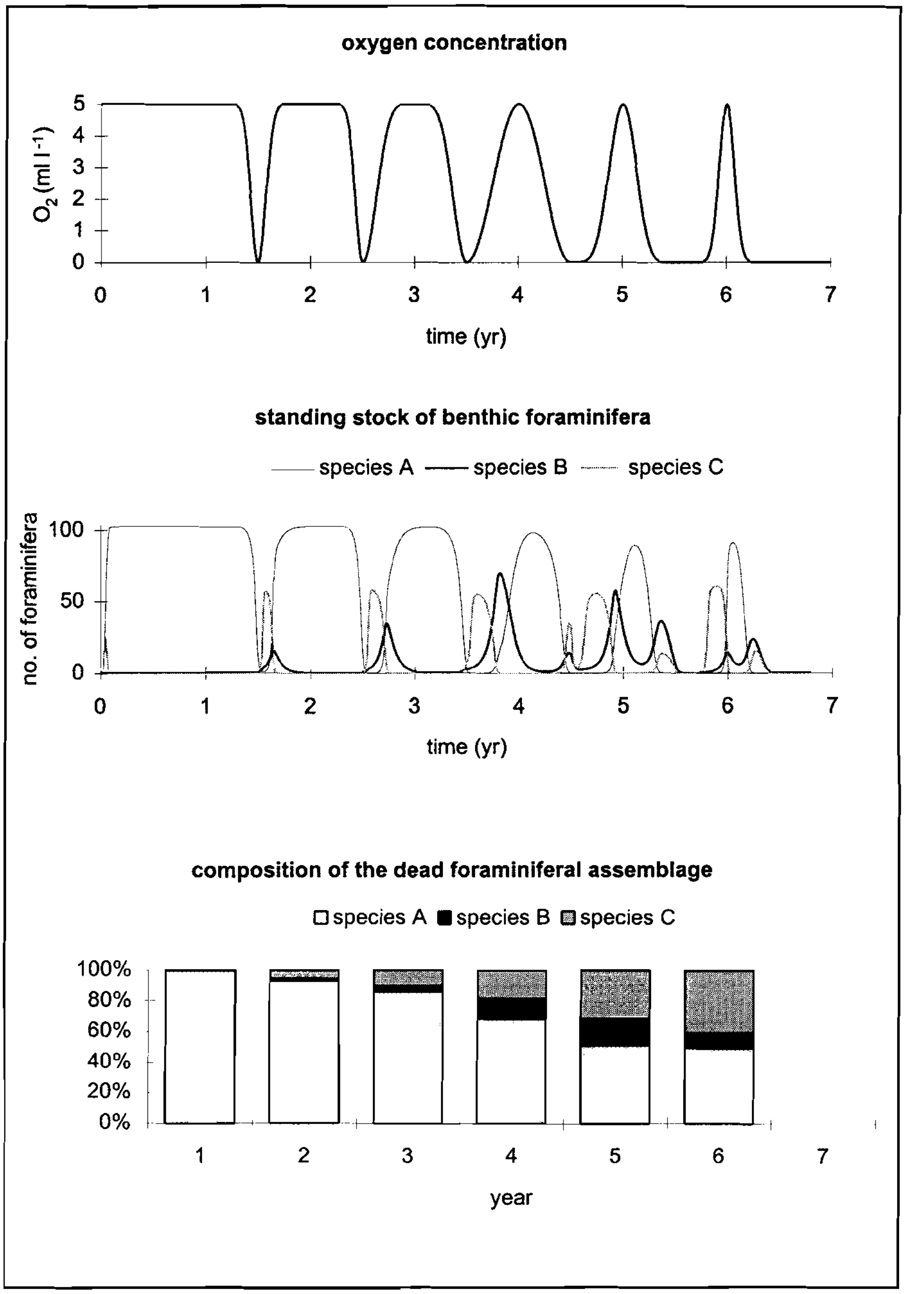

Fig. 9.4c. See text for discussion.

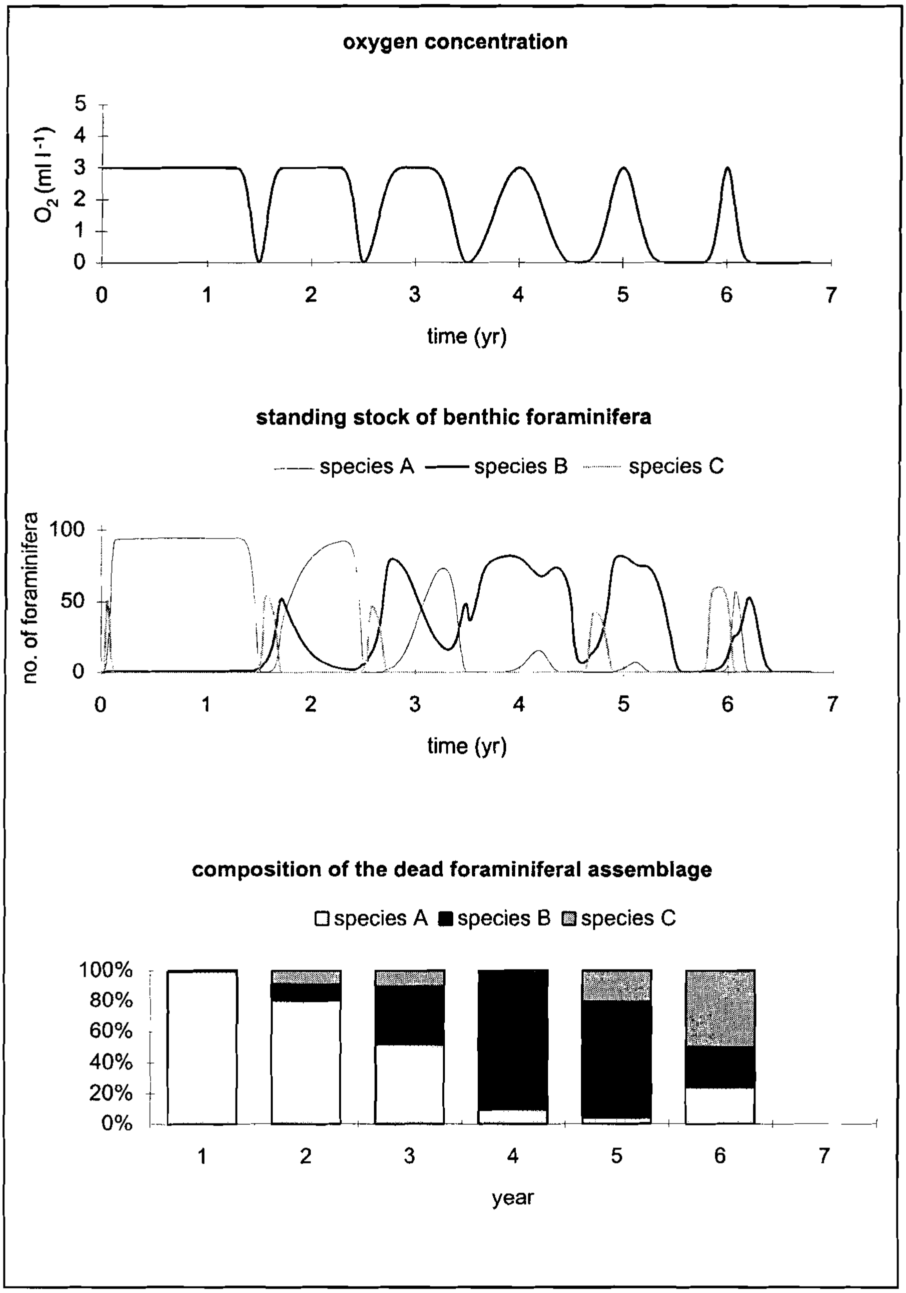

Fig. 9.4d. See text for discussion.

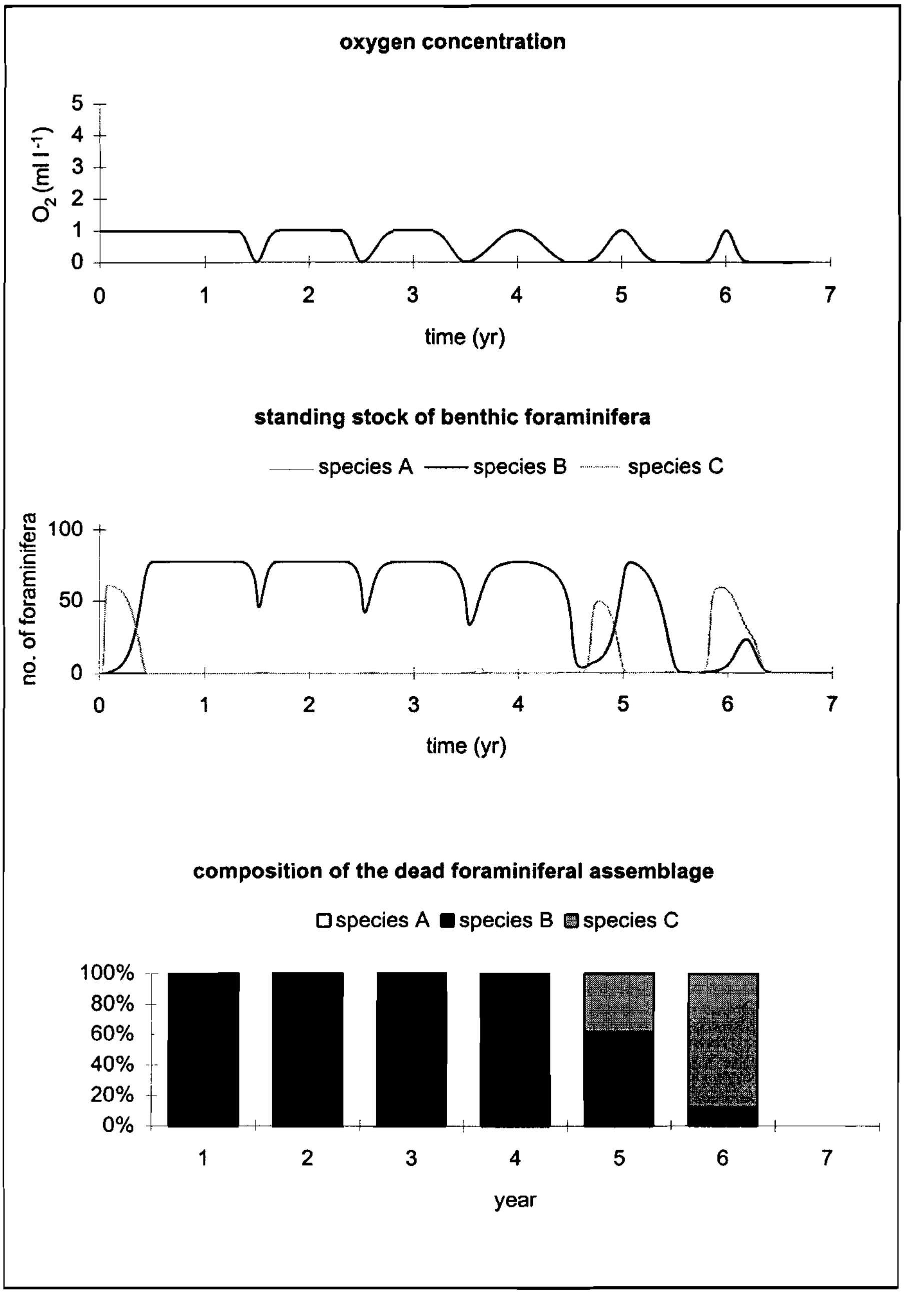

Fig. 9.4e. See text for discussion.

