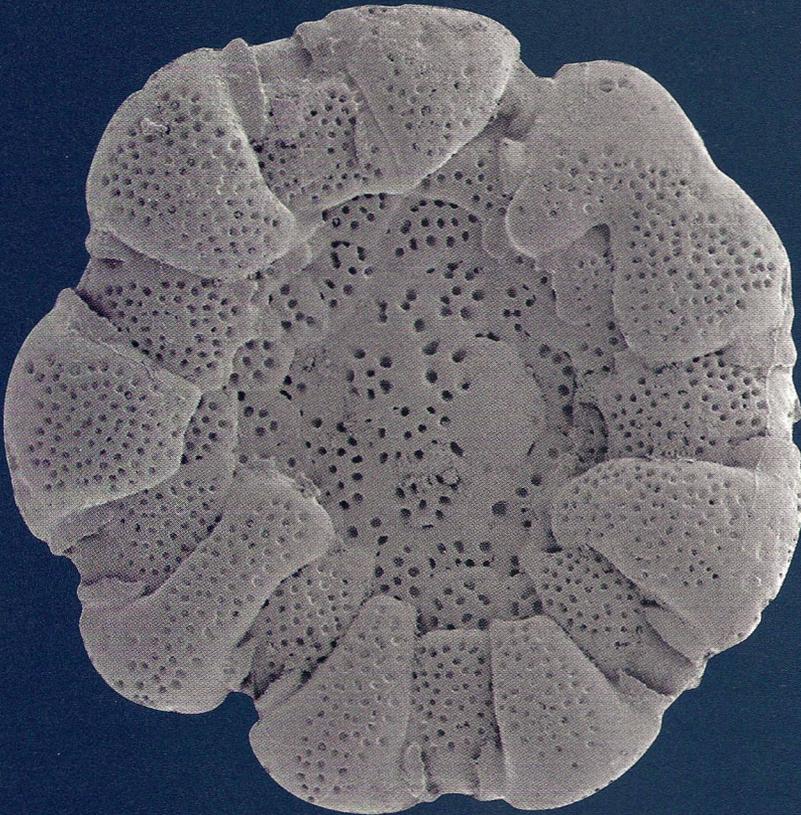


GEOLOGICA ULTRAIECTINA

Mededelingen van de
Faculteit Aardwetenschappen
Universiteit Utrecht

No. 203

Seasonality, biodiversity and microhabitats
in benthic foraminiferal communities



Natasja T. Jannink

G E O L O G I C A U L T R A I E C T I N A

Mededelingen van de
Faculteit Aardwetenschappen
Universiteit Utrecht

No. 203

Seasonality, biodiversity and
microhabitats
in benthic foraminiferal communities

Natasja T. Jannink

Promotores: Prof. Dr. G.J. van der Zwaan
Faculty of Earth Sciences, Utrecht University
Faculty of Biology, Nijmegen University

Prof. Dr. J.E. Meulenkamp
Faculty of Earth Sciences, Utrecht University

Co-promotor: Dr. A. Almogi-Labin
Geological Survey of Israel, Jerusalem

Front cover: Planorbulina mediterraneensis, d' Orbigny

Seasonality, biodiversity and microhabitats in benthic foraminiferal communities

Seizoensvariatie, biodiversiteit en microhabitats in
levensgemeenschappen van benthonische foraminiferen

(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. W.H. Gispen, ingevolge het besluit van het
College voor Promoties in het openbaar te verdedigen op
woensdag 2 mei 2001 des middags te 13.00 uur

door

Natasja Tamara Jannink

geboren op 29 januari 1972 te Hellendoorn

Members of the dissertation committee:

Prof. Dr. P.L. de Boer
Faculty of Earth Sciences, Utrecht University

Dr. A. Gooday
Southampton Oceanography Centre, Southampton, UK

Prof. Dr. C.H.R. Heip
NIOO-Centre for Estuarine and Coastal Ecology, Yerseke

Dr. F.J. Jorissen
Department of Geology and Oceanography, Bordeaux University

Prof. Dr. H. Visscher
Faculty of Biology, Utrecht University

ISBN: 90-5744-060-1

The research described in this thesis was carried out at the Institute of Paleoenvironments and Paleoclimate Utrecht (IPPU), Faculty of Earth Sciences, Utrecht University, Budapestlaan 4, P.O. Box 80021, 3508 TA Utrecht (The Netherlands), and at the Department of Biogeology, Faculty of Biology, Nijmegen University, Toernooiveld 1, P.O. Box 9010, 6500 GL Nijmegen (The Netherlands). Financial support was provided by the Netherlands Organisation for Scientific Research

(NWO, project 750.196.10A)

W

Contents

Chapter 1.	Introduction and summary	7
Chapter 2.	The seasonal dynamics of nutrient and chlorophyll-a concentrations on the SE Mediterranean shelf-slope.	11
Chapter 3.	Foraminiferal assemblages and diversity patterns along a depth transect off the Israeli coast (SE Levantine Basin).	25
Chapter 4.	Seasonal variation of benthic foraminiferal standing stocks in shallow water (40m) off the Israeli coast (SE Levantine Basin).	41
Chapter 5.	Life-strategies of shallow-water benthic foraminifera in the SE Levantine Basin.	57
Chapter 6.	Seasonal abundances and in-sediment distribution of benthic foraminifera living at a neritic station (120m) of the Israeli coast.	77
Chapter 7.	A seasonal study on patchiness of benthic foraminiferal assemblages at three adjacent stations (120m).	95
Chapter 8.	Foraminiferal patterns in two tropically different regions: the northern Adriatic Sea and the southern Levantine Basin.	105
Chapter 9.	A food-experiment with oligotrophic benthic assemblages: preliminary results.	125
Chapter 10.	Living (Rose Bengal stained) benthic foraminifera from the Pakistan continental margin (northern Arabian Sea).	135
Chapter 11.	A transfer function for the quantitative reconstruction of oxygen contents in marine paleo-environments.	161
Chapter 12.	Synthesis	171
	References	178
	Samenvatting in het Nederlands	185
	Dankwoord (Acknowledgements)	189
	Curriculum vitae	191

Chapter 1

Introduction and summary

Benthic foraminifera (Protista: Sarcodina) are one-celled organisms that are widely spread over the worlds' oceans. Most of the species can be distinguished by the morphology of their shell, and the high preservation potential of these shells makes them a useful tool to date sediment layers and reconstruct ancient environments. The latter, however, requires sufficient insight in the ecology.

After decades of research on the ecology of benthic foraminifera, still more questions than answers exist. Nevertheless, the last few years we seem to have come closer to some answers through experimental and monitoring studies. Whereas experiments are useful because of the possibility to standardise environmental parameters, monitoring studies are valuable because of repetitive sampling during one or several years. These time series provide us with knowledge on how foraminiferal communities change during the seasons, and develop over the years. With the repetitive sampling of several stations situated within one region we also gain insight in differences in foraminiferal community structures over distance.

In a monitoring study of the northern Adriatic Sea, Barmawidjaja et al. (1992) found large seasonal changes in foraminiferal abundances and in-sediment distribution. The combination of food flux and especially oxygenation of the sediment, was found to play a major role in the foraminiferal community structures. In 1995, Jorissen et al. presented the TROX-model, which describes the foraminiferal assemblages in the light of these two major controlling factors, food and oxygen.

To further unravel the importance of food and oxygen in benthic foraminiferal communities, a rather large-scale monitoring project was started in 1996. This project regarded two completely different regions within the Mediterranean Sea, the eutrophic Adriatic Sea and the oligotrophic Levantine Basin. In the Levantine basin, where nutrient levels are known to be low, the stability of the environment was expected to be relatively high. This in contrast with the Adriatic Sea, from which we knew that environmental circumstances change drastically throughout the year, which is reflect by the foraminiferal abundances (Barmawidjaja et al. 1992). In order to study seasonal changes in the foraminiferal communities both study areas were monitored bi-monthly between June '96 and June '98.

In the Levantine basin, we studied a down-slope transect perpendicular to the Israeli coast from 40 to 700m water depth. Several oceanographic properties (chlorophyll-a, temperature, salinity, and dissolved oxygen) were measured simultaneously with the sampling of sediments. The sediment oxygenation was measured in detail and living (Rose Bengal stained) benthic foraminifera were collected.

In Chapter 2, we present oceanographic data obtained at two sample stations S3 (120m) and S7 (400m) throughout the two years of monitoring. Each year in autumn, cooling of surface waters and strong winds cause mixing of the water layers. Through this mixing, nutrients are brought up from deeper water layers, eventually causing a relative peak in chlorophyll-a concentration. The (yearly) cyclicity of the system was clearly visible; during winter, clear peaks in chlorophyll-a concentrations were found above both stations, with the highest concentrations measured above station S3. In the euphotic zone, the integrated NO_3^- values were found to be opposite to the chlorophyll-a concentrations. The $\text{NO}_3^-/\text{PO}_4^{3-}$ ratios varied seasonally with low ratios during autumn and winter, and somewhat higher ratios during spring and summer. The euphotic waters were found to be N-limited during our monitoring period, instead of P-limited as was found during earlier studies.

An overview of the Levantine foraminiferal assemblages found at three downslope stations is presented in Chapter 3. The assemblages in the top 1cm sediment layer were found to be very different. The average abundance at the shallowest station was more than twice the average number of living foraminifera at station S3 (120m). At the deepest sample station (S9; 700m) densities were ten times lower than at the shallowest station S1.

Whereas a clear seasonal pattern was found in the total standing stocks of foraminifera at station S1 and S9, no such pattern could be distinguished in the total standing stocks at station S3. At stations S1 and S9, the seasonality was expressed in low numbers during autumn and beginning of winter, and relative higher standing stocks in spring and summer. Besides the differences in abundances downslope, a clear shift in the larger foraminiferal groups (perforate calcareous, miliolids, and agglutinants) was visible. The miliolids were very abundant at the shallowest station, but their densities decreased strongly downslope.

The foraminiferal standing stocks and in-sediment (vertical) distributions versus organic enrichment and oxygenation of the sediment at station S1 (40m), are discussed in Chapter 4. The foraminifera at this shallow sample station showed an (indirect) numerical response after increased primary productivity. Their in-sediment distribution seemed influenced by the oxygenation of the sediment, that changed drastically throughout the year. The delayed numerical response of the foraminifera, 2-4 months after increased organic matter influx, was most likely due to the interference of macrofauna (opportunistic tube worms) occurring very abundantly after increased primary productivity. Only after retreat of these tubeworms in spring, peak abundances of foraminifera were found.

In Chapter 5, the microhabitat partitioning of the most abundant species at station S1 (40m) are discussed in detail. The life strategy of epifaunal taxa is characterised by constant shallow in-sediment distribution and strong numerical response after organic enriched periods. The shallow infaunal species (e.g. bolivinids) were generally found dispersed over the 2cm sediment layer and the fluctuations in their overall low abundances showed no clear seasonal pattern. The deeper infaunal species displayed a stable (deeper) in-sediment position, even under anoxic circumstances. In spite of their deeper microhabitat, some infaunal taxa clearly reacted to increased organic matter concentrations.

The microhabitat partitioning of foraminifera as found at Levantine station S₃ (120m) was far less clear than in shallower water (Chapter 6). Although it was still possible to distinguish the more epifaunal and deeper infaunal species, no clear shallow infaunal group could be identified. The deeper oxygenation of the sediment at station S₃ could very well be the reason for this. Overall, the in-sediment distribution of foraminifera did not show an evident correlation with sediment oxygenation. The numerical response of the foraminifera was directly correlated with the periods following increased organic influx. Almost no macrofauna was present at S₃. The epifaunal species reacted most strongly to organic enrichment, whereas the deeper infaunal species showed a more stable abundance pattern throughout the years. Some deeper infaunal species (e.g. *Eggerella* spp.), however, displayed a numerical response after organic enrichment. Combining the results for the two stations S₁ and S₃, we suggest that these taxa probably reproduce in the top sediment layer, after which they disperse throughout the sediment again.

In Chapter 7 foraminiferal data from three adjacent stations (situated at 120m) is compared. The aim of this study was to get a grip on the phenomenon of spatial distribution, and to check whether seasonal differences and patchiness among the stations could blur the overall (yearly) foraminiferal signal. Through time large numerical differences were found between the stations, but the average numbers of the most abundant taxa over the years were quite similar. This may indicate that the effect of patchiness cannot be neglected on smaller time-scales, but becomes irrelevant on longer time-scales.

In Chapter 8 the foraminiferal communities as found in the northern Adriatic Sea are compared with the communities of the southern Levantine Basin. Although the trophic regimes in these areas are quite different, the standing stocks of foraminifera were found to be within the same range, suggesting that the amount of organic matter supply was not the major driving factor in this respect. It seems that the balance between food and oxygenation of the sediment probably was the important factor in both systems. The species diversity of the Adriatic Sea foraminiferal assemblages was much lower than the species diversities in the Levantine assemblages. The foraminiferal assemblages obtained from both regions had a lot of taxa in common. Comparison of the occurrences of five representative taxa show strong resemblances for both regions, implying that the microhabitat partitioning of these species is not so much dependent on their environment but probably inherent to the taxa themselves. For most of these taxa no clear correlation was found between the sediment oxygenation and their in-sediment distribution: only miliolids appeared to be strongly dependent on the oxygenation of the sediment.

In an experiment, food was added to part of the microcosms with benthic foraminifera obtained from the oligotrophic Levantine basin, while other microcosms were used as controls. The preliminary results (Chapter 9) indicate that the addition of food induced no clear increase in foraminiferal numbers. However, after calculations of the food mixture in terms of organic matter flux, the amount that was added turned out to be lower than the amount that probably arrives at the seafloor after productive periods. The concentration of the food-mixture may therefore not have been high enough to trigger foraminiferal reproduction.

Off the Pakistan margin (Indian Ocean), two transects were sampled, from within the Oxygen Minimum Zone (OMZ) to about 1500-2000m of water depth. The foraminiferal communities found at the sample stations changed drastically downslope (Chapter 10). The foraminiferal assemblages occurring within the OMZ were characterized by high abundance but low species diversity. Downslope the foraminiferal abundances decreased and the species diversities increased. At both transects the foraminiferal communities showed similar species distributions, in the $>63\mu\text{m}$ as well as the $>150\mu\text{m}$ size fraction, and displayed comparable in-sediment distributions. The fact that many foraminifera are able to persist under suboxic to anoxic circumstances indicates that oxygen is not a limiting factor for this group. The downslope species distributions as found for both transects was probably influenced by the amount or type of organic matter. The high foraminiferal abundances within the OMZ could also be due to the low predation pressure there.

In Chapter 11, a transfer function for quantitative reconstruction of oxygen concentrations in marine paleo-environments is presented. Foraminiferal data obtained from four very different regions (Bay of Biscay, Indian Ocean, northern Adriatic Sea and the Levantine basin) indicate that a specific group of benthic foraminifera is apparently oxyphilic. The abundances of these species are found to co-vary linearly with the oxygen content at the sediment-water interface. Application of the transfer function to the foraminiferal patterns in a core from the Adriatic Sea resulted in an accurate reconstruction of the oxygen concentrations over the past 160 years.

The seasonal dynamics of nutrient and chlorophyll-a concentrations on the SE Mediterranean shelf-slope

With: Barak Herut, Ahuva Almogi-Labin, and Isaac Gertman

Published in: Oceanologica Acta 23, (2000): 771-782

Abstract

We report the results of a sequence of twelve research cruises over a two-year period, from June 1996 through May 1998, that examined the seasonal variations in the nutrient (NO_3^- , PO_4^{3-} and $\text{Si}(\text{OH})_4$) and the chlorophyll-a concentrations at two permanent stations across the SE Mediterranean continental shelf and slope (120 and 400 m water depth off the Israeli coast). Seasonally-dependent chlorophyll-a concentrations ranged between 0.003 and 0.415 mg m^{-3} . Following autumn and winter a distinct biomass phytoplankton peak was produced ($\sim 30 \text{ mg chl-a m}^{-2}$ in the upper 120 m) and a subsequent moderate spring peak was observed. In the decomposition zone (120-400m), an opposite pattern was observed with decreasing amounts of NO_3^- and PO_4^{3-} during winter. The integrated $\text{Si}(\text{OH})_4$ pattern in the euphotic zone indicates that diatoms grow during spring and summer and that their frustules are rapidly settled during the breakdown of stratification. At depths between 150 to 400 m, the geometric mean $\text{NO}_3^-:\text{PO}_4^{3-}$ ratio (~ 24) was significantly higher than in the upper 150m (~ 7), where it varies seasonally with low ratios (3, 5) during fall and winter compared to summer and spring (9, 11). At the present time, it is not possible to reconcile the relatively low (<16) $\text{NO}_3^-:\text{PO}_4^{3-}$ ratios and apparent N dependence in the euphotic zone with the high (>20) ratios of exogenous upwelling and atmospheric inputs. The determination of the possible presence of additional nutrient phases and preferential uptake of nutrients by the phytoplankton is an important next step toward the understanding of nutrient limitation in such ultra-oligotrophic systems.

1. Introduction

Many studies have found evidence of extremely low nutrient concentrations and of exceptionally oligotrophic conditions in the waters of the central Levantine Basin (Berman et al., 1984, Berman et al., 1985, Dowidar, 1984, Krom et al., 1991, Krom et al. 1992, Krom et al., 1993, Salihoglu et al., 1990, Yacobi et al., 1995). These conditions have also been observed in the coastal waters of the SE Mediterranean (Abdel-Moati, 1990, Azov, 1986, Berman et al., 1986, Gitelson et al., 1996). In both areas, the chl-*a* concentrations were below 0.9 mg m^{-3} (Azov, 1986, Berman et al., 1984, Krom et al., 1992, Krom et al, 1993, Yacobi, et al, 1995). A deep chl-*a* maximum (DCM) develops between 75 and 150 m, which is typical of oligotrophic waters (Abdel-Moati, 1990, Berman et al., 1984, Dowidar, 1984, Kimor et al, 1987). The DCM has a regular distribution across the basin during summer and is not significantly affected by physical oceanographic structures (Yacobi et al. 1995). Remote sensing studies using the coastal zone color scanner showed some interannual and seasonal variations, but the different studies reported different patterns, probably as a result of the use of different algorithms to process the data (Antoine et al., 1995, Van Dijken and Arrigo, 1996).

Several studies have used the element ratios of dissolved nutrients (N, P and Si) in marine environments in order to determine which element might be limiting phytoplankton growth (Codispoti, 1989, Dortch and Whiteledge, 1992, Fanning, 1992, Justic et al., 1995, Krom et al., 1991). In the SE Mediterranean, Krom et al. (1991) found unusually high (>27) $\text{NO}_3^-:\text{PO}_4^{3-}$ ratios, and PO_4^{3-} (as compared to NO_3^-) was preferentially removed from the upper water column. They suggested that the productivity in that region might be limited by the availability of phosphorus (P). Nutrient enrichment experiments showed that P rather than N was the limiting nutrient for bacterial activity (Thingstad and Rassoulzadegan, 1995, Zohary and Robarts, 1998). The cause of this P-limitation and of the unusually high $\text{NO}_3^-:\text{PO}_4^{3-}$ ratios in the deep Eastern Mediterranean is still not known. However, up to now, no assessment of nutrient element ratios has been done for the pelagic waters across the continental shelf and slope of the SE Mediterranean.

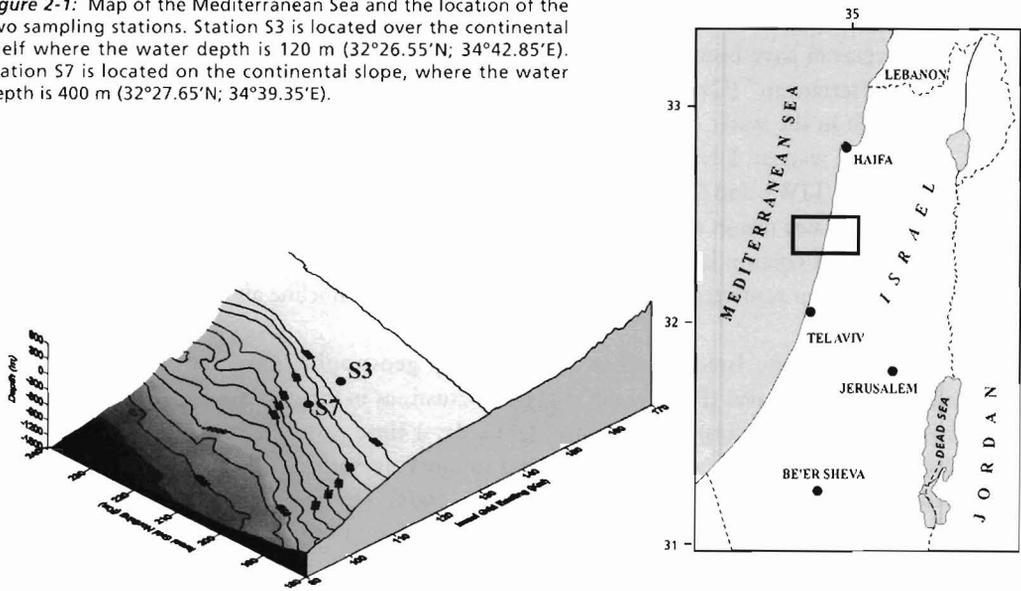
Krom et al. (1991) hypothesized that the P-limitation was due to the removal of PO_4^{3-} by adsorption on dust particles. Recently, it was estimated that this adsorption process can not explain such phosphate “deficits” (Herut et al., 1999a) and that the atmospheric input of N and P to this region reinforces the unusual $\text{NO}_3^-:\text{PO}_4^{3-}$ ratios (Herut et al. 1999a). Other theories suggested were nitrogen fixation (Bethoux et al., 1998) and NO_3^- enriched waters of Adriatic origin forming the deep Eastern Mediterranean waters (Civitarese et al., 1998).

Although water chemistry of the SE Mediterranean Sea has undoubtedly changed since the construction of the High Aswan dam in 1965 and the consequent drastic decrease in nutrients supplied

Table 2-1: Cruise dates arranged by the season of the year. Dates given as DD.MM.YY.

Summer	25.6.96	28.8.96	24.6.97	3.9.97
Fall	17.10.96	2.11.97		
Winter	24.12.96	5.2.97	14.1.98	2.3.98
Spring	6.5.97	17.5.98		

Figure 2-1: Map of the Mediterranean Sea and the location of the two sampling stations. Station S3 is located over the continental shelf where the water depth is 120 m (32°26.55'N; 34°42.85'E). Station S7 is located on the continental slope, where the water depth is 400 m (32°27.65'N; 34°39.35'E).



by the Nile outflow (Milliman, 1991), data that might document these long-term changes in the neritic and pelagic zones of this region are scarce. Prior to construction of the dam, the Nile floods peaked between August and October (Sharaf El Din, 1977) and triggered a major phytoplankton bloom off the Egyptian coast (Dowidar, 1984). A coincident phytoplankton bloom was also observed in the nearshore waters along the coast of Israel and Lebanon (Oren and Komarovskiy, 1961). Since 1965, according to Schneller et al. (1984), Berman et al. (1986), and Azov (1986), the seasonality of the phytoplankton blooms has changed to the winter-spring period. However, the existing data do not permit a detailed analysis of seasonal or time series changes of the nutrient and chl-a concentrations.

In order to address some of these problems, we developed a study to examine in detail the seasonal vertical distributions of nutrients and chl-a, as well as the physical properties of the water column, at two permanent stations off the Israeli coast (SE Mediterranean). A map with the sampling localities is shown in Figure 1. The stations were visited bi-monthly during two consecutive years, from June 1996 to May 1998. The aims were: (1) to determine the seasonal variations of the nutrient and chl-a profiles in the water column; (2) to examine the relationships between the nutrient and the chl-a concentrations; and (3) to examine the seasonal variations in the $\text{NO}_3^-:\text{PO}_4^{3-}$ ratio.

Hydrographic background

The extreme nutrient-depletion of the Eastern Mediterranean is apparently caused by the anti-estuarine circulation, which transports the deep-water nutrients from the Mediterranean into the

North Atlantic (Bethoux et al., 1998). The circulation patterns and water mass characteristics of the Eastern Mediterranean have been studied as part of the research initiative “Physical Oceanography of the Eastern Mediterranean” (Ozsoy et al., 1993, POEM group, 1992). Based upon the variations of salinity with depth in the water column, Hecht et al. (1988) identified four different water masses in the SE Levantine waters: Levantine Surface Water (LSW), Atlantic Water (AW), Levantine Intermediate Water (LIW), and Deep Water (DW).

The two upper water masses show seasonal variations in their properties. The upper 100 m (LSW and AW) of the water column is well mixed during winter, but stratified during the remainder of the year, with a mixed layer restricted to the upper 25 m and a sharp halocline and thermocline below the mixed layer.

The circulation on the Israeli shelf is dominated by geostrophic currents, which are mainly northward, and by shelf waves (Rosentraub, 1995). Fluctuations in the currents occur on both diurnal (from variations in sea breezes) and synoptic (3–14 days) time scales. The strongest currents are predominantly northward and occur in winter and summer. In spring and autumn, the currents are weaker and alternate from north to south (Rosentraub, 1995). During summer, the relatively strong but variable currents are confined to the upper layer and increase in intensity towards the continental slope to average speeds of 40 cm s^{-1} . In the winter period when there is mixing, the distribution of the currents is uniform throughout the water column.

2. Sampling and methods

The fieldwork for this study was conducted during twelve cruises on the R/V Shikmona, under the auspices of the Dutch-Israeli LEV project. The cruises took place bi-monthly, and each cruise visited the two permanent sampling stations which had been established for the project (Figure 1). The water depths, latitudes and longitudes for these stations are given in the caption of Figure 1. The dates of the cruises and their seasonal category are given in Table 1.

During each visit to the stations, water samples were collected with twelve 1.7 L Niskin bottles mounted on a General Oceanics Rosette. At the same time, a Sea-Bird SBE 9+ electronic CTD was used to obtain continuous vertical profiles of temperature (T), salinity (S) and oxygen. The bottles were closed at depths determined from the temperature and salinity profiles.

Immediately after the rosette was hauled aboard, sample aliquots were taken from each Niskin bottle for analyses of dissolved oxygen, nutrients ($\text{NO}_3^- + \text{NO}_2^-$, PO_4^{3-} and $\text{Si}(\text{OH})_4$) and chl-*a*. The dissolved oxygen samples were preserved. The nutrient aliquots were divided into triplicate samples and stored in 15 mL plastic scintillation vials that had been prewashed with 10% hydrochloric acid and rinsed three times with the sample prior to being filled. The nutrient samples were then immediately frozen (-18°C). For chl-*a* analyses a 400 mL aliquot from each Niskin bottle was pre-filtered through a $63 \mu\text{m}$ sieve and then filtered using glass fiber filters (GF/F). The filters were folded and packed in Al foil and immediately frozen (-18°C). During the last 7 cruises, in addition to the continuous CTD oxygen profile obtained on-station, oxygen measurements were carried out using the Carpenter-Winkler titration procedure (Carpenter, 1965) and a Radiometer Automatic Titrator

(TTT80) equipped with a dead-stop end point dual platinum electrode. The precision for these measurements was 0.4%. The two methods of measurement gave similar results ($\pm 2\%$), except for two cruises (May '97 and June '97) in which we used the titration values to correct the CTD data (by approximately 10%).

The amount of chl-a in each filtered sample was determined using acetone extraction and fluorometric measurements following the procedure developed by Holm-Iansen et al. (1965). The fluorometer has a detection limit of $0.1 \mu\text{g L}^{-1}$ that corresponds to a seawater concentration of $1.2 \text{ ng chl-a L}^{-1}$. Nutrient concentrations were determined in the laboratory using a segmented-flow, Technicon Autoanalyser II (AA-II) system following the methods described by Krom et al. (1992, 1993). The limit of detection for these procedures was defined as equal to 2 times the standard deviation of the blank. Our values for the detection limits were $0.05 \mu\text{M}$ for $\text{NO}_3^- + \text{NO}_2^-$, $0.008 \mu\text{M}$ for PO_4^{3-} , and $0.3 \mu\text{M}$ for Si(OH)_4 . The analytical precisions for $\text{NO}_3^- + \text{NO}_2^-$, PO_4^{3-} and Si(OH)_4 were $0.02 \mu\text{M}$, $0.003 \mu\text{M}$, and $0.06 \mu\text{M}$, respectively. In this paper, we refer to $\text{NO}_3^- + \text{NO}_2^-$ as NO_3^- .

3. Results

3.1 Physical structure of the water column

Because of its water depth (400 m), station S7 usually contained the complete range of the different water masses found in the Levantine Basin, including the Levantine surface water (LSW), the Atlantic water (AW), the Levantine intermediate water (LIW), and the uppermost zone of the deep water (DW). As discussed by Hecht et al. (1988) and also found here, each of these water masses is defined by a typical T-S shape diagram. The seasonal T and S depth profiles indicate that both the vertical and the lateral distribution of the three upper water masses changes seasonally and annually (Fig. 2).

At station S7 as well as S3 (120m), the mixed surface layer is approximately 20 m thick in summer, with a minimum thickness of ~ 13 m. In winter, it reaches a maximum depth of ~ 150 m (Fig. 2). The seasonal thermocline is usually located between 20 and 80 m, below the top of the mixed layer and above the weak permanent thermocline. During fall and winter, cooling and strong winds cause gradual convective mixing; they progressively erode and deepen the seasonal thermocline and halocline until these disappear during the height of winter (Fig. 2). The seasonal T-S variations have a characteristic pattern, with a wider range of temperatures and salinity during summer and fall than during winter and spring. Because of increased evaporation in summer, the AW is overlain by the saltier and warmer LSW. In the winter, AW cannot be distinguished from LSW, which progressively thins as winter proceeds.

During winter, the dissolved oxygen concentration profile was constant in the upper ~ 150 m of the water column, and decreased to a constant value ($\sim 6 \text{ mg L}^{-1}$) between 150 and 400 m. This decrease is characterized by three steps, between ~ 150 and 180 m, between 180 and 270 m, and between 270 and 330 m. In spring, a small maximum of dissolved oxygen ($\sim 7.4 \text{ mg L}^{-1}$) was detected between 30 and 80 m. During summer, it increased to a maximum value of $\sim 8 \text{ mg L}^{-1}$ at ~ 80 m water depth. Also

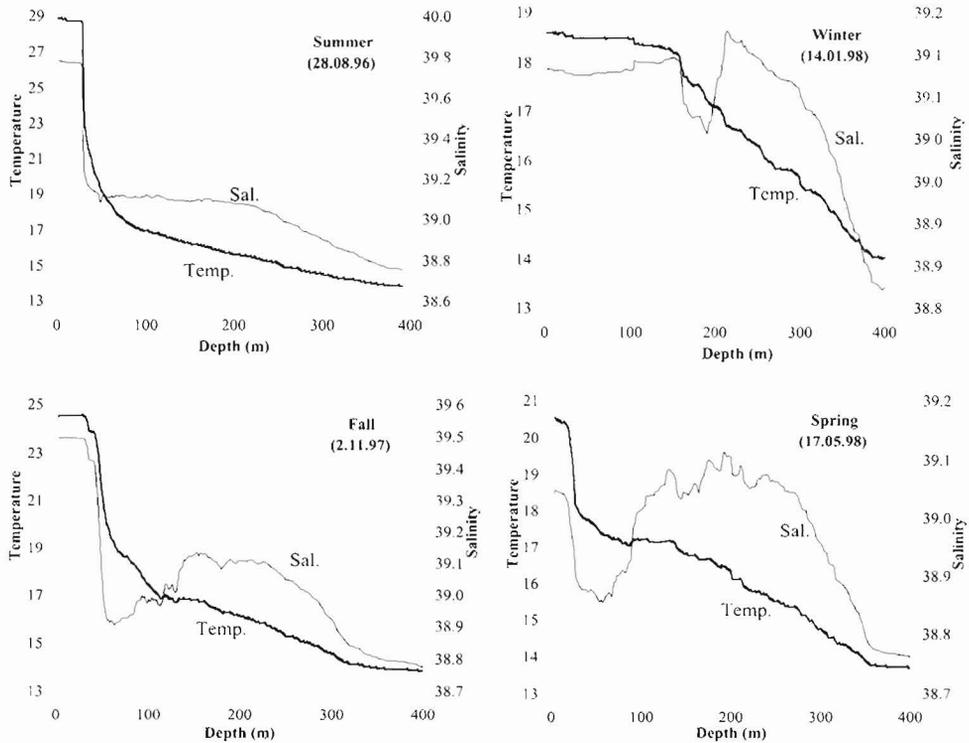


Figure 2-2: Representative seasonal vertical profiles of temperature (°C) and salinity (psu) at station 57.

in summer, the gradient beneath the oxygen maximum at ~80 m is steeper down to ~150 m depth. In fall, the well-established oxygen maximum starts to erode; this results in a shallower gradient between 150 and 400 m, similar to that observed during other seasons. In general, the oxygen profile was opposite to the nutrient profile (discussed below). During winter and spring, the highest dissolved oxygen concentrations were observed in the LSW and AW masses.

3.2 Nutrients

Our results show that the dissolved nutrient concentrations (PO_4^{3-} , NO_3^- and $\text{Si}(\text{OH})_4$) have a characteristic vertical profile, with low values in the upper water column between 0 and roughly 150–200 m depth. Nutrient values vary from below the detection limit to 0.09, 0.9 and 2.5 μM , respectively (Fig. 3). The nutricline becomes evident at 150–200 m depth, and nutrient concentrations increase to maximal values of 0.29, 6.12 and 16.0 μM respectively, at about 400 m water depth (Fig. 3). The nutricline shifts to shallower depths in summer (~150 m) than in winter and fall (~200 m), with generally higher nutrient concentrations in the decomposition zone (120–400 m) during summer.

The depth-integrated concentrations of $\text{Si}(\text{OH})_4$, PO_4^{3-} and NO_3^- in the upper 120 m layer (i.e.,

the euphotic zone; Parsons et al., 1977) varied from values near the detection limits up to maximum concentrations of 220, 5 and 50 mmole m^{-2} , respectively (Fig. 4). Generally, the data from station S₃ and the data from the more scattered sampling intervals in the upper 120 m of station S₇ show a similar pattern (Fig. 4). The depth-integrated concentration of Si(OH)_4 in the upper 120 m layer was higher during winter and fall and lower during spring (Fig. 4). We also detected quite low concentrations during the summer and fall, except during September 1997.

The PO_4^{3-} concentration in the euphotic zone showed no specific seasonal behavior in the first year; during the second year it reached maximum values in fall and winter. The NO_3^- concentrations were lowest from late fall through early winter and highest during spring and summer. In general, the neritic (S₃) and pelagic (S₇) waters had similar seasonal variations in their NO_3^- and Si(OH)_4 concentrations and differences in their seasonal concentrations of PO_4^{3-} .

Nutrient concentrations in the decomposition zone between 120 and 400 m were low during winter, after the convective mixing period. The nutrient concentration increased from the end of the winter until the end of the summer (Fig. 5). The PO_4^{3-} had an additional decline in September 1997.

Both nutrient species had similar absolute values during winter, but the stratification of the water column during the other seasons probably enhanced the decomposition of 'trapped' organic matter in the upper 120-200 m, and this is reflected by the higher nutrient integrated values (Fig. 5).

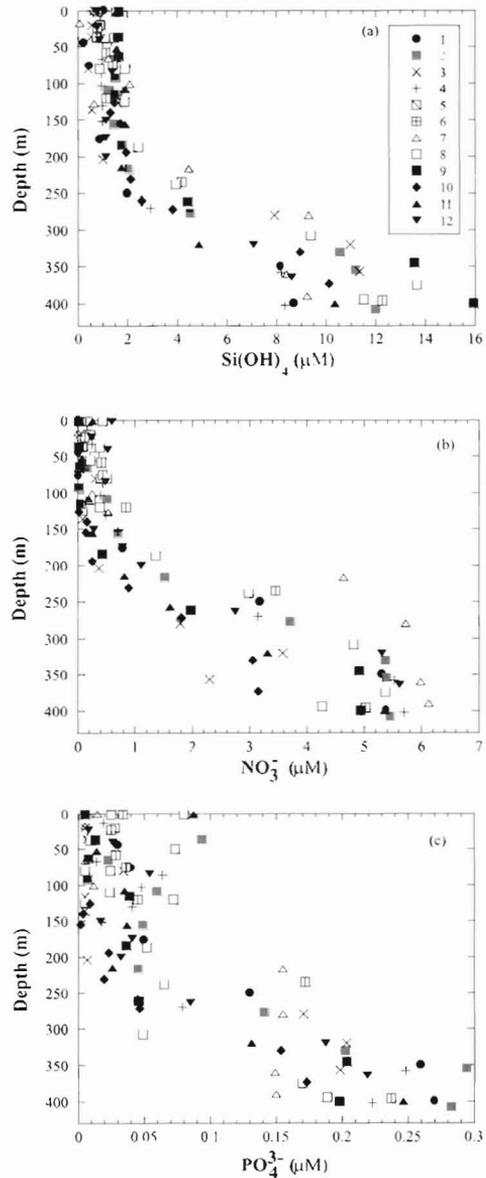


Figure 2-3: Vertical profiles of (a) Si(OH)_4 , (b) NO_3^- and (c) PO_4^{3-} concentrations (μM) at station S7 during 12 consecutive cruises: cruises 1 and 2 took place during fall (17.10.96 and 2.11.97); cruises 3 and 4 during spring (6.5.97 and 17.5.98); cruises 5 through 8 during summer (25.6.96, 28.8.96, 24.6.97, and 3.9.97); and cruises 9 through 12 occur during winter (24.12.96, 5.2.97, 14.1.98 and 2.3.98).

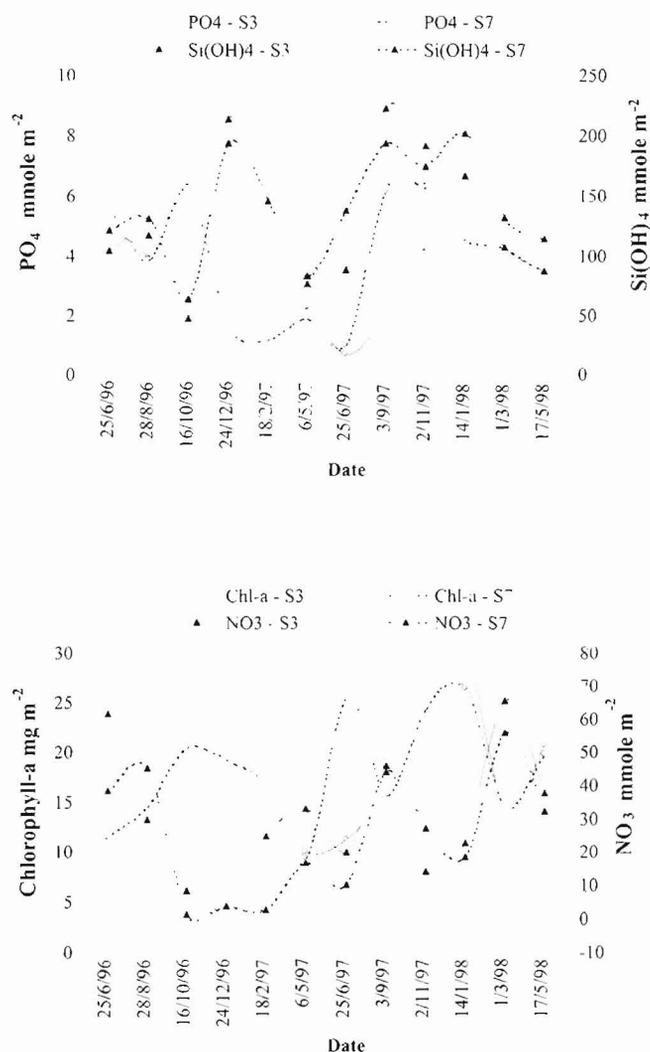


Figure 2-4: The depth-integrated concentrations (0-120 m, euphotic zone) of Si(OH)₄, NO₃⁻, PO₄³⁻ and chl-a over two annual cycles at stations S3 and S7.

3.3 Chlorophyll-a

Chl-a concentrations vary seasonally, and they range between 0.003 and 0.415 mg m⁻³, similar to chl-a concentrations in other areas of the Levantine Basin (Berman et al., 1986, Gitelson et al., 1996, Yacobi et al., 1995). We found the most pronounced seasonal differences in the surface water (Fig. 6), where chl-a concentrations were 2-5 times higher during fall and winter (mean values of 0.13 and 0.14 mg m⁻³) compared to summer and spring (mean values of 0.03 and 0.04 mg m⁻³). The chl-a vertical profile and the depth of the DCM vary seasonally at both stations. During winter, chl-a was more evenly distributed in the upper ~150 m of the water column (Fig 6). During spring and summer, a DCM was established, which was most pronounced between 100-120 m water depth. During fall, the DCM shifted upwards to water depths of approximately 80 m (Fig. 6). As shown in Figure 4, the depth-integrated values of chl-a ranged between 10 and 30 mg m⁻² in the upper 120 m and between 20 and 38 mg m⁻² in the upper 200 m. These values are similar to those for the upper 200 m of the Levantine Basin

(Yacobi et al., 1995). The integrated chl-a content in the euphotic zone (upper 120 m) was seasonally dependent, with fall and winter values higher by approximately a factor of 3 compared to summer values. Additional chl-a peak was detected during Spring 1997 and 1998 at station S7 (Fig. 4).

4. Discussion

During fall and winter, the water column in this region cools down and becomes mixed to a water depth of about 150 m (Fig. 2). This is thought to cause a significant input of nutrients into the euphotic zone from the water layers below. These nutrients are quickly consumed and produce a phytoplankton peak during winter time (Fig. 4). A similar seasonality has been observed in the boundary zone of the Cyprus Eddy in the eastern Mediterranean (Krom et al., 1992, 1993). There, increases in biomass during the winter (February) are related to a phytoplankton bloom of 44 mg chl-a m⁻², while in summer the concentration decreased to 10-13 mg chl-a m⁻². Our data show that the annual cycles of NO₃⁻ and PO₄³⁻ in the decomposition zone (120-400m) were opposite to the cyclicity in the overlying water. The lowest concentration of nutrients was observed during winter and coincided with a chl-a maximum in the upper water column (Fig. 4). A

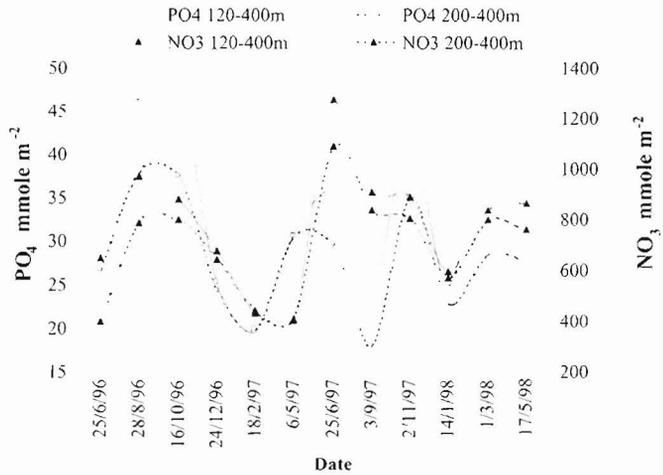


Figure 2-5: The depth-integrated concentrations (at 120-400 or 200-400 m, decomposition zone) of NO₃⁻ and PO₄³⁻ over two annual cycles at stations S7.

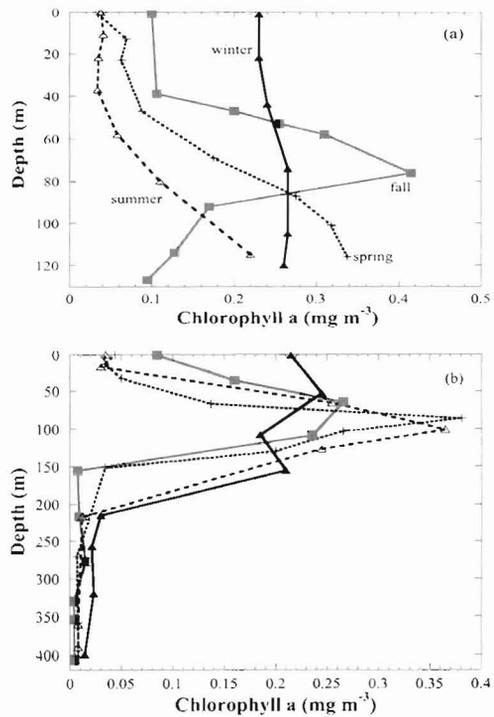


Figure 2-6: Representative seasonal vertical profiles of chl-a concentrations at stations (a) S3 and (b) S7.

moderate chl-a peak (upper 120 m) was observed at both stations during the spring of 1998. During 1997, we observed a similar increase in chl-a only in the offshore station (S7). This may be related to local in-offshore variability.

In the euphotic zone, the integrated NO_3^- values are generally opposite to those of the chl-a, and both are unrelated to the variability of PO_4^{3-} and Si(OH)_4 (Fig. 4). The concentrations of PO_4^{3-} vary interannually, but with no specific seasonal pattern in the first year. In the second year, PO_4^{3-} was low in late winter-spring and high during fall-early winter. This PO_4^{3-} behavior is not clear and might reflect a transfer or storage of dissolved P between/within different phases that were not measured in this study (i.e., dissolved organic P, adsorbed P, particulate P).

The Si(OH)_4 annual variability might reflect diatom blooms during periods of low silica concentrations and the settling of diatom frustules before periods of high silica peaks (Fig. 4). Some diatom species in the eastern Mediterranean (Kimor et al., 1987; Ignatiades et al., 1995) show a distinct adaptation to stratified oligotrophic waters (Abdel-Moati, 1990; Goldman, 1993; Villareal, 1991). The rapid silicate buildup in the euphotic zone (see slopes in Fig. 4) may represent a period of massive diatom sinking within the annual cycle. This generally occurs in the fall-winter (Sancetta et al., 1991). Thus, during spring and summer when the water column is stratified, diatom growth might occur, while during the breakdown of stratification by the winter mixing, the diatom growth filters followed by diatom deposition. High Si(OH)_4 concentrations were observed in September 1997 (Fig. 4), indicating a possible earlier diatom deposition event that may be related to unusual high salinity and temperature values and their depth profiles (Fig. 2). Both profiles of salinity and temperature suggest some breakdown of stratification.

To assess the export flux of diatoms (or associated organic carbon), we assumed that the difference of Si(OH)_4 between the spring/summer periods and the fall (when the highest values occur) represent the mass of precipitated diatoms. Using a biogenic Si:C ratio of 0.36 ± 0.1 in the DCM of the SE Mediterranean (Abdel-Moati, 1990), which exceeds the typical diatom ratio of 0.14 (Brezekinsky, 1985), and assuming that the integrated Si(OH)_4 increase of $\sim 130 \text{ mmole Si m}^{-2}$ (Fig. 4) represents the annual event of fast deposition, this mass is roughly $\sim 4.3 \text{ g C m}^{-2} \text{ yr}^{-1}$. Kemp et al. (1999) suggested that such rapid, massive annual deposition of diatoms is the main mechanism for the formation of Mediterranean sapropels in the late Quaternary. Assuming that the sum of the chl-a integrated values over an annual cycle represents the total phytoplankton load, the first (June '96 – June '97) and second (May '97 – May '98) years of our study had similar chl-a values of 112 and 124

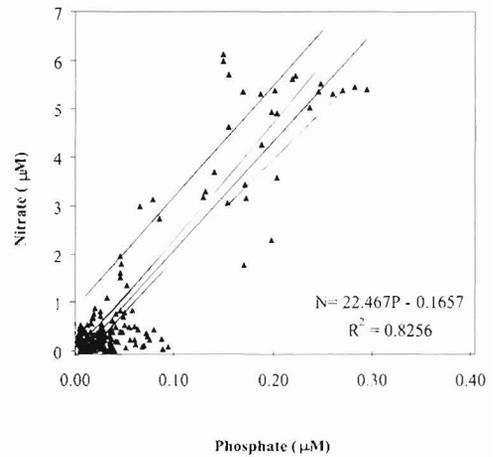


Figure 2-7: NO_3^- vs. PO_4^{3-} molar ratios of samples from all cruises. The linear regression curve and the 99% confidence bands for all the samples are included. The dotted line is the regression line calculated for the SE Levantine basin (200 – 2000 m) by Krom et al. (1991).

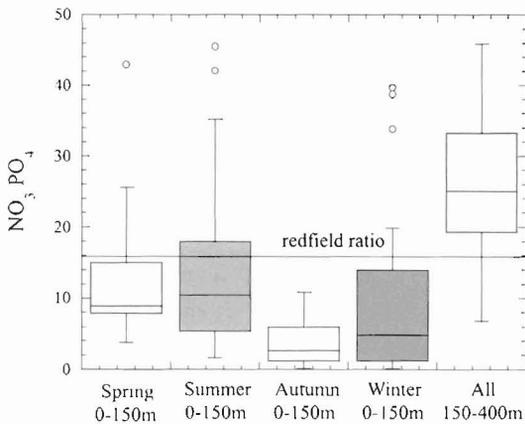


Figure 2-8: Box plots of the $\text{NO}_3^- : \text{PO}_4^{3-}$ molar ratios in the upper 150m for different seasons and in the 150-400 m depth interval for all samples. The bottom and the top edge of each box are located at the sample 25 and 75 percentiles. The central horizontal line is drawn at the sample median.

1996 and May 1998 at station S3 and S7, respectively) and similar to light intensities found in other oligotrophic areas. At station S7 the DCM was more developed during the summer and spring seasons ($\sim 0.3 \text{ mg m}^{-3}$), probably because of the physical structure of the water column and the consequent supply of nutrients to the euphotic zone. The DCM was always shallower than the main nutricline (between 150-200 m), similar to previous observations in the eastern Mediterranean (Yacobi et al., 1995).

Several possible sources may contribute nutrients to the euphotic zone. These may include the lower water masses as a result of winter mixing, transport across the nutricline by eddy diffusion, horizontal advection, input of terrigenous material, and atmospheric deposition (Eppley, 1989). In oceanic areas with almost no riverine input, similar to our study area, the continental shelf sediments are probably an important source of iron and other macronutrients (Johnson et al., 1999). Over the shelf (station S3), the PO_4^{3-} , NO_3^- and NH_4^+ concentrations in the interstitial waters of the upper sediment layers (0.5 cm) are more than 1 magnitude higher than in the bottom water (0.7-1.2, 13.5-23.7, and 8.3-32 μM , respectively; Herut, unpublished data), exporting nutrients to the water column. The combination of the relatively deep light penetration and the supply of nutrients from the sediment below, probably contributes to the deeper occurrence ($\sim 120 \text{ m}$) of the DCM location and the benthic production. In addition, especially during winter, sediment resuspension due to mixing and lateral advection of nutrients from the Nile delta by the northeasterly currents (Rosentraub, 1995) probably contribute significantly to the nutrient input. Over the continental slope (station S7) the winter vertical distribution of chl-a is mainly caused by the deep mixing and eddy diffusion across the nutricline, while the sharp summer peak may reflect a dominant in-situ supply of nutrients derived from the decomposition of 'trapped' phytoplankton on the distinct isopycnile layer. Indeed, the DCM was located at higher sigma-t values during summer (28.5-28.9) compared to the winter (28.0-28.6).

$\text{mg chl-a m}^{-2} \text{ yr}^{-1}$ in the upper 120 m (station S3 and S7), and 186 and 216 $\text{mg chl-a m}^{-2} \text{ yr}^{-1}$ in the upper 200 m (station S7). This load in the upper 200 m ($\sim 200 \text{ mg chl-a m}^{-2} \text{ yr}^{-1}$) is equivalent to approximately 41-49 $\text{g C m}^{-2} \text{ yr}^{-1}$, using $\text{C: chl-a} = 206-245$ (by weight; Abdel-Moati, 1990).

The depth range of the DCM between 80 and 120 m found in the present study is similar to the depth range found in previous studies in the SE Mediterranean (Abdel-Moati, 1990, Berman et al., 1986, Krom et al., 1992, Salihoglu et al., 1990, Yacobi et al., 1995) as well as in other oligotrophic regions (Cullen, 1982). The light penetration at these depths is 1% or less of the surface incident radiation (Abdel-Moati, 1990, Berman et al., 1986), in accordance with 32 and 41 m secchi disk depths (measured in August

As previously suggested (Yacobi et al., 1995), a slight gradient may exist between the DCM and the main nutricline as a possible additional source of nutrients. The upward shift of the nutricline during the summer might strengthen this process. However, due to the relatively large scatter of nutrient concentrations in the upper 200 m, it is not clear at what specific depth the nutricline becomes evident (Fig. 3). A possible additional source of nutrients may be atmospheric dry precipitates, especially from Saharan dust storms, which occur predominantly during autumn and spring (Herut et al., 1999a).

It has been suggested that ratios of dissolved N:P > 20–30 indicate that P is stoichiometrically limited, that N:P < 10 and Si:N > 1 indicate N-limitation, and Si:N < 1 and Si:P < 3 show Si-limitation (Dortch and Whiteledge, 1992, Justic et al., 1995). The above criteria are based principally on a phytoplankton nutrient uptake in Redfield ratios, as is observed in most oceanic areas. Limiting criteria may deviate with different nutrient uptake dynamics of site-specific biota. According to the above criteria, no Si-limitation was detected in this study. The scattergram of NO_3^- vs. PO_4^{3-} for all the samples showed a linear positive correlation ($r = 0.91$) with a slope of 22.5 and an intercept of -0.16 (Fig. 7). Similar best-fit was calculated for samples with NO_3^- and PO_4^{3-} concentrations $> 0.01 \mu\text{M}$ (on 142 of 187 samples). The correlation found here was similar to the pattern calculated across the Levantine basin with a slope of 22.9 (Krom et al., 1991). In the latter study, the surface depleted zone and the deepest samples ($\text{PO}_4^{3-} > 0.22 \sim \mu\text{M}$) were not included in the calculation.

In the euphotic zone, the $\text{NO}_3^-:\text{PO}_4^{3-}$ ratios we measured probably have a large error as a result of the low concentrations that were close to the analytical precision of both PO_4^{3-} and NO_3^- . The expected width of the $\text{NO}_3^-:\text{PO}_4^{3-}$ cluster for our data should be 4 times ($\pm 2\sigma$) the product of $\text{NO}_3^-:\text{PO}_4^{3-}$ ratio multiplied by its coefficient of variation (Fanning, 1992). For our data the width is centered on a $\text{NO}_3^-:\text{PO}_4^{3-}$ ratio of 22 and increases intensely and symmetrically in the euphotic zone owing to the extreme low NO_3^- and PO_4^{3-} concentrations. The actual $\text{NO}_3^-:\text{PO}_4^{3-}$ distribution in the euphotic zone has a different, asymmetrical shape with significantly lower ratios (Fig. 8). Excluding samples with concentrations $< 0.01 \mu\text{M}$ (45 samples), the $\text{NO}_3^-:\text{PO}_4^{3-}$ ratios scatter between 1 to 50 in the upper 150 m, but most of the samples (80%) have a ratio < 16 . The geometric mean and median values of the $\text{NO}_3^-:\text{PO}_4^{3-}$ ratios in this depth interval were 6.1 and 7.8, respectively. Between 150 and 400 m depth, the $\text{NO}_3^-:\text{PO}_4^{3-}$ ratios were somewhat more constant with geometric mean and median values of 23.8 and 24.9 (Fig. 8). Similar $\text{NO}_3^-:\text{PO}_4^{3-}$ depth profiles were observed in the core and the boundary of the Cyprus eddy (Krom et al., 1991), where ratios between 2 and 25 were calculated for the upper 100 m and 27 ± 4 below 300 m.

The $\text{NO}_3^-:\text{PO}_4^{3-}$ ratio appears to vary seasonally in the upper 150 m. During fall and winter (except March 1998), ratios were relatively low (2.7 and 4.8 median values), in comparison with 10.4 and 8.9 in summer and spring (Fig. 8). Thus, the autumn-winter phytoplankton bloom (highest integrated chl-*a* values) was associated with the lowest $\text{NO}_3^-:\text{PO}_4^{3-}$ ratios. It is debatable if the $\text{NO}_3^-:\text{PO}_4^{3-}$ ratios in the euphotic zone are related to phytoplankton uptake of nutrients and/or to the presence of other nutrient phases that were not measured in this study (i.e. dissolved organic phosphorus and nitrogen). It is not clear why the system exhibits N limitation when both the upwelling and atmospheric exogenous nutrient inputs have high (> 16) N:P ratios (Herut et al., 1999a,

Krom et al., 1991). If the water mixing is a main factor, we would have expected that the ratios would increase upon mixing with deeper waters with higher $\text{NO}_3^-:\text{PO}_4^{3-}$ ratios (~ 24). Similarly, atmospheric inputs have also higher N:P ratios (Herut et al., 1999a). If the phytoplankton uptake is close to the Redfield ratio (16:1) and the initial ratio of $\text{NO}_3^-:\text{PO}_4^{3-}$ before the blooming was <16 , the $\text{NO}_3^-:\text{PO}_4^{3-}$ ratio will further decrease. The N:P ratios in particulate organic matter in water layers above the DCM on the continental shelf off Egypt were ~ 20 (Abdel-Moati, 1990), suggesting that the $\text{NO}_3^-:\text{PO}_4^{3-}$ ratios there are lower than the Redfield ratio, similar to what we observed.

In the DCM layer, the particulate organic N:P ratios were close to the Redfield ratio (~ 16 ; Abdel-Moati, 1990), but were possibly affected by some preferential remineralization of P. A preferential uptake of nutrients by the phytoplankton may account for such a decrease. Preliminary data of relatively high dissolved inorganic N:P ratios in interstitial waters (>25 , Herut, unpublished data), may indicate the oxidation of P depleted organic matter (N:P >16).

The structure of the phytoplankton population in these sites was not examined and is not well known. Based on numerical abundances counted in a previous study (Kimor et al., 1987), monads and coccolithophorids ($<20 \mu\text{m}$) are dominant in their contribution to the total chlorophyll. However, there was a high spatial variability in the population percentages. Therefore, it remains to be determined if there is preferential uptake producing a fractionated nutrient covariance.

The nutrient phases measured in this study (dissolved inorganic NO_3^- and PO_4^{3-}) are probably dominant in the deep water, while the surface waters may contain other important phases. Thus, the determination of the possible presence and the contribution of additional nutrient phases is an important next step towards the understanding of nutrient limitation in such ultra-oligotrophic systems.

Acknowledgements

The authors would like to express their gratitude to L. Izraelov, Y. Gertner, E. Shoam-Frider and E. Shefer for their technical assistance in the sample collection and analyses, and to the crew of the R/V Shikmona. This project was supported by the Geo- and Life Sciences Foundation (A.L.W.) with financial aid from the Netherlands Organisation for Scientific Research (N.W.O.), project-number 750-19-610A and by the Israeli Ministry of Infrastructure.

Foraminiferal assemblages and diversity patterns along a depth transect off the Israeli coast (SE Levantine Basin)

With: Sandra Langezaal, Kees Hordijk, Ahuva Almogi-Labin, and Bert van der Zwaan

Abstract

Three stations (40m, 120m, and 700m depth) along a downslope transect perpendicular to the Israeli coast were monitored over a period of two years for their benthic foraminiferal assemblage.

At the shallowest station S1, the average total standing stock (TSS) is more than twice the average TSS at the 120m station S3, and even more than ten times higher than the one observed at the deepest station S9. The seasonal changes are most pronounced at the shallowest and deepest stations; at station S3 no clear seasonal pattern could be distinguished. The seasonality at S1 and S9 is mainly expressed in low numbers of living foraminifera during autumn and beginning of the winter, and higher numbers in spring and summer. The simple diversities at the two shallowest stations seem to be positively correlated with the TSS. This correlation is more pronounced at station S9.

The absolute as well as the relative numbers of some numerically important foraminiferal taxa distinctly change down-slope. The miliolids are abundantly present at the shallowest station but less so in deeper water. The ratio of perforate calcareous over agglutinated foraminifera is 1:1 in shallow water, but 2:1 at the deepest station.

The distribution patterns of the most common taxa suggest a distinct down-slope change of the species assemblages. Miliolids are very abundantly living at the shallowest station (S1); taxa as *Bulinina inflata* and the *Uvigerina* group (*U. mediterranea* and *U. peregrina*), become dominant in deeper water. Prominent factors in this change are the decrease of organic flux and possibly the CaCO₃ content with depth. Oxygen does not seem to play a prominent role.

I. Introduction

The ecological background of benthic foraminiferal distribution has been subject of study for several decades. Already in 1961, Bradshaw did experimental work in order to observe reactions to food supply, and changes in temperature and salinity. Although experimental studies have provided us with important information on the impact of oxygen deficiency (Alve and Bernhard, 1995, Moodley and Hess, 1992, Moodley et al., 1998) and organic matter input (Moodley et al., 2000, Widbom and Elmgren, 1988, Widbom and Frithsen, 1995), it is still difficult to relate these findings to the situation in the field. Therefore, field studies are valuable, and even more so are studies monitoring seasonal variations. Already in the late sixties Boltovskoy and Lena (1969) observed seasonal occurrences and standing stocks of benthic foraminifera off Puerto Deseado, for a period of more than 2 years. After that few such monitoring studies were performed. Although in the Mediterranean, several studies have been carried out, these mostly regard the eutrophic northern part of the Mediterranean (Barmawidjaja et al., 1992, Jorissen, 1988). In the more oligotrophic areas of the southern Mediterranean no such seasonal studies exist.

In the Levantine Basin off the Israeli coast, the waters are known to be extremely oligotrophic (Azov, 1986, Berman et al., 1984, 1986, see also Chapter 2). Unlike other oligotrophic sites (e.g. deep sea), it is possible here to survey foraminiferal assemblages on a high frequency basis. The coastal, neritic sediments are under the influence of seasonal changes in the upper water layers (Chapter 2), whereas deeper waters are expected to comprise a more stable benthic environment. The relatively low primary productivity is affected by the yearly cycle of mixing, the highest productivity occurring during the beginning of winter but remaining within the range of oligotrophy.

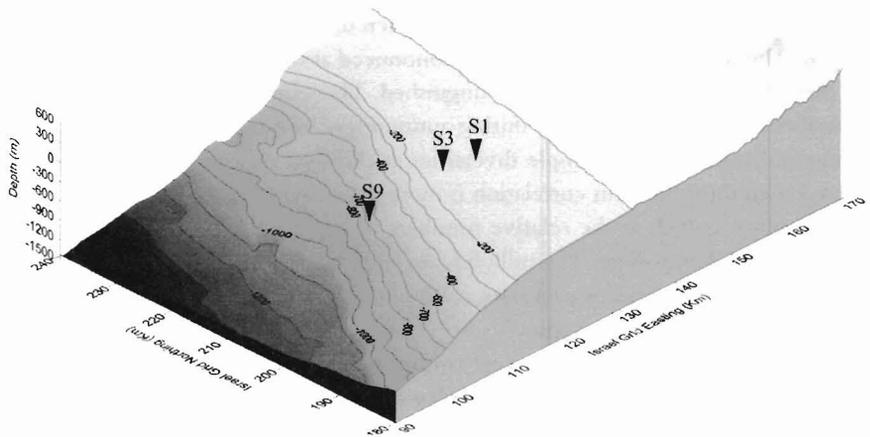


Figure 3-1: Sampling transect, off the Israeli coast, with stations S1 (40m), S3 (120m) and S9 (700m) indicated.

In the coastal waters off Netanya (Fig. 1), box core sediments were sampled and studied for the occurrence of living (Rose Bengal stained) benthic foraminifera. Through bi-monthly sampling (June '96 – May '98) we were able to get a clear picture of the seasonal changes in the benthic foraminiferal standing stocks and the processes driving these fluctuations. Three stations were sampled: S1 (40m), S3 (120m) and S9 (700m). The foraminiferal standing stocks, averaged over the 0–1cm part of the sediment column, in combination with the simple diversities are shown here. The distributions of the larger foraminiferal groups (agglutinants, perforate calcareous, miliolids, and soft-shelled) and of the 12 most common taxa in the top 0–1cm of the sediment column at the three stations are discussed in relation to the ambient environment.

2. Study area

As was shown and discussed in Chapter 2, the Levantine coastal waters are characterized by a rather high seasonality. During the monitoring of several water layer properties over the period June '96 – May '98, we observed a yearly cycle as was described earlier by Azov (1986) and Berman et al. (1984, 1986). During spring and summer the water layers stratify, to mix again from autumn until the end of winter down to a water depth of more than 120m.

Station S1 is situated at 40m water depth and therefore under strong influence of these seasonal changes. Every autumn, when the cool winds cause the water layers to be mixed, the temperature, salinity and dissolved oxygen concentrations change radically (Chapter 2). This change is also recorded at the sediment-water interface. At station S3, situated near the Deep Chlorophyll Maximum (about 120m; Berman et al., 1986), there are also fluctuations in temperature, salinity, and dissolved oxygen concentrations, but these are less extreme than at S1 (see Chapters 4 and 6). Station S9, located at 700m water depth, is the deepest station that was monitored during the two years of study. No seasonal changes in temperature, salinity and dissolved oxygen were observed here (see also Chapter 2).

The sediment at station S1 is coarse and sandy. At 120m it is less coarse, and at station S9 (700m) it is composed of silty clay. The overall oxygen penetration in the sediment at station S1 is relatively shallow (0.1–2.0cm, Chapters 4, 5). At 120m oxygen penetrates generally deeper (≥ 2.0 cm, see Chapter 6), although shallower during less well oxygenated periods. At the deepest station oxygen is found continuously deeper than 2.0cm, occasionally even as deep as 4.0cm.

3. Materials and methods

During the period of June '96 to May '98, box cores were taken along a depth transect perpendicular to the Israeli coast. Stations S1 and S3 were monitored bi-monthly. Station S9 was also sampled bi-monthly except for June '96 and March '98, due to bad weather. Physical and oceanographic parameters were monitored (see Chapters 2 and 4), and CTD profiles were taken (oxygen, temperature, salinity, see Chapter 2); chlorophyll-a concentrations were measured only at

station S3 (Chapters 2 and 6).

The box cores were sub-sampled for benthic foraminifera and oxygen measurements. The sediment tubes meant for study of benthic foraminifera ($\varnothing = 8.5\text{cm}$) were sliced in 0.5 cm slices and stored in ethanol (90%) containing Rose Bengal (1 gram/l). In the laboratory the samples were freeze-dried and subsequently wet-sieved over 63 μm , 150 μm and 595 μm sieves. The samples were studied wet, in order to allow for a good discrimination between living and dead foraminifera. Aliquots containing approximately 200 specimens were counted and species were sorted in a Chapman slide. The samples taken at station S9 were not split but studied completely. Because the counting of fragments originating from arborescent agglutinated foraminifera (only occurring in S9) is very dubious, these were excluded from our counts.

In this study we employ data from the 63–595 μm size fraction (>63 μm and the 150 μm size fractions). We focus on assemblages obtained from the 0–1cm sediment layer, because no data was available for sediment layers deeper than 1cm at station S9. Nevertheless, the two sediment samples combined in the top 0–1cm give a good impression of the foraminiferal assemblage living at the three stations.

