GEOLOGICA ULTRAIECTINA

Mededelingen van de Faculteit Geowetenschappen
Universiteit Utrecht

No. 286

The dynamic balance between food abundance and habitat instability: benthic foraminifera of Portuguese margin canyons

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Thesis layout: GeoMedia, Faculty of Geosciences, Utrecht University

ISBN 978-90-5744-151-6

The dynamic balance between food abundance and habitat instability: benthic foraminifera of Portuguese margin canyons

Het dynamisch evenwicht tussen voedselrijkdom en habitat instabiliteit: benthische foraminiferen uit onderzeese canyons voor de Portugese kust

(with a summary in English)

PROEFSCHRIFT

ter verkrijging van de graad van doctor aan de Universiteit Utrecht op gezag van de rector magnificus, prof. dr. J.C. Stoof, ingevolge het besluit van het college voor promoties 29 februari 2008 des middags te 14.30 uur

door

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geboren op 15 april 1979

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Contents

CHAPTER 1

Introduction

Benthic foraminifera are single celled protists which carve out an unlikely existence in one of Earth's least visited or understood habitats. Their home is the sediment accumulating on the world's ocean floors. Their sustenance is derived from the scraps of organic material which slip through the net of the marine pelagic food web, and their distribution is surprisingly broad. 'Forams' are found in seafloors warm and cold, shallow and deep, teeming with life or seemingly bereft of it. They were first described in 1700 by Dutch microscopist Antoine van Leeuwenhoek, who noted a creature ¨no bigger than a sand grain¨ in size, and in appearance not unlike ¨very little snail shells¨. Three centuries on, this simple description is the one I often still use when explaining to friends and family what I have been studying for the past four years.

Since the 1700s, however, our knowledge of these organisms has advanced a great deal, and it has become evident that the small bugs that look like snails actually have relatives in various shapes and sizes, measuring anything from tens of microns to several centimetres across. The shape of the shells, or tests as they are more commonly called, varies from a single chambered round sphere or an elongated tube, to more complicated spiral arrangements of multiple chambers. Today around 2140 species of benthic foraminifera have been recognised, the majority living on the sea floor, however a few have been discovered in fresh water (Holzmann and Pawlowski, 2002) and even in damp terrestrial environments (Meisterfeld et al., 2001).

Benthic foraminifera have been extensively studied by geologists due to the good fossilisation potential of their tests, which are composed of calcium carbonate or an 'agglutinated' bundle of mineral grains, and their abundant occurrence in marine sediments. Traditionally geologists have used changes in foraminiferal assemblages as stratigraphic markers without investigating the causes of such ecological shifts. However during the second half of the 20th century Fred B Phleger pioneered research into foraminiferal ecology, and accordingly it was understood that the modern foraminiferal distribution can be used as an analogue for the past distributions recorded in sediments. From this point, the organisms took centre stage in the science of palaeoclimatology – the interpretation of Earth´s climate history. Due to the inaccessibility of deep-sea environments, the ecology of foraminifera remains only partially understood, and many questions regarding the control of the distribution pattern of species remain open. However, during the last decade experimental and field studies have brought about many advances, such as the conceptual Trophic Oxygen model (TROX, Jorissen et al., 1995) which relates species distribution to the availability of food and oxygen. More recently the potential importance of benthic foraminifera in the global nitrogen cycle was discovered, when denitrification through an intracellular nitrate pool was observed in *Globobulimina pseudospinescens* (Risgaard-Petersen et al., 2006).

This thesis focuses on the distribution of benthic foraminifera in submarine canyons, which are dynamic sedimentary environments. Canyons, or deep chasms that cut across the sea bed, can act as under-water rivers transporting large quantities of sediment from the continental shelf towards the abyss. The sediment transport in canyons takes place in the form of gravity flows and/or turbidite currents. On their way the sediment mass flows scour the sea bed swiping away the top sediment and exposing previously covered sea floor. At their end destination, sediment is dumped and the previously existing sediment-water interface is sealed. Due to the active nature of these environments, organisms living in canyons must have adapted to the prevailing conditions, and thus the presence of highly specialised faunal assemblages may be anticipated. The canyon activity, however, may differ in time and space, thus during a dormant period more stable ecosystems can develop.

The foraminiferal and metazoan meiofaunal assemblages living in the Nazaré submarine canyon, located on the central Portuguese margin, are investigated in **Chapter 2.** A comparison with the adjacent slope communities revealed that the active sedimentary regime in the canyon may suppress foraminiferal numbers despite the higher food availability in the canyon than in the open slope environment. In the upper canyon axis a specialised nematode assemblage was discovered, consisting of *Sabatieria* sp. and *Metalinhomoeus* sp. These taxa have been previously described to inhabit environments with high sedimentary organic matter content (e.g Jensen et al., 1992; Hendelberg and Jensen 1993; Lampadariou et al., 1997) and areas disturbed by sediment dredging (e.g. Boyd et al., 2000).

The foraminiferal community structure in the Nazaré Canyon was further investigated in **Chapter 3**. A comparison was made between the frequently disturbed upper and middle canyon axis, and the low energy terraces and the lower canyon stations. The ecosystems on the canyon terraces were well-developed. In contrast, the canyon thalweg, experiencing frequent gravity flows and resuspension of surface sediment was found to be nearly barren. An interesting foraminiferal assemblage dominated by the genus *Technitella* spp., however, was found living in the upper canyon axis together with the specialised nematode species mentioned above. It was concluded that *Technitella* spp. can be regarded as a highly opportunistic recoloniser, indicating disturbed environments, high sedimentation rates, resuspension of surface sediments and fast current speeds.

Canyon sediments generally contain higher quantities of organic carbon than the adjacent slope environments. To investigate the influence of organic carbon enrichment on benthic foraminifera, a laboratory mesocosm experiment was set up, described in **Chapter 4**. A diatom bloom was simulated

under controlled laboratory conditions and the response of benthic foraminifera was monitored over time. Following the food impulse the number of foraminifera was observed to increase; the highest numbers coinciding with the highest food load. The distribution of infaunal species (species typically inhabiting relatively deep sediment units, close to the oxygen penetration depth in sediment), however, was not observed to change after the food impulse. Therefore, it seems that their in-sediment distribution is more controlled by redox processes or associated bacterial communities.

The field distribution of benthic foraminifera in relation to pore water redox chemistry (nitrate used as an indicator) and food availability (CPE, or chloroplastic pigment equivalents used as a measure for labile organic matter) was investigated in the Lisbon-Setúbal Canyon and along the adjacent open slope in **Chapter 5**. The studied regions, canyon and slope, were expected to provide an environmental range in the parameters of interest. A consistent relationship was found between the foraminiferal assemblages, labile organic matter content and sedimentary redox conditions, in accordance with the TROX model. Sediments rich in labile organic matter (CPE > 20 μg/cm^3) and with shallow nitrate penetration depth (~ 1.0 cm) were dominated by deep infaunal foraminifera (e.g. *Chilostomella oolina* and *Globobulimina* spp.). Once the nitrate penetration depth increased to two centimetres depth, shallow infaunal foraminifera including *Uvigerina* spp. became abundant. At the abyssal station, where nitrate penetration depth exceeded 5 cm and the surficial CPE content was very low (< 2 μg/cm^3), the only calcareous species found in relatively abundant numbers was *Nuttallides umbonifera*.

The majority of this thesis concentrates on investigation of modern foraminifera. In **Chapter 6**, however, the knowledge gained on living canyon foraminifera was applied to a paleo-record, dating back to the last glacial period. Two sedimentologically contrasting sites were chosen from the lower Nazaré Canyon, one experiencing significantly higher sediment accumulation rates and terrigenous input from the canyon (the northern bank) and the other more hemipelagic sedimentation (the southern bank). The contrasting sedimentary regimes, and especially the elevated accumulation of terrigenous sediments on the northern levee, were expected to be impressed in the foraminiferal assemblage.

The results of this thesis work are summarised in **Chapter 7**.

CHAPTER 2

Distribution of meiobenthos in the Nazaré canyon and adjacent slope (western Iberian Margin) in relation to sedimentary composition

Published as:
R. García, K.A. Koho, H.C. De Stigter, E. Epping, E. Koning, L. Thomsen (2007) Distribution of meiobenthos in the Nazaré canyon and adjacent slope (western Iberian Margin) in relation to sedimentary composition. Marine Ecology Progress Series 340, 207-220.

ABSTRACT

Abundance of metazoan meiofauna and foraminifera, and biomass and community structure of nematodes were investigated in the benthic zone along the Nazaré Canyon and adjacent continental slope in relation to concentration of organic matter and its suitability as a food source for the meiobenthos. The Nazaré canyon sediments were richer in organic carbon (C_{org}), total nitrogen, and phytopigments than the adjacent open slope. In addition, phytodetritus was fresher in the canyon sediment than on the slope (higher chlorophyll *a*: phaeopigments). Nevertheless, the abundance of polychaetes, copepods, bivalves, nematodes, total metazoans, and nematode biomass were not always higher in the canyon than on the adjacent open slope. Lower densities occurred in the upper and middle canyon, and living benthic foraminifers were significantly more abundant on the adjacent slope. The stations in the upper and middle canyon contained infinitesimal numbers of foraminifers. Reduced diversity and evenness and high *K*-dominance of the nematode assemblages in the upper part of the canyon indicated environmental stress, perhaps related to high C_{org} content and sediment disturbance. Non-selective deposit-feeders dominated the nematode assemblages of the upper and middle parts of the canyon, whereas a more diverse trophic structure was found in the deeper parts and the open slope. Conditions in the upper and middle areas of the Nazaré canyon are harsh, and only opportunistic organisms can survive there.

2.1 INTRODUCTION

Deep gullies and submarine canyons run perpendicular to the shoreline and can dissect the entire continental shelf and slope. Canyons can trap part of the suspended particulate organic matter transported along the continental margin, and serve as conduits for organic particles and sediments from the shelf and upper slope to the deep sea (Van Weering et al. 2002). Therefore, they represent areas of high sedimentary organic carbon (C_{org}) content and relatively high biochemical activity (Epping et al. 2002). Furthermore, some submarine canyons are very unstable environments, since tidal currents, episodic slumps and turbidity flows periodically transport sediments and organic particles into the canyon system (Puig et al. 2004). Currents inside canyons can reach velocities of 2 m s^{-1} (Vetter and Dayton 1998).

In the Nazaré canyon, sediments and fine particles are actively transported in nepheloid layers, and high sedimentation rates occur especially in its upper and middle regions (Van Weering et al. 2002). In the canyon, detritus of terrigenous origin predominates over pelagic detritus, and there is a higher C_{org} content than in the open continental shelf and slope (Epping et al. 2002, Van Weering et al. 2002). Enhanced remineralisation rates have been shown as a result of enrichment with C_{org} (Epping et al. 2002).

Meiofaunal communities are responsible for a significant amount of sediment remineralisation and support significant trophic pathways (Leguerrier et al. 2003). According to Tietjen (1992), on average, bacteria comprise 86%, macrofauna 7% and meiofauna 5% of living carbon in deep-sea sediments. Hence, despite comprising a relatively minor component of the living carbon compared to bacteria, macro- and meiofauna play an important role in the total carbon turnover of deep-sea environments. The meiofauna communities in the Nazaré canyon have rarely been studied: a few records of metazoan meiobenthos are available for the Western Iberian Margin (see Soltwedel 2000, Flach et al. 2002), while Flach (2003) reported very high densities of meiofauna in the canyon at all depths.

Benthic animal communities from canyon systems can reflect the unstable and organically enriched conditions of these systems. Indeed, the fauna communities inhabiting submarine canyons have been found to differ in structure from those on adjacent abyssal plains, continental shelf, or slope. Faunal densities and biomasses in canyon systems have been found to be higher (e.g. Gage et al. 1995, Vetter and Dayton 1998, Duineveld et al. 2001) and faunal diversities lower (e.g. Gage et al. 1995, Vetter and Dayton 1998, Curdia et al. 2004) than in adjacent habitats. These differences in faunal structure have been attributed to the higher organic content of canyon systems (see Gage et al. 1995, Duineveld et al. 2001). However, there are indications that abundances can also be lower in canyons than in adjacent areas (see Maurer et al. 1994); this could be related to factors other than the high C_{org} content of these systems.

In the Nazaré canyon, Flach (2003) reported lower numbers of macrofauna than on the Iberian continental slope. Polychaetes dominated the macrofauna in this canyon, and opportunistic polychaete communities occurred in regions with high organic matter content (Flach 2003, Curdia et al. 2004). Furthermore, macrofauna biomass in the canyon increases with increasing C_{org} fluxes (Flach 2003).

The present study investigated changes in the composition of meiofaunal assemblages along a depth gradient in the Nazaré canyon and the adjacent open slope. Organic matter concentrations and lability were also studied to investigate whether the content and freshness of the sedimentary organic matter in the canyon were the main driving factors controlling the meiobenthic community.

2.2 MATERIALS AND METHODS

2.2.1 Study area

The Nazaré canyon is the largest canyon on the Western Iberian Margin, and intersects the entire continental shelf (Vanney and Mougenot 1981). Inside the canyon there is a strong internal tide circulation of water, with velocities of up to 15 cm s^{-1} (Coelho et al. 2003). Sediment transported over the shelf and upper slope by alongshore currents is temporarily deposited in the very narrow upper and middle part of the canyon, until it is further transported to the deep sea in nepheloid layers or flushed down canyon by turbidite currents (Van Weering et al. 2002, Garcia et al. 2003).

The hydrography of the shelf is dominated by a poleward current in winter and an equatorward current during summer (Vitorino et al. 2002a, Coelho et al. 2003). The poleward current favours downwelling, while the equatorward current is generally associated with coastal upwelling, which triggers high primary production along the Iberian Margin (Vitorino et al. 2002a).

The canyon is characterised by a well-stratified water column. North Atlantic Deep Water (NADW) with temperatures of 2 to 7°C and salinities of 34.8 to 35.6 ppm is present between depths of approximately 2000 and 3000 m water depths (Garcia et al. 2003). Between approximately 600 and 1500 m, Mediterranean water is present, with temperatures of 8 to 13°C and salinities of 35.8 to 36.2 ppm. Temperatures of 14 to 18°C and salinities of 35.4 to 35.8 ppm characterise the upper water layer.

2.2.2 Sampling

Sediment cores for meiofauna and physicochemical analyses were collected in May 2004 during Cruise 64PE225 of the RV 'Pelagia'. For this study we analysed data from 8 stations located along a depth gradient in the Nazaré canyon axis (S41, S26, S34, S24 and S22) and adjacent open slope (S39, S27 and S25) (Figure 2.1). Sediment samples for physicochemical and faunal analyses were taken with the MUC 8+4 multiple corer developed by Octopus GmbH. This corer has an array of eight 6 cm diameter and four 10 cm diameter coring tubes, 61 cm in length. For each station, three 10 cm multicorer tubes were used for metazoan analysis, one 10 cm tube for sedimentological analysis, three 6 cm tubes for phytopigment analysis, and one 6 cm tube for foraminifer analysis. From a second deployment, four 6 cm tubes were used for analysis of total and organic C and N. Cores were stored at in situ temperature in a temperature-controlled room and processed within 3 h of collection.