Whereas under constant oxygen concentration the competition between two or three species inevitably leads to extinction of the weaker species, and stabilization at a constant population size of the one surviving species, a fluctuating oxygen concentration may at one time be in favour of one species, and at the next time in favour of another species. This is demonstrated by the results of our model simulation of foraminiferal population dynamics under fluctuating oxygen concentration (Fig. 9.4). Low-amplitude oxygen fluctuations between 5 and 3 ml l^{-1} (Fig 9.4a) produce very little variation in a foraminiferal community which is almost completely dominated by species A. The only effect of oxygen minima is a 10% decrease in abundance of species A, and a very minimal increase in species B, but this effect is quickly reversed again during subsequent oxygen maxima. The fossil assemblages produced over successive years are completely dominated by species A, irrespective the duration of the minima.

When the oxygen minima are lowered to 1 ml l^{-1} (Fig. 9.4b), the community composition changes markedly with increasing duration of the minima. This is due to the fact that species A has a lower population growth rate than species B under relatively low oxygen concentrations. Short oxygen minima, however, cause little response in species B, because of the relatively slow reproduction in this species. The rapid fall in abundance of species A observed during short oxygen minima is simply caused by the species' low reproduction efficiency at reduced oxygen concentration, and not by an increase in population size of species B. With increasing duration of the oxygen minima, species B can gain in momentum, and actively replace A. During subsequent reoxygenation events species A recovers, but with decreasing force as the duration of the oxygen maxima becomes shorter. The fossil assemblage is almost completely dominated by A in the first four years, while species B becomes an important component in the 5th year, to become dominant in the 6th and 7th year. As long as oxygen is not completely depleted, the available resources are efficiently partitioned among species A and B, leaving no room for species C.

This changes when the minimum oxygen concentration is reduced to zero (Fig. 9.4c). In such events the populations of both species A and B are severely affected, and resources become available in sufficient amount for species C to grow. As soon as the environment becomes reoxygenated again, species C appears on the scene, growing rapidly and taking maximum advantage of the available resource. The rapid population growth of species C retards the growth of the competing species, but after a while either species A or B, depending on the degree of oxygen replenishment, takes over and causes elimination of species C. Consequently, species C typically occurs in short bursts at the start of reoxygenation events, but it is also found at the end of reoxygenation events when the oxygen concentration has already fallen to a very low value approaching zero, and the competing species are unable to utilize much of the available resource. Due to its opportunistic behaviour and the relatively high shell production, species C is often well-represented in the fossil assemblage, especially where oxygen minima become more persistent. Destruction of most of the living stock of species B during extreme oxygen depletion, and the slow recovery of the species during reoxygenation events, results in much lower representation of species B in fossil assemblages produced under conditions of periodic extreme oxygen depletion, than in assemblages produced under moderate oxygen depletion. The initially low numbers of species B during reoxygenation events works to the advantage of species A, which as a result is well-represented in the fossil assemblage produced under periodic extreme oxygen depletion.

Lowering the maximum oxygen concentration to 3 ml l^{-1}, while keeping the minima at 0 ml l^{-1} (Fig. 9.4d) is to the disadvantage of species A when oxygen minima become more persistent, while species B builds up important stocks which are not destroyed either by increased growth of species A during oxygen maxima, or by oxygen depletion during oxygen minima. Only during persistent extreme oxygen depletion in the 6th year, the population of species B is eliminated, opening opportunities during the subsequent short reoxygenation event for species C at first, followed by species A. The fossil assemblage produced during years marked by short oxygen minima is dominated by species A, but as the oxygen minima become more persistent, the dominance shifts to species B. At a later stage the intermittent destruction of standing stocks, followed by recolonization, is reflected in the fossil assemblage by dominance of species C, and an important contribution of species A.

Under very low oxygen concentrations, fluctuating between 1 and 0 ml l^{-1} (Fig. 9.4e), species A is completely absent, whereas species B builds up a large population, persisting for as long as the duration of successive oxygen minima remains relatively short. Where oxygen minima persist over longer periods, the living stock of species B is largely or completely destroyed. The resulting ecological vacuum is rapidly filled by species C at the start of the subsequent reoxygenation event, while at a later stage species B may replace C, provided there is enough time during which oxygen is available. The fossil assemblage produced in the first years of relatively short oxygen minima is almost completely dominated by species B, while in later years of more persistent oxygen minima it becomes strongly dominated by species C.

Discussion and Conclusions

Obviously, the model presented here contains some gross oversimplifications. In the first place because real nature is infinitely more diverse and complex than possibly can be represented by three model species and two forcing parameter.

Whereas in the model each of the three species is deemed to either drive the other species into extinction, or to become extinct itself, a much greater degree of coexistence between species is realized in nature due to differentiation in a.o. resource utilization, microhabitat selection, and response to disturbance. A relatively simple improvement of the model could be realized by inclusion of a few infaunal compartments with decreasing levels of food availability and oxygen concentration. Under conditions of high oxygen concentration in the surface compartment, the subsurface compartments could serve low-oxygen tolerant species B and C as a permanent or temporary refuge against competition by species A. The maintenance of larger stocks of species B would significantly reduce the chances for the opportunistic species C. Clearly, in such a more elaborate model species B would be much better represented both alive and fossil than is the case in the present model, whereas species C would lose in importance under moderately oxygen-depleted conditions and become restricted to conditions of periodic extreme oxygen depletion.

Furthermore, the control of food availability and oxygen concentration on foraminiferal population dynamics was simplified to the point that these parameters affect only the birth rate, and not mortality. This seems not justified in view of the observation that foraminifera by increasing their lifespan may be able to bridge periods of adverse environmental conditions. By assuming a state of physiological dormancy, some species might be able to bridge periods of food scarcity or extreme oxygen depletion. This option is evidently not included in our model, resulting in a more rapid elimination of populations during anoxia than would probably occur in nature. Yet, if no viable offspring is generated, populations must sooner or later die out.

With respect to representation of foraminifera in the fossil assemblage, it is evidently not justified to assume that all individuals present in the living community are represented in the dead community. Apart from the fact that many arenaceous foraminiferal taxa have a very low preservation potential, calcareous taxa may also suffer from selective taphonomic destruction as a result of chemical and biological processes (e.g. Denne and Sen Gupta, 1989; Loubere et al., 1993). In this context it is worth mentioning that small-sized, thin-walled calcareous tests may be typical for some fast-growing opportunistic epifaunal species (e.g. Gooday, 1993), whereas thin-walled porous calcareous tests are also commonly observed among deep-infaunal species (Corliss, 1991).

Whereas in the model the supply of food is held constant in order to focus on the effect of oxygen, food supply is very unlikely to be constant in nature. Natural dysoxia are typically associated with conditions of enhanced productivity in the surface water and high organic carbon flux to the bottom. Food availability to foraminifera in low-oxygen environments may be further increased by the exclusion of macrofaunal competitors from such environments. The decrease in foraminiferal population growth rate resulting from reduced oxygen concentration, as observed in the model, may in nature be compensated by an increased growth rate due to the increased supply of food. The absence of foraminifera-consuming macrofauna may be an important additional cause of the extreme abundance of benthic foraminifera under severely oxygen-depleted conditions.

Taking into account the limitations of the model, we will shortly discuss what are the credits of it. In the first place, it is observed that where several species compete for a single source of food, stability of environmental conditions in a homogeneous medium results in the extinction of all but the most competitive species. Coexistence of species under stable conditions is only possible by resource partitioning, or in the presence of spatial environmental heterogeneity. In a typical deep-sea sediment, species A would occupy the oxic upper layer of the sediment, and species B the deeper, oxygen-depleted sediment layer, down to the boundary with the anoxic sediment, while species C would be outcompeted in both subzones. Introduction of a greater number of species, with different oxygen requirements, could result in a finer partitioning of species along the oxygen gradient, but each subzone would be inhabited by only one species.

It is demonstrated by the model, however, that coexistence of mutually competitive species may also occur in the presence of temporal variability in environmental conditions. Species A and B, which under stable conditions would occupy, respectively, the oxic and dysoxic zone of the sediment, may be found in temporal succession during successive oxygen minima and maxima. Where the populations of species A and B are periodically devastated by extreme oxygen minima, opportunistic foraminifera like species C may appear on the scene. As illustrated in the model, a high tolerance for ecological stress and a high reproductive potential are characteristics by which opportunistic species may succesfully compete with more specialized species under instable environmental conditions. If this category of foraminifera can be properly distinguished, it may be of diagnostic value for the recognition of high ecological instability in fossil environments.

Whereas typically epifaunal and deep-infaunal species from well-oxygenated deep-sea sediments stood model for, respectively, species A and B, species with the opportunistic characteristics of species C may be found associated with periodically anoxic environments below highly productive surface waters. Benthic foraminiferal taxa from productive shelf areas with a high tolerance for oxygen deficiency include infaunal or potentially infaunal species of the genera *Bulimina*, *Uvigerina*, *Bolivina*, *Fursenkoina* and *Buliminella*, as well as epifaunal species of *Valvulineria*, *Nonionella* and *Epistominella* (Van der Zwaan and Jorissen, 1991, and references therein). Especially the first three genera are of interest here, because they are often found associated with low-oxygen facies in Eastern Mediterranean Neogene and Quaternary sedimentary successions (e.g. Van der Zwaan, 1982; Ross and Kennett, 1983; Jonkers, 1984; Katz and Thunell, 1984; Verhallen, 1991; Rohling et al., 1993a). In recent oxygen-depleted basins along the eastern Pacific continental margin, Bolivinid species are often highly dominant (e.g. Harman, 1964; Phleger and Soutar, 1973; Ingle et al., 1980; Sen Gupta and Machain-Castillo, 1993). We propose that the high dominance of the above-mentioned taxa in low-oxygen environments is related to their relatively high productivity under oxygen-stressed and food-enriched conditions. Variable degrees of tolerance to moderate or severe oxygen depletion may be expected to exist also among opportunistic species. Those with a largely epifaunal microhabitat preference may perform better under relatively full reoxygenation, whereas opportunistic species with a more infaunal mode of life may predominate under conditions where slight increases in oxygen concentration periodically allow repopulation of otherwise azoic (with respect to protozoan and metazoan fauna) sediments. Repopulation of formerly anoxic sediment in a Norwegian fjord by *Stainfortia fusiformis* has been reported by Alve (1995). The same species dominates the foraminiferal assemblage of reoxygenated sediments in the seasonally dysoxic Adriatic Sea (Barmawidjaja et al., 1992).

Acknowledgements

The first author acknowledges support from the Netherlands Foundation for Scientific Research, grant nr. 751.356.021.