4. Results

4.1 Total standing stocks and the distribution patterns of foraminiferal groups

The three stations show remarkable differences in their foraminiferal assemblages. In figure 2 the average total standing stock (TSS) over the two-year sample period is plotted. It shows a striking decrease down-slope. The TSS of foraminifera at station S1 (40m) is more than twice the average TSS at station S3 (120m), and more than 10 times the average TSS at station S9 (700m). If we consider the primary productivity to be more or less homogenous over the study area and use the value given by Herut et al. (2000, Chapter 2; $\sim 4.5\text{gCm}^{-2}\text{y}^{-1}$), we can calculate the approximate amount of organic matter reaching the sediments of our three stations over the year, using a flux equation (Berger & Diester-Haass, 1988, see also Van der Zwaan et al., 1990):

$$J(d) = (k * PP/d) + (r * PP)$$

Here, $J(d)$ = amount of organic matter arriving at the bottom, d = water depth/100, k = export efficiency (taken here as 0.2), PP = primary production, and r = constant (here assumed to be 0.01, see also Berger and Diester-Haass, 1988). Figure 2 clearly shows that the decline in average TSS is very similar to the decrease of the calculated values for organic matter flux arriving at the sediment surface.

The ratio between perforate calcareous and agglutinated foraminifera is approximately 1:1 at stations S1 and S3, whereas it is 2:1 at station S9 (Fig 3). The average number of miliolids is much higher at station S1 than at stations S3 and S9; at the latter stations only 4.3% and 2.4% of the assemblage consist of miliolids, versus 19.7% at station S1 (Fig. 3).

The group of soft-shelled foraminifera (exclusively soft-shelled saccamminids) occurs most

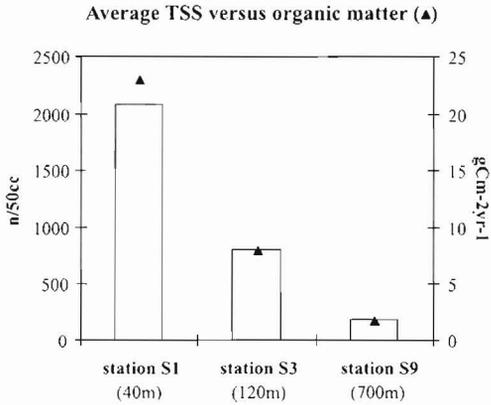


Figure 3-2: Average TSS of foraminifera (n/50cc) in the top 0-1cm of the sediment at the three sample stations versus the calculated average values of organic matter.

Down-slope species assemblages of benthic foraminifera

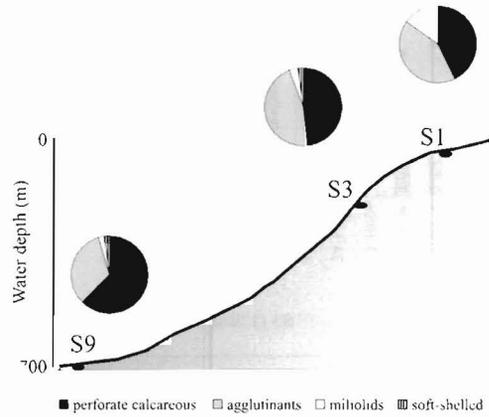


Figure 3-3: Relative abundances of the larger foraminiferal groups along the down-slope transect.

abundantly at station S₃, where they are almost as common as the miliolids. The proportion of soft-shelled saccamminids at station S₃ is very similar to their relative occurrence at station S₉, 2.7% and 2.3% respectively (Fig. 3).

LEV51 (40m)	LEV53 (120m)	LEV59 (700m)
<i>Quinqueloculina</i> spp. (12.4%)	<i>Bolivina</i> spp. (12.3%)	<i>Uvigerina</i> group (21.1%)
<i>Eggerella</i> spp. (8.1%)	<i>Bolivina striatula</i> (7.6%)	<i>Epistominella exigua</i> (11.0%)
<i>Bolivina</i> spp. (6.9%)	<i>Eggerella</i> spp. (7.4%)	<i>Cassidulina crassa</i> (6.6%)
<i>Caronia silvestrii</i> (5.2%)	<i>Verneuilinella</i> spp. (6.8%)	<i>Glomospira</i> sp.2 (6.4%)
<i>Adercotryma</i> sp.1 (5.0%)	<i>Cassidulina crassa</i> (6.7%)	<i>Glomospira charoides</i> (4.0%)
<i>Trochammina inflata</i> (4.6%)	<i>Criboelphidium poeyanum</i> (4.7%)	<i>Eggerella</i> spp. (3.6%)
<i>Asterigerinata mamilla</i> (4.3%)	<i>Textularia agglutinans</i> (4.2%)	<i>Bulimina marginata</i> (3.6%)
<i>Epistominella vitrea</i> (3.5%)	<i>Glomospira charoides</i> (3.7%)	<i>Glomospira</i> sp.1 (3.3%)
<i>Porosonion granosum</i> (2.9%)	<i>Epistominella vitrea</i> (3.7%)	<i>Haplophragmoides</i> spp. (3.2%)
<i>Nodophthalmidium</i> sp. (2.7%)	<i>Glomospira</i> sp.2 (3.5%)	<i>Adercotryma</i> sp. 1 (2.9%)
<i>Glomospira</i> sp.2 (2.4%)	Soft-shelled saccamminids (2.7%)	<i>Anomalina</i> sp. 1 (2.7%)
<i>Acostata mariae</i> (2.2%)	<i>Bigenerina nodosaria</i> (2.3%)	<i>Bulimina inflata</i> (2.4%)

Table 3-1: Species assemblages occurring at the three stations down-slope. The twelve most abundant taxa per station.

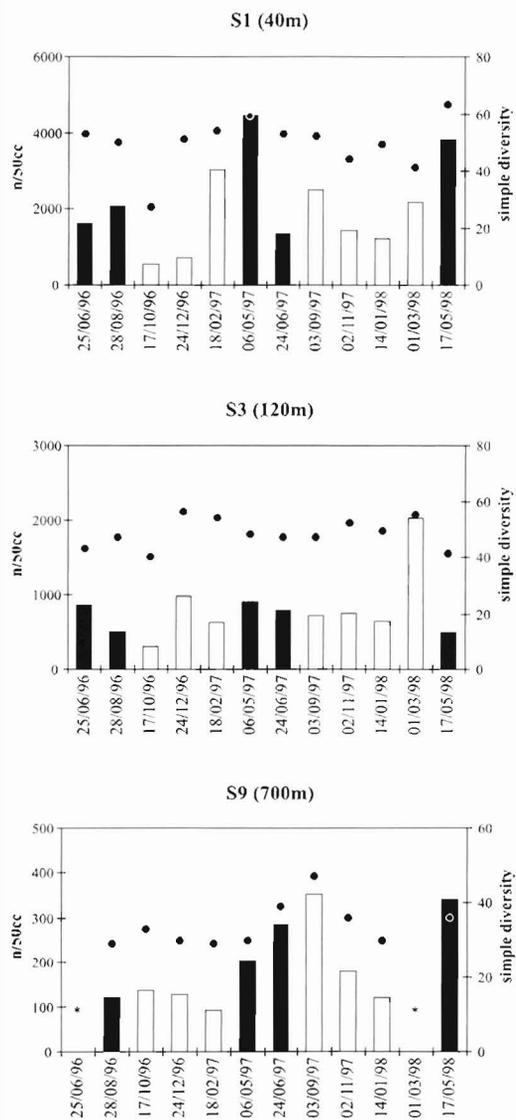


Figure 3-4: The TSS of foraminifera (averaged over the top 0-1cm of the sediment), throughout the two sampling years (bars) and the simple diversity (•). a) station S1 (40m); b) station S3 (120m); c) station S9 (700m, May '98 only 0-0.5cm). The periods of stratification are indicated by black colour (bars). Note differences in scaling. (* no data)

4.2 Species assemblages

In this paragraph we describe the species assemblages per station. The twelve most common foraminiferal taxa per station are shown in Table I; most of them are displayed in Plate I-III. At station S1, only five perforate calcareous taxa are among the twelve most common ones. *Asterigerinata mamilla* and *Porosonion granosum* are species which occur abundantly. They are scarce at station S3 and do not occur living at the deepest station S9 (700m). *Bolivina* spp., a group consisting of *Bolivina dilatata*, *Bolivina seminuda*, and *Bolivina spathulata*, occurs abundantly at stations S1 and S3, but far less so at S9. The relatively small taxon (only occurring in the 63-150µm size fraction) *Epistominella vitrea* is found abundantly living at station S1 as well as at station S3. The miliolid species *Nodophthalmidium* sp. occurs very abundantly at station S1, occasionally at station S3, but is completely absent at S9. The *Quinqueloculina* group, in which several *Quinqueloculina* species are included, is the most abundant group at station S1. However, already at 120m this group does not belong to the 12 most common taxa and at the deepest station (S9) it is almost absent. The agglutinated taxa occurring most abundantly at station S1 are *Adercotryma* sp. 1, *Eggerella* spp. and *Caronia silvestrii*. Whereas *Eggerella* spp. (*Eggerelloides* spp. sensu Cimerman and Langer, 1991), *Glomospira* sp. 2 and *Adercotryma* sp. 1 are common at all three stations, *Adercotryma* sp. 1 is only quantitatively important at stations S1 and S9. *Acostata maria* (= *Rcophax nana*) and *Trochammina inflata* occur very abundantly at the shallowest station S1, but only with low numbers at the other two stations.

At station S3, *Cassidulina crassa* is found living

abundantly. Other calcareous taxa which are specifically abundant at station S3 are *Bolivina striatula* and *Criboelphidium pocyantum*. Among the agglutinated taxa are *Glomospira charoides* and *Textularia agglutinans* (most abundant at S3). Also *Bigenerina nodosaria* is only abundant at the stations S3 and S9, whereas *Verneuilinella* sp. lives only abundantly at station S3 (120m.). Soft-shelled saccamminids are found at all three stations, but only at station S3 in high numbers. The most important perforate calcareous taxa at 700m differ from those at stations S1 and S3. Only *Bulimina marginata* and *C. crassa* occur also abundantly at the other stations. *Anomalina* sp., a species mostly occurring within the smaller size fraction (63–150µm), is typical for deeper water. The same holds for *Bulimina inflata*. As the *Uvigerina* group, also *Epistominella exigua* occurs most frequently at station S9. This *Epistominella* species is morphologically quite different from the earlier mentioned *E. vitrea* and resembles *E. exigua* (Goody and Lambshead, 1989, Fig. 1j-k; De Stigter, 1996, Plate III) very closely (see Plate I-III).

4.3 Seasonal variation in foraminiferal TSS versus simple diversity

The foraminiferal standing stock is highest at station S1 and decreases strongly with water depth. In figure 4 the standing stocks are plotted for the three stations versus the simple diversity. Indicated (black) are the periods of stratification of the water column, during which sediment oxygenation is less at S1 and S3.

Generally, we see a positive correlation between the numbers of living foraminifera and the numbers of taxa. The significance levels of these correlations are $0.01 < p < 0.05$.

In figure 4a the TSS of foraminifera at station S1 shows strong (seasonal) fluctuations over the two sampled years. The simple diversity and TSS seem to be positively correlated during the first year; both show a clear decrease during autumn. During the second year this correlation is far less obvious. At station S3, there are less seasonal fluctuations (Fig. 4b). Overall the standing stocks and simple diversity seem to be correlated. During the second year, the TSS shows a peak in March '98, while the species diversity remains more or less the same. At station S9, where we only sampled 10 times, relatively strong seasonal fluctuations are visible (Fig. 4c). Low numbers during autumn and winter alternate with relatively higher standing stocks during spring and summer. The simple diversity is strongly (positively) correlated with the TSS.

Although the numbers of species found over the two years at the three downslope stations were quite high (84, 90, and 72, respectively), the average species diversities were much lower and decreasing downslope (49, 47, and 33, respectively).

5. Discussion

The foraminiferal assemblages occurring at the three stations along our down-slope transect off the Israeli coast show remarkable differences. The total standing stock (TSS) of benthic foraminifera, averaged over the 0–1cm of the sediment, is highest at the shallowest station S1. The high total

numbers of benthic foraminifera could be a result of a relatively higher organic matter input at the shallowest station compared to the deeper ones. This is supported by the calculated amount of organic input at various depth intervals using the flux equation of Berger and Diester-Haass (1988; see also Van der Zwaan et al., 1990, De Stigter, 1996). However, one has to bear in mind that measurements and observations by Azov (1984), Berman et al. (1984, 1986) and Herut et al. (2000, Chapter 2) indicate that the coastal waters are possibly somewhat more enriched with organic matter than the offshore waters. Apparently, the TSS is to a high extent controlled by organic flux, as was suggested earlier (e.g. Gooday, 1986; Jorissen et al., 1992). In the southern Adriatic Sea De Stigter (1996) found decreasing standing stocks of foraminifera with increasing water depth, and suggested this to be a result of decreasing organic matter flux downslope. Apparently, a similar control holds true for the Levantine Basin, although this is overall a very oligotrophic system with only an occasional increase in primary productivity due to mixing of water layers. The level of sediment oxygenation seems not to control the TSS: highest values at station S1 occur in the less oxygenated sediment samples.

The seasonality in standing stocks is high in shallow water (S1) and seems to be driven by a delayed response on winter mixing which results in increased chlorophyll-a concentrations. The delay is even longer for the deep water station S9 suggesting that other factors (e.g. degree of ventilation, or properties of the deep Mediterranean water which is present at this site) interfere with the impact of the surface flux. At 120m (S3) no seasonal pattern in TSS can be detected; we attribute this to the presence of the DCM which continuously provides the benthic environment with additional resources.

The species assemblages are rather similar for the two shallowest stations, but the assemblage found at station S9 differs. At station S9, the species group *Uvigerina* (including *U. mediterranea* and *U. peregrina*) is very abundant, whereas at the shallower stations it is almost absent. Moreover, *Bulimina inflata* and *Epistominella exigua*, which are not found living at the shallower stations S1 and S3, are relatively abundantly present at S9. They all are known to prefer deeper waters, although the *Uvigerina* group and *E. exigua* are generally found abundantly in organic enriched areas (Gooday, 1993, Harloff & Mackensen, 1997, Jannink et al., 1998, Murray, 1991, Smart et al., 1994, Schmiedl et al., 1997). *U. mediterranea* is most frequent at water depths deeper than approximately 80-90m (Jorissen, 1988, Parker, 1958), whereas *U. peregrina* occurs often deeper than 200m water depth. Both taxa seem to prefer a muddy substrate (Murray, 1991), a factor which apparently is more important than the somewhat decreased level of flux prevailing in the deeper waters.

The proportions of the larger foraminiferal groups (perforate calcareous, agglutinated, miliolid, and soft-shelled) change drastically down-slope. The miliolids occur abundantly at station S1, but decrease towards deeper stations. This not only regards the absolute numbers; also the proportions are much lower than the proportion of miliolids found at the shallowest station. This pattern cannot be due to oxygen deficient circumstances, which most miliolids (*Quinqueloculina* spp. and *Nodophthalmidium* sp.) seem to be unable to cope with (see Chapter 5), as the oxygenation of the sediment increases with water depth.

The fact that most miliolids were found living at our shallowest station S1 coincides with the observations of several researchers who also noted miliolids to occur most abundantly at shallow water depths, predominantly in coarse grained sandy sediments (Murray, 1991, De Stigter, 1996, Moodley,

1992, Sgarrella & Moncharmont Zei, 1993). Parker (1958) found most miliolid taxa to occur in sediments situated at less than 25m water depth, where they made up more than 40% of the total assemblage. In the Adriatic Sea, Jorissen (1988) observed the miliolids to be significantly correlated with the percentage of CaCO_3 in the sediment. He suggested that the availability of calcium carbonate might act as a limiting factor for this group. The porcelaneous shell of the miliolids mainly consists of randomly oriented calcite needles (Debenay et al., 1996). The process of calcification in miliolids is facilitated if the carbonate saturation state of the seawater increases (Hallock, 1999). The surface waters off the Israeli coast are known to be oversaturated with calcium carbonate, whereas its percentage in the sediments decreases somewhat downslope (Goldsmith, 1997). The deeper waters of the Levantine (station S9) might contain less CaCO_3 and together with lower temperatures of the ambient water, formation of calcium carbonate might be more difficult for the miliolids.

The stations S1 and S3 show similar ratios of perforate calcareous versus agglutinated taxa (1:1); however, the ratio shifts to 2:1 at the deepest station. A considerable part of the agglutinated foraminifera at the shallower stations consists of *Eggerella* spp.; this species is mainly responsible for the fact that the amount of agglutinated species is twice as high at S1 and S3 compared to the deepest sample station. The exclusion of arborescent agglutinated foraminifera, like *Rhizammina* sp. and *Rhabdammina* sp., of which fragments were found very abundantly at S9, also causes an underestimate of the proportion of agglutinated species at this station. The average numbers of soft-shelled saccamminids occurring at S1 and S9 are approximately the same, but due to the higher TSS at S1 the proportion of soft-shelled saccamminids is much smaller there. At station S3 the soft-shelled foraminifera are more common but still make up for only a small part of the TSS. The saccamminids were the only soft-shelled species (group) which was encountered during this study. Whether this is an artefact, as result of sample treatment (freeze-drying and wet-sieving), remains unclear.

Summarising our discussion so far, it seems that factors that play a role in the observed bathymetric change are substrate and most likely the impact of a decreasing organic flux with increasing depth. It is remarkable that from our data it is obvious that oxygenation does not play a role at all: the shallowest station is the least oxygenated.

The correlation between the simple diversity and the TSS is not very strong. A positive correlation can be observed; at times of relatively higher TSS (e.g. May '97 and May '98) simple diversity was highest. It seems likely that during organic enriched periods foraminifera profit, whereas the organic load is still too low to cause any negative side-effects. (e.g. oxygen deficiency). The positive correlation between the TSS and species diversity only holds for the seasonal changes per station. At station S3, where the overall organic matter input was calculated to be far less than at station S1, the overall diversity of species is even somewhat higher. This can be due to the more stable circumstances and the lesser seasonality at this station. According to Buzas and Gibson (1969) a considerable period of environmental stability would be required to achieve a complex organization and thus high diversity. In the Arabian Sea, Jannink et al. (1998, Chapter 10) found a distinct increase in species diversity down-slope, most likely due to increasing sediment oxygenation and increasingly stable environmental circumstances.

6. Conclusions

The benthic foraminiferal assemblages found at three stations off the Israeli coast, showed very different standing stocks, species diversities and taxonomic compositions. The total standing stocks decrease sharply downslope. The average flux of organic matter which decreases with depth seems one of the major factors influencing the TSS. The miliolids are most abundantly present at the shallowest station (S1). This might be due to the more sandy sediment and/or to the higher CaCO_3 content in the shallow waters along the Israeli coast. The absolute and relative numbers of agglutinated taxa are lowest at the deepest station S9 (700m). This is mostly due to much lower numbers of *Eggerella* spp.

The species diversity and the TSS of foraminifera are positively correlated. This indicates that the foraminifera profit from increased flux without being hampered by possible negative side effects as oxygen deficiency. The species assemblages occurring downslope show large differences in taxonomic composition. Change in substrate (from sandy to clay) and increased stability play an important role in this respect. Levels of organic flux decrease with depth and are probably important as well. Oxygenation is best in the deepest station but seems to be irrelevant for the observed faunal change.

Plate I

Figure 1-2 *Epistominella vitrea* Parker, sample LEV12S1 (0-0.5cm)

Figure 3 *Adelosina* sp., sample LEV12S1 (0-0.5cm)

Figure 4 *Quinqueloculina* sp., sample LEV12S1 (0-0.5cm)

Figure 5 *Asterigerinata mamilla* (Williamson), sample LEV12S1 (0-0.5cm)

Figure 6 *Caronia silvestrii* Bronnimann, Whittaker, and Valleri, sample LEV10S1 (1-1.5cm)

Figure 7 *Nodophthalmidium* sp., sample LEV5S1 (0-0.5cm)

Figure 8 *Eggerella* sp. (*Eggerelloides* sp. sensu Cimerman and Langer, 1991), sample LEV12S1 (0-0.5cm)

Figure 9 *Adercotryma* sp. 1, sample LEV12S1 (0-0.5cm)

Figure 10 *Glomospira* sp. 2, sample LEV12S1 (0-0.5cm)

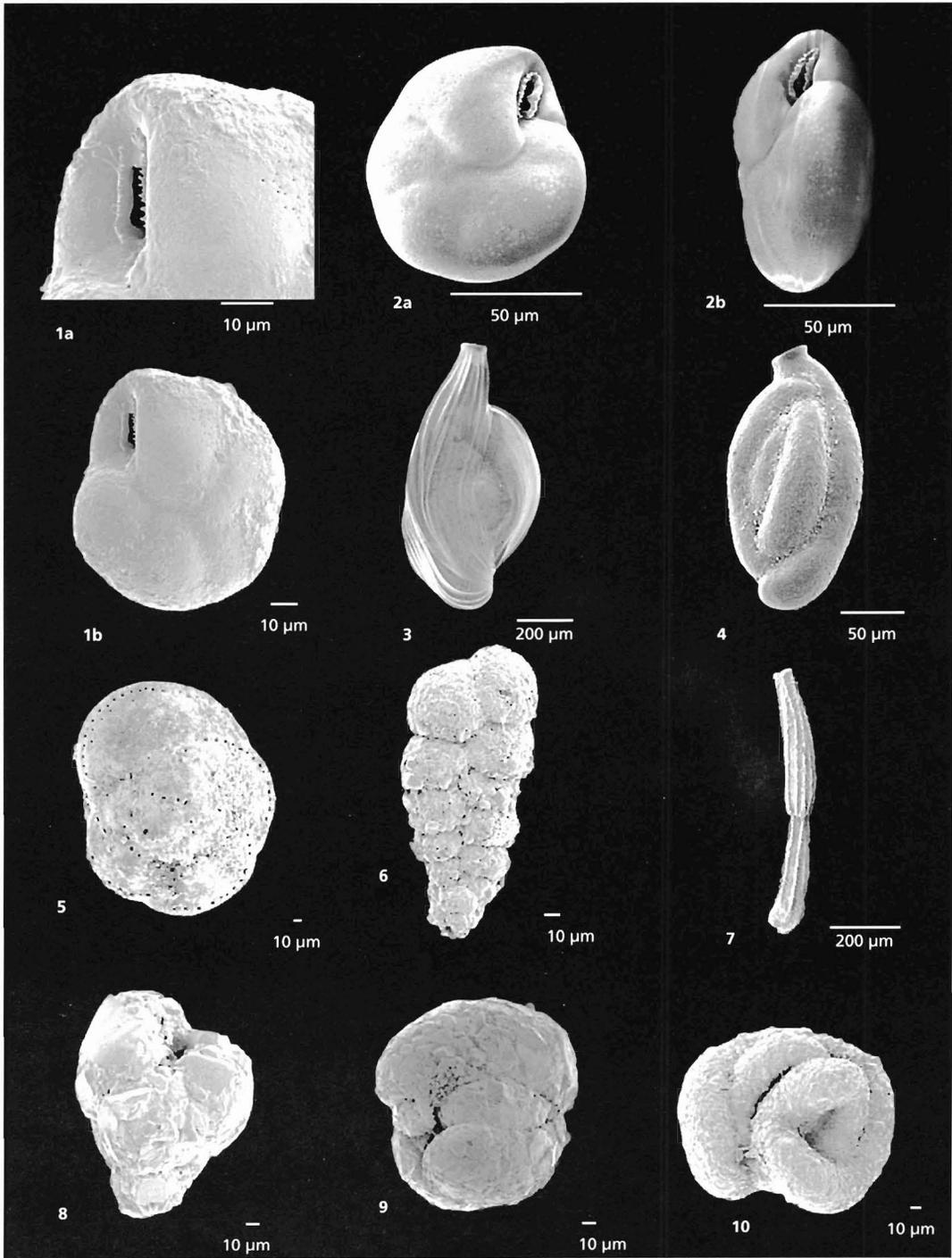


Plate I

Plate II

Figure 1-2 *Bolivina striatula* Cushman, sample LEV1S3 (1.5-2cm)

Figure 3 *Bolivina dilatata* Reuss, sample LEV12S1 (0.5-1cm)

Figure 4-5 *Bolivina spathulata* (Williamson), sample LEV1S3 (1-1.5cm)

Figure 6-7 *Bolivina seminuda* Cushman, sample LEV9S1 (0-0.5cm)

Figure 8 *Bigenerina nodosaria* d'Orbigny, sample LEV1S3 (0-0.5cm)

Figure 9 *Textularia agglutinans* d'Orbigny, sample LEV11S1 (1-1.5cm)

Figure 10 *Verneuilinulla* sp., sample LEV1S3 (1-1.5cm)

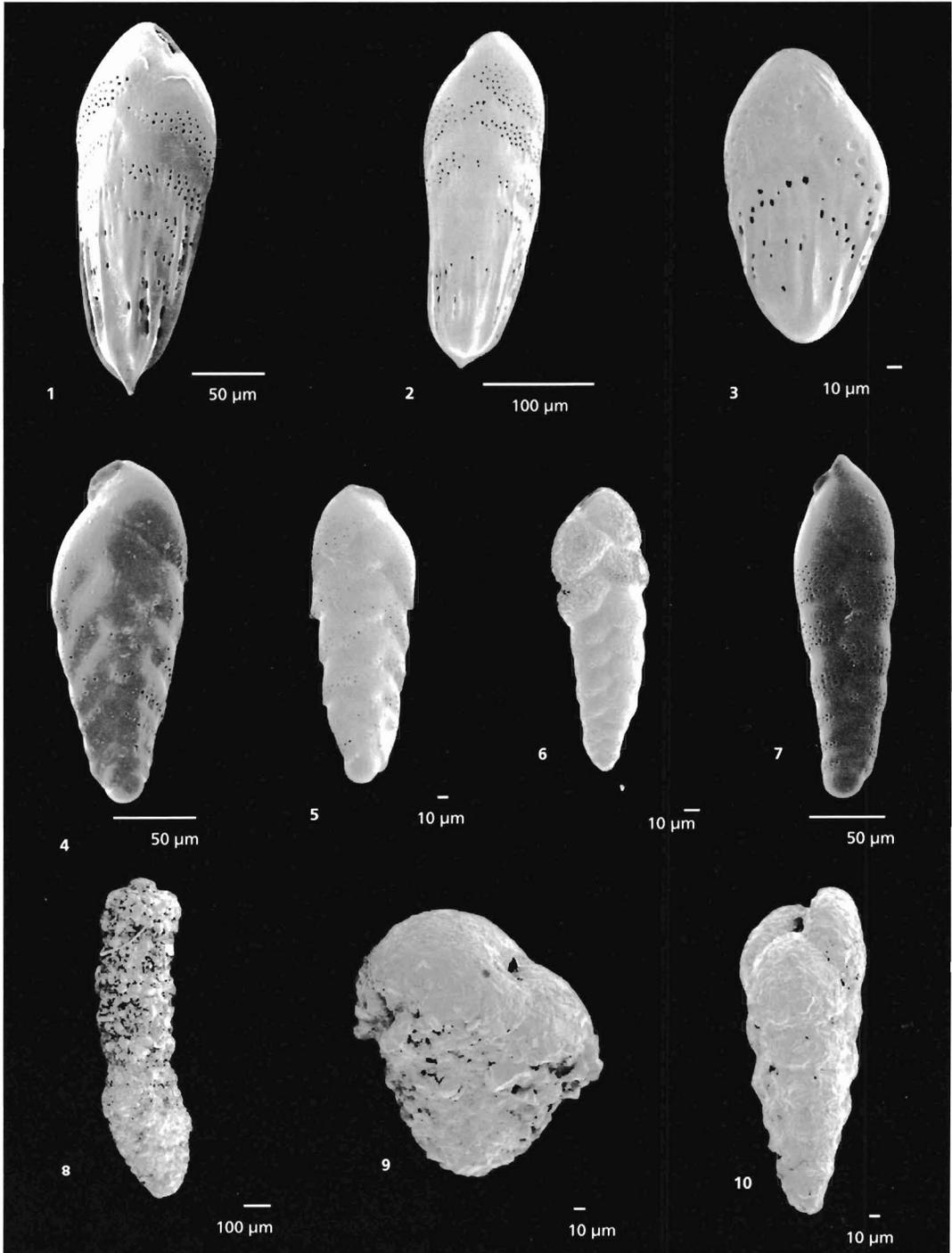


Plate II

Plate III

Figure 1 *Cassidulina crassa* d'Orbigny, sample LEV1S3 (1.5-2cm)

Figure 2 *Epistominella exigua* Brady, sample LEV2S9 (0-0.5cm)

Figure 3 *Uvigerina mediterranea* Hofker, sample LEV3S9 (0-0.5cm)

Figure 4 *Bulimina marginata* d'Orbigny, sample LEV12S1 (0-0.5cm)

Figure 5 *Bulimina inflata* Sequenza, sample LEV12S9 (0-0.5cm)

Figure 6 *Bolivina alata* (Sequenza), sample LEV3S9 (1-1.5cm)

Figure 7-8 *Glomospira charoides* (Jones and Parker), sample LEV1S3 (0.5-1cm)

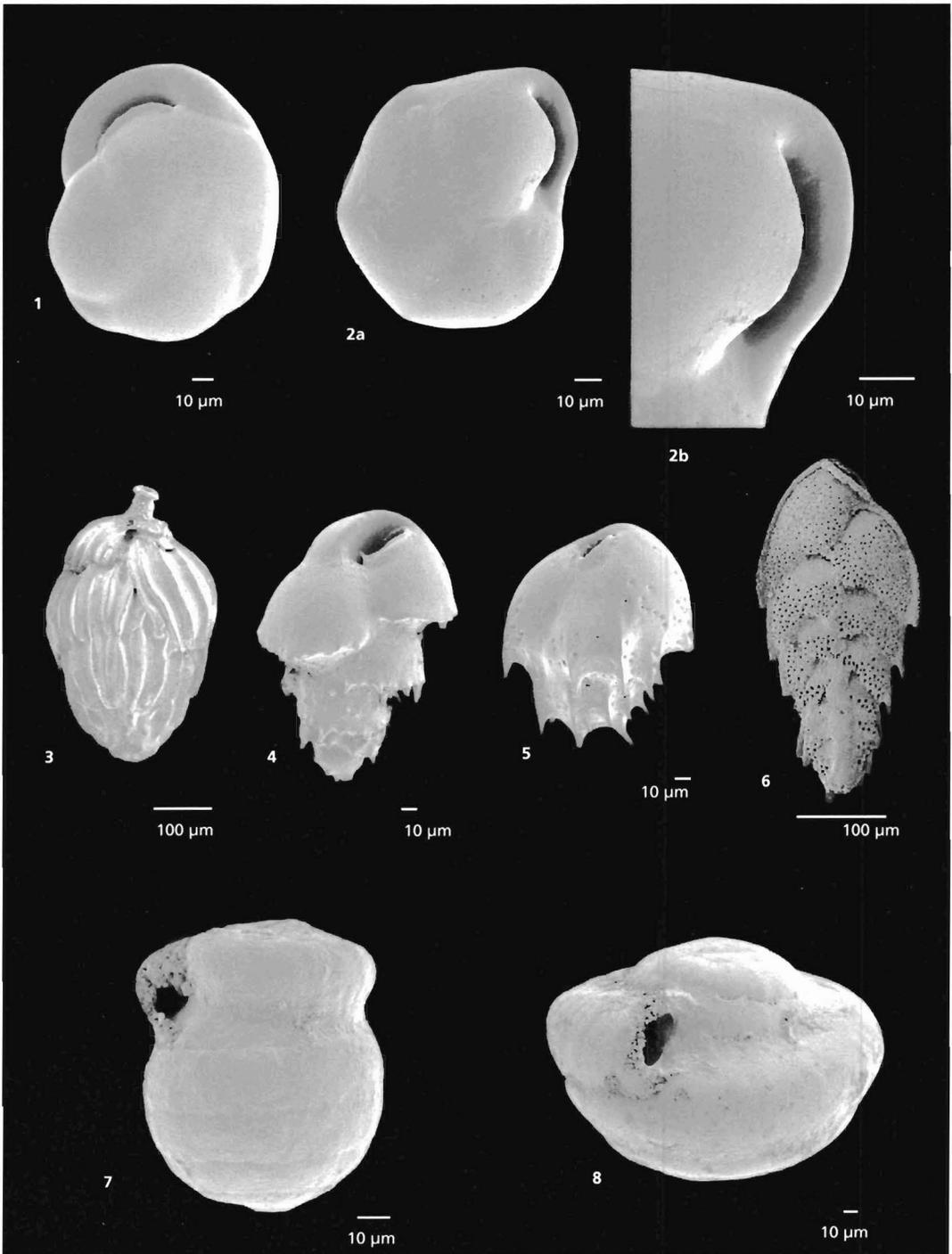


Plate III

Seasonal variation of benthic foraminiferal standing stocks in shallow water (40m) off the Israeli coast (SE Levantine Basin)

With: Sandra Langezaal, Ahuva Almogi-Labin, Barak Herut, and Bert van der Zwaan

Abstract

Between June '96 and May '98, a depth transect perpendicular to the Israeli coast off Netanya was sampled bimonthly during twelve cruises. During these cruises a neritic station (40m) was sampled for water column properties and box core sediments. Our data indicate that during summer the water column is highly stratified, whereas throughout autumn and winter the water layers become mixed down to at least 150m water depth.

The abundance of living (Rose Bengal stained) benthic foraminifera exhibits a strong seasonal pattern. The total abundance displays peak values at the end of the winter season and during spring, whereas the lowest standing stocks are found during autumn and the beginning of winter. These variations seem to be related to the availability of organic matter. We speculate that foraminiferal response to increased primary production (occurring in winter) was delayed by the presence of *Polydora* tube worms.

The in-sediment distribution of the benthic foraminifera appears to be strongly related to the oxygen profile in the sediment. Together with decreasing oxygen contents the foraminiferal standing stocks display a very steep decline in the top 2cm of the sediment column. Under better oxygenated circumstances, however, the benthic foraminifera become more evenly distributed.

1. Introduction

Recently, a considerable amount of research has been performed in order to gain more insight into the ecological background of benthic foraminiferal distributions. Field and experimental studies were directed at unravelling the response of assemblages to oxygen stress (Alve, 1995, Alve and Bernhard, 1995, Barmawidjaja et al., 1992, Bernhard, 1992, Bernhard and Reimers, 1991, Bernhard et al., 1997, Jannink et al., 1998, Jorissen et al., 1998, Loubere et al., 1995, Moodley and Hess, 1992, Moodley et al., 1997, 1998b, 1998c, Rathburn and Corliss, 1994). Since oxygen and organic flux are intricately coupled (Jorissen et al., 1995, Kitazato and Ohga, 1995), one would expect a similar research effort directed at the effects of food supply. Unfortunately, far less research has been performed to study the response of foraminifera to food (e.g., Altenbach, 1992, Gooday, 1988, 1994, Gooday and Turley, 1990). The abundance of benthic foraminifera is found to be positively related to the flux of (fresh) organic matter (Gooday, 1988, Gooday and Turley, 1990), with some species reacting in a more opportunistic way than others (Gooday, 1988, 1993, Gustafsson and Nordberg, 1999, Levin et al., 1999). For example, Gooday (1988) found some taxa to react very rapidly, within 1–2 months, on the arrival of organic matter. Faubel et al. (1983) recorded a tenfold increase in the foraminiferal population density within six weeks after food input. This suggests that some species are able to respond very quickly to variation in food supply.

The relation between foraminiferal distribution and oxygenation of the sediment has been studied rather intensively over the past few years. Alve and Bernhard (1995) found in an experimental study that benthic foraminifera migrate upwards during decreased oxygenation. After re-oxygenation of the sediment, they observed that the foraminifera re-occupied deeper positions. Also in field studies a relationship between the faunal distribution and sediment oxygenation has been found, although some foraminifera were found living (well) beneath the oxygenated surface layers (Jannink et al., 1998, Jorissen et al., 1998). In oxygen experiments, Bernhard (1993) and Moodley et al. (1997, 1998c) found that many benthic foraminiferal taxa are able to survive prolonged anoxia. However, recently performed experimental work by Moodley et al. (1998b) revealed that benthic foraminifera were not capable of surviving prolonged exposure to the combination of anoxia and high sulphide concentrations. The phenomenon of tracking oxygen gradients by benthic foraminifera, either indirectly by grazing on different stocks of bacteria as suggested by Jorissen et al. (1998) and Van der Zwaan et al. (1999), or by limitation through oxygen itself, still needs to be verified and examined more closely.

To study the response of benthic foraminifera to changes in organic enrichment and/or oxygenation of the sediment, clearly more experiments and field studies are needed. By studying benthic foraminifera under laboratory conditions one is able to control almost all parameters, but the translation of the experimental outcome to real nature still remains difficult. Field studies, on the other hand, give us the opportunity to study foraminifera in their own habitat under natural circumstances. Obviously, such studies have the disadvantage that regular monitoring is difficult. In the “ADRIA-LEV” project, which started in 1996, we focussed on two ecologically different areas within the Mediterranean bioprovince, which were regularly monitored over a period of two years. The study areas are the Adriatic Sea, characterised by highly variable and eutrophic conditions, and the

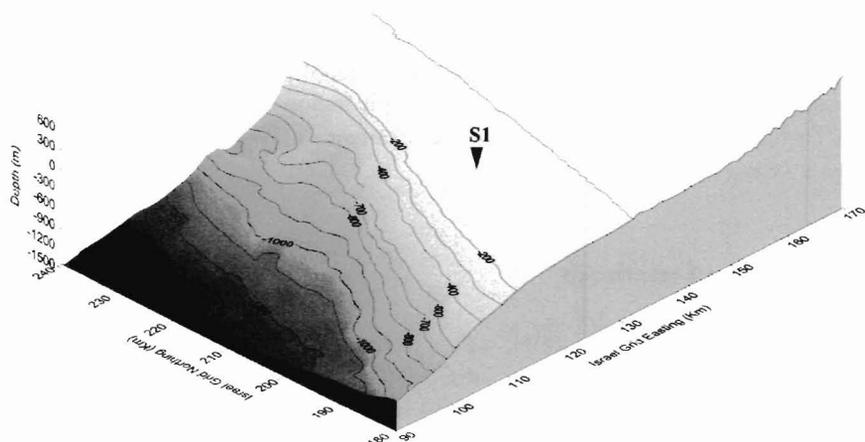


Figure 4-1: Location map of the permanent station S1 (40m).

oligotrophic Levantine Basin. We presumed the food fluxes to be the driving force in seasonal changes of benthic foraminiferal assemblages in the Adriatic Sea, as was also suggested by other authors (Barmawidjaja et al., 1992, 1995; Jonissen et al., 1992). In the oligotrophic Levantine Basin, however, we expected stable oligotrophic conditions to prevail (Berman et al., 1984; Krom et al., 1991; Yacobi et al., 1995), and therefore minor effects of seasonal change.

In the Levantine Basin nine permanent stations, situated off the Israeli coast (Netanya), were sampled. The stations are located along a depth transect from 40 to 700m. Water column properties, such as chlorophyll-a concentration and CTD-profiles, were monitored during all 12 cruises. Oxygen penetration in the sediment was recorded at every sampled station. By studying the seasonal and in-sediment distribution of the benthic foraminifera, together with the above mentioned parameters, we hoped to be able to shed more light on their intricate ecological background.

In this paper we present data on the distribution through time of living (stained) benthic foraminiferal stocks (63–595µm) at the 40m station (S1, Fig. 1). Data on oxygen penetration in the sediment, CTD-profiles and chlorophyll-a concentrations are also discussed. Data on specific species patterns will be presented in a separate paper

2. Study site

The Levantine Basin is a very oligotrophic part of the Mediterranean Sea (Azov, 1986; Kimor et al., 1987; Krom et al., 1991). Primary productivity is even considered to be low in the coastal regions (Berman et al., 1984; Azov, 1986). Azov (1986) found that the annual average chlorophyll-a

concentration at a neritic station (30m) off the coast of Haifa (Israel) was $\sim 0.34 \text{ mgm}^{-3}$. He found considerable fluctuations in phytoplankton concentrations throughout the year ($0.13\text{--}1.46 \text{ mgm}^{-3}$). His data showed elevated chlorophyll-a concentrations in autumn and a peak concentration occurring in February/March. The Coastal Zone Colour Scan (CZCS) pigment concentrations, averaged over the period 1979–1985 (OCEAN-project webpage), suggest elevated concentrations during winter and peak values occurring around February. Our sample station S1 (40m) is situated in the distal part of the nilotic (= Nile influenced) province and the sediment can be categorised as silty sand ($<2\mu\text{m} = 8.8\%$; $<63\mu\text{m} = 48.8\%$; $63\text{--}250\mu\text{m} = 42.4\%$).

3. Material and methods

At station S1 (40m, $32^{\circ}22.53'\text{N}$, $34^{\circ}48.36'\text{E}$) twelve box cores were taken (Fig. 1; Table I). Continuous profiles of temperature, salinity, density and oxygen were measured with a Sea-Bird Electronics CTD. The chlorophyll-a data was obtained at another sample station (S3, 120m), that was situated close to station S1. Immediately upon arrival aboard the box core sediments were subsampled using two tubes, one for sampling benthic foraminifera and one for *in situ* oxygen measurements. The oxygen measurements were carried out using micro-electrodes attached to a micromanipulator. The other tube was subsampled for benthic foraminifera by slicing the top 2cm into 0.5cm intervals and the deeper part of the column, down to 10cm, into 1cm intervals. The samples were preserved in a Rose Bengal solution (1 g L^{-1} ethanol 96%).

The sediment samples were wet-sieved over $>63\mu\text{m}$, $>150\mu\text{m}$ and $>595\mu\text{m}$ sieves. The residues were wet-studied in order to facilitate distinction between living (Rose Bengal coloured) and dead benthic foraminifera. The Rose Bengal colouring was used very strictly, as described in Jannink et al. (1998).

Cruise number	date	season	Cruise number	date	season
Levc1	25-06-'96	Summer	Levc7	24-06-'97	Summer
Levc2	28-08-'96	Summer	Levc8	03-09-'97	Summer
Levc3	17-10-'96	Autumn	Levc9	02-11-'97	Autumn
Levc4	24-12-'96	Winter	Levc10	14-01-'98	Winter
Levc5	18-02-'97	Winter	Levc11	01-03-'98	Winter
Levc6	06-05-'97	Spring	Levc12	17-05-'98	Spring

Table 4-1: Overview of the LEV-cruises (cruise-numbers, dates, and seasons).

4. Results

4.1 CTD-profiles and chlorophyll-a concentrations

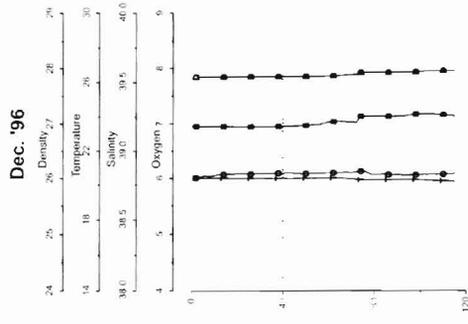
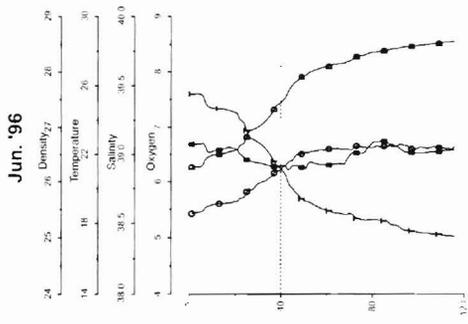
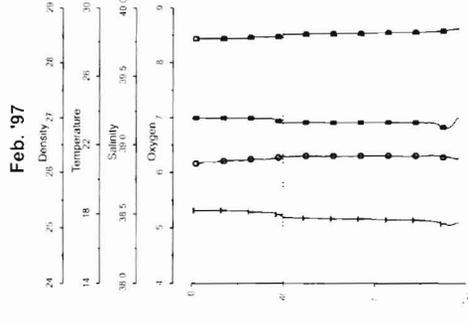
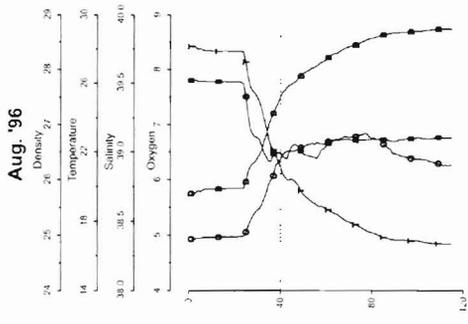
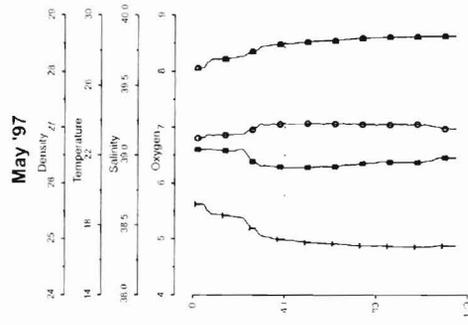
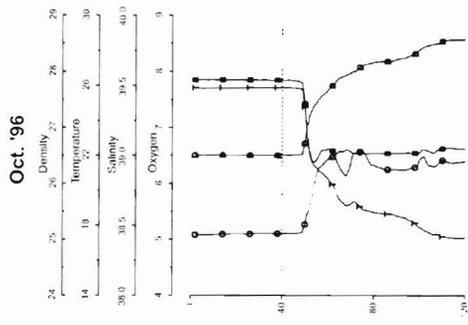
The CTD-profiles (S3; 0–120m) as obtained over the two year sample period are shown in figure 2. A shallow thermocline developed during early spring and summer. During autumn (Oct. '96 and Nov. '97) the thermocline weakened and deepened, resulting in a completely mixed water column during winter down to at least 150m water depth (Dec. '96, Feb. '97, Jan '98 and Mar.'98). This yearly cycle is also clearly visible in the depth of the mixed layer through time as shown in figure 3a. The water temperature measured at 40m water depth (station S1) shows a similar seasonality (Fig. 4a). In winter, when the water column was mixed, the lowest temperatures were measured (Feb. '97 and Mar. '98: 17.8°C and 17.4°C, respectively). Highest temperatures were observed in summer (26.1°C and 26.9°C in Aug. '96 and Sept. '97, respectively) and autumn (26.0°C and 24.7°C in Oct. '96 and Nov. '97, respectively). The halocline developed more or less in line with the thermocline, with the salinity at 40m exceeding 39.5‰ during autumn (Fig. 4a, Oct. '96 and Nov. '97). The dissolved oxygen concentrations measured at 40m water depth, just above the sediment–water interface, varied considerably throughout the year. The lowest values were measured in autumn, whereas peak concentrations of dissolved oxygen were found at the end of winter and spring (Fig. 4b). During the first year the oxygen concentrations were somewhat lower than during the second year.

Chlorophyll-a concentrations at station S3 (120m) show strong seasonality (Fig. 3b). Throughout the year the chlorophyll-a concentrations, integrated over the entire upper 120m, varied between 10 and 30mg m⁻². The highest values were found in autumn and winter (Oct. '96, Dec. '96, Nov. '97 and Jan. '98).

4.2 Total standing stocks of benthic foraminifera (63–595µm) and observations on macrofauna (>595µm)

The total standing stocks (TSS) of benthic foraminifera (63–595µm, per 50cc) in the top 2cm of the sediment (Fig. 4c) display a clear seasonal pattern throughout the two years. The lowest values occurred in autumn and early winter. Numbers of living benthic foraminifera increased at the end of winter and reached a peak during spring. A distinct peak occurred also in late summer of 1997 (Sept. '97). The TSS variations in both years are very similar. The maximum values are in the order of 2–3 times higher than the minimum ones. The ratio between the foraminifera occurring in the >63µm versus the >150µm size fraction is about 10:1 (data not shown here).

In the >595µm size fraction hardly any living benthic foraminifera were observed. In February '97 and March '98, many sand tube-worms of the genus *Polydora* were found living in the top part of the sediment (Fig. 4c). In May '97 and May '98 only degraded *Polydora* remains were found. During this period bivalves and a few benthic foraminifera (>595µm) lived in the topmost sediment layer. In September '97, when a high number of living benthic foraminifera (63–595µm) was observed, many (empty) tubes of a calcareous tube-worm species belonging to the genus *Filograna/Salmacina* were found to be present (>595µm, Fig. 4c).



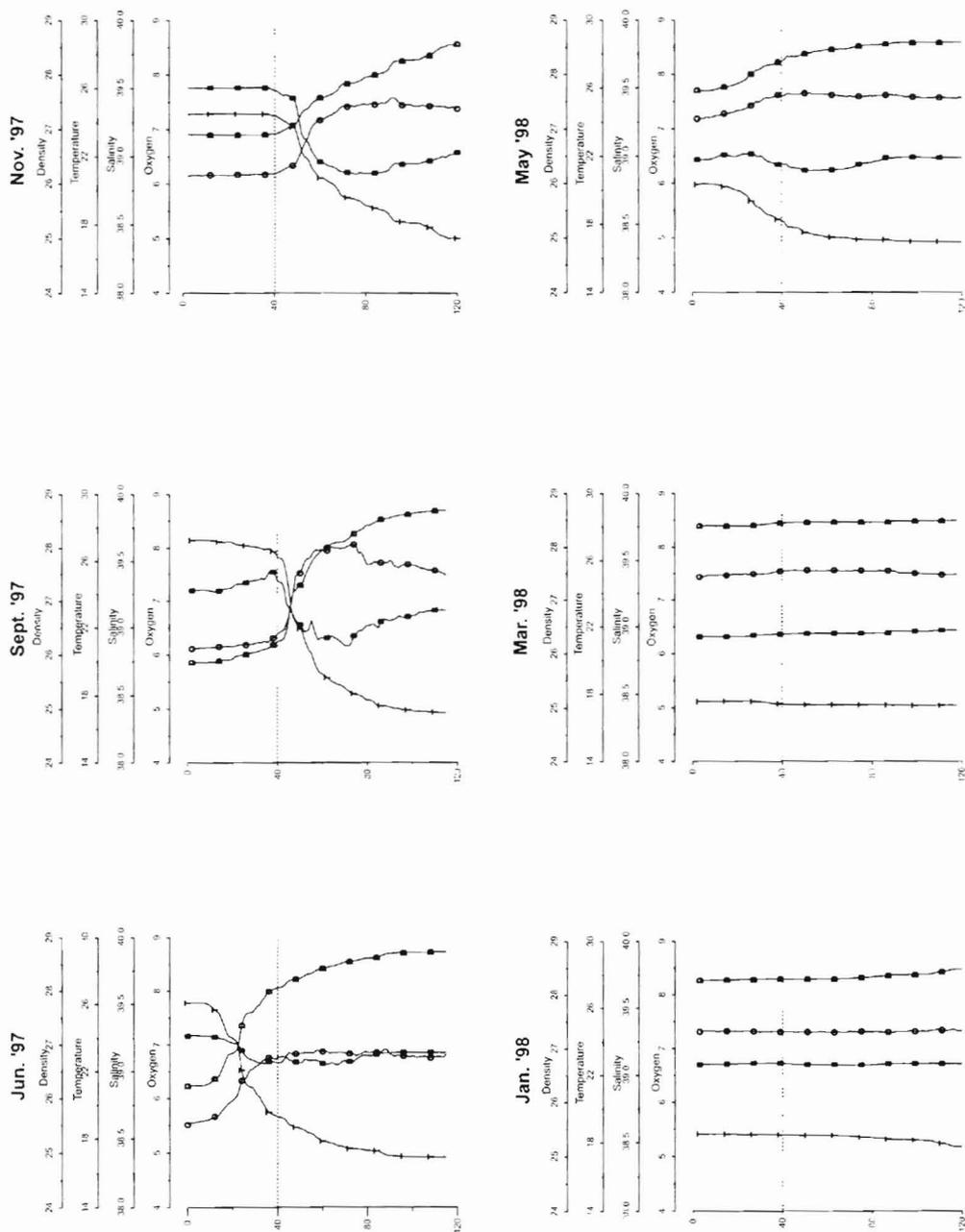


Figure 4-2: CTD-profiles obtained from June'96 - May '98 (station S3, 120m) with dotted line indicating the depth position of station S1 (40 m). (T= temperature, S= salinity, O= oxygen (mg/l), D= density).

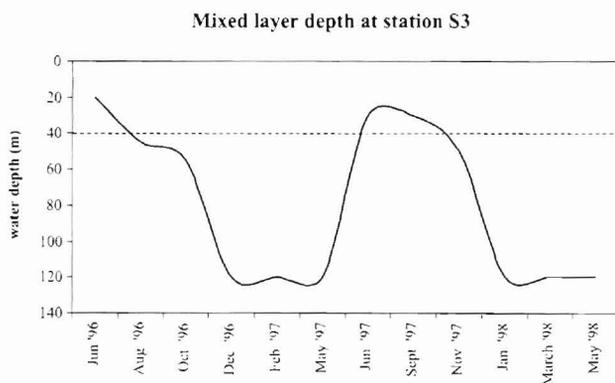
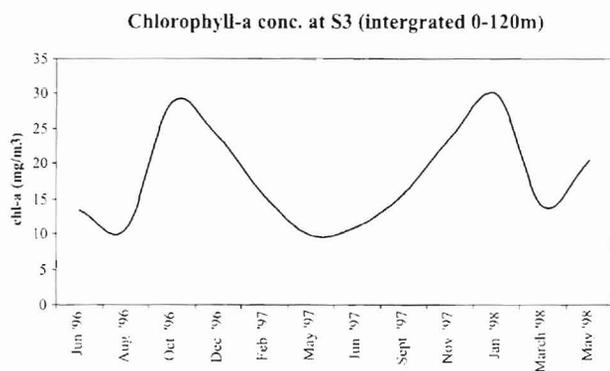


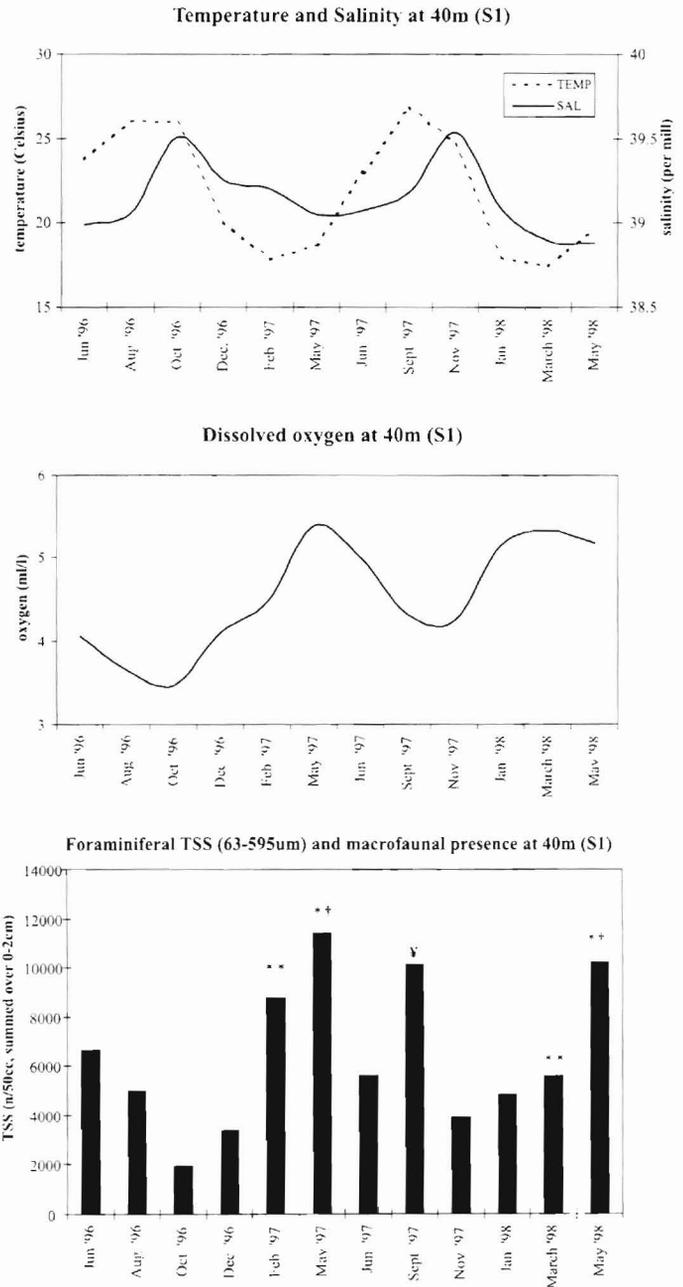
Figure 4-3: Water column properties over the two sampling years obtained at station S3 (120m): a. Mixed layer depth (S1 indicated by dotted line); b. Chlorophyll-a concentrations (integrated over the water column).



4.3 In-sediment distribution of benthic foraminifera (63-595 μ m) and sediment oxygen profiles

The distribution of the benthic foraminiferal standing stock (TSS) and the oxygen profiles in the upper 2cm of the sediment are shown in figure 5. In June '96, the TSS of benthic foraminifera was distributed more or less equally over the top 2cm of the sediment. During this sampling event no oxygen measurements could be carried out. In August '96, benthic foraminiferal numbers displayed a sharp decline with depth. At that time there was virtually no free oxygen in the sediment. In October '96 and December '96, when oxygen was more abundantly available, the benthic foraminifera were distributed evenly over the top 2cm. Later, in February '97, a clear sub-surface maximum developed. At that time oxygen penetrated relatively deep into the sediment. In spring (May '97) high numbers of foraminifera and elevated oxygen concentrations were confined to the sediment top-layer; during summer until the winter of the second year (June '97, Sept. '97, Nov. '97 and Jan. '98; Fig. 5) oxygen became available again in the sediment, and benthic foraminifera were found to be distributed more or less evenly over the sediment column. Although at the end of the winter of the second year (March '98) ample oxygen was present, the TSS of benthic foraminifera declined sharply with sediment depth.

Figure 4-4: Water column properties over the two sampling years obtained at station S1 (40m): a. Water temperature (°C) and salinity (‰) at 40m; b. Dissolved oxygen concentration in the water layer (ml/l) at 40m; c. Total standing stock of benthic foraminifera (n/50cc, summed over the top 2cm) with occurrences of *Polydora* tube worms (living: ** and degraded: +) and dead calcareous tubes (*Filograna/Salmacina* sp., see ¥) indicated.



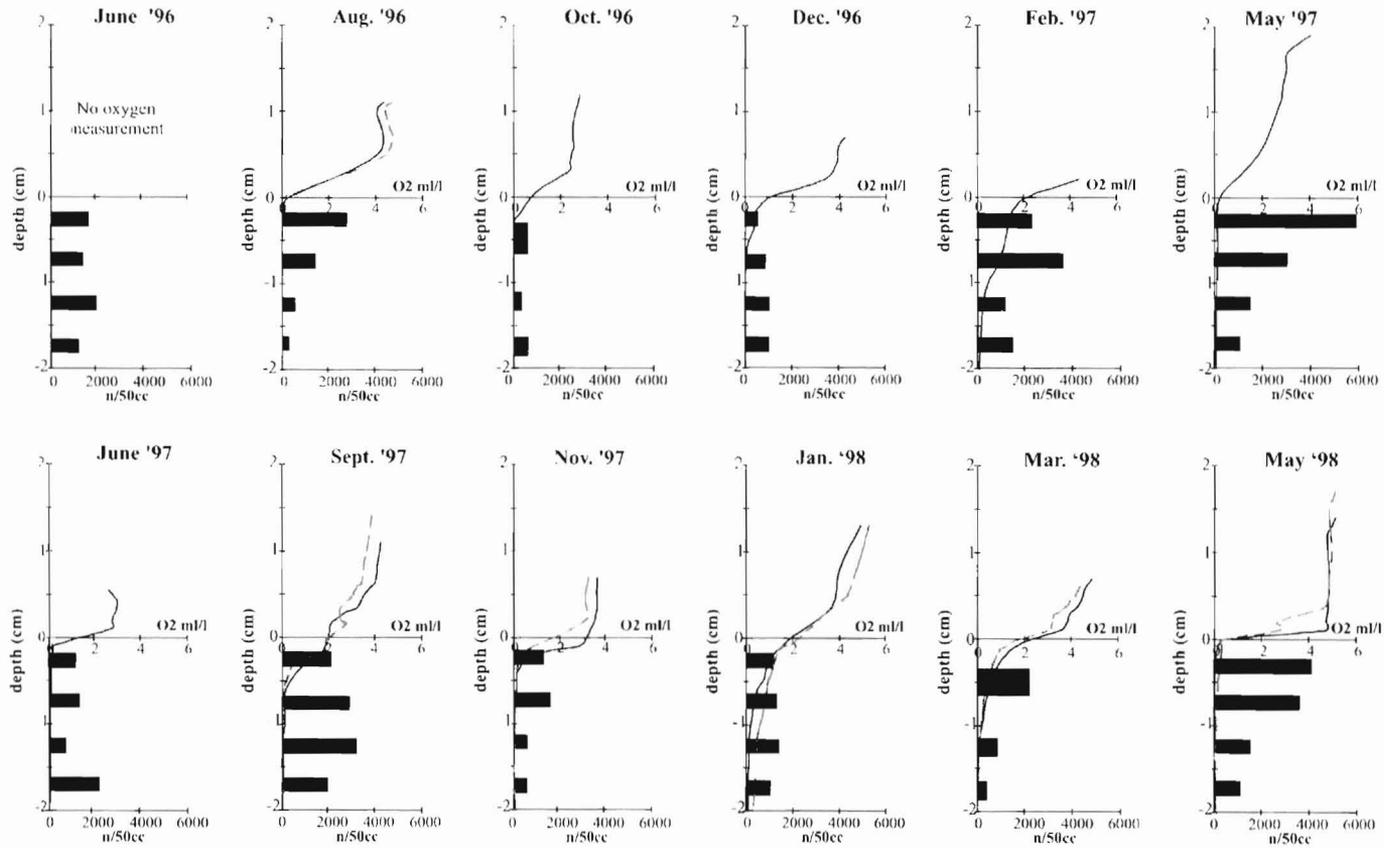


Figure 4-5: In sediment distribution of the total standing stock (TSS) of benthic foraminifera in the upper 2 cm, and the in situ oxygen profile as measured by micro-electrodes (indicated as dotted and/or closed lines), from June '96 till May '98.

This preceded the situation of the spring of 1998 (May), when just as in the previous year, oxygen was only available in very low concentrations and the foraminiferal TSS showed a very sharp in-sediment decrease.

Summarizing the patterns, it seems that the sediment oxygenation was relatively high during autumn and winter. During those seasons the benthic foraminiferal standing stocks were distributed evenly throughout the top 2cm of the sediment. In spring and summer, the oxygenation of the sediment was relatively poor and the benthic foraminifera occurred most abundantly at the sediment-water interface.

5. Discussion

5.1 CTD-profiles and chlorophyll-a concentrations

At our 40m station (S1) we found a distinct seasonality (Fig. 2). Throughout summer surface waters warm up, resulting in stratification of the water column. In autumn the upper layers of the water column mix as a result of rather strong surface water cooling. The base of the mixed layer deepens throughout the winter to a depth of at least 150m at the end of winter. In spring, stratification builds up again, resulting in a stratified water column throughout summer. A similar seasonal cycle is described by Krom et al. (1991) and Yacobi et al. (1995). Cooling and deepening of the mixed layer causes the injection of nutrients from the underlying water layers and sediments. These nutrients are used by phytoplankton, resulting in elevated chlorophyll-a concentrations in autumn (Oct. '96 and Nov. '97) and the beginning of winter (Dec. '96 and Jan. '97). We did not observe a second peak in chlorophyll-a concentration at the end of winter as found by Azov (1986). This can be due to two reasons: either we just missed the peak in two successive years (which seems unlikely), or in shallow water there is really only a single chlorophyll-a peak occurring in autumn/winter. The latter seems to be the most likely explanation, considering the fact that other researchers also found the most pronounced chlorophyll-a peak at the beginning of winter (Antoine et al., 1995).

5.2 Foraminiferal standing stocks and observations on macrofauna

The variations throughout the year in foraminiferal abundances seem to be related more closely to the flux of organic matter than to the oxygenation of the sediment. After the peak concentration of chlorophyll-a, during autumn and the first part of winter, the TSS of benthic foraminifera increases (Figs. 3 and 4), and eventually peaks at the end of winter (Feb. '97) and most clearly in spring (May '97 and May '98). The time lag between the peak in primary productivity (autumn/winter) and the peak abundance of the benthic foraminifera (end of winter/spring) is rather long and may be due to the presence of macrofauna. We found abundant living *Polydora* tube worms (>595µm size fraction) in the top sediment layer during February '97 and March '98. In May of both years these tube worms were nearly absent and only degraded remains were found. Tube worm species belonging to this genus are known for their opportunistic reaction to organic enrichment of the sediment (Grassle and Grassle, 1974, Widbom and Frithsen, 1995). Widbom and Frithsen (1995) observed *Polydora* tube

worms in an experimental set up. There, the tube worms had a significantly higher abundance after organic enrichment, whereas benthic foraminifera had a significant lower abundance compared to their abundance in the control mesocosm. Widbom and Frithsen (1995) suggested that competition for space by a few opportunistic macrofauna species (such as *Polydora*), could limit the response of other species within a benthic community. Also Moodley et al. (1998a) suggested that biological interaction by macrofauna could have negative effects on meiofaunal densities. The distribution pattern as found in February '97, when the benthic foraminifera showed a clear sub-surface maximum (Fig. 5), could well be a result of competition pressure of the *Polydora* tube worms. The peak abundance of the benthic foraminifera in May '97 then would be a result of more degraded organic matter which became available at the time the tube worms no longer caused competition. The remains of the tube worms could even serve the foraminifera as source of (degraded) food. The high primary production in winter, followed by a peak occurrence of *Polydora* and later of benthic foraminifera, was repeated in the second year.

The peak abundance of the benthic foraminifera during September '97 seems anomalous. It only occurred during that particular year, when the top part of the sediment contained large amounts of tubes of dead calcareous tube worms (*Filograna/Salmacina*). These worms are known to occur between 5-60m water depth (Ben-Eliahu and Fiege, 1996), but generally live on rocky substrates (Ten Hove, pers. comm., 1999). The winds and currents that caused the water layers to be mixed already down to 40m in September '97 (Fig. 2), probably transported these *Filograna/Salmacina* remains from shallower (rocky) substrates along the Israeli coast to our sampling site. The presence of the transported tubes could have provided a special niche for the benthic community: they may have provided shelter from currents, and the organic material left in the tubes possibly was available for consumption by the foraminifera.

time	process	effect
AUTUMN/ WINTER	mixing →	high primary productivity
WINTER	maximum mixing and ventilation	high benthic macrofaunal abundance
SPRING	stratification →	high foraminiferal abundance <i>limitation of primary productivity</i>
SUMMER	maximum stratification	<i>decrease meiofauna</i> ↓ limitation of meiofauna

Figure 4-6: A summary of the annual processes that influence the foraminiferal TSS at the 40m station (S1) in the SE Levantine Basin (for explanation see text).