The sediment samples for phytopigment, total and organic C and N analysis were stored at -20°C until analysis; 4 to 6 replicate sub-cores were taken from the core tubes for metazoan analysis using 60 ml syringes with cut-off anterior ends. These sediment samples were preserved in 4% buffered formaldehyde solution. The sediment samples from the core used for analysis of foraminifers were preserved in 96% ethanol solution with Rose Bengal. Only the upper 5 cm of the cores were used in this study.

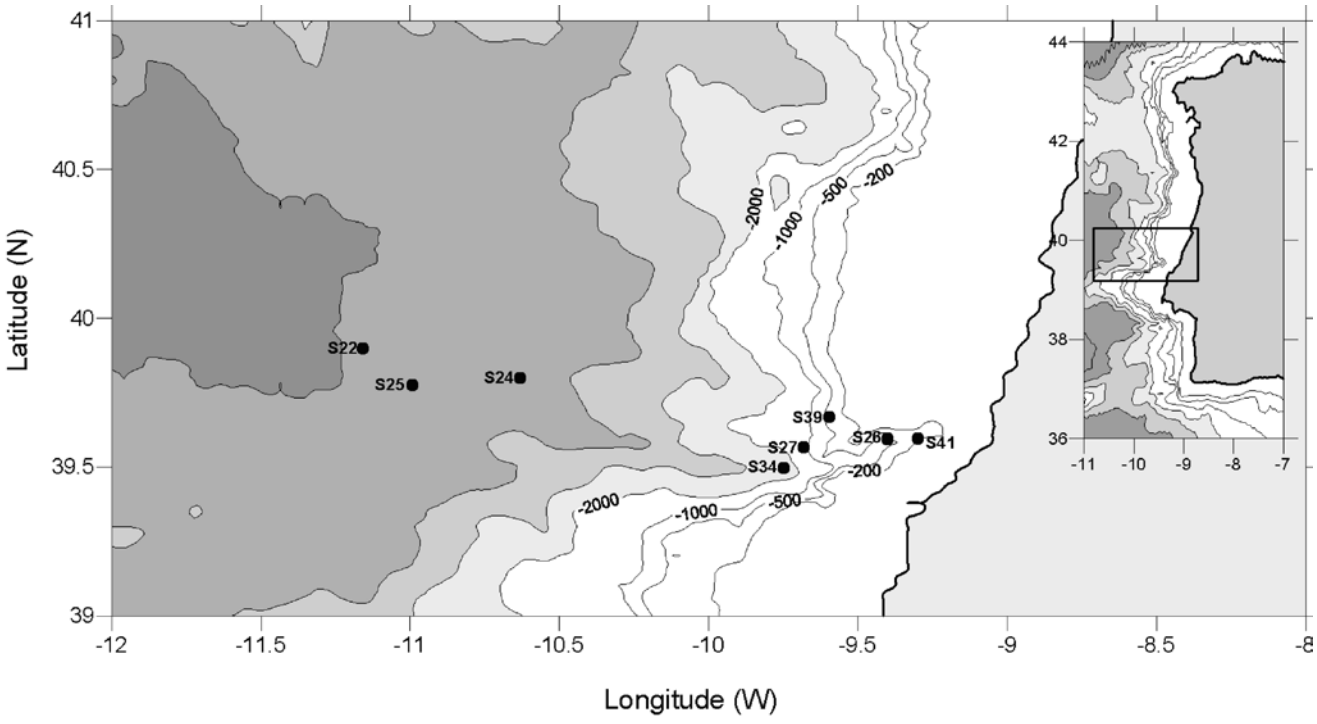


Figure 2.1. Nazaré canyon showing stations sampled during cruise 64PE225

2.2.3 Grain-size analysis

Sediment samples were freezedried, and then crumbled and mixed. Subsequently, ~100 mg of sediment was dispersed in water, applying ultrasound for mechanical dispersal but without addition of chemical dispersatives. The dispersed sediment was then introduced into a Coulter LS 230 laser particle-sizer for determination of particle size spectra.

2.2.4 Geochemical analysis

Phytodetritus input to the seafloor was assessed by fluorometric measurement of sediment-bound chlorophyll *a* (chl *a*) and phaeopigment (phaeo) concentrations following the method of Yentsch and Menzel (1963). Sediment samples were first freeze-dried and homogenised in a mortar. Pigments were subsequently extracted in 10 ml 90% acetone solution and measured in a Turner fluorometer following Shuman and Lorenzen (1975). The bulk of pigments measured with this method were termed 'chloroplastic pigment equivalents', CPE (Thiel 1978). Chl *a* versus phaeo concentrations were used to assess the fresh organic matter of photosynthetic origin that reached the seafloor.

Sediment total carbon, total nitrogen (TN) and C_{org} were measured using a Thermo Finnigan flash element analyser following the procedures described by Lohse et al. (2000).

2.2.5 Meiofauna analysis

In the laboratory, sediment samples for metazoan investigations were washed through a 48 µm sieve and metazoans were extracted using Ludox (colloidal silica polymer) diluted in water to a specific gravity of 1.209 (Ólafsson and Elmgren 1997). The metazoans were counted and identified to major taxa in a Petri dish under a stereomicroscope. All the nematodes were picked and put in a watch glass with a glycerine solution (5% glycerine, 5% pure ethanol and 90% distilled water). After 24 h at 50°C, the nematodes were mounted on micro-slides, using anhydrous glycerine as mounting medium, for identification to genus under a compound microscope. To estimate nematode biomasses, nematode length (excluding filiform tails) and width were measured by the semiautomatic images system (analySIS®2.1) at the Alfred Wegener Institute. Nematode volume and biomass (wet weights) were calculated using Andrassy's (1956) formulas. Nematode wet weights were then converted into carbon biomass assuming that 100% wet weight corresponds to 12.4% carbon weight (Jensen 1984). Nematode feeding types (1A, 1B, 2A and 2B) were determined after the classification provided by Wieser (1953).

Sediment samples for investigations of foraminifers were washed through 150 and 63 µm sieves. Only the 150 µm fraction was used for this study. Well-stained foraminifers were counted in a Petri dish under a stereomicroscope, and transferred to Chapman slides for identification. For the quantification of arborescent foraminifers (a type of branching agglutinant foraminifer), a standard minimum size of 1.5 ± 0.1 mm was adopted because these foraminifers can easily break apart when sorting. The estimate of total individuals thus included fragments of various sizes.

2.2.6 Data analysis

Shannon-Wiener diversity index *H'* (Krebs 1989), evenness *J'* (Pielou, 1969) and *K*-dominance curves (Lambshead et al. 1983) were calculated for the nematode assemblage at each site.

Univariate 2-way ANOVAs were used to investigate differences in faunal abundance, nematode biomass, diversity and evenness between the 2 locations (i.e. canyon vs. open slope) and between different water depths. A nested design was constructed with depth nested within location. A 1-sample Kolmogorov-Smirnov test was used to check the normality of the taxa counts, nematode biomass data and ecological indices. The data was not normally distributed, and was therefore $\log_2$ (x + 1)-transformed prior to ANOVA analysis. To test for possible relationships between the various meiofaunal and geochemical parameters and for possible differences between the Nazaré canyon and the adjacent open slope, 2 non-parametric correlation analyses were performed; one with canyon data the other with open slope data. The Kendall's tau statistic from the statistical package SPSS 12.0 was used, as this is extremely conservative, with a low number of measurements.

Stn	Latitude (°N)	Longitude (°W)	Depth (m)	Clay (% vol)	Silt (% vol)	Sand (% vol)	CPE (µg 5cm^{-3})	chl *a*:phaeo	TN (%)	C_{org} (%)	C:N
Canyon											
S41	39° 34.8′	9° 09.2′	354	7.72	78.87	13.42	89.1	0.09	0.22	1.73	9.0
S26	39° 35.9′	9° 23.9′	1121	5.06	42.036	52.89	92.4	0.18	0.19	1.78	10.9
S34	39° 30.0′	9° 45.0′	2847	6.02	44.63	49.38	48.6	0.03	0.20	1.86	10.9
S24	39° 48.0′	10° 37.9′	4810	13.21	73.63	13.18	13.9	0.03	0.15	1.54	12.1
S22	39° 53.9′	11° 10.0′	4969	14.06	81.18	4.75	5.7	0.03	0.14	1.52	12.5
Open slope											
S39	39° 39.9′	9° 35.9′	300	4.89	29.58	65.54	22.3	0.02	0.04	0.30	8.5
S27	39° 33.9′	9° 40.9′	1000	15.31	71.32	13.36	9.4	0.03	0.13	1.02	8.9
S25	39° 46.5′	10° 59.9′	4798	23.62	75.21	1.18	1.7	0.02	0.09	0.54	7.0

Table 2.1. Sediment granulometry (clay = <2 µm, silt = >2 to <63 µm, sand = >63 µm), concentrations of chloroplastic pigments equivalents (CPE), total nitrogen (TN), organic carbon (C_{org}), chlorophyll *a*: phaeopigment ratio (chl *a*:phaeo), and carbon to nitrogen molar ratio (C:N) for top 5 cm of sediment at each station as a function of water depth

2.3 RESULTS

2.3.1 Sediment granulometry

Sediments in the canyon were predominantly muddy (silt and clay), except at Stns S26 and S34 (Table 2.1), where silt and clay comprised only about 50% of the sediment, with the other 50% consisting of sand, and the finer material occurring in the top centimetres. On the open slope, sediments became muddier with increasing water depth. In the shallow open slope station (S39), about 35% of the sediment particles were silt and clay, whereas in the deepest open slope (S25) station about 98% of the sediment particles were silt and clay.

2.3.2 Geochemical characteristics of sediments

The canyon sediments were organically enriched compared to the adjacent open slope (Table 2.1), containing higher CPE, a measure of phytodetritus content. The upper part of the canyon (Stns S41 and S26) had the highest CPE values, which decreased with increasing water depth. Furthermore, the quality of the phytodetritus was highest in the upper part of the canyon (Stns S41 and S26) (chl *a*:phaeo = 0.09 to 0.18), and TN and C_{org} contents were also higher in the canyon, especially in the upper and middle parts (Stns S41, S26 and S34). The canyon detritus had a higher proportion of terrigenous organic matter (C:N = 9 to 12.5) than open slope detritus.

On the open slope, CPE values were low, decreasing with increasing water depth. The quality of the phytodetritus was low and similar to the quality at the middle and deeper parts of the canyon. TN and C_{org} contents were lower than in the canyon, and the detritus had a higher proportion of organic material of pelagic origin (C:N = 7 to 8.9).

2.3.3 Meiofauna

We identified a total of 12 major taxa within the 2 study areas. Nematodes were the most abundant group within the canyon and the adjacent open slope, comprising between 40 and 90% of total metazoan abundance (Figure 2.2). Copepods were the second most abundant group in both study areas, comprising between 10 and 40% of total metazoan abundance, followed by polychaetes. Bivalves were more abundant in the canyon stations, but in low percentages, except at Stn S34. Amphipoda, Cumacea, Decapoda, Ostracoda, other Crustacea, Kinorincha and Halcaroidea occurred occasionally and in very low numbers, being insignificant in terms of abundance. On average, these taxa together represented about 1 to 2% of the total meiofauna. These taxa will not be analysed below in more detail.

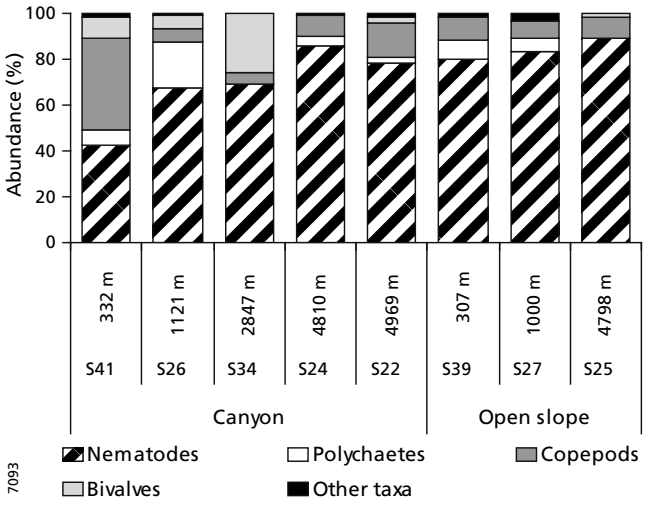


Figure 2.2. Relative abundance of nematodes, polychaetes, copepods, bivalves and minor taxa along a depth gradient at Stns S41, S26, S34, S24, S22, S39, S27 and S25 in Nazaré canyon and on adjacent open slope

Foraminiferal abundance is not expressed as a percentage of total meiofauna because foraminifers were only investigated in the >150 µm fraction, the >48 µm fraction being used to examine metazoans abundance.

Foraminifera

Low to insignificant numbers of foraminifers were recorded in the upper and middle canyon (Figure 2.3a). The highest total standing stocks were found in the deep canyon station, S24. Below this station the system widens into a fan, and foraminifer abundances here were similar to those on the nearby slope. In contrast, high total standing stocks of foraminifers were recorded along the open slope, displaying a clear decreasing trend with increasing water depth.

Elevated numbers of arborescent foraminifers (branching agglutinant) were observed in the open slope sediments, most being recorded at Stn S27 (Figure 2.3b). In the canyon arborescent foraminifers were almost completely absent, with the exception of Stn S22 at the lower end of the canyon.

In general, the canyon stations were dominated by agglutinated foraminifers (Figure 2.3c), representing between the 60 and 80% of all individuals; the only exception being Stn S34, where >80% of the assemblage comprised calcareous foraminifera. At the head of the canyon (Stn S41), calcareous and agglutinated foraminifers were present in similar numbers. At the open slope stations, arborescent, calcareous and agglutinated foraminifers were well represented. Agglutinated foraminifers dominated at the shallow open slope station accounting for 70% of total foraminifers abundance. At 1000 m (Stn S27), calcareous and arborescent foraminifers were numerically dominant (80% of all individuals). The deepest site was numerically dominated by arborescent foraminifers (>60% of all individuals).

Metazoans

On the open slope, the abundance of most taxonomical groups and also nematode biomass decreased with increasing water depth (Figure 2.4a,b,c,e,f). In contrast, in the canyon no clear decrease was observed. Stn S26 at 1121 m contained the highest abundance of most taxonomical groups and also the highest nematode biomass (Figure 2.4a,b,d,e,f). The only depth-related pattern in the canyon was that the highest abundance of taxa and highest nematode biomass occurred in the upper part of the canyon (Stns S41 and S26).

Statistically, there were significant inter-station differences in the abundances of metazoans and nematode biomass as a function of depth at each location (canyon and open slope) (all $p \leq 0.001$, Table 2.2). There were also significant differences in the mean abundance of nematodes and bivalves between the canyon and the slope ($p \leq 0.004$ and $p \leq 0.001$ respectively, Table 2.2). Mean abundance of nematodes was lower in the canyon than on the slope (53.5 ± 21.1 ind. 10 cm^{-2} and 73.1 ± 16.4 ind. 10

cm^{-2}, respectively, mean ± SE), and mean abundance of bivalves was higher in the canyon (4.6 ± 2.6 ind. 10 cm^{-2} and 0.2 ± 0.2 ind. 10 cm^{-2}, respectively).