CHAPTER 10

SYNTHESIS

A central conclusion of this thesis is that the abundance of both living and dead benthic foraminifera in seafloor sediments generally is observed to decrease with water depth (Chapters 2 and 3). This pattern is not unique for benthic foraminifera, but is observed in other groups of marine benthos as well (e.g. macrofauna: Rowe, 1983; metazoan meiofauna: Tietjen, 1992). Probably, the decreasing faunal abundance with water depth basically reflects the decreasing availability of organic carbon on the seafloor, fuelling benthic life. Very few species, however, are interested in organic carbon as such; probably the only species which does is *Homo sapiens*, and then only that particular variety engaged in the budgeting of organic carbon. From common experience it is clear that certain types of organic matter, wood for example, may be readily consumed by some organisms like termites, but not by others like man. Further, special skills may be required for the procurement of some food items, for example food that runs away, or swims, flies or floats. Although on a different scale, foraminifera living on the seafloor are likely to face the same problem of finding suitable food. Organic carbon useful for foraminiferal consumption may occur in particulate form, swimming or floating in suspension above the sediment surface, or lying or living on top of the sediment or buried in the sediment, or it may occur in dissolved form. To a certain extent, the morphology of benthic foraminiferal tests may reflect various types of feeding behaviour (see Jones and Charnock, 1985). For example, the remarkable tests constructed by certain Astrorhizid foraminifera, rooted in the sediment but projecting an arborescent array of agglutinated tubes into the overlying water, must be an adaptation to a suspension-feeding mode of life. Some foraminifera of this type may also take up dissolved organic carbon from the sediment via the root system (DeLaca et al., 1981). Predominance of epifaunal Astrorhizids in living communities of benthic foraminifera, as observed on the slope of the South Adriatic Basin (Chapters 3, 4 and 5), may be indicative of bottom currents which keep organic matter in suspension. Unfortunately, these arenaceous foraminifera are of little use as fossil indicators, because of their low fossilization potential. Evidence for a suspension-feeding mode of life has also been reported for the deep-sea calcareous species *Cibicidoides wuellerstorfi* and *Rupertina stabilis* (Lutze and Altenbach, 1988; Linke and Lutze, 1993). Next to suspension-feeding, deposit-feeding and various forms of carnivory, parasitism, commensalism and use of algal symbionts have been observed in benthic foraminifera (Lipps, 1983). Deep-sea foraminifera are presumably mostly deposit-feeders. Slender, elongate test morphologies may be an adaptation to an actively burrowing, subsurface deposit-feeding mode of life (Jones and Charnock, 1985), although it may also represent an adaptation enhancing gas-exchange in oxygen-limited environments (Bernhard, 1986; Corliss, 1985; 1991). In the Adriatic Sea, foraminifera with a serial morphology (largely equivalent with slender-elongate) are most abundant on the shelf and upper slope, and decrease in abundance with increasing water depth (Chapter 3). The downslope decrease of serial morphotypes may be indicative of a decreasing availability of organic carbon in the sediment, and an increase in pore-water oxygen concentration, both due to a decreasing organic flux. A similar observation has been made by Corliss and Chen (1988) on the NW Atlantic continental margin.

Organic matter present in the benthic environment is not only differentiated in terms of its physical state (particulate suspended, particulate deposited, or dissolved), but also in terms of its composition. Although actually consisting of a great number of different components, all with different chemical and biological characteristics, the organic matter may be considered as consisting of three main fractions: a relatively labile fraction which is readily available for consumption by most benthic organisms, a more slowly degrading fraction which may be consumed by benthic fauna only after first being processed by bacteria, and finally a fraction which appears resistant to biological degradation, possibly as a result of sorption on mineral surfaces (Mayer, 1993; Keil et al., 1994). The distribution of these three fractions in marine sediments is schematically drawn in Figure 10.1. The labile fraction is usually concentrated in the upper few millimetres of the sediment. Rapid consumption of this material at the sediment-water interface largely prevents it from being transported deeper into the sediment. Due to seasonal variation in primary production of organic matter and the rapid consumption of the labile organic fraction, the availability of labile organic material is usually highly variable with time. The slowly degrading fraction has a longer residence time, and is mixed down to several centimetres depth by bioturbation, its concentration decreasing gradually with depth. The degradation-resistant fraction, unaffected by biological activity, is distributed homogeneously in the sediment, and remains after complete consumption of the other two fractions.

The exponential decrease in abundance of living benthic foraminifera with depth in the sediment, as observed in the South Adriatic Sea (Chapter 3), may be assumed to reflect the overall decrease in metabolizable organic matter down into the sediment. More speculatively, it can be observed that vertical distribution patterns of individual species are to some extent reminiscent of the vertical distribution of the labile and more slowly degrading organic fractions, as drawn in Figure 10.1. It seems reasonable to state that the presence of a species over a certain depth interval gives an indication of the

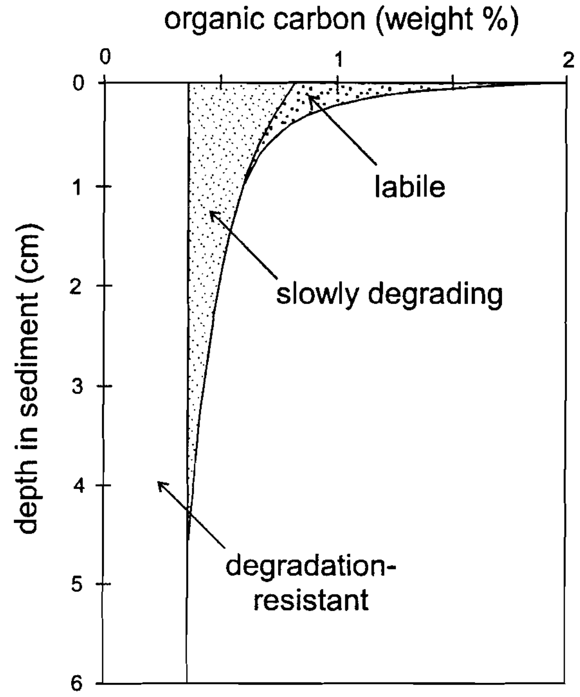

Fig. 10.1. Vertical distribution of labile, slowly-degrading, and degradation-resistant fractions of organic carbon in a generalized deep-sea sediment. Vertical scale hypothetical, centimetres below the sediment-water interface.

minimum depth range over which it finds suitable food. Therefore, species occurring from the sediment surface down to several centimetres depth may be considered to depend for their nutrition at least partly on the more slowly degrading organic fraction. Species which are largely restricted to the uppermost sediment layer may tentatively be assumed to feed selectively on the labile organic material. However, the limited penetration of these species deeper into the sediment may as well be related to other factors. As argued in a number of Chapters (3, 4, 5, 9), oxygen probably plays an important role next to food in structuring benthic foraminiferal communities.

The possible association of certain foraminiferal species with different types of organic material is evidently of great interest for the reconstruction of paleocarbon fluxes, as it may allow differentiation of material deriving from different sources. This possibility is hinted at in Chapter 2, where it is observed that the productivity of benthic foraminifera on the upper continental slope (as estimated from the abundance of benthic relative to planktonic foraminifera) is often higher than expected on the basis of organic flux equations. Exclusion of presumably infaunal, deposit-feeding species of the genera

Bolivina, Bulimina, Uvigerina, Globobulimina, yields a better correspondence between benthic production and expected organic flux. Tentatively it is assumed that enrichment of upper slope sediments with laterally transported, partially degraded organic matter, is responsible for the enhanced production of infaunal foraminifera. As observed in the Adriatic Sea, the genera just mentioned may not be exclusively infaunal. In fact, although occurring down to several centimetres depth, the species *Bolivina spathulata, B. dilatata, Bulimina marginata/aculeata, Uvigerina mediterranea* and *U. peregrina* all have maximum abundances in the upper sediment layer. Selective feeding offers an interesting explanation for the coexistence of these partially infaunal species with more exclusively epifaunal species in the surface sediment layer. It needs to be clarified, however, by which means epifaunal species would be able to utilize the labile, easily degradable organic fraction, whereas (partially) infaunal foraminifera would have to content themselves with more resistant, slowly degrading material. Differences in reproduction rate of epifaunal and infaunal species (Chapter 4) may provide an answer to this question. Rapid reproduction in response to intermittent supply of fresh organic matter may allow epifaunal foraminifera to sequester a substantial part of this valuable resource (see also Gooday, 1988; 1993). After being stripped of the labile components, the remaining organic material may be available for consumption by more slowly reproducing foraminifera. Although possibly of lower nutritional quality, the partially degraded material buried in the sediment represents a substantial and relatively stable resource pool. Access to this resource depends on the ability of species to utilize this slowly degrading material, and also on the ability to operate under oxygen-poor conditions which usually prevail in the subsurface sediment. Whereas infaunal foraminifera evidently must possess both qualities, typical epifaunal species may well be limited to near-surface habitats by their dependence on fresh organic matter and normal oxygen concentration. As illustrated by a model simulation (Chapter 9), the limitation of species within a certain range of oxygen concentrations does not necessarily mean that these species are unable to live under concentrations of oxygen beyond this range, but is rather a consequence of a lesser ability to compete with better adapted species.

Generally, the vertical distribution of benthic foraminifera in the sediment may be controlled by the availability of food and oxygen in the sediment (Chapter 4, see also Corliss and Emerson, 1990). Under a low organic carbon flux, as characterizing vast areas of the oceans' abyssal plains, the vertical distribution of foraminifera in the sediment is limited by food scarcity in the sediment, although free oxygen may be available down to considerable depth. Under a high organic flux, on the other hand, as characteristically found on the shelf and upper slope below areas of high surface-water productivity, lack of oxygen in the sediment, possibly combined with accumulation of toxic hydrogen sulfide, may prevent foraminifera to exploit metabolizable organic matter present below the sediment surface. Maximum penetration of foraminifera occurs under intermediate organic flux. A modified version of the model presented in Chapter 4, which includes the concepts of food and oxygen-dependent differentiation of foraminiferal habitats, is presented in Figure 10.2. It is assumed, as discussed above, that epifaunal species of foraminifera feed predominantly on the labile fraction of fresh organic material, and require a relatively high concentration of dissolved oxygen. As a consequence, these species are present in near-surface habitats under low to intermediate organic flux, but absent under very high organic flux, due to reduced oxygen concentration. Shallow-infaunal foraminifera are assumed to tolerate lower concentrations of oxygen, and therefore to be present from the sediment surface down to near the oxic-anoxic boundary, provided that food is available. Where shallow-infaunal species coexist with epifaunal species, the former group may predominantly feed on the more resistant, slowly degrading fraction of organic matter, not consumed by the latter. However, where

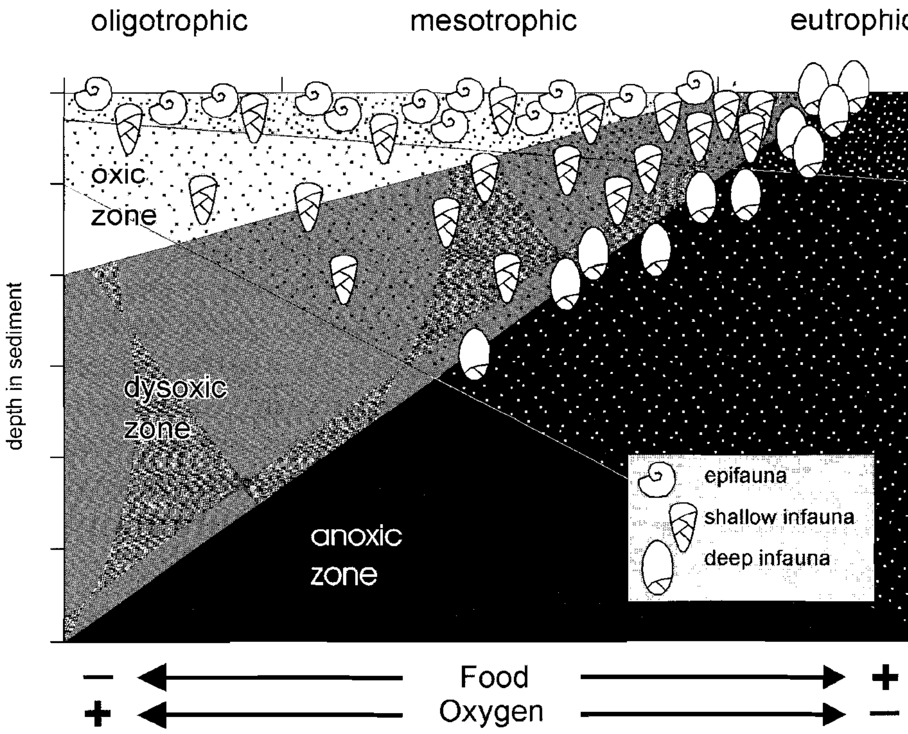

Fig. 10.2. Distribution of epifaunal, shallow-infaunal and deep-infaunal benthic foraminifera in marine sediments, with respect to pore-water oxygen concentration and the availability of labile organic matter (densely dotted) and more slowly degrading organic matter (sparsely dotted). Depth scale hypothetical.

epifaunal species are excluded by oxygen deficiency, shallow-infaunal species may display a more generalistic feeding behaviour, and utilize both the labile and more resistant organic fractions. Deep-infaunal species, finally, may be assumed to have a high tolerance to extreme oxygen deficiency, possibly surviving even periodic anoxia, but may be unable to compete for food under higher concentrations of oxygen. As a consequence, these deep-infaunal species invariably occupy the deepest level of vertical microhabitat successions, provided that metabolizable organic matter is available in sufficient quantity. Only under exceptional conditions where extreme oxygen deficiency occurs up to the sediment surface, deep-infaunal foraminifera may replace both shallow-infaunal and epifaunal foraminifera.