The larger standing stock of benthic foraminifera as a response to an increase in organic matter has been observed by many researchers. Some found only a short time lag between organic enrichment of the sediment and increase in foraminiferal abundance (Faubel et al., 1983, Gooday, 1988). Faubel et al. (1983) recorded a tenfold increase within six weeks after the arrival of organic matter at the seafloor. Levin et al. (1999) found agglutinated foraminifera to ingest $\delta^{13}\text{C}$ -labeled diatoms within 1-1.5 days. From deep-sea benthic foraminifera it is known that they react within 1-2 months following organic enrichment (Gooday, 1988). Therefore, the time lag between the peak of primary productivity and increased benthic foraminiferal standing stock as found in our data, seems to be extremely long. As discussed earlier, macrofaunal competition could have been an important factor in this respect, as was also suggested by Widbom and Frithsen (1995). Following this line of reasoning it seems logical to assume that the relatively low values of TSS as found in October '96 and November '97 respectively, are a result of the exhaustion of food resources. The annual cycle as described above is summarised in figure 6.

5.3 Foraminiferal in-sediment distributions and sediment oxygenation

In contrast with the standing stock patterns, the in-sediment distribution of the benthic foraminifera appeared to be influenced less by the organic matter flux than by the oxygen concentration (Fig. 4). The oxygenation of the sediment seemed, in its turn, to be closely related to dissolved oxygen concentrations in the overlying water layer. After mixing of the water column in autumn, the concentration of dissolved oxygen in the water at 40 m water depth increased. This is reflected in the relatively deeper oxygenation of the sediment during autumn and winter. In summer, when the concentration of dissolved oxygen in the water layer was relatively low, the depth of oxygen penetration in the sediment became rather shallow (Aug. '96 and Jun. '97).

In general, the foraminiferal distribution in the sediment followed the profile of the in-sediment oxygen concentration. This demonstrates the influence of the penetration depth of oxygen, and the amount of available free oxygen in the sediment, on the distribution of living benthic foraminifera. With shallow penetration of oxygen in the sediment, or with low amounts of free oxygen, the numbers of living benthic foraminifera decreased sharply with sediment depth (Aug. '96, May '97, and May '98). With increasing oxygen penetration or concentration, benthic foraminifera were more or less evenly distributed (Oct. '96, Dec. '96, Feb. '97, Sept. '97, and Jan. '98). A similar response was observed by Alve and Bernhard (1995) and Ohga and Kitazato (1997). Alve and Bernhard (1995) found the benthic foraminifera moving upwards in the sediment to avoid oxygen deficiency; they re-migrated after re-oxygenation. In our case, the in-sediment distribution profiles of the benthic foraminifera in both May '97 and May '98 display a steep decline, following a sharp oxygen gradient. The dissolved oxygen concentrations in the overlying water, however, were relatively high. The steep sediment oxygen profiles were probably due to degradation of organic matter, which had taken place before and during that period. Kitazato and Ohga (1995) also found steeply declining benthic foraminiferal distribution patterns after input of organic matter. They suggested that the degradation process consumes the oxygen in the sediment column and would therefore cause the benthic

foraminifera to migrate vertically in order to reach the more oxygenated surface of the sediment. Van der Zwaan and Jorissen (1991) proposed a model for microhabitat occupation during various stages of oxygen deficiency, which was based on the assumption that the presence of infaunal life is controlled by a critical oxygen level. According to Jorissen et al. (1998) oxygen would influence the foraminiferal distribution in the sediment only in an indirect way. They recently found a clear relationship between depth of maximum occurrence of infaunal species and pore water profiles of oxygen and nitrate. They suggested a very close coupling of the benthic foraminiferal zonation in the sediment and prevailing geochemical processes.

Although we found a clear relationship between the oxygenation of the sediment and the foraminiferal distribution in the Levantine Basin, some foraminifera were found living also well beneath the oxygenated sediment layers. From experimental studies we already know that some taxa are capable of surviving anoxia (Bernhard, 1993; Moodley et al., 1997), and even mild H_2S stress for some time (Moodley et al. 1998b). This suggests that some species are microaerophilic and/or facultative anaerobic (see Bernhard, 1996 and references therein). However, according to Moodley et al. (1998b) the tolerance to anoxia and short-term sulphidic conditions is limited to survival. This could imply that, although benthic foraminifera are capable of surviving anoxia, they need oxygen in order to complete their life-cycle. It should be noted that the species in our assemblages differ from the taxa discussed by Bernhard (1993) and Moodley et al. (1997, 1998b). But it cannot be excluded that in an oligotrophic area as the Levantine Basin the proportion of obligate aerobic taxa is high, leading to a strong regulation of the assemblage by the oxygenation of the sediment. This is supported by the changes in vertical distribution of the benthic foraminifera over the years at our Levantine station.

The question whether the benthic foraminifera are actively tracking a critical oxygen level and/or related geochemical zones, or are attracted by the accompanying bacteria in these different zones, still remains to be resolved. Jorissen et al. (1998) and Van der Zwaan et al. (1999) suggested that the vertical distribution of the foraminifera could be caused by the succession of various stocks of bacteria, which in its turn would be influenced by the oxygenation of the sediment. Our data are inadequate to solve this issue.

6. Conclusions

The Levantine Basin is known for its oligotrophic waters. Although we expected a more or less stable benthic community, we found that in shallow water the abundances of the foraminiferal assemblages as well as their in-sediment distribution changed drastically throughout the two years we sampled.

The overall abundance of living benthic foraminifera in the sediment column seems to be regulated by the seasonal increase of organic matter following the winter primary productivity peak. The foraminiferal reaction to the increased flux probably was delayed by the presence of *Polydora* tube worms. Oxygen plays a major and limiting role in the vertical distribution of the benthic foraminiferal community at our station St. With good oxygenation of the sediment a more or less even distribution

of benthic foraminifera over the first 2cm of the sediment column prevailed. Under less ventilated circumstances the bulk of the benthic foraminifera retracted to the uppermost layer of the sediment. Nevertheless, considerable amounts of foraminifera were found to survive in deeper sediment layers, under anoxic conditions.

Life-strategies of shallow-water benthic foraminifera in the SE Levantine basin

With: Sandra Langezaal, Ahuva Almogi-Labin, and Bert van der Zwaan

Abstract

During twelve bimonthly cruises, box core sediments were obtained from a shallow water sample station (S1, 40m) in the Levantine basin. We examined the topmost layers of the sediment (0-2cm) for the abundance and in-sediment distribution of the benthic foraminiferal species, and compared these with the sediment oxygenation. From the total foraminiferal assemblage the 28 most common taxa were selected and used for a hierarchical clustering, resulting in a dendrogram with five clusters. The three major species clusters could be categorized as epifaunal, shallow infaunal, and deeper infaunal. Our data suggest that the life-strategy of epifaunal species as *Quinqueloculina* spp., *Nodophthalmidium* sp., and *Epistominella vitrea* involves that they attempt to avoid oxygen deficiency by inhabiting the surface sediments; only when oxygen penetrates the deeper sediment layers these species are found living there. The epifaunal taxa show a strong numerical response after increasing primary productivity and organic enrichment of the sediment. The numbers of *E. vitrea* increased in May only, suggesting that this species needs a higher organic matter concentration in order to respond by reproduction.

The shallow infaunal taxa (*Bolivina striatula*, *Bolivina seminuda*, and *Bolivina dilatata*) are generally found to be dispersed over the top 2cm of the sediment. Their abundance fluctuates over the two years, but their overall relatively low standing stocks display no clear seasonal pattern. The life-strategy of these species seems to be one of surviving and coping under less favourable conditions (e.g. oxygen deficiency), together with avoiding competition stress from other fauna.

The species categorized as deeper infaunal species (*Eggerella* spp., *Caronia silvestrii*, and *Bulimina marginata*) occupy a relatively stable in-sediment microhabitat, even under anoxic circumstances. They occupy a niche which cannot be inhabited by other benthic foraminifera because of its unfavourable conditions (oxygen deficiency). Not only are the deeper infaunal species able to survive, they are even capable of thriving under these circumstances.

1. Introduction

The distributions of living (Rose Bengal stained) benthic foraminifera have been studied already for more than half a century. Bradshaw (1955), for example, observed the reactions of benthic foraminifera to changes in environmental parameters such as food, temperature and oxygenation. Today, this research is still of tremendous value in order to assess the microhabitat of benthic foraminifera and their specific niche therein. Much emphasis has been placed on the environmental parameter oxygen, and the reaction of benthic foraminifera to variations in its concentration (Alve and Bernhard, 1995, Bernhard, 1993, Moodley et al., 1997, 1998b). From what we know now, some benthic foraminifera are able to survive under anoxia (Bernhard, 1993, Bernhard and Alve, 1996, Jannink et al., 1998, Jorissen et al., 1998, Moodley et al., 1997, 1998b, see also Chapter 4), but most foraminifera cope less well with negative side effects as sulphide production (Moodley et al., 1998a). Whereas laboratory experiments are providing us with a lot of valuable information, the results are sometimes hard to translate to the natural situation. Therefore detailed and extensive field-evidence is still required.

To be able to unravel the ecology of benthic foraminifera under their natural environmental circumstances, frequent monitoring is imperative. In the course of the LEV-project we sampled every two months for a period of two years in order to study the seasonal distribution and abundances of the benthic foraminifera living in the oligotrophic Levantine waters, off the Israeli coast. In Chapter 4, we presented and discussed the variations in the total standing stocks at station S1 (40m). We concluded that although the Levantine waters are thought to be stable and oligotrophic, there is a strong seasonal cycle in the oceanography which is clearly reflected by the benthic foraminifera that live in the sediment. The mixing of the water layers, which starts every year in autumn, brings nutrients to the surface waters resulting in an increase in primary productivity during winter (Antoine et al. 1995, Dowidar, 1984, see also Chapters 2 and 4). The abundance of benthic foraminifera seems to be positively influenced by organic matter enrichment, with a delay in reaction time that probably is caused by interference of macrofauna (Chapter 4). High foraminiferal standing stocks were found from the end of the winter till spring (Feb. '97, May '97, March '98 and May '98). An additional peak in total abundance occurred in September '97. This is possibly due to early deep mixing that year. Although the TSS seems to be controlled to some extent by the organic flux, it is clear that the in-

Cruise number	date	season	Cruise number	date	season
Levc1	25-06-'96	Summer	Levc7	24-06-'97	Summer
Levc2	28-08-'96	Summer	Levc8	03-09-'97	Summer
Levc3	17-10-'96	Autumn	Levc9	02-11-'97	Autumn
Levc4	24-12-'96	Winter	Levc10	14-01-'98	Winter
Levc5	18-02-'97	Winter	Levc11	01-03-'98	Winter
Levc6	06-05-'97	Spring	Levc12	17-05-'98	Spring

Table 5-1: Table of sampling events

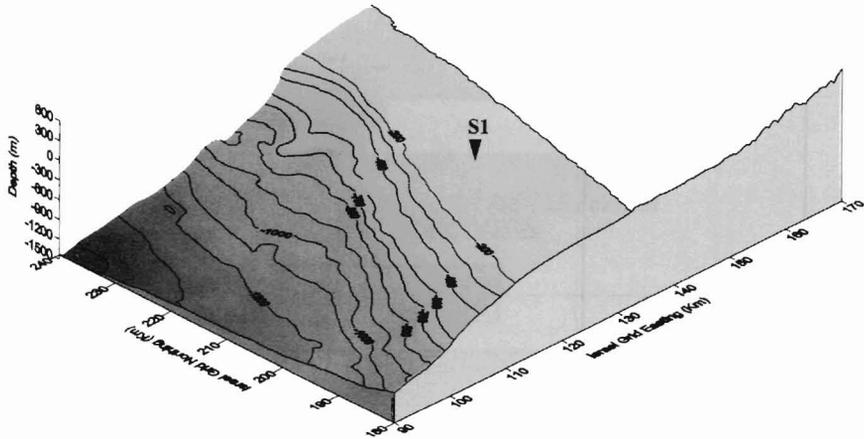


Figure 5-1: Location map of the sampling area, with sample station S1 indicated

sediment (vertical) distribution of the foraminiferal assemblage is strongly affected by the sediment oxygenation. Under conditions of shallow oxygen penetration most benthic foraminifera were found living at the sediment surface. However, if the sediment was well oxygenated benthic foraminifera occurred abundantly deeper.

In this chapter we discuss the data obtained at our station S1 (40m) in more detail. Using a species data-set including the 28 most abundant and important taxa we carried out hierarchical clustering and performed a Principal Component Analysis (PCA). We discuss the three major clusters (out of five) from the resulting dendrogram, and focus on the distribution of the key taxa from each cluster in an attempt to assess the various life-strategies of benthic foraminifera

2. Materials and methods

At station S1 (40m, $32^{\circ}22.53'N$, $34^{\circ}48.36'E$) twelve box cores were taken (Fig. 1; Table I). In addition continuous profiles of temperature, salinity, density and oxygen were obtained using a Sea-Bird electronics CTD (see Chapters 2 and 4). Chlorophyll-a concentrations (integrated over the water column) were measured at the nearby sample station S3 (120m).

The box core sediments were sub-sampled using two perspex tubes, one for *in situ* oxygen measurements and one for sampling benthic foraminifera. Immediately upon arrival on board the oxygen measurements were carried out with micro-electrodes attached to a micromanipulator. The other tube was sampled for benthic foraminifera by slicing the top 2cm into 0.5cm and the 2-10cm into 1cm intervals. The samples were preserved in a Rose Bengal solution (1 g L^{-1} ethanol 96%). The

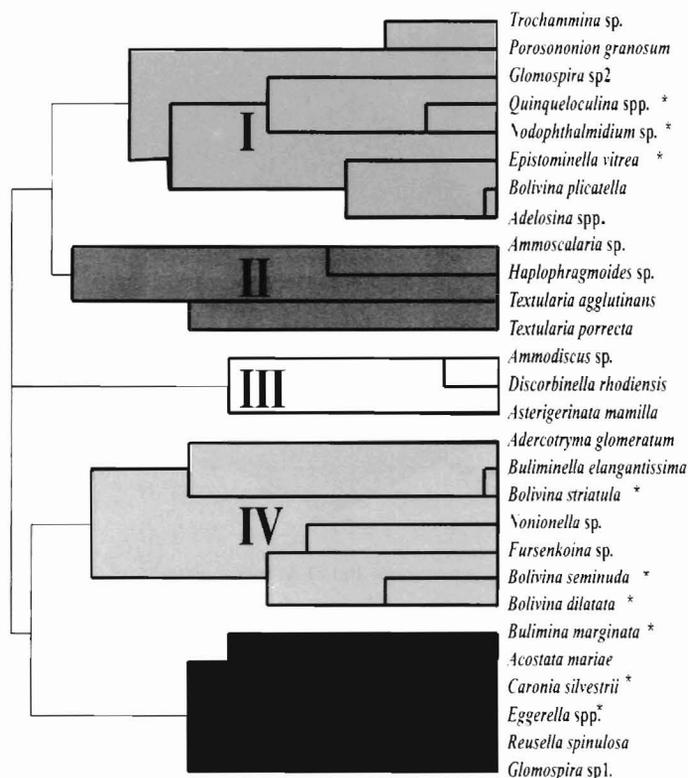


Figure 5-2: Dendrogram obtained by hierarchical clustering of the 28 most abundant and important occurring species. Species indicated with * are used for detailed study.

sediment samples were wet-sieved over $>63\mu\text{m}$, $>150\mu\text{m}$ and $>595\mu\text{m}$ sieves. The residues were studied in a petri-dish with ethanol in order to be able to distinguish between living (Rose Bengal coloured) and dead foraminifera. The Rose Bengal colouring was used very strictly, as is described in Jannink et al. (1998). Although there has been some dispute about using this staining method for recognition of "living" foraminifera (Bernard, 1988), Murray and Bowser (2000) state that results obtained by using the Rose Bengal staining method are as reliable as those of other techniques. Moreover, the temperatures at our stations in the Levantine basin ($>17^{\circ}\text{C}$) do not limit biodegradation; therefore our strict use of Rose Bengal as stain should suffice to indicate specimens living at the time of collection.

A hierarchical clustering was carried out employing the relative abundances of 28 common taxa ($63\text{--}595\mu\text{m}$). We used the statistical program SPSS (version 7.0: average linkage, Pearson correlation, between groups). A Principal Component Analysis (PCA) with environmental parameters was obtained by using the program Canoco (version 4.0). In order to compare the outcome of the hierarchical clustering with the PCA-diagram, it was necessary to exclude sample event June '96 when

no oxygen measurements were performed. Key species were selected of which in-sediment distribution and abundance patterns versus environmental parameters are presented and discussed in detail.

3. Results

3.1 Hierarchical clustering of the 28 most important and abundant species

The data set containing relative numbers of 28 species, was used to perform a hierarchical cluster analysis resulting in the dendrogram shown in figure 2. Five clusters can be distinguished, three larger and two smaller ones. The miliolids (*Quinqueloculina* spp., *Nodophthalmidium* sp. and *Adelosina* spp.) cluster together (Cluster I). This cluster also includes *Epistominella vitrea*. Cluster II consists of only the agglutinated taxa, *Ammoscalaria* sp., *Haplophragmoides* sp., *Textularia agglutinans* and *Textularia porrecta*. The small cluster III consists of *Ammodiscus* sp., *Discorbina rhodiensis* and *Asterigerinata mammila*. Cluster IV consists mainly of bolivinids (*B. dilatata*, *B. senmuda*, *B. striatula*) together with the less common species *Nomonella* sp., *Fursenkoma* sp., *Buliminella elegantissima* and *Adarcotryma glomeratum*. Cluster V includes, among others, the species *Eggerella* spp., *Bulimina marginata*, *Caronia silvestrii*, and *Reussella spinulosa*.

3.2 Principal component analysis

We performed a Principal Component Analysis, without log-transformation, using Canoco (version 4.0, Ter Braak and Smilauer, 1998). The first axis describes 29.6% of the variation, the second axis 12.4% and the third 11.1%. In figure 3 we present the 3rd instead of the 2nd axis; between these axes there is a minor difference in amount of described variation. However, plotting the 3rd axis results in a much better separation of species within the diagram. The available (environmental) parameters are plotted as vectors (Fig. 3). On the first axis, depth plots positively, whereas Shannon diversity plots negatively. On the third axis autumn loads positively, opposite to the vector winter. The total standing stock (TSS) and oxygen vectors are parallel but the vector of TSS is somewhat stronger, meaning that TSS is loading more on these two axes. Note that oxygen and depth are not completely opposite, indicating that oxygen is not linearly related to sediment depth and must be influenced by other factors as well.

The three major clusters of the dendrogram are clearly separated in the two dimensional PCA-diagram. The Cluster I taxa plot negatively on the first axis, with *Quinqueloculina* spp. very close to the oxygen vector. *Nodophthalmidium* sp. and *Epistominella vitrea* are also exactly opposite to sediment depth, but their position is less closely related to oxygen. The species grouped within Cluster IV plot perpendicular to the vectors of oxygen and sediment depth. *Bolivina dilatata* and *Bolivina senmuda* are very close to the base of both axes, suggesting that their ecological behaviour is not really explained by any of these. *Bolivina striatula*, however, is positively related to the vector autumn. All Cluster V species load positively on the 1st axis. *Caronia silvestrii* is negatively related to

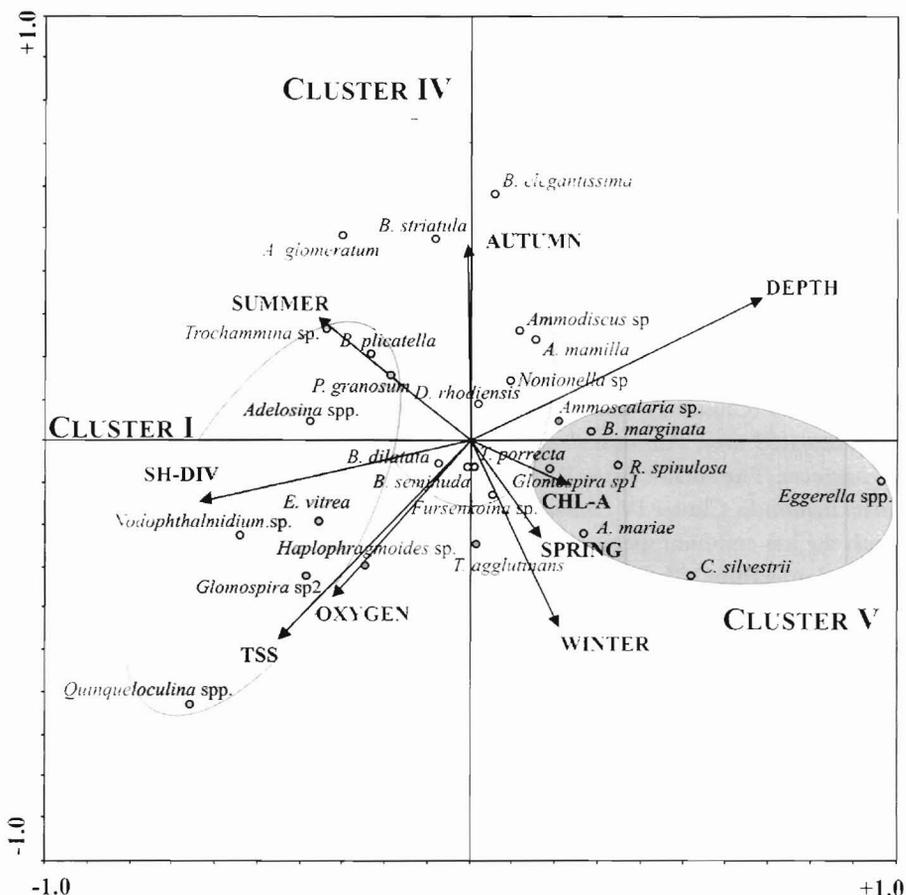


Figure 5-3: PCA-plot obtained from the 28 most abundant and important occurring species. The three major clusters are indicated. Snannon diversity is indicated by SH-DIV.

the 3rd axis, and plots in between the winter and sediment depth vectors. *Bulinna marginata* loads positively on the 1st axis, whereas *Eggerella* spp. seems strongly correlated with sediment depth and, to a lesser extent, winter

Studying the general features of the PCA-diagram, we can distinguish the three species clusters very easily. We categorize the Cluster I taxa, plotting opposite to sediment depth and parallel to the vector oxygen, as epifaunal. Based on their intermediate position between the oxygen and sediment depth vectors, the taxa joined in Cluster IV are categorized as shallow infaunal. We categorize the species included in Cluster V as deeper infaunal, because of their positive loadings on the 1st axis (sediment depth).

3.3 Vertical distribution and abundance of key-taxa

3.3.1 Epifaunal taxa

The *Quinqueloculina* specimens are found living mostly in the top cm of the sediment column (Fig. 4a). Deeper in the sediment, they always occur in relatively low abundances. The group *Quinqueloculina* spp. displays a clear seasonal pattern in its abundance over the two sampling years (Fig. 4b). Following the peak in chlorophyll-a concentration at the end of winter and in May, they occur in high numbers. In September '97, when calcareous tubes are found abundantly at the sediment surface (Fig. 4), an additional peak in numbers of living *Quinqueloculina* spp. is found. The total standing stock (TSS) of *Quinqueloculina* spp. and the primary productivity, as reflected by chlorophyll-a, seem to be in antiphase.

Nodophthalmidium sp. occurs, as *Quinqueloculina* spp., mainly in the top 1cm of the sediment column (Fig. 4c). The total standing stocks of *Nodophthalmidium* sp. display more or less the same seasonality as *Quinqueloculina* spp.: relatively low numbers of living specimens during autumn/midwinter, and higher numbers at the end of winter and in spring (Fig. 4d).

Epistominella vitrea displays the strongest seasonal abundance pattern of all taxa (Fig. 4f). It occurs with high abundances in spring and summer of both years, whereas it is found only in very low numbers (or not at all) during the remainder of the year. Compared to *Quinqueloculina* spp. and *Nodophthalmidium* sp., the increase of *E. vitrea* specimens is timed somewhat later: *E. vitrea* peaks only in May and June. The numerical response of *E. vitrea* may well be due to the organic matter which becomes available at the sediment surface after the degradation of tube worms (Jannink et al., Ch. 4). In May most *E. vitrea* specimens are found living in the upper 1cm of the sediment column, whereas in June, the specimens are living more equally dispersed over the top 2cm of the sediment column (Fig. 4e).

3.3.2 Shallow infaunal taxa

Bolivina striatula is found to live most dominantly in the upper 1cm of the sediment, but occasionally occurs deeper (Fig. 5a). The total standing stock (TSS) of *B. striatula* is highly fluctuating over the years, but shows no clear seasonal pattern (Fig. 5b). Numbers are quite low during the first year with minimum values occurring in autumn/midwinter, whereas during the winter of the second year it reaches its peak. There is no clear relation between the TSS of *B. striatula* and the chlorophyll-a concentrations throughout the two years.

Bolivina seminuda displays, like *B. striatula*, no clear seasonal TSS pattern (Fig. 5d). Throughout the two years its numbers are quite stable, except for two occasions of increased numbers in June '96 and February '97. The in-sediment distribution of *B. seminuda* shows that this species generally is living evenly dispersed over the first 2cm of the sediment column (Fig. 5c). Like the TSS of *B. striatula*, also the TSS pattern of *B. seminuda* displays no clear correlation with primary productivity throughout the years.

Like the other bolivinids, *Bolivina dilatata* displays no seasonality in its TSS pattern. Its numbers vary throughout the different seasons and years, but no repetitive pattern can be distinguished (Fig. 5f). The highest numbers of *B. dilatata* are found in May '98, while in the same period of the

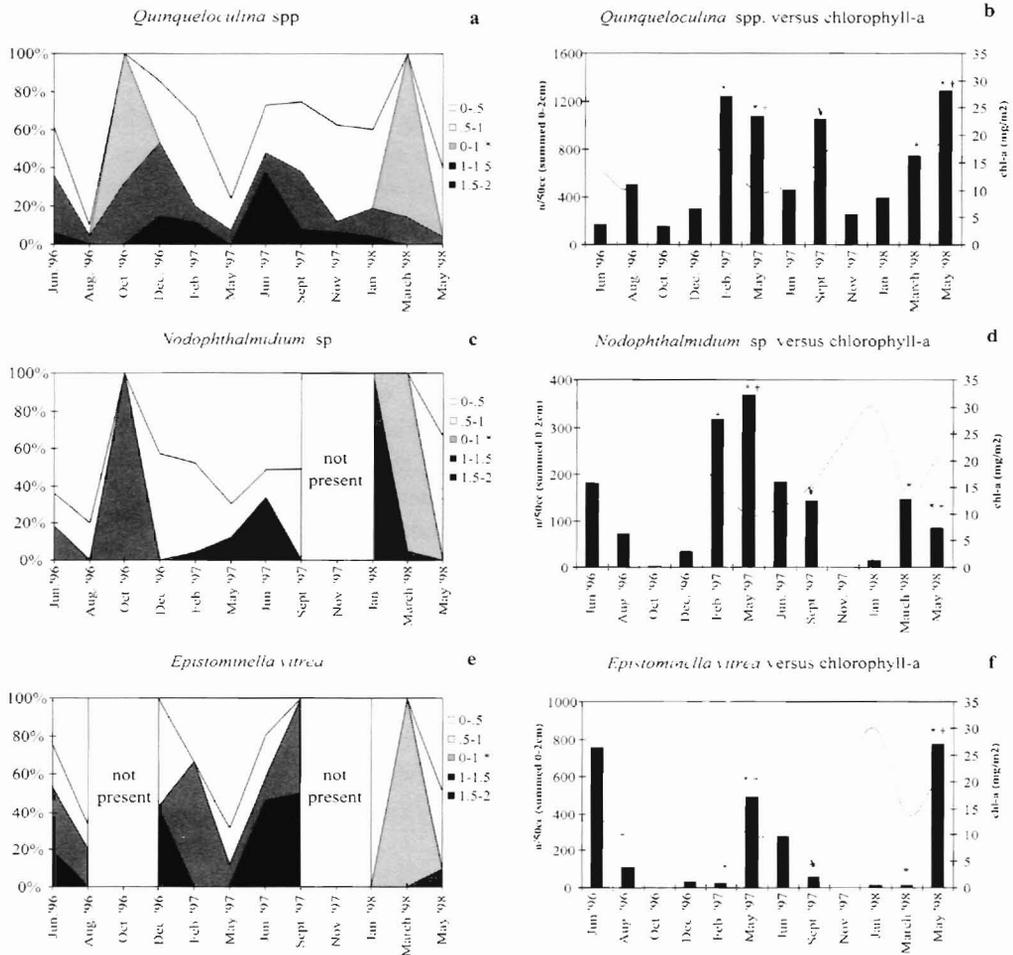


Figure 5-4: Vertical distribution (in % of its total standing stock) and abundance of the three epifaunal species versus chlorophyll-a concentration
 a-b) *Quinqueloculina* spp., c-d) *Nodophthalmidium* sp., e-f) *Epistominella vitrea*. * = occurrence of *Polydora* tube worms, * + = degraded tube worm remains, † = calcareous tubes.

preceding year it occurs with minimum values. The abundances of *B. dilatata*, as for the other bolivinids, do not show any relation with the chlorophyll-a concentrations throughout the years. Its in-sediment distribution differs over the two years, with most specimens occurring just below the top sediment layer (Fig. 5e). The standing stock patterns of the three taxa just discussed show no resemblance to each other.

3.3.3 Deeper infaunal taxa

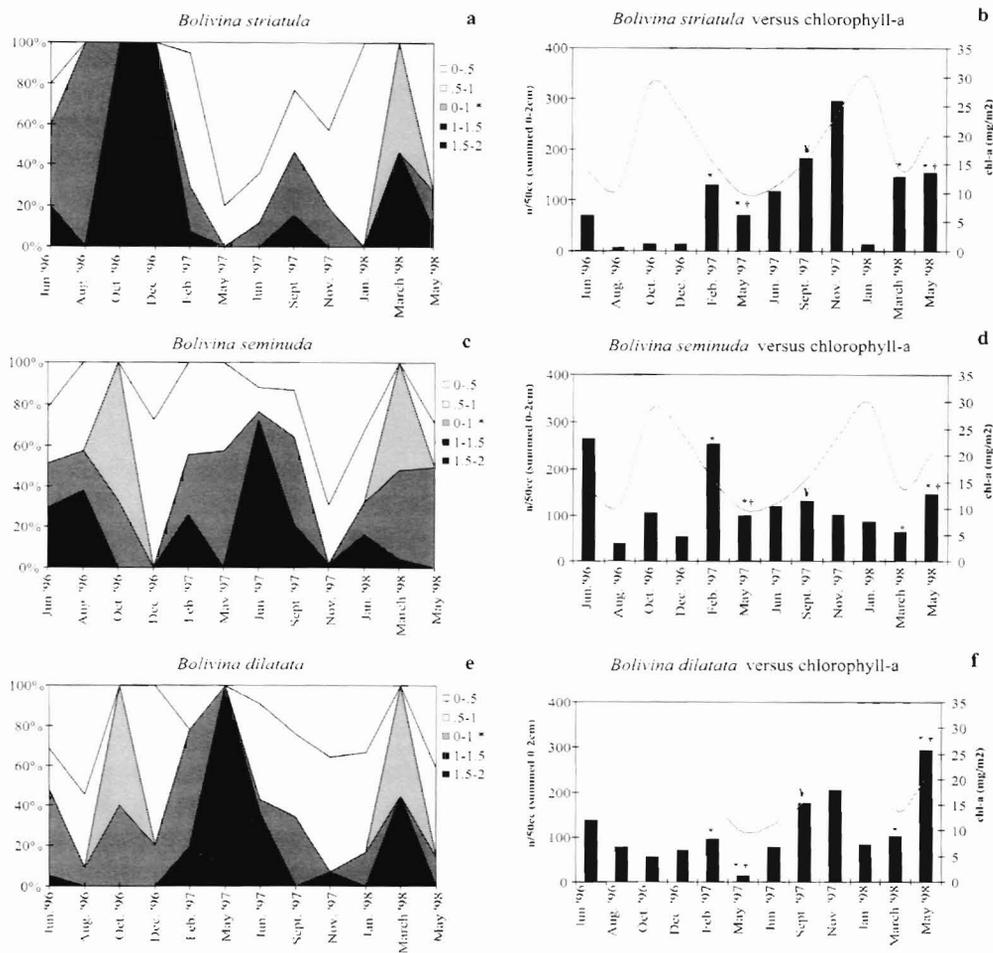


Figure 5-5: Vertical distribution (in % of its total standing stock) and abundance of the three shallow infaunal species versus chlorophyll-a concentration: a-b) *Bolivina striatula*; c-d) *Bolivina seminuda*, e-f) *Bolivina dilatata*. For explanation of inserted symbols see figure 4.

Species which are found to consistently inhabit the deeper sediment samples are *Eggerella* spp., *Caronia silvestrii*, and *Bulimina marginata* (Fig. 6). *Eggerella* spp. is found to live very abundantly at our sampling site. Whereas its numbers are clearly fluctuating throughout the two years, the highest standing stocks are found in spring (Fig. 6b). *Eggerella* spp. displays a relatively quicker numerical response after the mixing of the water layers, and resulting peaks in chlorophyll-a concentration, than the epifaunal taxa. Already in December '96 and January '98 *Eggerella* spp. becomes more abundant, whereas the numbers of the epifaunal taxa increase only in February '97 and March '98. The in-sediment distribution of *Eggerella* spp. is fairly stable, with its relative numbers being spread equally

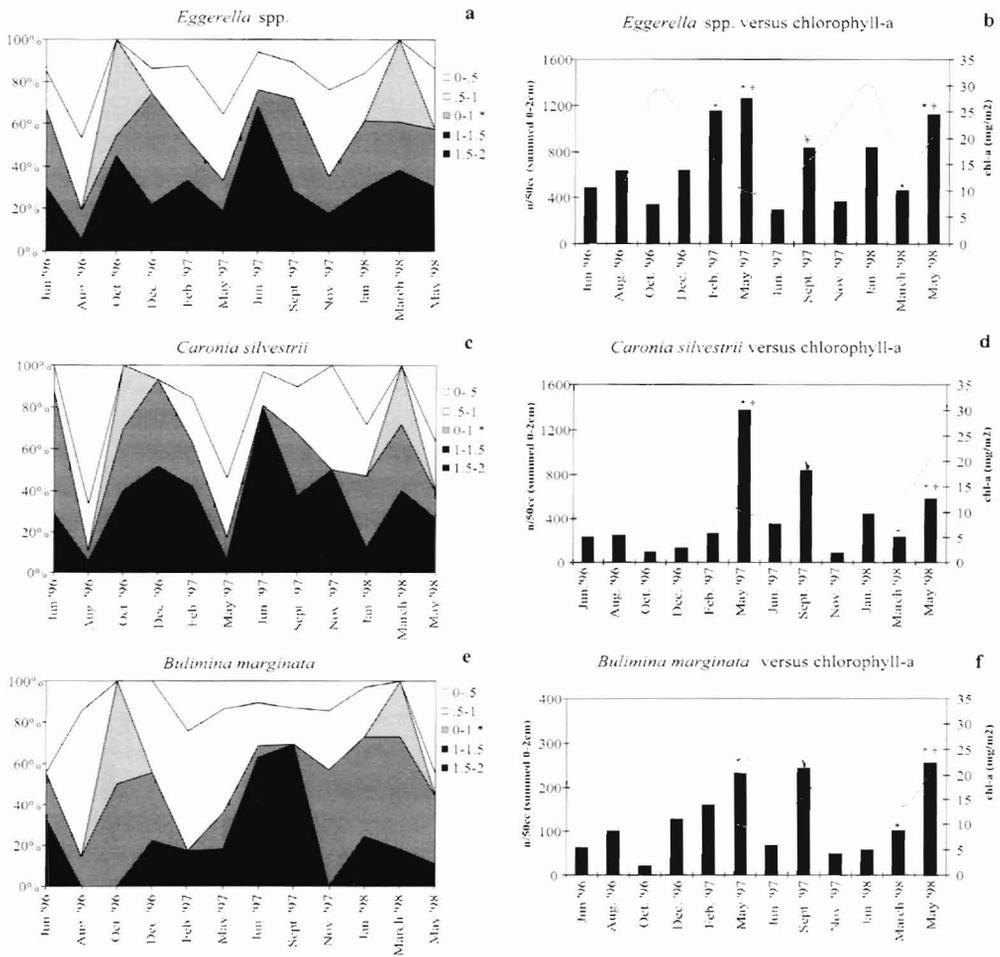


Figure 5-6: Vertical distribution (in % of its total standing stock) and abundance of the three deeper infaunal species versus chlorophyll-a concentration: a-b) *Eggerella* spp.; c-d) *Caronia silvestrii*; e-f) *Bulimina marginata*. For explanation of inserted symbols see figure 4.

over the first 2cm of the sediment column (Fig. 6a)

Although *Caronia silvestrii* generally does not occur in very high numbers, it peaks in May '97 and to a lesser extent again in September '97 and May '98 (Fig. 6d). The primary productivity does not seem to influence the TSS of *C. silvestrii*, but the organic enrichment caused by degradation of tube worms at the sediment surface clearly does (Fig. 6d, and Chapter 4). The specimens of *C. silvestrii* are generally found to live abundantly in the deeper sediment layers (1-2cm), but its peak occurrences in May are found shallower (Fig. 6c).

Bulimina marginata, which is a common but not very abundant species, occurs with elevated numbers in May '97, September '97 and May '98 (Fig. 6f). Similar to *Eggerella* spp. it already exhibits increasing numbers immediately after the increase in chlorophyll-a concentration (Dec. '96 and Jan. '98). The in-sediment distribution varies strongly throughout the two years (Fig. 6e); *B. marginata* even occurs occasionally with relatively high numbers in the deepest sediment layer (1.5–2cm).

3.4 In-sediment distribution of the three species groups versus sediment oxygenation

In the figures 7–9 the vertical distribution of the three species groups versus the sediment oxygenation is shown. The in-sediment distribution of the epifaunal species is overall shallow. Especially when the oxygenation of the sediment is poor, the specimens are found mostly concentrated in the topmost sediment layer (e.g. Aug. '96). In May of both years the oxygen seems to be consumed already at the sediment–water interface, whereas the epifaunal species reach their highest abundance here. However, their vertical standing stock patterns display a very steep decrease with sediment depth. When the sediment is re-oxygenated the epifaunal species are found living deeper in the sediment (Dec. '96, Feb. '97, and Sept. '97).

Throughout the two years the shallow infaunal taxa are generally evenly dispersed over the first 2cm of the sediment column (Fig. 8). Only at some occasions, when oxygenation of the sediment is fairly poor, they are found to live shallower. The shallow infaunal species occur living under suboxic as well as anoxic circumstances, but generally reach higher abundances under more oxygenated conditions. When the oxygenation of the sediment is very poor (May '97 and May '98) they occur with relative lower numbers, and are distributed clearly shallower than the deeper infaunal species.

The deeper infaunal species are generally found to be equally distributed throughout the top 2cm of the sediment column, even under suboxic to anoxic conditions (Fig. 9). In February '97, September '97 and January '98 the in-sediment distribution seems to reflect the deeper oxygenation, but very high sub-surface abundances are found under oxygen deficient circumstances in May '97 and May '98. This suggests that oxygen deficiency within the sediment is generally not severely limiting these taxa.

3.5 Average total standing stock (TSS) versus mean Average Living Depth (ALD).

In figure 10 the average TSS of the species is plotted against the mean ALD (Average Living Depth, see Jorissen et al., 1995). The group of shallow infaunal taxa (*Bolivina striatula*, *Bolivina seminuda*, and *Bolivina dilatata*) forms a tight cluster. The standard deviations of their ALDs are rather large due to the large variations in their vertical distribution.

For the epifaunal and the deeper infaunal group, the TSS of the taxa varies strongly. However, on basis of the ALD the two groups can be distinguished very easily. The standard deviations for both the mean ALD and the average TSS of *Epistominella vitrea* are fairly large, due to its extreme fluctuations in abundance and in-sediment distribution over the two years. The miliolid species

Epifaunal taxa

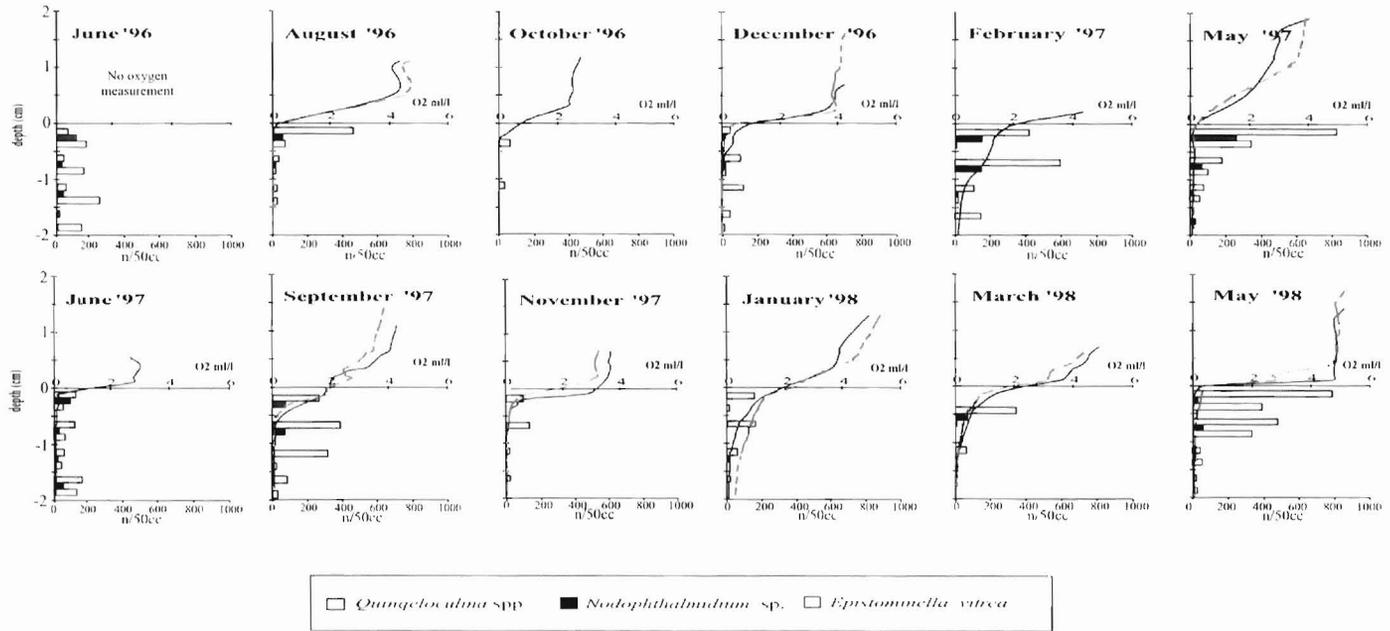


Figure 5-7: In sediment distribution of the epifaunal species versus sediment oxygenation per sampling period.

Shallow infaunal taxa

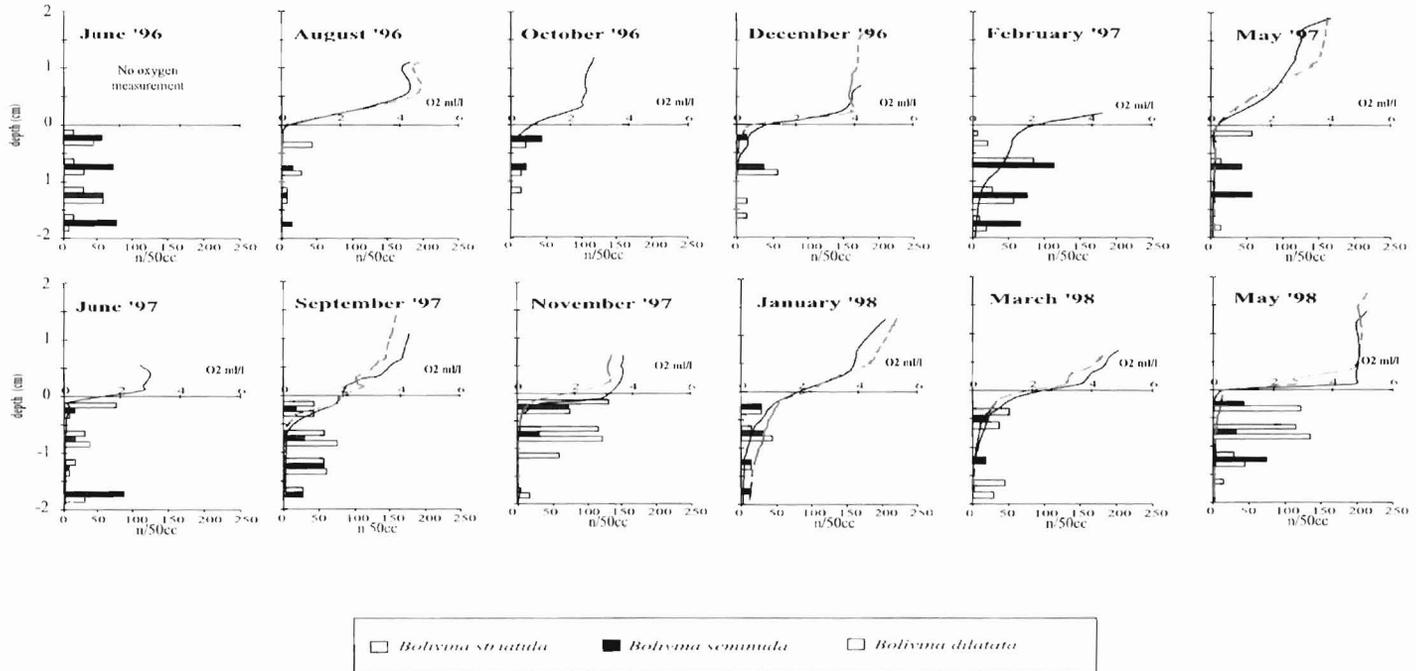


Figure 5-8: In-sediment distribution of the shallow infaunal species versus sediment oxygenation per sampling period.

Deeper infaunal taxa

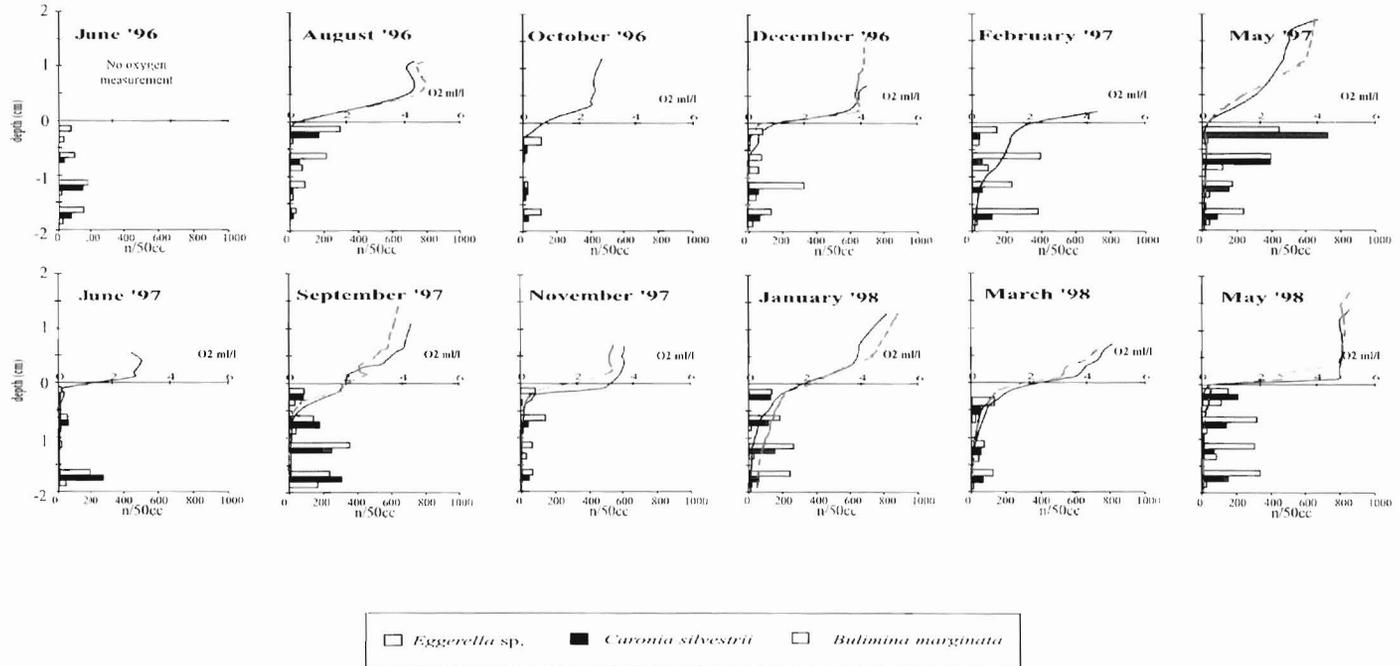


Figure 5-9: In sediment distribution of the deeper infaunal species versus sediment oxygenation per sampling period

Nodophthalmidium sp. and *Quinqueloculina* spp. have shallow mean ALDs with smaller standard deviations than *E. vitrea*, indicating a preference for the top part of the sediment and a less fluctuating in-sediment distribution. Whereas *Nodophthalmidium* sp. is found to occur with low numbers and relatively high standard deviations for the average TSS, *Quinqueloculina* spp. has a high average TSS, but with a smaller standard deviation. This suggests that the fluctuations in TSS of *Nodophthalmidium* sp. were somewhat larger over the two years than the fluctuations in TSS of *Quinqueloculina* spp.

The standard deviations of the TSS of both *Bulinna marginata* and *Caronia silvestrii* are large, due to their fluctuating abundances over the two sample years. Because the abundance of *Eggerella* spp. is generally high, its standard deviations are quite small. The standard deviations of *B. marginata* and *Eggerella* spp. for the mean ALD are relatively small compared to the other taxa, indicating that their deeper in-sediment position is fairly stable.

If we plot the average ALD of the nine taxa versus the standardized (i.e. the standard deviation as a proportion of the average standing stock) standard deviations of their TSS (Fig. 11), we see that the deeper infaunal taxa like *Eggerella* spp. and *B. marginata* show far less extreme fluctuations than, for instance, the epifaunal *E. vitrea*.

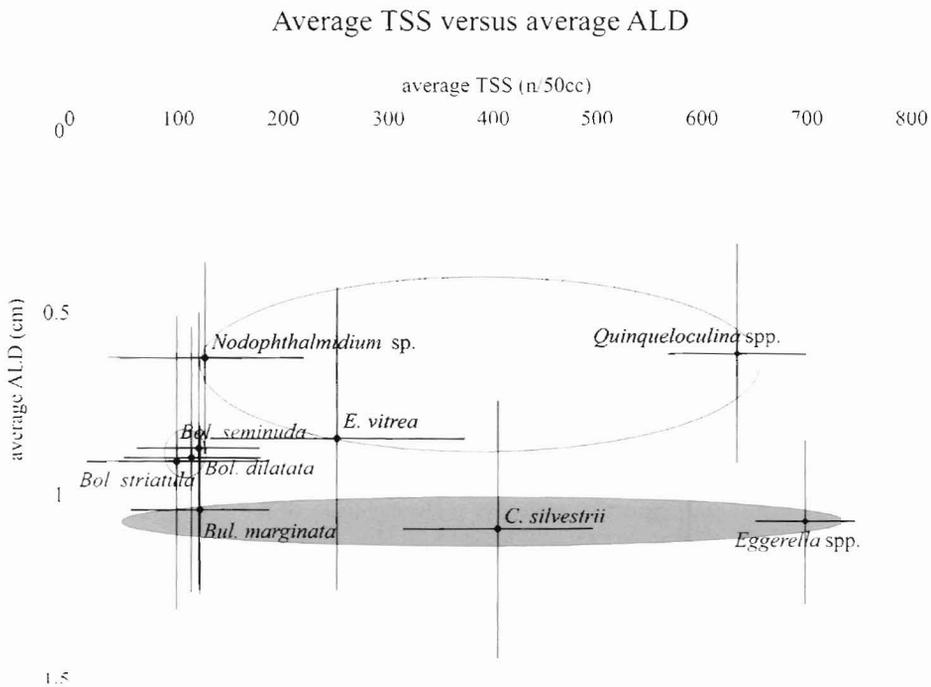


Figure 5-10: The average total standing stock (TSSavg) versus the mean Average Living Depths (ALD) of the nine selected species. The standard deviation of TSS is standardized per species (as % of TSSavg).

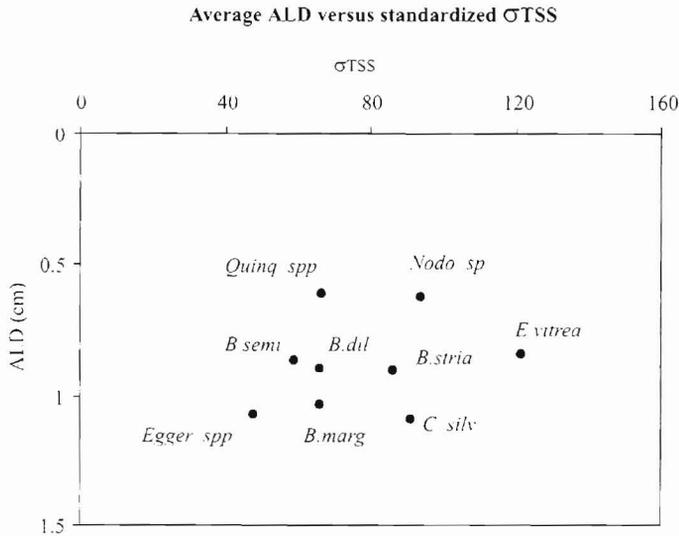


Figure 5-11: The average ALD versus the standardized standard deviation of TSS (for explanation see text).

4. Discussion

Our sample station is situated in the stable, oligotrophic waters off the Israeli coast. In spite of this, the benthic foraminiferal assemblage displays a strong seasonal pattern in total standing stock as well as in vertical distribution (Chapter 4). The in-sediment distribution of the benthic foraminiferal assemblage seems closely related to the sediment oxygenation, whereas the total standing stocks appear to be related to the availability of organic matter as well. Both years, the highest standing stocks are found at the end of winter and the beginning of spring. After the elevated chlorophyll-a levels in early winter, the numbers of benthic foraminifera increase to eventually reach maximum values in May. This delay is probably caused by the presence of sandy tube worms, which are found very abundantly living in February '97 and March '98. After this macrofauna dies off, the competition for space is diminished and the top part of the sediment becomes enriched with the degraded organic matter originating from the tube worms.

The 28 most abundant and important taxa give a clear picture of the ecological range occurring within the foraminiferal community. Hierarchical clustering analysis leads to two small and three major groups. The taxa in these clusters are characterized by a predominantly epifaunal, shallow infaunal, or deeper infaunal position in the sediment. Throughout the two years of sampling the species comprising these different groups display a distinct ecological behaviour, which can be summarized as life-strategies.

The overall vertical distribution of the species within the epifaunal group is very shallow, with occasional occurrences in the deeper sediment layers. They occupy a similar habitat, and also their

fluctuations in total standing stocks are alike. The species occur with relatively low numbers throughout winter, while their highest standing stocks are found at the end of winter and in spring. The somewhat aberrant occurrence in September '97 might have been caused by the presence of empty calcareous tubes (Chapter 4). These could have provided shelter and created a perfect niche for these epifaunal taxa. Moreover, the tubes could very well have contained organic matter originating from the former inhabitants (tube worms) or bacteria, which can also serve as food for the foraminifera. This latter possibility was also suggested by Thomsen and Altenbach (1993), who found an increased biomass of bacteria and benthic foraminifera in and around macrofaunal tubes. The miliolids (*Quinqueloculina* spp. and *Nodophthalmidium* sp.) occurring at our sample site display a clear preference for the top layers of the sediment, which in turn seems strongly related to the oxygenation of the sediment. As for *Quinqueloculina* spp., the relation between its in-sediment distribution and the oxygenation of the sediment was also suggested by Moodley et al. (1998b). When they placed *Quinqueloculina seminula* in the anoxic part of the sediment it dispersed evenly; once the specimens encountered subsurface oxic conditions they did not move further into deeper (anoxic) sediment layers. At our sample station *Quinqueloculina* spp. occurs with relatively high numbers, especially following the input of organic matter. In combination these data suggest a life-strategy of *Quinqueloculina* spp. which involves that it lives in shallow sediment layers in order to avoid the stress of oxygen deficiency and that it reacts rather quickly to increasing organic matter concentrations. This life-strategy seems also valid for *Nodophthalmidium* sp., although this species is far less abundant. *Epistominella vitrea*, the species which shows the most extreme changes in abundance over the years, peaks in the upper sediment layers during May. Later, in June, it occurs abundantly throughout the top 2cm of the sediment column. In the Adriatic Sea this species is known as an opportunistic one, reacting quickly to food supply (Barmawidjaja et al. 1992, Jorissen et al., 1992). In our case, its relatively long reaction time after the elevations in chlorophyll-a concentration could be due to the still very low peak concentrations of chlorophyll-a at our sample station if compared to other areas. Only the amount of organic matter (for instance degraded tube worms) available in May is likely to be high enough to trigger *E. vitrea* to reproduce and reach its peak values, although other factors might have played a role as well. The shift in vertical distribution which takes place between May and June, from shallow to deeper sediment layers, would imply that reproduction of *E. vitrea* takes place at the sediment surface layer after which the specimens disperse more evenly throughout the sediment.

The group of so-called shallow infaunal taxa, mainly consisting of bolivinids (*Bolivina striatula*, *Bolivina seminuda*, and *Bolivina dilatata*) displays somewhat more divergent TSS patterns than the epifaunal taxa. However, all three bolivinid species exhibit a strongly fluctuating in-sediment distribution with no clear seasonal pattern. Their abundances show the same irregularity. While *B. striatula* and *B. dilatata* occur with relatively low values during the winter and spring of '96/'97, they reach their relatively highest numbers in the winter and spring of '97/'98. Also *B. seminuda* shows irregular TSS and in-sediment distribution patterns over the two years. Most remarkable is that the increase in numbers of bolivinids does not seem to be related to the availability of organic matter (chlorophyll-a, degraded tube worms), as is clearly the case with the epifaunal species. In the Adriatic Sea, Barmawidjaja et al. (1992) found these bolivinids to occupy deeper sediment layers, but their

maxima in TSS were mostly found at the top part of the sediment. At our sample station, however, the numbers of bolivinids were found to be high also in the deeper sediment layers, suggesting that they did not solely reproduce in the top sediment layer. The ecological strategy of the shallow infaunal species at our sample station is not quite clear. They do not seem to be positively influenced by increase of organic matter concentration, and their in-sediment distribution is not directly related to sediment oxygen levels. They occur most abundantly at times when other species are not so common. In November '97 for instance, when the epifaunal taxa as well as the deeper infaunal species are almost absent, the shallow infaunal bolivinids occur with quite high absolute numbers. Similar behaviour of bolivinids was noticed during an experiment performed by Ernst et al. (1999), in which they were found living throughout the topmost 3cm of the sediment. Generally, the bolivinids showed a sub-surface maximum which was most pronounced when other species were abundantly present in the topmost sediment. However, this situation changed after the sediment column was turned upside down and the earlier common taxa occurred only in relatively small numbers; then most bolivinids were found living in the top sediment layer. The life-strategy of the bolivinids therefore seems to be one of avoiding competition, together with surviving and coping under oxygen deficiency. This lifestyle results in moderate numbers after reproduction, which probably takes place only when local circumstances are profitable.

The taxa referred to as deeper infaunal (*Eggerella* spp., *Caronia silvestri* and *Bulimina marginata*) display rather similar distribution patterns. They occur with relatively low numbers during autumn (Oct. '97 and Nov. '98) whereas in winter and spring the numbers of living specimens increase substantially. The (sub-surface) maxima of the deeper infaunal species in winter could be related to better oxygenation in the sediment caused by the mixing of the water layers. However, the low numbers of specimens under the rather well oxygenated circumstances during autumn indicate that oxygenation of the sediment cannot sufficiently explain the total standing stock patterns of the deep infaunal species. A combination of organic enrichment and sediment oxygenation seems therefore more feasible. It is already known that *Eggerella* spp. and *B. marginata* prefer to live in deeper sediment layers (Barmawidjaja et al., 1992, Collison, 1980, Corliss and Van Weering, 1993, de Stigter et al., 1998, Jorissen et al., 1998). Due to our seasonal monitoring we may be able to discern where in the sediment they are most likely to reproduce. At our sampling station, the numerical increases of both *Eggerella* spp. and *B. marginata* are found to occur throughout the top 2cm of the sediment, not only at the sediment surface. This indicates that reproduction probably also has taken place in the deeper sediment layers; these may become enriched with organic matter due to bioturbation. However, the amount of organic matter reaching the deeper sediment layers in areas as oligotrophic as our sample station is probably only a small portion of the amount that arrived on the sediment surface in the first place. Yet, the fact that both *Eggerella* spp. and *B. marginata* increase in numbers shortly after the peak in primary productivity could suggest that they need less organic enriched circumstances to be triggered to reproduce than the epifaunal taxa.

The numbers of *C. silvestri* only increase after winter, like those of *Epistominella vitrea*. During their peak abundance in May '97 most *C. silvestri* specimens are found in the topmost sediment sample. This implies that, whereas it generally is distributed over the top 2cm of the sediment, it probably reproduces at the sediment-water interface. Barmawidjaja et al. (1992), who found

Morulaepecta bulbosa (= *Caronia silvestrii*) with maximum numbers in the top cm of the sediment, also suggested that although this species generally displays an infaunal life-style, it reproduces in the top sediment layer. The reason for this could be that it needs a higher level of organic enrichment than *Eggerella* spp. and *B. marginata* to reproduce. This would explain the generally low abundance of *C. silvestrii*, and its peak occurrence in the topmost sediment sample during May '97. Summarizing, the deeper infaunal species are able to survive and thrive under less oxygenated circumstances, thus providing themselves with a niche that is not available for most benthic foraminifera.

5. Conclusions

In the neritic waters of the Levantine basin, off the Israeli coast, three categories could be distinguished within the benthic foraminiferal assemblage: epifaunal, shallow infaunal and deeper infaunal. This subdivision was defined on the basis of the in-sediment distribution patterns. Taxa characterizing these categories seem to possess different life-strategies.

The epifaunal taxa (e.g. *Quinqueloculina* spp., *Nodophthalmidium* sp. and *Epistominella vitrea*) avoid oxygen stress by living generally in the shallowest sediment layers and only live in deeper sediment layers when the sediment is sufficiently oxygenated. In the absence of macrofaunal competition they react rather strongly to an increase in organic matter input. Although *E. vitrea* belongs to this group it seems to need a higher level of organic matter enrichment before it reproduces.

The ecological niche of the shallow infaunal species is less pronounced but still fairly clear. The life-strategy of the bolivids (*Bolivina striatula*, *Bolivina seminuda*, and *Bolivina dilatata*) is one of avoiding competition together with surviving and coping under less favourable conditions. Throughout the year they occur in moderate numbers, even after reproduction. No clear periodicity can be recognized in their standing stocks, this in contrast to the epifaunal and deeper infaunal foraminiferal species.

Deeper infaunal species, such as *Eggerella* spp., *Caronia silvestrii*, and *Bulimina marginata*, are found most abundantly in the deeper sediment layers where they seem to prosper quite well. They are found living in relatively high numbers, *Eggerella* spp. even being the most abundant species occurring at our study site. Besides coping with the stress of oxygen deficiency, the deeper infaunal taxa are able to react (strongly) to increasing organic matter and deeper oxygenation of the sediment. Through their ability to withstand oxygen deficiency they can occupy niches which are not available to other (micro- and macrofaunal) species. Therefore they suffer less from competition and predation.

Seasonal abundances and in-sediment distribution of benthic foraminifera living at a neritic station (120m) off the Israeli coast

With: Kees Hordijk, Ahuva Almogi-Labin, and Bert van der Zwaan

Abstract

Over a period of two years, twelve box cores were taken at 120m water depth (station S3), along the coast of Israel (SE Levantine basin). The foraminiferal assemblages (>63µm and >150µm size fractions) were compared to sediment oxygenation and chlorophyll-a concentrations. The total standing stock (TSS) of living (Rose Bengal stained) benthic foraminifera showed only a clear correlation with primary productivity if a delay in response of about two months was taken into account. The increase in TSS as reaction to increased organic matter input was most pronounced in the top part of the sediment.

The microhabitat patterns of the foraminifera did not show a clear correlation with the sediment oxygenation. During times of relatively shallow sediment oxygenation (spring and summer) the foraminifera were found to live relatively deep in the sediment, whereas during times of deeper oxygenation of the sediment the foraminifera occurred most prominently in the top sediment layers (December '96 and March '98). This is in contrast with the pattern observed in shallower water where in-sediment distribution was found to be correlated to the sediment oxygenation. The patterns displayed by the >63µm and the >150µm size fraction were quite similar, suggesting that in general microhabitat occupation is rather independent of the ontogenetic stage.

The standing stock patterns and in-sediment distributions of the eight most abundant foraminiferal taxa are discussed in some detail. Most of these taxa showed lifestyles that were rather comparable to those prevailing in shallow water (40m), varying from almost exclusively epifaunal to completely infaunal. The most outspoken epifaunal species reacted most strongly to organic enrichment. The infaunal taxa (e.g. *Eggerella* spp.) reached occasionally large numbers in the top sediment, apparently

also related to organic enrichment at the sediment surface. This seems to suggest that these species reproduce in the upper sediment layer, after which they disperse over the sediment column again.

1. Introduction

It is, by now, fairly well established that foraminiferal assemblages are influenced by organic matter availability (Gooday, 1988; Gooday and Turley, 1990), sediment oxygenation (Bernhard, 1993; Bernhard et al., 1997; Alve and Bernhard, 1995), or both (Jonssen et al., 1995; Schmiedl et al., 1997; Van der Zwaan et al., 1999). A pulse of organic matter to the sea floor is thought to induce reproduction (Gooday, 1993), but a negative side effect can be that the oxygen consumption due to degradation of the organic matter results in suboxic to anoxic sediments (Gooday et al., 2000; Jonssen et al., 1995; Jannink et al., 1998; Chapter 10). Therefore, it is generally difficult to discriminate between the two parameters (Van der Zwaan et al., 1999, and references therein).

The south-eastern part of the Mediterranean, the Levantine basin, is extremely oligotrophic (Azov, 1986; Berman et al., 1984). The pelagic region along the Israeli coast is suitable for seasonal studies of benthic fauna because it is relatively easy to assess the influence of parameters as food supply and sediment oxygenation. Since the organic matter flux is strictly linked to the yearly mixing of water layers, and oxygenation of the sediment is generally sufficient for the foraminifera, the two parameters do not interfere strongly with each other.

Sample station S3 is situated at 120m, the water depth at which the deep chlorophyll maximum occurs in the Levantine Basin. The station was sampled on a two-monthly basis with a box corer, and water column properties as CTD-profiles and chlorophyll-a concentrations were measured at every sample event (Herut et al., 2000; Chapter 2). From the box cores, the top 0-2cm of the sediment was studied for the benthic foraminifera that occurred living in the 63-150µm size fraction, whereas the 150-595µm size fraction was studied down to a sediment depth of 5cm. In addition to the sub-cores taken for foraminiferal studies, others were used to measure the concentration of dissolved oxygen in the sediment.

In this chapter we discuss the TSS of the foraminiferal assemblage and its in-sediment distribution throughout the two years in relation to the environmental parameters. The distributions of the eight most common (groups of) species are treated in detail.