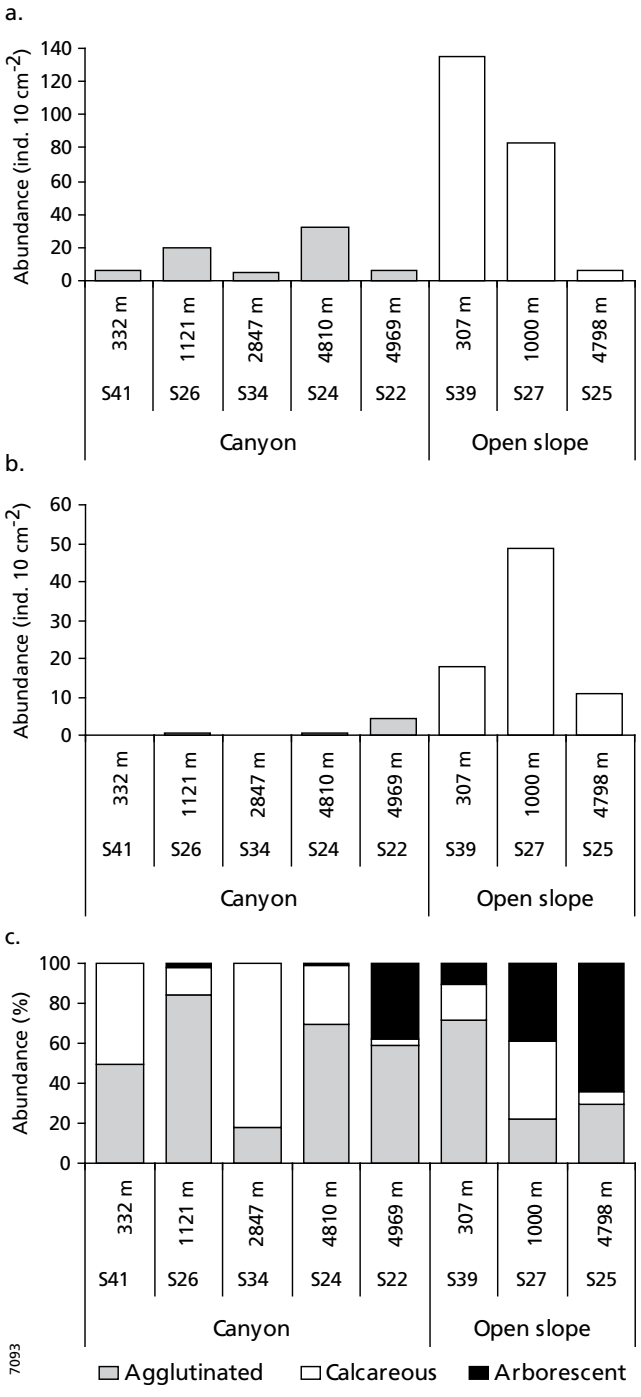


Figure 2.3. (a,b) Abundance of total standing stock of (a) agglutinated and calcareous foraminifers and (b) arborescent foraminifers, and (c) relative abundance of agglutinated, calcareous and arborescent foraminifers, along bathymetric gradient and at Stns S41, S26, S34, S24, S22, S39, S27 and S25 in the Nazaré canyon and on adjacent open slope (n = 1, data from one replica)

Parameter	Location		Depth(Location)	
	F	p ≤	*F*	p ≤
Total meiofauna	3.249	0.081	14.410	0.001
Polychaeta	0.444	0.510	22.744	0.001
Nematoda	9.606	0.004	11.548	0.001
Copepoda	0.119	0.732	12.941	0.001
Bivalvia	24.514	0.001	8.775	0.001
Nem. Biomass	1.866	0.181	8.724	0.001
Diversity (*H'*)	52.189	0.001	11.247	0.001
Eveness (*J'*)	5.735	0.023	2.335	0.065

Table 2.2. Results of univariate 2-way nested ANOVA; df = 1 and 5 for Location and Depth(Location) respectively. Nem.: nematode

Nematode assemblage

A total of 85 genera of nematodes were recorded (Table 2.3). For the canyon a total of 55 genera was recorded, of which only 3 (*Metalinhomoeus, Sabatieria* and *Sphaerolaimus*) were present at all canyon stations and 16 genera were exclusively present in the canyon. The open slope had a total of 68 genera, of which 11 (*Acantholaimus*, *Camacolaimus*, *Cervonema*, *Halaimus*, *Marylinia*, *Metalinhomoeus*, *Neochromadora*, *Paralongicyatholaimus*, *Sabatieria*, *Sphaerolaimus* and *Terschellingia*) were present at all open slope stations and 31 genera were exclusively present in the open slope (Table 2.3). *Metalinhomoeus* and *Sabatieria* were the most abundant genera for both canyon and open slope, being highest in the canyon.

The mean diversity (*H'*) and evenness (*J'*) indexes for the nematode assemblage were significantly higher on the open slope than in the canyon. Diversity on the slope was 2.3 ± 0.1 and 1.3 ± 0.2 in the canyon (p ≤ 0.001, Table 2.2). Evenness was 0.9 ± 0.01 on the slope and 0.7 ± 0.1 in the canyon (p ≤ 0.023, Table 2.2). Diversity decreased with increasing water depth on the open slope (Figure 2.5a). In the canyon, it only did so in the upper and middle parts. Evenness did not change along the depth gradient on the slope (Figure 2.5b), and in the canyon, Stns S26 and S34 had lower evenness values than the remaining canyon stations. Inter-station differences in diversity with depth at each location (canyon and open slope) were statistically significant (p ≤ 0.001, Table 2.2).

K-dominance curves of nematode abundance (Figure 2.6) revealed 2 groups of curves in the canyon and 1 in the open slope. The curves for Stns S26, S34 and S41 indicated higher nematode dominance within these assemblages than at Stns S24 and S22 (Figure 2.6a). In addition, the curves for Stns S24 and S22 were similar to those for the 3 open slope stations (Figure 2.6b), indicating that all these stations had similar nematode dominance.

The trophic structure of the nematode assemblages differed between canyon and open slope. On the open slope, the four different feeding types of Wieser (1953) were well represented in terms of abundance (Figure 2.7a) and biomass (Figure 2.7b), and no differences in the trophic structure were observed along the depth gradient. In contrast, in the canyon, non-selective deposit-feeding nematodes (Feeding Type 1B) dominated in terms of abundance (Figure 2.7a) and biomass (Figure 2.7b). The assemblages of the upper and middle part of the canyon differed from that in the deeper part: Non-selective deposit

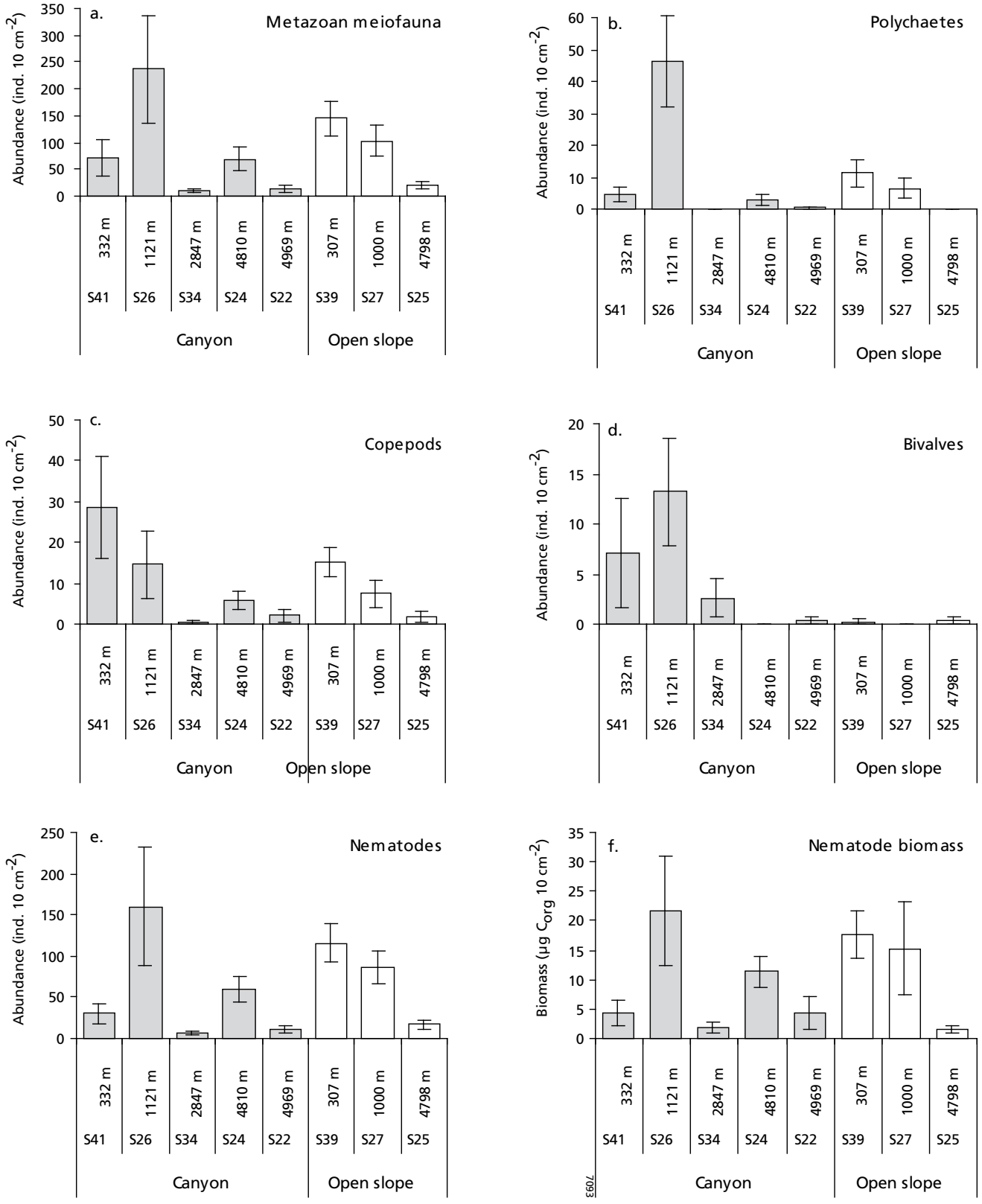


Figure 2.4. (a) to (e) Mean ± SE abundance of (a) metazoan meiofauna, (b) polychaetes, (c) copepods, (d) bivalves and (e) nematodes, and (f) nematode biomass (Corg 10 cm^{-2}) along bathymetric gradient and at Stns S41, S26, S34, S24, S22, S39, S27 and S25 in Nazaré canyon and on adjacent open slope

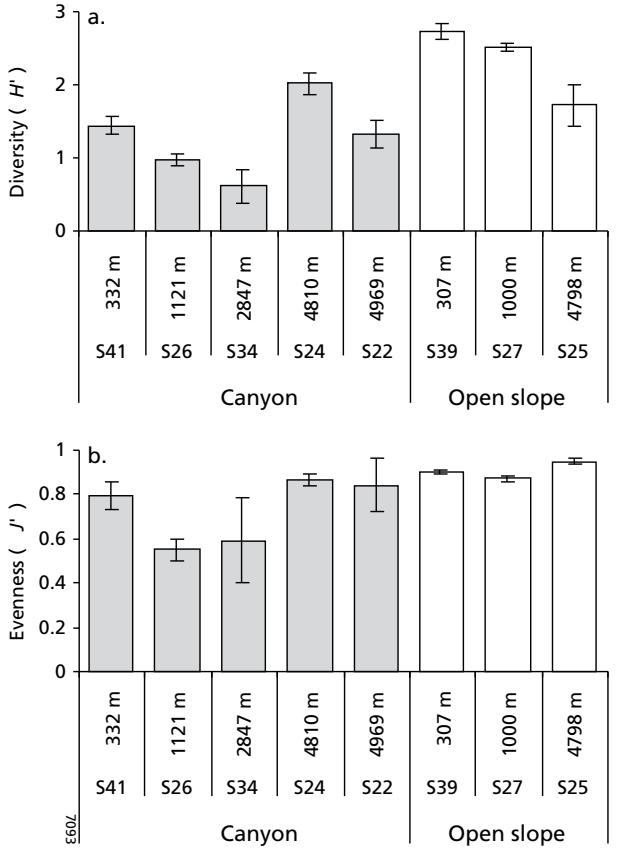


Figure 2.5. Mean ± SE (a) diversity (Shannon-Wiener *H'*), and (b) evenness (*J'*) of nematode assemblage along bathymetric gradient and at Stns S41, S26, S34, S24, S22, S39, S27 and S25 in Nazaré canyon and on adjacent open slope

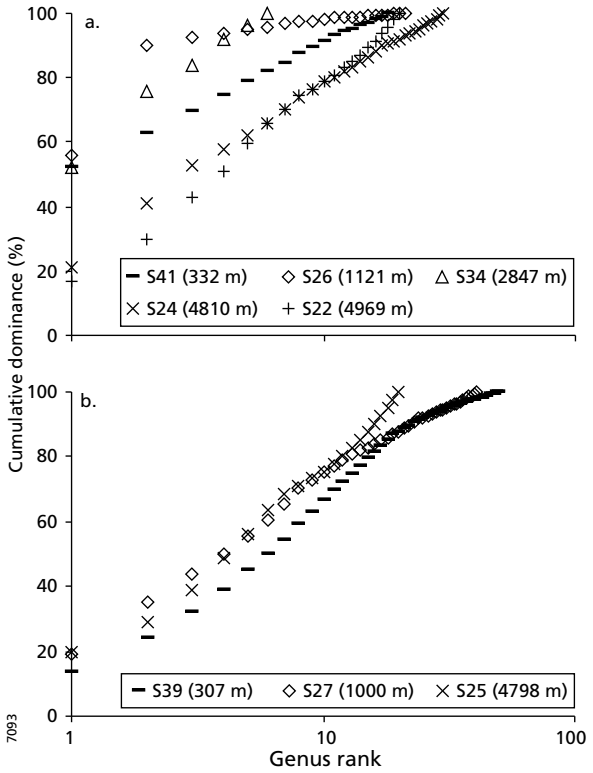


Figure 2.6. Nematode abundance K-dominance curves along depth gradient in (a) Nazaré canyon and (b) adjacent open slope stations

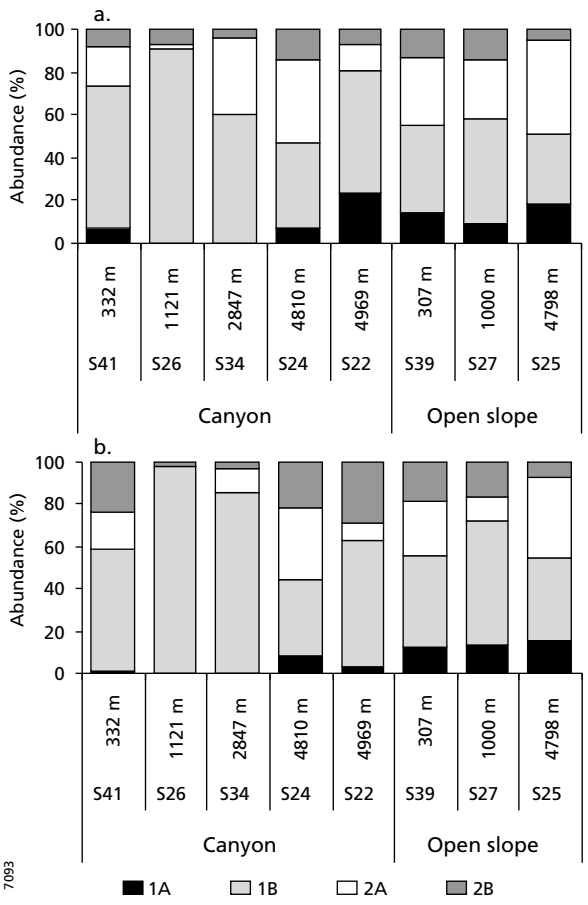


Figure 2.7. (a) Relative abundance and (b) biomass of nematodes belonging to the 4 different feeding types described by Wieser (1953), along bathymetric gradient and at Stns S41, S26, S34, S24, S22, S39, S27 and S25 in Nazaré canyon and on adjacent open slope (1A = selective deposit-feeder, 1B = non-selective deposit-feeder, 2A = epigrowth feeder, 2B = predator/omnivor)

feeders (Type 1B) were dominant in the upper and middle canyon areas, whereas selective deposit feeders (Type 1A) were unimportant; however, the latter feeding type was more important in the deeper part of the canyon, where it was present in proportions similar to those on the open slope.