Whereas the total production of benthic foraminifera may be proportional to the total organic carbon flux to the benthos, the implication of this model is that the proportion of labile versus more slowly degrading organic material may be estimated on the basis of the relative abundances of epifaunal and infaunal foraminifera. Epifaunal production may be most directly related to the vertical flux of fresh organic matter from the surface water to the bottom. Enhanced infaunal production, on the other hand, may reflect lateral supply of more aged material by transport along the bottom. As mentioned in Chapter 2 and 3, this may especially occur on the upper continental slope, due to export of organic material from the adjacent productive shelf areas. It must be noted, however, that the association of infaunal foraminifera with relatively degraded organic material is valid only as long as the bottom water and surface sediment layer remain relatively well-oxygenated. Under oxygen-deficient conditions, low-oxygen resistant infaunal species replace less tolerant epifaunal species (see for example Chapters 6, 7 and 8). Extreme oxygen depletion has a profound impact on benthic foraminiferal production; populations may initially grow strongly, due to the lack of food-competition and predation by benthic macrofauna (see also Phleger and Soutar, 1973; Bernhard and Reimers, 1991), but ultimately benthic foraminiferal life is destroyed by a permanent lack of oxygen. Evidently, reconstruction of paleocarbon flux from benthic foraminiferal abundance data should be avoided or regarded with great circumspection if the foraminiferal assemblage bears the marks of oxygen-deficient conditions.

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APPENDIX A

counting lists of Rose Bengal stained benthic foraminifera

Core AD91-32 (41°54.80 N, 16°41.75 E, 146 m)														
depth in sediment (cm)	0.0-0.5		0.5-1.0		1.0-1.5		1.5-2.0		2.0-3.0		3.0-4.0		4.0-5.0	
approx. sample volume (cc):	16		16		16		16		32		32		32	
fraction f: 63-150µm; m: >150µm	f	m	f	m	f	m	f	m	f	m	f	m	f	m
Astrorhizids														
Rhabdammina sp.2	4	15				7				4				
Rhizammina sp.		3		1								2		
non-fossilizing arenaceous														
Adercotryma glomeratum	12		28		14		1		5				1	
Ammobaculites sp.	8	5		3		2	1	1	2			3		
Ammodiscus spp.	3	3	3	1	2	3	3	2						
Ammolagena clavata		1		1										
Cribrostom. subglobosum		7		1		2		1						
Cribrostomoides sp.1		2		1		1		1	1					
Cribrostomoides sp.2	1													
Eggerella scabra	23	15	7	2	4	2	2	2	7		1	1	2	
Eggerella sp.1	32		7		7		4		5		3		2	
Eggerella sp.2									2					
Eggerella subconica	1	3		1		2								
Glomospira charoides	4	1	9		13	5	13		3	1				
Glomospira sp.1	16		5		7		2		2					
Glomospira sp.2	13		4		5	1					2			
Hapl. membranaceum	35		34		16				6		5		2	
Haplophragmoides bradyi	31		21		6		1				1			
Lagenammina fusiformis	26	6	1	1	1	1	1	2	4	3	1			
Martinottiella sp.		6		3	1	4	1	10	3	10		7		
Pseudobolivina sp.	2		4		2									
Reophax dentaliniformis	8	14	7	13	3	3	1			2		3	1	1
Reophax nana			2		3									
Reophax scotti	2								1		1			
Reophax sp.1	2	11	3	5		4				3		1		
Reophax spp.	22	3	6		4	4	2		5					
Saccammina atlantica	3	8	3	3	4	4				5	1		1	1
Saccammina sp.		1		3	1			1						
Textularia porrecta			1						1		1			
Tritaxis brittannica	17				2		1		1					
Tritaxis fusca	6	2	1		1	1	1		1					
Troch. globigeriniformis	46	1	11		2		1		1		1			
Trochammina chitinosa							1		15		5		4	
Trochammina inflata	4	1	2		5		4		1				1	
Trochammina sp. 1	2				2									
Trochammina sp.3					2						1			
other arenaceous	6	2		1	5		2		1		1		1	
fossilizing arenaceous														
Bigenerina nodosaria	18	28	4	8	3	3	3		7	1	4	1		
Pseudoclavulina crustata		1										1		
Siphotextularia concava		1					2	1		2				
Textularia agglutinans	8	8		5	3	5	4	1	2	7	2	3	4	
Textularia conica		1			1									
Textularia sagittula	15	7	5	1	7	1	2	1	12	1	3		8	
imperforate calcareous	37	9	5	2	8		2		6					

APPENDIX A

counting lists of Rose Bengal stained benthic foraminifera

Core AD91-32 (41°54.80 N, 16°41.75 E, 146 m) continued														
depth in sediment (cm)	0.0-0.5		0.5-1.0		1.0-1.5		1.5-2.0		2.0-3.0		3.0-4.0		4.0-5.0	
approx. sample volume (cc):	16		16		16		16		32		32		32	
fraction f: 63-150µm; m: >150µm	f	m	f	m	f	m	f	m	f	m	f	m	f	m
perforate calcareous:														
Alliatina primitiva	2		6		4		2		1		1			
Amphicoryna scalaris	1	3		1		1						1		
Anomalina sp.1	5		2		2						1			
Anomalinoides minimus	3				1									
Anomalinoides sp.1	1		2		2		2		4		3		1	
Bolivina albatrossi	6		4		4				3		2			
Bolivina dilatata	58		26		18		16		20		3		2	
Bolivina spathulata	166	1	39	1	23		5		13		10	1	13	
Bolivina subspinescens	9		3		3						2		1	
Bulimina aculeata	2	2						1	1		1	1		
Bulimina costata	8	1												
Bulimina marginata	5	5	2		2	1	1	1	1					
Cassidulina crassa	28		5		3		1							
Cassidulina laevigata	34	1	4		3		1		1	1	1			
Cassidulina oblonga	3	2	2		1					1				
Cassidulinoides bradyi	1				4	1	1		7	1	4	2		1
Chilostomella czizeki				1										1
Cibicides lobatulus		1											1	
Cibicides pachydermus	4	12		4		1		1		1			1	
Dentalina spp.			1	2		1			1	1		1		
Epistominella exigua	4		2		2				1					
Epistominella vitrea	1				2				1		2			
Eponides sp.1	32		7		2		1		11		6		2	
Fissurina spp.	6		5		3						1			
Fursenkoina tenuis	1						1		1		1		3	
Gavelinopsis praegeri	25	2	3		3	1	1		2					
Globobulimina pyrula						1		1		2		3		
Globocass. subglobosa	5	1	1		2								1	
Gyroidina orbicularis		1					1							
Gyroidina umbonata	12	2	2		2					1				
Gyroidinoides sp.	4										1			
Hanzawaia boueana	3	2		1					1		1		1	
Hanzawaia rhodiense	4	1			3				2					
Hyalinea balthica		1												
Lagena spp.	4								1					
Lenticulina spp.		1				1			1	1				
Melonis barleeanum	15	5	27	3	21	4	22		11	2	2	1		
Nonionella sp.1	2													
Nonionella sp.2	7		11		1						1		1	
Nonionella turgida									2		1		1	
Planorb. mediterranensis	1	1		1						2				
Planulina ariminensis	2	2								1			1	
Polymorphina sp.				1										
Pullenia quinqueloba	1		1		1									
Robertina translucens					1									
Rosalina bradyi	6		5		2				2		2		1	
Rosalina sp.	2	2							1					
Seabrookia earlandi	4				4									
Siphonina reticulata	4		1		1									

Core AD91-32 (41°54.80 N, 16°41.75 E, 146 m) continued

depth in sediment (cm)	0.0-0.5		0.5-1.0		1.0-1.5		1.5-2.0		2.0-3.0		3.0-4.0		4.0-5.0	
approx. sample volume (cc):	16		16		16		16		32		32		32	
fraction f: 63-150µm; m: >150µm	f	m	f	m	f	m	f	m	f	m	f	m	f	m
perforate calcareous (continued)														
Stainfortia fusiformis	2				1									
Svratkina tuberculata	3		3		1		1				1		1	
Trifarina angulosa	14	4	3	1	11	1						1		
Trifarina pauperata	5		3				1				5		5	
Uvigerina med.	17	34		7	1	7			1	3	1	1		
Uvigerina peregrina	5	1	1	2	2	1	1							
Valvulineria bradyi			1											
other perforates	1													

Core AD91-30 (41°59.80 N, 16°55.50 E, 398 m)

depth in sediment (cm)	0.0-0.5		0.5-1.0		1.0-2.0		2.0-3.0		3.0-4.0		4.0-5.0	
approx. sample volume (cc):	10		10		20		20		20		20	
fraction f: 63-150µm; m: >150µm	f	m	f	m	f	m	f	m	f	m	f	m
Astrorhizids												
Rhabdammina sp.2	1			5								
Rhizammina sp.		13										
Saccorhiza ramosa	25	71	2	18	12	60	2	1				
non-fossilizing arenaceous												
Adercotryma glomeratum	17		6		4							
Ammobaculites sp.							1	1		2		
Ammodiscus spp.	4				1	1	7					
Ammolagena clavata										1		
Cribrostom. subglobosum						2		2				
Eggerella scabra	2	2			1	1	2		2		1	
Eggerella sp.1	2		1		3		4					
Eggerella subconica	1	1	1									
Glomospira charoides	1	2	2	1	2							
Glomospira sp.1	2											
Glomospira sp.2	10	1	6		4		1					
Hapl. membranaceum	6											
Haplophragmoides bradyi	3											
Lagenammina fusiformis	7				3			1				1
Martinottiella sp.		1				1		2		3		
Meandrospira sp.	1				1		1		1			
Placopsilina sp.		2								1		
Pseudobolivina sp.	2											
Reophax dentaliniformis	3	3	2			2	1					
Reophax scotti	1											
Reophax sp.1						1						
Reophax spp.	4		8		2		1					
Saccammina atlantica	2	11	4	3	4	4	1	3	1	3		
Saccammina sp.		1										
Textularia porrecta					1							
Tritaxis fusca		1					1					
Troch. globigeriniformis			1				1					
Trochammina inflata	2		1						1			