2. Material and methods

At sample station S3 (120m, 32°26.58'N, 34°42.84'E) twelve box cores were taken (Fig. 1). The times of sampling are given in Table I of Chapter 4. Continuous profiles of temperature, salinity, density and oxygen were measured with a Sea-Bird electronics CTD (see Chapters 2 and 4). Chlorophyll-a concentrations were measured and integrated over the total water column.

The box core sediments were sub-sampled using two perspex tubes, one for *in situ* oxygen measurements and one for sampling benthic foraminifera. The oxygen measurements were carried out

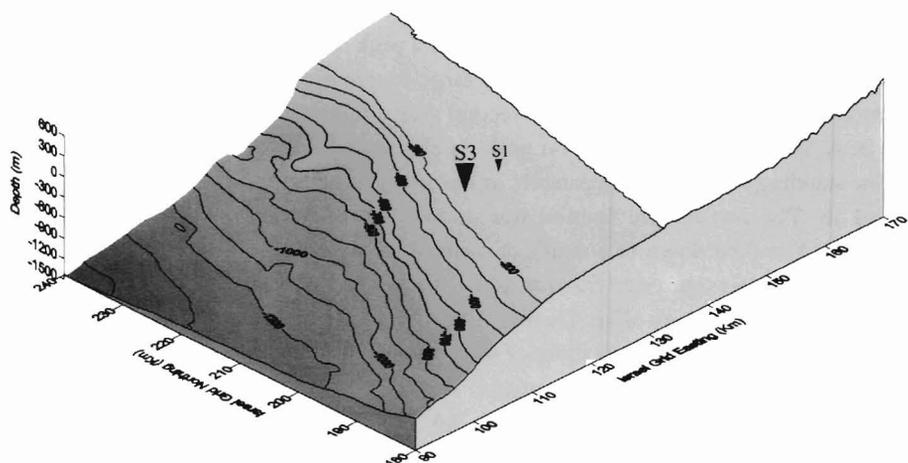


Figure 6-1: Location map, with station S3 (and S1) indicated

immediately upon arrival onboard, with micro-electrodes attached to a micromanipulator. The other tube was sampled for benthic foraminifera, by slicing the top 2cm into 0.5cm and the subsequent 2-10cm into 1cm intervals. The samples were preserved in a Rose Bengal solution (1 g L^{-1} ethanol 96%). The sediment samples were wet-sieved over $>63\mu\text{m}$, $>150\mu\text{m}$ and $>595\mu\text{m}$ sieves. For reasons of time, only the samples from the top 2cm in the smallest size fraction ($63\text{--}150\mu\text{m}$) were studied, since analysis of the $>150\mu\text{m}$ size fraction is less time consuming, we counted these from the top 5cm. The samples were studied in a petri-dish with ethanol in order to be able to distinguish between living (Rose Bengal coloured) and dead benthic foraminifera. The Rose Bengal colouring was used very strictly, as is described in Jannink et al. (1998). For comments on the use of Rose Bengal as a "vital stain" see Chapter 5.

We used the statistical program SPSS (version 7.5) to carry out a hierarchical clustering analysis (average linkage, Pearson correlation, between groups) employing the relative abundances of 35 important and abundant taxa ($63\text{--}595\mu\text{m}$). A Principal Component Analysis (PCA) including environmental parameters was obtained by using the program Canoco (version 4.0, Ter Braak and Simlaauer, 1998). From each of the clusters, key taxa were selected of which in-sediment distribution and abundance patterns are discussed in more detail.

3. Results

3.1 Total standing stocks (TSS) of benthic foraminifera

In figure 2, the TSS ($63\text{--}595\mu\text{m}$) of benthic foraminifera found living in the top 2cm is shown. The

chlorophyll-a concentrations in the water layer, integrated over the water column above station S3, are also plotted. During the first year, the TSS shows low numbers in autumn and the beginning of winter, followed by an increase at the end of winter (Dec. '96), mainly in the top half cm. Over the second year, the TSS is very constant except for a peak density of foraminifera in March '98. Here, the TSS is suddenly doubled again due to a large increase of foraminifera in the top half cm of the sediment. Overall, the TSS during the second year is higher and less variable than during the first year. The peaks in TSS seem to follow on peaks in chlorophyll-a with a time lag of about two months.

The standing stocks found separately in the >63µm and >150µm size fractions are shown in figures 3a and 3b. The >63µm size fraction was studied for the 0-2cm sediment samples, the >150µm size fraction was studied down to a depth of 5 cm. The overall ratio between TSS of foraminifera in the >63µm and the >150µm size fraction is 9:1. Over the first year fluctuations in the >63µm and the >150µm size fractions are alike. During the second year, the fluctuations in TSS of the >63µm size fraction are more extreme than those of the >150µm size fraction.

The benthic foraminifera in the >63µm size fraction are more or less evenly distributed over the top 2cm of the sediment, except in June '96, December '96 and March '98. The patterns in the >150µm size fraction suggest that the numbers of (adult) living foraminifera decrease with depth (0-5cm). Almost no foraminifera are found living deeper than 3 cm.

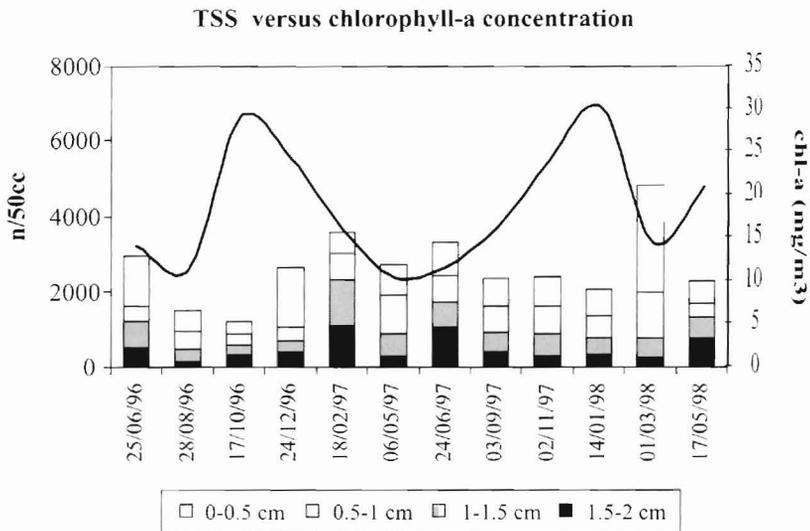


Figure 6-2: Total standing stocks (TSS) of benthic foraminifera (63-595µm) at station S3 (120m) versus the chlorophyll-a concentration (integrated over the water column). The shadings represent the in-sediment layers (0-2cm).

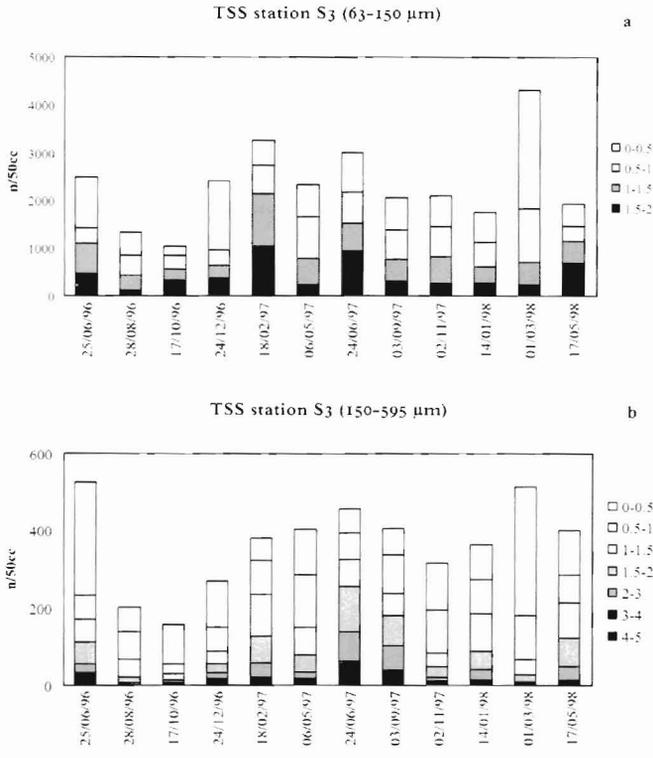


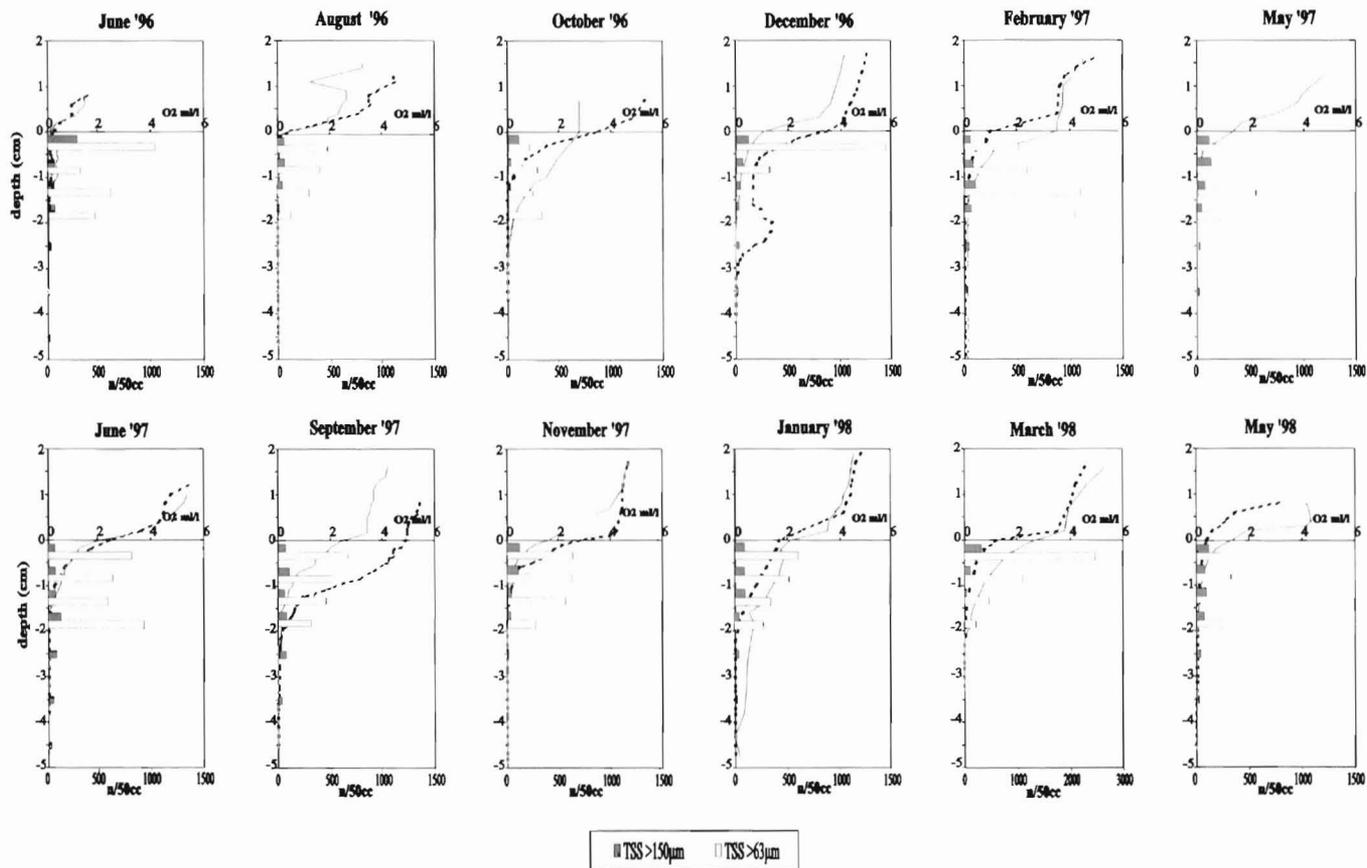
Figure 6-3: a) TSS of benthic foraminifera found living in the 63-150µm size fraction, at station S3 (120m). The shadings represent the in-sediment layers (0-2cm). b) TSS of benthic foraminifera found living in the 150-595µm size fraction, at station S3 (120m). The shadings represent the in-sediment layers (0-5cm)

3.2 TSS versus sediment oxygenation

In figure 4 the concentration of dissolved oxygen within the sediment is shown in combination with the TSS of living foraminifera in both the >63µm and the >150µm size fractions. The oxygen penetration differed largely over the two years: overall it was relatively deep, down to about 1-2cm depth. It was relatively shallow during spring and summer (e.g. June '96, August '96, May '97 and May '98), whereas during autumn and winter the sediment was better aerated (Oct. '96, Dec. '96, Sept. '97, Jan. '98).

The foraminiferal standing stocks do not show a clear correlation with the sediment oxygen penetration. The TSS in the >63µm size fraction generally decreases with sediment depth, irrespective of the oxygen concentration. In for instance June '96 and May '98, when oxygen penetration was shallow, the foraminifera were found to live with high standing stocks in the deeper sediment layers. In periods of deeper oxygenation (e.g. Dec. '96, Sept. '97, and Jan. '98), the TSS of foraminifera found in the >63µm size fraction decreased with sediment depth. The >150µm fraction generally follows the patterns displayed by the >63µm size fraction. The TSS of foraminifera found living in the >150µm size fraction sharply decreased below 2cm. During the two years of sampling, almost no foraminifera in the larger size fraction were found living deeper than 4cm sediment depth.

Figure 6-4: In-sediment distribution of the TSS of the benthic foraminifera found living in the $>63\mu\text{m}$ and $>150\mu\text{m}$ size fraction, versus the sediment oxygenation. Note the deviating scale of TSS for March '98.



3.3 Hierarchical clustering of the 35 most abundant taxa

With the relative abundances of the 35 most common species or groups (63–595µm), a hierarchical cluster-analysis was performed (SPSS version 7.5, between groups, Pearson correlation), resulting in the dendrogram shown in figure 5.

Four clusters are obvious. Cluster I includes the miliolids *Quinqueloculina* spp. and *Adelosina* sp., together with the *Bolivina seminuda/spathulata* group, *Cassidulina crassa*, *Melonis barleeanum* and the agglutinated taxon *Lagenammuna* sp. The agglutinated species *Adercotryma* sp.1 and *Adercotryma glomeratum* cluster very closely together. The calcareous species *Amphicoryna scalaris* clusters together with the agglutinated species *Bigenerina nodosaria* (Cluster II). Next to these two species, *Glomospira charoides*, *Criboelphidium poeyanum*, *Pyrgo* sp., a number of agglutinants and the soft-shelled saccaminids are included. The small Cluster III comprises *Epistominella vitrea*, *Bolivina dilatata*, *Sigmoilopsis* sp., and *Textularia porrecta*. Cluster IV includes the species *Bulimina marginata*, *Bolivina striatula*, and the agglutinated taxa *Eggerella* spp. and *Textularia agglutinans*. *Verneulinulla* sp. is loosely attached to this cluster

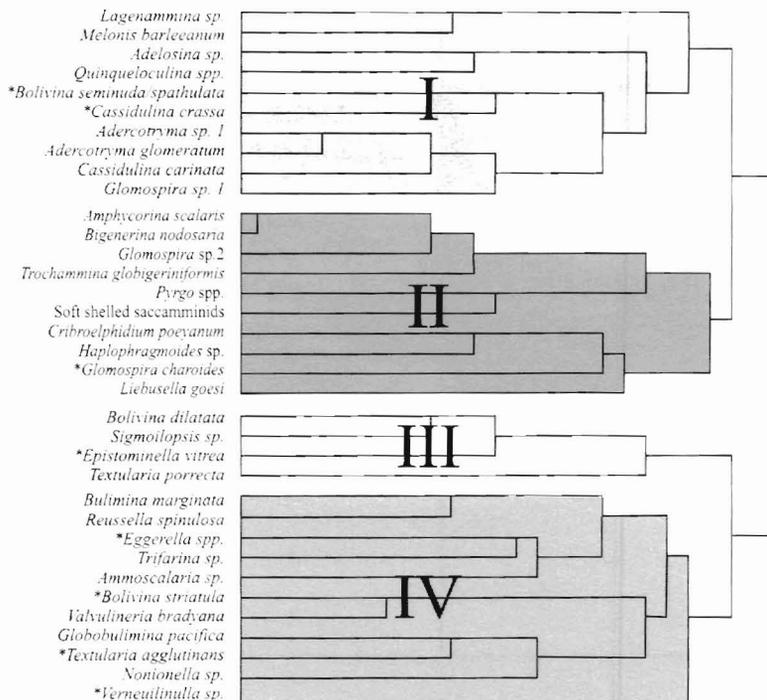


Figure 6-5: Dendrogram obtained by hierarchical clustering of relative abundances of the 35 most common and abundant foraminiferal species at station S3 (SPSS version 7.5; Pearson correlation, between groups).

3.4 Principal component analysis (PCA)

With the program Canoco (4.0) a Principal Component Analysis was performed on the same data set that was used for the hierarchical cluster analysis. In figure 6, the 1st and 2nd axis of the PCA, explaining respectively 26.5% and 16.1% of the variation, are plotted. Next to the PCA-scores of the 35 taxa, some environmental variables (oxygen, sediment depth, temperature and salinity, chlorophyll-a) as well as the seasons were included. The four clusters of the dendrogram are indicated within the PCA-graph. The parameter *chl_a_delay* needs explanation, because it is derived from the measured chlorophyll-a concentration (*chl_a*). In figure 2, the TSS peaks follow the peaks in chlorophyll-a concentration with a time lag of two months. This could indicate that there is a response time of the foraminiferal assemblage to the increasing chlorophyll-a of about two months. In order to check what influence the chlorophyll-a concentration (including a possible time lag) has on the individual foraminiferal taxa, *chl_a_delay* was introduced in the PCA-graph; we obtained this parameter for a certain period by using the value of the previous sample period. The seasons as used

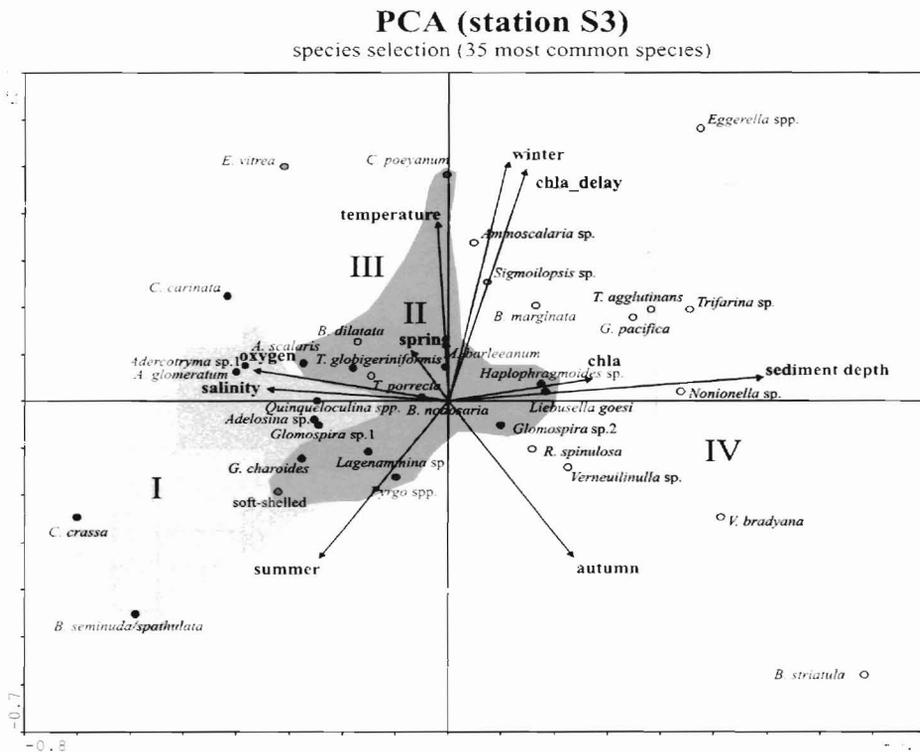


Figure 6-6: Principal Component Analysis (PCA) diagram obtained by using the relative abundances of the 35 most common and abundant species at station S3 (Canoco 4.0) including some (environmental) parameters. Indicated are the four clusters obtained by hierarchical clustering (figure 5). For explanation see text.

in this PCA-graph are defined in Table I of Chapter 4.

The parameter chlorophyll-a (chl_a) loads positively on the first axis, but the derived parameter chl_a_delay loads heavier on the second axis. This indicates that the first axis probably represents only sediment oxygenation and sediment depth, together with some influence of salinity (which changes only very slightly throughout the years). The second axis is more influenced by the seasonal cyclicality of the system; the seasons together with temperature and the delayed chlorophyll-a concentrations load rather strongly.

Clusters I and IV are clearly separated by the 1st axis. Cluster I plots negatively on the 1st axis together with increasing oxygenation. Cluster IV plots positively on the first axis with increasing sediment depth, indicating infaunal behaviour. The Clusters II and III, however, do not take a clear position in this PCA graph, suggesting that the relative numbers of these taxa are not very strongly affected by the factors loading on the two axes. *Epistominella vitrea* and *Criboelphidium poeyanum* are exceptions. These two species plot positively along the 2nd axis, suggesting peaks in winter following chlorophyll-a increases.

3.5 Absolute and relative abundance patterns of eight common taxa

The eight most common taxa occurring at station S3 are *Cassidulina crassa*, *Bolivina seminuda/spathulata*, *Glomospira charoides*, *Epistominella vitrea*, *Textularia agglutinans*, *Verneuilinulla sp.*, *Eggerella spp.*, and *Bolivina striatula*. These taxa were selected because they are relatively abundant and are likely to be representative of the clusters in which they occur.

The ALD₂'s (Average Living Depths over 2cm sediment column) of the eight taxa are given in Table I. *C. crassa* is found to have the shallowest ALD₂, followed by *B. seminuda/spathulata* and *G. charoides*. The ALD₂ of *E. vitrea* and *T. agglutinans* (around 1cm) indicates that they occurred living more or less evenly distributed over the top 2cm of the sediment column. For *Verneuilinulla sp.*, *Eggerella spp.*, and *B. striatula*, the ALD₂-values are somewhat larger than 1cm, indicating that these taxa had a slight preference for the deeper sediment layers.

	avg. ALD ₂
<i>Cassidulina crassa</i>	0.63
<i>Bolivina seminuda/spathulata</i>	0.78
<i>Glomospira charoides</i>	0.82
<i>Epistominella vitrea</i>	0.88
<i>Textularia agglutinans</i>	0.98
<i>Verneuilinulla sp.</i>	1.01
<i>Eggerella spp.</i>	1.03
<i>Bolivina striatula</i>	1.03

Table 6-1: The ALD₂ (Average Living Depth calculated over top 2cm) of the eight most common foraminiferal taxa occurring at station S3.

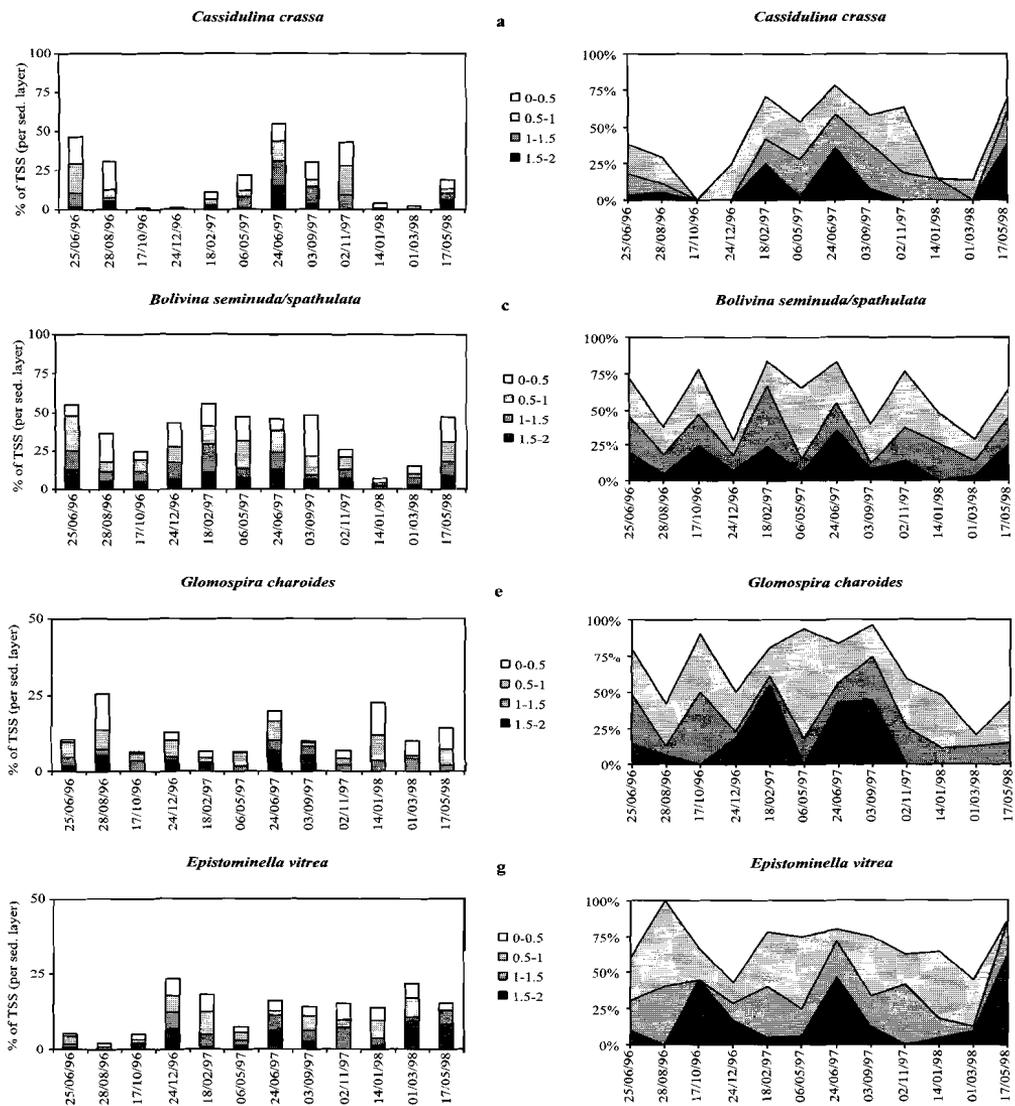


Figure 6-7: Relative abundances of 4 most common species (Clusters I to III; as % of TSS) and their in-sediment distribution over the two sampling years.

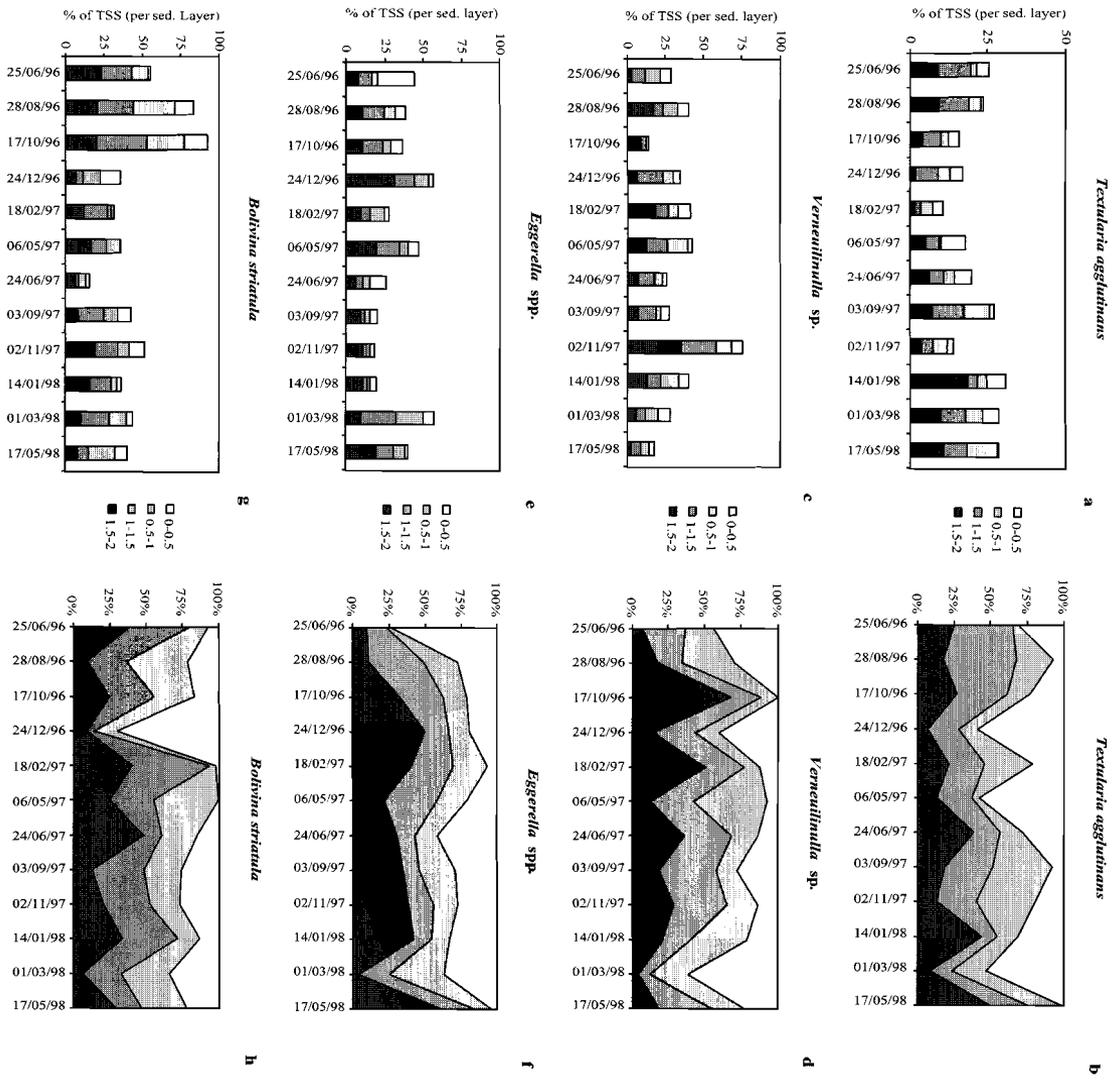


Figure 6-8: Relative abundances of 4 most common species (Cluster IV) as % of TSS) and their in-sediment distribution over the two sampling years.

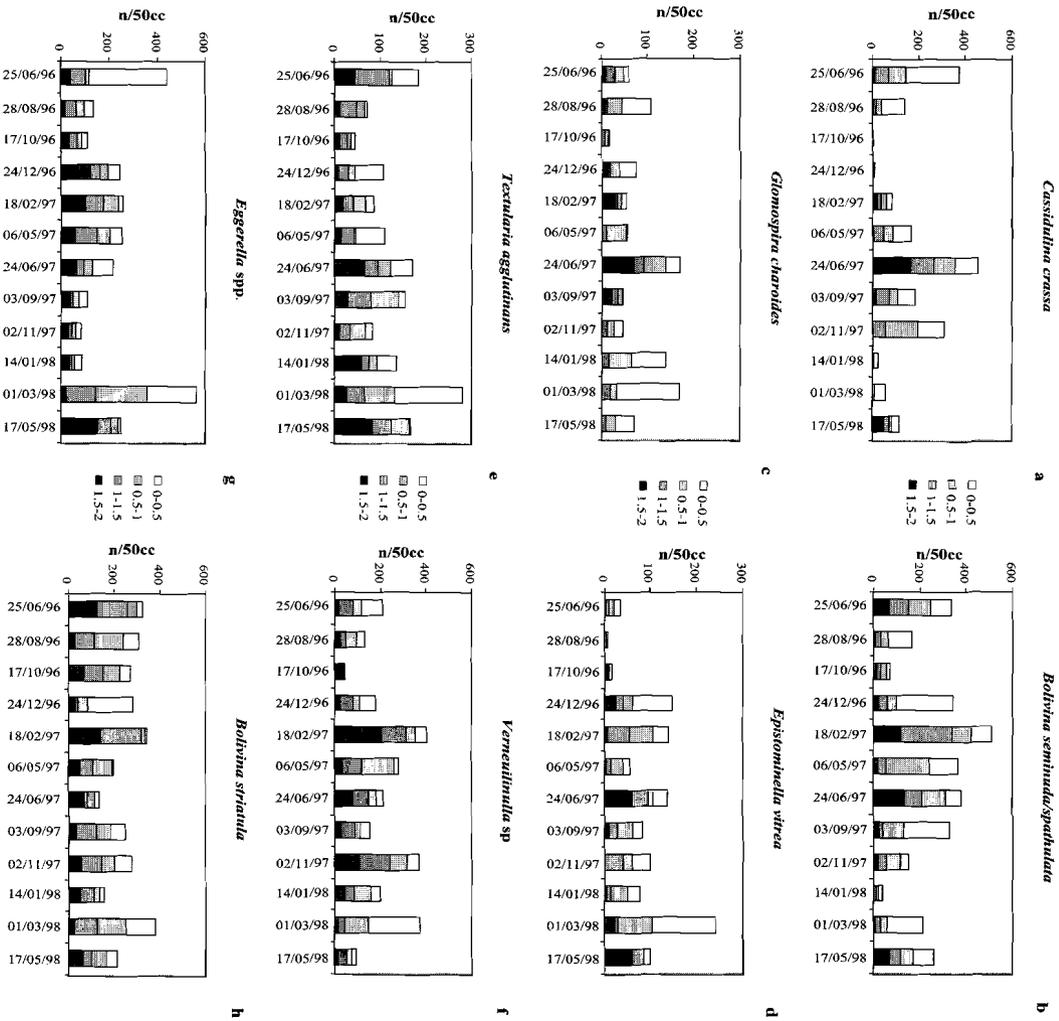


Figure 6-9: Absolute abundances of 8 most common species (Cluster I-IV) over the two sampling years.

The relative abundances of Cluster I species *C. crassa* and *B. seminuda/spathulata* are plotted in figures 7a and 7c. *C. crassa* clearly displayed its highest relative abundance in summer, whereas *B. seminuda/spathulata* showed overall stable relative numbers except for its low values in autumn. The in-sediment distribution of *C. crassa* was typically epifaunal; it was only sporadically abundant in the deeper sediment layers (Fig. 7b). Its absolute abundance pattern was very similar, with highest absolute numbers occurring during summer (Fig. 9a). *B. seminuda/spathulata* showed high relative numbers in spring and summer (Fig. 7c). Its in-sediment distribution fluctuated throughout the years, but generally highest abundances were found within the top 1cm of the sediment (Figs. 7d and 9b).

The relative abundances of *Glomospira charoides* were somewhat lower than the proportions of *C. crassa* and *B. seminuda/spathulata*, and showed no clear seasonal pattern (Fig. 7e). Its in-sediment distribution was mainly shallow, but occasionally it was also found in deeper sediment layers (Fig. 7f). Like its relative abundance, its absolute numbers displayed no seasonal pattern, but generally highest values occurred in summer and winter (Fig. 9c).

During the first year *Epistominella vitrea* was abundant in winter, whereas its relative abundances were quite stable throughout the remainder of the monitoring period (Fig. 7g). It is a shallow living species, and only twice significant numbers were found in the deeper sediment layers (Figs. 7h and 9d).

Textularia agglutinans, clustering together with *Verneuilinulla* sp., *Eggerella* spp., and *Bolivina striatula* in Cluster IV, displayed a rather stable pattern of relative abundances (Fig. 8a). Throughout the two years, it was found more or less evenly over the top 2cm of the sediment (Fig. 8b). The absolute numbers of *T. agglutinans* showed quite a different pattern than its relative abundance pattern, with high abundances at the end of winter, in spring and in summer (Fig. 9e). The relative abundances of *Verneuilinulla* sp. and *Eggerella* spp., were quite constant (Figs. 8c and 8e). Both species were found distributed more or less evenly over the top 2cm sediment layers (Figs. 8d and 8f), with occasional deeper in-sediment distribution. The absolute numbers of *Verneuilinulla* sp. were highest in winter (Fig. 9f), whereas the absolute numbers of *Eggerella* spp. were highest in June '96 and March '98. During the latter periods *Eggerella* spp. was most abundant in the topmost sediment layer. *B. striatula* showed its highest relative abundances during summer and autumn of the first year (Fig. 8g). Except for Dec. '96, it was spread rather evenly over the sediment layers (Fig. 8h). The pattern of the absolute abundances of *B. striatula* was far more stable than its relative values. The first year of monitoring its numbers were quite stable, during the second year they fluctuated, but were highest at the end of winter (Fig. 9h).

4. Discussion

4.1 Total standing stocks and in-sediment distribution

The total standing stock (TSS) in both size fractions does not show a clear correlation with sediment oxygenation. When sediment oxygenation was very shallow (June '96, August '96, May '97 and May '98) the TSS values in the deeper sediment layers were still considerable. In May '97 and May '98 the TSS of foraminifera occurring in both the >63µm and the >150µm size fraction, even

showed sub-surface maxima. However, in January '98 when the sediment was oxygenated down to at least 4 cm, no large amounts of living foraminifera were found in the deeper sediment layers.

Because of the overall deeper oxygenation of the sediment at this station (120m), compared to the sediments in shallower water (Chapter 4), there was probably less reason for the (epifaunal) foraminifera to be restricted to the shallower sediment layers. This seems even more true if we take into account that most foraminifera can cope with periods of suboxia and with short-term anoxia (Bernhard, 1996). During an experiment, Moodley et al. (1997) even found that many hard-shelled foraminifera survived prolonged anoxia for more than 2 months. At our station there was always some dissolved oxygen present in the sediment. This, in combination with the knowledge that most foraminifera would be able to survive a two-month period of suboxia in the deeper sediment layers, supports the idea that most taxa did not actively track oxygen gradients. Alve and Bernhard (1995) found foraminifera migrating to the sediment surface during anoxia. However, a large difference between their experimental set-up and the situation at our station S₃ is that during the experiment the bottom water oxygen concentration was kept very low (<0.2ml/l O₂), whereas at our sample station the bottom water remained always oxygenated (see CTD-profiles, Chapter 2).

The total standing stocks fluctuated strongly throughout the two sampling years. The TSS in the first year was lower than that of the second year, but lowest values were found both years in autumn and at the beginning of winter. The TSS pattern would fit the chlorophyll-a concentration pattern rather well, if two-month time-lapse would be considered as a reasonable period for the foraminifera to react to the increase of organic matter flux to the sea bottom. In December '96 the TSS increased, following the relative peak in chlorophyll-a concentration during October '96. In the first year, the chlorophyll-a concentration built up quickly but decreased slowly during the next three sample events; the TSS of foraminifera increased in December '96 but stayed rather high. The second year, in contrast to the first year, the chlorophyll-a concentrations built up slowly, but decreased very rapidly in March '98. The TSS followed this pattern more or less.

Despite the fact that the foraminiferal TSS at 40m (station S₁, see Chapters 4 and 5) is much higher (and received a higher organic flux from the surface layer), the TSS of foraminifera at 120m appeared to react more directly to the primary productivity change in the water column. However, the seasonal control could have been related also to the fact that at 120m meiofauna is not simply dependent on direct flux, but also profits from the late spring to early fall DCM-maximum. The DCM is located at about the depth of our station and subject to strong seasonal variation. Macrofaunal interference might be yet another interfering factor (see Chapter 4, for discussion). At station S₃, however, not much macrofauna was found living in the sediments. The foraminiferal TSS values at station S₃ (>63µm and >150µm size fraction) displayed less fluctuations during the two years than the foraminiferal TSS values in shallower water. This could indicate that at station S₃ the environmental circumstances were more stable. The numerical difference of the foraminiferal TSS between stations S₁ and S₃ was most likely due to lower organic matter concentrations that eventually reached the sea floor at the latter station (see Chapter 3).

During the two years of study only very few specimens (>150µm) were found living deeper than 4cm. Moreover, the similarity of the in-sediment distribution in the >63µm and the >150µm size fractions, suggests that also smaller foraminifera probably did not occur abundantly deeper than 5cm.

4.2 Hierarchical clustering and PCA

The clustering of the 35 most common foraminiferal species (groups) results in three large clusters and a smaller one. Cluster I, consisting of species (groups) like *Quinqueloculina* spp., *Adelosina* sp., *Bolivina seminuda/spathulata*, and *Cassidulina crassa*, loads strongly on the 1st axis of the PCA. This 1st axis seems to represent the sediment depth quite well and, to a lesser extent, the oxygen concentration in the sediment. The fact that Cluster I plots negatively on the first axis, indicates that this group of foraminifera has an epifaunal to shallow infaunal lifestyle. Also at our shallowest sample station S1 (40m; Chapter 4), the in-sediment distribution of *Quinqueloculina* spp. was very shallow and found to be strongly influenced by the sediment oxygenation. Barmawidjaja (1991) observed only high abundances of *Quinqueloculina* specimens in sediments obtained during periods with the highest oxygen values. This supports our findings.

Most of the species included in Cluster II plot with very low scores on both the 1st and 2nd axis. Only *Criboelphidium poeyanum* loads positively on the 2nd axis, apparently due to its higher occurrence in the somewhat more eutrophic winter season. Wintertime is a distinct period in the Levantine region, because just before winter sets in water layers mix, resulting in elevated chlorophyll-a concentrations. As already mentioned, a clear correlation of the foraminiferal TSS with the chlorophyll-a concentration only exists if a time-lag of the period between two sample events is taken into account. The introduced parameter (chl_a_delay), representing the expected organic enrichment after the relative peak in chlorophyll-a concentration, loads rather strongly on the 2nd axis. From Cluster III, *Epistominella vitrea* loads strongly on the second axis and to a lesser extent on the first axis. This implies that the relative abundance of *E. vitrea* correlates rather poorly with oxygenation, but strongly with the presence of organic matter in winter.

All Cluster IV taxa plot positively on the first axis suggesting that all of them occurred with considerable relative abundances deeper in the sediment. Especially *Eggerella* spp., *Trifarina* sp., *Nonionella* sp., *Valvulineria bradyana*, and *Bolivina striatula* display a strong positive correlation with sediment depth. Moreover, *B. striatula* plots negatively on the second axis because its highest relative abundances occur in autumn, and not after the organic enrichment of the sediment during winter when most taxa were frequent.

4.3 Distribution of the eight abundant taxa

From Cluster I to Cluster IV, a trend in in-sediment distribution can be recognized. Cluster I taxa dominantly inhabited the upper part of the sediment, whereas the Cluster IV species were mainly found living in the deeper sediment layers. This can also be inferred from the PCA-diagram, in which most Cluster I species plot negatively on the first axis, opposite to sediment depth and together with oxygen. Most Cluster IV taxa correlate positively with increasing sediment depth. The epifaunal taxa of Cluster I display a more spiky abundance pattern, whereas the deeper infaunal species showed more constant numbers over the years.

The peak abundances of *C. crassa* were found in summer. Also other Cluster I species seem to

display a rather clear seasonality, highest numbers occurring during spring and summer. At our station *B. seminuda/spathulata* was found to react strongly to availability of organic matter, as was found in the Adriatic Sea; Barmawidjaja (1991) placed both species in opportunistic categories. At station S1 (40m; see Chapter 5), however, no opportunistic behaviour of *B. seminuda/spathulata* was found, and it showed no clear standing stock pattern throughout the two years. This could be due to competition with other, more opportunistic, taxa (see Chapter 5). The numbers of *E. vitrea* clearly increased after the arrival of (fresh) organic matter. The species *E. exigua*, a deeper water counterpart of *E. vitrea*, is known for its opportunistic response to food supply (Gooday, 1993, Gooday and Turley, 1990), and was found living within the phytodetritus with very high numbers after phytodetritus deposition (Gooday, 1988).

The species grouped within Cluster IV inhabited an overall deeper in-sediment niche. *T. agglutinans* was found evenly spread over the top 2cm of the sediment. This (deeper) infaunal life strategy was also described by Barmawidjaja et al. (1992) who found *T. agglutinans* to be distributed evenly over the top 6cm sediment in the Adriatic Sea. Its highest abundance in our material, however, was found in the topmost sediment layer at the end of winter (particularly of the second year), just after increased food supply. This might indicate that it reproduced in the top sediment layer, following increased (fresh) organic matter supply. *Verneuilinulla* sp. was not common at other water depths that were monitored in the Levantine basin. Although its abundance did not show a clear correlation with increased organic matter supply, it was found with relatively high numbers at the end of winter. *Verneuilinulla* sp. displayed a shallow in-sediment distribution only during the winter of the second year. During other peak abundances it was found more evenly dispersed over the sediment. The fact that *Eggerella* spp. plotted positively on both PCA-axes suggests that this species inhabited a rather deep in-sediment niche and that its relative abundances were surprisingly well correlated with supply of (fresh) organic matter. Although deep infaunal, its (strong) increases in the sediment top layer during organic enriched periods suggest that it reproduced at the sediment-water interface (similar to *T. agglutinans*). This concurs with our findings in the shallowest sample station S1, where *Eggerella* spp. was also found to be abundant in the top 1cm sediment layers after organic enrichment (Chapter 5). Also *B. striatula* was abundant in the uppermost sediment layers in December '96 and March '98; however, its overall abundances over the 2cm sediment were quite stable and no clear seasonal pattern can be distinguished. The fact that it correlates very strongly with autumn in the PCA, is due to very low density of other taxa. The epifaunal life strategy that was found for *B. striatula* by Barmawidjaja et al. (1992) and Jorissen et al. (1992) in the Adriatic Sea is not evident in the Levantine Basin. Overall, its specimens were found spread evenly over the sediment (0-2cm). An opportunistic behaviour of *B. striatula*, as described by Jorissen et al. (1992), could not be confirmed. Whereas its in-sediment distribution was shallower at station S1, here also no opportunistic behaviour could be inferred.

5. Conclusions

In contrast with patterns found in shallow water, at station S3 (120m) we found no correlation between the sediment oxygenation and the in-sediment distribution of the foraminifera. This could

be partly due to the overall better oxygenation of the sediments at station S3. In deeper water the microhabitat partitioning of the foraminiferal taxa is more difficult to detect than in shallower waters (station S1), possibly caused by the overall better oxygenation of sediments in deeper water. The fact that at 120m seasonal oxygen deficiency was nearly absent resulted in more stable microhabitats for the foraminifera, compared to the ones found in shallower water.

Although the microhabitat partitioning was not very clear, species with a more epifaunal and others with a more infaunal mode of life could be distinguished. Epifaunal taxa showed strongly fluctuating abundance patterns, in contrast to the shallow to deeper infaunal species, which displayed more stable patterns.

Cassidulina crassa and *Bolivina seminuda/spathulata* lived predominantly as epifauna and their abundance pattern showed large (seasonal) fluctuations. Also *Glomospira charoides* was mainly found to live in shallow sediment layers. Its absolute numbers fluctuated without a clear seasonal pattern. *Epistominella vitrea* exhibited a rather opportunistic life style, reacting on increased organic flux. The deeper infaunal taxa, *Textularia agglutinans*, *Verneuilinulla* sp., *Eggerella* spp., and *Bolivina striatula* displayed more stable abundance patterns. *T. agglutinans* and *Eggerella* spp., were found to respond to organic enrichment, and their increase in numbers was mainly found in the topmost sediment layer. This might suggest reproduction in the top sediment layers, where the sediment is most enriched with (fresh) organic matter.

Chapter 7

A seasonal study on patchiness of benthic foraminiferal assemblages at three adjacent stations (120m)

With : Kees Hordijk, Ahuva Almogi-Labin, and Bert van der Zwaan

Abstract

Three stations in the SE Levantine basin, situated at a water depth of approximately 120m, were sampled every two months over the period June '96 – May '97. The seasonal sampling of these stations was carried out in order to get some grip on the issue of patchiness of benthic foraminiferal distribution.

Whereas considerable differences were found between the standing stocks of the foraminiferal species found living in the $>63\mu\text{m}$ size fraction samples, the most common taxa did not display strong patchiness. This was different for the $>150\mu\text{m}$ size fraction, where more inter-station differences were found.

Although the seasonal distributions of the seventeen most common foraminiferal taxa ($>150\mu\text{m}$) displayed large differences, the year-averaged standing stocks were quite similar. The same holds for the relative frequencies of these species in the averaged assemblage at the three stations.

In spite of some differences on a local and seasonal scale, our results suggest that the overall similar foraminiferal assemblages indicate that patchiness is not of major importance.

1. Introduction

As benthic foraminifera are often used as paleoecological tools to reconstruct past environments (Kouwenhoven, 2000), it is important to get sufficient grip on their ecological background. Many field and experimental studies revealed relevant knowledge on the microhabitat of foraminiferal taxa under certain circumstances (e.g. Alve and Bernhard, 1995, Corliss, 1991, Gooday, 1986, Moodley et al, 1997). Only some of these were studies in which sample stations were monitored for a longer period. Such studies enable one to keep track of temporal (seasonal) changes in the foraminiferal species distributions and the impact of environmental circumstances on these (e.g. Jorissen et al, 1992, Barmawidjaja et al., 1992, Chapters 4, 5, and 6). In addition to monitoring studies directed at temporal variation, it is important to get insight in the spatial heterogeneity, i.e. the patchiness of the foraminiferal assemblages. The heterogeneity can be considerable, caused by patchy distribution of organic material (Gooday and Turley, 1990) or presence of submarine vegetation (Murray, 1991). Schafer (2000) considers it of great importance in nearshore environments. This is further illustrated by Murray and Alve (2000); in the Hamble estuary (England) they found the benthic foraminiferal assemblages, sampled only a few centimetres apart, to differ highly. In contrast, during a seasonal study in the San Pedro Basin, Silva et al. (1996) found no substantial differences between foraminiferal species assemblages in two sub cores taken 200m apart. There, the seasonal changes in species distribution appeared to be much larger than the difference between the two spatially separated stations.

To obtain information on the degree of patchiness in the spatial distribution of foraminifera in the Levantine coastal sediments, three adjacent stations were sampled at a water depth of approximately 120m. From June '96 until May '97, these stations were sampled on a two-monthly basis. The benthic foraminifera occurring in the 63–150 μ m size fraction were studied only for the box cores taken in June '96. The assemblages occurring in the 150–595 μ m were studied from the top sediment samples throughout one year, i.e. six sampling moments from June '96 to May '97.

2. Material and methods

For sampling methods see the Chapters 3 to 6. For the present study (only) the top sediment samples of the three stations at ~120m (0–0.5cm) were studied for benthic foraminifera occurring in the >63 μ m (only June '96) and the >150 μ m size fractions (one year cycle). Due to bad weather, station S5 was not sampled in October '96 (Table I, Fig. 1). A large part of the total standing stock

Stations	Water depth (m.)	Latitude	Longitude
S3	121	32°26.58'N	34°42.84'E
S4	122	32°26.40'N	34°42.75'E
S5	121	32°26.51'N	34°42.85'E

Table 7-1: The water depth and coordinates of the three sample stations.

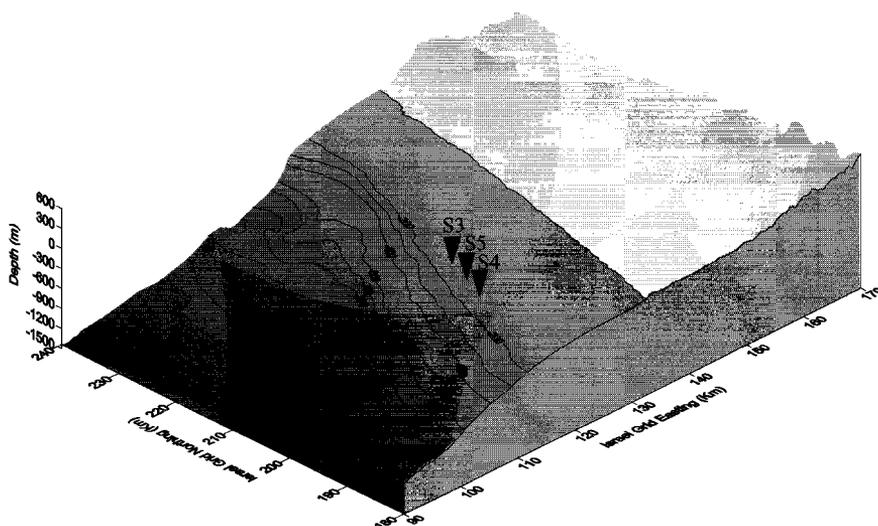


Figure 7-1: Bathymetrical map, showing the sample station localities (S3, S4, and S5).°

(TSS) is occurring in the topmost sediment layer (>35%, see also Chapter 6) and we assumed that this sample would give an appropriate impression of spatial differences between the stations.

3. Results

3.1 Species assemblages found in the >63 μ m size fraction

In June '96, we observed a relatively large variation between the species assemblages occurring at the three sample stations (Fig. 2). The samples all contained more or less the same taxa, but some occurred in highly deviating densities. *Cassidulina crassa*, *Epistominella vitrea*, *Eggerella* spp., *Textularia agglutinans*, soft-shelled saccamminids, and *Verneuilinulla* sp. were present in rather similar numbers at all three stations, but the standing stocks of *Bolivina seminuda*/*spathulata*, *Glomospira* sp.2 and especially *Bolivina striatula* differed highly.

3.2 Seasonal changes in TSS of benthic foraminifera found in the >150 μ m size fraction

The total standing stocks (TSS) of benthic foraminifera found in the >150 μ m size fraction over the period June '96 – May '97 are presented in figure 3. At station S3, there was a clear peak occurrence of benthic foraminifera in June '96, whereas during remainder of the year the TSS were relatively stable but low: only 30%–50% of the TSS value found in June '96. The TSS values of benthic foraminifera

June '96 (>63µm)

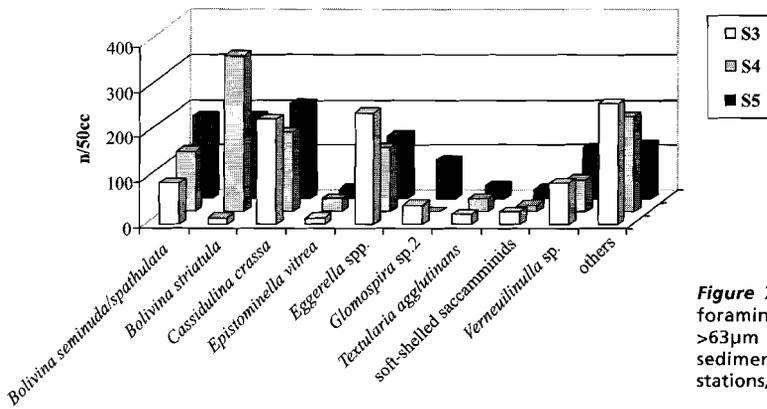


Figure 7-2: The nine most common foraminiferal species found in the >63µm size fraction of the top sediment, sampled at the three stations, June '96.

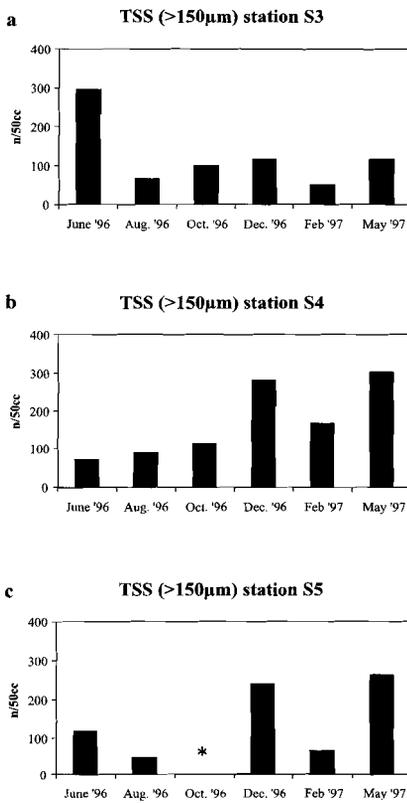


Figure 7-3: The standing stocks of the total foraminiferal assemblages found throughout the year, at a) station S3, b) station S4, and c) station S5 (* = no data).

(>150µm) at station S4 were relatively stable at the first three sample events, i.e. during summer and autumn. However, in winter (December '96) the foraminifera occurred with peak abundances, after which the TSS was found to be lower in February '97, but higher again in May '97. The TSS pattern of foraminifera at station S5 was similar to the pattern at station S4, but the numbers of foraminifera were generally somewhat lower.

3.3 The seasonal abundance changes of the most common foraminiferal species (>150µm) at the three stations

The seasonal changes in the abundance of the seventeen most common foraminiferal taxa, found at the three stations throughout the monitoring period, are presented in figure 4. These abundances differed greatly between the stations. In October '96, when only a few species occurred living, *Valvulineria bradyana* was relatively abundant at station S4, whereas it was not present at that time at station S3 (Fig. 4c). At the same sample event *Bolivina striatula* and *Bigenerina nodosaria* were abundantly present at station S3, whereas only a few specimens of these taxa were found living at station S4. In February '97, *Lagenammia* sp., *Textularia agglutinans*, and *Bigenerina nodosaria* occurred with relatively high abundances at station S4, but only low numbers of these species were found at the other two sample stations (Fig. 4e). In May '97 most of the seventeen taxa were found living at all three stations; however, large differences between the abundances of the species are noticeable (e.g. *Amphicoryna scalaris*, *Eggerella* spp., and *Lagenammia* sp., see Fig. 4f).

3.4 Average standing stocks of foraminiferal species occurring in the >150µm size fraction

In figure 5, the average standing stocks of the seventeen most common species at the stations S3, S4, and S5, are presented. The five most abundant taxa in the >150µm size fraction are *Amphicoryna scalaris*, *Eggerella* spp., *Lagenammia* sp., *Textularia agglutinans*, and *Bigenerina nodosaria*. The yearly averages at the three stations are quite similar for most species, but these differ from station to station for some (e.g. *Eggerella* spp. and *B. nodosaria*).

In figure 6 the stacked bars represent the year-averaged percentages of the most common taxa at the three stations. Although there are some dissimilarities, the patterns look very much alike. Also the proportions of the five most common taxa mentioned above, are very similar.

4. Discussion

Although several researchers mentioned the issue of patchiness in living foraminiferal assemblages (Murray, 1991, Gooday and Turley, 1990, Murray and Alve, 2000, Schafer and Mudie, 1980, Schafer and Cole, 1982, Schafer, 2000), it is a not well studied feature. The distributions of the seventeen most common species found at our stations, differ largely if we compare them over time. This concurs with the findings of Murray and Alve (2000), who studied the seasonal changes in species distributions at

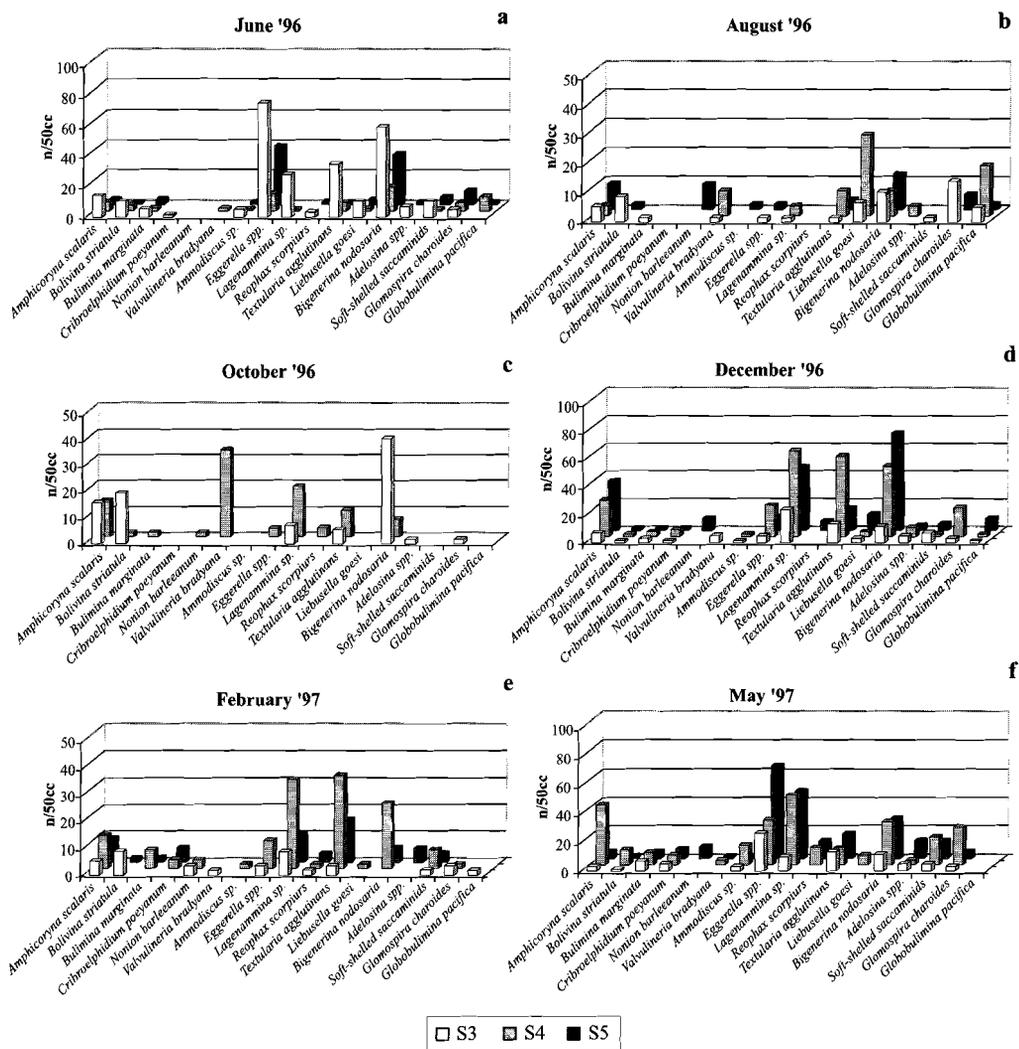


Figure 7-4: The total standing stocks of foraminiferal species throughout the year, at the three stations. Note the different scales (n/50cc). Station S5 was not sampled in Oct. '96

Average numbers (>150µm)

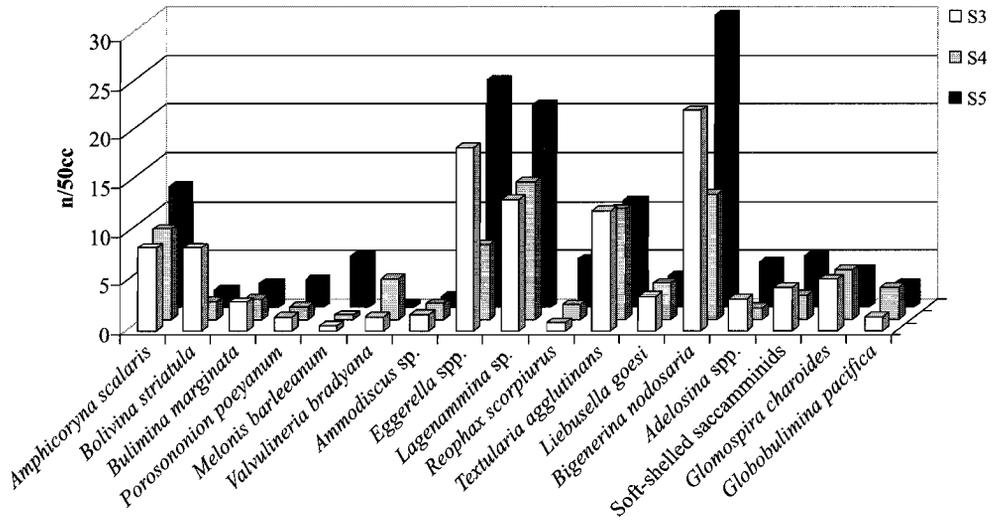


Figure 7-5: The total standing stocks, averaged over the year, of the seventeen most abundant species in the >150µm size fraction, as found at the three stations.

Average foraminiferal assemblages (>150µm)

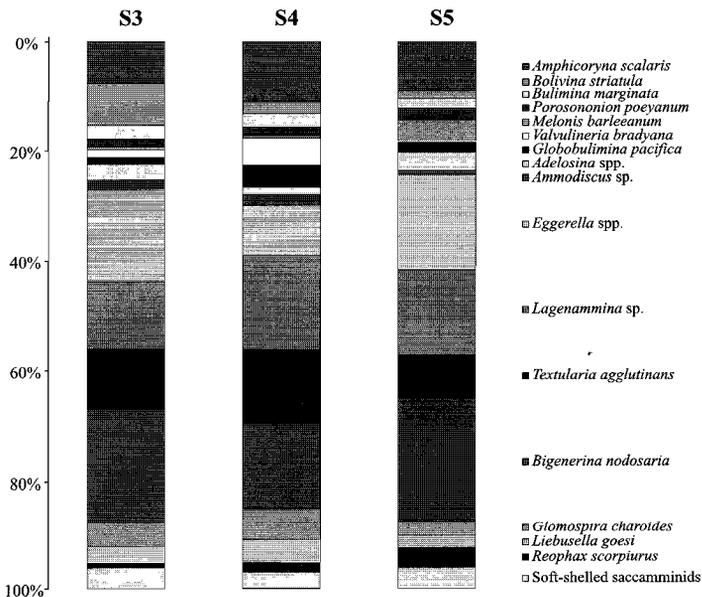


Figure 7-6: Stacked bars, showing the relative abundance abundances of the foraminiferal species, averaged over the year.

two intertidal stations in the Hamble estuary (England). They sub-sampled the top sediment (0-10cm) at both stations on a monthly basis, for more than two years, and found large differences between these sub-cores in the abundances of their three most abundant species. This patchiness was suggested to be the reason why no clear seasonal patterns were found (Murray and Alve, 2000). However, Silva et al. (1996) found during their seasonal study on foraminiferal assemblages in the San Pedro Basin (~720m), that the sediment columns (0-10cm) sampled at two different localities 200m apart, displayed very similar standing stocks for the most common species. Moreover, they found the seasonal changes throughout the year much more important than the differences between the two sub-cores. During a seasonal study on intertidal foraminifera Basson and Murray (1995) found overall similar species abundances in replicate samples taken in the Arabian Gulf. Whereas some replicates showed aberrant TSS values for the species, most samples taken throughout the two year period had a replicate similarity of >75 % (Basson and Murray, 1995).

If we consider the benthic foraminifera we found living in the >63µm size fraction of samples taken in June '96, the standing stocks of the species *Bolivina seminuda/spatulata*, *Cassidulina crassa*, *Eggerella* spp., and *Verneuilinulla* sp., were quite comparable for the stations; *Bolivina striatula* was the only abundant species which displayed large differences. The seasonal changes in the total foraminiferal assemblage were comparable for stations S4 and S5, but deviated at station S3. Also per species the total numbers differed considerably. Generally, however, if a species occurred with relatively high abundances at a certain station during a certain sampling event, it occurred also relatively abundant at the other two stations. Only October '96 forms an exception; here the assemblages found at stations S3 and S4 differ substantially.

The differences between our three stations could imply that the foraminiferal assemblages are distributed with a certain patchiness along the Israeli coast. However, we have to keep in mind that only the topmost part of sediment was studied. Also the differences in foraminiferal species abundances that were found by Murray and Alve (2000) during their seasonal study, were obtained from top sediment samples. In contrast, the study of Silva et al. (1996), in which no patchiness was found, was based on sediment columns of 0-10cm sediment depth. This suggests that the patchiness we found can be an overestimate because of lack of a more complete picture of the total sediment column. The year average of the foraminiferal abundances in the top sediment samples for the three stations were very similar. This indicates that over time the influence of vertical distribution, which is probably the most important reason for the seasonal dissimilarities between the stations, levels out. This results in the large resemblance between the average foraminiferal assemblages. In order to study patchiness it would be better to take a bulk sediment sample from 0-5cm of sediment depth (>90% of foraminiferal assemblage, Chapter 6), instead of only the upper part of the sediment.