2.3.4 Relationships between benthic meiofauna and geochemical parameters

The correlation analysis revealed different levels of interactions for the canyon system and adjacent open slope (Table 2.4). In the canyon there were 21 correlations, with an average Kendall's tau correlation coefficient of 0.5. The abundance of total metazoans, copepods, polychaetes, bivalves, nematodes and also nematode biomass were positively correlated ($p \leq 0.01$) with the lability of the phytodetritus (chl *a*:phaeo). Diversity and evenness were negatively correlated with C_{org} ($p \leq 0.01$) and phytodetritus (CPE) content ($p \leq 0.05$ and 0.01 respectively). The nematode trophic group 1B was positively correlated with chl *a*:phaeo ($p \leq 0.01$) and CPE ($p \leq 0.01$). On the open slope, there were 13 correlations with an average Kendall's tau correlation coefficient of 0.6. The abundance of total metazoans, copepods, polychaetes, nematodes and the nematodes biomass was positively correlated

Genera	FT	Canyon system					Open slope		
		S41	S26	S34	S24	S22	S39	S27	S25
Acantholaimus	2A		2.1±1.4	1.4±0.9	1.4±1.4		0.9±0.9	4.6±1.2	1.4±0.6
Amphimonhystrella	1B					0.2±0.2			0.4±0.4
Araeolaimus	1A				0.3±0.3		0.2±0.2		
Ascolaimus	1B						0.7±0.5		
Axonolaimus	1B	0.5±0.3	3.3±1.2				4.7±2.1		
Bathyeuristomina	2B							0.4±0.4	
Camacoliamus	2A				0.6±0.3		0.5±0.3	0.4±0.4	0.4±0.4
Campylaimus	1B		0.2±0.2				1.2±1.2		
Cervonema	1B		0.2±0.2		0.3±0.3	0.2±0.2	3.5±0.8	1.8±1.1	0.4±0.4
Chaetonema	1B					0.5±0.4	0.5±0.5		
Chromadora	2A	0.7±0.5	0.7±0.5		0.3±0.3		6.8±1.3	1.4±1.0	
Chromadorita	2A	0.2±0.2					0.5±0.3		
Comesa	1B							0.4±0.4	
Comesoma	1B					0.2±0.2			
Crenopharynx	1A						0.7±0.5	0.7±0.4	
Cricolaimus	2A						0.2±0.2		
Cyatolaimus	2A						0.5±0.5		
Cylicolaimus	2B						3.1±2.8		
Daptonema	1B		0.9±0.7				0.2±0.2	0.7±0.7	
Desmocolex	1A				0.3±0.3				
Desmodora	2A						5.2±4.1	3.5±1.2	
Desmolaimus	1B		0.2±0.2						
Disconema	1B				0.3±0.3			0.4±0.4	
Diplopeltoides	1A							0.7±0.4	0.4±0.4
Diplopeltula	1A					0.2±0.2	0.5±0.3		0.4±0.4
Dolicholaimus	2B						0.2±0.2		
Dorylaimopsis	2B						0.2±0.2	0.4±0.4	
Elzalia	1B					0.2±0.2		0.4±0.4	
Endeolophos	2A							0.7±0.4	0.4±0.4
Enoploides	2B				0.6±0.3				
Enoplolaimus	2B	0.2±0.2	0.5±0.5				0.2±0.2		
Filoncholaimus	2B						0.2±0.2		
Halalaimus	1A	0.2±0.2			0.8±0.6		4.2±1.6	1.4±0.6	0.4±0.4
Hopperia	2B							0.7±0.7	
Kraspedonema	2A				0.3±0.3				
Laimella	2A						0.2±0.2		
Leptolaimus	1A				0.3±0.3				
Limhomoeus	2A						0.2±0.2		
Longicyatholaimus	2A				7.1±0.4		1.7±0.8	0.7±0.4	
Marylinnia	2A	1.7±0.6			0.8±0.6		6.4±0.9	0.4±0.4	1.4±0.8
Metacyatholaimus	2A					0.2±0.2			
Metadesmolaimus	1B				0.3±0.3				
Metalinhomoues	1B	13.0±5.6	85.4±39.2	3.1±1.1	4.2±1.4	0.4±0.2	14.1±2.6	11.3±1.7	2.8±1.0
Metoncholaimus	2B	0.2±0.2			0.6±0.3				
Microlaimus	2A	1.2±0.4			0.3±0.3		0.5±0.3		0.4±0.4
Molgolaimus	1A							0.4±0.4	
Nemanema	1A				0.3±0.3			0.7±0.7	0.7±0.7
Neochromadora	2A	0.7±0.5	0.2±0.2	0.2±0.2			8.0±2.2	6.4±0.9	1.1±0.7
Neotonchus	2A				0.3±0.3				
Onchium	2A				0.3±0.3				
Oncholaimus	2B				0.3±0.3		0.2±0.2		0.4±0.4
Oncholaimellus	2B							0.7±0.7	
Oxystomina	1A	0.2±0.2	0.2±0.2			0.2±0.2	0.9±0.6	1.1±0.7	
Paracanthonchus	2A				1.7±1.0				
Paracomesoma	1B				1.4±1.4	0.2±0.2		0.4±0.4	

Genera	FT	Canyon system					Open slope		
		S41	S26	S34	S24	S22	S39	S27	S25
Paracyatholaimus	2A	0.2±0.2			0.6±0.6		2.1±1.1	1.8±1.8	
Paradontophora	1B					0.2±0.2			
Paralongicyatholaimus	2A		0.7±0.7	0.5±0.3	0.6±0.6	0.7±0.5	1.9±1.1	0.4±0.4	1.4±0.6
Paramesacanthion	2B		0.2±0.2		1.7±1.0		0.5±0.3		
Paralinhomeus	1B		1.7±1.7						
Paranticoma	2A								0.7±0.4
Pareudesmocolex	1A						0.2±0.2		
Parasphaerolaimus	2B		0.2±0.2						
Pierrickia	1B							3.5±1.7	
Polysignia	2A							0.4±0.4	
Pomponema	2B	0.5±0.3	0.2±0.2				2.1±1.1	0.4±0.4	
Prooncholaimus	2B	0.5±0.3							
Pselionema	1A					0.2±0.2	2.6±1.4	0.7±0.7	
Pterygonema	1A						0.2±0.2		
Quadricoma	1A						0.7±0.5		
Sabatieria	1B	2.6±0.7	53.1±21.3	0.5±0.3	7.6±2.8	1.1±0.5	11.1±1.9	14.1±4.0	0.4±0.4
Setosabatieria	1B		0.2±0.2				4.7±1.5	3.9±1.9	
Sphaerolaimus	2B	0.7±0.3	1.4±1.4	0.2±0.2	1.4±0.8	0.2±0.2	1.9±1.0	3.9±2.0	0.4±0.4
Subsphaeroplimus	2B						0.7±0.7	0.4±0.4	
Steineria	1B							0.4±0.4	
Synodontium	1B						0.2±0.2		
Synonchiella	2B						0.2±0.2	0.4±0.4	
Syringolaimus	2B					1.4±0.6		0.7±0.4	0.4±0.4
Terschellingia	1B	1.2±0.7	1.4±1.4			1.1±0.6	2.8±0.6	0.4±0.4	1.1±1.1
Thalassoalaimus	1A						0.2±0.2		
Thalassomonhystera	1B					0.2±0.2	0.2±0.2		
Thoracostomopsis	2B							0.4±0.4	
Vasostoma	2A		0.2±0.2		0.6±0.3	0.4±0.2			
Viscosia	2B	0.2±0.2			0.6±0.3	0.7±0.4	2.8±0.7	1.1±1.1	
Wieseria	1A						0.7±0.7		
Total		24.8±11.8	153.5±72.2	5.9±3.1	35.9±18.0	8.3±5.6	103.5±41.4	72.9±32.5	14.5±10.0
No Genera		18	23	6	30	21	51	41	20

Table 2.3. List of nematode genera – showing feeding type, FT (Wieser 1953) – and mean ± SE abundance (ind. 10 cm^{-2}) for Nazaré canyon and adjacent open slope stations (1A = selective deposit-feeder, 1B = non-selective deposit feeder, 2A = epigrowth feeder, and 2B = predator/omnivore)

with CPE ($p \leq 0.01$, nematode biomass $p \leq 0.05$). Diversity was also positively correlated with CPE ($p \leq 0.05$), as were the nematode trophic groups 1B, 2A ($p \leq 0.01$) and 2B ($p \leq 0.05$).

2.4 DISCUSSION

2.4.1 Meiofauna and organic matter levels

The meiofauna abundance recorded in the Nazaré canyon and adjacent open slope ranged between 9.9 and 236.5 ind. 10 cm^{-2}. These values are low compared to those in temperate regions of the east Atlantic and off the Iberian Peninsula (see Soltwedel 2000), but within the range observed during springtime in the Western Iberian Margin. Most present-day studies on meiofauna use a mesh size ≤32 µm. We used a 48 µm mesh size, which could have underestimated actual meiofauna densities. Using a comparable mesh size (50 µm), Rachor (1975) found meiofauna abundances at 38°N (~1°S from the Nazaré study area) ranging between 18 and 294 ind. 10 cm^{-2} during springtime at depths of 1469 to 5112 m. In wintertime, also at 38°N, and using a 40 µm mesh size, Thiel (1975) recorded meiofauna abundances ranging between 123 and 1387 ind. 10 cm^{-2} at depths of 250 to 5250 m, suggesting strong seasonality. On the NW Iberian margin (42 to 43°N) during summertime, Flach et al. (2002) observed meiofauna abundances ranging between 250 and 1800 ind. 10 cm^{-2}, at depths of 200 to 5000 m, but they used a smaller 32 µm mesh size. In terms of biomass, the values recorded for the Nazaré canyon and adjacent open slope are about 3 to 4 times lower than those reported for the NW Iberian margin during summer (Flach et al. 2002).

The average C_{org} content of the top 5 cm of sediment in the Nazaré canyon ranged between 1.52 and 1.86%, while on the adjacent open slope C_{org} contents ranged between 0.3 and 1.02%. These values are similar to those found in the past for the Nazaré canyon and slope in the NW Iberian margin (Epping et al. 2002). At other continental margins, similar C_{org} contents

Parameter	Metazoans	Copepods	Polychaetes	Bivalves	Nematodes	NemBiom	*H'*	*J'*	1A	1B	2A	2B
Canyon												
CPE	**0.424**	0.274	***0.457***	***0.549***	0.218	0.220	**-0.338**	***-0.455***	-0.126	***0.460***	-0.084	-0.311
clh *a*:phaeo	***0.734***	***0.629***	***0.753***	***0.465***	***0.565***	***0.485***	0.059	**-0.323**	-0.087	***0.693***	0.187	0.115
Corg	0.011	-0.174	0.012	0.247	-0.173	-0.118	***-0.622***	***-0.426***	-0.049	0.038	**-0.354**	***-0.556***
TN	0.100	0.204	0.062	0.230	-0.170	-0.118	-0.235	-0.250	-0.068	0.098	-0.052	-0.245
C:N	-0.277	**-0.374**	-0.259	**-0.415**	-0.070	-0.059	0.176	**0.308**	0.107	-0.279	0.020	0.221
Open slope												
CPE	***0.666***	***0.786***	***0.653***	0.051	***0.649***	**0.550**	***0.603***	-0.288	0.343	***0.678***	***0.800***	**0.559**
clh *a*:phaeo	-0.240	-0.360	-0.208	-0.153	-0.225	-0.131	-0.288	-0.131	-0.041	-0.244	-0.373	-0.123
C_{org}	-.0.240	-0.360	-0.208	-0.153	-0.225	-0.131	-0.288	-0.131	-0.041	-0.244	-0.373	-0.123
TN	-0.240	-0.360	-0.208	-0.153	-0.225	-0.131	-0.288	-0.131	-0.041	-0.244	– 0.373	-0.123
C:N	0.400	0.280	**0.458**	-0.255	0.411	**0.498**	0.288	***-0.655***	0.398	0.407	0.267	**0.532**

Table 2.4. Results of non-parametric Kendall's tau correlations analyses for metazoans, copepods, polychaetes, bivalves, nematodes, nematode biomass (Nem Biom), diversity (*H'*), evenness (*J'*), selective deposit feeder (1A), non-selective deposit feeder (1B), epigrowth feeder (2A), predator/omnivore (2B) for Nazaré canyon and adjacent open slope. Bold: $p \leq 0.05$; bold italics: $p \leq 0.01$. Abbreviations as in Table 2.1

have also been observed (Duineveld et al 2001, Grémare et al. 2002).

The CPE ranged between 5.7 and 92.4 µg 5 cm^{-3} in the Nazaré canyon sediments, and between 1.7 and 22.3 µg 5 cm-3 on the open slope. The open slope values fall within the range given for other continental margins at similar depths (Soltwedel 1997, Soltwedel et al. 2000). In contrast, the values we found in the Nazaré canyon sediments are several others of magnitudes higher than those found in other continental margins.

The lability of the phytodetritus in the canyon and adjacent slope sediments is refractory compared to that of other continental margins at similar depths. Soltwedel et al. (2000) found chl *a*: phaeo ratios of 0.4 to 0.7 at ~500 m, of 0.07 to 0.21 at ~1000 m, of 0.03 to 0.12 at ~3000 m and of 0.05 at ~4000 m depths on the Yermak Plateau. In the canyon and adjacent slope sediments chl *a*:phaeo ratios ranged between 0.02 and 0.18.