Core AD91-30 (41°59.80 N, 16°55.50 E, 398 m) continued												
depth in sediment (cm)	0.0-0.5		0.5-1.0		1.0-2.0		2.0-3.0		3.0-4.0		4.0-5.0	
approx. sample volume (cc):	10		10		20		20		20		20	
fraction f: 63-150µm; m: >150µm	f	m	f	m	f	m	f	m	f	m	f	m
non-fossilizing arenaceous (continued)												
Trochammina sp. 1	2											
other arenaceous			1		1		1					
fossilizing arenaceous												
Bigenerina nodosaria	6	6	2	1	4	3	5					
Pseudoclavulina crustata		1		1		1						
Textularia agglutinans	1	2		1			8	4		1		
Textularia conica												
Textularia sagittula	2				1						2	
imperforate calcareous	6	1	1	1			3				1	1
perforate calcareous:												
Alliatina primitiva	3								1			
Amphicoryna scalaris	1	1										
Anomalina sp.2					1							
Anomalinoides minimus	6		3									
Bolivina albatrossi	3		2									
Bolivina dilatata	3		1				3		1		1	
Bolivina seminuda					1	1	1		1		1	
Bolivina spathulata	5		2								1	
Bulimina costata	2		1									
Bulimina marginata	1	2		1	1		1	1				
Cassidulina crassa	3		1						1			
Cassidulina oblonga	1				2				3			
Cassidulinoides bradyi	3		1				5	2	2	1		
Cibicides lobatulus	2											
Cibicides pachydermus		2							1			
Dentalina spp.	1				1							
Epistominella exigua	15		6		2							
Epistominella vitrea	1											
Eponides sp.1	4		2		2		3		3		1	
Fursenkoina tenuis							1	3		1		
Gavelinopsis praegeri	3	1									1	
Globobulimina pyrula						2						
Globocass. subglobosa	2				1		4		1		1	
Gyroidina umbonata	1											
Gyroidinoides sp.	1				2							
Hanzawaia boueana	1											
Lenticulina spp.				1		1						
Melonis barleeanum		1			1		1					
Nonionella sp.1	1											
Planulina ariminensis	1	1					1					
Pullenia quinqueloba		1		1			6	2				
Robertina translucens								1				
Rosalina bradyi	9	7										
Seabrookia earlandi	2											
Siphonina reticulata	1	1	2		1		1					
Sphaeroidina bulloides	1											

Core AD91-30 (41°59.80 N, 16°55.50 E, 398 m) continued												
depth in sediment (cm)	0.0-0.5		0.5-1.0		1.0-2.0		2.0-3.0		3.0-4.0		4.0-5.0	
approx. sample volume (cc):	10		10		20		20		20		20	
fraction f: 63-150µm; m: >150µm	f	m	f	m	f	m	f	m	f	m	f	m
perforate calcareous (continued)												
Trifarina angulosa						1	1					
Trifarina pauperata							1					
Uvigerina med.		7								1		
Uvigerina peregrina			1									

Core AD91-29 (41°59.50 N, 16°58.75 E, 487 m)														
depth in sediment (cm)	0.0-0.5		0.5-1.0		1.0-1.5		1.5-2.0		2.0-3.0		3.0-4.0		4.0-5.0	
approx. sample volume (cc):	14		14		14		14		28		28		28	
fraction f: 63-150µm; m: >150µm	f	m	f	m	f	m	f	m	f	m	f	m	f	m
Astrorhizids														
Rhabdammina sp.2				1										
Rhizammina sp.		4												
Saccorhiza ramosa	40	32	4	18	3	1		3	1	1		1		
non-fossilizing arenaceous														
Adercotryma glomeratum	15		12		3		1		1					
Ammobaculites sp.	1		1											
Ammodiscus spp.	6		2				3							
Ammolagena clavata				1										
Cribrostom. subglobosum										1		1		1
Cribrostomoides sp.1		1		1										
Eggerella subconica	4													
Eggerella scabra	1		1				2							
Eggerella sp.1	1													
Glomospira charoides	1	2	2	1	1		1						1	
Glomospira sp.2	41		8		1		4		1					
Haplophragmoides bradyi	6													
Hapl. membranaceum	6								1					
Lagenammina fusiformis	6	2			4		1	1	3	1	11			
Martinottiella sp.		2		2		2				2				
Meandrospira sp.	3				1	1	4				1			
Pseudobolivina sp.	1		1											
Reophax dentaliniformis										1				1
Reophax scotti													2	
Reophax spp.	21	3	7		1						1			
Saccammina atlantica	11	32	6	6		2	2	3	3			2		2
Saccammina sp.		4												
Tritaxis fusca									1					
Troch. globigeriniformis	1													
Trochammina inflata	22		30	1	10		2		2		1			
Trochammina sp. 1	4				1		1							
other arenaceous	5	4	1		1		2							
fossilizing arenaceous														
Bigenerina nodosaria	2	1	1	1		3	4	1	4	3	2	1		
Pseudoclavulina crustata		1												
Textularia agglutinans								1			1		1	
Textularia sagittula			1						1				1	

APPENDIX A

counting lists of Rose Bengal stained benthic foraminifera

Core AD91-29 (41°59.50 N, 16°58.75 E, 487 m) continued														
depth in sediment (cm)	0.0-0.5		0.5-1.0		1.0-1.5		1.5-2.0		2.0-3.0		3.0-4.0		4.0-5.0	
approx. sample volume (cc):	14		14		14		14		28		28		28	
fraction f: 63-150µm; m: >150µm	f	m	f	m	f	m	f	m	f	m	f	m	f	m
imperforate calcareous	6	1	5	5		4	1		1		3	1		
perforate calcareous:														
Alliatina primitiva									2					
Anomalinoides minimus	14		5		1		5		3					
Asterononion sp.					1									
Bolivina albatrossi	3										1			
Bolivina dilatata	4		1						1					
Bolivina spathulata	4						1		1					
Bolivina subspinescens	2													
Bulimina costata			1											
Bulimina marginata							1					1		
Cassidulina crassa	6				1		1				2		1	
Cassidulina oblonga	1		1											
Cassidulinoides bradyi			1	2	2		6		9	1	12	4	1	
Cibicides lobatulus							1							
Dentalina spp.	1			1	1				1					
Epistominella exigua	2		1						1				1	
Epistominella vitrea											1			
Eponides sp.1	2						2				1			
Fursenkoina tenuis										1		3		4
Gavelinopsis praegeri			1											
Globobulimina pyrula								1						8
Globocass. subglobosa			1						1		1			
Gyroidina orbicularis	1	1	1						1					
Gyroidina umbonata	4						1							
Gyroidinoides sp.	2						1				2			
Lagena spp.													1	
Lenticulina spp.	1													
Melonis barleeanum	2	1	3	2										
Planulina ariminensis							1						1	
Polymorphina sp.										1				
Rotamorphina involuta			2				1							
Seabrookia earlandi	4				1						1			
Siphonina reticulata				1			2	1	2					
Svratkina tuberculata									1					
Uvigerina med.		2		1		2								
Uvigerina peregrina	1						1							
other perforates							1							

Core AD91-28 (41°59.00 N, 17°01.00 E, 578 m)										
depth in sediment (cm)	0.0-1.0		1.0-2.0		2.0-3.0		3.0-4.0		4.0-5.0	
approx. sample volume (cc):	30		30		30		30		30	
fraction f: 63-150µm; m: >150µm	f	m	f	m	f	m	f	m	f	m
Astrorhizids										
Rhabdammina sp.1	311	8	32	2						
Rhizammina sp.		3								
Saccorhiza ramosa	104	72	39	60	6	12				2

Core AD91-28 (41°59.00 N, 17°01.00 E, 578 m) continued										
depth in sediment (cm)	0.0-1.0		1.0-2.0		2.0-3.0		3.0-4.0		4.0-5.0	
approx. sample volume (cc):	30		30		30		30		30	
fraction f: 63-150µm; m: >150µm	f	m	f	m	f	m	f	m	f	m
non-fossilizing arenaceous										
Adercotryma glomeratum	12		10		1		1			
Ammodiscus spp.	8		1		2		2			
Eggerella subconica			1							
Eggerella scabra	1	1								
Eggerella sp.1	2									
Glomospira charoides	3						1			
Glomospira sp.2	28		3						1	
Haplophragmoides bradyi	2		1							
Hapl. membranaceum	6									
Lagenammina fusiformis	5	1								
Meandrospira sp.	1	2	12		1			1		
Reophax sp.1		1								
Reophax spp.	12									
Saccammina atlantica	2	14				1	1	3		1
Saccammina sp.		3				1				
Troch. globigeriniformis	5									
Trochammina inflata	22		22		4		2			
Trochammina sp. 1	5									
Trochammina sp.3	1									
other arenaceous	4									1
fossilizing arenaceous										
Bigenerina nodosaria	2	1	3	2	2					
Pseudoclavulina crustata		2								
Siphotextularia concava			1							
imperforate calcareous	7	1		2	1					
perforate calcareous:										
Alliatina primitiva	4		1				1			
Amphicoryna scalaris	1	1								
Anomalinoides minimus	28		12						2	
Asterononion sp.	1									
Bolivina albatrossi			1							
Bolivina dilatata	3									
Bolivina seminuda					3				1	
Bolivina spathulata	2						1		1	
Bulimina costata	1									
Cassidulina crassa	7		1		1		1			
Cassidulina oblonga	3									
Cassidulinoides bradyi			1		2		10		16	
Dentalina spp.									1	
Epistominella exigua	8		2						1	
Eponides sp.1	2						3		1	
Gavelinopsis praegeri					1					
Gyroidina altiformis	1					1	1			
Gyroidina orbicularis	2		1		1					
Gyroidina umbonata	1		1							
Melonis barleeanum		1	13							

Planulina ariminensis	1									
Pullenia quinqueloba	1		1	1		1			1	
Rosalina bradyi	1						1			
Rotamorphina involuta	2		3		2		1			
Siphonina reticulata	2	1			1	1	1	1	1	
Sphaeroidina bulloides				1						
Uvigerina med.	2			1						
Uvigerina peregrina	2				1					
Uvigerina proboscidea									1	
Valvulineria bradyi	2									

Core AD91-27 (41°59.50 N, 17°02.75 E, 664 m)														
depth in sediment (cm)	0.0-0.5		0.5-1.0		1.0-1.5		1.5-2.0		2.0-3.0		3.0-4.0		4.0-5.0	
approx. sample volume (cc):	21		21		21		21		42		42		42	
fraction f: 63-150µm; m: >150µm	f	m	f	m	f	m	f	m	f	m	f	m	f	m
Astrorhizids														
Saccorhiza ramosa	19	16	3	2			2							
non-fossilizing arenaceous														
Adercotryma glomeratum	14		1											
Ammodiscus spp.			2		2		1							
Glomospira charoides	3	3	6		2		4		4		3		1	
Glomospira sp.2	1													
Haplophragmoides bradyi	1													
Martinottiella sp.				1										
Meandrospira sp.	1													
Reophax spp.			1											
Saccammina atlantica						1				1				1
Saccammina sp.						1								
Tritaxis fusca								1			1			
Trochammina inflata	6													
fossilizing arenaceous														
Bigenerina nodosaria					2						1			
Pseudoclavulina crustata		1												
imperforate calcareous	1	1		1	2	1						1		
perforate calcareous:														
Anomalinoides minimus	7		2										1	
Bulimina costata	1		1											
Cassidulina crassa	1													
Epistominella exigua	2													
Eponides sp.1	1				1				1		1		1	
Fissurina spp.							1		1		1			
Gavelinopsis praegeri							1							
Gyroidina orbicularis	3				2		1							
Gyroidina umbonata	2													
Gyroidinoides sp.	1													
Lagena spp.	1		1											
Melonis barleeanum	2													
Pullenia quinqueloba	2								1					
Rosalina globularis	1													
Rotamorphina involuta					2		2							
Siphonina reticulata				1			1			1				
Uvigerina med.		1				1								
Uvigerina peregrina	1													