Our study indicates that patchiness could be present, in view of the differences in the TSS patterns at the three stations. However, the total standing stocks of foraminifera were always found to be within the same order of magnitude, implying that the numerical differences are not enormous. The fact that the composition of the species assemblages at the stations is rather comparable, and the average species assemblages almost identical, indicates that patchiness is probably not of great importance, certainly if the possibility of differences in vertical distributions at the sample sites is taken into account. The oligotrophic circumstances in our study area might be one of the reasons for the

absence of large spatial differences in the foraminiferal assemblages. This might be due to lack of patchy distributed organic matter on the sea bottom, which is suggested to be a reason for spatial heterogeneity (Gooday and Turley, 1990).

The outcome of the present study is of importance, since it suggests that we are able to clarify the ecologically driven influences on the foraminiferal assemblages in the coastal sediments off Israel without having to take into account large discrepancies due to patchiness.

Foraminiferal patterns in two trophically different regions: the northern Adriatic Sea and the southern Levantine Basin

With: Ivo Duijnste and Bert van der Zwaan

Abstract

In spite of the fact that the northern Adriatic Sea and southern Levantine Basin are trophically quite different, the benthic foraminiferal standing stocks through the seasons were found to be in the same range. This suggests that the amount of food (organic matter) available at the sediment-water interface was not the major factor that determined the foraminiferal abundances. Our data suggest that not simply the amount of food, but the delicate balance between organic matter supply and oxygenation was the important ecological factor.

The assemblages of the two areas have a lot of taxa in common but they differ significantly with respect to diversity. The Levantine assemblages contain a high amount of species occurring in low frequencies. In the more eutrophic Adriatic Sea the simple diversity is considerably lower, as can be expected in such a seasonally highly variable setting. These assemblages contain more opportunistic taxa than those of the oligotrophic Levantine basin. In the latter, an increase of infaunal taxa with water depth can be observed.

A comparison of the in-sediment distributions of five representative taxa demonstrate a large resemblance for the different stations. Considering the substantial differences in oxygenation as well as organic matter concentration, this implies that the general microhabitat partitioning is inherent to these taxa themselves and not dependent on environmental variation. For most of these taxa, no correlation was found between the average living depth, or the in-sediment distribution, versus oxygenation. An exception formed the miliolids, their in-sediment distribution appeared to be rather strongly dependent on sediment oxygenation.

1. Introduction

Our LEV-ADRIA project started in 1996 with the intention to monitor foraminiferal assemblages occurring in two ecologically completely different regions within the Mediterranean Sea, the eutrophic northern Adriatic Sea and the oligotrophic southern Levantine Basin. The rather extreme eutrophication of the northern Adriatic Sea occasionally results in high total standing stocks of foraminifera, certainly as long as oxygen is present (Jorissen et al., 1992). The marine system is strongly controlled by spring run-off from the Po river and by yearly autumn mixing, both playing a major role in the eutrophication. The occasionally high organic loads arriving at the sea bottom in front of the Po-delta cause severe side-effects for the benthic community in the form of anoxia (e.g. Van der Zwaan and Jorissen, 1991; Justic, 1991; Jorissen et al. 1992).

Because of its oligotrophic waters (Azov, 1986, Berman et al., 1984, 1986, Chapter 2), the Levantine basin was expected to represent a more stable environment. The sediments receive relatively low organic loads and offer a more stable environment for the benthic fauna. However, considering the data described in the preceding chapters of this thesis we can conclude that even in this region strong seasonal fluctuations in the foraminiferal assemblage occur, probably driven by increased organic enrichment after seasonal mixing of water layers.

To define more precisely what the differences are between the two systems, and which effects they have on the foraminiferal assemblages, we compared diversity patterns and general assemblage compositions in the two areas. In addition, the abundance patterns, average living depth (ALD) and overall in-sediment distribution for the miliolid group and four taxa that occur relatively abundant at all stations (*Epistominella vitrea*, *Eggerella* spp., *Caronia silvestrii*, and *Bulimina marginata*) are discussed. In order to gain more insight in the impact of oxygen availability, time series of ALD patterns over two years were plotted against sediment oxygenation.

2. Material and methods

Foraminiferal data was obtained through monitoring cruises in the southern Levantine Basin and northern Adriatic Sea (Fig. 1, Table I). The two Levantine stations S1 and S3 were sampled bimonthly through box coring over the period June '96 to May '98. The two Adriatic Sea stations AD108 and AD203 were sampled eight times between November '96 and June '98. At these stations sampling was done by SCUBA diving. In the Adriatic as well as in the Levantine sediments oxygen-profiles were obtained immediately upon arrival onboard, using micro-electrodes.

Station	Water depth (m)	Latitude	Longitude
LEV51	41	32°22.5'N	34°48.4'E
LEV53	121	32°26.6'N	34°42.8'E
AD108	32	44°45.4'N	12°45.0'E
AD203	36	44°34.0'N	12°48.0'E

Table 8-1: Localities (longitude, latitude, water depth) of the sample stations in the Adriatic Sea and the Levantine Basin

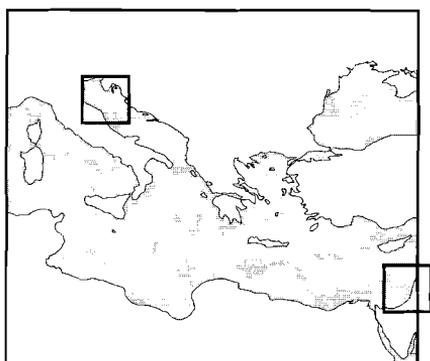
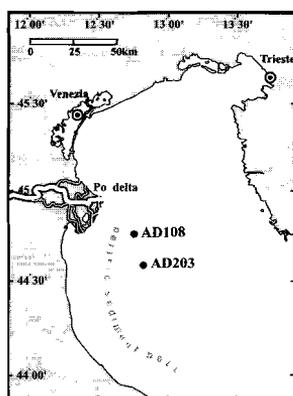
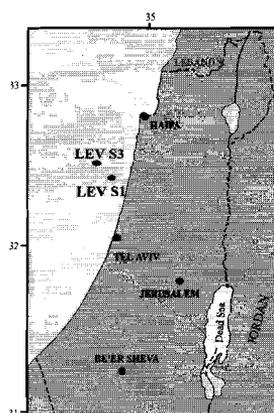


Figure 8-1: Sample localities in the Levantine Basin (S1 and S3) and the Adriatic Sea (AD108 and AD203).



northern
Adriatic Sea



southern
Levantine Basin

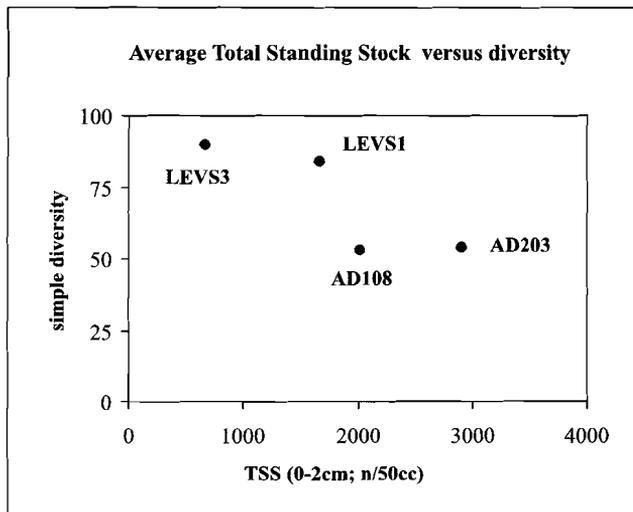
The sediment cores were sliced in slices of 0.5 cm (0-2 cm) and 1 cm (2-10 cm); the samples were stored in a mixture of Rose Bengal and ethanol (1 g/L). In the laboratory the samples were washed and sieved. Foraminiferal data used for this study is obtained from the 63-595 μm size fraction of the four top half cm slices (0-2 cm).

3. Results

3.1 Diversity and total standing stock patterns

A comparison of simple diversities demonstrates that the assemblages from the stable Levantine area are far more differentiated than those from the ecologically more stressed Adriatic Sea (Fig. 2a). Yet, the bulk of the fauna is not very different: species abundant in the Adriatic Sea are often also common in the Levantine assemblages. More than 70% of the taxa occurring in the Adriatic Sea, also occurs in

a



b

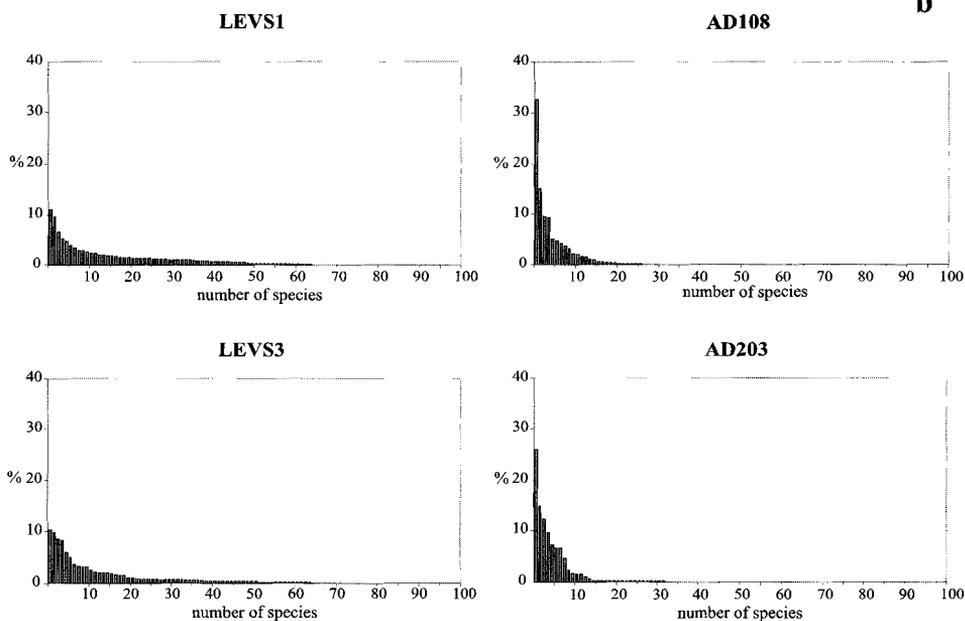


Figure 8-2: a) Average total standing stock (two-years) versus simple diversity found at the four stations; b) histograms of the relative abundances of species averaged over time for the four stations.

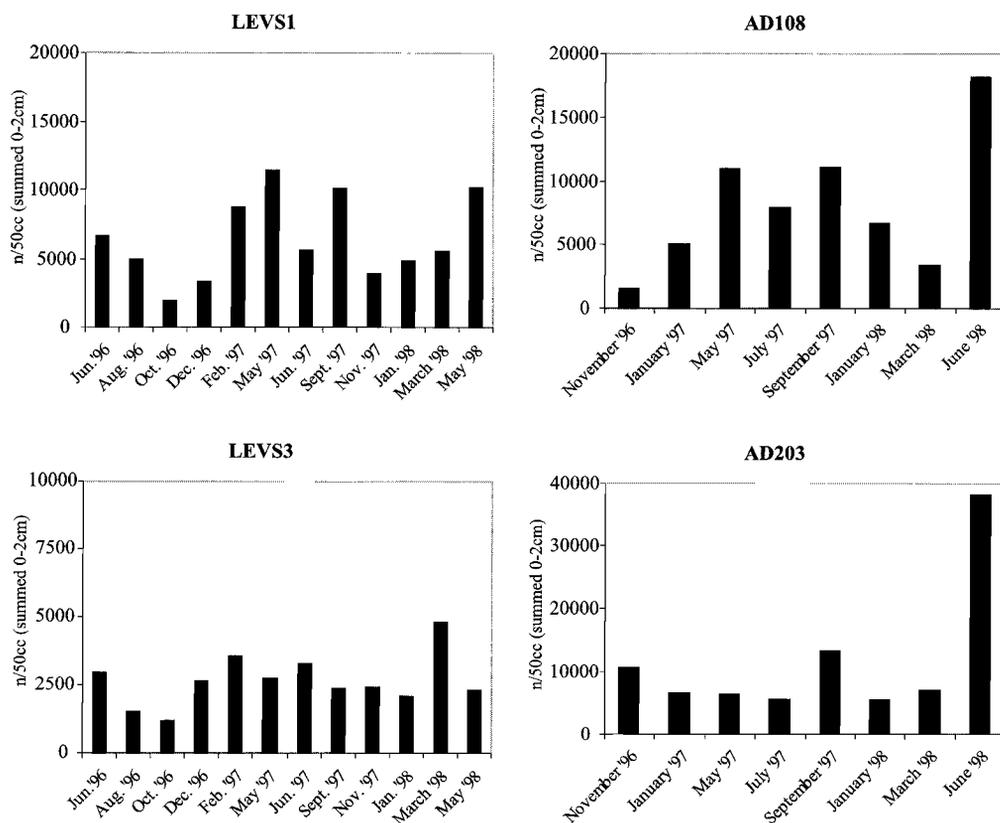


Figure 8-3: Total standing stocks (top 2cm; n/50cc) at the four stations over time.

the Levantine basin (data not shown). The higher diversity in the latter is mainly related to a large number of taxa which are present in low to extremely low relative frequencies (Fig. 2b). The average total standing stocks are inversely related to the diversities and are higher in the Adriatic Sea (Fig. 2a). This can be expected looking at the higher seasonal input of organic matter in the Adriatic Sea compared to the Levantine.

In figure 3 the total standing stocks (TSS) are shown as time series. In stations S1 and AD108 the numbers of foraminifera fluctuated strongly over the two years. At S1 there was a clear seasonal pattern, with increasing numbers after winter/spring and decreasing numbers during autumn and the beginning of winter. At station AD108 the TSS pattern displayed an almost identical pattern, except for the exceptional peak value in June '98. At station AD203 the pattern appeared more stable, with somewhat elevated numbers in November '96 and September '97, and a peak standing stock in June '98. The TSS pattern at S3 was the most constant of the four stations discussed here; the overall abundances were approximately twice as low as the TSS found at S1. The total abundances at S1 were very similar to the TSS found at AD108, but generally 1-2 times lower than those found at AD203.

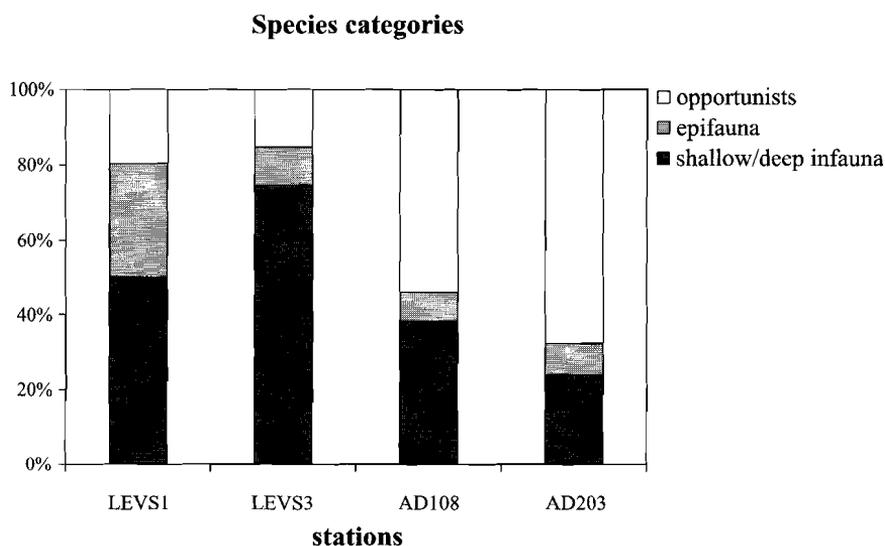


Figure 8-4: Relative abundances of the foraminifera at the four stations categorized within the groups: opportunists, epifauna, or shallow/deep infauna (see text for explanation).

3.2 Ecological categories

In figure 4 we summarise the general assemblage composition to get some insight in the main differences. Based on earlier studies we distinguished three categories, i.e. epifaunal, infaunal and opportunistic taxa (see Appendix 1). Although we realise that the assignment of taxa to either of these groups is often arbitrary, we think they give relevant information on the ecological structure of the benthic community.

The proportion of epifaunal taxa decreases with diversity, being highest in both Levantine stations. In station S3 the proportion of (mostly shallow) infauna increases, possible because of the deeper sediment oxygenation at this station (Chapter 6). The largest difference is constituted by the higher proportion of opportunistic species occurring in the Adriatic Sea, being 2–3 times the amount occurring in the Levantine assemblages.

3.3 Abundance patterns of the miliolids and four common taxa

In figure 5 the standing stock patterns of the miliolid group and four common taxa (*Epistominella vitrea*, *Eggerella* spp., *Caronia silvestrii*, and *Bulimina marginata*) are shown for all four stations.

At the Levantine station S1 the standing stock of miliolids displayed large fluctuations, and a clear seasonality was visible: low numbers in autumn and winter, highest standing stocks at the end of winter and in spring, and reduced standing stocks again in summer. At station S3 the group of

miliolids was far less abundant and the seasonal pattern less clear. In the Adriatic Sea, the miliolids were more abundant at station AD203 than closer to the Po delta, at AD108. The standing stock at AD203 displayed high numbers in November '96 and June '98, and slightly increased numbers in spring (May '97). At AD108 their numbers increased in spring (May '97) and the following autumn, and peaked in June '98.

Just as for the miliolids, the standing stock pattern of *E. vitrea* at station S1 was almost identical in both years. At station S3 the numbers of *E. vitrea* initially were very low after which they increased (end of winter) and stayed more or less stable for the remainder of the monitoring period. The standing patterns in the Adriatic were similar for both stations although *E. vitrea* was far more abundant at station AD203. At both stations *E. vitrea* occurred with peak values in June '98.

Although the patterns of the miliolids and *E. vitrea* were rather similar for both areas, the absolute numbers differed. Miliolids were more abundant in the Levantine basin whereas *E. vitrea* was more abundant in the Adriatic Sea. The seasonal variability of both taxa was most clear in the shallow station S1 and the Adriatic station 108. The seasonal change was considerably reduced in station AD203 and even more so in the deeper water station S3.

Eggerella spp., *Caronia silvestrii* and *Bulimina marginata* basically display a similar pattern as both taxa described before. The seasonal variation reduced going from station 108 in the Adriatic Sea to station S3 in the Levantine. The regularity of the displayed seasonal cycle was often rather disappointing. In this sense absolute standing stocks seem to be decided by a rather complex chain of events instead of being a straightforward response to ventilation or eutrophication.

3.4 Average Living Depths (ALD) versus sediment oxygenation

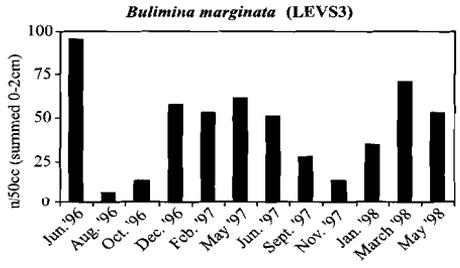
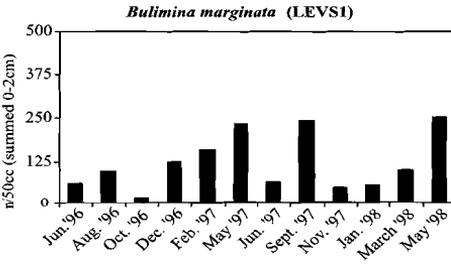
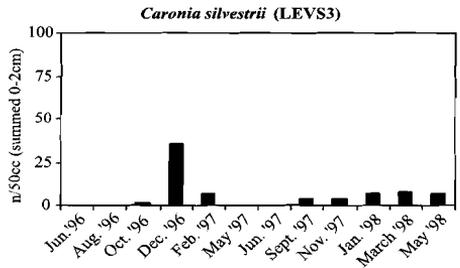
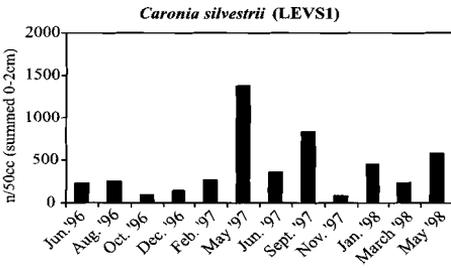
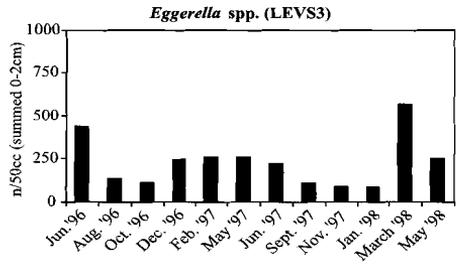
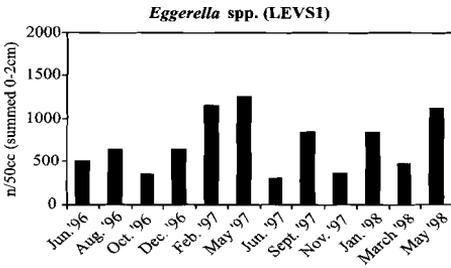
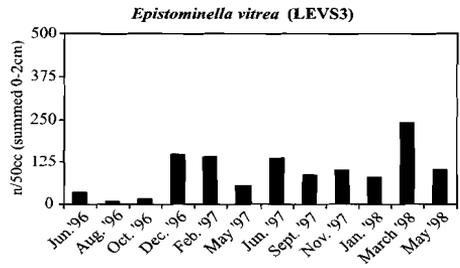
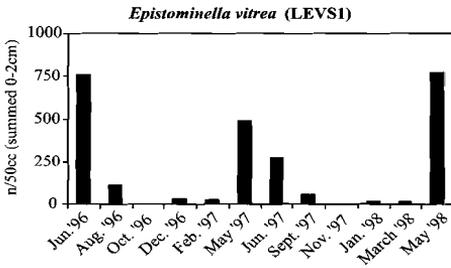
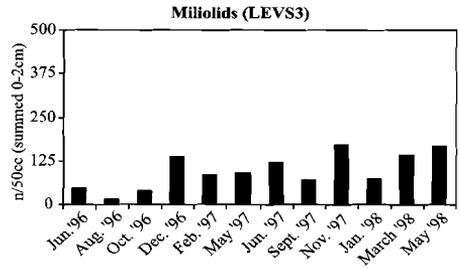
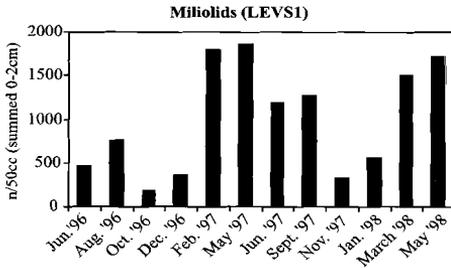
In figure 6 the ALD₂ (average living depth over 0–2cm) of the miliolids and the four other taxa are plotted against the sediment oxygenation. Also the correlation between the relative in-sediment distribution of the species and sediment oxygenation, was calculated (Table II).

The ALD₂ of the miliolids versus oxygenation is shown in figure 6a. The average ALD₂ was rather shallow, but no correlation was found between the ALD₂ and the level of oxygenation. In general, the ALD₂ seemed shallower than the level of 0.1 ml/L oxygen; only at the stations S1 and AD108 it was found to be occasionally below this level. Although there is no clear correlation between the ALD₂ and oxygenation, at all four stations a significant positive correlation was found between the miliolid in-sediment abundance and sediment oxygenation.

Epistominella vitrea displayed a variable in-sediment distribution, but generally its ALD₂ was rather

	LEVS1	LEVS3	AD108	AD203
miliolids	+	++	+	+++
<i>Epistominella vitrea</i>	n.s.	n.s.	n.s.	+
<i>Eggerella</i> spp.	n.s.	n.s.	-	n.s.
<i>Caronia silvestrii</i>	n.s.	n.s.	n.s.	n.s.
<i>Bulimina marginata</i>	n.s.	n.s.	+	n.s.

Table 8-II: Correlation between the relative in-sediment distribution and sediment oxygenation. (p<0.05 = +/- (positive/negative); p<0.01 = ++; p<0.001 = +++; n.s. = no significant correlation)



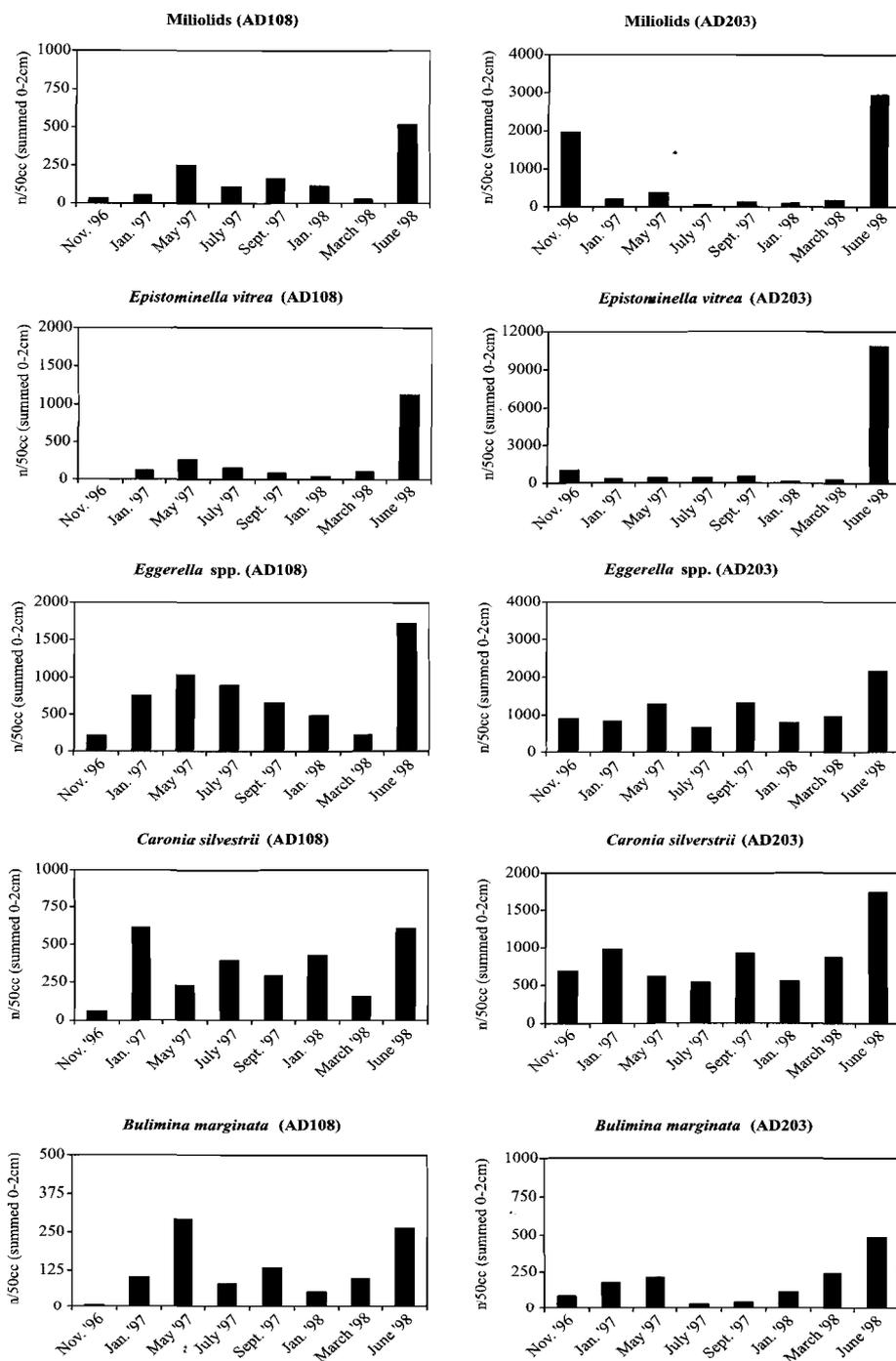
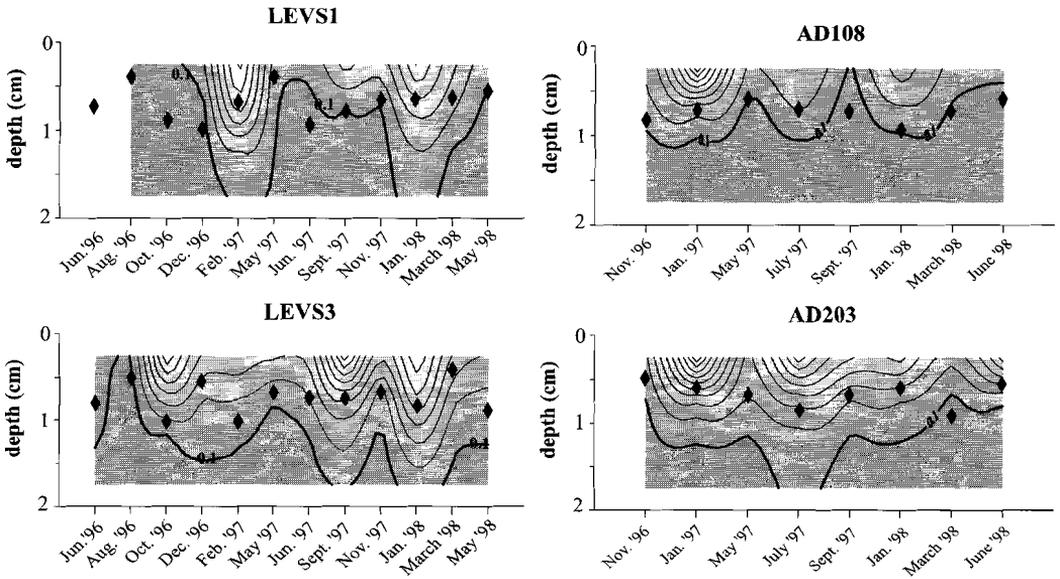


Figure 8-5: Total standing stocks (top 2cm; n/50cc) of the miliolids, *Caronia silvestrii*, *Epistominella vitrea*, *Eggerella* spp., and *Bulimina marginata* at the Levantine and the Adriatic stations.

Miliolids

a



Epistominella vitrea

b

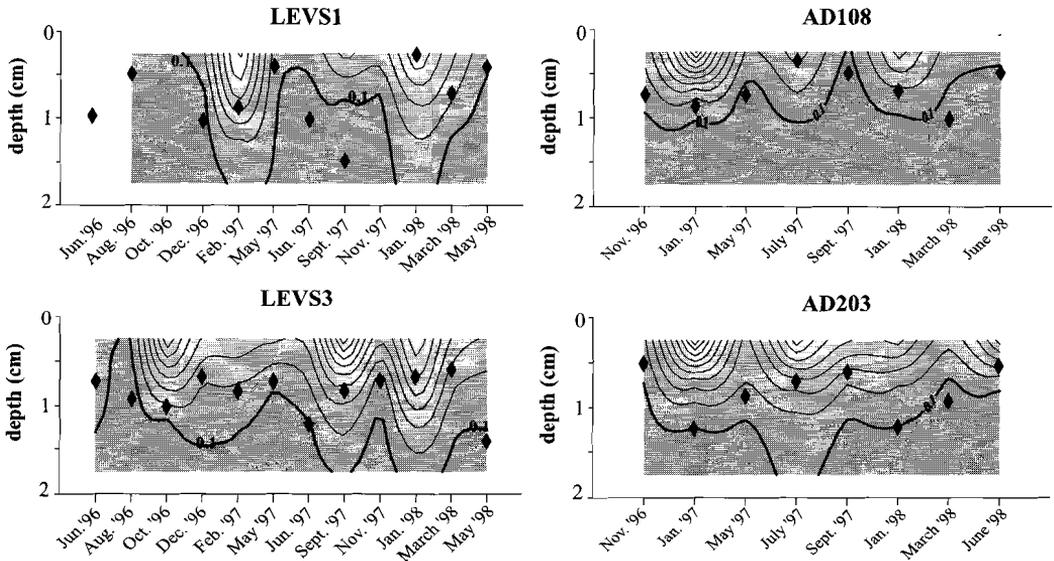
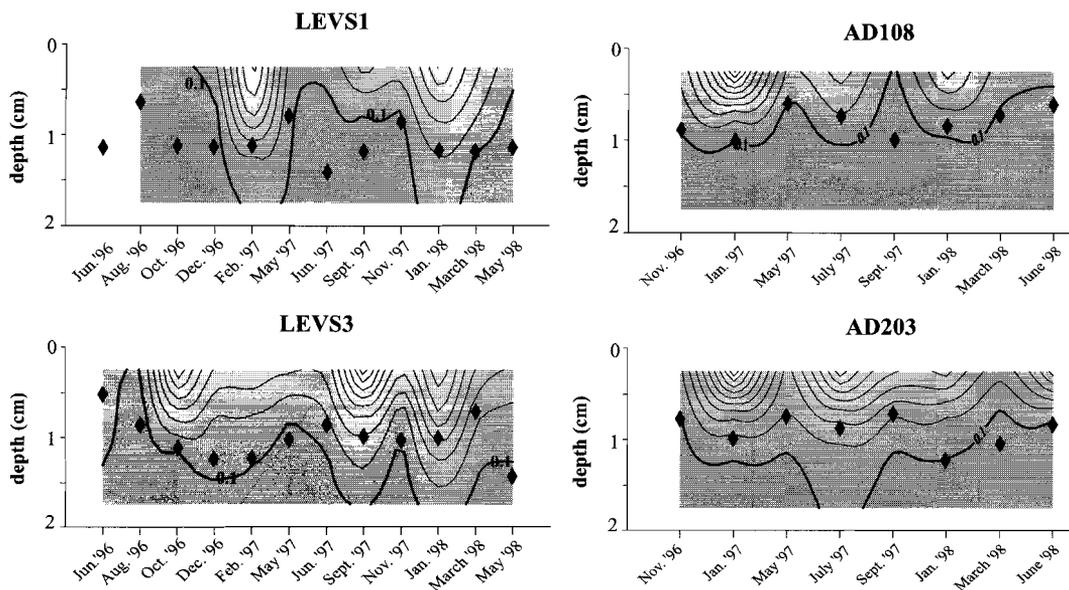


Figure 8-6: The ALD₂ of the miliolids and four common taxa at the four sample stations versus the occurring sediment oxygenation. a) miliolids; b) *Epistominella vitrea*; c) *Eggerella* spp.; d) *Caronia silvestrii*. The thick line indicates the level of 0.1ml/L oxygen, the ♦ symbols indicate the ALD₂. At S1 no oxygen was measured in June '96.

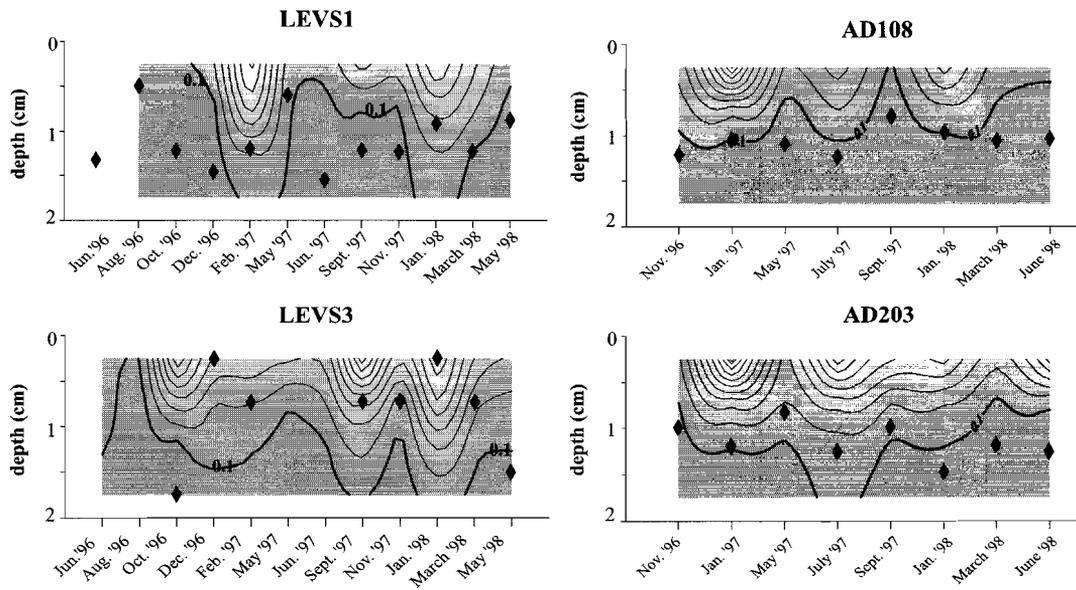
Eggerella spp.

c



Caronia silvestrii

d



Bulimina marginata

e

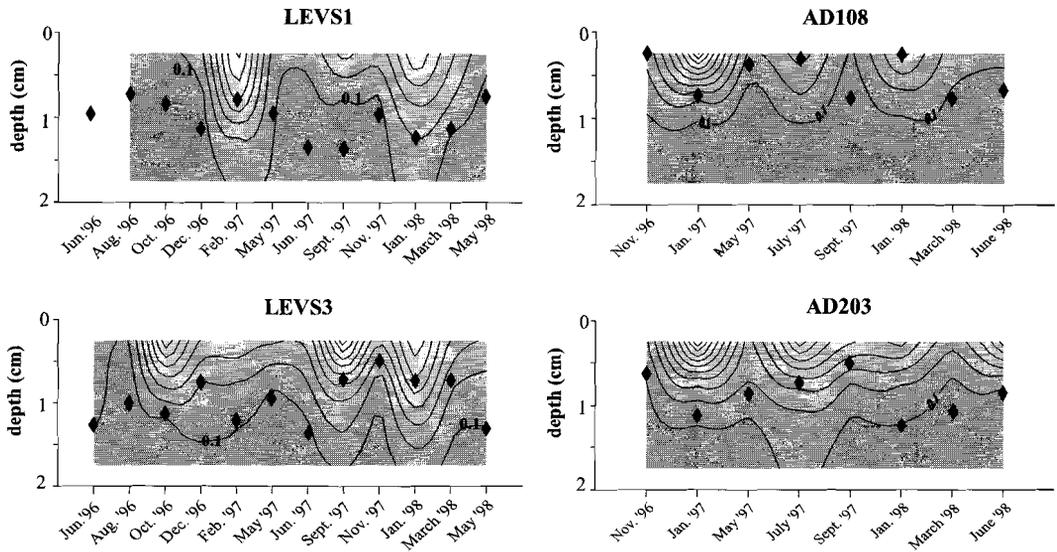


Figure 8-6: The ALD_2 of the miliolids and four common taxa at the four sample stations versus the occurring sediment oxygenation. e) *Bulimina marginata*. The thick line indicates the level of 0.1 ml/L oxygen, the \blacklozenge symbols indicate the ALD_2 . At S1 no oxygen was measured in June '96.

shallow (Fig. 6b). The ALD_2 , as well as its relative abundance at all stations (except AD203) were not correlated with sediment oxygenation; it should be noted, however, that the species was only rarely found below the level of 0.1 ml/L oxygenation.

At station S1 the ALD_2 of *Eggerella* spp. seasonally fluctuated considerably, between 0.5 cm and 1.5 cm, with no correlation to the sediment oxygenation (Fig. 6c). Its ALD_2 at station S3 was less variable through time. At station AD108 and AD203 *Eggerella* occurred slightly shallower and showed less variation than in the Levantine stations. In none of the stations a correlation between the ALD_2 , or the in-sediment abundance, versus oxygenation was found.

Caronia silvestrii appeared to be a rather deeply residing taxon (Fig. 6d); generally its ALD_2 was found to be around 1 cm or deeper and only occasionally shallower than 0.75 cm (S1 and S3). At the Adriatic Sea sample stations its in-sediment distribution was more or less stable ($ALD_2 \sim 1$ cm), whereas in the Levantine stations it changed drastically throughout the years. The vertical distribution of *C. silvestrii* over the sediment column at S3 is based on only a few specimens, which makes the ALD_2 not reliable. No correlation was found between the ALD_2 , and sediment oxygenation. The in-sediment abundance of this species was not correlated to the sediment oxygenation, except at AD108 where a negative correlation was found. This could very well be due to its preference for the deeper sediment layers. It should be noted that the ALD_2 of *C. silvestrii* was often found to be below the level of 0.1 ml/L oxygenation.

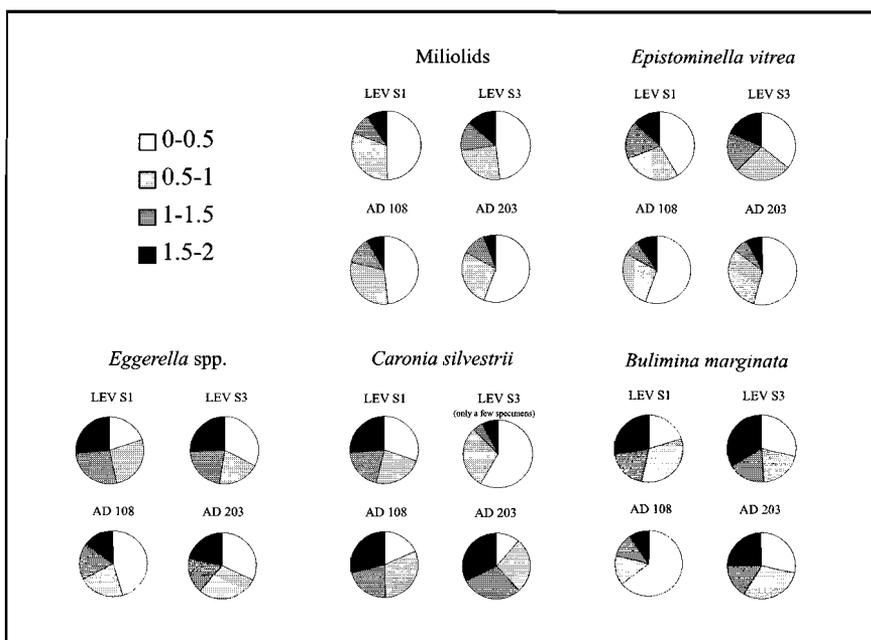


Figure 8-7: The in-sediment distribution of the miliolids and four abundant taxa.

The ALD₂ of *Bulimina marginata* displayed large fluctuations at all stations (Fig. 6e). At station S1 it was frequently well below the level of 0.1 ml/L oxygenation and also at S3 it was occasionally found below this level. At station AD108 the species occurred much shallower than at the Levantine stations, but also here the ALD₂ was occasionally below the 0.1 ml/L oxygen level. The ALD₂ of *B. marginata* at station AD203 was similar to that in the Levantine basin. As for the other species, no correlation existed between the sediment oxygenation and the ALD₂. Only at AD108 a positive correlation between its in-sediment distribution and sediment oxygenation was found.

The ALD₂ of the five taxa exhibited a more fluctuating pattern at the Levantine stations than in the Adriatic stations. Except for the miliolids, for none of the five taxa a consistent correlation between the ALD₂ or the in-sediment distribution patterns and sediment oxygenation was found.

3.5 Ecological niches

In figure 7, the two year averaged in-sediment distribution of the taxa over the top 2 cm is shown. The miliolids occurred, in the Levantine as well as in the Adriatic Sea, with 50% of their specimens in the topmost sediment layer and with 75% in the top 1cm. *Epistominella vitrea* was also most prominently living in the top cm of the substrate. In the Levantine, most specimens were found in 0-1cm (>60%); the remainder was equally spread out over the deeper sediment layers. In the Adriatic

Sea more than 80% of the living specimens were found in the top cm of the sediment, with the remaining specimens evenly distributed deeper.

Eggerella spp. is clearly a deeper living species, almost equally distributed over the top two cm sediment column. Only at site AD108 it showed a slight preference for the topmost sediment sample. Also *Caronia silvestrii* is occurring all over the sediment column. In the Adriatic sites it displayed a preference for the deeper sediment samples. The aberrant picture at site S3 was based on only a few specimens. The overall in-sediment distribution of *Bulimina marginata* is very similar to that of *Eggerella* spp., including the preference for the top sediment layer at site AD108.

4. Discussion

4.1 TSS patterns and biodiversity

Our data clearly demonstrate that diversity is highest in the most oligotrophic and stable area: the Levantine basin. We used simple diversity, because the data-sets are all based on approximately the same counting quantities. The high simple diversity as found in the Levantine basin can be related to stability, but more likely is that the less regularly occurring periods of severe stress play a prominent role (see for example Sanders, 1968). In the Levantine stations a large amount of taxa are rare, in contrast to most taxa in the Adriatic stations. One may assume that with stress, for instance related to anoxia as occurring in the Adriatic Sea, many rare species are eliminated. Following a period of stress, it apparently takes time to re-establish diversity at a high level (see also Sanders, 1968). This hypothesis finds some support if we look at the overall composition of the assemblages. The Adriatic samples are clearly characterised by a higher number of opportunistic species, whereas in the Levantine a rather large and sometimes highly diversified group of epifaunal and infaunal taxa dominates.

Although on the average the standing stocks in the Levantine Basin were lower than those in the Adriatic Sea, the TSS patterns displayed considerable fluctuations throughout the two years. In the Levantine station S1, they follow a rather clear seasonal cycle (see also Chapters 4 and 5). In station S3 the foraminiferal TSS increased during the first year in December '96 and during the second year in March '98, both times just after relative peak concentrations of chlorophyll-a (Chapter 6). At the shallow water Levantine site S1 no major factor next to the seasonal mixing of water layers in autumn and winter drives the marine system; this eventually results in a rather clear seasonal TSS pattern. The less clear-cut seasonal TSS pattern at station S3 is most likely due to much lower increase in food supply arriving here, resulting in less extreme numerical responses of the foraminifera. At this water depth additional food supply from the DCM is likely, which also could blur the seasonal cycle. Wollenburg & Kuhnt (2000) found that episodic supply of food was the critical environmental parameter influencing Arctic benthic foraminifera. In this overall low productive area they found maximum standing stocks during a phytoplankton bloom. But in our case apparently other factors interfere and lead to a somewhat blurred response of the TSS on the yearly productivity cycle.

At the Adriatic Sea stations, strong fluctuations in foraminiferal TSS throughout the years were found. The seasonal repetition here was even less obvious than at S3. This may be due to the fact that

sampling occurred rather irregularly, making it more difficult to keep track of seasonal changes. But even taking that into account, one has to acknowledge that the TSS pattern displayed no obvious (seasonal) repetition over the years. Especially the TSS pattern at station AD108 is characterised by large fluctuations. The high values in May '97 probably reflected organic enrichment of the sediment due to increased run-off, which is known to occur during spring (Jorissen et al., 1992). When water layers mix in autumn nutrients are brought up to the surface; also then increasing primary productivity eventually causes an increase in food supply at the sea floor. At station AD108 this was reflected in the high TSS in September '97 and at station AD203 high numbers of foraminifera were found in November '96 and September '97. Because station AD203 is located further from the Po-delta, the river run-off has less influence on the environmental circumstances at this station; this could explain why no clear peak in TSS was found during spring. The enormous peaks occurring in June '98 were aberrant and no clear explanation can be given for this. Considering that these peaks in foraminiferal TSS occurred simultaneously at both Adriatic stations, the obviously very profitable ecological circumstances occurred on a larger geographical scale.

In the highly eutrophic Sagami Bay, Kitazato et al. (2000) found the foraminiferal population size to be strongly driven by seasonal phytodetritus deposition. They suggest that seasonal flux is the most important determinant for population size. We have no reason to doubt this although in our case the correlation between flux and standing stock seems to be far more complex. The two different study areas are known to have completely different levels of trophication. However, the foraminiferal numbers found at stations S1 and AD203 were quite comparable. This suggests that the overall level of organic matter availability is not the major or only controlling factor. We assume that populations are limited also by stress. The latter is far more pronounced in the Adriatic Sea than in the Levantine, due to the regular anoxia events that occur over large areas. In this view the foraminiferal TSS would be decided by a delicate balance between food supply and stress.

4.2 Standing stock patterns of the miliolids and four abundant taxa

The standing stock patterns of the miliolids and four foraminiferal taxa are overall very comparable for the four stations. The miliolids displayed numerical responses after increase of the organic matter load in the both the Adriatic Sea and the Levantine. The delayed numerical response of foraminifera living at station S1 is probably due to macrofaunal interference (extensively discussed in Chapters 4 and 5). At station S3 the miliolids reacted more directly to increased food supply and also in the Adriatic Sea the numerical responses of the miliolids seem related to times of organic enrichment. At station AD203 their standing stocks increased during autumn and spring of the first year, although in the second year no autumn peak was found. Overall, part of the life-strategy of the miliolid group seems to be to profit rather directly from increase in organic matter availability. This is even more pronounced in the case of *Epistominella vitrea*, that obviously profited during short periods from increased supply. Quick numerical response was also found for the deeper living counterpart of *E. vitrea*, *Epistominella exigua* which is known to occur abundantly after organic enrichment (Goody & Turley, 1990, Goody, 1988). As discussed by Goody (1993), this species is also able survive under

low trophic conditions but reproduces very opportunistically after food arrival on the seafloor. The same behaviour was found in the Arctic for *Epistominella arctica* by Wollenburg and Kuhnt (2000).

Surprisingly, also the standing stock patterns of *Eggerella* spp. and *Bulimina marginata* seemed to be controlled by increase of organic matter supply. This is less obvious for *Caronia silvestrii* that was far less abundant at station S3 than at the other stations. Our data suggest that even these deeper living taxa can respond rather promptly to organic matter enrichment. In many cases this seems to result in reproduction at the surface layer, where a higher proportion of the assemblage is then concentrated for some time (e.g. *Eggerella* spp., see Chapters 5 and 6).

4.3 Average living depth (ALD₂) versus sediment oxygenation

At all four stations the ALD₂ of the miliolids was quite shallow. In the Levantine their ALD₂ fluctuated strongly, whereas in the Adriatic sediment it was more stable. At none of the stations there was a clear correlation between the ALD₂ of the miliolids and the sediment oxygenation. However, at all stations a significant positive correlation between their relative in-sediment distribution and sediment oxygenation was found. The fact that the ALD₂ is less sensitive to abundance patterns, explains why no clear correlations were found between ALD₂ and oxygenation. The deepest ALD₂ of the miliolids is found at times they occurred in relatively low numbers. The averaged standing stocks of miliolids, however, showed the clear tendency to live most abundantly in the shallowest sediment layers. The fact that this was found at all four stations, indicates that this epi- to shallow infaunal lifestyle is inherent to miliolids and not the result of local ecological conditions.

The ALD₂ of *Epistominella vitrea* fluctuated strongly at all stations, but showed no clear correlation with the sediment oxygenation. At S1 its ALD₂ displayed its most extreme fluctuations. As for the miliolids, the in-sediment standing stock distribution of *E. vitrea*, summarised over the years, suggests that the ecological niche it generally occupies within the sediment is a rather shallow one.

The other three taxa are obviously residing deeper in the sediment column. Also here, there seems to be a considerable similarity between the patterns from the different regions. *Eggerella* spp. had a relatively deeper ALD₂ than both the miliolids and *E. vitrea*, its ALD₂ being mostly deeper than 1 cm. Like *Eggerella* spp., *C. silvestrii* displayed relatively deep average living depths at all stations. Its in-sediment habitat is very similar to the one of *Eggerella* spp. *Bulimina marginata* was characterised by a relatively deep ALD₂ in the Levantine sediments, but in the sediments at AD108 it was found to be mostly rather shallow. The three deeper living (infaunal) species show less extreme fluctuations in their standing stock patterns through time than the more shallow living taxa. This could be due to the fact that the niche of the infaunal taxa is generally less crowded and that compared to the shallower sediment layers competition is less severe. Under conditions of sufficient food supply, there is probably no need to migrate to shallower sediment layers. Kitazato et al. (2000) also found deep infaunal foraminifera to generally show less pronounced seasonal fluctuations in population size. Nevertheless, even some of these deep infaunal taxa exhibited response to phytodetrital deposition. This is comparable to the pattern found for the deeper infaunal *Eggerella* spp., living very abundantly in the top sediment layer after organic enrichment. Afterwards, however, it was found to be dispersed

evenly again over the sediment column (see Chapters 5 and 6). This implies that it probably needs increased (fresh) organic matter supply in order to be triggered for reproduction. Its re-migration to deeper and less organic rich sediment layers might be caused by the much smaller foraminiferal densities here, which minimise competition stress.

It seems likely that the more shallow living taxa, that generally display more irregular TSS patterns, are somewhat more demanding with respect to food availability. Their relatively opportunistic life-style, e.g. quick numerical response after increased food availability, strengthens their competitive position and makes it possible for them to survive successfully in the shallow sediment layers. The positive correlation between miliolid abundance and oxygen implies that they are not able to thrive under oxygen deficient circumstances. This may force them to adopt a more epi- to shallow infaunal lifestyle in spite of the inherent relatively large competition stress.

5. Conclusions

The major factors controlling the foraminiferal standing stock patterns are (seasonal) organic matter enrichment and oxygen stress. The fact that foraminiferal numbers found in the Levantine basin were not much lower than those found in the Adriatic, suggests that standing stocks do not simply reflect the amount of organic flux, but probably more the balance between flux and limitation by stress. Diversity seems to be inversely related to average standing stock, possibly because quite a number of taxa occurring in low abundances are more easily eliminated by stress, resulting in low diversity but high standing stocks in the Adriatic Sea.

In spite of the differences between the Adriatic Sea and the Levantine Basin, five taxa that were studied in some detail occupied very constant microhabitat positions, suggesting that these are inherent to the species and not exclusively the result of the ambient in-sediment environment.

Whereas there was a significant correlation between the relative in-sediment distribution of miliolids and sediment oxygenation at both Levantine stations, no clear correlations were found for the ALD₂ versus oxygenation. For none of the other taxa a consistent correlation between in-sediment distribution and oxygenation was found.

Some deeper living taxa seemed to react on food supply by reproducing in the top sediment; after that, they re-migrated again in the deeper sediment layers. Epifaunal taxa reacted sharper to organic flux supply, but might experience stronger competition; this could be the cause of the more variable standing stock patterns over the years.

Appendix 8-1

1= opportunists
2= epifaunal
3= shallow-deep infaunal

LEVS1	category	LEVS3	category
Acostata mariae	3	Acostata mariae	3
Adelosina spp.	2	Adelosina spp.	2
Ammobaculites spp.	2	Adercotryma glomerata	3
Ammodiscus sp.	3	aggl. milio	3
Ammonia spp.	1	Agglutinated (monoserial)	3
Ammoscalaria sp.	3	Ammodiscus sp.	3
Amphicoryna scalaris	3	Ammonia spp.	1
Anomalina globulosa	2	Ammoscalaria sp.	3
Astaculus sp.	2	Amphicoryna scalaris	3
Asterigerinata mamilla	2	Articulina sagra/tubulosa	2
Asteronion stelligerum	2	Astaculus sp.	2
Asterorotalia (Hottinger)	2	Asterigerinata mamilla	2
Biloculinella labiata	2	Asteronion stelligerum	2
Bolivid aggl. sp.	3	Asterorotalia (Hottinger)	2
Bolivina dilatata	3	Bigenerina nodosaria	2
Bolivina plicatella	3	Biloculinella labiata	2
Bolivina seminuda/spatulata	3	Bolivid aggl. sp.	3
Bolivina sp.	3	Bolivina alata	3
Bolivina striatula	3	Bolivina dilatata	3
Buccella granulata	2	Bolivina seminuda/spatulata	3
Bulimina aculeata	2	Bolivina sp.	3
Bulimina elongata	3	Bolivina striatula	3
Bulimina marginata	3	Bolivina subspinensis	3
Bulimina sp.	2	Bulimina elongata	3
Buliminella elegantissima	3	Bulimina marginata	3
Buliminella spp.	3	Bulimina striata	3
Caronia silvestrii	3	Buliminella elegantissima	3
Cassidulina carinata	2	Buliminella spp.	3
Cassidulina crassa	3	Caronia silvestrii	3
Cassidulina leavigata	2	Cassidulina carinata	2
Cassidulina subglobosa	2	Cassidulina crassa	3
Cibicides lobatulus	3	Cassidulina leavigata	2
Cornuspira sp.	2	Cassidulina subglobosa	2
Criboelphidium poeyanum	3	Cibicides lobatulus	3
Cribrostomoides sp.	3	Cornuspira sp.	2
Dentalina spp.	2	Criboelphidium poeyanum	3
Disconorbis bulbosus	2	Cribrostomoides sp.	3
Discorbinella rhodiensis	2	Dentalina spp.	2
Eggerella spp.	1	Discorbinella rhodiensis	2
Elphidium crispum	2	Eggerella spp.	1
Elphidium spp.	2	Epistominella vitrea	1
Epistominella vitrea	1	Fissurina sp.	3
Fursenkoina spp.	1	Fursenkoina spp.	1
Gavelinopsis preageri	2	Gavelinopsis preageri	2
Glomospira sp.1	3	Globobulimina pacifica	3

Appendix 8-1 (continued)

1= opportunists
2= epifaunal
3= shallow-deep infaunal

LEVS1	category	LEVS3	category
Gyroidinoides sp.	3	Glomospira sp.2 (geel)	3
Haplophragmoides spp.	3	Gyroidina sp.	3
Hopkinsina pacifica	1	Haplophragmoides spp.	3
Hyalinetriion sp.	2	Hopkinsina pacifica	1
Lagena striata	2	Hyalinetriion sp.	2
Lagenammina sp.	3	Lagena striata	2
Lenticulina peregrina	3	Lagenammina sp.	3
Lenticulina sp.	3	Lenticulina peregrina	3
Leptohalysis scotti	2	Lenticulina sp.	3
Melonis barleeaanum	3	Leptohalysis scotti	2
Miliolids (lump)	2	Liebusella goesi	2
monothalaam	2	Melonis barleeaanum	3
Nodophthalmidium sp.	2	Miliolids (lumb)	2
Nodosaria sp	2	Miliolinella sp.	2
Nonionella spp.	1	monothalaam	2
Planorbulina mediterraneensis	2	Neandrospira glomerata	3
Polymorphina sp.	2	Nodosaria sp	2
Porosonion granosum	3	Nonionella spp.	1
Quinqueloculina spp.	2	Nonionella turgida	1
Rectoglandulina rotundata	2	Planorbulina mediterraneensis	2
Rectouvirgerina cilindrica	2	Planulina araminensis	3
Reophax scorpiurs	2	Polymorphina sp.	2
Reophax sp.	2	Pyrgo spp.	2
Reusella spinulosa	3	Quinqueloculina spp.	2
Rosalina floridensis/spp.	3	Rectouvirgerina cilindrica	2
Sigmoilopsis spp.	3	Reophax scorpiurs	2
Soft-shelled saccaminids	3	Reophax spp.	2
Spiroloculina sp.	2	Reusella spinulosa	3
Stainforthia complanata	1	Robertinoides sp	3
Textularia agglutinans	3	Rosalina spp.	3
Textularia porrecta	3	Sigmoilopsis sp.	3
Trifarina spp.	3	Soft-shelled saccaminids	3
Trochaminna globi.	3	Spiroloculina sp.	2
Trochaminna inflata	3	Stainforthia complanata	1
Uvigerina meditt/semiornata	3	Svratkina sp.	3
Uvigerina sp.	3	Technitella legumen	2
Valvulineria bradyana	3	Textularia agglutinans	3
Valvulineria sp.	3	Textularia porrecta	3
		Textularia sp.	3
		Trifarina spp.	3
		Triloculina sp.	2
		Troch. glob.	3
		Trochaminna inflata	3
		Uvigerina mediterranea	3
		Uvigerina sp.	3

Appendix 8-1 (continued)

1= opportunists
2= epifaunal
3= shallow-deep infaunal

AD108	category	AD203	category
Acostata mariae	3	Acostata mariae	3
Adercotryna glomerata	3	allogromids	3
Ammodiscus spp.	3	Ammonia spp.	1
Ammoglobigerina globigeriniformis	3	Ammoscalaria pseudospiralis	3
Ammoscalaria pseudospiralis	3	Amphicoryna spp.	3
Amphicoryna spp.	3	Bolivina dilatata/spatulata/seminuda	3
Bolivina dilatata/spatulata/seminuda	3	Buccella granulata	2
Bulimina marginata	3	Bulimina marginata	3
Buliminella elegantissima	3	Buliminella elegantissima	3
Buliminella spp.	3	Buliminella spp.	3
Caronia silvestrii	3	Caronia silvestrii	3
Cassidulina crassa	3	Cassidulina crassa	3
Criboelphidium poeyanum	3	Cibicides lobatulus	3
Eggerella spp.	1	Criboelphidium poeyanum	3
Elphidium spp.	3	Eggerella spp.	1
Epistominella vitrea	1	Elphidium spp.	3
Fissurina spp.	3	Epistominella vitrea	1
Fursenkoina spp.	1	Fissurina spp.	3
Glomospira spp.	3	Fursenkoina spp.	1
Gyrogonoides spp.	3	Haplophragmoides spp.	3
Haplophragmoides spp.	3	Hopkinsina pacifica	1
Hopkinsina pacifica	1	Hyalinonetrix spp.	2
Lagena spp.	2	Lagena spp.	2
Lenticulina gibba	3	Lenticulina gibba	3
Leptohalysis scottii	2	Leptohalysis scottii	2
miliolids	2	miliolids	2
Nodosaria spp./Dentalina spp.	2	Nodosaria spp./Dentalina spp.	2
Nonionella turgida	1	Nonionella turgida	1
Nouria polymorphinoides	3	Nouria polymorphinoides	3
Oolina globosa	2	Oolina globosa	2
Polymorphina spp.	2	Planorbulina spp.	2
Porosonion granosum	3	Polymorphina spp.	2
Pseudoeponides falsobeccarii	2	Porosonion granosum	3
Reophax scorpiurus	2	Porosonion spp.	3
Reussella spinulosa	3	Pseudoeponides falsobeccarii	2
Rosalina bradyi	3	Reophax scorpiurus	2
Saccamina sp1.	3	Reussella spinulosa	3
Saccamina spp.	3	Rosalina bradyi	3
Sigmoilopsis schlumbergeri	3	Saccamina sp1.	3
soft-shelled Saccamina	3	Saccamina spp.	3
Stainforthia fusiformis	1	Sigmoilopsis schlumbergeri	3
Textularia agglutinans	3	Stainforthia fusiformis	1
Textularia porrecta	3	Textularia agglutinans	3
Textularia spp.	3	Textularia porrecta	3
Trifarina angulosa	3	Textularia sagittula	3

Chapter 9

A food-experiment with oligotrophic benthic assemblages: preliminary results

With : Marijke van Kuijk and Bert van der Zwaan

Abstract

A food-experiment was performed with assemblages obtained from the oligotrophic southern Levantine basin. Microcosms with foraminifera containing sediments were divided over two aquaria. To one experimental situation a food-mixture (*Dunaliella* sp., *Nitzschia laevis*, and *Navicula lenzi*) was added; the other was used as control. The microcosms were harvested five times over a period of twelve weeks. Each time duplos were taken from the food-enriched as well as from the control situation. Stained foraminifera were counted from the 63-150µm and >150µm size fractions resulting from all five sample moments; from three sample moments also the 37-63µm size fraction was studied.

Addition of the food-mixture induced no clear increase in foraminiferal numbers. Calculation of the added food-mixture in terms of organic flux suggests that the food supply added during our experiment probably did not reach the level of the organic loads arriving at the Levantine seafloor after productive periods. We therefore suggest that the concentration of our food-mixture may not have been high enough to trigger high reproduction among the foraminifera. As an alternative, the outcome of our experiment could suggest that benthic assemblages in the shallow water realm are not as food limited as was thought previously.

1. Introduction

To get some grip on the main factors controlling the foraminiferal assemblages in the Levantine Basin, we started a monitoring study in 1996 (Chapters 4 and 5). In the two years of study, the density of the foraminiferal community at the shallowest station S1 (40m) appeared to be determined by the seasonality of the system. The yearly cycle of stratification and mixing of water layers regulates the primary productivity, and therefore also to a large extent the foraminiferal assemblages and densities. In another study (Chapter 8) we inferred that the main factor controlling the foraminiferal numbers is the balance between organic matter concentration and oxygen consumption. Earlier, the importance of organic flux was discussed for example by Gooday (1993), Gooday and Turley (1990), Wollenburg and Kuhnt (2000) and Kitazato et al. (2000).

In order to test the impact of food addition on the population dynamics of foraminifera without the interfering effects of oxygen, an experiment was carried out with assemblages from the oligotrophic Levantine basin. The experimental set-up consisted of a control situation with normal conditions (as prevailing in the Levantine), and a food-enriched situation. Food was added after 3 weeks to give the assemblages time to settle. From the samples taken during the experimental period, three different size

time in weeks	procedure
t = 0	samples taken at onset of experiment (n=3)
t = 3	samples taken before addition of food (n=2) in order to observe possible stress response following experimental treatment
t = 6	samples taken 3wks after food input (n=2)
t = 9	samples taken 6wks after food input (n=2)
t = 12	samples taken 9wks after food input (n=2)

Figure 9-1: Experimental set-up (n= numbers of samples counted per treatment).

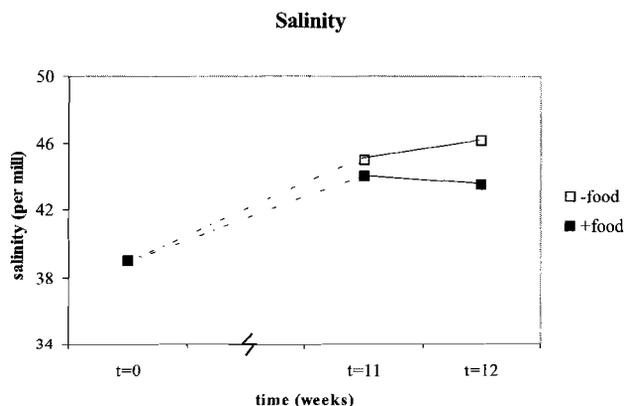


Figure 9-2: Salinity in both aquaria during the experiment.

fractions were studied in order to survey the population dynamics. Sampling took place over a period of twelve weeks in order to allow foraminifera to reproduce and respond to the food pulse. In this study, we present preliminary data and discuss the population dynamics of the most common taxa.

2. Materials and methods

Sediment obtained at our shallowest sample station S1 (40m) in the Levantine basin (February 2000), was used for the experiment. From several box cores the top sediment layer was collected and stored in plastic jars together with ambient seawater. In the laboratory the sediment was sieved over a 500 μ m sieve, to exclude macrofauna and larger predators. After sieving, the sediment was gently mixed and left to settle for 24 hours. A grid was used to divide the sediment evenly over 80 microcosms. Every microcosm (100cc) was filled with 40cc sediment and placed in one of the two aquaria, except for eight microcosms that were taken as control for the time of incubation $t=0$. In each of the aquaria containing artificial seawater (Reef Crystals, synthetic sea salt; $T=17^{\circ}\text{C}$, $S=39\text{‰}$) 36 microcosms were placed. The aquaria were continuously aerated throughout the experiment.