2.4.2 Distribution of meiofauna abundance and biomass

For continental margins, the abundance and biomass of benthic communities have been reported to decrease with increasing water depth (Tietjen 1992, Soltwedel 2000, Flach et al. 2002). This decrease has been related to decreased food availability (Gage and Tyler 1991). In the canyon and adjacent open slope sediments, phytodetritus decreased with increasing water depth, and C_{org} content tended to be lower at greater depths (Table 2.1). However, a parallel decrease in meiofauna abundance and biomass only occurred on the open slope (Figure 2.4). This is supported by the stronger positive correlation between the metazoan taxa and CPE contents on the open slope than in the canyon (Table 2.4).

For submarine canyons, higher abundances of fauna and higher biomasses have been reported and related to the higher organic content of these environments (Gage et al. 1995, Vetter and Dayton 1998, Duineveld et al. 2001). Moreover, the quality of organic matter also plays an important role in controlling benthic communities. In areas with high quantities of labile organic matter, faunal density and biomass have been found to be higher than in areas where similar quantities of refractory organic matter were observed (Dauwe and Middelburg 1998).

Higher organic contents (C_{org}, TN and CPE) were found throughout the canyon than on the adjacent slope, especially in the upper/middle parts (Table 2.1). Despite the fact that the bulk of the organic matter in the canyon was very refractory (C:N ≈ 9 to 12), the amount and quality of organic matter available for direct consumption was higher in the upper part of the canyon (higher CPE contents and chl *a*:phaeo ratios; Table 2.1). This suggests that the upper and middle canyon areas would constitute better feeding grounds for the benthos, and higher densities and biomass would be expected there. However, higher meiofaunal abundance and nematode biomass were not always observed in the canyon. Although meiofaunal densities in the deeper parts of the canyon seemed to parallel environmental organic levels, in the upper and middle areas this was not the case. Stns S41, S26 and S34 were always depleted in foraminifers compared to the open slope (Figure 2.3). Metazoans in general, and polychaetes and nematodes specifically (Figure 2.4) were very abundant at St S26 (1121 m), but were depleted at St S41 and S34. This was also true for nematode biomass. In general, organisms on the adjacent open slope seemed to survive better with lower or similar background levels of C_{org} and CPE than those in the canyon.

The absence of a clear relationship between faunal abundance and biomass with organic content and metabolisable organic matter in the canyon suggests that some other environmental parameter(s) is/are responsible for faunal distributions. De Stigter et al. (2007) measured high near-bed tidal currents, average horizontal particle flux and deposition flux in the upper and middle parts of Nazaré canyon. The high currents may cause frequent resuspension and transport of surface sediments, leading to unstable sediment substrate, and high sedimentation rates may lead to fauna being buried by sediment. Such an environment is difficult to colonise because the meiofauna is either swept away by high currents or buried by unstable sediments and episodic depositional events, as confirmed by the lack of fragile arborescent foraminifers in the upper and middle canyon. Gage et al. (1995) also reported the absence of fragile surface-feeding macrofauna in the Setúbal canyon, where indications of vigorous bottom currents were found. In the Nazaré canyon, low numbers of calcareous and agglutinated foraminifers were found in the upper and middle parts. Previously, low abundances of foraminifers were recorded in the Wilmington canyon off the coast of New Jersey, and their

absence was related to periodic mass wasting and high current activity in the study area (Jorissen et al.

1994). Further, the nematodes *Sabatieria* sp. and *Metalinhomoeus* sp., which have been shown to persist and thrive in very disturbed environments resulting from dredging and trawling activities (Schratzberger and Jennings 2002) were very dominant in the upper and middle parts of the Nazaré canyon. These observations seem to indicate that meiofauna abundance and biomass in the upper and middle canyon is strongly controlled by physical factors.

2.4.3 Nematode community structure

In the upper and middle parts of the Nazaré canyon, higher phytopigments and C_{org} concentrations were recorded, and the phytodetritus was less refractory. Here, low nematode diversity and evenness, and high *K*-dominance curves were found, and non-selective deposit-feeding nematodes were especially important. In agreement, the correlation analyses showed negative correlations of diversity and evenness with C_{org} and CPE, and a positive correlation of non-selective deposit-feeders with CPE and chl *a*:phaeo (Table 2.4). In the deeper canyon area and adjacent open slope, lower contents of phytopigments and C_{org} were recorded, and the phytodetritus was more refractory. Higher diversity and evenness, and lower *K*-dominance curves were found here. The trophic structure of the nematode assemblages was more diverse. The correlation analysis supported this, showing a positive correlation of diversity with CPE, and a higher number of trophic groups correlated to CPE (Table 2.4). Thus, diversity patterns of the nematode community and trophic structure both indicate that the differences in metabolisable organic matter between upper canyon regions and adjacent open slope, and deeper canyon regions play an important role in controlling the composition of the meiobenthos inhabiting these regions.

Two nematode genera, *Sabatieria* sp. and *Metalinhomoeus* sp., accounted for ~70% of the abundance in the upper canyon (Fig. 6a). Both these genera are non-selective deposit-feeders. *Sabatieria* sp. is well adapted to living in fine-sediment environments, with high C_{org} loads, low oxygen concentrations, and high sulphide concentrations (Jensen et al. 1992, Soetaert and Heip 1995). Suboxic sediments also characterise the upper part of the Nazaré canyon (Epping et al. 2002). *Metalinhomoeus* sp. has also been found to be very abundant in silty and very fine sand environments with high C_{org} content (Buchholz and Lampadariou 2002). Further, these genera are also found in highly physically-disturbed sedimentary conditions resulting from dredging and trawling. Thus, in the more disturbed and organically enriched conditions of the upper canyon, *Sabatieria* sp. and *Metalinhomoeus* sp. may constitute opportunistic colonisers. Flach (2003) also found that the macrobenthic community in the Nazaré canyon was dominated by two small opportunistic polychaetes.

2.5 CONCLUSIONS

The Nazaré canyon contains higher amounts of organic matter than the adjacent open slope. In its upper and middle parts, the phytodetritus is fresher, and thus of higher nutritional value for the meiobenthos. However, contrary to expectations, the meiobenthos in this part of the canyon seem unable to fully exploit the high amounts of food resources the canyon provides. In comparison, the meiobenthos on the open slope is more abundant, although with less abundant food resources. The low abundance of fauna in the canyon may be due to the local high-velocity bottom currents and unstable sedimentary conditions hindering the settlement of meiobenthic communities. The upper canyon was dominated by 2 very opportunistic nematode genera (*Sabatieria* sp. and *Metalinhomoeus* sp.) that are able to withstand great sedimentary disturbance, high organic loads and suboxic conditions. The nematode community structure was related to organic concentrations. In the organically enriched upper canyon, lower diversities of the nematode assemblages and of the trophic structure were observed. Finally, the stations sampled in the canyon were situated in the thalweg, where physical disturbance by sediment transport and deposition is likely to be highest. A comparison with potentially less disturbed sites on terraces adjacent to the thalweg has yet to be made.

Acknowledgements.
This research was supported by EUROSTRATAFORM project, EC contract EVK3-CT-2002-00079 funded by the European Commission, DG-XII, and the HERMES project, EC contract OCE-CT-2005-511234 funded by the European Commission's Sixth Framework Programme under the priority Sustainable Development, Global Change and Ecosystems. Shiptime on RV 'Pelagia' was provided by Royal NIOZ, Texel, The Netherlands. The authors thank all the crew of the research vessel 'Pelagia' for their work in getting the samples on deck, Dr. T. J. Kouwenhoven for helping out with sample processing on board and comments on the manuscript, and Dr. T. Soltwedel and Dr. C. Hasseman for providing the semiautomatic images system (analySIS®2.1) from the Alfred Wegener Institute. We also thank Dr. A. Lerchl from Jacobs University Bremen for providing microscopes, and the students A. Palacz (for his help with phytopigment analyses) and B. Alexander (for proof-reading the English of the manuscript).

CHAPTER 3

Benthic foraminifera in the Nazaré canyon, Portuguese continental margin: sedimentary environments and disturbance

Published as:
K.A. Koho, T.J. Kouwenhoven, H.C. De Stigter, G.J. van der Zwaan, 2007. Benthic foraminifera in the Nazaré canyon, Portuguese continental margin: sedimentary environments and disturbance. Marine Micropaleontology 66, 27-51.

ABSTRACT

Living (rose Bengal stained) benthic foraminifera were investigated from thirteen stations ranging from 146-4976 m water depth in the Nazaré Canyon, located on the Western Iberian continental margin. The total standing stocks (TSS), species assemblages and in-sediment distributions are compared between stations located on the highly disturbed axis of the upper (< 2700 m) and middle canyon (2700-4000 m), the adjacent low energy terraces and the lower canyon (> 4000 m). In addition, the community changes were investigated in relation to water depth and bio-available, organic carbon.

Overall, low total standing stocks of foraminifera were found in the disturbed canyon axis, which experiences frequent sediment resuspension and gravity flows. At the upper canyon axis station at 1118 m a rather exceptional fauna was recovered, dominated by a species of *Technitella* that made up 75 % of the TSS.

The highest TSSs were recorded in the upper canyon terrace stations, where fine grained sediment and organic carbon are able to accumulate. Standing stocks on the terraces decreased with increasing water depths. The quiescent terrace stations recorded high abundances of infaunal species, including *Melonis barleeanum*, *Globobulimina* spp. and *Chilostomella oolina*. The occurrence of these species reflects the low pore water oxygen concentrations and high bio-available carbon supply.

Several tubular *Bathysiphon* species were found in the upper canyon terrace stations. Instead, the deepest stations of the lower canyon were dominated by another large agglutinated protozoan, *Saccorhiza ramosa*. The change in the arborescent/tubular foraminiferal community may reflect the increase in sediment oxygenation with increasing water depth in the canyon, *Bathysiphon* spp. occurring in sediments with higher bio-available carbon flux and *S. ramosa* inhabiting more oligotrophic areas.

3.1 INTRODUCTION

Submarine canyons are dynamic environments where vast quantities of sediment are transported, together with organic carbon, from the shallow seas towards the abyss. The down-slope transport of material and the associated turbidity currents can scour and erode the seafloor and lead to accumulation of sediment at a distal location. Scouring of the seafloor can bring about a sudden exposure of older sediments to oxygen, leading to remineralisation of old carbon (Cowie et al., 1995, Prahl et al. 1997), and uncovering of a new habitat for faunal colonisation. Redistribution of the sediment, together with organic carbon (C_{org}), can influence the geochemical gradients and their stability. The sediment deposited by turbidites and gravity flows can seal off the oxygen supply of former surficial sediments and lead to the development of a new redox zonation. This type of disturbance is expected to have an adverse impact on the living benthos: laboratory experiments indicate that unstable geochemical gradients and sudden changes in pore water oxygen levels can be lethal for fauna that cannot withstand sub- to anoxic conditions (e.g. Moodley et al., 1997, Moodley et al. 1998b, Ernst et al. 2002).

Submarine canyons can capture sediment transported along the shelf and slope and thus actively trap material, including fine particles and organic carbon (C_{org}), from the surrounding environment (Van Weering et al., 2002). High organic carbon fluxes prevail in the Nazaré canyon, consequently leading to enhanced oxygen consumption rates. This was demonstrated by Epping et al. (2002), who measured high mineralisation rates with an important contribution of anaerobic processes, including denitrification in the canyon in relation to the open slope, which was dominated by aerobic oxidation.

Benthic foraminifera are among the most common living organisms in today's oceanic environments (e.g. Bernstein et al., 1978, Snider et al., 1984, Gooday, 1986, Gage et al., 1995). However, the living foraminiferal populations in submarine canyons are not well documented. Some studies have been conducted in recent years, including the Wilmington Canyon off the coast of New Jersey (Jorissen et al., 1994), the Cap Breton and Cap Ferret Canyons in the Bay of Biscay, eastern Atlantic (Anschutz et al, 2002, Fontanier et al., 2005, Hess et al., 2005) and the Lacaze-Duthiers Canyon in the Gulf of Lions, western Mediterranean (Schmiedl et al., 2000). These studies suggest that specific ecological conditions must exist, either due to frequent mass flows (Jorissen et al, 1994), turbidity current activity (Anschutz et al., 2002, Hess et al., 2005), or to high organic carbon fluxes (Schmiedl et al., 2000, Fontanier et al., 2005).

This study aims to investigate further the influence of sedimentary disturbance in the form of current activity and resuspension of surface sediments, and of localised input of organic matter on benthic foraminifera. In this study we do not focus on seasonal characteristics. Instead, the foraminiferal abundance and distribution are examined and compared between the highly disturbed upper and middle canyon axial stations and the relatively undisturbed terrace sites, where fine grained material is able to accumulate. In addition, the changes in the foraminiferal assemblages are studied along the depth gradient in the canyon and in relation to changes in the amount of bio-available (labile) organic carbon.

3.2 STUDY REGION

3.2.1 Regional setting: hydrography of the Portuguese margin

The Portuguese margin, situated along the western side of the Iberian Peninsula, is influenced by seasonally changing hydrodynamics. During winter the prevailing southerly winds lead to downwelling events and offshore bottom water Ekman transport (Vitorino et al. 2002 a). Winter dynamics are also characterised by intense storms with wave heights exceeding 5 m. These high-energy events are capable of eroding sediments at mid-shelf depths and can lead to significant offshore transport of fine grained sediments in the form of nepheloid layers (Vitorino et al., 2002 a,b). During summer the conditions are reversed leading to an active upwelling regime induced by northerly winds and southward surface currents (Vitorino et al. 2002a). The conditions favourable for upwelling occur between June and September (Huthnance et al. 2002). The development of upwelling is followed by a clear increase in primary productivity in surface waters during summer (Joint et al 2001).

Different water masses can be identified in the water column of the Iberian margin (Fiuza et al. 1998, Garcia et al., 2003). At the surface, below the seasonally varying thermocline, a light (warm and salty, ≤36.0 psu) body of subtropical Eastern North Atlantic Central Water (ENACW) can be distinguished. Below ENACW, between 600-1600m water depth, relatively warm (~10 °C) and saline (>36.0 psu) Mediterranean Outflow Water (MOW) is found, its salinity peak centred at 1100 m depth. North Atlantic Deep Water (NADW) dominates below the MOW, having a cooler (6-2 °C) and less salty (~35.0 psu) nature.

3.2.2 Nazaré Canyon

The Nazaré Canyon is located off the coast of Portugal around 39º 40'N; 009°-011° W. It is one of the largest submarine canyons in Europe, measuring approximately 230 km in length and reaching down to 5000 m water depth in its distal part. Upper, middle and lower canyon were defined following Vanney and Mougenot (1990) and De Stigter et al. (in press). The proximal section of the canyon is dissecting the entire continental shelf, with the canyon head located very close to the shore. The upper canyon (<2700 m water depth) is deeply incised in the shelf and characterised by a V-shaped morphology, and a rapid increase in depth. Towards the middle section (2700-4000 m water depth) the canyon remains deeply cut, but widens to a U-shaped profile with a V-shaped axial channel. The lower canyon floor slopes very gently, becoming more or less flat. Close to 4000 m water depth the canyon floor begins to widen from 3 km to 15 km at the distal end. The changes in the canyon morphology coincide with changes in the sedimentological processes observed in the canyon, including tidal currents, suspended sediment load and sedimentation rate (Table 3.1).