APPENDIX A

counting lists of Rose Bengal stained benthic foraminifera

Core AD91-26 (41°59.80 N, 17°08.70 E, 794 m)										
depth in sediment (cm)	0.0-1.0		1.0-2.0		2.0-3.0		3.0-4.0		4.0-5.0	
approx. sample volume (cc):	25		25		25		25		25	
fraction f: 63-150µm; m: >150µm	f	m	f	m	f	m	f	m	f	m
Astrorhizidae:										
Rhabdammina sp.1									2	
Rhizammina sp.		3								
Saccorhiza ramosa	248	17	1	1						
non-fossilizing arenaceous										
Adercotryma glomeratum	21									
Ammodiscus spp.	2	1	2				1	1		
Ammolagena clavata	2									
Eggerella scabra	2									
Eggerella sp.1	3						1			
Glomospira charoides	17	4	14		6	1	4	1	6	
Glomospira sp.1			1				4			
Glomospira sp.2	4									
Haplophragmoides bradyi	5									
Meandrospira sp.	4		1		1					
Reophax spp.			1		1					
Trochammina inflata	9									
other arenaceous	2									
imperforate calcareous	1	1		1	1	2		1		
perforate calcareous:										
Alliatina primitiva	2									
Anomalinoides minimus	26		2		2		5		1	
Bolivina albatrossi	1									
Bolivina subspinescens			1							
Bulimina costata	1									
Bulimina marginata		1								
Cassidulina crassa	2									
Epistominella exigua	8									
Eponides sp.1	1		8		1					
Gavelinopsis praegeri			1		1					
Globocass. subglobosa	1									
Gyroidina altiformis	1									
Gyroidina orbicularis	3	1					1			
Gyroidina umbonata	2				2					
Melonis barleeanum	3	1	3							
Planulina ariminensis	1									
Pullenia quinqueloba		1								
Robertina translucens			1							
Rosalina globularis	1									
Rotamorphina involuta	4									
Sphaeroidina bulloides		1								
Uvigerina med.		1		1		2				

APPENDIX A

counting lists of Rose Bengal stained benthic foraminifera

Core AD91-25 (42°00.00 N, 17°11.75 E, 898 m)														
depth in sediment (cm)	0.0-0.5		0.5-1.0		1.0-1.5		1.5-2.0		2.0-3.0		3.0-4.0		4.0-5.0	
approx. sample volume (cc):	17		17		17		17		33		33		33	
fraction f: 63-150µm; m: >150µm	f	m	f	m	f	m	f	m	f	m	f	m	f	m
Astrorhizidae:														
Rhabdammina sp.1	4	2												
Saccorhiza ramosa	241	147	36	20	2	4	1							
non-fossilizing arenaceous														
Adercotryma glomeratum	19		3						1					
Ammodiscus spp.			2		1		1	1	1		1	1	1	
Cribrostomoides sp.1		1		1										
Eggerella subconica		1	1											
Eggerella sp.1	1		2											
Glomospira charoides	4	2	5	2	3		5		5		2		1	
Glomospira sp.1	1				2						1			
Glomospira sp.2	8		4				1		2		3		3	
Haplophragmoides bradyi	2													
Hapl. membranaceum	1				1									
Meandrospira sp.	7		3											
Reophax spp.					1									
Trochammina inflata	21		9		9		1							
Trochammina sp. 1			1											
other arenaceous	1					2								
fossilizing arenaceous														
Bigenerina nodosaria							1		1	1		1		
Pseudoclavulina crustata				1										
Textularia sagittula			1											
imperforate calcareous	1	1				2		1			1			
perforate calcareous:														
Anomalinoides minimus	19		5		1		1							
Bulimina costata	1													
Cassidulina crassa		1												
Dentalina spp.	1													
Epistominella exigua	4						1							
Eponides sp.1			1		3		3		4		6		6	
Fissurina spp.	1								1					
Gavelinopsis praegeri			1						1					
Gyroidina orbicularis	3		2		1									
Gyroidina umbonata	1													
Gyroidinoides sp.													1	
Lagena spp.	1		1				1							
Lenticulina spp.	1													
Melonis barleeanum		1					1		1					
Planulina ariminensis												1		
Rotamorphina involuta	6		5		1		1		2		1			
Siphonina reticulata								1	1					
Uvigerina med.		3				1		1				1		1
Uvigerina peregrina		1		1							3			
Valvulineria bradyi	1													
other perforates			1		1									

APPENDIX A

counting lists of Rose Bengal stained benthic foraminifera

Core AD91-01 (41°50.84 N, 17°52.48 E, 1200 m)

depth in sediment (cm)	0.0-0.5		0.5-1.0		1.0-1.5		1.5-2.0		2.0-3.0		3.0-4.0		4.0-5.0	
approx. sample volume (cc):	10		10		10		10		20		20		20	
fraction f: 63-150µm; m: >150µm	f	m	f	m	f	m	f	m	f	m	f	m	f	m
Astrorhizids														
Saccorhiza ramosa	18	16	3	2		5								
non-fossilizing arenaceous														
Adercotryma glomeratum	1		1											
Glomospira charoides	1	1	2				1				2			
Glomospira sp.2	4	1												
Reophax scotti			1											
Trochammina inflata	2		1											
imperforate calcareous		1												
perforate calcareous:														
Alliatina primitiva											1			
Anomalinoides minimus	1		1		1									
Epistominella exigua	5		1											
Eponides sp.1					1									
Fissurina spp.	1													
Globocass. subglobosa	1													
Gyroidina orbicularis			1						1	1		1		
Melonis barleeanum	2		1											
Rotamorphina involuta	3		3				1		1					
Seabrookia earlandi	1													
other perforates					1									

APPENDIX B

counting lists of dead benthic foraminifera in AD91- box cores

surface layer (0-1 cm)																
station:	**32**		**30**		**29**		**28**		**27**		**26**		**25**		**1**	
sample volume (cc):	16		10		14		30		21		25		17		10	
splitfraction 1/x	512	128	205	43	205	43	205	43	102	8	85	2	128	2	5.3	1
sieve fraction:																
f:63-150µm, m: >150µm	f	m	f	m	f	m	f	m	f	m	f	m	f	m	f	m
Astrorhizids																
Rhabdammina sp.2																
Rhizammina sp.						2										
Saccorhiza ramosa			4	5	7	10	14	10	2	9	25	24	46	328	111	21
non-fossilizing aren.																
Adercotryma glomeratum			2		1		1	1			3		6		2	
Ammobaculites sp.											1					
Ammodiscus spp.						1	1						2	8	1	
Ammolagena clavata								2						1		4
Cribrostom. subglobosum									1			3				
Cribrostomoides sp.2																
Eggerella scabra					2		2	1	1	1	2	2		7		
Eggerella subconica			1									1		3	2	1
Glomospira charoides				3	2	5	1	7	6	3	7	12	3	25	26	14
Glomospira sp.1														1	6	1
Haplophragmoides bradyi			1		1						2				2	
Lagenammina fusiformis														1		
Meandrospira sp.						2				3		4		1		3
Placopsilina sp.																
Pseudobolivina sp.	1															
Reophax nana																
Reophax spp.						3		4	1		1		1		1	
Saccammina atlantica								2						2		
Tritaxis brittannica.													1			
Tritaxis fusca					1	2								1		
Troch. globigeriniformis			1			1							1			
Trochammina inflata					1				1		1		3		1	
other arenaceous		1	1	2		2	1	1		1		1	3	11	6	1
fossilizing arenaceous																
Bigenerina nodosaria	2	22	5	7	3	17	3	4	2	5		4	1			
Pseudoclavulina crustat	1	1		1		3		5		5		3		4		1
Siphotextularia concava	1	7	1	2	2	2		1	1	4	1		2	3		
Textularia agglutinans	7	35	9	15	4	4	6	6	4	1	1	1		2	2	
Textularia conica		3	1	3	1	5	2	3	1	2						1
Textularia sagittula	3	8	2	7	3	1	1	1	1				2	1		
imperforate calcareous	17	28	14	29	23	20	25	28	22	23	35	20	40	50	33	21

APPENDIX B

counting lists of dead benthic foraminifera in AD91- box cores

subsurface layer (4-5 cm)																
station:	**32**		**30**		**29**		**28**		**27**		**26**		**25**		**1**	
sample volume (cc)	32		20		28		30		42		25		33		20	
splitfraction 1/x	3277	1024	1024	128	205	85	410	85	341	16	85	2.1	205	4	14	1
sieve fraction:																
f:63-150µm, m: >150µm	f	m	f	m	f	m	f	m	f	m	f	m	f	m	f	m
Astrorhizids																
Rhabdammina sp.2								1								
Rhizammina sp.																
Saccorhiza ramosa			1	1		2	1	1			1	37	11	30	54	6
non-fossilizing aren.																
Adercotryma glomeratum											1		1	1	2	
Ammobaculites sp.		1				1										
Ammodiscus spp.							1	1				4		11	5	4
Ammolagena clavata				1				1				2		1		9
Cribrostom. subglobosum													1			
Cribrostomoides sp.2														1		
Eggerella scabra						1						6		4	2	2
Eggerella subconica							1							1		
Glomospira charoides			1	1	6	4	1	2	1	5	4	27	3	18	10	20
Glomospira sp.1					2								1	8	3	
Haplophragmoides bradyi							2						3		3	
Lagenammina fusiformis														1		
Meandrospira sp.				1		3		1				5	1			3
Placopsilina sp.						1										
Pseudobolivina sp.																
Reophax nana	1															
Reophax spp.																
Saccammina atlantica																
Tritaxis brittannica.																
Tritaxis fusca				1										1		1
Troch. globigeriniformis							1									
Trochammina inflata			1										1		2	
other arenaceous		1		1	1		1		2	1		4		5	4	15
fossilizing arenaceous																
Bigenerina nodosaria	4	13	1	6	2	10	1	3	2	3	1	2	1	1		
Pseudoclavulina crustata		1			1			4		2		3				
Siphotextularia concava	1	2	2	8	6	5		4	2	5	1	1		1		
Textularia agglutinans	5	18	1	7	6	9	3	10	1	4	1	1	1	1		
Textularia conica	2	2		4	1	3	4	7		1						
Textularia sagittula	3	3	3	7	7	5	2	1	2	1		1			1	
imperforate calcareous	23	27	28	36	42	18	17	18	21	27	26	34	29	47	32	41