After 3 weeks ($t=3$) 8 microcosms were harvested, and 1.65 mg (dry weight) of a food-mixture was added to the remaining 32 microcosms in one of the aquaria. This mixture, containing heat-killed *Dunaliella* sp., *Nitzschia laevis*, and *Navicula lenzi*, was injected with a syringe onto the sediment surface in the microcosms. The microcosms in the second aquarium were not enriched and considered to be control experiments. Both aquaria were closed circuits, in order to prevent contamination.

Two microcosms were taken randomly from each aquarium after 6, 9, and 12 weeks (Fig. 1). The microcosms of $t=3$ were taken just before the addition of the food-mixture. For harvesting, the water was removed and a mixture of ethanol and Rose Bengal (1 g/L) was added. The Rose Bengal stained sediments were sieved over several sieves, leaving aliquots of $>150\mu\text{m}$, 63–150 μm , and 37–63 μm .

Because of the considerable amount of time involved in studying all the samples, from $t=3$, $t=6$, and $t=9$ all three size fractions were studied; from $t=0$ and $t=12$ only the 63–150 μm and $>150\mu\text{m}$ size fractions were counted.

During the experiment we observed some lowering of the water level in the aquaria, in spite of the fact that we had covered them to prevent evaporation. Salinity was only measured at the beginning ($t=0$) and from $t=11$ onwards. These measurements suggest that evaporation took place and affected the salinity significantly. However, it approximately was the same in both aquaria (Fig. 2); the salinity went up from 39 ‰ (ambient salinity, $t=0$) to 46.1 ‰ and 43.5 ‰ , respectively, at $t=12$.

3. Results

3.1 Total standing stocks in the three size fractions

The total standing stocks (TSS) as found in the three size fractions throughout the experiment are shown in figure 3. The TSS increased most pronouncedly between $t=3$ and $t=6$. Strangely enough

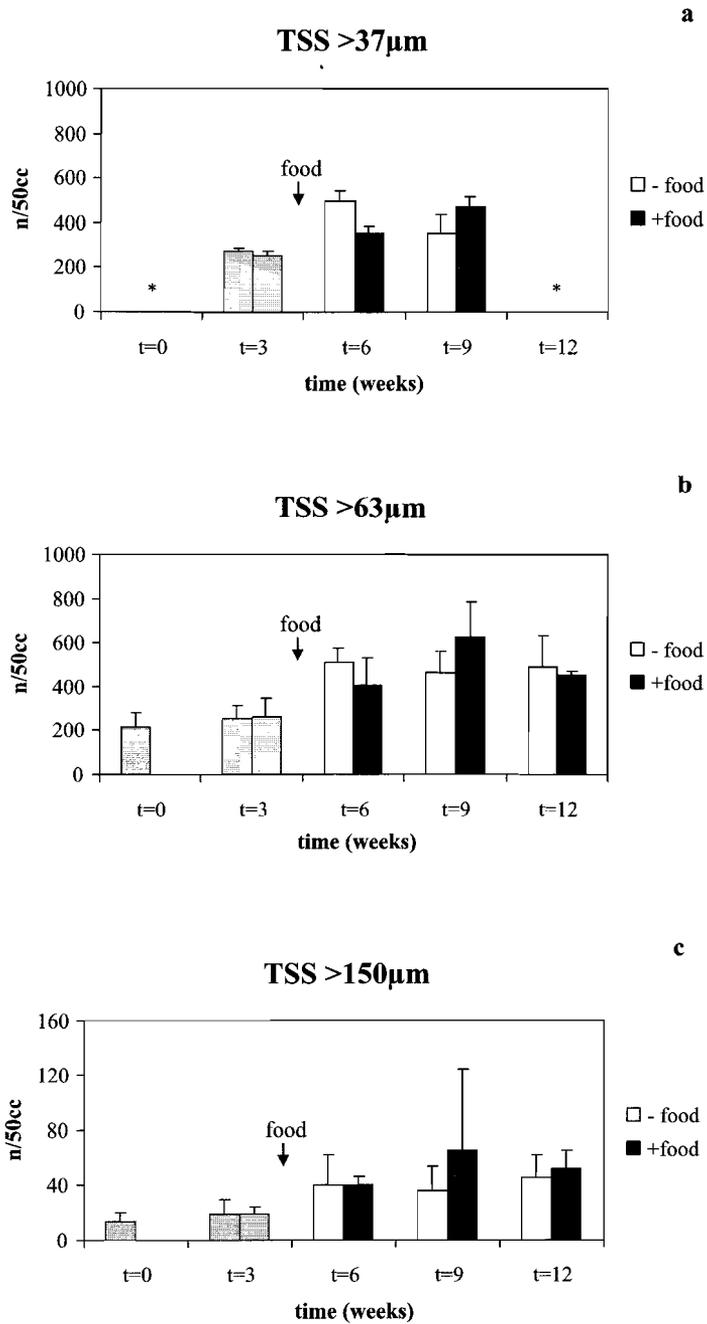


Figure 9-3: Total standing stocks in the three size fractions; a) 37-63µm; b) 63-150µm; c) >150µm. The * symbol indicates that the >37µm was not counted.

this holds for both the food-enriched and the control situation. In two out of three size fractions, the increase is even stronger in the control situation where no food was added. At $t=9$, the numbers were highest in the enriched situation. The patterns in the $>37\mu\text{m}$ and the $63\text{--}150\mu\text{m}$ size fractions are similar. In the larger size fraction the differences are less outspoken but still visible.

3.2 A few common taxa

The numerical responses of a few common taxa are shown in figure 4. In view of the difficulty to determine taxa in the smallest size fraction at the species level, we distinguished groups.

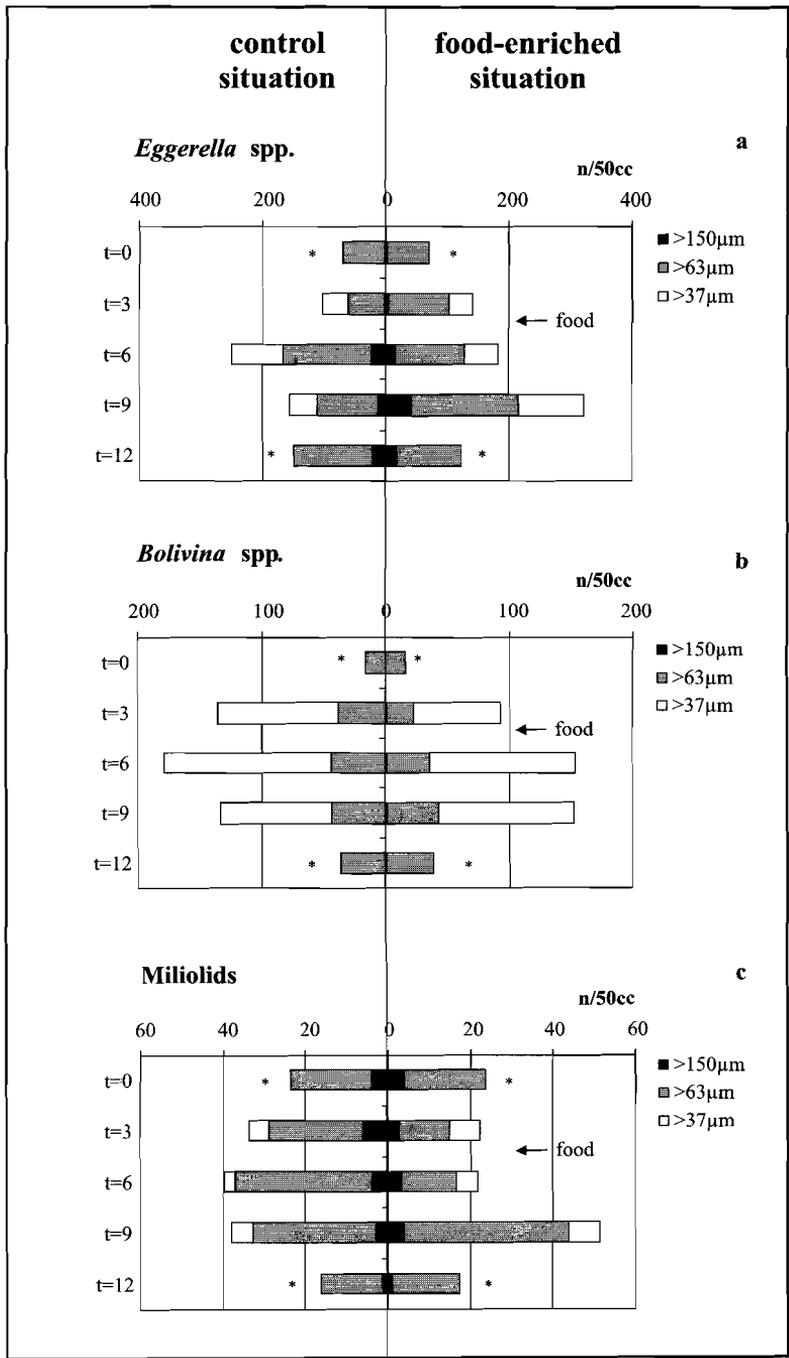
The numbers of *Eggerella* spp. increased most quickly in the control aquarium, although also in the food-enriched one its numbers went up (Fig. 4a). At $t=9$, its numbers were significantly higher in the enriched situation compared to the numbers in the control situation. Nine weeks after the food input the numbers of *Eggerella* spp. ($t=12$; $>63\mu\text{m}$ and $>150\mu\text{m}$ size fraction) in both aquaria were more or less the same, about twice as high as at $t=0$.

Almost no *Bolivina* spp. were found in the $>150\mu\text{m}$ size fraction, most specimens apparently living in the $>37\mu\text{m}$ size fraction (Fig. 4b). Three weeks after the food input numbers increased in both the food-enriched and the control situation. At $t=9$, the numbers of *Bolivina* spp. decreased in the control situation, but its numbers in the enriched situation stayed more or less the same. Nine weeks after the food input ($t=12$), the numbers of *Bolivina* spp. found in the $>63\mu\text{m}$ size fraction were very similar for both situations. It is remarkable that the increase in TSS is completely realised by the increase in the smaller size fractions ($>37\mu\text{m}$ and $>63\mu\text{m}$).

At the start of the experiment ($t=0$) only few miliolids were found living (Fig. 4c). After three weeks ($t=3$) the numbers had increased somewhat but less than the taxa discussed before. Overall the numbers of miliolids were higher in the control situation, but at $t=9$ an increase was found in the food-enriched situation. In the three weeks after $t=9$, the numbers of miliolids in both situations decreased to half the density at $t=9$.

The most obvious response in both experimental situations was displayed by *Caronia silvestrii*. A few specimens were found at $t=0$; between $t=3$ and $t=9$ the population increased, but declined after that. *C. silvestrii* was found consistently to be most abundant in the control situation. As a smaller foraminiferal species, it was only found abundantly in the two smallest size fractions.

The numbers of *Ammonia* spp. (mainly *Ammonia tepida*) in the $>150\mu\text{m}$ and $>63\mu\text{m}$ size fractions were relatively low between $t=0$ and $t=9$. At $t=3$ *Ammonia* spp. ($>63\mu\text{m}$) was slightly more abundant in the control aquarium compared to the food-enriched situation, but its numbers in the $>37\mu\text{m}$ size fraction were found to be similar for both situations. At $t=9$ the numbers of *Ammonia* spp. increased in both situations, but most strongly in the food-enriched one. After that its numbers in the $>63\mu\text{m}$ size fraction increased somewhat in the food-enriched aquarium ($t=12$).



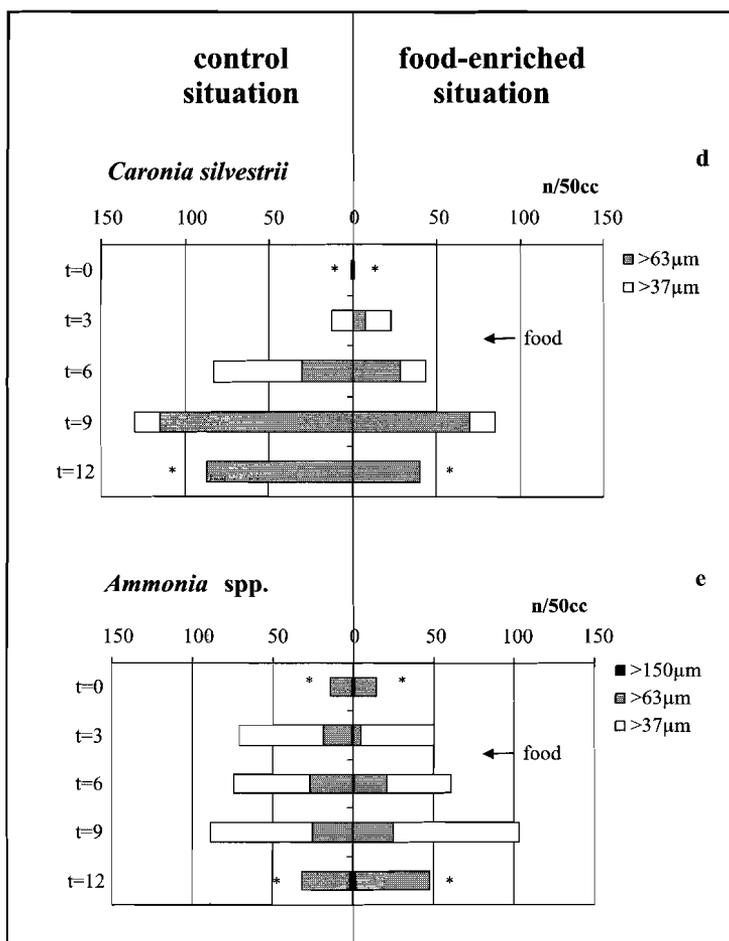


Figure 9-4: The standing stocks of five common taxa throughout the experiment; a) *Eggerella* spp.; b) *Bolivina* spp.; c) Miliolids; d) *Caronia silvestrii*; e) *Ammonia* spp. The * symbol indicates that the >37μm was not counted, the shading represent the numbers in the different size fractions, and food addition is indicated by arrow. Note the different scaling.

4. Discussion

The results obtained by this experiment, during which food (a mixture of heat-killed algae and diatoms) was added to microcosms containing foraminifera, are rather striking. Many researchers found a clear correlation between the foraminiferal standing stocks and food availability, in eutrophic as well as oligotrophic waters (Gooday, 1993, Gooday and Turley, 1990, Kitazato et al., 2000, Wollenburg and Kuhnt, 2000, see also Chapter 8). The uptake and ingestion of food supply by foraminifera is even found to occur within several hours or a few days (Levin et al., 1999, Moodley et al., 2000). During our experiment we found no significant food-triggered numerical response in the foraminiferal population as compared to the control situation.

Results from an earlier experiment (Duijnste, 2001) revealed an initial increase in foraminiferal numbers, probably triggered by the stress caused during the start of the experiment itself. We therefore allowed the foraminifera to settle in the microcosms for three weeks before starting the food experiment. In this way we would be able to distinguish between an increase in numbers after the onset of the experiment (possibly induced by stress), and a possible response to food input. As is obvious from our results, there was no clear indication of an early (stress-induced) reproduction: the standing stocks in the $>63\mu\text{m}$ and the $>150\mu\text{m}$ size fractions were very similar at $t=0$ and $t=3$. Probably our methods were adequate enough to prevent this reproduction.

An overall increase in foraminiferal numbers was found in both experimental situations (control and food-enriched). The TSS of foraminifera kept under the food enriched circumstances indeed started to increase after food input, to reach maximal values at $t=9$, i.e. six weeks later. Although some minor discrepancies in time occur, more or less the same holds for the standing stocks in the control situation. The absence of a clear numerical difference between the experimental situations leads us to conclude that in general food did not trigger foraminiferal reproduction. This could be due to the fact that the food influx was not sufficient enough to act as a stimulus for reproduction. As alternative one could surmise that the food-mixture was not suitable as source of food for the foraminifera. Knowing that several researchers found (heat-killed) *Dunaliella* sp. an adequate resource for foraminifera (Bradshaw, 1961, Anderson et al., 1991), the latter explanation evidently is not valid. Bradshaw (1961) added *Dunaliella* sp. cells to *Ammonia tepida* cultures and found that only after input of a certain concentration of these cells *A. tepida* increased in numbers. His experiment demonstrated that below a specific concentration, the foraminifera did not show any reproduction or even growth. This supports the suggestions made earlier (see Chapter 8) that foraminifera probably need a certain level of food supply in order to start reproduction.

We added 1.65 mg dry weight of the food-mixture per 19.63 cm^2 (the surface area of the microcosms), i.e. 0.0001 g (dry weight) per cm^2 . For the eastern Levantine, Herut et al. (2000, see Chapter 2) calculated an average flux of $0.000012\text{ g C/cm}^2/\text{day}$. The food pulse we added is maximally 10 times larger if all our food would consist of particulate C. This may not have been enough. But as an alternative one has to consider seriously whether food is a major limiting factor in these shallow water sediments, even as oligotrophic as in the Levantine.

Widbom and Frithsen (1995) also found no increase of foraminiferal densities after food enrichment. They observed an even lower density of foraminifera in the enriched microcosms

compared to the controls, and suggested that the lack of a positive numerical response by the foraminifera could have been caused by biotic interactions (e.g. predators). However, due to sieving the sediment before the on-set of our experiment most macrofauna (predators) was excluded, rendering this idea unsuitable for explaining our results.

Eggerella spp., *Bolivina* spp., the miliolids, *Caronia silvestrii*, and *Ammonia* spp., all showed the same features throughout the experiment. Initially, their numbers increased most strongly in the control situation (t=6), and somewhat later also in the food-enriched situation (t=9). In the case of *Eggerella* spp. the numbers were significantly higher in the food enriched situation. If this increase was caused by the organic supply, the *Eggerella* specimens needed a relatively long time to react (six weeks), indicating that they did not react very opportunistically.

Also *Ammonia* spp. were more numerous in the food-enriched situation (t=9), possibly as reaction to the food supply. However, in that case the response is extremely late especially when we take into account that Bradshaw (1961) found reproduction of *Ammonia tepida* within less than ten days after input of *Dunaliella* sp. During a labelling experiment Moodley et al. (2000) also found *Ammonia* spp. to react rapidly to the supply of (¹³C-labelled) algae. Already within 2 days the *Ammonia* specimen had ingested a considerable amount of the algae. Both the experiments by Bradshaw (1961) and Moodley et al. (2000) clearly indicate that *Ammonia* has a large potential to respond to increased food supplies. The absence of such a rapid response during our experiment indicates again that most likely the concentration of the supplied food was not sufficient enough. The high salinity that was measured in the course of the experiment should not have been a major limiting factor for *Ammonia* spp. (mainly *A. tepida*), because this species is found to survive under much higher salinities (~54‰, Almogi-Labin et al., 1992).

The *Bolivina* spp., generally considered to be a rather opportunistic group, did not show a clear response after food addition. They probably need a more extensive organic enrichment before reproduction takes place. The same may hold for some other taxa although it cannot be excluded that some taxa are rather loosely or not correlated to flux. This could be the case for *C. silvestrii* which showed higher numbers in the control experiment. Also in the Adriatic Sea and the Levantine basin its standing stock patterns display no clear correlation to increased organic enrichment (Chapter 8).

The increase in salinity that was found during the experiment probably did not negatively affect the foraminiferal densities. Generally, the standing stocks increased over time and the microcosms in the aquarium with the highest salinity contained even higher foraminiferal densities than the microcosms in the other.

5. Conclusions

No clear increase of foraminiferal numbers was found after the addition of a food-mixture. The added amount of food (less than 10 times the average daily flux), probably was too low to induce effects. However, it cannot be excluded that foraminiferal populations in these shallow waters are not food limited.

Only for *Eggerella* spp. a significant difference in density was found between the two treatments. Its numerical response (after 6 weeks) could indicate that this deeper infaunal species needs a lower amount of food to be triggered to reproduce, compared to most foraminifera.

Living (Rose Bengal stained) benthic foraminifera from the Pakistan Continental Margin (northern Arabian Sea)

With: Jan-Willem Zachariasse and Bert van der Zwaan

Published in: Deep Sea Research I 45, (1998): 1483-1513

Abstract

The Arabian Sea is characterized by one of the world's most pronounced Oxygen Minimum Zones ($< 0.1 \text{ O}_2 \text{ ml/l}$), which impinges the seafloor from 200–1000 m. The OMZ results from extremely high surface water productivity and moderate thermocline ventilation. Nine box cores were taken at two parallel down-slope transects covering a depth from 500 to 2000 m. From these nine box cores living (Rose Bengal stained) benthic foraminifera were studied in detail.

Within the upper part of the Oxygen Minimum Zone, *Bolivina dilatata* and *Bulimina exilis* are the most abundant species. In the lower part of the OMZ, *Uvigerina peregrina* and *B. exilis* occur most abundantly. Just below the OMZ, at a water depth of about 1250 m, the assemblage is typically dominated by *Rotaliatinopsis semiinvoluta* and *U. peregrina*; in still deeper waters (1500–2000 m) *Bulimina aculeata* and *Epistominella exigua* are the most prominent species.

Transect II was sampled three weeks after transect I; on the average, standing stocks were four times higher in transect II. However, down-slope species distributions are similar in the transects, both in the 63 μm and the 150 μm size fractions. Also vertical (in-sediment) distributions are remarkably similar. This indicates that standing stock differences between the two transects can either be ascribed to the effect of patchiness or, more likely, to the nature and the amount of organic flux.

We found unambiguous evidence that in and below the OMZ many benthic foraminifera persist in suboxic to anoxic microhabitats. This regards surface as well as subsurface habitats. Evidently, oxygen is not a limiting factor for a considerable number of species. The obvious relationship between species distribution and the OMZ might then be explained in terms of preferences for amount or type of organic flux. An alternative explanation involves favourable effects resulting from the absence of larger predators. The various models pertaining to the limiting balance between organic flux and oxygen are discussed.

I. Introduction

During the last decades, much research has been performed on the ecology of living (stained) benthic foraminifera (e.g. Alve, 1995; Alve & Bernhard, 1995; Barmawidjaja *et al.*, 1992; Bernhard, 1992; Corliss, 1991; Corliss & Van Weering, 1993; Gooday, 1986, 1993; Jorissen *et al.*, 1992, 1995; Van der Zwaan & Jorissen, 1991). It is now widely accepted that benthic foraminiferal distribution patterns are controlled to a considerable extent by organic carbon flux (Altenbach & Sarnthein, 1989; Caralp, 1984, 1989a,b; Corliss, 1991; Gooday, 1986, 1988, 1993, 1994; Gooday *et al.*, 1992; Jorissen *et al.*, 1992, 1995; Loubere *et al.*, 1993; Lutze & Coulbourn, 1984; Mackensen, 1987; Mackensen *et al.*, 1985, 1993; Maio & Thunell, 1993; Miller & Lohmann, 1982; Moodley *et al.*, 1993; Rathburn & Corliss, 1994; Silva *et al.*, 1996; Sjoerdsma & Van der Zwaan, 1992; Van der Zwaan & Jorissen, 1991). However, there is convincing evidence that oxygen levels, both in bottom waters and pore waters, affect distributions as well (Alve, 1995; Alve & Bernhard, 1995; Barmawidjaja *et al.*, 1992; Bernhard, 1986, 1992; Gooday, 1986, 1994; Jorissen *et al.*, 1992, 1995; Kaiho, 1994; Loubere *et al.*, 1993, 1995; Mackensen *et al.*, 1985; Maio & Thunell, 1993; Moodley *et al.*, 1993; Perez-Cruz & Machain-Castillo, 1990; Phleger & Soutar, 1973; Rathburn & Corliss, 1994; Sen Gupta & Machain-Castillo, 1993). With regard to these two parameters, the ecological characteristics of some species such as *Uvigerina peregrina* and *Epistominella exigua* are rather well described (Altenbach & Sarnthein, 1989; Gooday & Turley, 1990; Gooday, 1994; Hermelin & Scott, 1985; Hermelin & Shimmield, 1990; Loubere *et al.*, 1993, 1995; Lutze & Coulbourn, 1984; Mackensen *et al.*, 1985; Peterson, 1984; Turley *et al.*, 1993). The ecological background of most benthic foraminiferal species, however, is not well known.

Jorissen *et al.* (1995) presented a conceptual model (the *TROX*-model) in which food availability (*TR*ophic conditions) and *OX*ygen concentrations were supposed to affect the in-sediment penetration depth of benthic foraminifera. The model implies that in oligotrophic environments the maximum penetration depth is mainly controlled by food availability, whereas in eutrophic environments it is controlled by the pore-water oxygen content. A sample transect through the Adriatic Sea was used to illustrate their *TROX*-model.

An area perfectly suited to study this assumed combined effect of oxygen and food availability on the distribution of living benthic foraminifera is the northern Arabian Sea. The combination of high primary production and moderate ventilation (You & Tomczak, 1993) leads to an intense OMZ at water depths between 200–1000 m (Olson *et al.*, 1993; Wyrki, 1973). According to the *TROX*-model, oxygen is expected to be the limiting factor for living benthic foraminifera within the OMZ, where oxygen concentrations are less than 1 μM ($< 0.1 \text{ O}_2 \text{ ml/l}$, suboxic according to the classification used by Tyson & Pearson, 1991), whereas the limiting factor below the OMZ would be food supply.

Box cores, which were taken from the northern edge of the Arabian Sea during the Netherlands Indian Ocean Program, were examined for the presence of Rose Bengal stained benthic foraminifera in two size fractions (63–150 μm and 150–595 μm). The vertical (in-sediment) microhabitat distribution was studied using 0.5–1 cm sediment slices.

The aim of this study is to establish the ecological background of the most abundant benthic

foraminifera occurring in the north-east Arabian Sea. In this way, we hoped to gather data to verify the *TROX*-model and to determine which factors control the species distribution, on macro-scale as well as on micro-scale, in this specific ecosystem. This information could also be potentially valuable to reconstruct past variations in OMZ intensity.

2. Material, methods and geochemical data

During the NIOB D2-leg in October 1992, nine box cores were taken from the continental margin south of Karachi, Pakistan. Two depth-transects were sampled (Figure 1); transect I consists of five box cores from 500 to 2000 m, transect II consists of four box cores from 500 down to 1500 m (Table I).

The box cores (\varnothing 50 cm) were taken according to standard procedures (for details see Van der Linden *et al.*, 1994). Visually, they appeared undisturbed: the water above the sediment was clear. All box cores were (sub)sampled by slowly pushing in 3–4 tubes (\varnothing 8.5 cm) for the various analyses. One tube per box core was subsampled by cutting the sediment in precise slices of 0.5 cm for the top 2 cm and slices of 1 cm for 2–10 cm. Exceptions are box cores 455 and 477. From the former only the 1–2 cm of the box core was sliced into 0.5 cm intervals and the remainder in 1 cm intervals; the latter was only sampled in 1 cm intervals. Each sample was put immediately into a bottle containing ethanol and

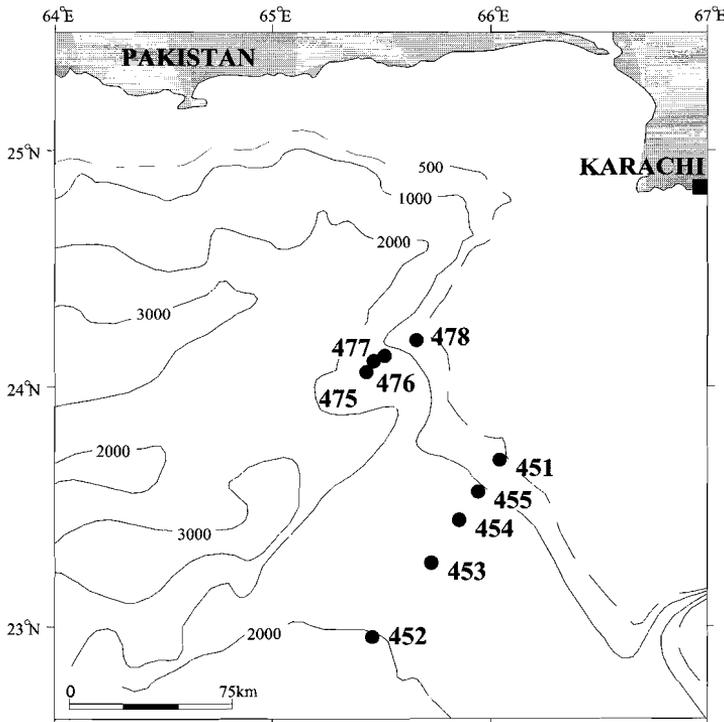


Figure 1: Location map of sites 451-455 (transect I) and 475-478 (transect II).

NIOP-box cores	Latitude (N)	Longitude (E)	Depth (m)	Date
451	23°41'.4	066°02'.9	495	04-10-92
455	23°33'.3	065°57'.2	998	06-10-92
454	23°26'.9	065°51'.2	1254	06-10-92
453	23°14'.0	065°44'.0	1555	05-10-92
452	22°56'.4	065°28'.1	2001	05-10-92
478	24°12'.7	065°39'.7	556	23-10-92
477	24°07'.6	065°30'.9	1000	23-10-92
476	24°06'.1	065°28'.9	1226	23-10-92
475	22°11'.9	065°26'.8	1472	23-10-92

Table 1: List of NIOP box cores and their location, water depth and sampling date.

Rose Bengal (Walton, 1952), and stored in a cooling facility until further processing. In the laboratory, the samples were wet-sieved over 63 μm and 150 μm sieves. We studied the 150–595 μm size fractions of all box-core samples; however, of the available samples in the 63–150 μm size fraction we studied only those from box cores 451 and 478 completely. In view of the time-consuming character, the 63–150 μm size fractions from the other seven box cores were only studied in the upper two samples (0–

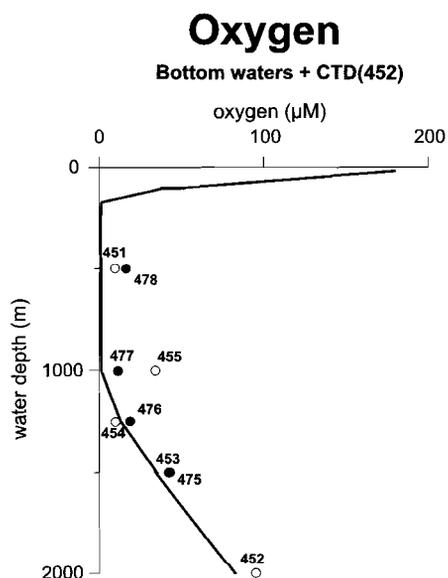


Figure 2: Bottom water oxygen values obtained by Winkler titrations of box-core bottom waters (○ = transect I; ● = transect II) and oxygen profile measured at CTD-station 452 (Van Bennekom & Hiehle, 1994).

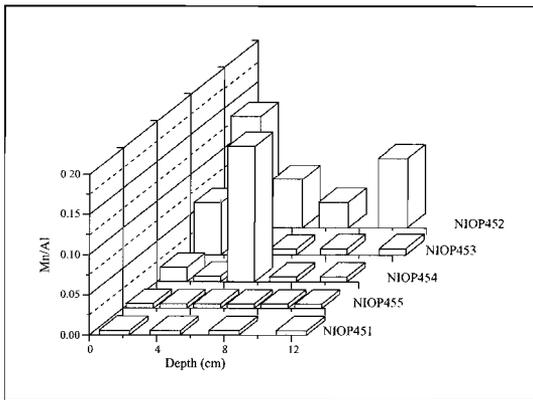
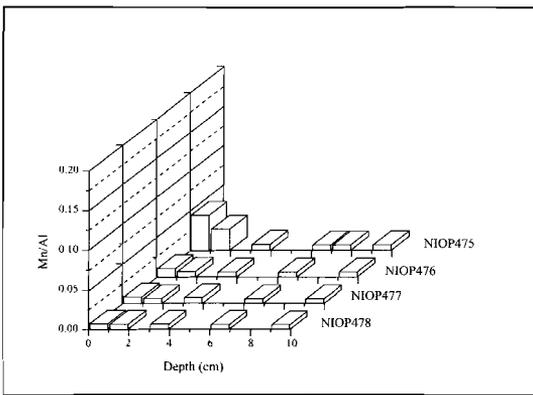


Figure 3: Mn/Al profiles within the box core sediments.



0.5 and 0.5–1.0 cm). The samples were studied in a gridded dish containing ethanol. The stained benthic foraminifera were sorted and counted in a Chapman slide. When possible 200–300 specimens were collected, but most of the samples in the 150–595 μm size fraction contained fewer specimens. In some samples from the 63–150 μm size fraction stained specimens were so abundant that the samples needed to be split. Fragments of *Rhizammina sp.* and *Rhabdammina sp.* were not included in our counts because in our view there is no proper way to convert counts of these fragments to number of specimens.

Whereas the use of Rose Bengal stained foraminifera to interpret living associations was critically discussed by Bernhard (1988), it is still the method most often used for foraminiferal research (Barmawidjaja *et al.*, 1992; Corliss, 1991; Corliss & Van Weering, 1993; Jorissen *et al.*, 1992; Loubere *et al.*, 1995; Mackensen & Douglas, 1989; Murosky & Snyder, 1994; Murray, 1992; Perez-Cruz & Machain-Castillo, 1990). Recently, Alve & Bernhard (1995) concluded that the use of Bengal Rose is as accurate as the ATP method, in distinguishing live from dead foraminifera, in certain cases, and considerably less time consuming. Our definition of “stained” was quite strict: all chambers, except for the last (youngest), had to be stained bright red/rose. Foraminiferal tests that showed boreholes and/or were not stained properly according to our definition, were excluded.

a.

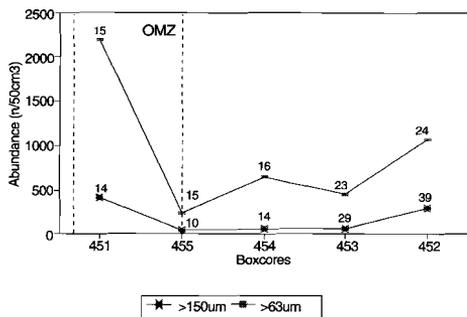
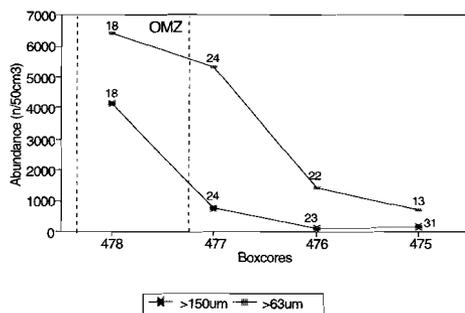


Figure 4: Total abundances of living (stained) benthic foraminifera in the 63-150 μm and 150-595 μm size fractions, and simple diversity (labels) within the top 0.5 cm (sometimes 1 cm) of the sediment, at transect I (a) and transect II (b).

b.



The oxygen concentration in the bottom waters on top of the box cores (Winkler-titration, onboard ship) and the oxygen profile at CTD-station 452 (Van Bennekom & Hiehle, 1994) are given in Figure 2. Box core bottom water oxygen concentrations follow the oxygen profile at CTD-station 452 (with box core oxygen values being generally slightly higher). The bottom water oxygen concentration of box core 455, however, is somewhat aberrant being higher than the concentrations at neighbouring sample sites. At transect II, the oxygen concentrations in the bottom waters are about the same for sites 478, 477, and site 476, whereas the oxygen level in the bottom waters at site 475 is clearly higher.

The Mn/Al profiles of the box cores are based on ICP analyses (Fig. 3). The ratios show persistent low values, from near the sediment surface down to a depth of 12 cm, within the box-cores of 500 m and 1000 m at both transects. This demonstrates that in the sediments of these box cores no free oxygen is available (Calvert & Pedersen, 1993), which is supported by the much higher values of the Mn/Al ratio in average deep sea clays (Turekian & Wedepohl, 1961).

In the box cores further downslope, Mn/Al ratios are somewhat higher in the upper part of the sediment than deeper down, indicating that here is (little) oxygen available. More downslope, the Mn/Al ratios become higher and the level of free oxygen availability resides deeper in the sediment.

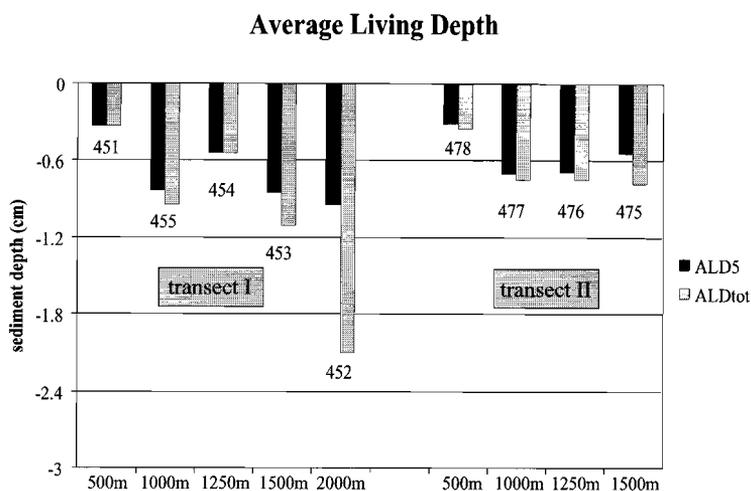


Figure 5: Average living depths of the calcareous benthic foraminifera (150-595 μm) in each box core.

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

x = lower boundary of the deepest sample

n_i = number of specimens in interval

D_i = midpoint of sample interval i

N = total number of individuals for all levels

(See Jorissen et al., 1995). (ALD_5 = average living depth of the foraminifera living in the topmost 5 cm; ALD_{tot} = average living depth of the total assemblage).

3. Results

Total abundances of living benthic foraminifera (per 50 cm^3) in the 150-595 μm and 63-150 μm size fractions (top 0.5 cm), together with simple diversities, are shown in Figure 4. In general, abundances decrease with water depth, whereas simple diversity increases. Total abundances in both size fractions of box core 455 and 452 (transect I) deviated slightly from this general trend. The total abundances in the box cores of transect II are about four times higher than those of transect I. At both transects, the total abundances in the 63-150 μm size fractions are substantially higher than in the 150-595 μm size fractions.

Most living benthic foraminifera are found within the top 5 cm of the sediment, highest abundances occurring at the sediment-water interface. The average living depth distribution (ALD, see Jorissen *et al.*, 1995) shows a clear down-slope trend. Within the OMZ, living foraminifera are mostly found at the sediment-water interface, whereas below the OMZ they are living substantially deeper. In general, however, the average living depth of the calcareous benthic foraminifera remains shallower than 2 cm sediment depth irrespective of the OMZ (Fig. 5).

Figure 6 shows that, the species composition changes with increasing water depth. The succession of assemblages, however is quite comparable for both transects. The most relevant information per box core is summarized in the following sections.

3.1 Transect I

NIOP 451 (495m; Fig. 6a): In the 63–150 μm as well as in the 150–595 μm size fraction *Bolivina dilatata*, *Cassidulina laevigata* and *Ammodiscus* sp. are very abundant. *Bulimina exilis* is dominant only in the 63–150 μm size fraction. The maximum living depth of the foraminifera in the 150–595 μm size fraction is 5 cm, but most (>98%) are found living in the topmost 1 cm. The ALD_5 (= average living depth of all calcareous benthic foraminifera 150–595 μm living in the topmost 5 cm) and ALD_{tot} (= average living depth for the total calcareous assemblage), are about identical and less than 0.5 cm (Fig. 5).

NIOP 455 (998m; Fig. 6b): The most abundant species in the 63–150 μm and 150–595 μm size fraction are *Rotaliatinopsis semiinvoluta*, *Uvigerina peregrina*, *Ammodiscus* sp., and *Recurvoides* sp. The species *Anomalina* sp., *Cassidulina bradyi*, and *Cibicides bradyi* are very abundant in the 63–150 μm size fraction. Only a few benthic foraminifera in the 150–595 μm fraction occur down to a depth of 7 cm, and the majority (>98%) are found within the topmost 3 cm. The ALD_5 of the calcareous benthic foraminifera is somewhat shallower than their ALD_{tot} , but both are less than 1 cm (Fig. 5).

NIOP 454 (1254m; Fig. 6c): *Rotaliatinopsis semiinvoluta*, *Bulimina exilis*, *Ammodiscus* sp., and *Eggerella* sp. are very abundant in both the 63–150 μm and the 150–595 μm size fraction. *Haplophragmoides* sp. occurs abundantly only in the 150–595 μm size fraction. The maximum living depth of the living benthic foraminifera (150–595 μm) is 2 cm, whereas the ALD_5 and ALD_{tot} of the calcareous species (Fig. 5) both are just below 0.5 cm.

NIOP 453 (1555m; Fig. 6d): *Ceratobulimina pacifica*, *Melonis barleeanum* and *Reophax pilulifer* are the most abundant species in the 150–595 μm size fraction, with *M. barleeanum* occurring down to a sediment depth of 7 cm. Fragments of *Rhizammina* sp. and *Rhabdammina* sp., although very abundant, are not included in the counts. In the 63–150 μm size fraction the most abundant species are *Eggerella* sp., *Epistominella exigua*, and *Anomalina* sp. In this size fraction *Bolivina seminuda* and *Ammodiscus* sp. reach their highest abundances below the topmost 0.5 cm. Maximum depth at which benthic foraminifera in the 150–595 μm size fraction occur is 7 cm, with more than 88% of the foraminifera living within the top 2 cm. The ALD_5 of the calcareous species is less than 1 cm, whereas their ALD_{tot} is somewhat deeper than 1 cm (Fig. 5).

NIOP 452 (2001m; Fig. 6e): *Bulimina aculeata* and *Lagenammina* sp. are abundant in both the 63–150 μm and the 150–595 μm size fraction. The 63–150 μm size fraction is dominated by *Epistominella exigua*. In the larger size fraction, living benthic foraminifera occur to a depth of at least 8 cm, but more than 70% is living in the topmost 2 cm. The ALD_5 of the calcareous benthic foraminifera is less than 1 cm, whereas their ALD_{tot} exceeds the 2 cm sediment depth (Fig. 5).

3.2 Transect II

NIOP 478 (556m; Fig. 6f): *Bolivina dilatata* and *Ammodiscus* sp. are the most dominant species in both the 63–150 μm and 150–595 μm size fraction. *B. dilatata* occurs to a depth of at least 10 cm, but displays a pronounced maximum in the topmost sediment layer. Whereas a few benthic foraminifera

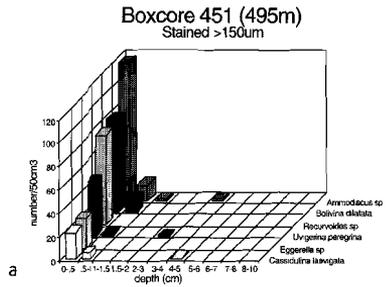
occur down to a depth of 10 cm, more than 98% of the total assemblage lives within the topmost sediment layer. The ALD_5 and ALD_{tot} of the calcareous species are both less than 0.5 cm (Fig. 5).

NIOP 477 (1000m; Fig. 6g): The species *Uvigerina peregrina*, *Eggerella* sp., and *Osangularia culter* are abundant in both size fractions. Next to these species, *Cibicides bradyi* and *Anomalina* sp. are dominant in the 63–150 μ m size fraction. The maximum penetration depth of the total assemblage in the 150–595 μ m size fraction is 10 cm, whereas 99% of the benthic foraminifera live in the uppermost 3 cm. The ALD_5 and the ALD_{tot} of the calcareous benthic foraminifera are both less than 1 cm (Fig. 5).

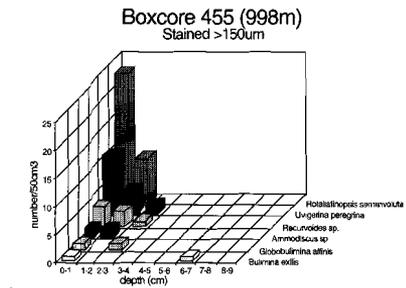
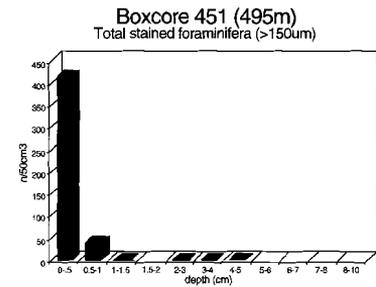
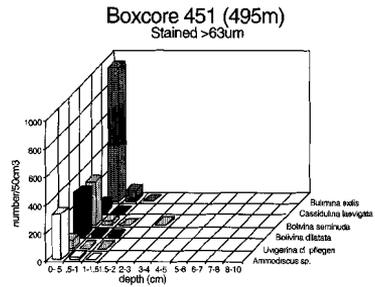
NIOP 476 (1226m; Fig. 6h): *Bulimina exilis*, *Rotaliatinopsis semiinvoluta*, *Ammodiscus* sp. and *Bulimina aculeata* are abundant in both size fractions. *Globobulimina pacifica* displays a subsurface maximum at 0.5–1.5 cm. In the 63–150 μ m size fraction, *R. semiinvoluta* is an abundant species, together with *Epistominella exigua* and *Cibicides bradyi*. The maximum penetration depth of the benthic foraminifera in the 150–595 μ m size fraction is 6 cm, with more than 97% of the assemblage living within the topmost 3 cm. The ALD_5 and ALD_{tot} of the calcareous species are both less than 1 cm (Fig. 5).

NIOP 475 (1472m; Fig. 6i): *Melonis barleeaanum*, *Bulimina aculeata*, *Reophax dentaliniformis* and *Reophax nana* are the most abundant species in the 150–595 μ m size fraction. Most specimens in this size fraction occur living in the topmost 0.5 cm of the sediment. In the 63–150 μ m size fraction *Epistominella exigua* is by far the most abundant species. In the 150–595 μ m size fraction, living benthic foraminifera occur down to a depth of 7 cm, but more than 90% of the assemblage lives in the topmost 2 cm. The average living depth of the calcareous species within the top 5 cm is just over 0.5 cm deep, and their ALD_{tot} is still less than 1 cm (Fig. 5).

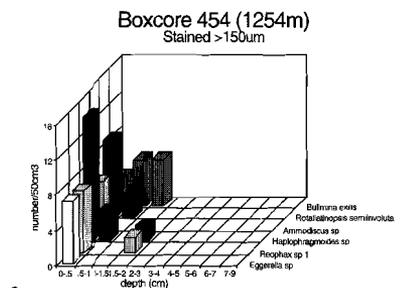
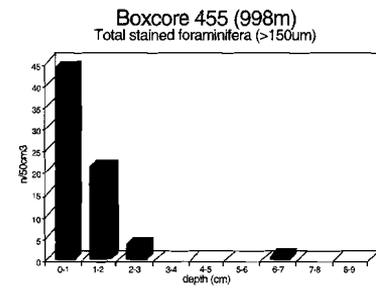
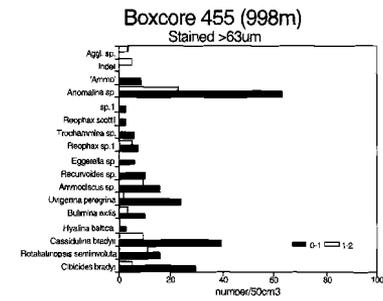
The assemblages from both transects are dominated by 8 species: *Bolivina dilatata*, *Ammodiscus* sp., *Bulimina exilis*, *Uvigerina peregrina*, *Rotaliatinopsis semiinvoluta*, *Melonis barleeaanum*, *Epistominella exigua*, and *Bulimina aculeata* (Fig. 7). *Bolivina dilatata* only occurs at both shallowest stations 451 and 478 (Fig. 7a), but its in-sediment distribution is different: down to 1.5 cm and 10 cm respectively. Moreover, its total abundance in transect II is considerably higher than in transect I. *Ammodiscus* sp. (Fig. 7b) displays a rather similar pattern, being far more abundant in transect II than in transect I, and in shallower than in deeper waters. Both species seem to characterize the upper part of the OMZ. *Bulimina exilis* and *U. peregrina* occur most abundantly within the OMZ, the latter being also more frequent in transect II (Fig. 7 c,d). Just below the OMZ, *R. semiinvoluta* dominates the living assemblages between 1000 m and 1250 m (Fig. 7e). This species is most frequent in the 63–150 μ m size fraction. Below the OMZ at about 1500 m, *M. barleeaanum* is found with a few specimens living in the 150–595 μ m size fraction from box cores 453 and 475 (Fig. 7f); it also occurs in box core 452, which is situated at 2000 m water depth. In the 63–150 μ m size fraction of box core 477 (1000m) *M. barleeaanum* has its highest abundance. *Epistominella exigua* (Fig. 7g) is extremely dominant in the 63–150 μ m size fractions of box cores 475 (transect II) and 452 (transect I), and has its highest abundance in box core 475. At about the same water depth (box cores 475 and 452) but living deeper in the sediment, specimens of *B. aculeata* occur (Fig. 7h).



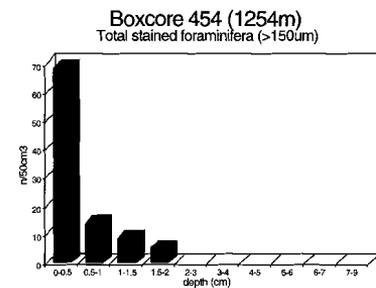
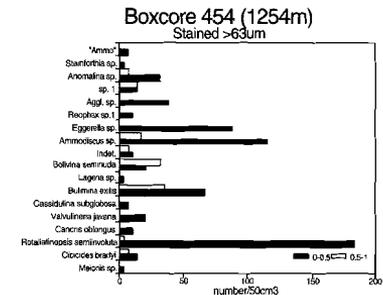
a

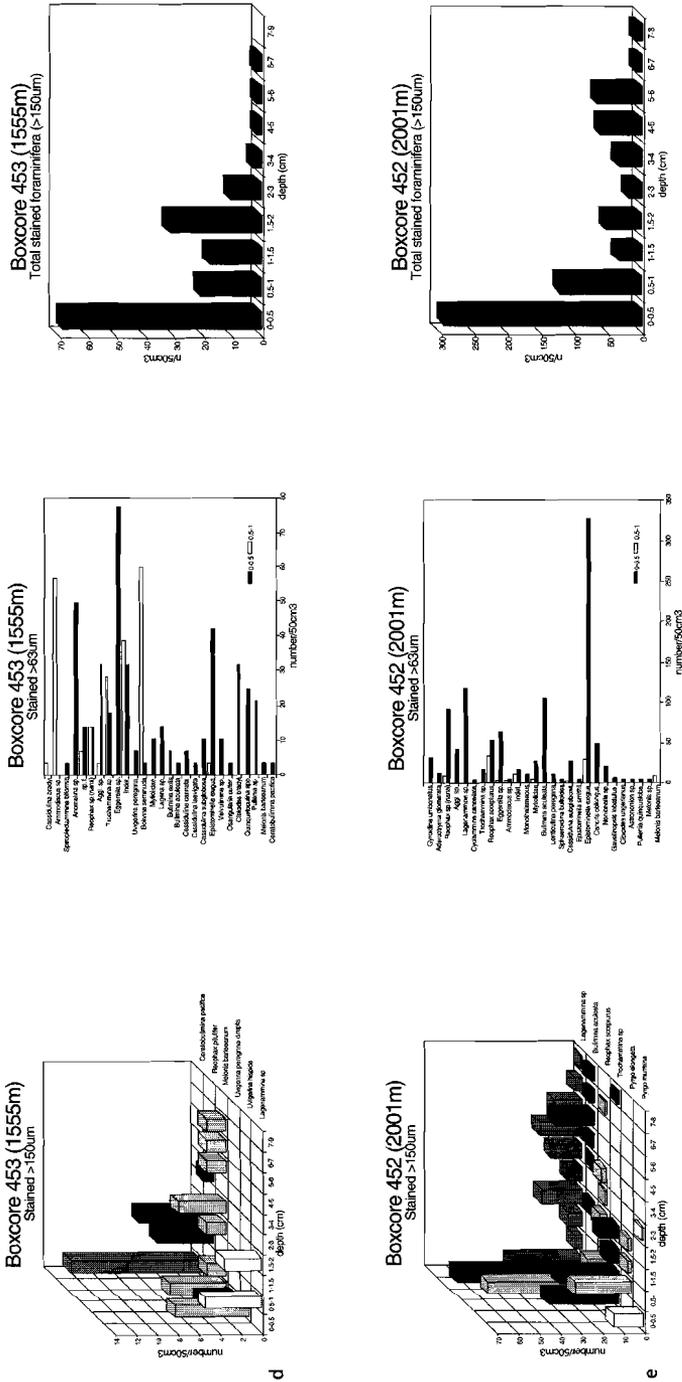


b

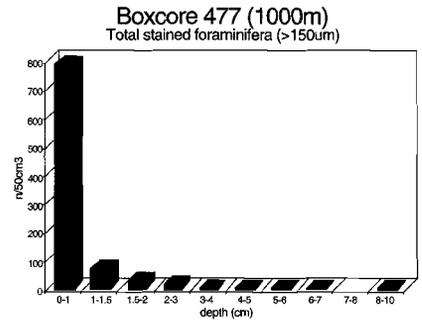
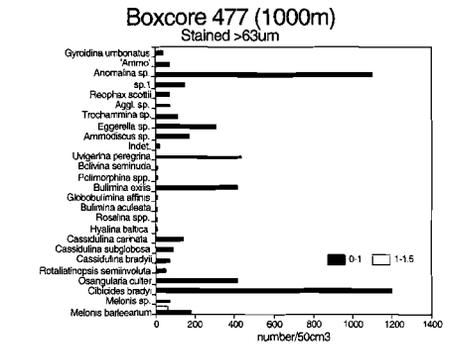
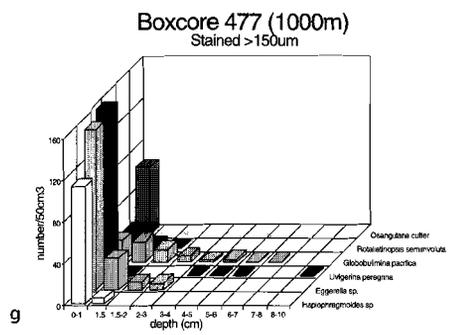
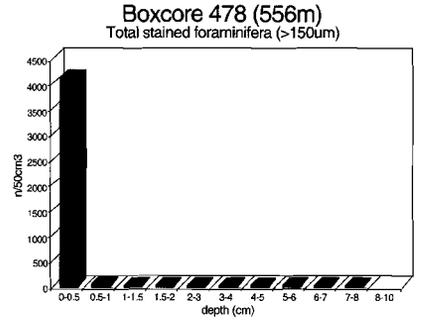
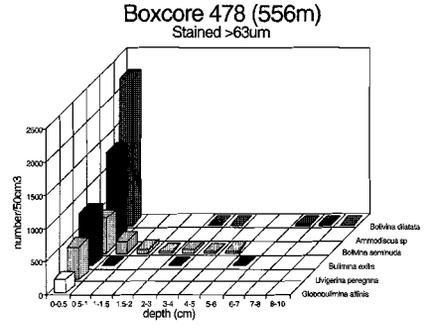
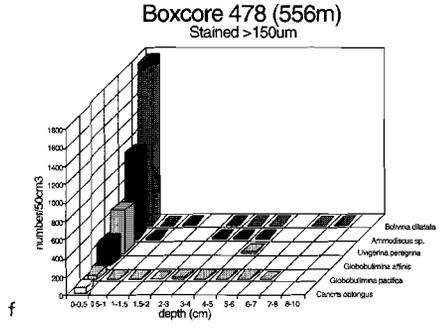


c





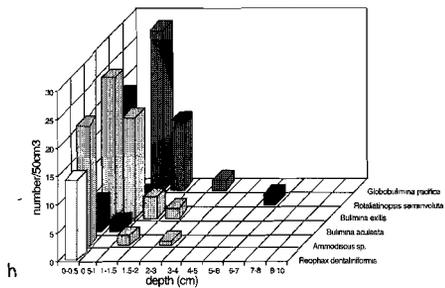
Figures 6 a-i: Vertical distribution of the most abundant species (numbers per 50cm³) in the 150-595 µm and 63-150 µm size fraction of each box core. On the right-hand side in-sediment distribution of the total number stained foraminifera (150-595 µm) per station.



f

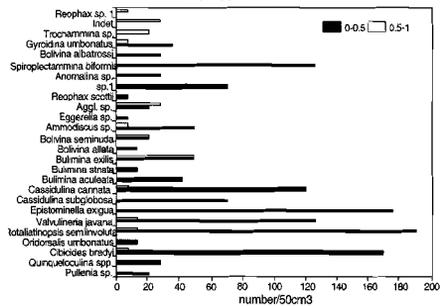
g

Boxcore 476 (1226m)
Stained >150um

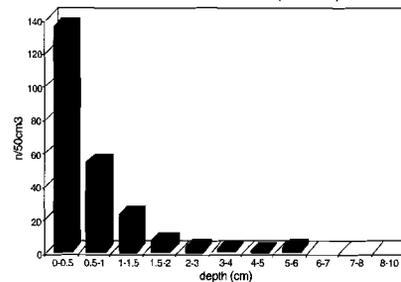


h

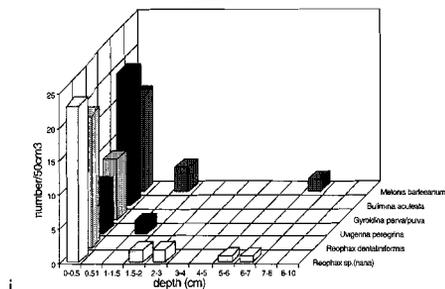
Boxcore 476 (1226m)
Stained >63um



Boxcore 476 (1226m)
Total stained foraminifera (>150um)

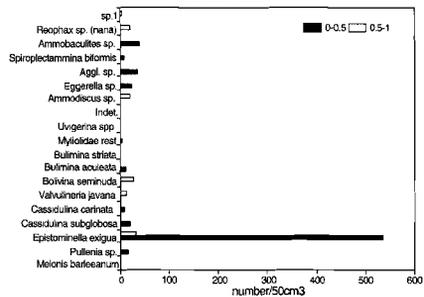


Boxcore 475 (1472m)
Stained >150um

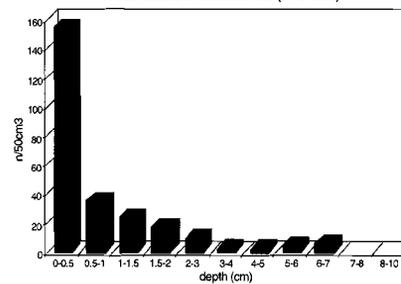


i

Boxcore 475 (1472m)
Stained >63um

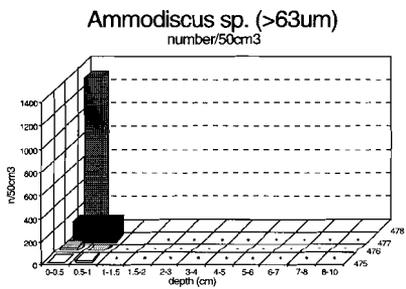
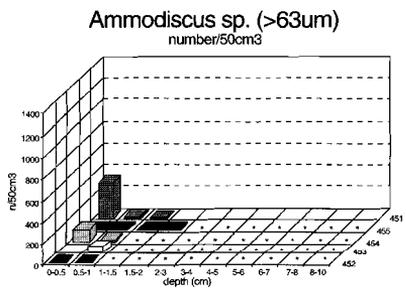
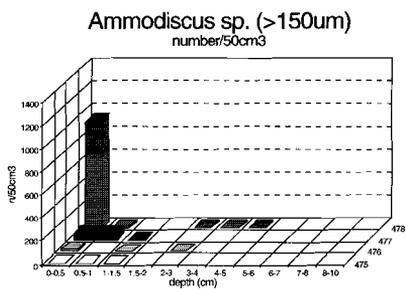
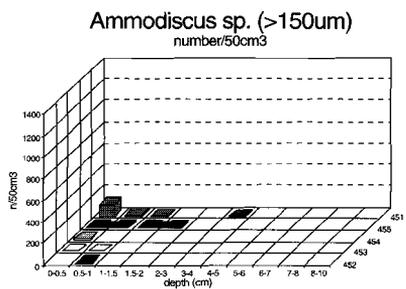
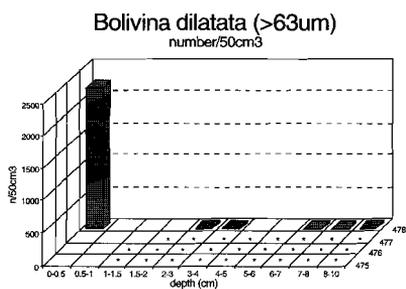
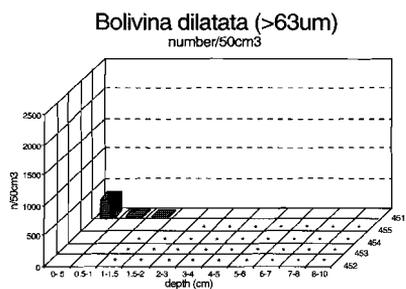
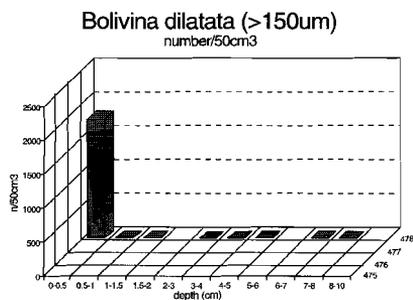
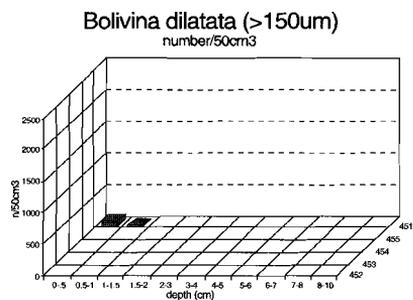


Boxcore 475 (1472m)
Total stained foraminifera (>150um)



Transect I

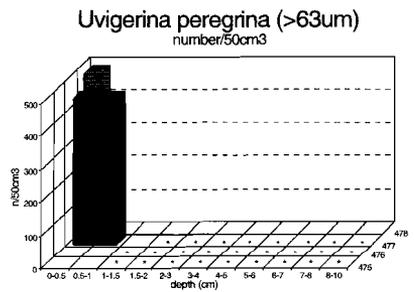
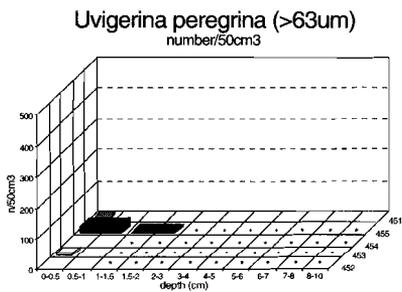
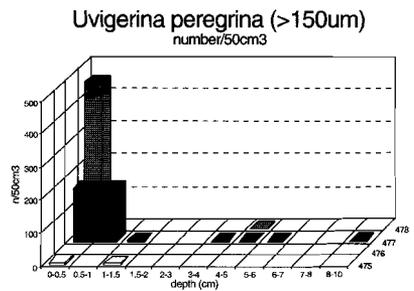
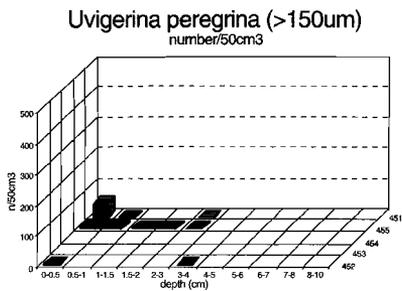
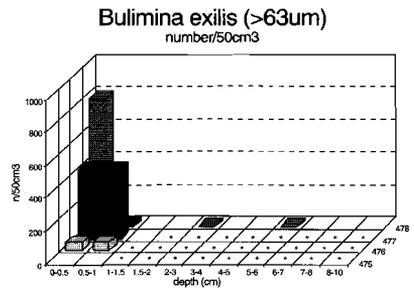
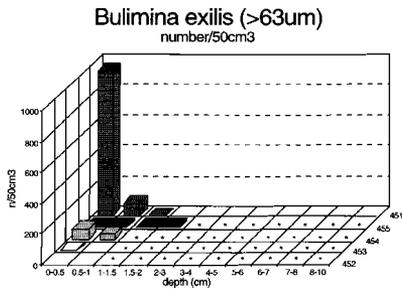
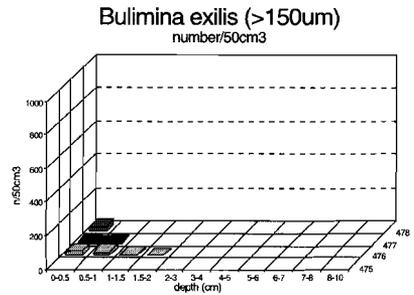
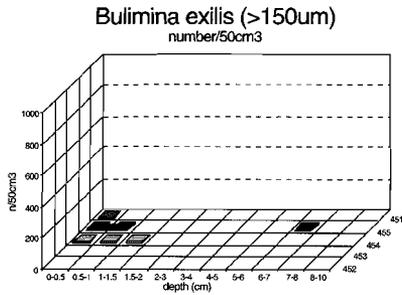
Transect II



Figures 7 a-b: Distributional patterns of eight abundant species, at transect I and II (* = no data).