The canyon activity and the disturbance of surface sediments are greatest along the upper and middle canyon axis, where time series observations with benthic landers (De Stigter et al., in press; Table 3.1 and 3.2) provided evidence for frequent resuspension and transport of bottom sediments by tidal currents and by intermittent sediment gravity flows. The dynamic sedimentation regime is reflected by the often very watery and non-cohesive appearance of surface sediments in cores retrieved from the canyon axis, in contrast to more consolidated sediments from the adjacent terraces.

Nazaré	Upper canyon	Middle canyon	Lower canyon
Suspended particle load	1-10 mg/L	0.2 mgl/L	0.05 mg/L
Sediment accumulation rate *1	2-76 g/m²·d (rates highly variable locally; frequent erosion)	8-33 g/m²·d (permanent sedimentation loci)	0.6-0.9 g/m²·d
Shape of the canyon	V-shaped incised	U-shaped incised	U-shaped flat floor
Semi diurnal tides	20-30 cm/s	up to ~30 cm/s	5-10 cm/s
Disturbance	Frequent re-suspension and gravity flows	Gravity flows	Centennial-millennial scale; last major turbidite 1755 AD*2

*1 derived from ^{210}Pb *2 Lisbon earthquake

Table 3.1. Sedimentary regime in Nazaré Canyon axis and the general characteristics (data from De Stigter et al., in press).

	Station name (this paper)	Original station name	Sample moment	Latitude (N)	Longitude (W)	depth (m)	C_{org} (wt %)	O_2 penetration depth (cm)	C/N (molar)	CPE (µg/5cm³)	Chla: Phaeo	Mode (µm)	SAR (g/m²·d)	Maximum current speed (cm/s)	SPM (g/m²)	Max mass flux (g/m²·d)
Upper canyon	146T	225-42	May 2004	39°38′29″	009°16′29″	146										
	151T	218-57	Oct 2003	39°38′30″	009°16′59″	151	1.5[a]					14.3[a]	2.9[a]			
	301A	225-41	May 2004	39°34′43″	009°09′11″	301	2.0[a], 1.7[c]	~0.1*[d]	9.0[c]	89.1[c]	0.09[c]	12.1[a]	46.2[a]	(35)[a]		
	321T	218-05	Oct 2003	39°38′48″	009°05′00″	321	1.7[a]					10.3[a]	14.6[a]			
	344T	138-12	May 1999	39°38′52″	009°14′43″	344	3.3[a, b]	0.5[b]	9.9[b]			13.6[a]	2.2[a]			
	890T	138-16	May 1999	39°35′43″	009°24′14″	890	3.0[a, b]		10.0[b]			14.9[a]	12.9[a]			
	927T	236-13	May 2005	39°35′52″	009°24′16″	927						16.4[a]				
	1118A	225-26	May 2004	39°35′58″	009°24′0″	1118	1.8[a], 1.8[c]	~0.5*[d]	10.9[c]	92.4[c]	0.18[c]	13.0[a]		(>30)[a]	(up to 10)[a]	(788.3)[a]
Middle canyon	2847A	225-34	May 2004	39°30′13″	009°45′0″	2847	1.6[a], 1.9[c]	~1.25*[d]	10.9[c]	48.6[c]	0.03[c]			(25-35)[a]	(0.2)[a]	(43.6)[a]
	3097T	138-14	May 1999	39°30′46″	009°51′3″	3097	3.8[b]	1.5[b]	11.1[b]			30.1[a]	32.6[a]			
Lower canyon	4810	225-24	May 2004	39°48′2″	010°37′58″	4810	1.5[a], 1.5[c]	~4.5*[d]	12.1[c]	13.9[c]	0.03[c]					
	4969	225-22	May 2004	39°53′54″	011°09′25″	4969	1.8[a], 1.5[c]	~5.0*[d]	12.5[c]	5.7[c]	0.03[c]	6.5[a]	0.8[a]			
	4976	218-07	Oct 2003	39°54′00″	11°10′00″	4976	1.5[a]					105.9[a] 7.8[a]	0.9[a]	(5)[a]	(0.05)[a]	(0.2)[a]

*Nitrate (NO_3^-) declines sharply at this depth in the pore waters and ammonium (NH_4^+) begins to build up.

[a] De Stigter et al., in press (measured in 0-1 cm of sediment; except for station 4976 where sediment grain size mode is reported for 0-0.5 cm and 0.5-1.0 cm depth in sediment, to illustrate the heterogeneity at the site)

[b] Epping et al. 2002 (measured in 0-1 cm of sediment)

[c] Garcia et al. 2007 (measured in 0-5 cm of sediment)

[d] E. Koning (pers. comm.)

Table 3.2. Environmental variables measured in the canyon sediments. The location inside the canyon is indicated by a letter after the station name: T = terrace and A = axis. For visual clarification, the shaded stations are located along the canyon axis. CPE stands for the chloroplastic pigments equivalents, representing the sum of the chlorophyll *a* and its degradation products phaeopigments (Garcia et al., 2007). Chla:Phaeo, Chl *a* versus phaeopigment can be used to indicate the freshness of the phytodetritus (Garcia et al. 2007). Grain size mode and sediment accumulation rate (SAR) after De Stigter et al. (in press). SAR based on sediment profiles of ^{210}Pb. Maximum current speed, suspended matter load (SPM) and mass sediment flux is presented in brackets as measurements were carried out with benthic landers. Lander deployments were located at or relatively close to the stations where foraminiferal samples were collected.

Considerably higher sediment transport has been recorded inside the Nazaré Canyon in comparison to the adjacent continental margin (Schmidt et al. 2001, Van Weering et al. 2002). An overview of the sediment transport and deposition in the Nazaré Canyon was presented by De Stigter et al. (in press), further demonstrating the activity of the canyon environment. Due to vigorous internal tidal activity in the upper canyon, surficial sediments are nearly constantly resuspended and under momentum, suspended matter load measuring up to 10 mg/L. In the middle canyon, the surface material is only resuspended during the spring tide maximum; therefore at times the seabed can remain undisturbed for up to two weeks. In the lower canyon, sedimentary disturbance occurs via gravity flows on timescales of a year or even longer, tidal activity being too weak to mobilise sedimentary material at these depths.

On average, the highest sedimentation rates are recorded in the mid-canyon (Table 3.1), which appears to act as a locus for sediment deposition. High rates are also noted in the upper canyon, however due to active resuspension and erosion by currents, the upper canyon can only serve as a temporary location for the settling sediment. In the lower canyon the activity is minimal and major turbidity currents occur only on a centennial-millennial timescale. The youngest major event has been tentatively dated to an age corresponding with the Lisbon earthquake in the 18th century.

The canyon surface sediments have a very characteristic composition. The entire canyon floor, including the walls and terraces of the canyon, is covered by fine grained mud that is strikingly uniform in composition throughout the system (De Stigter et al., in press). The surface mud has a distinct unimodal particle size distribution around 10-20 μm, contains 10-15% of carbonate and has a high C_{org} content (up to 3.8 wt %; Table 3.2). The thickness of the mud drape can vary within the canyon. For instance, along the upper canyon thalweg, the mud cover is relatively thin (5-20 cm) and is underlain by medium sand, whereas at the terraces it is more substantial (no sand was recovered from multicores sampled from the terraces). The organic carbon content of the sediments is high, reaching up to 3.8 wt % in station 3097T (Table 3.2). No systematic trend was observed between sedimentary organic carbon and water depth. Epping et al. (2002) measured low reactivity of carbon, indicating that the canyon is enriched in older, laterally advected organic material. The molar C/N ratios are high and do increase with water depth. The bulk sedimentary C_{org} has a high terrigenous component, which is confirmed by the abundance of flaky and woody particles.

The oxygen penetration depth in the canyon sediments increases with water depth (Epping et al. 2002; Table 3.2). In the upper canyon sediments, anoxic sediments occur at < 0.5 cm depth in sediment. The shallow oxygen penetration depth is also reflected in high pore water ammonium concentrations (92.7 μmol/L at 0.45 cm depth in sediment) measured by E. Koning et al. (pers. comm.) in May 2004 at around 1000 m water depth. The pore water oxygen penetration increases to ~1.5 cm depth in sediment in the middle canyon and to more than 3 cm depth in sediment in the lower canyon.

3.3 METHODS

3.3.1 Collection and processing of samples

The study material was collected during cruises 64PE138, 64PE218, 64PE225 and 64PE236 of R.V. Pelagia of Royal NIOZ, taking place in May 1999, October 2003, May 2004 and May 2005, respectively. Altogether, 13 stations are included in this study, of which eight are located in the upper canyon, two in the middle canyon and three in the lower canyon (Figure 3.1 and Table 3.2). From here on the stations will be referred to by their water depth. Where relevant, a distinction is made between stations on the axis, marked by A, and on terraces, T (Table 3.2).

Most samples were collected using a MUC 8+4 multiple corer developed by Oktopus GmbH, equipped with eight 6

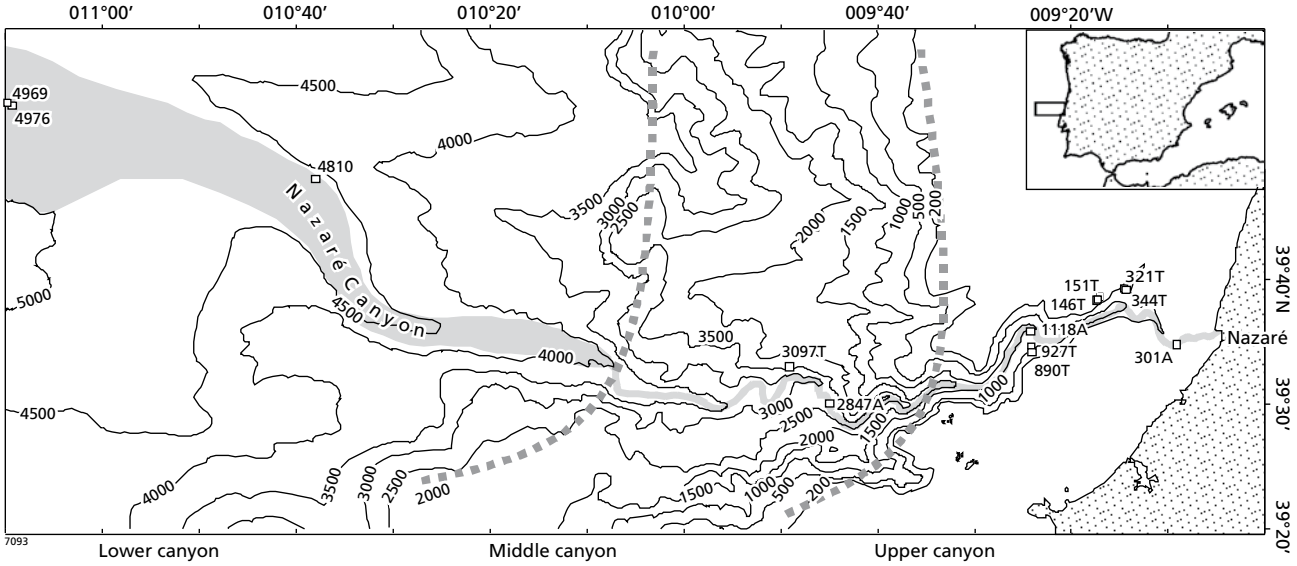


Figure 3.1. Map of the Nazaré Canyon showing the sampled stations, station numbers labelled with a T (terrace) and A (axis), where appropriate. Inset shows the Iberian Peninsula and the location of the Nazaré Canyon. The dashed lines indicate the subdivision into upper, middle and lower canyon as outlined in De Stigter et al. (in press) which in turn follows Vanney and Mougenot (1990). Figure modified from De Stigter et al (in press).

cm diameter and four 10 cm diameter coring tubes. For the foraminiferal analyses the smaller 6 cm tubes were used. From sites 146T and 151T boxcores were collected and subsampled with 6 cm diameter tubes.

On board the cores were sliced down to 10 cm depth. The top 2 cm was cut in slices of 0.5 cm thick. The remaining 8 cm was cut into 1 cm thick slices. Immediately after slicing the samples were stored in a solution of rose Bengal in 96% ethanol (1 g/L) until further treatment.

In the Utrecht laboratory the samples were wet-sieved into >150 and 63-150 µm size fractions. The samples were kept wet at all times and picked as soon as possible after sieving. Samples collected during cruise 64PE138 were freeze dried, and foraminiferal specimens were picked from a Petri dish containing 50% ethanol. The rose Bengal stained foraminifera were hand-picked and most were identified at species level. Results are presented of the >150 µm fraction down to 5 cm depth in sediment. Low numbers or no stained foraminifera were found below 5 cm depth in the cores. Only well-stained specimens were regarded as living and any patchy colouring was interpreted to indicate material that was already dead at the moment of sampling. If in doubt, tests were broken and protoplasm was inspected in more detail.

3.3.2 Analyses

Total standing stocks (TSS), the number of living foraminifera (excluding branching/tubular agglutinated foraminifera) per core (under 28.3 cm^2), were calculated by summation of the number of stained foraminifera in depth levels 0-5 cm. The numbers per core-slice were converted to densities by standardising the number of individuals to 50 cc. The species richness (S), a count of living foraminiferal species per station, was used to indicate foraminiferal diversity per station.

The numbers of rose Bengal stained arborescent and tubular foraminifera are reported separately, because of limitations of the counting method. Arborescent and tubular foraminifera break apart easily when processed in the laboratory, and therefore it is difficult to distinguish single individuals. In this paper, numbers of these foraminifera are noted as whole specimens if an aperture or a middle bulge (e.g. in *Rhabdammina* spp.) or a terminal bulb is present (e.g. in *Saccorhiza ramosa*); otherwise they are counted as living (rose Bengal stained) fragments.

The average living depth (ALD_x), used as an indication of the vertical distribution of the total foraminiferal standing stock or of individual species, is calculated following Jorissen et al. (1995) as:

$$ALD_x = \sum_{i=0,x} (n_i D_i)/N,$$

where x describes the lower boundary of the deepest sample, n_i is the number of foraminifera in the interval *i*, D_i is mid-depth of the sample interval *i*, and N is the total standing stock for all levels. The ALD for individual species was calculated only when five or more specimens were found from one site, and labelled as ALD5. In this study we report the living depth down to 5 cm in sediment.

A hierarchical cluster analysis applying squared Euclidean distances, average linkage was performed using statistical software SPSS 11.0 for Windows. The analysis was based on the total assemblages, including the arborescent and tubular foraminifera, and all the rare species. The clustering was derived from absence or presence of taxa, a value of 1 given to a taxon if present and 0 if absent. The presence/absence method was chosen to establish the similarity of the stations based solely on the total assemblage of foraminifera found in each station, in order to evaluate whether the stations sampled in October could be studied together with the stations sampled in spring.

In addition, Pearson correlation was carried out using statistical software SPSS 11.0 for Windows. The correlations were based on absolute counts of all foraminifera, including arborescent and tubular taxa (N=146). The analysis was performed to further investigate the relationships and comparability of the stations sampled in different seasons and years.