APPENDIX B

counting lists of dead benthic foraminifera in AD91- box cores

surface layer (0-1 cm) continued																
station:	**32**		**30**		**29**		**28**		**27**		**26**		**25**		**1**	
sample volume (cc):	16		10		14		30		21		25		17		10	
splitfraction 1/x	512	128	205	43	205	43	205	43	102	8	85	2	128	2	5.3	1
sieve fraction:																
f:63-150µm, m: >150µm	f	m	f	m	f	m	f	m	f	m	f	m	f	m	f	m
perforate calcareous																
Alliatina primitiva									1		1		1		8	
Ammonia spp.	1	3														
Amphicoryna scalaris		2		5	1	6	1	5	1	1	1	2		2		
Anomalinoides minimus			2		3		6		6		6		8		15	
Asterigerinata spp.	6	3	4	1	1		2		1				2			
Asterononion sp.									1							
Asterononion sp.2	1		3	1	1			1	1	1			2	1		
Bolivina albatrossi			1		2		4		3		5		4		1	
Bolivina dilatata	2				3		1		2		1					
Bolivina seminuda						1					1					
Bolivina spathulata	28	14	37	12	18	5	24	7	17	4	4		7	1	2	
Bolivina subspinescens.	1				1		1		1				3			
Buccella spp.	2	4	2													
Bul.aculeata	8	25	2	7	4	1	2		1	1		1	1			
Bulimina costata	3	1	13	36	3	29	13	15	9	9		1	6	3		
Bulimina marginata	14	5	11	32	6	32	6	28	6	24	5	2	3	5		
Cassidulina crassa	23	1	52	1	54	4	23	7	68	6	61	6	53	8	47	8
Cassidulina laevigata	28	8	43	42	22	21	30	17	26	8	9		12	2	2	
Cassidulina oblonga	7	11	5	5	8	4	2									
Cassidulinoides bradyi									1							
Chilostomella czizeki								1								
Cibicides lobatulus	9	18	7	10	3	19	5	3	1	3	3	5	4	3	5	7
Cibicides pachydermus		3		6	1	6	1		1	3						1
Dentalina spp.		1	1		1	2			1	1	2	1		2	3	3
Elphidium spp.	23	39	2	8	1	2	3		3							
Epistominella exigua			1		3		2		5		15		21		8	
Epistominella vitrea	2		5		3		4		17		13		13		3	
Eponides sp.1	3		5		3		2		7		10		8		2	
Eponides sp.2					1				2		2					
Fissurina spp.	1		1	3	2		2	1	5	3		1	9	2	3	1
Gavelinopsis praegeri	13	2	16	7	13	5	9	10	15		1		8	4	2	
Globobulimina pyrula																
Globocass. subglobosa	4		15		22	3	28	2	37	9	27	22	26	11	14	3
Gyr.orbicularis		1		3	1	4		7		4		2		2	3	7
Gyroidina altiformis		2		1	1	4	1	2		5	1	15		11	8	27
Gyroidina umbonata	2	2	4	10	6	5	4	6	11	3	6	1	8	1	12	1
Gyroidinoides sp.			1		7		4		3		9		8		5	
Hanzawaia boueana	2	2		10		4	1	2	2	2	2		2			
Hanzawaia rhodiense		2		1												

subsurface layer (4-5 cm) continued																
station:	**32**		**30**		**29**		**28**		**27**		**26**		**25**		**1**	
sample volume (cc)	32		20		28		30		42		25		33		20	
splitfraction 1/x	3277	1024	1024	128	205	85	410	85	341	16	85	2.1	205	4	14	1
sieve fraction:																
f:63-150µm, m: >150µm	f	m	f	m	f	m	f	m	f	m	f	m	f	m	f	m
perforate calcareous																
Alliatina primitiva					1		1		1		1		1		1	
Ammonia spp.	1	3														
Amphicoryna scalaris		3		12	3	9		4	1	6	1		1	2		
Anomalinoides minimus			1		11		2		6		18		5		20	
Asterigerinata spp.	13	1	3	2	2		1		1							
Asterononion sp.		1	1		1					1				3		1
Asterononion sp.2			1		3		2		2		1					
Bolivina albatrossi	2		5		1		1		2		2		4		1	
Bolivina dilatata		1	1		2		2		1		1		1		1	
Bolivina seminuda							1									
Bolivina spathulata	34	26	26	9	36	9	18	7	20	5	7		9	2	3	
Bolivina subspinescens.	1		3		6		1		1		1		1			
Buccella spp.																
Bul.aculeata	6	19	4	3	7	5	5	3	3	4	2		1	1		
Bulimina costata		2	5	33	11	23	4	14	3	15	3	1	1	6		
Bulimina marginata	11	10	10	32	16	32	10	22	5	23	6	12	7	11	1	
Cassidulina crassa	35	1	31	5	77	12	35	10	36	6	63	9	48	3	35	4
Cassidulina laevigata	23	14	18	40	53	10	25	17	21	10	11	3	15	14	2	
Cassidulina oblonga	4	9	3	4	3			6			1	1				
Cassidulinoides bradyi																
Chilostomella czizeki																
Cibicides lobatulus	10	13	2	9	11	5	7	1	1	3	3	2	3	6	3	7
Cibicides pachydermus		4		3	1	1		2		6						1
Dentalina spp.			1		1			1			2			1		1
Elphidium spp.	26	43	4	9	5		3	1	1		2					
Epistominella exigua	1		4		1		1		2		10		8		10	
Epistominella vitrea	13		6		9		7		16		17		20		11	
Eponides sp.1	9		2		7		10		6		18		11		6	
Eponides sp.2					2				2				1			
Fissurina spp.			1	5	5	1	3		1	6	3	4	2	1	8	2
Gavelinopsis praegeri	11	1	17	21	22	10	10	8	6	9	10	1	7	5	2	
Globobulimina pyrula					1					1				1		
Globocass. subglobosa	17		17		44	1	25		15	8	22	13	30	13	6	6
Gyr.orbicularis	1			2	3	7		6	1	4		12		6		11
Gyroidina altiformis		1			1		1	3		2	2	23	2	4	2	15
Gyroidina umbonata	1	2	4	6	7		1	4	4	5	18		9	1	6	
Gyroidinoides sp.			2		10		5		3		6		9		2	
Hanzawaia boueana	2	6	2	9	2	6	1	3	2	3			1	3		
Hanzawaia rhodiense			1	1				1								

APPENDIX B

counting lists of dead benthic foraminifera in AD91- box cores

surface layer (0-1 cm) continued																
station:	**32**		**30**		**29**		**28**		**27**		**26**		**25**		**1**	
sample volume (cc):	16		10		14		30		21		25		17		10	
splitfraction 1/x	512	128	205	43	205	43	205	43	102	8	85	2	128	2	5.3	1
sieve fraction:																
f:63-150µm, m: >150µm	f	m	f	m	f	m	f	m	f	m	f	m	f	m	f	m
perforate calcareous (continued)																
Hoeglundina elegans		1														
Hyalinea balthica	2	9	5	14	3	4	6	5	2	1	5		4	1		
Lagena spp.	1	2		4	1	5		5	3	3	1	1	2	3	4	1
Lenticulina spp.				3	2	5	2	3	1	2	2	6		4	1	1
Melonis barleeanum	4	5		4		3		3	1			2		2		2
Nonionella sp.1			2		2		2		3		3		6		9	
Nonionella sp.2	1				3				2		5		3			
other perforates	5		2	1	1	1	5	1	5		10	4	3	3	3	1
Patellina rugosa											1					
Planorb. mediterranensi	1	1												1		
Planulina ariminensis				2	3	4		8	1	7		2		1	1	2
Polymorphina sp.																
Pullenia bulloides													1			
Pullenia quinqueloba		1		1		2			4	1		2	1	3		
Reussella spinulosa		6												1		
Robertina translucens			1				2	1	1	1			1	6	1	
Rosalina globularis			2	2	1	1	1	5	2							
Rosalina bradyi	2	2	3	4	1		1		1	1	2		2	2		
Rosalina sp.				1			1	2	4		1		3		2	
Rotamorphina	1	1			1	1			3		2		6	4	23	1
Seabrookia earlandi			2				1		1				2			
Siphonina reticulata					1	1				2	1					
Sphaeroidina bulloides		6	1	5		2	2	1		2		1		1		
Spirillina sp.								2					1	2		
Stainfortia fusiformis																
Svratkina tuberculata			2		1											
Trifarina angulosa	2	4	8	10	3	7	2	19	1	4				3		
Trifarina pauperata	4		2				2		2		2		3			
Uvigerina med.	2	30	4	12	1	12	3	16	2	29		38		26		35
Uvigerina peregrina	4	20	5	15	1	8	4	12	4	49	3	60	2	31	1	15
Uvigerina proboscidea				3		1		3		1						
Valvulineria bradyi	1				1											

APPENDIX B

counting lists of dead benthic foraminifera in AD91- box cores

subsurface layer (4-5 cm) continued																
station:	**32**		**30**		**29**		**28**		**27**		**26**		**25**		**1**	
sample volume (cc)	32		20		28		30		42		25		33		20	
splitfraction 1/x	3277	1024	1024	128	205	85	410	85	341	16	85	2.1	205	4	14	1
sieve fraction:																
f:63-150µm, m: >150µm	f	m	f	m	f	m	f	m	f	m	f	m	f	m	f	m
perforate calcareous (continued)_																
Hoeglundina elegans				1				1								
Hyalinea balthica		12	4	12	4	1	6	3	4	4	1	1	1	1		
Lagena spp.			1	2				2		2	3	1		3	4	2
Lenticulina spp.	1	2	1	6		3	2	3	2	4	1	2				5
Melonis barleeanum	2	4	2	6	4	2	3	2		3	2	6		2		2
Nonionella sp.1			4		2		3		3		7		3		7	
Nonionella sp.2	1		1		3		1		1		4		4		3	
other perforates	1	5			2		4		2		1		3		8	
Patellina rugosa			2				1								1	
Planorb. mediterranensis		2														
Planulina ariminensis			2	5	3	7	1	7	1	15		6		1		4
Polymorphina sp.					1							2		1		1
Pullenia bulloides									1		1					
Pullenia quinqueloba		2	1	1	1			1	2	2		2	1	3		
Reussella spinulosa		2														
Robertina translucens		1	1		2	1					2	1		4	2	1
Rosalina globularis			2	3		2		4	1	6			1	2		
Rosalina bradyi	4	3	1	4	7		2	1	1	3	1	1	4	2		
Rosalina sp.		3	1		5	1	1		4	3	1		1			
Rotamorphina	1		1	1	1	1	1	1		2	2	1	4		4	2
Seabrookia earlandi					3		3		1				2		1	
Siphonina reticulata				1		1	1			1			1			
Sphaeroidina bulloides		4	1	3		1		3	1							
Spirillina sp.	1		1					2	1	2			2	2	1	
Stainfortia fusiformis	1				1		1								1	
Svratkina tuberculata	1				2											
Trifarina angulosa	1	9	6	19	4	8	4	8	2	11		2	2	4		
Trifarina pauperata	2				5		4						2		1	
Uvigerina med.	3	30	1	24		29		29	1	60		91	2	46	1	94
Uvigerina peregrina	6	11	4	10	3	6	2	9	5	44	4	65	1	36	2	16
Uvigerina proboscidea		1		1		1		1								
Valvulineria bradyi			2	1	1				1				2			

SAMENVATTING

De gestage toename van de hoeveelheid kooldioxide in de aardse atmosfeer, als gevolg van het opstoken van fossiele brandstoffen, en de daarmee samengaande klimaatsveranderingen, maken de vraag welke processen de koolstofhuishouding op aarde beïnvloeden zeer actueel. Fixatie van koolstof door fytoplankton in de oppervlaktelaag van de oceaan, en het bezinken van een deel van de zo vastgelegde organische koolstof naar de diepzee, vormt een belangrijk proces waardoor kooldioxide aan de atmosfeer wordt onttrokken. De hoeveelheid organisch materiaal dat op deze wijze naar de diepzee verdwijnt kan, behalve door middel van sedimentvallen (waarvan de effectiviteit omstreden is), mogelijk ook worden bepaald aan de hand van de verspreiding van diepzee-organismen. Deze organismen zijn voor hun voeding vrijwel geheel afhankelijk van de export van organisch materiaal vanuit de oppervlaktelaag van de oceaan. In het verleden is reeds meerdere malen aangetoond dat benthische foraminiferen, een groep ééncellige bodemorganismen, zeer geschikt kunnen zijn als indicatoren van de flux van organisch koolstof naar de zeebodem. Benthische foraminiferen zijn meestal talrijk aanwezig in Recente diepzeeafzettingen en zijn daarom geschikt voor kwantitatieve analyses, en daarbij produceren veel soorten benthische foraminiferen schaaltjes van kalk of geagglutineerd sedimentmateriaal, die over het algemeen zeer goed bewaard blijven in fossiele sedimenten.