Transect I

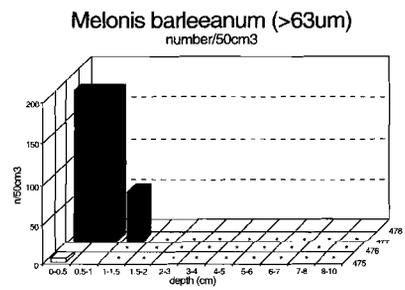
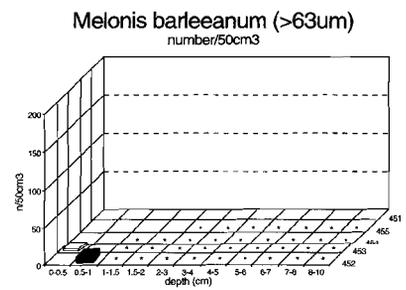
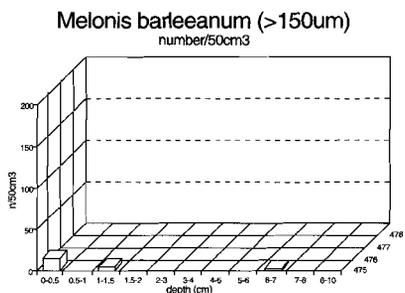
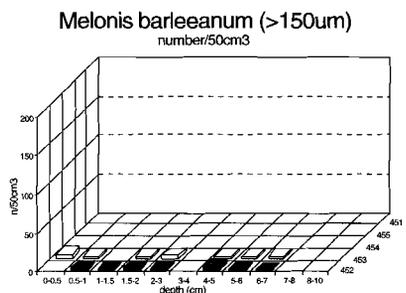
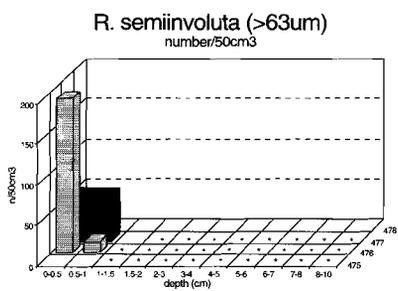
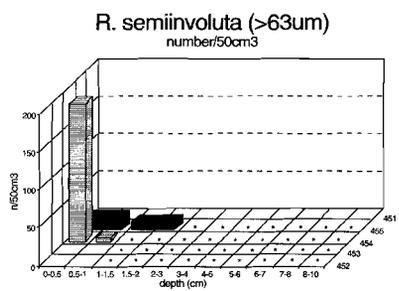
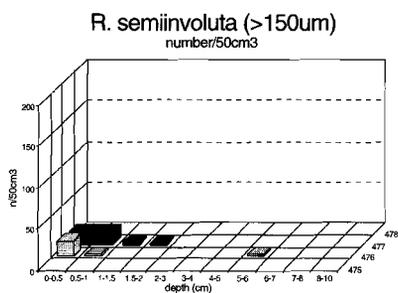
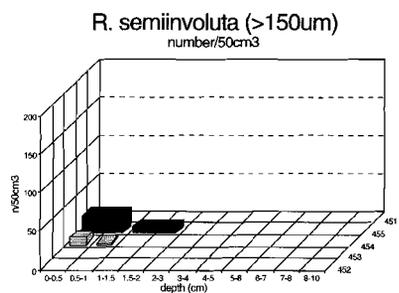
Transect II



Figures 7 c-d

Transect I

Transect II

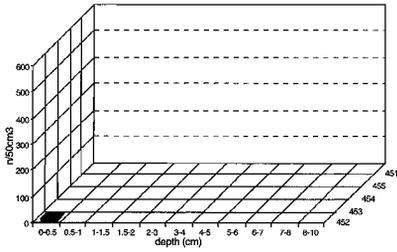


Figures 7 e-f

Transect I

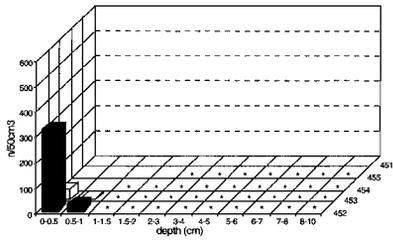
Transect II

Epistominella exigua (>150µm)
number/50cm³

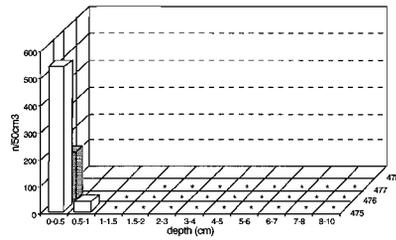


E. exigua did not occur in the 150-595 µm of Transect II

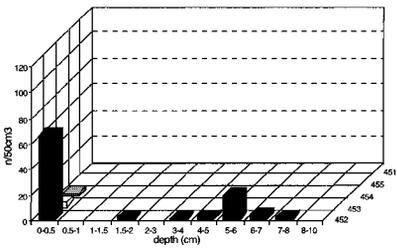
Epistominella exigua (>63µm)
number/50cm³



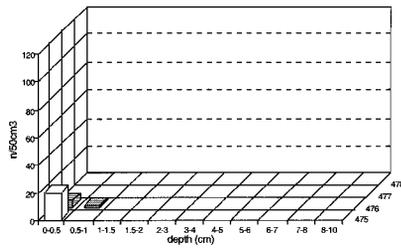
Epistominella exigua (>63µm)
number/50cm³



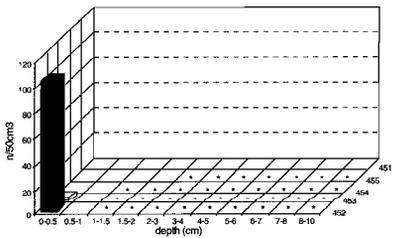
Bulimina aculeata (>150µm)
number/50cm³



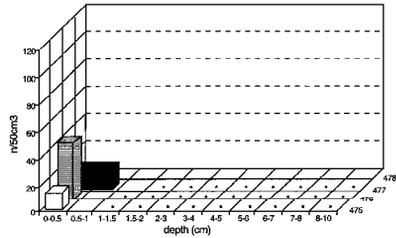
Bulimina aculeata (>150µm)
number/50cm³



Bulimina aculeata (>63µm)
number/50cm³



Bulimina aculeata (>63µm)
number/50cm³



Figures 7 g-h

4. Discussion

Oxygen measurements in the water column and at the sediment–water interface, together with the Mn/Al profiles suggest that, from the sediment–water interface downwards, suboxic to anoxic conditions prevail at the stations within the OMZ. The living foraminiferal population at these stations is dominated by only a few species that reach very high abundances. In both size fractions of box cores 451 and 478 (500 m), *Bolivina dilatata*, *Bulimina exilis*, and *Ammodiscus* sp. account for 50–70% of the living population. Also other authors (e.g. Bernhard, 1986) describe dysoxic assemblages to have a low diversity and a high standing stock. Noteworthy is that in spite of the presumed anoxic conditions at the OMZ stations many species still persist, indicating that oxygen itself does not seem to be a strongly limiting factor. This idea is supported by the outcome of a number of experimental studies published recently (Bernhard, 1993; Bernhard and Alve, 1996; Moodley and Hess, 1992; Moodley *et al.*, 1997a,b).

The species dominating within and below the OMZ are part of a faunal succession. *Bolivina dilatata*, which only occurs in the shallowest box cores (500 m), tolerates prevailing low-oxygen bottom waters. This concurs with observations of Barmawidjaja *et al.* (1992), who stated that this species is common in low oxygen environments. The agglutinated species *Ammodiscus* sp. is, like *B. dilatata*, far more abundant in transect II than in transect I, and it is co-dominant with *B. dilatata* in the shallowest parts of both transects. *Ammodiscus* sp. has its highest abundance in the box cores located at 500m, but it also occurs deeper. It is scarcely found living deeper in the sediment and seems to be a typically epifaunal species. Thies & Kuhnt (1995) also found *Ammodiscus* sp. to be common in samples from the Arabian Sea OMZ. In the 63–150 µm size fractions of the shallow box cores, but also in some of the deeper box cores, *Bulimina exilis* is highly abundant. Zalesny (1959) described *Bulimina denudata* (= *B. exilis* sensu Jonkers, 1984) as “a prolific species which reached very high numbers in living assemblages” and suggested temperature and depth to be the main factors controlling its distribution. According to Jonkers (1984), *B. exilis* can be regarded as a “very productive species under low oxygen and high food conditions”. This coincides with the circumstances at both sites, 451 and 478, where the bottom oxygen levels are low (although we lack data for organic flux). Caralp (1989a) found the distribution of *B. exilis* to be related to organic carbon content and quality. Her findings were that *B. exilis* prefers high contents of “unaltered” organic matter. In general, it appears that the upper part of the OMZ is characterized by species preferring a high organic flux which is relatively unaltered, and for which oxygen per se is not a seriously limiting factor.

Characteristic for the upper part of the OMZ, but also occurring somewhat deeper, is *Uvigerina peregrina*. In both size fractions of box core 478 (transect II, 500 m) it is highly abundant although less so in the shallowest box core of transect I (box core 451). Thies & Kuhnt (1995) also found *U. peregrina* in the OMZ of the north Arabian Sea. Rathburn & Corliss (1994) found *Uvigerina* species living abundantly at the 510 m and 1005 m sites in the Sulu Sea. Altenbach & Sarnthein (1989) observed *U. peregrina* *in vivo* and saw it living within the uppermost sediment layer. They found that “the microhabitat of *U. peregrina* is characterized by high concentrations of bacteria, exoenzymes and meiofauna, and is typical of sediments enriched in organic carbon and depleted in oxygen, as

found in areas below upwelling productivity". Also Loubere *et al.* (1993) recorded *U. peregrina* as a dominantly near-surface dweller with smaller infaunal populations. Our results support this view: *U. peregrina* occurs most abundantly in the top 0.5 or 1 cm of the box cores in both transects and is only scarcely found deeper in the sediment. Our data further suggest that *U. peregrina* is not clearly limited by oxygen deficiency. The relationship between the occurrence of *U. peregrina* and the organic carbon content of the sediment is widely accepted (Altenbach & Sarthain, 1989; Jonkers, 1984; Lutze & Coulbourn, 1984; Maio & Thunell, 1993; Miller & Lohmann, 1982; Rathburn & Corliss, 1994; Van der Zwaan & Jorissen, 1991). The position of *U. peregrina*, in somewhat deeper water than the species discussed before, could suggest that it tolerates somewhat lower food levels and/or more degraded organic matter.

Rotaliatinopsis semiinvoluta appears to be restricted to conditions occurring in the lower range of the OMZ and just below it. Although the sampling resolution of the box cores is low, this species seems to have its highest abundances in the 63–150 µm size fraction of box cores 454 and 476, at approximately 1250 m water depth. If this position is really related to the specific conditions at the lower edge of the OMZ, then it would be an ideal marker species for tracing past variability in the lower depth limit of the OMZ in the Arabian Sea. This, however, requires further study. Not much is known about this species, but we think *R. semiinvoluta* requires a relatively high amount of organic matter, while it is not able to survive the suboxic to anoxic conditions in the OMZ. In between the suboxic to anoxic conditions within the OMZ and the relatively lower amounts of organic matter in deeper waters, the lower boundary of the OMZ could provide the perfect niche for *R. semiinvoluta*.

Still deeper, and consequently under even lower organic flux, *Epistominella exigua* only lives abundantly in the 63–150 µm size fractions of box cores situated below the OMZ. It obtains its highest abundance at the deepest site of transect II (475; 1500 m). At transect I, it reaches its highest abundance in box core 452, at 2000 m water depth. *E. exigua* is a cosmopolitan species, known to live at abyssal depths (Hermelin & Scott, 1985; Hermelin & Shimmield, 1990; Mackensen *et al.*, 1985; Peterson, 1984; Schafer & Cole, 1982). Mackensen *et al.* (1985) found *E. exigua* southwest of Norway, between 1200–4000 m water depth, with its highest abundance at approximately 2000 m. They also found that it prefers high primary productivity with relatively much organic detritus, and tolerates a relatively low oxygen content in the interstitial water of the sediment. These findings are supported by Gooday (1988) and Turley *et al.* (1993). In our box cores, *E. exigua* is found living most abundantly within the top 0.5 cm of the sediment and seems thus to avoid deep infaunal positions. In box core samples taken after phytodetritus deposition, Gooday (1988) found *E. exigua* only living in the phytodetritus itself but not in the underlying sediment. According to Gooday (1988), the greenish protoplasm observed in these *E. exigua* specimens suggests that they ingest the phytodetritus. Turley *et al.* (1993) observed *E. exigua* feeding on cyanobacteria and microalgae during their experiments. Gooday (1988) suggested that *E. exigua* is a "specialist feeder that blooms opportunistically when the appropriate food becomes available". Our findings suggest that *E. exigua* indicates far more oligotrophic conditions than the other species discussed previously (*Bolivina dilatata*, *Ammodiscus* sp., *Bulimina exilis*, *Uvigerina peregrina* and *Rotaliatinopsis semiinvoluta*). However, it is apparently able to react sharply on supply of organic matter within the context of an oligotrophic deep sea environment. To be able to do so, *E. exigua* certainly would require an epifaunal position.

Melonis barleeanum displays a rather diffuse distributional pattern, but in the larger size fraction it is restricted to the deepest box cores, and apparently able to survive in a large range of infaunal habitats: it occurs down to 7 cm. Its position so far below the OMZ would concur with the idea of Caralp (1989a) who suggested that this species would prefer altered organic matter. However, the patterns in the smaller size fractions are somewhat different, highest abundance occurring in transect II also at shallower sites. *Bulimina aculeata* displays a rather comparable pattern. It reaches its overall highest abundance in both size fractions of box core 452: at approximately 1250 and 1500 m water depth, this species occurs more abundantly in transect II than in transect I. Zobel (1973) found *B. aculeata* in the northeast Arabian Sea between 1500–2800 m, whereas Miller & Lohmann (1982) found this species to be restricted to the OMZ. Maio & Thunell (1993), however, found *B. aculeata* most abundant living below the OMZ, at a water depth of 1700–2000 m, where the organic carbon content was relatively high. Our data indeed suggest that this species is an opportunistic deeper dwelling one, not particularly dependent on high amounts of fresh and unaltered organic matter, but certainly thriving under a high flux.

It is striking that generally (with exception of *Melonis barleeanum*) the distributions of the species discussed so far, show great similarity in the 63–150 μm and the 150–595 μm size fractions. This suggests that there is only limited change in their microhabitat preferences during their ontogeny.

4.1 *Transect I versus transect II.*

Whereas the distributions of individual species are very similar for both transects, total abundances are very different. The overall standing stock of living benthic foraminifera is about four times higher in transect II than at transect I. The latter transect was sampled three weeks earlier than transect II. This difference in standing stock can simply be explained by patchiness. Alternatively, in the three week time period between the sampling of transect I and II, build up of standing stocks, after arrival of fresh organic matter, could have progressed further. Gooday (1988) found that some benthic foraminifera bloomed opportunistically after the arrival of phytodetritus at the seafloor. Since transect II was sampled later, the amount of organic matter and/or its state of degradation, could be different to such an extent that faunal differences are induced. This could explain the relatively higher abundance in transect I of living *B. exilis*, which presumably prefers fresh organic matter, and the relatively higher abundance in transect II of living *M. barleeanum*, which would prefer more altered organic matter.

4.2 *Overall distribution of benthic foraminiferal assemblages*

The two transects show approximately the same down-slope succession of assemblages, suggesting a correlation with water depth. A similar depth-related succession of assemblages has been observed by others in completely different settings and at different depths (Corliss, 1991; Hermelin & Shimmield, 1990; Mackensen & Douglas, 1989). We suggest that assemblage distribution is controlled by two

factors: food availability and (bottom water) oxygen levels. Food availability is clearly expressed in the decrease in standing stock with increasing depth and is related to the downward diminishing flux which can be observed in many oceans (e.g. Corliss, 1991). However, in this area the flux is so high (200–400 gC/m²yr; Codispoti, 1991, Kabanova, 1968, Qasim, 1982) that even in deeper waters relatively eutrophic conditions prevail.

In our data species diversity is (poorly) inversely correlated with abundance. Buzas & Gibson (1969) explain the low diversities in shallow water by the extreme physiological stress placed on organisms there. Within the OMZ, the oxygen content is probably so low that, as suggested by Gooday (1986), predators are scarce and competition low. Therefore, the species that are able to withstand the physiological stress of low oxygen, can opportunistically bloom here because of relatively high food availability, low competition and the absence of predators. A similar mechanism was described by Sjoerdsma & Van der Zwaan (1992), who suggested that dysoxic environments with high but sometimes unpredictable food availability are inhabited by *r*-selected species that put maximum effort in reproduction. This mechanism is supported by the high abundances of certain benthic foraminifera we found living within the OMZ. Below the OMZ, food availability is relatively lower, but oxygen contents are higher. Therefore more species are able to live here resulting in a higher diversity. This latter type of environment is, according to Sjoerdsma & Van der Zwaan (1992), mainly inhabited by keen competitors (called *K*-strategists). The relatively lower standing stock below the OMZ can be explained by the shift in energy allocation, between both life-strategies. While the *r*-strategists are known to put most of their energy in reproduction, which results in high abundances, the *K*-strategists put most of their energy in competition, which results in a diverse assemblage with low abundances.

The trend of low simple diversity within the OMZ and higher simple diversities below the OMZ is present at both transects, except for the 63–150 µm size fractions of box cores 452 and 475. The relatively lower simple diversities here are most likely due to the high dominance of *E. exigua*. The general trend is understandable if we realize that in the deep water sites a wider infaunal inhabitation is possible due to increased oxygen contents. Indeed, a more developed infaunal microhabitat pattern with increasing depth is visible.

Some species are known to be typically deep infaunal dwellers; they even sometimes develop a subsurface maximum (see Jorissen *et al.*, 1995 for discussion). Although, in our samples, some species do occur at great in-sediment depth, for instance *Globobulimina pacifica* at site 478, it is striking that a clear subsurface maximum is never visible. Instead, looking at the faunal densities, the patterns are rather abruptly truncated at 1–1.5 cm, indicating that even in the more oxygenated deeper waters infaunal microhabitats were rather inhospitable. The average living depths of the calcareous benthic foraminifera in the 150–595 µm size fractions do not give a clear down-slope pattern, but the ALD's within the OMZ are distinctively shallower than the ALD's below the OMZ. Both the maximum penetration depths of the total benthic foraminiferal assemblage and the ALD's of the calcareous benthic foraminifera, point to a predominantly epifaunal lifestyle for the benthic foraminifera living within the OMZ and an epifaunal to shallow infaunal lifestyle of the benthic foraminifera living below the OMZ.

Our results contradict the predictions of the *TROX*-model of Jorissen *et al.* (1995) to some extent.

Although within the OMZ mostly shallow microhabitats are occupied, oxygen per se is not limiting to species occurring here, since Mn/Al profiles indicate sub- to anoxic conditions. Some species are even able to produce significant standing stocks. We suggest that here the successive redox fronts within the sediment could be an alternative and better limiting mechanism, although data in this respect are mostly lacking. Also the deepening of the microhabitat occupation, predicted by *TROX* with decreasing flux in deeper waters, is only partially observed. Most of the species occurring below the OMZ are probably more effectively limited by oxygen than species occurring within it, but in-sediment penetration is still very shallow. However, in an environment so loaded with organic matter, one probably still can not speak of a normally ventilated benthic environment. Consequently, the redox front could reside rather shallow even in the deeper water sites, although also here we lack data.

5. Conclusions

The results of this study give a good overall view of the distributional patterns of benthic foraminifera living on the Karachi continental margin in the southeast Arabian Sea. Benthic foraminiferal distribution is remarkably little limited by oxygen: even in the presumably anoxic infaunal microhabitats within the OMZ we found many species, some of which had considerable standing stocks. Species proliferating here, among them *Bolivina dilatata*, *Bulimina exilis*, *Uvigerina peregrina* and *Ammodiscus* sp., seem to be dependent more on the high flux of unaltered organic matter as occurring in the OMZ, than on oxygen limitation. Below the OMZ, species presumably dependent on lower and/or more altered organic matter appear in some order: first *Rotaliatinopsis semiinvoluta*, then *Epistominella exigua*, and still deeper *Bulimina aculeata* and *Melonis barleeaanum*. We suggest that this order can be used to reconstruct past variability in oxygen minimum zones. Also the position of *R. semiinvoluta* at or near the base of the OMZ, might be useful in fossil reconstructions.

Even in deeper water, where flux is lower and more oxygen is present, faunal penetration is not very deep. Moreover, faunal density patterns are truncated at the 1 to 2 cm depth level along the total depth transect. This indicates that everywhere deeper in-sediment inhabitation is prevented by some mechanism: since from our data it appears that oxygen per se is not a very effective limiting factor, we suggest the ensuing redox conditions within the sediment act as barrier for deeper penetration. If so, these redox fronts reside rather shallow along the whole depth range; that could be caused by the high organic load of the benthic environment, even in deeper waters.

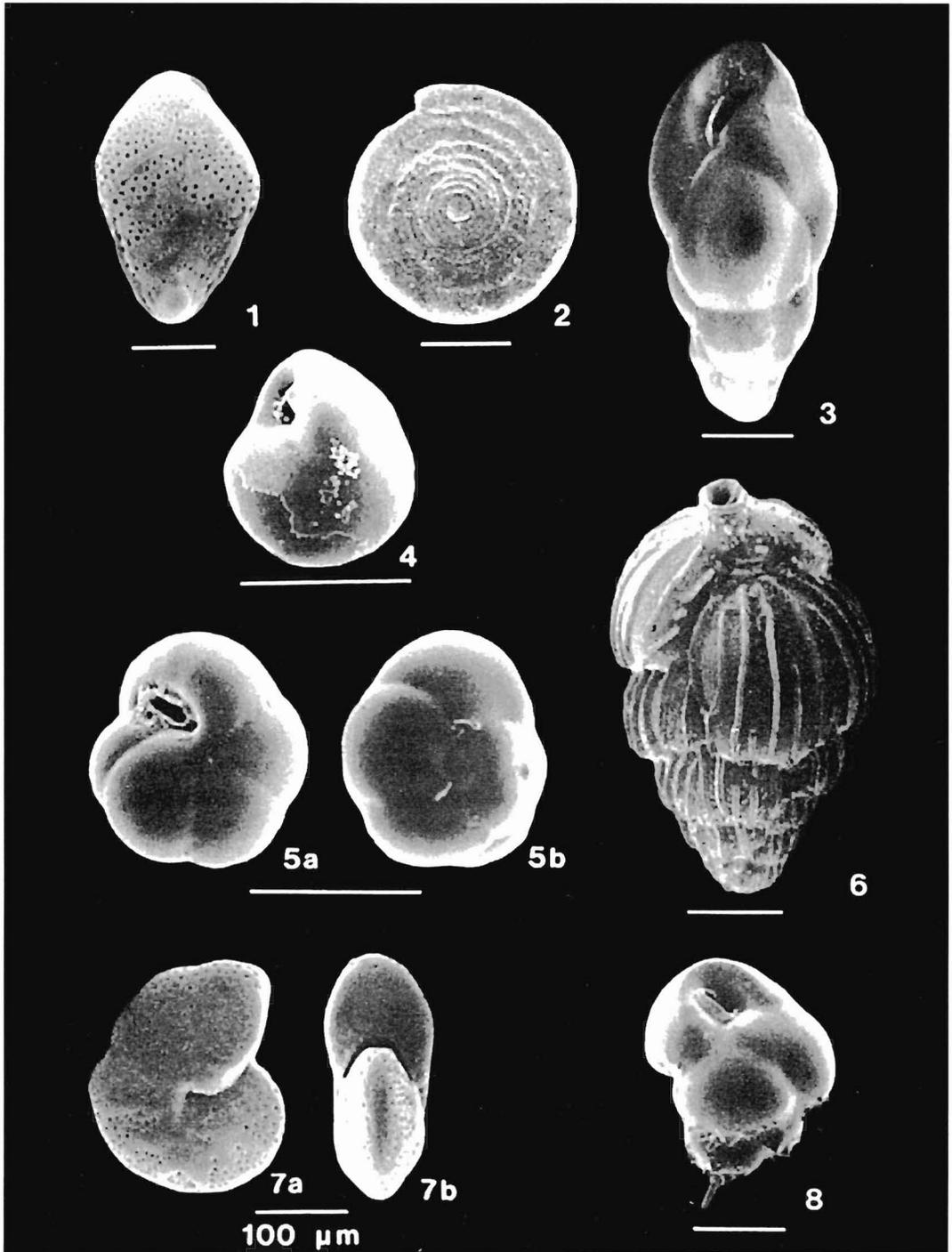
Benthic foraminiferal standing stocks are clearly no simple function of organic flux although in one transect faunal densities indeed decrease with inferred decreasing flux. The densities in the OMZ are very high, which is probably the combined effect of flux and absence of predation. Simple diversity increases with depth, indicating that for some species oxygen, possibly in combination with the effects of high organic flux in shallow water, is limiting: in deeper waters more species inhabit a somewhat extended microhabitat range.

Acknowledgements

This research was carried out in a joint Dutch-Pakistan marine geosciences program, as part of the Netherlands Indian Ocean Programme 1992-1993. We thank the director and our colleagues A.R. Tabrez and A.A. Khan of the National Institute of Oceanography, Karachi, for their cooperation. The chief scientists of the cruise were W.J.M. van der Linden and C.H. van der Weijden. We thank the officers and crew of the R/V Tyro and the technical support given by technicians of the Netherlands Institute of Sea Research (NIOZ). Special thanks are due to G.J. Reichart his help in collecting the material, analytical support and discussion. We thank E.A. Koning for analytical support (Winkler titrations), G. Van 't Veld and G. Ittmann for processing the samples, W. den Hartog for making the SEM-pictures and T. van Hinte for preparing some illustrations. The help of H.C. de Stigter in constructing the "sediment slicer" is greatly appreciated. We also thank the two anonymous reviewers for their useful remarks. Also M. den Dulk and T. Kouwenhoven are thanked for their part in the discussions. This is publication **970160** of the NSG.

PLATE:

- Fig. 1. *Bolivina dilatata* (Reuss); NIOP 451, 63-150 μm (400x)
Fig. 2. *Ammodiscus* sp.; NIOP 478, 150-595 μm (250x)
Fig. 3. *Bulimina exilis* (Brady); NIOP 478, 150-595 μm (200x)
Fig. 4. *Epistominella exigua* (Brady); NIOP 452, 63-150 μm (400x)
Fig. 5. *Rotaliatinopsis semiinvoluta* (Banner & Blow); NIOP 454, 63-150 μm (400x) a. apertural view; b. side view
Fig. 6. *Uvigerina peregrina* (Cushman); NIOP 451, 150-595 μm (200x)
Fig. 7. *Melonis barleeaanum* (Williamson); NIOP 453, 150-595 μm (200x)
a. side view; b. apertural view
Fig. 8. *Bulimina aculeata* (d'Orbigny); NIOP 452, 150-595 μm (200x)



Chapter 11

A transfer function for the quantitative reconstruction of oxygen contents in marine paleo-environments

With : Bert van der Zwaan, Ahuva Almogi-Labin, Ivo Duijnste, and Frans Jorissen

Abstract

We observed living (Rose Bengal stained) foraminifera in the Indian Ocean, Atlantic Ocean and Mediterranean Sea, and compared the distributional patterns with micro-profiled oxygen contents in the sediment column. Our data demonstrate that one group of species is apparently oxyphilic and that their abundances co-vary linearly with the oxygen content at the sediment-water interface. We developed a transfer function and tested this on a historic record from the Adriatic Sea. We show that application of this transfer function to benthic foraminiferal patterns in a core from the Adriatic Sea results in an accurate quantitative reconstruction of the oxygenation history over the past 160 years. The reconstructed record shows that the marine system rapidly became prone to hypoxia between AD 1890 and 1935. We suggest that this was due to the man-induced increased nutrient load of Po waters, related to the introduction of artificial fertiliser in the drainage area.

1. Introduction

For a better understanding of global change it is essential to quantitatively constrain ocean circulation and ventilation. In this respect, oxygen content patterns are helpful to determine present and past changes in the state of the oceans. Of all available proxies for oxygenation benthic foraminifera are still among the best (Sen Gupta and Marchain-Castillo, 1993; Kaiho, 1999). Foraminifera are uni-cellular protozoans that are abundant in marine waters. They play an important role in benthic ecosystems (Snider et al., 1984; Lee and Capriulo, 1990) and in some environments they even are the most abundant meiofaunal component (Shirayama and Hirokoshi, 1989). Although they often live in the sediment column down to a depth of more than 15 cm, densest populations occur at the sediment-water interface (Gooday, 1994; Jorissen et al., 1995; Van der Zwaan et al., 1999). It has been suggested that taxa occupy a distinct microhabitat (Corliss, 1985), but field observations indicate that various factors contribute to a dynamic distribution throughout the year (Barmawidjaja et al., 1992; Silva et al., 1996). Important among the ecological factors is certainly food, often regarded equal to the organic flux arriving at the sea floor (Gooday, 1994; Jorissen et al., 1995). Oxygen is considered to be a prime variable as well. Experimental research and field observations suggest, however, that it is not as important in limiting the distribution as previously thought, since many species seem to be facultative anaerobes or micro-aerophylic (Alve and Bernhard, 1995; Moodley et al., 1997; Jannink et al., 1998).

In an attempt to further assess the role of oxygen, we collected living (Rose Bengal stained) foraminifera from the Adriatic Sea, the Levantine Basin off Israel, the Atlantic Ocean off NW Africa and the Indian Ocean off Pakistan (Table 1). Pertinent data regarding to some of the sample localities and oceanographic conditions were published elsewhere earlier (Van der Linden and Van der Weijden, 1994; Reichart, 1997; Jorissen et al., 1998). We measured oxygen concentrations in the water column using CTD. Concentrations at the sediment-water interface were observed in water collected from the boxcores or with Niskin bottles. The oxygen concentrations were later determined by standard methods (Van der Linden and Van der Weijden, 1994). In the Mediterranean and Atlantic boxcores we additionally measured the oxygen concentrations in the sediment column by careful micro-profiling with oxygen-probes. Detailed geochemical data for sediments, bottom waters and pore waters were obtained for the Atlantic and Arabian Sea cores (Reichart, 1997; Jorissen et al., 1998). For the Indian Ocean boxcores, from which no oxygen probe measurements were available, Mn concentrations were used to establish the penetration level of free oxygen (Corliss and Emerson, 1990). In the case of the Indian Ocean and the Mediterranean Sea cores we analysed the foraminiferal assemblages from every 0.5 cm interval over the first 2 cm. In the Indian Ocean material we further analysed every cm-slice down to a depth of 5 cm, and sometimes to 10 cm. In the Atlantic Ocean boxcores we counted assemblages from every cm-slice, down to a depth of 5-10 cm.

2. In-sediment distribution patterns

We used the Average Living Depth (ALD; Jorissen et al., 1995) as measure to evaluate how the

	Station	Depth (m)	Oxygen content ($\mu\text{mol/L}$)	Oxyphilic taxa
Indian Ocean (geographical co-ordinates of stations see Jannink et al., 1998	451	495	9.5	miliolids, <i>Gavellinopsis</i> , <i>Cibicides wuellerstorfi</i>
	478	556	11.5	
	455	998	9.7	
	477	1000	16.3	
	476	1226	18.7	
	454	1254	34.1	
	475	1472	42.9	
	453	1555	42.3	
	452	2001	95.2	
Atlantic Ocean (geographical co-ordinates of stations see Jorissen et al., 1998	1	507	74,1	<i>Cibicides kullenbergi</i> , <i>Cibicides wuellerstorfi</i> , <i>Cibicides ungerianus</i> , <i>Lenticulina</i> , <i>Hoeglundina</i> <i>elegans</i> , <i>Rosalina</i> , <i>Gavellinopsis</i> , <i>Sphaeroidina</i> <i>bulloides</i> , <i>Planulina ariminensis</i> , miliolids
	2	1407	182,1	
	3	2075	171,8	
	7	3010	219,1	
	8	2530	191,5	
	9	2002	161,6	
	10	1525	140,1	
	11	1200	220,1	
	15	1000	145,9	
	17 ^c	1890	119,2	
	20b	1200	129,9	
	21	750		
	22	765		
<i>Adriatic Sea</i> (co-ordinates: - 108 : 44°45.4' N, 12°45.0' E - 203 : 44°34.0' N, 12°48.0' E)	<u>Station 108</u>	32	155 ^(*)	<i>Ammonia beccarii</i> , <i>Amphicoryna scalaris</i> , <i>Buccella granulata</i> , <i>Lenticulina</i> , <i>Reussella</i> , <i>Rosalina</i> , miliolids ^(*) Not included in fig. 2: for this month only whole cm. samples available
	Aug 96 ^(*)		51	
	Nov 96		264	
	Jan 97		213	
	May 97		115	
	Jul 97	86		
	Sep 97			
	<u>Station 203</u>	36	236 ^(*)	
	Aug 96 ^(*)		73	
	Nov 96		249	
	Jan 97		296	
May 97	165			
Jul 97	175			
Sep 97				
<i>Levantine</i> (co-ordinates: - S1 : 32°.22.53' N, 34°.48.36' E; - S3 : 32°.26.58' N, 34°.42.84' E)	<u>Station Lev 1</u>	40	206	<i>Ammonia beccarii</i> , <i>Amphicoryna scalaris</i> , <i>Anomalina globulosa</i> , <i>Buccella granulata</i> , <i>Lenticulina</i> , <i>Elphidium crispum/ advenum/</i> <i>macellum</i> , <i>Reussella</i> , <i>Rosalina</i> , miliolids
	Aug 96		207	
	Dec 96		195	
	Feb 97		179	
	May 97		119	
	Jun 97		194	
	Sept 97		163	
	Nov 97		237	
	Jan 98		229	
	May 98			
	<u>Station Lev 3</u>	120	199	
	Aug 96		238	
	Oct 96		225	
	Dec 96		213	
	May 97		243	
Sept 97	233			
Jan 98	185			
May 98				

Table 11-1: Data on stations and oxyphilic taxa. Upon arrival on board all collected samples were immediately stored in ethanol and Rose Bengal. For this study the >150 mm size fractions were employed. Only vividly stained foraminifers, regarded as living at the time of collection, were picked and stored in slides. The criteria for distinction between living and dead are well standardised between the various laboratories. Samples printed in bold (Jan 97 station 108; Jan 97 and May 97 station 203; stations 7 and 8 Atlantic) are considered to be not representative due to unusual circumstances at time of sampling. Only species categorised as oxyphilic (thus if present at a station showing most abundant occurrences in topmost cm layers) are listed in the last column.

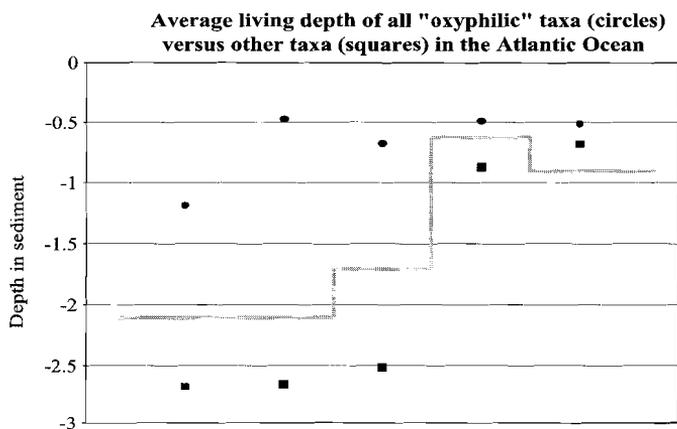
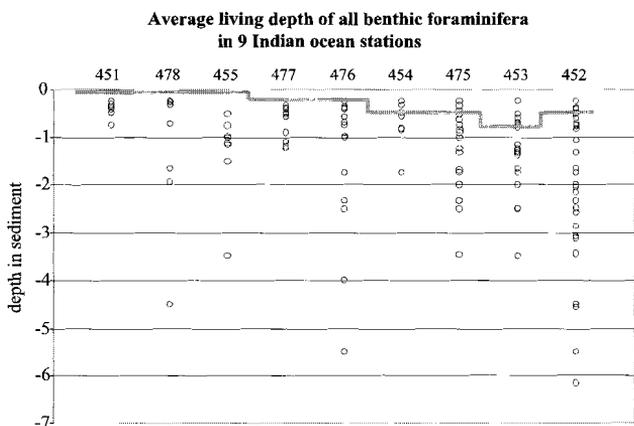
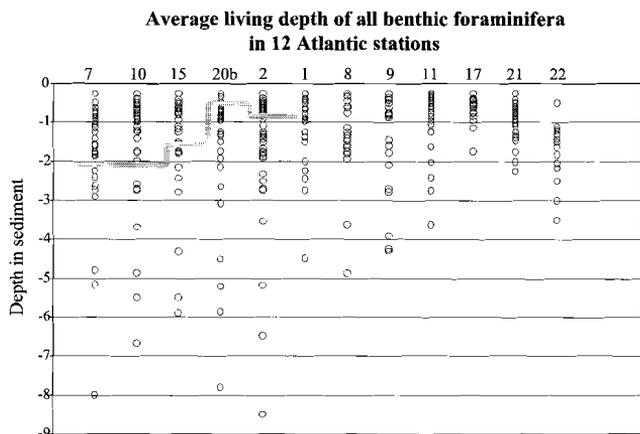


Figure 11-1: Average Living Depth of all living taxa (open circles) encountered in the Atlantic and Indian Ocean stations. Data from Jorissen et al. (1998) and Jannink et al. (1998). Grey line indicates the depth of penetration of free oxygen, in the Indian Ocean based on Mn profiles (see text). Vertical axes represent depth in the sediment column (cm). In fig. 1c (bottom panel) average living depth of all oxyphilic taxa is plotted against average living depth of all other calcareous taxa. Data are same as in topmost panel, first five stations.

foraminifera inhabit the sediment column. The ALD is a weighted average of the depth at which a taxon occurs in the total sediment column regarded. Although we studied quite different environments, the ALD data from all sites indicate that species are living so closely packed together that the individual distributional patterns must have considerable overlap. As an example we graphically summarized (fig. 1) the ALD patterns of all living taxa encountered at the Indian and Atlantic Ocean stations. Many species occur below the zone where free oxygen is available, suggesting that they are able to tolerate anoxic conditions at least temporarily. This is supported by earlier experimental evidence (Alve and Bernhard, 1995; Moodley et al., 1997).

After careful inspection of all our data, it appeared that some species are living consistently, although never exclusively, in the uppermost sediment layers of all localities studied. Among them are a number of fragile agglutinated taxa. Their chances to fossilise successfully are often poor (Murray and Alve, 1999). In order to arrive at proxies that have a general applicability even under fossil conditions with poor preservation, we removed all agglutinated taxa from the census counts. From the remaining calcareous taxa we further selected (see Table 1) only those that in all localities are most abundant in the topmost sediment layer. These apparently live as epifauna and most of them indeed meet the general morphological characteristics considered to be indicative for such species (Corliss, 1988). Their average ALD is consistently shallower than the level where free oxygen becomes absent (fig. 1c). We term this group 'oxyphilic', since one could suspect that the availability of oxygen is the reason for this shallow occurrence. Further evidence supports this notion. Some species (*Cibicides wuellerstorfi*, *Planulina ariminensis*) were earlier described as living preferentially at or above the sediment-water interface (Corliss and Fois, 1991; Linke and Lutze, 1992). Others, like *Sphaeroidina bulloides*, *Lenticulina* spp. and miliolids were reported to be infrequent under adverse oxygen conditions (Corliss, 1988; Den Dulk et al., 1998; Kaiho, 1999). From still other taxa, like *Ammonia*, *Rosalina*, *Gavellinopsis* and *Buccella*, the morphology indicates that infaunal behaviour, and thus tolerance to low oxygen contents, is unlikely. Moreover, specific species belonging to these genera were reported recently as preferring elevated microhabitats as well (Schönfeld, 1997; Debenay et al., 1998).

We plotted the abundance of 'oxyphilic' taxa in the Adriatic Sea and the Levantine Basin versus the in-sediment oxygen contents (fig. 2). Only from these areas we have enough data to compose time series. From these time series it is obvious that the group indeed tracks the oxygen gradient in the sediment column, being only abundant in the topmost sediment layers where and when oxygen is available. Given our data we estimate that it takes some two months before the foraminiferal density patterns have adjusted to changing oxygen conditions. This lag results for a short time in the presence of the 'oxyphilic' group deeper in the sediment when the redox front has already moved upwards. In this context it is worthwhile to recall evidence (Alve and Bernhard, 1995; Moodley et al., 1997), also pertaining to species belonging to this group, which suggests that adult specimens can survive experimental anoxia for at least 60 days. Since we consider here the larger size fraction, the retarded response can be explained by survival of adults although these probably are not able to reproduce anymore. From our data it is also evident that the primary production and organic flux to the sediment have no strong correlation with the occurrence of the taxa considered; the periods of their highest density coincide with the times of deepest oxygen penetration.

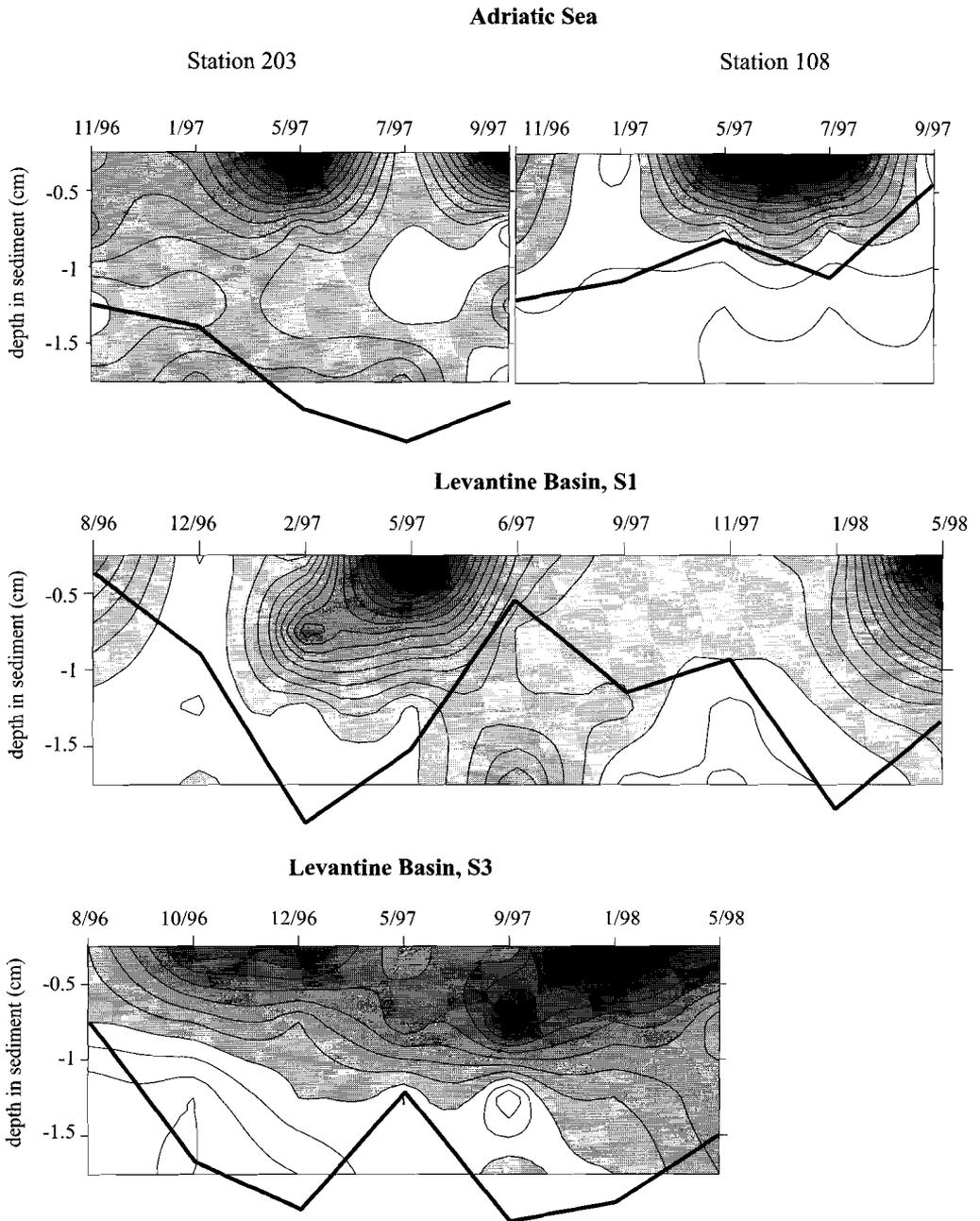


Figure 11-2: Time series of the distribution of oxyphilic taxa in the topmost 2 cm of two Adriatic Sea and two Levantine permanent stations. Level of penetration of free oxygen was measured with microprobes and is indicated by bold line. Contoured foraminiferal densities in the Adriatic Sea vary between 0 and 40 specimens/50cc. Densities in the Levantine station S1 vary between 7 and 220 specimens/50cc, those of Levantine station S3 between 0 and 15 specimens/50 cc.

3. Paleo-oxygenation: transfer function and application

In fig. 3 we plotted the relative proportion of the oxyphilic taxa in the calcareous assemblage, versus the oxygen content at the sediment-water interface. The correlation between oxygen and the oxyphilic species is statistically significant, but we identified five deviating samples. Samples taken in January or May from the Adriatic Sea are from periods of sudden change; well-mixed conditions and the onset of spring production led to sudden oxygen supersaturation even at the sediment-water interface. Samples from stations 7 and 8 in the Atlantic Ocean were taken after an upwelling event; given the exceptionally high abundance of *Globobulimina* specimens, the sediment oxygen demand at these stations was clearly out of balance with the rather well-ventilated bottom water. The deviating faunal composition in these five samples is likely to be attributable to a time lag between changes in oxygen contents and the subsequent faunal response (see also fig. 2 for time lag).

The observation that the oxyphilic taxa are favouring the oxic microhabitat, provides no explanation why their total abundance is positively correlated with the oxygen contents as measured at the sediment-water interface. Oxygen is limiting foraminiferal distribution only at the lowest concentrations (Alve and Bernhard, 1995; Moodley et al., 1997); there is no evidence that it directly regulates population density at higher oxygen contents. Our data indicate that the foraminiferal microhabitat expands with deeper oxygen penetration (fig. 1c). It can be assumed that in general the volume of aerated sediment correlates rather well with the bottom water oxygen contents. Increasing oxygenation will thus lead to larger volume of inhabitable sediment for the oxyphilic group and subsequent increase of their population size. Since that is a universal relationship, the observed regression probably is structural and valid also for other areas and different time slices

The regression (O_2 [$\mu\text{mol/l}$] = $7.23 + 5.62 * \{\% \text{ oxyphilic}\}$, $R^2 = 0.66$) as given in fig. 3 leads to the possibility to reconstruct average paleo-oxygenation at the sediment-water interface if the

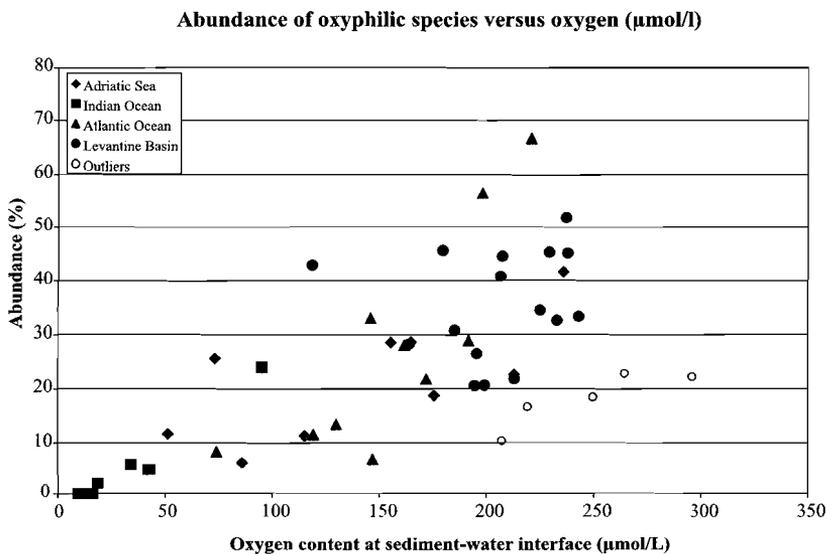


Figure 11-3: Relationship between oxyphilic taxa and oxygen concentration at the sediment water – interface.

abundance of the oxyphilic group is known. The relationship is statistically significant and that is remarkable if we take into account that samples are included from very different trophic regimes. In the NW Atlantic average primary production is between 65-235 gC.m⁻².yr⁻¹, in the Indian Ocean it is 200-400 gC.m⁻². yr⁻¹ and in the Levantine Basin it is only 35 gC.m⁻².yr⁻¹ (Oren, 1970; Codispoti, 1991; Jorissen et al., 1998). This further strengthens our argument that the distribution of the species mentioned is indeed to a large extent dependent on the availability of oxygen.

We applied the new proxy to a well-dated core located in the muddy zone in front of the Po River at 32 m water depth and covering the past 160 years (Barmawidjaja et al., 1995) . The resulting quantitative oxygenation curve (fig. 4) can be compared with historic data as far back as AD 1911 (Justic et al., 1987; Justic, 1991). There is a high similarity in trends of our reconstruction representing average oxygenation at the sediment-water interface and the calculated year-average trend based on historic data (Justic et al., 1987). The later is based on observations 2 m above sea bottom. The difference between the curves amounts to 80-100 µmol/l, a difference that we also observed in the field. In our Levantine data, the average difference between oxygenation at 0.5m above sea bottom and at the sediment-water interface amounted to 92 µmol/l. It is clear that since AD 1890 a steady deterioration took place. This is clearly related to the use of artificial fertilisers (Barmawidjaja et al., 1995; Justic, 1991). Our data show that since AD 1930 the environment has been forced close to hypoxia, as indeed has become evident (Justic et al., 1987); the total drop in average oxygenation amounts to 100 µmol/l. Following a short-term amelioration after World War II and since 1970, the

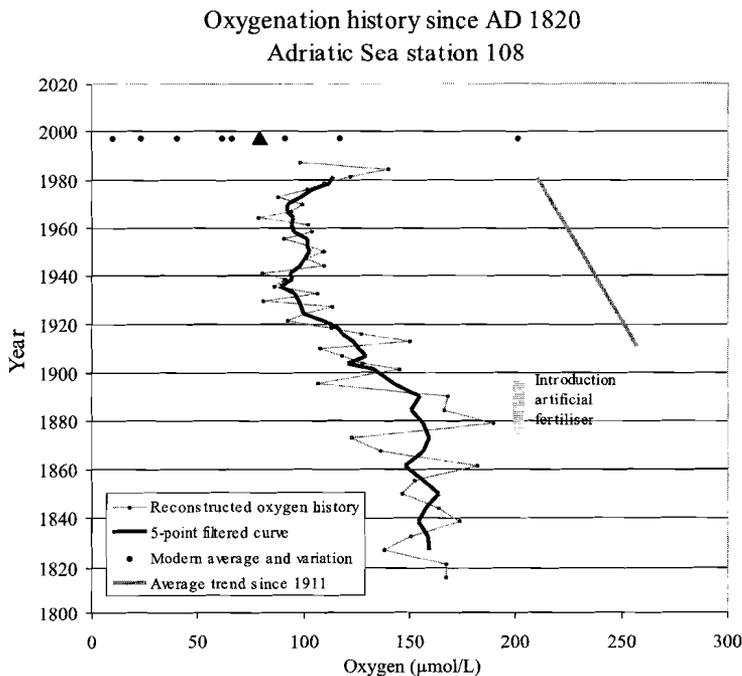


Figure 11-4: Oxygenation history covering the past 160 years of core 108, located in the northern Adriatic Sea just in front of the Po River (coordinates 44 45,4 N, 12 45,0 E). Oxygenation curve based on faunal data and datings of Barmawidjaja et al. (1995); historic trend in oxygenation is here represented by calculated fit of historic (1911-1982) oxygen data (see Justic et al., 1987, and Justic, 1992). Monthly variation of modern values (1998, own observations) is indicated by dots, their average by triangle.

last part of our reconstructed curve suggests again deterioration. This is confirmed by the modern values of which the average one fits our reconstruction very well, indicating that the proxy is a valuable tool for the accurate reconstruction of average oxygenation in paleoceanography.

Synthesis

In this synthesis we summarise some of the main features described in the previous chapters. We will attempt to arrive at some generalised conclusions, mainly directed at the impact of oxygen and organic flux, and the underlying causes of spatial and biological heterogeneity (i.e. biodiversity and the problems of patchiness). Where possible, we will try to specify possible consequences for the use of foraminifera in paleoecological reconstructions.

The starting point of our discussion is the TROX model as published by Jorissen et al. (1995) and Van der Zwaan et al (1999). In both models organic flux and oxygen are paramount in describing species microhabitat patterns. Yet, our seasonal studies suggest that also other factors are of importance.

The balance between organic flux and oxygen

Although the southern Levantine basin is known to be an oligotrophic and stable area, considerable fluctuations in foraminiferal numbers were observed throughout the two years of our study (Chapter 4). Seasonality appeared to be of much higher importance than previously thought. Some species seemed adapted to specific times of the year, i.e. spring or summer periods. No evidence was found that this seasonality was driven by preferences for temperature, light or type of food. In all cases we have the impression that the balance between food and oxygen is decisive, although sometimes in a complex chain of events. After winter mixing elevated levels of primary productivity occurred in the Levantine (Chapter 2), which resulted eventually in settling of organic matter to the seafloor. Especially in shallow water the total foraminiferal numbers seemed to co-vary with these periods of organic matter enrichment. The time-lapse between the arrival of fresh organic matter and the foraminiferal response was found to be different at the Levantine stations S1 (40m) and S3 (120m). The foraminifera living at the shallowest station reacted to the organic matter arrival with a rather long time-lapse, apparently due to strong interference by macrofauna. This effect of macrofauna diminished with depth; at 120 m the foraminifera were found to respond more rapidly, within a 1-2 month period following the relative peak in chlorophyll-a concentrations. The seasonality patterns here were blurred, however, possibly because of additional nutrients leaking from the DCM. If true, this demonstrates yet again that not only vertical flux is important, but also additional sources of nutrients (DCM, sediment) play a role. In the Levantine and the Adriatic Sea we found that the TROX models correctly predict a balance between organic flux and species limitation due to the increased oxygen demand (Chapter 8, and Duijnste, 2001). In contrast to what TROX predicts, not only epifaunal taxa were sensitive to flux; also deep infaunal species like *Eggerella* spp. reacted

opportunistically. With decreasing flux the TROX models correctly predicted an increasing amount of epifaunal taxa.

An experiment performed with foraminifera from the Levantine station S1, gave some insight in foraminiferal response to food supply. The fact that none of the foraminiferal taxa (except possibly *Eggerella* spp.) showed a numerical response to the added food, was explained by an insufficient food supply. Rough calculations reveal that the concentration of the mixture was (only) a fraction of the expected seasonal enrichment under field conditions. The significant numerical response of *Eggerella* spp. (6 weeks after food supply) again suggested that in spite of its deep infaunal microhabitat, it is more opportunistic than other species.

Throughout the two years of monitoring the sediments in the Levantine basin always contained some free oxygen, although the level of anoxia (<0.1 ml/l O_2 , Bernhard & Alve, 1996) was occasionally found close to the sediment-water interface. The sediment at the shallow water station (S1, 40m) was less oxygenated than the sediment at 120m. The Average Living Depth of the foraminifera fluctuated largely during the two years. However, in the Levantine basin and at both Adriatic stations none of the taxa studied in detail appeared to be strictly dependent on oxygen. The miliolids formed the exception being (statistically significant) controlled by oxygenation. In the Levantine a number of taxa clearly was not affected at all, and these are the taxa also abundant in the occasionally highly stressed Adriatic environment. Studies in the Adriatic Sea (Chapter 8) and Indian Ocean (Chapter 10) indeed suggest that a substantial part of the benthic foraminiferal community is at least able to survive under dysoxic to anoxic conditions. Also experimental results obtained by Moodley et al. (1998) and Bernhard (1993) indicate that anoxia in itself is not immediately limiting for foraminifera. In the Levantine the number of relatively rare (epifaunal) taxa is much higher than in the Adriatic Sea. These taxa, correctly predicted by TROX to live at the sediment water interface or deeper if oxygen allows it (compare S1 to S3 patterns), appear to be affected by oxygen in a much more direct way. In this they resemble the miliolids. Oxygen is severely limiting for them if it lowers to less than 0.1 ml/L at the sediment water interface; in such periodically stressed habitats diversities are much lower.

In Chapter 11, we make use of this so-called oxyphilic behaviour of some taxa. We present an oxygen transfer function that is derived from foraminiferal data obtained from four completely different regions with very different trophic regimes: Levantine Basin, Adriatic Sea, Indian Ocean, and Bay of Biscay. We show that the abundance of oxyphilic foraminiferal species allows one to calculate the level of oxygen in (paleo) bottom waters. From the distribution of these taxa it is obvious that they track the oxygen contents of the sediment, but do so with a time lapse. Because this transfer function is based on such a wide variety of foraminiferal communities it seems suitable for wide geographic application. Den Dulk (2000) and Kouwenhoven (2000) already made use of this and found it to be quite successful in reconstructing paleo-oxygenation of Indian Ocean waters during the last 120ky, and oxygenation of the Mediterranean waters during the Miocene, respectively.

Stability and biological control: the problem of biodiversity

The diversity of (foraminiferal) communities is an important feature for biologists as well as palaeontologists, because potentially it gives a quick indication of the (paleo)environmental circumstances. Especially if one has data with similar sample volumes from more sample localities within one region, comparisons between the data-sets might give important clues on differences in ecology. In case of fossil sediment samples, diversity might provide an indication of ecological differences through time (e.g. oxygenation, eutrophication).

Moseley (1880) described samples from the deep sea characterised by very low species diversity. He suggested this to be caused by competitive exclusion of species. Almost a century later Sanders (1968) presented data from deep sea sites where species diversity appeared to be relatively high. To explain this he introduced the stability-time hypothesis. This hypothesis describes two contrasting situations, a physically controlled one and a biologically accommodated one. The first assumes that adaptations are primarily to the physical environment. These communities are expected to be characterized by small numbers of species. Biologically accommodated communities are expected to evolve only under relatively stable conditions. Because the physical environment is constant for a longer period, the success of species is not physically controlled but more affected by the biological stress (e.g. competition, predation) within the community. Therefore, these communities are characterized by large numbers of (stenotopic) species (see Sanders 1968). In figure 1 this hypothesis is summarized.

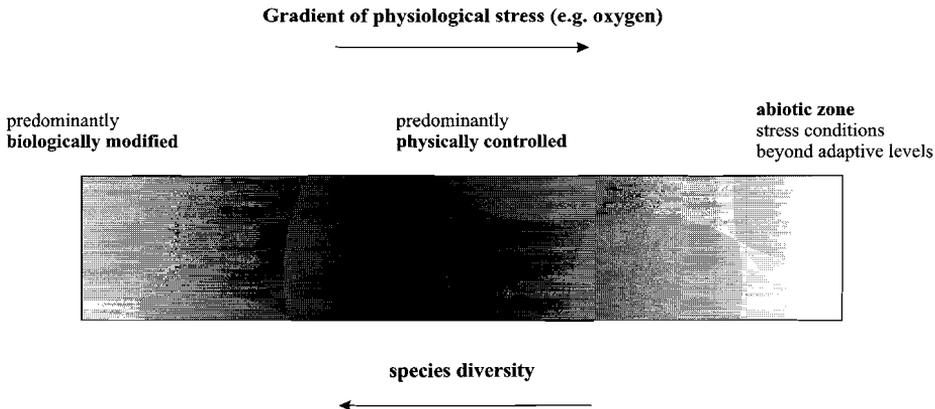


Figure 12-1: Stability-time hypothesis modified after Sanders (1968); shading represents abundance.

An alternative for the stability-time model, is formed by the equilibrium- nonequilibrium model. For instance, Connell (1978) suggested that high diversities as in tropical rain forests and coral reefs are based on the nonequilibrium state these ecosystems are in. He suggested that when reaching an equilibrium state, the communities would progress towards lower species diversity. In this sense, high diversities are the sign of long term variability. Also Hutchinson (1961) stated that coexistence of many

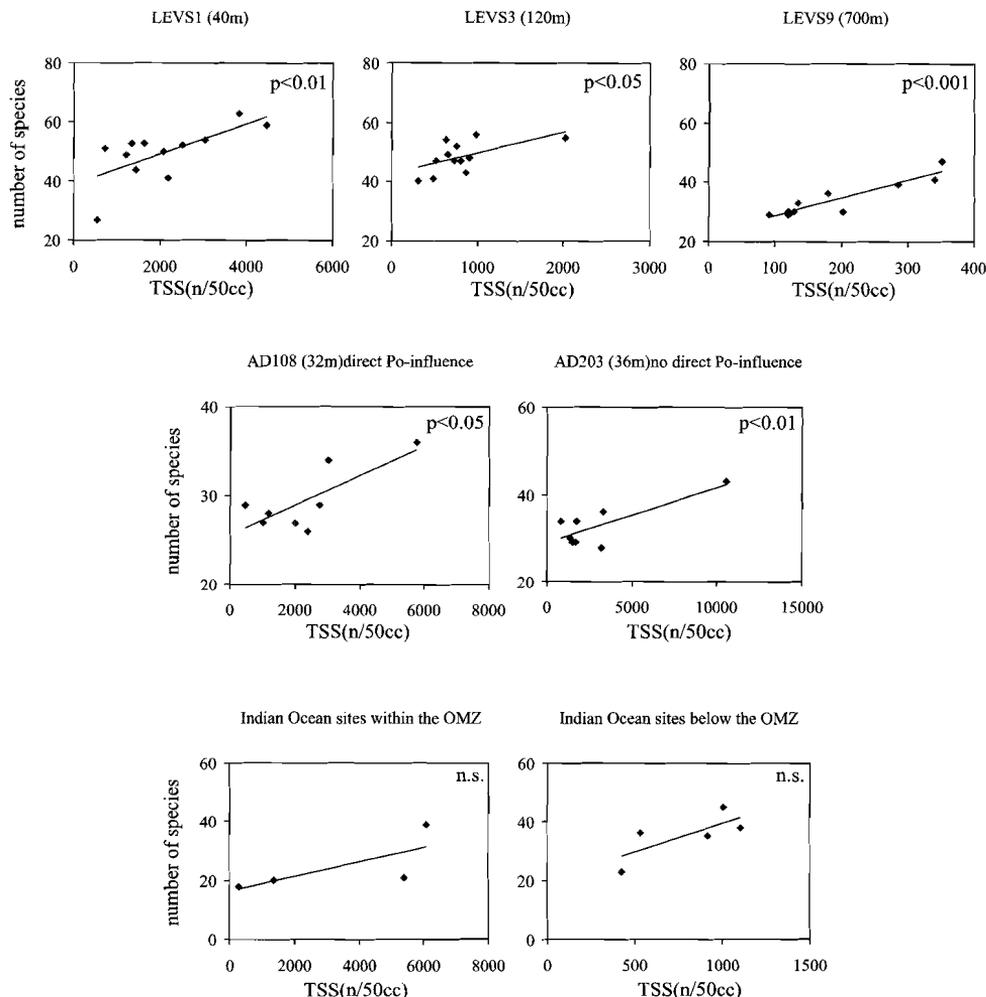


Figure 12-2: Foraminiferal total standing stocks versus simple diversity (0-1cm), at the three Levantine and the two Adriatic stations, and the station within and below the OMZ in the Indian Ocean. In the upper right of each graph the significance level of the correlation is given (n.s.= not significant).

species is a nonequilibrium rather than an equilibrium phenomenon. He argued that the competition theory (at equilibrium) predicts that the diversity of coexisting species cannot exceed the number of limiting resources (e.g. “paradox of plankton”, Hutchinson, 1961). However, a solution for this matter was recently presented by Huisman and Weissing (1999). They showed that resource competition models can generate oscillations and chaotic fluctuations in species abundances, which in turn allow the coexistence of many species on only few resources. The debate on whether to put diversity theories in an equilibrium or non-equilibrium perspective still continues.

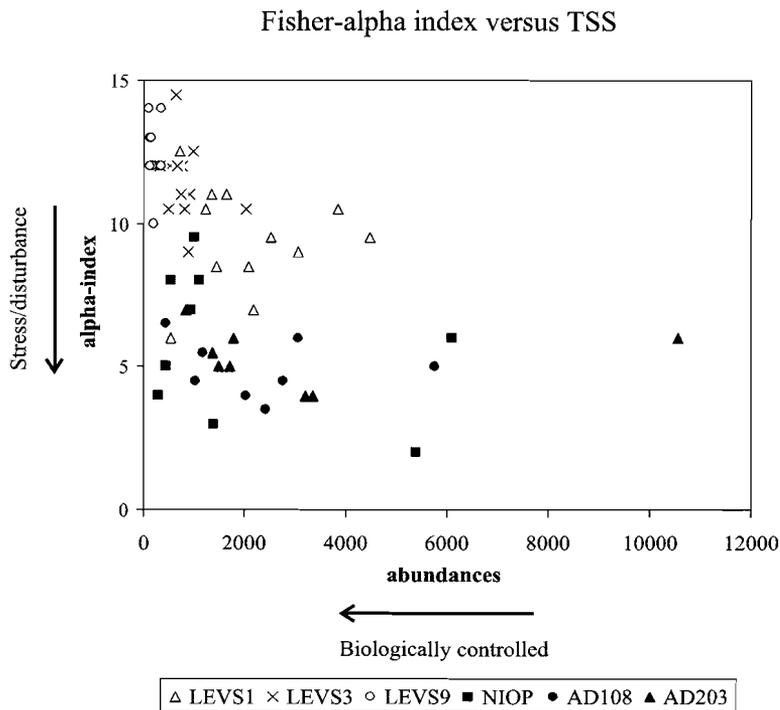


Figure 12-3: The Fisher- α diversity index versus total standing stocks

In the Levantine Basin the simple diversities at 40m depth and 120m were much higher than the simple diversity at 700m (station S9). At each station, the simple diversity was significantly positively correlated with the foraminiferal total standing stock (Fig. 2, see also Chapter 3). In the Indian Ocean, simple diversity was generally found to be lowest at the shallowest stations which were situated within and at the lower boundary of the Oxygen Minimum Zone (OMZ). Within the OMZ the most densely populated sediments were dominated by only a few (opportunistic) species; these were most resistant to the stressful circumstances (e.g. oxygen deficiency (Chapter 10)). Below the OMZ, simple diversities increased, but the standing stocks decreased strongly due to the decreasing flux with depth. Off the Oman margin, Gooday et al. (2000) found also lower species diversities within the OMZ compared to the diversity below the OMZ. If we plot the total standing stock and the simple diversity separately for the various regions, we see that the simple diversity and total standing stock are positively correlated (Fig. 2). A positive correlation between numbers of species and the number of individuals was also found by Sanders (1968) and Lambshead et al. (2000) for polychaete and bivalve species from shallow water and deep-sea nematodes, respectively.

The problem with using simple diversity is that it is closely coupled to standing stocks. As a consequence it is difficult to make inter-regional comparisons solely on basis of simple diversities. To standardize the diversities for abundances in a simple and rather straightforward manner, we used the

Fisher-alpha index (c.f. Murray, 1991). In figure 3 we plotted the α values versus total abundance. Highest values are found in the Levantine Basin, where no (seasonal) stress occurred. Off the Israeli coast, the food supply decreases downslope and consequently foraminiferal abundances decrease (Chapter 3). At the deepest station (S9), under low trophic levels but highly stable physical conditions, highest α values occur (Fig. 3). To some point this can be described by the stability-time hypothesis of Sanders (1968): where conditions are least stable (S1) α values are lowest. However, in that view the deepest Indian Ocean stations are most stable and should have highest α values. This is not true, and here stability as sole factor evidently falls short.

The α values in the Adriatic Sea again demonstrate that stress is the most prominently acting factor in deciding diversity. In this sense, it should be noted that the TROX models adequately describe the microhabitats, but that they fail to predict presence-absence of species. Stress and especially variability in stress decides on the absence from the Adriatic Sea of a large number of infrequent, mostly epifaunal taxa that are present in the Levantine. Here, biological control prevails allowing for many (possibly specialised) species to compete successfully at the sediment water interface. With somewhat higher fluxes (likely to prevail even in the deeper Indian Ocean), or with higher (variation in) stress (as in the Adriatic Sea) diversity drops and stress tolerant species prevail in low density assemblages and opportunistic species dominate high density assemblages. This coincides more or less with the ideas of Grassle and Sanders (1973), who suggested that under extreme and variable conditions of low predictability a highly opportunistic life-strategy evolves. Such species, with wide physiological tolerance, high reproductive rates, and large offspring are favoured in highly variable environments because they are able to adapt rather quickly to environmental changes. This in contrast with the species occurring at the deeper Indian Ocean sites (below the OMZ) and certainly the deeper Levantine station, where communities mainly consist of species that display relatively low and constant numbers. Grassle and Sanders (1973) suggested that in such more oligotrophic environments diversity is high and population size relatively low, and the community is characterized by species with

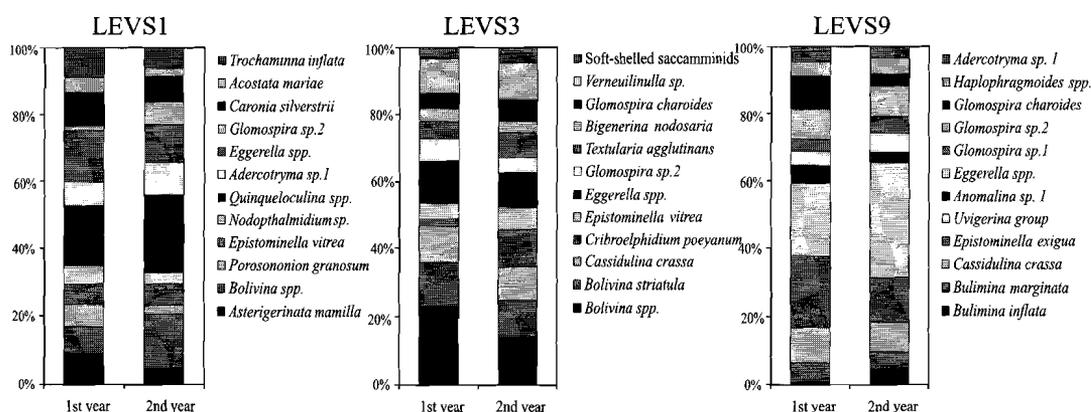


Figure 12-4: Relative abundances of the most abundant species at the three Levantine sites, averaged for the first and the second sampling year.

a lower reproductive potential, and a longer life span.