Station		TSS	Arborescent/tubular foraminifera		ALD5	Species richness
		per core (28.3 cm^2)	Whole (28.3 cm^2)	fragment (28.3 cm^2)	(cm)	(S)
Upper canyon	146T	565	1	17	1.2	47
	151T	578	0	9	1.7	49
	301A	15	0	0	1.3	6
	321T	627	0	0	1.0	43
	344T	519	2	20	1.0	54
	890T	564	7	7	1.2	33
	927T	896	52	79	1.0	30
	1118A	54	0	3	0.5	10
Middle canyon	2847A	16	0	0	1.8	4
	3097T	176	5	7	1.6	30
Lower canyon	4810	84	0	2	2.5	19
	4969	18	0	31	1.2	8
	4976	27	1	51	0.8	10

Table 3.3. Total standing stock (TSS) of foraminifera and arborescent and tubular taxa recorded in the canyon (per core/below 28.3 cm^2, in 141.5 cm^3 of sediment). The average living depth (ALD5) is based on calcareous and agglutinated species only, excluding the branching and tubular agglutinants. The location inside the canyon is indicated by a letter (T = terrace and A = axis) after the station name, where applicable.

3.4 RESULTS

3.4.1 Total Standing Stocks

Total standing stocks (TSS) of living foraminifera are reported in Table 3.3, including the number of arborescent/tubular individuals and fragments found. The highest numbers, with more than 500 specimens per core (5 cm deep, 28.3 cm^2), were recorded in the upper canyon terrace stations (146T, 151T, 321T, 344T, 890T and 927T). These stations contained at least ten times more living fauna than the stations in the adjacent canyon axis, where only low total numbers of living individuals were encountered (15 and 54 specimens). The mid canyon axis (2847A) was also nearly barren with only 16 living individuals. In contrast, the terrace station located at 3097 m water depth recorded a relatively high abundance (176 specimens). In the lower canyon, 84 specimens were counted in station 4810 and only 18 and 27 in stations 4969 and 4976. All in all, a decrease in the TSS was recorded on the terrace stations when moving from the upper canyon to the middle and lower canyon. Along the canyon axis, this pattern was not observed.

3.4.2 Vertical distribution of foraminifera in the sediment

The vertical distribution of the foraminiferal fauna is shown in Figure 3.2 (left hand panels). The average living depth (ALD5) per station is presented in Table 3.3. A clear decrease in the total abundance with increasing sediment depth was observed only in four stations: 344T, 927T, 1118A, and 4969. Unimodal subsurface maxima were recorded at stations 151T, 301A, 321T, 890T, 2847A and 4976. However, only few individuals were found at the axial (301A, 2847A) and the lower canyon stations (4979), thus the significance of the mode of distribution may be questionable at these sites. Bimodal distributions were found at stations 146T, 3097T and 4810.

On average, the living depth of benthic foraminifera in the canyon was located between 1-2 cm depth in the sediment (Table 3.3). Shallow ALD5 were found only in the upper canyon station 1118A and the lower canyon station 4976, where most foraminifera were found close to the surface (ALD5 0.5 cm and 0.8 cm). A deeper ALD5 of 2.5 cm was found in the lower canyon station 4810.

3.4.3 Assemblage distribution in canyon sub-environments

The foraminiferal assemblages differed between the axis and terrace stations, and changed with increasing water depth. The abundant foraminiferal species, making up more than 4 per cent of the total standing stock per station, are represented in Figure 3.2 (right hand panels). The species richness (S) is shown in Table 3.3. Appendix 3A summarises the number of common species and the ALD5 throughout the canyon.

The upper canyon axis stations (301A, 1118A) were characterised by low numbers of foraminifera and low species richness. Only individuals of *Chilostomella oolina* and *Nouria polymorphinoides* were encountered more than once in station 301A. Station 1118A was dominated by *Technitella* spp. contributing around 75 % of the total standing stock.

The upper canyon terrace stations had more abundant and diverse fauna (Table 3.3). The shallow stations (146T and 151T) were dominated by infaunal species, such as *Bigenerina cylindrica*, *B. nodosaria*, *Reophax* sp.1 and *Uvigerina peregrina*. In addition, *C. oolina* and *Globobulimina* spp. were recorded in high numbers. Stations 321T and 344T were dominated by *C. oolina*, and showed relatively high abundances of *Nouria polymorphinoides* and *Valvulineria bradyana*.

Stations 890T and 927T had many species in common, although differences were noted in the relative abundance of species. Both stations recorded high numbers of *Melonis barleeanum*. In addition, *C. oolina* and *Veleroninoides scitulus* were found at both sites. *C. oolina* was more abundant in station 927T whereas *V. scitulus* was more numerous in station 890T. Taxa, such as *Bulimina inflata*, *Bolivina alata* and *B. cylindrica,* were also more common in station 890T. A fragile spinous agglutinated species, *Crithionina hispida,* appeared mainly in station 927T together with *Discammina compressa*.

The assemblages found in the middle canyon axis (2847A) and terrace (3097T) stations were dominated by few species (Figure 3.2), however the very low total standing stocks (16 specimens) at site 2847 must be kept in mind, when interpreting the results. Two of the main species, *Fursenkoina* sp. and *Fursenkoina bradyi*, were not present in the upper canyon assemblage, thus differentiating the mid-canyon foraminiferal community from the upper canyon one. *Globobulimina* spp. were abundant only in the terrace station. The ALD5 of *Fursenkoina* spp. (>2 cm on the axis, ~1.5 cm on the terrace) and *Globobulimina* spp. (2.5 cm) indicate an infaunal habitat.

In the lower canyon stations (4810, 4969, and 4976) predominantly agglutinated species were found, including *Hormosinella distans, Psammosphaera fusca*, *Reophax* spp. and *Lagenammina* spp. The only abundant calcareous species, *Pullenia simplex*, was found in station 4810. *Pullenia simplex* occurred relatively deep in the sediment, suggesting an infaunal microhabitat (ALD5: 2.9 cm).

The dendrograms displayed in Figure 3.3(a, b) illustrate the correlations between stations as based on presence-absence of all foraminiferal taxa. In Figure 3.3b the stations sampled in October are included. Both dendrograms reflect a logical grouping: stations at similar water depths cluster together and the axial stations are separated from the terrace stations. In addition, the lower canyon stations with their distinct assemblages cluster separately.

The relationships between stations were further illustrated by the Pearson correlation, performed on the absolute counts of all foraminifera (Table 3.4). In general, a relatively high correlation was found between stations sampled from similar water depths (e.g. 146T and 151T, $r = 0.690$, $p < 0.01$). In addition, some degree of correlation is found between stations sampled from similar canyon sub-environments, such as upper canyon terrace sites. Stations located at similar water depths but sampled at different seasons, also show relatively good correlation. For instance, station 321T (sampled in October 2003) correlates with station 344T (sampled in May 1999, $r = 0.698$; $p < 0.01$). An even higher correlation coefficient ($r = 0.977$, $p < 0.01$) is found for the deepest sites, also sampled at different seasons.

3.4.4 Arborescent and tubular foraminifera species

Whereas the arborescent and tubular foraminifera were common on the upper and middle canyon terraces, and in the lower canyon, they were (nearly) absent from the canyon axis (Table 3.3, Appendix 3B). The highest abundances were

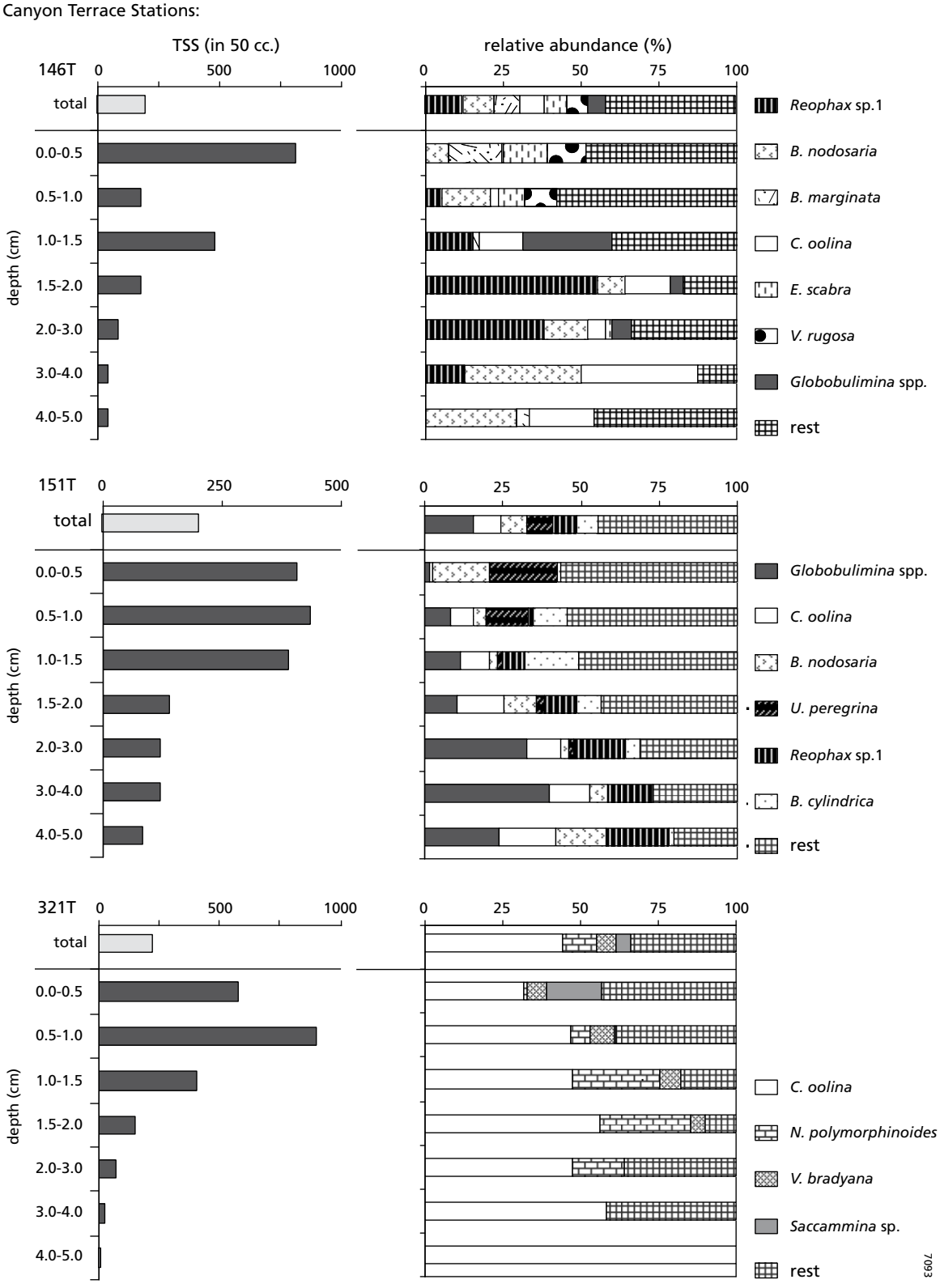
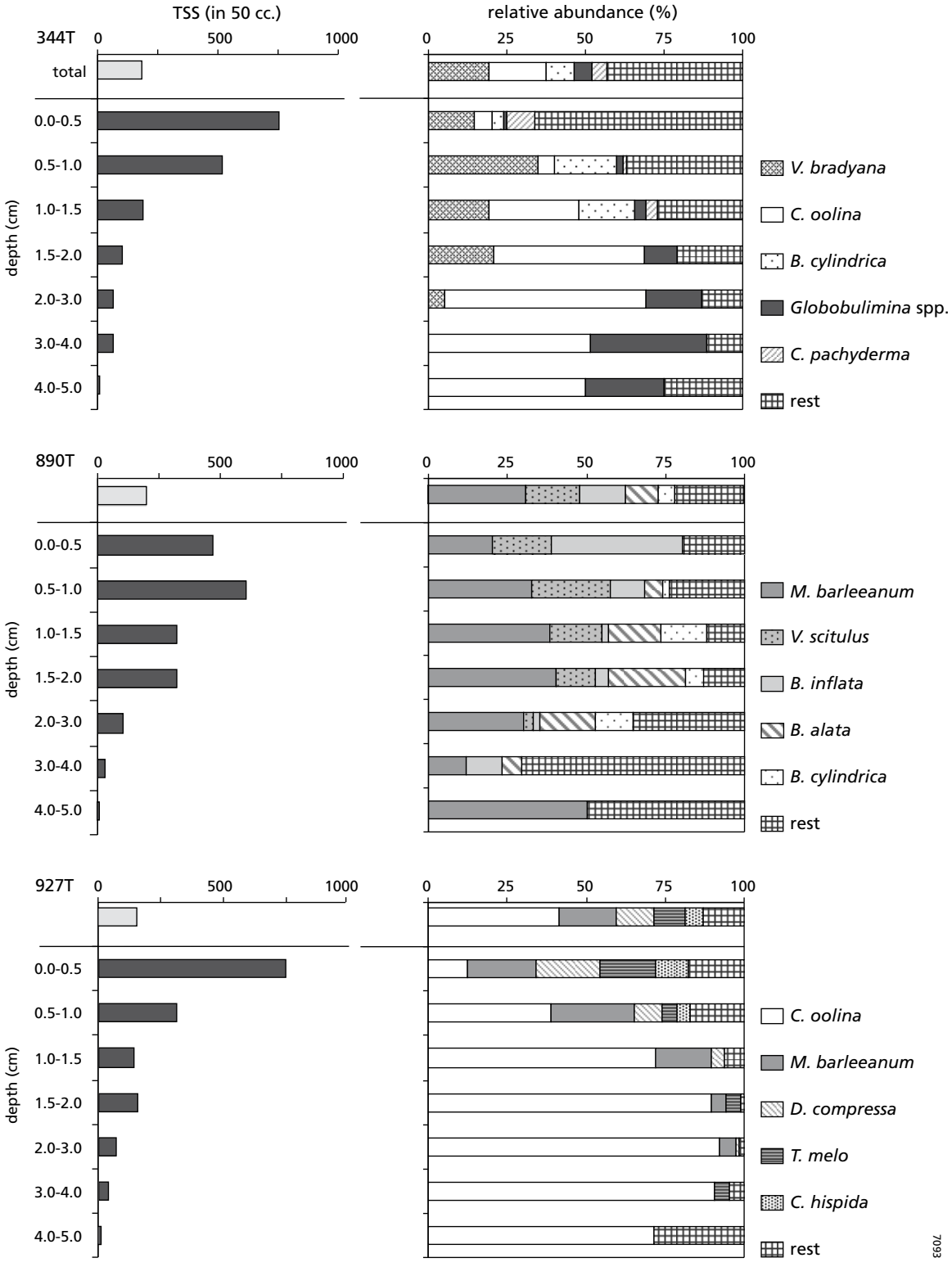


Figure 3.2. Left hand panels: The vertical distribution of foraminifera in the sediment. The counts are standardised to 50 cc. per sediment slice. The total standing stock (light grey bar) is also standardised to 50cc. Right hand panels: Relative abundance and vertical distribution of common taxa. Foraminiferal species counting more than four per cent of the total standing stock per station are represented in the figure.