In deze studie van Recente en fossiele benthische foraminiferen in de Adriatische Zee wordt het belang van de flux van organisch materiaal als bepalende factor van de verspreidingspatronen bevestigd. Zowel levende als fossiele benthische foraminiferen nemen in aantal af met toenemende waterdiepte, wat een weerspiegeling vormt van de afnemende aanvoer van organisch materiaal. Waar in afwijking van dit algemene patroon een verhoogde productie van foraminiferen wordt waargenomen, bijvoorbeeld op het bovenste deel van de continentale helling, is dit verklaarbaar door laterale aanvoer van organisch materiaal via bodemstromingen. Op plaatsen met een dergelijke verhoogde productie zijn endobenthische (in het sediment levende) foraminiferen vaak relatief talrijk. Gespeculeerd wordt dat deze endobenthische soorten in staat zijn om het reeds gedeeltelijk afgebroken organisch materiaal dat via bodemstromingen wordt aangevoerd te consumeren. Vers bezonken organisch materiaal, dat vanuit voedingsoogpunt veel waardevoller is, wordt waarschijnlijk vooral door epibenthische (op het sedimentoppervlak levende) foraminiferen gegeten.

De oorzaak waardoor deze epibenthische foraminiferen het verse en voedingsrijke voedsel kunnen bemachtigen, terwijl endobenthische soorten genoegen moeten nemen

met tweede keus voedsel, is mogelijk dat epibenthische soorten zich snel kunnen vermeerderen in tijden van voedselrijkdom. Hierdoor kunnen zij een groot deel van het met onregelmatige tussenpozen bezinkend organisch materiaal claimen. Een aanwijzing voor een hogere reproductiesnelheid van epibenthische foraminiferen, en daarmee een grotere productie van foraminiferenschaaltjes, wordt gevonden in de in verhouding grote aantallen lege schelpjes van epibenthische soorten in het oppervlaktesediment, in vergelijking met de hoeveelheid levende exemplaren. Dieper in het sediment levende soorten zijn daarentegen vaak beter vertegenwoordigd in levende populaties dan in vergelijkbare dode associaties.

Als het hierboven gesuggereerde verband tussen verschillende kwaliteiten organisch materiaal en het voorkomen van epibenthische en endobenthische foraminiferen reëel blijkt, kan de verspreiding van deze groepen foraminiferen in fossiele sedimenten mogelijk gebruikt worden om de verticale en laterale organisch koolstofflux in het verleden te reconstrueren. Een belangrijk probleem daarbij is dat de indeling van foraminiferen als epibenthisch of endobenthisch problematisch is. De meeste algemeen voorkomende soorten in de Adriatische Zee worden levend in grootste aantallen gevonden dicht aan het sedimentoppervlak, maar komen ook - in afnemende hoeveelheid - dieper in het sediment voor. Een zeker onderscheid is wel mogelijk tussen soorten die zeer snel in aantal afnemen met diepte in het sediment, en soorten die meer geleidelijk in aantal afnemen. Eerstgenoemden zouden als hoofdzakelijk epibenthisch aangemerkt kunnen worden. Een beperkt aantal soorten wordt levend hoofdzakelijk dieper in het sediment aangetroffen, en kan met recht aangeduid worden als endobenthisch.

Behalve de voedselverdeling in het sediment speelt waarschijnlijk ook de zuurstofconcentratie een rol bij het bepalen van de verticale verdeling van foraminiferen. Endobenthische soorten mogen worden verondersteld in het algemeen beter bestand te zijn tegen lage zuurstofconcentraties, en de daarbij optredende biologische en chemische processen, dan veel epibenthische soorten. Dit steunt vooral op het feit dat de eerstgenoemden aangetroffen worden in diepere niveaus van het sediment, waar zuurstof schaars of zelfs geheel afwezig is. Epibenthische soorten houden zich meestal op in de doorgaans goed beluchte bovenste sedimentlaag, en zijn mogelijk slecht aangepast aan zuurstofarme omstandigheden. Wanneer de zuurstofconcentratie in het bodemwater en in het sediment daalt, zal dit vaak negatieve gevolgen hebben voor de epifauna, ondanks de vaak met lage zuurstof samengaande voedselrijkdom. Onder deze omstandigheden nemen lage-zuurstof-tolerante endobenthische soorten de plaats in van epibenthische foraminiferen. Onder aanhoudend zuurstofarme of zuurstofloze omstandigheden verdwijnen op den duur ook de meest resistente soorten.

Dit komt duidelijk naar voren uit de studie van twee sapropelen (sedimenten afgezet onder zuurstofarme condities) uit de Adriatische Zee en van een landsectie in Zuid-Italië.

Terwijl benthische foraminiferen in een belangrijk deel van beide sapropelen geheel afwezig zijn, worden op bepaalde niveau's opvallende soortenarme associaties aangetroffen. Deze associaties duiden op periodieke beluchting van het bodemwater, hetgeen mogelijk een gevolg was van afkoeling van het oppervlaktewater. Door middel van een modelsimulatie van de groei van foraminiferenpopulaties wordt geïllustreerd hoe regelmatige eliminatie van foraminiferenfauna's door aanhoudende zuurstofschaarste, gevolgd door snelle repopulatie tijdens verbeterde bodemwaterbeluchting, kan leiden tot dominantie van lage-zuurstof-tolerante opportunistische soorten.

De conclusie van dit onderzoek is dat schatting van tegenwoordige en vroegere flux van organisch koolstof bij de zeebodem, met onderscheid van relatief vers en gedeeltelijk afgebroken ouder materiaal, mogelijk is door het bepalen van aantallen levende of accumulatie van dode benthische foraminiferen in het sediment. Zuurstofarmoede in het bodemwater kan echter de normale patronen ingrijpend doen veranderen, waardoor betrouwbare schatting van organische flux niet onder alle omstandigheden mogelijk is.

DANKWOORD

Dit proefschrift vormt de weerslag van onderzoek, verricht in de jaren 1989 - 1993 aan de Faculteit Aardwetenschappen van de Universiteit Utrecht, met financiële steun van de Nederlandse Organisatie voor Wetenschappelijk Onderzoek (NWO). Aan de totstandkoming van dit proefschrift hebben een groot aantal mensen hun medewerking verleend, en ik wil hen hierbij nog eens speciaal bedanken voor hun grote en belangeloze inzet.

Om te beginnen mijn begeleider van het eerste uur, Johan Meulenkamp, die in de heuvels van Centraal Sicilië de eerste steen hakte waarmee mijn onderzoek zou beginnen, en die met wijze raad de voortgang van mijn onderzoek bespoedigde. Bert van der Zwaan begeleidde met enthousiasme en grote deskundigheid mijn paleoecologische studies, en heeft met grote volhardendheid aangedrongen op verdere publicatie van de resultaten. Frans Jorissen droeg bij aan mijn onderzoek met een mooie verzameling monsters uit de Adriatische Zee. Met groot enthousiasme voor microskopisch detail was hij gaarne bereid elke door mij gevangen foram nog eens drie keer om te draaien om tot een juiste determinatie te komen, maar daarnaast was hij ook een groot voorstander van pragmatische werkhypothesen, en een vlotte schrijver van verhalen.

Gert-Jan Reichart leverde met zijn doctoraalonderzoek aan Adriatische foraminiferen een bijdrage aan hoofdstuk 5 van dit proefschrift. Eelco Rohling schreef een belangrijk deel van hoofdstukken 7 en 8, en liet mij profiteren van zijn kennis op oceanografisch gebied. Willem Renema en Jelmer Cleveringa hebben dagenlang forams zitten pikken, kwamen met veel zinvolle suggesties, en droegen zeer bij aan het verlevendigen van mijn werkplek. Leonardo Langone, Joen Widmark, Ronald Zaalberg en Colette Vergnaud-Grazzini leverden eveneens bijdragen aan delen van dit proefschrift.

Voor goede microskopen en microskooplampen, essentieel bij het bestuderen van foraminiferen, en voor allerhande technisch advies, kon ik altijd terecht bij Gerrit in 't Veld en Geert Ittman. Arnold van Dijk en Gijs Nobbe hielpen met chemische analyses. Ank Pouw wil ik bedanken voor al het papierwerk rondom mijn promotie, en voor het ontmoedigen van mijn gebruik van fossiele tekstverwerkingsprogramma's. Tom van Hinte leerde mij tekenen met de computer, nog voor ik fatsoenlijk kon schrijven, en Wil den Hartog verzorgde de SEM foto's van foraminiferen. Dankzij de goede zorg van de medewerkers van de Aardwetenschappen bibliotheek in Utrecht, en de NIOZ bibliotheek op Texel, had ik toegang tot een ruim aanbod aan vakliteratuur.

Voor ideeën over benthische foraminiferen en nog veel andere zaken vond ik een luisterend oor en goede repliek bij mijn collega's Deddy Barmawidjaja, Rob Speijer, Neven Loncarić, Kati Baldi, en mijn leermeester op het gebied van planktonische foraminiferen, Jan Willem Zachariasse. Mijn dank betreft ook mijn Utrechtse collega's Jan van Dam, Lucas Lourens en Frits Hilgen.

Voor een zeer plezierige en buitengewoon leerzame tijd op Texel ben ik in de eerste plaats veel dank verschuldigd aan Tjeerd van Weering, die mij betrok bij het Ocean Margin Exchange (OMEX) project, en die hiermee mijn denken over organische fluxen in de oceaan zeer heeft beïnvloed. Het delen van een werkkamer en een computer met Henk de Haas is voor mij zeer voordelig gebleken, maar Henk heeft het vooral veel tijd gekost. In de wandelgangen van het NIOZ, en tijdens vaartochten op zee, heb ik veel geleerd van collega's waaronder Ellen Okkels, Wim Boer, Els Ufkes, Hauke Gipp, Geert Jan Brummer, Lutz Lohse, Eric Epping, Wim Helder, en vele anderen.

Familie en vrienden wil ik bedanken voor morele ondersteuning en voor het regelmatig doorbreken van inslijtende werksleur. Mijn schoonvader Ton Stephan hielp mij aan een goed werkende computer, en wist die op kritieke momenten ook draaiend te houden. Mijn vader zette zich in als leerling-forampikker, en hielp met het verbeteren van mijn engelse teksten. Ik wil dit boekje opdragen aan mijn vader en moeder, aan mijn zussen Hilde en Pien, en aan Erzsébet, voor alle gedeelde momenten van verwondering en enthousiasme over de prachtige schepping waarin wij mogen leven.

CURRICULUM VITAE

Hendrik Corstiaan de Stigter werd geboren op 18 november 1964 te Bennekom. In juni 1983 behaalde hij het diploma voor het Voortgezet Wetenschappelijk Onderwijs aan het Christelijk Streeklyceum te Ede. In de maand september van hetzelfde jaar begon hij zijn studie Geologie aan de Faculteit Aardwetenschappen van de Universiteit Utrecht. Het doctoraalexamen Geologie, met specialisatierichting Stratigrafie/Micropaleontologie, en bijvak Structurele Geologie, werd op 28 augustus 1988 behaald (cum laude). Van mei 1989 tot mei 1993 was hij als onderzoeker in opleiding verbonden aan de Vakgroep Geologie van de Faculteit Aardwetenschappen, Universiteit Utrecht. Sinds februari 1994 is hij betrokken bij het Ocean Margin Exchange (OMEX) program aan het Nederlands Instituut voor Onderzoek der Zee (NIOZ) te Texel, het eerste jaar als erkend gewetensbezwaarde militaire dienst, en daarna als projectmedewerker.