In figure 3 we can clearly distinguish several environments, from highly variable (e.g. food) and occasionally stressed (e.g. oxygen) in the Adriatic Sea, to physically stressed but less variable (e.g. oxygen stress) within the OMZ (Indian Ocean), to little physical stress and medium variability (shallow Levantine), to no physical stress and stable, oligotrophic conditions (deep Levantine and less so, the deep Indian Ocean below the OMZ). Consequently, the diversity seems an excellent measure of the type of environment, in particular the degree of biological control and environmental variability. As such, diversity models form a welcome addition to TROX models dealing with microhabitats.

In order to safely assume that field observations can be used to reconstruct the fossil record, we have to deal with the problem of spatial heterogeneity. Patchiness in benthic foraminiferal communities is a phenomenon that has been addressed earlier by several researchers (Gooday and Lamshead, 1989, Murray and Alve, 2000, Schafer and Cole, 1982, Schafer, 2000). In case of patchy distributed foraminiferal assemblages, the information on species distribution versus environmental parameters is not straightforward. Therefore, patchy distributed assemblages are less useful for ecological studies, if the reason for the patchiness cannot be revealed. Occasionally, however, such reasons are very obvious, for instance patchy distributed organic flux, carcasses of fishes, or high macrofaunal activity. We studied the importance of patchiness in the Levantine, by comparing faunal data from three stations situated at 120m water depth. Whereas the abundance patterns of the species were not alike, the averaged (yearly) foraminiferal assemblages were very similar (Chapter 7).

The value of average assemblages to reduce temporal heterogeneity is confirmed by the yearly averages of the taxa observed at the three downslope stations (S1, S3, and S9). These display very similar average proportions if the two consecutive years are compared (Fig. 4). The obvious consequence, however, is that from the point of view of fossil studies yearly averages or dead faunas might better reflect the environment than a single sample of living foraminifera. The latter is prone to be the product of environmental conditions prevailing during the previous couple of months.

- Abdel-Moati, A.R., 1990. Particulate organic matter in the subsurface chlorophyll maximum layer of the Southeastern Mediterranean. *Oceanologica Acta* 13, 307-315.
- Almogi-Labin, A., Perelis-Grossovicz, L., and Raab, M., 1992. Living *Ammonia* from a hypersaline inland pool, Dead Sea area, Israel. *Journal of Foraminiferal research*, 22(3), 257-266.
- Altenbach, A.V., 1992. Short term processes and patterns in the foraminiferal response to organic flux rates. *Marine Micropaleontology*, 19, 119-129.
- Altenbach, A.V., and M. Sarnthein, 1989. Productivity record in benthic foraminifera. In: *Production of the Ocean: Present and Past*. W. H. Berger, V.S. Smetacek, and G. Wefer, editors, John Wiley & Sons Limited, 255-269.
- Alve, E., 1995. Benthic foraminiferal distribution and recolonization of formerly anoxic environments in Drammensfjord, southern Norway. *Marine Micropaleontology*, 25, 169-186.
- Alve, E., and Bernhard, J. M., 1995. Vertical migratory response of benthic foraminifera to controlled oxygen concentrations in an experimental mesocosm. *Marine Ecology Progress Series*, 116, 137-151.
- Anderson, O.R., Lee, J.J., Faber, W.W.Jr., 1991. Collection, maintenance and culture methods for the study of living foraminifera. In: J.J. Lee and O.R. Anderson (eds.), *Biology of foraminifera*. Academic Press, United Kingdom, 335-357.
- Antoine, D., Morel, A., and Andre, J-M., 1995. Algal pigment distribution and primary production in the eastern Mediterranean as derived from coastal zone color scanner observations. *J. Geophys. Res.* 100, 16193-16209.
- Azov, Y., 1986. Seasonal patterns of phytoplankton productivity and abundance in nearshore oligotrophic waters of the Levant Basin (Mediterranean). *J. Plankton Res.* 8, 41-53.
- Barmawidjaja, D.M., 1991. Studies in living and fossil foraminifera from seasonally productive regions. *Geologica Ultraiectina*, 82, Thesis, Utrecht University.
- Barmawidjaja, D.M., Jorissen, F.J., Puskaric, S., and Van der Zwaan, G.J., 1992. Microhabitat selection by benthic foraminifera in the northern Adriatic Sea. *Journal of Foraminiferal Research*, 22(4), 297-317.
- Barmawidjaja, D., Van der Zwaan, G., Jorissen, F. and Puskaric, S., 1995. 150 years of eutrophication in the northern Adriatic Sea: Evidence from a benthic foraminiferal record. *Marine Geology*, 122, 367-384.
- Basson, P.W., and Murray, J.W., 1995. Temporal variations in four species of intertidal foraminifera, Bahrain, Arabian Gulf. *Micropaleontology*, 41 (1), 69-76.
- Ben-Eliahu, M.N., and Feige, D., 1996. Serpulid Tube-Worms (Annelida: Polychaeta) of the Central and Eastern Mediterranean with particular attention to the Levant Basin. *Senckenbergiana Maritima*, 28 (1/3), 1-51.
- Berger, W.H., and Diester-Haass, L., 1988. Paleoproductivity: The benthic/planktonic ratio in foraminifera as a productivity index. *Marine Geology*, 81, 15-25.
- Berman, T., Townsend, D.W., El Sayed, S.Z., Trees, C.C., and Azov, Y., 1984. Optical transparency, chlorophyll and primary productivity in the Eastern Mediterranean near the Israeli coast. *Oceanologica Acta*, 7, 367-371.
- Berman, T., Walline, P.D., Schneller, A., Rothenberg, J., and Townsend, D.W., 1985. Secchi disk depth record: A claim for the eastern Mediterranean. *Limnol. Oceanogr.*, 30, 447-448.
- Berman, T., Azov, Y., Schneller, A., Walline, P.D., and Townsend, D.W., 1986. Extent, transparency and phytoplankton distribution of the neritic waters overlying the Israeli coastal shelf. *Oceanologica Acta*, 9, 439-447.
- Bernhard, J.M., 1986. Characteristic assemblages and morphologies of benthic foraminifera from anoxic, organic-rich deposits: Jurassic through Holocene. *Journal of Foraminiferal Research*, 16(3), 207-215.
- Bernhard, J.M., 1988. Post-mortem vital staining in benthic foraminifera: duration and importance in population and distributional studies. *Journal of Foraminiferal Research*, 18, 143-146.
- Bernhard, J.M., 1989. The distribution of benthic Foraminifera with respect to oxygen concentration and organic carbon levels in shallow-water Antarctic sediments. *Limnol. Oceanogr.*, 34(6), 1131-1141.
- Bernhard, J.M., 1992. Benthic foraminiferal distribution and biomass related to the pore-water oxygen content: central California continental slope and rise. *Deep-Sea Research I*, 39, (3/4), 585-605.
- Bernhard, J.M., 1993. Experimental and field evidence of Antarctic foraminiferal tolerance to anoxia and hydrogen. *Marine Micropaleontology*, 20, 203-213.
- Bernhard, J.M., 1996. Microaerophilic and facultative anaerobic benthic foraminifera: a review of experimental and ultrastructural evidence. *Revue de Paleobiologie*, 15 (1), 261-275.
- Bernhard, J.M. and Reimers, C.E., 1991. Benthic foraminiferal population fluctuations related to anoxia: Santa Barbara Basin. *Biogeochemistry*, 15, 127-149.
- Bernhard, J.M., and Alve, E., 1996. Survival, ATP pool, and ultrastructural characterization of benthic foraminifera from the Drammensfjord (Norway): response to anoxia. *Marine Micropaleontology*, 28, 5-17.
- Bernhard, J.M., Sen Gupta, B.K. and Borne, P.F., 1997. Benthic foraminiferal proxy to estimate dysoxic bottom-water oxygen concentrations: Santa Barbara Basin, U.S. Pacific continental margin. *Journal of Foraminiferal Research*, 27(4), 301-310.
- Bethoux, J.P., Morin, P., Chaumery, C., Connan, O., Gentili, B., and Ruiz-Pino, D., 1998. Nutrients in the Mediterranean Sea,

- mass balance and statistical analysis of concentrations with respect to environmental change. *Mar. Chem.*, 63, 155-169.
- Boltovskoy, E., and Lena, H., 1969. Seasonal occurrences, standing crop and production in benthic foraminifera of Puerto Deseado. *Contributions from the Cushman Foundation for Foraminiferal Research*, 20 (3), 87-95.
- Bradshaw, J.S., 1955. Preliminary laboratory experiments on ecology of foraminiferal populations. *Micropaleontology*, 4, 351-358.
- Bradshaw, J. S., 1961. Laboratory experiments on the ecology of foraminifera. *Contributions from the Cushman Foundation for Foraminiferal Research*, 7(3), 87-106.
- Brezekinsky, M.A., 1985. The Si:C:N ratio of marine diatoms: interspecific variability and the effect of some environmental variables. *J. Phycol.*, 21, 347-357.
- Buzas, M.A., and Gibson, T.G., 1969. Species diversity: benthonic foraminifera in western North America. *Science*, 163, 72-75
- Calvert, S.E. and T.F. Pedersen, 1993. Geochemistry of Recent oxic and anoxic marine sediments: Implications for the geological record. *Marine Geology*, 113, 67-88.
- Caralp, M.H., 1984. Impact de la matiere organique dans des zones de forte productivite sur certains foraminiferes benthiques. *Oceanologica Acta* 7(4), 509-515.
- Caralp, M.H., 1989a. Abundance of *Bulimina exilis* and *Melonis barleeanum*: Relationship to the quality of marine organic matter. *Geo-Marine Letters* 9, 37-43.
- Caralp, M.H., 1989b. Size and morphology of the benthic foraminifer *Melonis barleeanum*: relationships with marine organic matter. *Journal of Foraminiferal Research*, 19(3), 235-245.
- Carpenter, J.H., 1965. The Chesapeake Bay Institute technique for the Winkler dissolved oxygen method. *Limnol Oceanogr.*, 10, 439-447.
- Cimerman, F., and Langer, M., 1991. Mediterranean Foraminifera. Razred za naravoslovne vede, classis IV: historia naturalis, opera 30, pp 1-118. Pls 1-93. Slovenska Akademia, Ljubljana.
- Civitaresse, G., Gacic, M., Vetrano, A., Boldrin, A., Bregant, D., Rabitti, S., and Souvermezoglu, E., 1998. Biochemical fluxes through the Strait of Otranto (Eastern Mediterranean). *Cont. Shelf Res.*, 18, 773-789.
- Codispoti, L.A., 1989. Phosphorus vs. nitrogen limitation of new and export production, in: W.H. Berger, V.S. Smetacek., Wefer, G. (Eds.), *Productivity of the ocean: Present and past. Dahlem Konferenzen Research Report 44*, John Wiley & Sons Ltd., Chichester, 377-408.
- Codispoti, L.A., 1991. Primary productivity and carbon and nitrogen cycling in the Arabian Sea. In: S.L. Smith, K. Banse, J.K. Cochran, L.A. Codispoti, H.W. Ducklow, M.E. Luther, D.B. Olsen, W.T. Peterson, W.L. Prell, N., Surgi, J.C. Swallow and K. Wishner, (Editors), *U.S. JGOFS: Arabian Sea Process Study*, U.S. JGOFS Planning Report, 13, 75-85.
- Collison, P., 1980. Vertical distribution of foraminifera off the coast of Northumberland, England. *Journal of Foraminiferal Research*, 10 (1), 75-78.
- Connell, J.H., 1978. Diversity in Tropical Rain Forests and Coral Reefs. *Science*, 199, 1302-1310.
- Corliss, B.H., 1985. Microhabitats of benthic foraminifera within deep-sea sediments, *Nature*, 314, 435-438.
- Corliss, B.H., 1988. Morphotype patterns of Norwegian Sea deep-sea foraminifera and ecological implications. *Geology*, 16, 716-719.
- Corliss, B.H., 1991. Morphology and microhabitat preferences of benthic foraminifera from the northwest Atlantic Ocean. *Marine Micropaleontology*, 17, 195-236.
- Corliss, B.H., and Emerson, S., 1990. Distribution of Rose Bengal stained deep-sea benthic foraminifera from the Nova Scotia continental margin and Gulf of Maine. *Deep Sea Research*, 37, 381-400.
- Corliss, B.H., and Fois, E., 1991. Morphotype analysis of deep-sea benthic foraminifera from the Northwest Gulf of Mexico. *Palaios*, 5, 589-605.
- Corliss, B.H., and Van Weering, T.C.E., 1993. Living (stained) benthic foraminifera within surficial sediments of the Skagerrak. *Marine Geology*, 111, 323-335.
- Cullen, J.J., 1982. The deep chlorophyll maximum: comparing vertical profiles of chlorophyll a. *Can. J. Fish Aquat. Sci.*, 391, 791-803.
- De Stigter, H.C., 1996. Recent and fossil benthic foraminifera in the Adriatic Sea: distribution patterns in relation to organic carbon flux and oxygen concentration at the seabed. *Geologica Ultraiectina*, No. 144, Thesis, Utrecht University, 254pp.
- De Stigter, H.C., Jorissen, F.J., and Van der Zwaan, G.J., 1998. Bathymetric distribution and microhabitat partitioning of live (Rose Bengal stained) benthic foraminifera along a shelf to bathyal transect in the southern Adriatic Sea. *Journal of Foraminiferal Research*, 28(1), 40-65
- Debenay, J.-P., Bénéteau, E., Zhang, J., Stouff, V., Geslin, E., Redois, F., Fernandez-Gonzalez, M., 1998. *Ammonia beccarii* and *Ammonia tepida* (Foraminifera): morphological arguments for their distinction. *Marine Micropaleontology*, 34, 235-244.
- Debenay, J.-P., Guillou, J.-J., and Lesourd, M., 1996. Colloidal calcite in foraminiferal test: Crystallization and texture of the test. *Journal of Foraminiferal Research*, 26(4), 277-288.
- Den Dulk, M., Reichart, G.J., Memon, G.A., Roelofs, E.M., Zachariasse, W.J., Van der Zwaan, G.J., 1998. Benthic foraminiferal response to variations in surface water productivity and oxygenation in the northern Arabian Sea. *Marine Micropaleontology*, 35, 43-66

- Den Dulk, M., 2000. Benthic foraminiferal response to Late Quaternary variations in surface water productivity and oxygenation in the northern Arabian Sea. *Geologica Ultraiectina*, Thesis, Utrecht University, 205pp.
- Dortch, Q., and Whiteledge, T.E., 1992. Does nitrogen or silicon limit phytoplankton production in the Mississippi river plume and nearby regions? *Cont. Shelf Res.*, 12, 1293-1309.
- Dowidar, N.M., 1984. Phytoplankton biomass and primary productivity of the southeastern Mediterranean. *Deep-Sea Res.*, 31, 983-1000.
- Duijnste, I.A.P., 2001. Experimental ecology of foraminifera: towards better quantitative paleoecological reconstructions. PhD-thesis, Utrecht University.
- Eppley, R.W., 1989. New production: history, methods, problems, in: W.H. Berger, V.S. Smetacek., Wefer, G. (Eds.), *Productivity of the oceans: present and past*. Dahlem Konferenzen Research report 44, John Wiley & Sons Ltd., Chichester, 85-98.
- Fanning, K.A., 1992. Nutrient provinces in the sea: concentration ratios, reaction rate ratios, and ideal covariation. *J. Geophys. Res.*, 97, 5693-5712.
- Faubel, A., Hartwig, E, and Thiel, H., 1983. On the ecology of sublittoral sediments, Fladen Ground, North Sea. I. Meiofauna standing stock and estimation of production. *Meteor. Forssch.-Ergebnisse D*, 36, 35-48.
- Gitelson, A., Karnieli, A., Goldman, N., Yacobi, Y.Z., and Mayo, M., 1996. Chlorophyll estimation in the Southeastern Mediterranean using CZCS images: adaptation of an algorithm and its validation. *J. Mar. Sys.*, 9, 283-290.
- Goldman, J.C., 1993. Potential role of large oceanic diatoms in new primary production. *Deep-Sea Res.*, 40, 159-168.
- Goldsmith, S. L., 1997. Provenance of marine Sediments off the Mediterranean Coast of Israel. Master thesis, University of Leeds.
- Gooday, A.J., 1986. Meiofaunal foraminiferans from the bathyal Porcupine Seabight (northeast Atlantic): size structure, standing stock, taxonomic composition, species diversity and vertical distribution in the sediment. *Deep Sea Research*, 33 (10), 1345-1373.
- Gooday, A.J., 1988. A response by benthic foraminifera to the deposition of phytodetritus in the deep sea. *Nature*, 332, 70-73.
- Gooday, A.J., 1993. Deep-sea benthic foraminiferal species which exploit phytodetritus: Characteristic features and controls on distribution. *Marine Micropaleontology*, 22, 187-205.
- Gooday, A.J., 1994. The Biology of Deep-Sea Foraminifera: a review of some advances and their applications in paleoceanography. *Palaios*, 9, 14-31.
- Gooday, A.J., and Lambshead, P.J.D., 1989. The influence of seasonally deposited phytodetritus on benthic foraminiferal populations in the bathyal northeast Atlantic: the species response. *Marine Ecology Progress Series* 58, 53-67.
- Gooday, A.J., and Turley, C.M., 1990. Responses by benthic organisms to input of organic material to the ocean floor: a review. *Phil. Trans. R. Soc. Lond. A*, 331, 119-138.
- Gooday, A.J., L.A. Levin, P. Linke, and T. Heeger, 1992. The role of benthic foraminifera in deep-sea food webs and carbon cycling. In: *Deep-Sea Food Chains and the Global Carbon Cycling*. G.T. Rowe and V. Pariente, editors, Kluwer Academic Publishers, The Netherlands, 63-91.
- Gooday, A.J., Bernhard, J.M., Levin, L.A., and Suhr, S.B., 2000. Foraminifera in the Arabian Sea oxygen minimum zone and other oxygen-deficient settings: taxonomic composition, diversity, and relation to metazoan faunas. *Deep-Sea Research*, II, 47, 25-54.
- Grassle, J.F., and Grassle, J.P., 1974. Opportunistic Life Histories and Genetic Systems in Marine Benthic Polychaetes. *Journal of Marine Research*, 32(2), 253-284.
- Grassle, J.F., and Sanders, H.L., 1973. Life histories and the role of disturbance. *Deep Sea Research*, 20, 643-659.
- Gustafsson, M. and Nordberg, K., 1999. Benthic foraminifera and their response to hydrography, periodic hypoxic conditions and primary production in the Koljö fjord on the Swedish west coast. *Journal of Sea Research*, 41, 163-178.
- Hallock, P., 1999. Symbiont-Bearing Foraminifera. In: *Modern Foraminifera*, ed. Sen Gupta, B. K., Kluwer Academic Publishers, 123-140.
- Harloff, J., and Mackensen, A., 1997. Recent benthic foraminiferal associations and ecology of Scotia Sea and Argentine Basin. *Marine Micropaleontology*, 31, 1-29.
- Hecht, A., Pinardi, N., and Robinson, A.R., 1988. Currents, water masses, eddies and jets in the Mediterranean Levantine Basin. *J. Phys. Oceanogr.*, 18, 1320-1353.
- Hermelin, J.O.R., and D.B. Scott, 1985. Recent benthic foraminifera from the central North Atlantic. *Micropaleontology* 31(3), 199-220.
- Hermelin, J.O.R. and G.B. Shimmield, 1990. The importance of the Oxygen Minimum Zone and Sediment Geochemistry in the Distribution of Recent Benthic Foraminifera in the Northwest Indian Ocean. *Marine Geology* 91, 1-29.
- Herut, B., Krom, M.D., Pan, G., and Mortimer R., 1999a. Atmospheric input of nitrogen and phosphorus to the SE Mediterranean: sources, fluxes and possible impact. *Limnol. Oceanogr.*, 44, 1683-1692.
- Herut, B., Zohary, T., Robarts, R.D. and Kress, N., 1999b. Adsorption of dissolved phosphate onto loess particles in surface and deep Eastern Mediterranean water. *Mar. Chem.*, 64, 253-265.
- Herut, B., Almogi-Labin, A, Jannink, N.T., and Gertman, I., 2000. The seasonal dynamics of nutrient and chlorophyll a concentrations on the SE Mediterranean shelf-slope. *Oceanologica Acta*, 23, 771-782.

- Holm-Hansen, O., Lorenzen, C.J., Holmes, R.W., and Strickland, J.D.H., 1965. Fluorometric determination of chlorophyll. *J. du Conseil Permanent International pour l'Exploration de la Mer*, 30, 2-15.
- Huisman, J., and Weissing, F.J., 1999. Biodiversity of plankton by species oscillations and chaos. *Nature*, 402, 407-410.
- Hutchinson, G.E., 1961. The paradox of the plankton. *American Naturalist*, 95, 137-145.
- Ignatiades, L., Georgopoulos, D., and Karydis, M., 1995. Description of the phytoplankton community of the oligotrophic waters in the SE Aegean Sea (Mediterranean). *Mar. Ecol.*, 16, 13-26.
- Jannink, N.T., Zachariasse, W.J., and Van der Zwaan, G.J., 1998. Living (Rose Bengal stained) benthic foraminifera from the Pakistan continental margin (northern Arabian Sea). *Deep Sea Research I*, 45, 1483-1513.
- Johnson, K.S., Chavez, F.P., and Friederich, G.E., 1999. Continental-shelf sediment as a primary source of iron for coastal phytoplankton. *Nature*, 398, 697-700.
- Jonkers, H.A., 1984. Pliocene benthonic foraminifera from homogeneous and laminated marls on Crete. *Utrecht Micropaleontological Bulletins* ed. Vol. 31. Loonletterij Abé, Hoogeveen. 179 pages.
- Jorissen, F.J., 1988. Benthic Foraminifera from the Adriatic Sea: Principles of Phenotypic Variation. *Utrecht Micropaleontological Bulletin*, 37, 176pp.
- Jorissen, F.J., Barmawidjaja, D.M., Puskaric, S, and Van der Zwaan, G.J., 1992. Vertical distribution of benthic foraminifera in the northern Adriatic Sea: the relation with the organic flux. *Marine Micropaleontology*, 19, 131-146.
- Jorissen, F.J., de Stigter, H.C., and Widmark, J.G.V., 1995. A conceptual model explaining benthic foraminiferal microhabitats. *Marine Micropaleontology*, 22, 3-15.
- Jorissen, F.J., Wittling, I., Peypouquet, J.P., Rabouille, C., and Relexans, J.C., 1998. Live benthic foraminiferal faunas off Cape Blanc, NW-Africa: Community structure and microhabitats. *Deep Sea Research I*, 45, 2157-2188.
- Justic, D., Legovic, T., and Rottini-Sandri, L., 1987. Trends in oxygen content 1911-1984 and occurrence of benthic mortality in the northern Adriatic Sea. *Estuarine, Coastal and Shelf Science*, 25, 435-445.
- Justic, D., 1991. Hypoxic conditions in the northern Adriatic Sea: historical development and ecological significance. In: R.V. Tyson and T.H. Pearson (eds.), *Modern and Ancient Continental Shelf Anoxia*. Geological Society Special Publication, 58, 95-105.
- Justic, D., Rabalais, N.N., Turner, R.E., and Dortch, Q., 1995. Changes in nutrient structure of river dominated coastal waters: stoichiometric nutrient balance and its consequences. *Estuar. Coast. Shelf Sci.*, 50, 339-356.
- Kabanova, Y.G., 1968. Primary production of the northern part of the Indian Ocean. In: *Oceanology, of the academy of sciences of the USSR (English translation)*, 19: 214-225.
- Kaiho, K., 1994. Benthic foraminiferal dissolved-oxygen index and dissolved-oxygen levels in the modern ocean. *Geology* 22, 719-722.
- Kaiho, K., 1999. Effect of organic flux and dissolved oxygen on the benthic foraminiferal oxygen index (BFOI). *Marine Micropaleontology*, 37, 67-77.
- Kemp, A.E.S., Pearce, R.B., Koizumi, I., Pike, J., and Rance, S.J., 1999. The role of mat-forming diatoms in the formation of Mediterranean sapropels. *Nature*, 398, 57-61.
- Kimor, B., Berman, T., and Schneller, A., 1987. Phytoplankton assemblages in the deep chlorophyll maximum layers off the Mediterranean Coast of Israel. *J. Plankton Res.*, 9, 433-443.
- Kitazato, H., and Ohga, T., 1995. Seasonal changes in deep-sea benthic foraminiferal populations: Results of long-term observations at Sagami Bay, Japan. In: *Biogeochemical Processes and Ocean Flux in the Western Pacific*. Sakai, H., and Nozaki, Y. (Eds.). Terra Scientific Publishing Company, Tokyo, 331-342.
- Kitazato, H., Shirayama, Y., Nakatsuka, T., Fujiwara, S., Shimanaga, M., Kato, Y., Okada, Y., Kanda, J., Yamaoka, A., Masuzawa, T., and Suzuki, K., 2000. Seasonal phytodetritus deposition and responses of bathyal benthic foraminiferal populations in Sagami Bay, Japan: preliminary results from "Project Sagami 1996-1999". *Marine Micropaleontology*, 40, 135-149.
- Kouwenhoven, T.J., 2000. Survival under stress: benthic foraminiferal patterns and Cenozoic biotic crises. *Geologica Ultraiectina*, 186, thesis Utrecht University, 205 pp.
- Krom, M.D., Kress, N., Brenner, S., and Gordon, L.I., 1991. Phosphorus limitation of primary productivity in the E. Mediterranean Sea. *Limnol. Oceanogr.*, 36, 424-432.
- Krom, M.D., Brenner, S., Kress, N., Neori, A., and Gordon, L.I., 1992. Nutrient dynamics and new production in a warm-core eddy from the eastern Mediterranean. *Deep-Sea Res.*, 39, 467-480.
- Krom, M.D., Brenner, S., Kress, N., Neori, A., and Gordon, L.I., 1993. Nutrient distributions during an annual cycle across a warm-core eddy from the eastern Mediterranean Sea. *Deep-Sea Res.*, 40, 805-825.
- Lamshead, P.J.D., Tietjen, J., Ferrero, T., and Jensen, P., 2000. Latitudinal diversity gradients in the deep sea with special reference to North Atlantic nematodes. *Marine Ecology Progress Series*, 194, 159-167.
- Lee, J.J., Capriulo, G.M., 1990. The ecology of marine protozoa. In: *Ecology of marine protozoa*, G.M. Capriulo (ed.). Oxford University Press, 3-45.
- Levin, L.A., Blair, N.E., Martin, C.M., DeMaster, D.J., Plaia, G. and Thomas, C.J., 1999. Macrofaunal processing of phytodetritus at two sites on the Carolina margin: in situ experiments

- using ¹³C-labeled diatoms. *Marine Ecology Progress Series*, 182, 37-54.
- Linke, P., and Lutze, G.F., 1992. Microhabitat preferences of benthic foraminifera – a static concept of dynamic adaptation to optimise food acquisition?. *Marine Micropaleontology*, 20, 215-234.
- Loubere, P., A. Gary, and M. Lagoe, 1993. Generation of benthic foraminiferal assemblages: Theory and preliminary data. *Marine Micropaleontology* 20, 165-181.
- Loubere, P., Meyers, P., and Gary, A., 1995. Benthic foraminiferal microhabitat selection, carbon isotope values and association with larger animals: a test with *Uvigerina peregrina*. *Journal of Foraminiferal Research*, 25(1), 83-95.
- Lutze, G.F., and W.T. Coulbourn, 1984. Recent benthic foraminifera from the continental margin of northwest Africa: community structure and distribution. *Marine Micropaleontology* 8, 361-401.
- Mackensen, A., H.P. Sejrup, and E. Jansen, 1985. The distribution of living benthic foraminifera on the continental slope and rise off southwest Norway. *Marine Micropaleontology* 9, 275-306.
- Mackensen, A., 1987. Benthische Foraminiferen auf dem Island-Schottland Rücken: Umwelt-Anzeiger an der Grenze zweier ozeanischer Räume. *Palaeontologische Zeitschrift* 61(3/4), 149-179.
- Mackensen, A., and Douglas, R.G., 1989. Down-core distribution of live and dead deep-water benthic foraminifera in box cores from the Weddell Sea and the California continental borderland. *Deep-Sea Research*, 36 (6), 879-900.
- Mackensen, A., D.K. Fütterer, H. Grobe, and G. Schmiedl, 1993. Benthic foraminiferal assemblages from the eastern South Atlantic Polar Front region between 35° and 57°S: Distribution, ecology and fossilization potential. *Marine Micropaleontology* 22, 33-69.
- Maio, Q., and Thunell, R.C., 1993. Recent deep-sea benthic foraminiferal distributions in the South China Sea and the Sulu Seas. *Marine Micropaleontology* 22, 1-32.
- Miller, K.G., and G.P. Lohmann, 1982. Environmental distribution of Recent benthic Foraminifera on the northeast United States continental slope. *Geological Society of America Bulletin* 93, 200-206.
- Milliman, J.O., 1991. Flux and fate of fluvial sediment and water in coastal seas, in: Mantoura, R.F.C., Martin, J.M. Wollast, R. (Eds.), *Ocean Margin Processes in Global Change*, John Wiley & Sons Ltd., Chichester, 69-89.
- Moodley, L., S.R. Troelstra, and T.C.E. Van Weering, 1993. Benthic foraminiferal response to environmental change in the Skagerrak, northeastern North Sea. *Sarsia* 78, 129-139.
- Moodley, L., 1992. Experimental ecology of benthic foraminifera in soft sediments and its (paleo) environmental significance. Thesis, Free University, Amsterdam.
- Moodley, L., and Hess, C., 1992. Tolerance of infaunal Benthic Foraminifera for Low and High Oxygen Concentrations. *Biological Bulletins*, 183, 94-98.
- Moodley, L., Van der Zwaan, G.J., Herman, P.M.J., Kempers, A.J., and Van Breugel, P., 1997. Differential response of benthic meiofauna to anoxia with special reference to Foraminifera (Protista: Sarcodina). *Marine Ecology Progress Series*, 158: 151-163.
- Moodley, L., Heip, C.H.R., and Middelburg, J.J., 1998a. Benthic activity in sediments of the northwestern Adriatic Sea: sediment oxygen consumption, macro- and meiofauna dynamics. *Journal of Sea Research*, 40, 263-280
- Moodley, L., Schaub, B.E.M., Van der Zwaan, G.J., and Herman, P.M.J., 1998b. Resistance of benthic foraminifera (Protista: Sarcodina) to hydrogen sulphide. *Marine Ecology Progress Series*, 169, 77-86.
- Moodley, L., Van der Zwaan, G.J., Rutten, G.M.W., Boom, R.C.E. and Kempers, A.J., 1998c. Subsurface activity of benthic foraminifera in relation to porewater oxygen content: laboratory experiments. *Marine Micropaleontology*, 34, 91-106.
- Moodley, L., Boschker, H.T.S., Middelburg, J.J., Pel, R, Herman, P.M.J., de Deckere, E., and Heip, C.H.R., 2000. Ecological significance of benthic foraminifera: ¹³C labelling experiments. *Marine Ecology Progress Series*, 202, 289-295.
- Moseley, H.N., 1880. Deep-sea Dredging and Life in the Deep Sea. *Nature*, 21, 543-547, 569-572, 591-593.
- Murosky, M.W., and S.W. Snyder, 1994. Vertical distribution of stained foraminifera in sediments of southern Onslow Bay, North Carolina continental shelf. *Journal of Foraminiferal Research* 24(3), 158-170.
- Murray, J.W., 1991. *Ecology and Palaeoecology of Benthic Foraminifera*. Longman, New York, 397pp., ISBN 0-582-05122-3.
- Murray, J.W., 1992. Distribution and population dynamics of benthic foraminifera from the southern North Sea. *Journal of Foraminiferal Research* 22(2), 114-128.
- Murray, J.W., and Alve, E., 1999. Natural dissolution of modern shallow water benthic foraminifera: taphonomic effects on the paleoecological record. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 146, 195-209
- Murray, J.W., and Alve, E., 2000. Major aspects of foraminiferal variability (standing crop and biomass) on a monthly scale in an intertidal zone. *Journal of Foraminiferal Research*, 30 (3), 177-191.
- Murray, J.W., and Bowser, S.S., 2000. Mortality, protoplasm decay rate, and reliability of staining techniques to recognize 'living' foraminifera: a review. *Journal of Foraminiferal Research*, 30 (1), 66-70.
- OCEAN-project, Mediterranean Trend Analysis, web-page: <http://me-www.jrc.it/cgi-bin/ocean/mkgraph_czcs_fm.pl>

- Ohga, T., and Kitazato, H., 1997. Seasonal changes in bathyal foraminiferal populations in response to the flux of organic matter (Sagami Bay, Japan). *Terra Nova*, 9(1), 33-37.
- Olson, D.B., G.L. Hitchcock, R.A. Fine, and B.A. Warren, 1993. Maintenance of the low-oxygen layer in the central Arabian Sea. *Deep-Sea Research II*, 40, 673-685.
- Oren, O.H., 1970. Seasonal changes in the physical and chemical characteristics, and the productivity at the low trophic level of the Mediterranean waters off Israel. PhD. Thesis, Hebrew University, Jerusalem, 238pp.
- Oren, O.H., and Komarovskiy, B., 1961. The influence of the Nile flood on the shore waters of Israel. *Rapp. Comm. Int. Mer. Medit.*, 16, 655-659.
- Ozsoy, E., Hecht, A., Unluata, U., Brenner, S., Sur, H.I., Bishop, J., Latif, M.A., Rozentraub, Z., and Oguz, T., 1993. A synthesis of the Levantine Basin circulation and Hydrography 1985-1990. *Deep-Sea Res. II*, 40, 1075-1119.
- Parker, F.L. 1958. Eastern Mediterranean Foraminifera. Reports of the Swedish Deep-Sea expedition, Vol. VIII: Sediment cores from the Mediterranean Sea and the Red Sea, No 4.
- Parsons, T.R., Takahashi, M., and Hargrave, B., 1977. *Biological Oceanographic Processes*, 2nd edition, Pergamon Press, Oxford, , 332 pp.
- Perez-Cruz, L.L., and M.L. Machain-Castillo, 1990. Benthic foraminifera of the oxygen minimum zone, continental shelf of the Gulf of Tehuantepec, Mexico. *Journal of Foraminiferal Research* 20 (4), 312-325.
- Peterson, L.C., 1984. Recent abyssal benthic foraminiferal biofacies of the eastern e-quatorial Indian Ocean. *Marine Micropaleontology* 8, 479-519.
- Phleger, F.B., and Soutar, A., 1973. Production of benthic foraminifera in three east Pacific oxygen minima. *Micropaleontology*, 19 (1), 110-115.
- POEM Group, 1992. General circulation of the Eastern Mediterranean. *Earth-Science Reviews*, 32, 285-309.
- Qasim, S.Z., 1982. Oceanography of the northern Arabian Sea. *Deep-Sea Research*, 29: 1041-1068.
- Rathburn, A.E., and Corliss, B.H., 1994. The ecology of living (stained) deep-sea benthic foraminifera from the Sulu Sea. *Paleoceanography* 9 (1), 87-100.
- Reichert, G.J., 1997. Late Quaternary variability in the Arabian Sea monsoon and oxygen minimum zone. *Geologica Ultraiectina*, 154, 152pp.
- Rosentraub, Z., 1995. Circulation on the Mediterranean continental shelf and slope of Israel. IAEPSO 21 General Assembly, Honolulu, Hawaii, 5-12 August.
- Salihoglu, I., Saydam, C., Basturk, O., Yilmaz, K., Gocmen, D., Hatipoglu, E., and Yilmaz, A., 1990. Transport and distribution of nutrients and chlorophyll-a by mesoscale eddies in the north-eastern Mediterranean. *Mar. Chem.*, 29, 375-390.
- Sancetta, C., Villareal, T., and Falkowski, P., 1991. Massive fluxes of Rhizosolenid diatoms: a common occurrence? *Limnol. Oceanogr.*, 36, 1452-1457.
- Sanders, H.L., 1968, Marine benthic diversity: a comparative study. *The American Naturalist*, 102, 243-282.
- Schafer, C.T., 2000. Monitoring nearshore marine environments using benthic foraminifera: Some protocols and pitfalls. *Micropaleontology*, 46 (1), 161-169.
- Schafer, C.T., and Mudie, P.J., 1980. Spatial distribution of foraminifera and pollen in two nearshore sediment sites, St. Georges Bay, Nova Scotia. *Canadian Journal of Earth Sciences*, 17, 313-324.
- Schafer, C.T., and Cole, F.E., 1982. Living benthic foraminifera distributions on the continental slope and rise east of Newfoundland, Canada. *Geological Society of America Bulletin*, 93, 207-217.
- Schmiedl, G., Mackensen, A., and Müller, P.J., 1997. Recent benthic foraminifera from the eastern South Atlantic Ocean: Dependence on food supply and water masses. *Marine Micropaleontology*, 32, 249-287.
- Schneller, A., Kimor, B., and Azov, Y., 1984. Seasonal distribution of diatoms and dinoflagellates (>65 m) off the coast of Israel. XXIXth Congress and Plenary Assembly, Lucerne, Plankton Committee, Rapp. PV Reun. CIESM, October 11-19.
- Schönfeld, J., 1997. The impact of the Mediterranean Outflow Water (MOW) on the benthic foraminiferal assemblages and surface sediment at the southern Portuguese continental margin. *Marine Micropaleontology*, 29, 211-236.
- Sen Gupta, B.K., and M.L. Machain-Castillo, 1993. Benthic foraminifera in oxygen-poor habitats. *Marine Micropaleontology* 20, 183-201.
- Sgarrella, F., and Moncharmont Zei, M., 1993. Benthic foraminifera of the Gulf of Naples (Italy): systematics and autoecology. *Bollettino della Societa Paleontologica Italiana*, 32(2), 145-264.
- Sharaf El Din, S.H., 1977. Effect of Aswan High Dam on the Nile flood and on the estuarine and coastal circulation pattern along the Mediterranean Egyptian coast. *Limnol. Oceanogr.*, 22, 194-207.
- Shirayama, Y., and Hirokoshi, M., 1989. Comparison of the benthic size structure between sublittoral, upper slope and deep-sea areas of the western Pacific. *International Revue Hydrobiology*, 74, 1-13.
- Silva, K.A., Corliss, B.H., Rathburn, A.E., and Thunell, R.C., 1996. Seasonality of living benthic foraminifera from the San Pedro Basin, California borderland. *Journal of Foraminiferal Research*, 26 (1), 71-93.
- Sjoerdsma, P.G., and G.J. Van der Zwaan, 1992. Simulating the

- effect of changing organic flux and oxygen content on the distribution of benthic foraminifera. *Marine Micropaleontology* 19, 163-180.
- Smart, C.W., King, S.C., Gooday, A.J., Murray, J.W., and Thomas, E., 1994. A benthic foraminiferal proxy of pulsed organic matter paleofluxes. *Marine Micropaleontology*, 23, 89-99.
- Snider, L.J., Burnett, B.R., and Hessler, R.R., 1984. The composition and distribution of meiofauna and nanobiota in a central North Pacific deep-sea area. *Deep Sea Research*, 31, 1225-1249.
- Ter Braak, C.J.F., and Smilauer, P., 1998. CANOCO reference manual and user's guide to Canoco for Windows: software for canonical community ordination (version 4.0). Microcomputer Power, Ithaca NY USA, 352pp.
- Thies, A., and W. Kuhnt, 1995. Benthic Foraminifera in Modern Oxygen Depleted Environments and Cretaceous Black Shales - a Comparison. Geologisch-Paläontologisches Institut, Kiel (internal report).
- Thingstad, T.F., and Rassoulzadegan, F., 1995. Nutrient limitations, microbial food webs and 'biological C-pump': suggested interactions in a P-limited Mediterranean. *Mar. Ecol. Prog. Ser.*, 117, 299-306.
- Thomsen, L., and Altenbach, A.V., 1993. Vertical and areal distribution of foraminiferal abundance and biomass in microhabitats around inhabited tubes of marine echiurids. *Marine Micropaleontology*, 20, 303-309.
- Turekian, K.K., and K.H. Wedepohl, 1961. Distribution of the Elements in Some Major Units of the Earth's Crust. *Geological Society of America Bulletin*, 72, 175-192.
- Turley, C.M., A.J. Gooday, and J.C. Green, 1993. Maintenance of abyssal benthic foraminifera under high pressure and low temperature: some preliminary results. *Deep-Sea Research* 40(4), 643-652.
- Tyson, R.V. and T.H. Pearson, 1991. Modern and ancient continental shelf anoxia: an overview. In: *Modern and Ancient Continental Shelf Anoxia*, R.V. Tyson and T.H. Pearson, Geological Society Special Publication No 58, 1-24.
- Van Bennekom, A.J. and M.A. Hiehle, 1994. CTD operations and calibrations during leg D1, D2 and D3 of the Netherlands Indian Ocean Programme. In: *Geological study of the Arabian Sea*. W.J.M. van der Linden and C.H. van der Weijden, editors, Netherlands Geosciences Foundation, The Hague, 37-66.
- Van der Linden, W.J.M., and Van der Weijden, C.H., 1994. Geological study of the Arabian Sea. Netherlands Geosciences Foundation, The Hague, 66pp
- Van der Linden, W.J.M., W.J. Zachariasse, and C.H. Van der Weijden, 1994. The Arabian Sea Oxygen Minimum Zone (OMZ). In: *Geological study of the Arabian Sea*. W.J.M. van der Linden and C.H. van der Weijden, editors, Netherlands Geosciences Foundation, The Hague, 9-16.
- Van der Zwaan, G.J., Jorissen, F.J., and De Stigter, H.C., 1990. The depth dependency of planktonic foraminiferal ratios: Constraints and applications. *Marine Geology*, 95, 1-16.
- Van der Zwaan, G.J., and Jorissen, F.J., 1991. Biofacial patterns in river-induced shelf anoxia. In: *Modern and Ancient Continental Shelf Anoxia*. Tyson, R.V., and Pearson, T.H. (Eds.). Geological Society Special Publication, 58, 65-82.
- Van der Zwaan, G.J., Duijnste, I.A.P., den Dulk, M., Ernst, S.R., Jannink, N.T., and Kouwenhoven, T.J., 1999. Benthic foraminifers: proxies or problems? A review of paleoecological concepts. *Earth-Science Reviews* 46, 213-236.
- Van Dijken, G.L., and Arrigo, K.R., 1996. Ocean color remote sensing of the southeastern Mediterranean Sea. *EOS*, 76, 167.
- Villareal, T.A., 1991. Nitrogen-fixation by the cyanobacterial symbiont of the diatom genus *Hemiaulus*. *Mar. Ecol. Prog. Ser.*, 76, 201-204.
- Walton, W.R., 1952. Techniques for recognition of living foraminifera. *Contr. Cushman. Fnd. Foram. Res.*, 3, 56-60.
- Widbom, B., and Elmgren, R., 1988. Response of benthic meiofauna to nutrient enrichment of experimental marine ecosystems. *Marine Ecology progress Series*, 42, 257-268.
- Widbom, B., and Frithsen, J.B., 1995. Structuring factors in a marine soft bottom community during eutrophication - an experiment with radio-labelled phytodetritus. *Oecologia*, 101, 156-168.
- Wollenburg, J.E., and Kuhnt, W., 2000. The response of benthic foraminifers to carbon flux and primary production in the Arctic Ocean. *Marine Micropaleontology*, 40, 189-231.
- Wyrtki, K., 1973. *Physical Oceanography of the Indian Ocean*. In: *The Biology of the Indian Ocean*, ed. B. Zeitschel, 18-36, Springer, Berlin.
- Yacobi, Y.Z., Zohary, T., Kress, N., Hecht, A., Robarts, R.D., Waiser, M., Wood, A.M., and Li, W.K.W., 1995. Chlorophyll distribution throughout the southeastern Mediterranean in relation to the physical structure of the water mass. *Journal of Marine Systems*, 6, 179-190.
- You, Y. and M. Tomczak, 1993. Thermocline circulation and ventilation in the Indian Ocean derived from water mass analysis. *Deep-Sea Research I*, 40, 13-56.
- Zalesny, E.R., 1959. Foraminiferal ecology of Santa Monica Bay, California. *Micropaleontology* 5(1), 101-126.
- Zobel, B., 1973. Biostratigraphische Untersuchungen an Sedimenten des in-disch-pakistanischen Kontinentalrandes (Arabisches Meer). "Meteor" *Forsch.-Ergebnisse C*(12), 9-73.
- Zohary, T., and Robarts, R.D., 1998. Experimental study of microbial P limitation in the Eastern Mediterranean. *Limnol. Oceanogr.*, 43, 387-395.

Introductie en samenvatting

(Summary in Dutch)

Benthonische foraminiferen (Protista: Sarcodina) zijn eencellige organismen die wijdverspreid voorkomen in de oceanen. De schelpdragende soorten kunnen worden onderscheiden op basis van de morfologie van hun schelp. Doordat de meeste schelpen (langdurig) bewaard blijven na de dood van het organisme kunnen we ze terugvinden in zeer oude mariene afzettingen. Met voldoende inzicht in de ecologische achtergrond van de verschillende soorten, verkregen door onderzoek aan recente foraminiferen, zijn we in staat reconstructies te maken van fossiele mariene milieus.

Na decennia van ecologisch onderzoek aan benthonische foraminiferen zijn er nog steeds meer vragen dan antwoorden. Echter, door middel van experimenteel en (seizoenaal) veldwerk, zijn we de laatste jaren dichterbij antwoorden gekomen. Experimentele studies zijn voornamelijk van belang doordat ze de mogelijkheid bieden bepaalde variabelen constant te houden, terwijl veldwerk, indien uitgevoerd over een langere periode, belangrijke informatie verschaft over seizoensvariaties en ontwikkeling van de levensgemeenschappen onder natuurlijke omstandigheden. Naast verschillen in de tijd, geeft veldwerk inzicht in eventuele verschillen over afstand.

Tijdens het bestuderen van foraminiferen voorkomend in het noorden van de Adriatische Zee werden door de seizoenen heen grote verschillen gevonden in zowel de dichtheid als de verticale verdeling van foraminiferen over de sedimentkolom (Barmawidjaja et al., 1992). De combinatie van de hoeveelheid beschikbaar voedsel en het zuurstofgehalte in het sediment bleek van enorm belang voor de samenstelling van de foraminiferen associaties. Het in 1995 door Jorissen en anderen geïntroduceerde TROX-model beschrijft levensgemeenschappen van foraminiferen aan de hand van deze twee factoren, voedsel en zuurstof.

In 1996 werd een relatief grootschalig onderzoeksproject gestart met als doel de invloed van deze twee factoren op benthonische foraminiferen verder te doorgronden. Tijdens dit project werden twee heel verschillende gebieden in de Middellandse Zee bestudeerd, de voedselrijke (eutrofe) Adriatische Zee en het voedselarme (oligotrofe) Levantijnse Bekken. In het Levantijnse Bekken werd een stabiele omgeving verwacht, terwijl van de Adriatische Zee al bekend was dat er drastische verschillen in omgevingsvariabelen voorkomen gedurende het jaar. Door eerder uitgevoerd onderzoek was ook bekend dat deze veranderingen werden gereflecteerd in variaties in dichtheden van foraminiferen (Barmawidjaja et al., 1992). Om de seizoensvariatie binnen de levensgemeenschappen te kunnen bestuderen werden beide gebieden iedere twee maanden bezocht en bemonsterd in de periode van juni 1996 tot juni 1998.

In het Levantijnse Bekken werd een diepte-transect (van 40 tot 700m) loodrecht ten opzichte van de Israëliëse kust bestudeerd. Verscheidene oceanografische parameters (chlorophyll-a, temperatuur, saliniteit, en zuurstof) werden gelijktijdig gemeten met het bemonsteren van de sedimenten. Het zuurstofprofiel in de sedimentkolom werd gemeten met zeer nauwkeurige apparatuur, waarna het

sediment werd behandeld voor het bestuderen van levende (gekleurd met een kleurstof: Bengaals roze) foraminiferen.

De oceanografische gegevens die we tijdens de twee jaar van ons onderzoek verzameld hebben op stations S3 (120m) en S7 (400m) worden besproken in Hoofdstuk 2. De jaarlijkse afkoeling van het oppervlaktewater en de sterke wind gedurende het najaar, zorgen ervoor dat de bovenste waterlagen gemengd worden. Hierdoor worden voedingstoffen naar het wateroppervlak gebracht. De jaarlijkse cycliciteit in dit systeem resulteert in hoge primaire productie (chlorophyll-a) gedurende de herfst- en wintermaanden, met name gemeten op station S3. De concentraties van NO₃- en chlorophyll-a zoals die gemeten zijn gedurende twee jaar lieten een tegenovergesteld patroon zien. De ratio NO₃-/PO₄₃- varieerde sterk gedurende het jaar; de hoogste waarden werden gemeten gedurende de lente- en zomermaanden. In tegenstelling tot eerdere bevindingen, werd gevonden dat de oppervlaktewateren voor de kust van Israël niet fosfaat (P) maar stikstof (N) gelimiteerd zijn.

Een overzicht van de levensgemeenschappen van foraminiferen wordt gepresenteerd in Hoofdstuk 3. De aantallen levende foraminiferen per volume-eenheid waren het hoogst in het ondiepste station S1 (40m) en namen af met diepte. De verhoudingen in aantallen foraminiferen op de verschillende dieptes (40m, 120m, en 700m) waren 10:5:1.

In het ondiepste en diepste station werd een duidelijke seizoensvariatie in aantallen foraminiferen gevonden. Deze uitte zich in lage dichtheden van foraminiferen gedurende de herfst en het begin van de winter, en hoge dichtheden aan het eind van de winter en in de lentemaanden. Naast het verschil in dichtheden, werd er ook een duidelijk verschil in soortensamenstelling langs het diepte-transect gevonden. Hoewel de milioliden zeer veelvuldig aanwezig waren in het ondiepste station, namen ze duidelijk in aantal af met waterdiepte.

In Hoofdstuk 4 worden de faunapatronen in station S1 (40m) gecombineerd met de resultaten van de zuurstofmetingen en de organische verrijking van het sediment. De foraminiferen reageerden (vertraagd) op een verhoging in primaire productie. De verdeling van de foraminiferen over de sedimentkolom leek afhankelijk van de zuurstofconcentratie in het sediment, die sterk veranderde gedurende het jaar. De vertraging (2-4 maanden) in de numerieke respons van de foraminiferen na organische verrijking van het sediment werd waarschijnlijk veroorzaakt door de aanwezigheid van macrofauna (opportunistische kokerwormen). Deze waren zeer talrijk aanwezig na stijging van het organisch gehalte. Een toename van foraminiferen werd pas gevonden in de lente, na afsterving van de macrofauna.

De microhabitat verdeling van de meest voorkomende soorten foraminiferen wordt in detail besproken in Hoofdstuk 5. De levensstrategieën van de epifaunale soorten uitte zich in het dominant voorkomen aan het sedimentoppervlak en in een sterke numerieke reactie na organische verrijking van het sediment. De ondiep infaunale soorten (o.a. boliviniden) waren verspreid over de bovenste 2cm van de sedimentkolom en vertoonden een minder duidelijke reactie op voedselverrijking. De diep infaunale soorten bevonden zich voornamelijk in de diepere sedimentlagen, zelfs onder zuurstofloze omstandigheden. Hoewel voedselverrijking plaatsvindt aan het sedimentoppervlak reageerden sommige infaunale soorten duidelijk op verhoging van het voedselgehalte.

De microhabitat verdeling van de verschillende soorten in station S3 (120m) was veel minder

duidelijk dan die in station S1 (40m). In Hoofdstuk 6 wordt de verdeling van verscheidene soorten in station S3 besproken, in combinatie met de omgevingfactoren zuurstof en voedsel. Hoewel het mogelijk was een onderscheid te maken tussen epifaunale en diep infaunale soorten, kon er geen duidelijke ondiep infaunale groep worden onderscheiden. Dit werd waarschijnlijk veroorzaakt door het gemiddeld dieper doordringen van zuurstof. Er kon echter geen relatie worden gelegd tussen de diepteverdeling van de foraminiferen in de sedimentkolom en de zuurstofpenetratie in het sediment. Direct volgend op een periode van relatief voedselrijke omstandigheden, werd een toename van foraminiferen gevonden. In de sedimenten van station S3 werd bijna geen macrofauna gevonden. Door het jaar heen reageerden de epifaunale soorten sterk op voedselverrijking, terwijl de dieper infaunale soorten een stabielere dichtheidspatroon lieten zien. Sommige diep infaunale soorten (zoals *Eggerella* spp.) vertoonden wel een numerieke reactie op voedselverrijking. Wanneer we de resultaten van station S1 en station S3 combineren, vinden we sterke aanwijzingen dat deze soorten reproduceren aan het sedimentoppervlak, waarna ze zich opnieuw verspreiden door het sediment.

In Hoofdstuk 7 combineren we data van drie naast elkaar gelegen stations, gesitueerd op 120m waterdiepte. Het voornaamste doel hiervan was vast te stellen in hoeverre spatiele variatie in distributie een fenomeen is waar rekening mee gehouden dient te worden. Ook is het belangrijk een beeld te krijgen in hoeverre seizoensverschillen en verschillen in de micro-biotopen ("patchiness") doorwerken in het gemiddelde (jaarlijkse) faunasignaal. Hoewel de stations, door het jaar heen, redelijk grote verschillen in soortensamenstelling en dichtheden lieten zien, waren de gemiddelde aantallen van de meest voorkomende soorten heel vergelijkbaar voor de drie stations. Dit duidt erop dat, gemiddeld over een jaar, de levensgemeenschappen van foraminiferen in de drie stations min of meer hetzelfde zijn. Dit betekent dat verschillen op microschaal, die bestaan over een korte tijd, worden gereduceerd over een langere periode (b.v. jaar).

De levensgemeenschappen van foraminiferen in de noord Adriatische Zee worden vergeleken met die in het Levantijns Bekken in Hoofdstuk 8. Hoewel deze twee regio's zeer verschillen qua milieuomstandigheden (voedselrijk versus voedselarm) verschilden de dichtheden van foraminiferen niet substantieel. Dit duidt erop dat het voedselgehalte alleen niet bepalend is voor de aantallen benthonische foraminiferen per volume-eenheid. Waarschijnlijk worden de foraminiferen in beide marine systemen voornamelijk beïnvloed door de delicate balans tussen voedselgehalte en zuurstofconcentratie. Hoewel deels dezelfde soorten voorkomen, is de soortdiversiteit per station in het Adriatische Zee gebied veel lager dan de soortdiversiteit in het Levantijns Bekken. De seizoensvariëaties van de vijf meest voorkomende soorten lieten een duidelijke overeenkomst zien tussen beide gebieden. Het bleek dat de microhabitat verspreiding van de verschillende soorten niet zozeer afhankelijk was van hun omgeving maar dat deze inherent was aan de soort. Voor de meeste soorten gold, dat hun verdeling over de sedimentkolom onafhankelijk was van de zuurstofpenetratie in het sediment. Alleen de verdeling van milioliden over de sedimentkolom was duidelijk gecorreleerd aan het zuurstofgehalte.

Tijdens een experiment, uitgevoerd met fauna afkomstig uit het Levantijns Bekken, werd voedsel (algenmix) toegevoegd aan een deel van de experimentele opstelling terwijl het andere deel als blanco functioneerde (Hoofdstuk 9). Voorlopige resultaten duiden erop dat het toevoegen van voedsel geen stijging van aantallen foraminiferen tot gevolg had. Na grove berekening van de toegevoegde hoeveelheid organisch materiaal bleek dat deze waarschijnlijk lager was dan de hoeveelheid organisch

materiaal die na een piek in primaire productie op het sediment terecht komt. Dit zou kunnen betekenen dat de toegevoegde hoeveelheid voedsel niet hoog genoeg was om reproductie onder de foraminiferen te initialiseren.

In de Indische Oceaan (Pakistan) werden twee diepte-transecten bestudeerd, van 500m tot een waterdiepte van 1500-2000m (Hoofdstuk 10). De levensgemeenschappen van foraminiferen, gemonsterd op verschillende waterdieptes, verschilden erg van elkaar. Binnen de Zuurstof Minimum Zone werden de levensgemeenschappen van foraminiferen gekenmerkt door lage diversiteit en hoge aantallen. Met waterdiepte nam de diversiteit toe en de aantallen foraminiferen af. Langs beide transecten werden dezelfde soorten gevonden, in zowel de $>63\mu\text{m}$ als de $>150\mu\text{m}$ fractie. Het feit dat aanzienlijke hoeveelheden foraminiferen onder zeer lage zuurstofconcentraties en zelfs in zuurstofloze sedimenten leefden, geeft aan dat zuurstof voor sommige soorten geen beperkende factor is. Hoewel de hoge aantallen foraminiferen in de ondiepere stations verklaard kunnen worden door het hogere voedselgehalte op deze plekken, speelt de afwezigheid van predatoren in deze zuurstofloze sedimenten zeker ook een rol.

In Hoofdstuk 11 wordt een rekenkundige vergelijking gepresenteerd waarmee kwantitatieve reconstructies van zuurstofconcentraties kunnen worden berekend. Datasets van foraminiferen, verkregen door studies in vier heel verschillende mariene milieus (Golf van Biskaje, Indische Oceaan, Noord Adriatische Zee, Levantijnse Bekken) indiceren dat een specifieke groep foraminiferen zuurstofminnend is. De relatieve aantallen van deze soorten blijken lineair te correleren met de zuurstofconcentratie aan het sedimentoppervlak. Toepassing van de vergelijking op een historische record uit de Adriatische Zee resulteerde in een accurate reconstructie van de variatie in zuurstof op de zeebodem gedurende de laatste 160 jaar.

Dankwoord (Acknowledgements)

Ik zou graag iedereen willen bedanken die betrokken is geweest bij het onderzoek dat heeft geleid tot dit proefschrift. Als eerste ben ik veel dank verschuldigd aan mijn promotoren Professor Bert van der Zwaan en Professor Johan Meulenkamp voor het initiëren van dit onderzoek. Beide hebben me de mogelijkheid gegeven, binnen dit onderzoek, het grensvlak tussen de biologie en de geologie te verkennen. Mijn co-promotor dr. Ahuva Almogi-Labin wordt enorm bedankt voor haar participatie in het project en haar persoonlijke begeleiding.

Tijdens mijn studie in Nijmegen leerde ik Bert van der Zwaan kennen als een zeer enthousiaste overbrenger van kennis, niet alleen voor de collegebanken maar ook tijdens een zeer geslaagde excursie naar de Boulonnais (Noord-Frankrijk). De door hem opgewekte interesse voor het overgangsgebied tussen biologie en geologie resulteerde in een korte, interessante stage op foram-gebied. Toen hij eind 1995 vroeg, of ik trek zou hebben in een jaar foram-onderzoek te Utrecht, twijfelde ik dan ook geen moment. Het enthousiasme van de foram-groep in Utrecht werkte zeer aanstekelijk, binnen heel korte tijd was ik verkocht aan de wereld der foraminiferen. Ik heb Bert van der Zwaan leren kennen en waarderen als iemand met een enorm voorraadvat aan kennis, waaruit ten allen tijde getapt kan worden. Discussies over het werk werden vaak opgeluisterd door de tot de verbeelding sprekende anekdotes van zijn kant.

Toen ik juni '96 naar Israël afreisde om daar te beginnen met het veldwerk voor mijn promotieonderzoek stond Ahuva Almogi-Labin me vol enthousiasme op te wachten (ondanks 1,5 uur vertraging). Naast de theoretische kennis die ik van haar kado kreeg, heeft ze me tijdens de vaartochten altijd bijgestaan met raad en daad. Ahuva, thanks for your support throughout the years, thanks for the numerous discussions on science, for your effort during the cruises and for your hospitality, inviting me several times to stay over at your house.

Ivo Duijnste, degene met wie ik samen het foram-avontuur in de Middellandse Zee ben aangegaan (en op 2 mei zal afsluiten), wil ik bedanken omdat hij een geweldige collega is. Hij heeft altijd tijd voor anderen en is altijd te porren voor discussies over data en voor het uitleggen van ingewikkelde (vaak statistische) zaken. Ik verheug me daarom ook erg op de aankomende jaren van samenwerking! Tanja Kouwenhoven wil ik graag bedanken voor de ongelofelijk inzet en het enthousiasme waarmee ze zich door de teksten van mijn proefschrift heeft heen geworsteld. Deze kwamen enorm ten goede van het eindresultaat. Ook wil ik Tanja bedanken voor de interesse waarmee ze regelmatig informeerde "hoe het ermee ging". Sandra Langezaal bedank ik voor haar interesse en haar aandeel in mijn promotieonderzoek. Met veel plezier denk ik terug aan die keer dat ze me vergezelde tijdens een van de vaartochten. Ik ben blij dat Tanja en Sandra me willen bijstaan tijdens de verdediging van mijn proefschrift. Sander Ernst bedank ik als fijne collega en voor zijn (morele) steun tijdens de "laatste loodjes" (dmv icq-tjes). Het was heel prettig werken met deze club, en het is fijn te weten dat de samenwerking nog weer met 3 jaar verlengd is. Ik wil ook graag Maryke den Dulk bedanken, voor de jarenlange prettige samenwerking. We moeten nu echt snel weer eens wat afspreken. Jan-Willem Zachariasse en Gert-Jan Reichart worden bedankt voor hun samenwerking binnen het Indische Oceaan-project.

Naast mijn directe (foram) collega's wil ik graag Jan-Berend Stuut, Maarten Prins, Hayfaa Abdul Aziz, Joris Steenbrink, overige collega's en ex-collega's en de vaste staf van de afdeling Stratigrafie & Paleontologie (IvA, Utrecht) bedanken voor de gezellige werksfeer. Henko de Stigter

wordt bedankt voor het enthousiasme waarmee hij me wegwijst in de wereld van roze gekleurde forams. Gerrit van 't Veld en Geert Ittman wil ik bedanken voor het "microscopisch-klaar" maken van de sedimentmonsters, vooral omdat deze vermengd waren met een smerige oplossing van kleurstof in alcohol. Wil den Hartog bedank ik voor het maken en bewerken van foto's en Paul van Oudenallen (AV-Dienst) wil ik graag bedanken voor de opmaak van dit boekje. De mensen die als student een belangrijke bijdrage hebben geleverd aan het onderzoek; Kees Hordijk, Jeroen Reiniers, en Marijke van Kuijk, wil ik graag bedanken voor hun inzet en de prettige samenwerking.

De collega's in Nijmegen (KUN); Lex Kempers en de collega's van de afdeling Experimentele Plant-Oecologie, wil ik met name bedanken voor de morele steun tijdens de koffie/thee-pauzes gedurende de laatste maanden van mijn promotieonderzoek. Huub Geurts wil ik graag bedanken voor zijn hulp en uitleg bij het maken van SEM-foto's.

I would like to thank the captains and crew of the R/V Shikmona for their help and support during the cruises. Special thanks I owe to Barak Herut (Israel Oceanographic and Limnological Research, Haifa) who organised the cruises very adequately and was always prepared to help out with the "foram-work", while being also responsible for the measurements of the oceanographic properties (see Chapter 2). Efrat, Yaron, Isaac, Edna and Daniella are thanked for their help, support and happy company during the cruises. Also Yacov Rafael (GSI, Jerusalem) is thanked for his support during the cruises. Whereas I do not have "sea-legs", the sea has been good to me and made it possible to enjoy the cruises together with the people mentioned above. To all of you: "Toda raba" (thanks very much).

Mijn familie en vrienden wil ik bedanken voor hun morele steun en belangstelling. Mijn moeder wil ik bedanken voor haar steun, haar interesse, en het voortdurende stimuleren in het maken van die keuzes die mij belangrijk leken. Aan haar zou ik dit boekje willen opdragen.

Mijn zus Belinda wil ik bedanken voor haar belangstelling en steun tijdens mijn onderzoek, en voor de regelmatige afleiding in de vorm van sporten (en winkelen). Mijn vriendin Petra ter Brugge bedank ik voor de leuke en interessante uren waarin we ons onderzoek bespraken (soms onder het genot van een Rodenbach), en haar bemoediging en steun gedurende de afrondingsfase van het proefschrift.

Als laatste wil ik Christian bedanken, als belangrijk rust- en steunpunt door de jaren heen. Zijn voortdurende aan- en bemoediging en zijn onverstoortbaar vertrouwen in mij als "onderzoekster" hebben me enorm gestimuleerd. Hoewel ik een grote kans loop cliché te worden: Chris heel erg bedankt, zonder jou had ik deze kar niet kunnen/willen trekken.

I would like to thank the members of the dissertation committee, Prof. Dr. P.L. de Boer (Faculty of Earth Sciences, Utrecht University), Dr. A. Gooday (Southampton Oceanography Centre), Prof. Dr. C.H.R. Heip (NIOO-Centre for Estuarine and Coastal Ecology, Yerseke), Dr. F.J. Jorissen (Department of Geology and Oceanography, Bordeaux University), and Prof. Dr. H. Visscher (Faculty of Biology, Utrecht University), for thorough reading of the manuscript and for valuable suggestions.

Curriculum vitae

Natasja Tamara Jannink werd geboren op 29 januari 1972 te Hellendoorn. In 1990 behaalde zij het diploma voor het Voortgezet Wetenschappelijk Onderwijs aan het Pius X College te Almelo. In datzelfde jaar werd de studie Biologie begonnen aan de Faculteit Natuurwetenschappen van de Katholieke Universiteit Nijmegen. Na het behalen van het doctoraalexamen Biologie in maart 1995, werd ze aangesteld als toegevoegd onderzoeker op de afdeling Stratigrafie & Paleontologie, Faculteit Aardwetenschappen (UU). Van mei 1996 tot mei 2001 was zij werkzaam als onderzoeker in opleiding op deze afdeling en de afdeling Biogeologie, Faculteit Natuurwetenschappen (KUN). Vanaf mei 2001 zal ze werkzaam zijn als postdoc op dezelfde Faculteiten in Nijmegen en Utrecht.