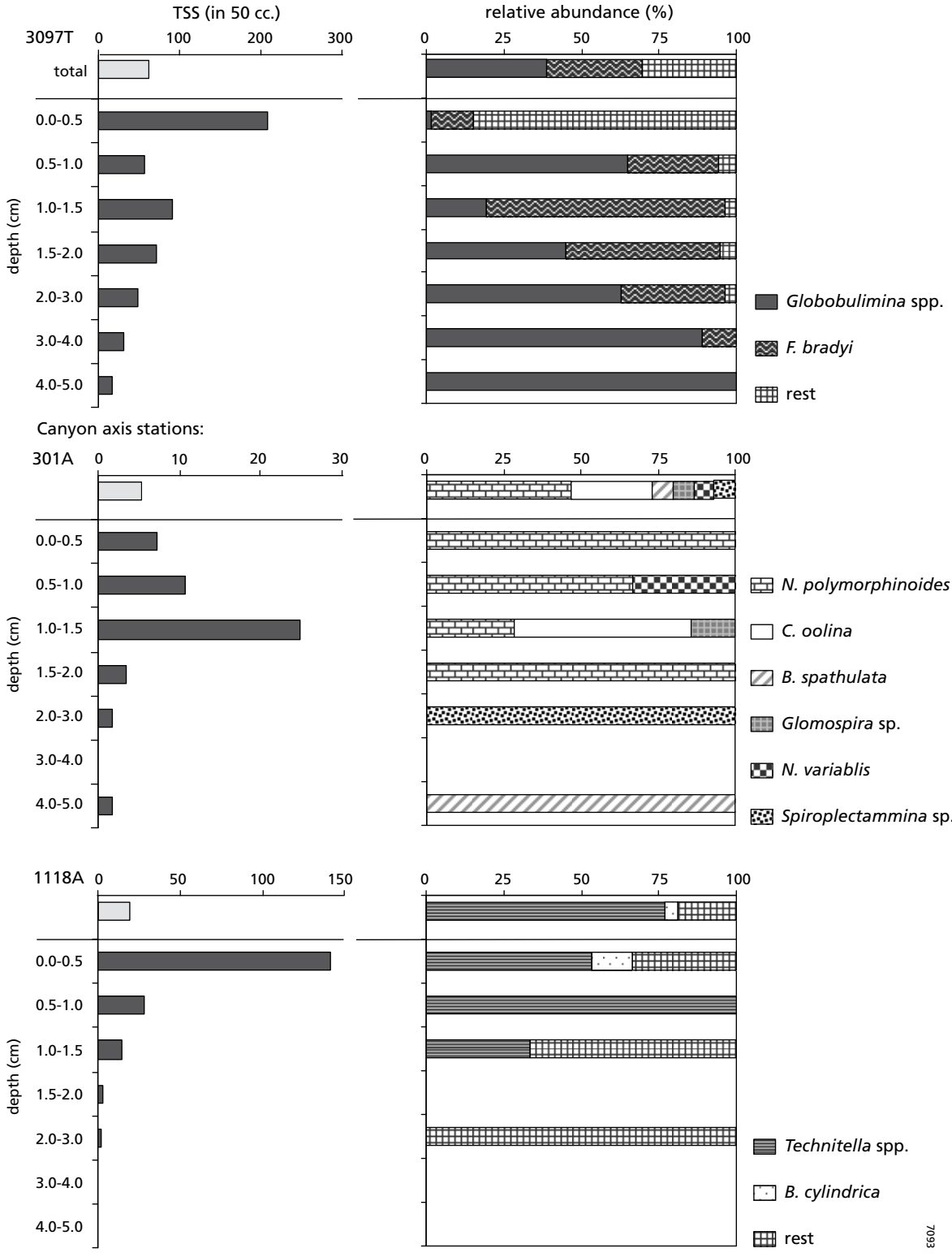
Figure 3.2. (continued)



encountered in the upper canyon terrace station 927T, where a significant number of specimens could be counted as whole individuals. Three *Bathysiphon* species were encountered in station 927T, including *Bathysiphon filiformis* that was found down to 3 cm sediment depth in sediment; the majority of specimens were located in the top 0.5 cm. In addition, a slightly spinous *Hyperammina?* sp. was very common in this station.

The lower canyon stations (4969, 4976) recorded the second highest total abundance of arborescent foraminifera but only fragments were found. In these stations predominantly *Saccorhiza ramosa* was found, a species not present in the upper canyon (apart from a single specimen found in station 890T). Fragments of *S. ramosa* were found in the top 1 cm of sediment, indicating an epifaunal habitat.

Figure 3.2. (continued)



3.5 DISCUSSION

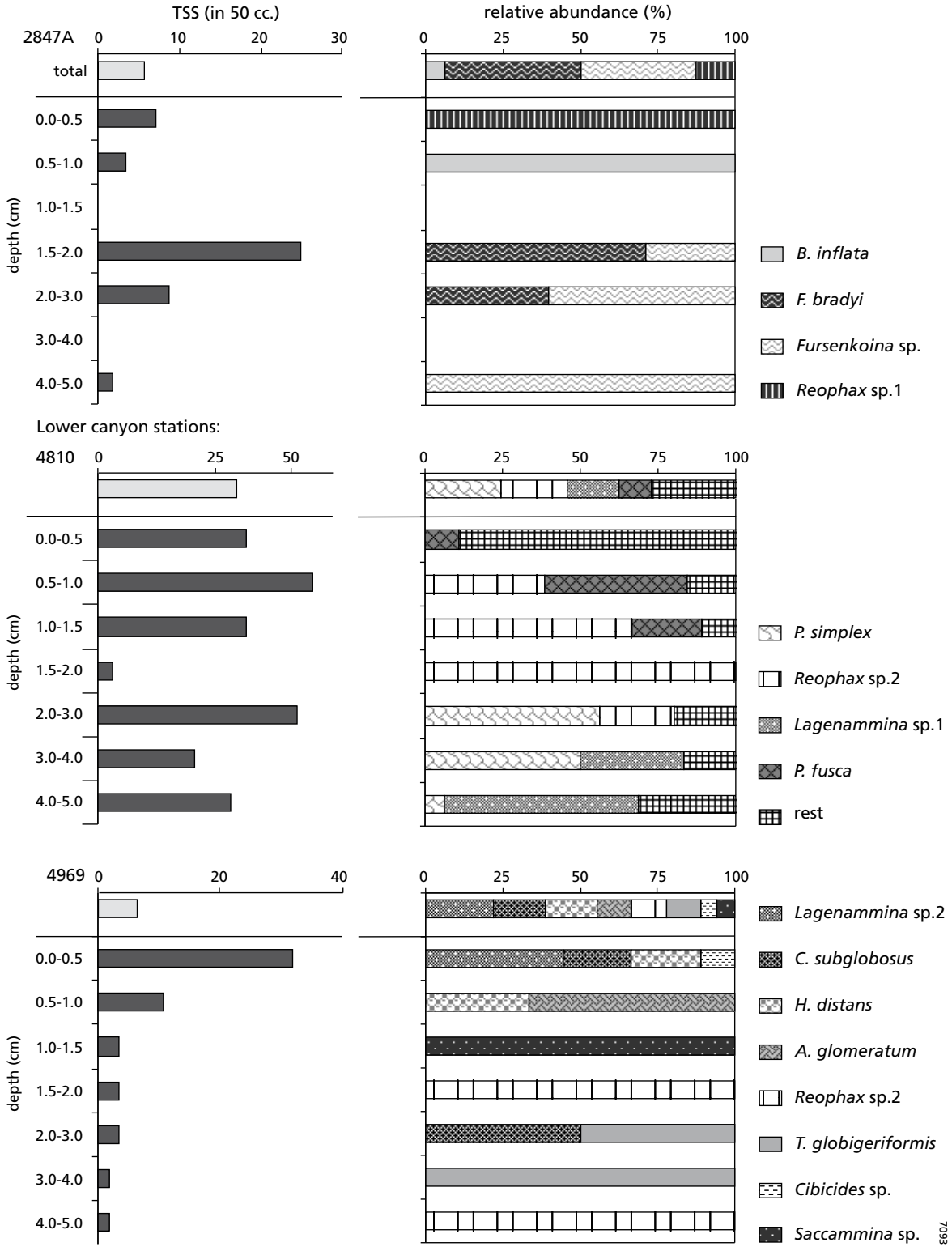
3.5.1 A priori considerations

Benthic foraminiferal faunas in the Nazaré Canyon will be discussed against the background of the studied sub-environments of the canyon. The environmental aspects and an evaluation of the study limitations are summarised below.

Nazaré Canyon environments

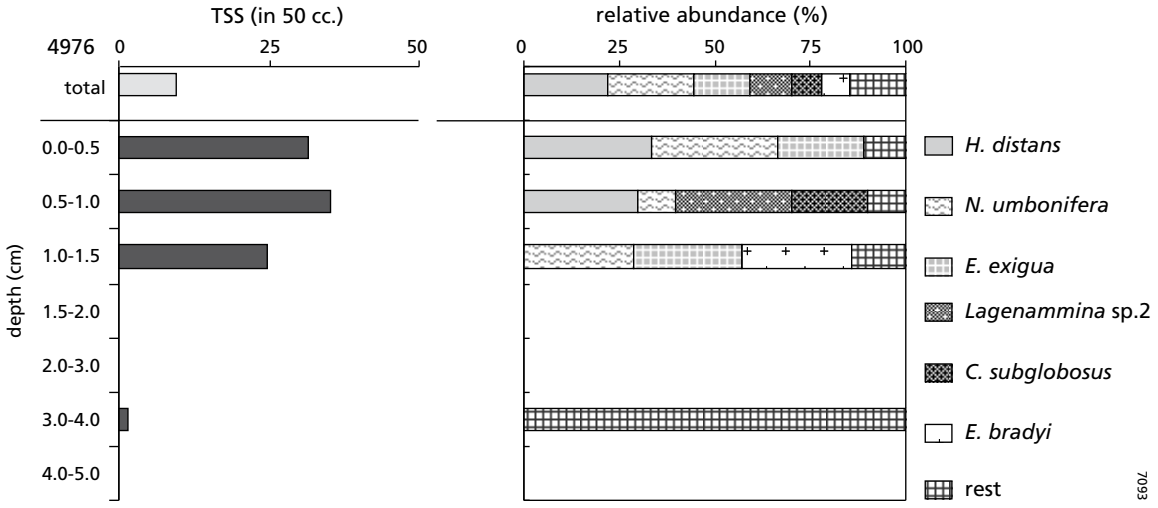
Benthic foraminiferal data is derived from the canyon axis (3 stations), terraces (7 stations) and the lowermost canyon (3 stations; Figure 3.1 and Table 3.2). In terms of sedimentary disturbance, the upper canyon axis (down to 2700 m; stations 301A and 1118A) is characterised by high-speed tidal currents, associated continuous resuspension of surface sediments, and

Figure 3.2. (continued)



intermittent gravity flows (De Stigter et al., in press; Tables 3.1 and 3.2). Thin turbidite layers in the sedimentary record at station 1118A and in-situ observations of near-bottom currents and turbidity indicate that sediment gravity flows must be relatively common at this depth. High sedimentation rates are counteracted by remobilisation and downward transport of the sediment load. In the middle canyon axis (2700 – 4000 m; station 2847A) tidal currents and resuspension are limited to spring tide maxima. The sediment accumulation appears to be higher in the middle canyon in comparison to the upper canyon. In the lower canyon (>4000 m; station 4810), sedimentary disturbance occurs via gravity flows on timescales of a year or longer. The deep canyon is characterised by low current velocities (< 5 cm/s; Table 3.2).

Figure 3.2. (continued)



Disturbance inside the canyon decreases away from the axis towards the terraces, where fine particles and organic carbon accumulate. The relatively lower energy conditions on the terraces are evident from higher cohesiveness of the surface sediments and the absence of sand in the collected multicores.

High organic carbon concentrations were measured throughout the canyon sediments. However, most of the bulk C_{org} is refractory and thus not profitable for benthic organisms. The more labile organic carbon, deriving from phytodetritus input was assessed by Garcia et al. (2007) from chloroplastic pigment equivalents (CPE), representing the sum of the chlorophyll *a* and phaeopigment. The freshness of the phytodetritus in turn is indicated by the ratio of Chl *a* versus Phaeo (phaeopigment) content. As Table 3.2 indicates, the upper canyon sediments (measurements along the axis) were enriched in labile, bio-available carbon (high CPE and Chla:Phaeo values); the labile carbon content decreasing towards the middle and lower canyon. The CPE values were still elevated in the lower canyon in relation to the adjacent slope (Garcia et al. 2007) but the Chla:Phaeo rations were similar. The lower canyon sediments are poor in relatively fresh organic matter and have oxygen penetration down to several centimetres. The lower canyon can be considered a moderately stable, food-limited environment and overall more comparable to the adjacent slope.

Limitations of the study

The rose Bengal staining method has disadvantages and it has been shown that under anoxic conditions the specimens may stain several months after the death of an organism (Bernhard, 1988, Hannah and Rogerson, 1997). Nevertheless, Murray and Bowser (2000) conclude that after the death of a foraminifer, under "natural conditions" (i.e. below oxygenated bottom waters), the problem of staining of dead specimens is negligible as tests that contribute to the sediment are emptied of protoplasm due to reproduction, growth stages, or predation. In addition, comparative analyses of different methodologies with rose Bengal stain, e.g. studies of Bernhard et al. (1997) and Lutze and Altenbach (1991), gave comparable results, and if rose Bengal is used with care, results can be 96 % correct.

As outlined in section 3.3.1, rose Bengal stained fragments of arborescent and tubular benthic foraminifera were included in the counts. These fragments (and complete individuals) were mainly found in the deep canyon, where current velocities do not exceed 5 cm/s, or on the more stable terrace sites. Therefore, it seems likely that the fragmentation occurred during sample processing and not as a result of sediment transport and subsequent burial. We considered the stained fragments to be part of live individuals at the time of collection (Appendix 3B).

The samples were collected during four different cruises, three of which during spring and one during autumn (64PE218, 2003), and hence a seasonal or inter-annual bias may play a role in the studied data-set. Nonetheless, clustering of presence/absence data of the stations (Figure 3.3a, b) leads to a consistent grouping of the sites sampled from similar canyon sub-environments and from similar water depths, indicating that despite different sample moments in time, total foraminiferal assemblages at a single site remain relatively stable through time. The relationships between sampling sites were further supported by the Pearson correlation (Table 3.4). Relatively good correlations were found for sites sampled at similar water depths and from similar canyon sub-environments. Therefore, it seems that the seasonal and inter-annual fluctuations in foraminiferal assemblages are not a major factor, and a direct comparison between stations can be made, with inclusion of the stations sampled in October 2003.

With this in mind, some relevant observations can be made concerning the distribution of foraminiferal faunas in Nazaré Canyon.

3.5.2 Foraminifera on the canyon axis

Upper and middle canyon axis

The stations located on the canyon axis recorded low total standing stocks of foraminifera (TSS) and low species richness (S). The physical disturbance along the axis of the canyon is likely to have an adverse effect on the development of stable benthic communities. The high sedimentation rates may bury the fauna, continuous resuspension of surface sediments may lead to unstable geochemical gradients in the sediments and

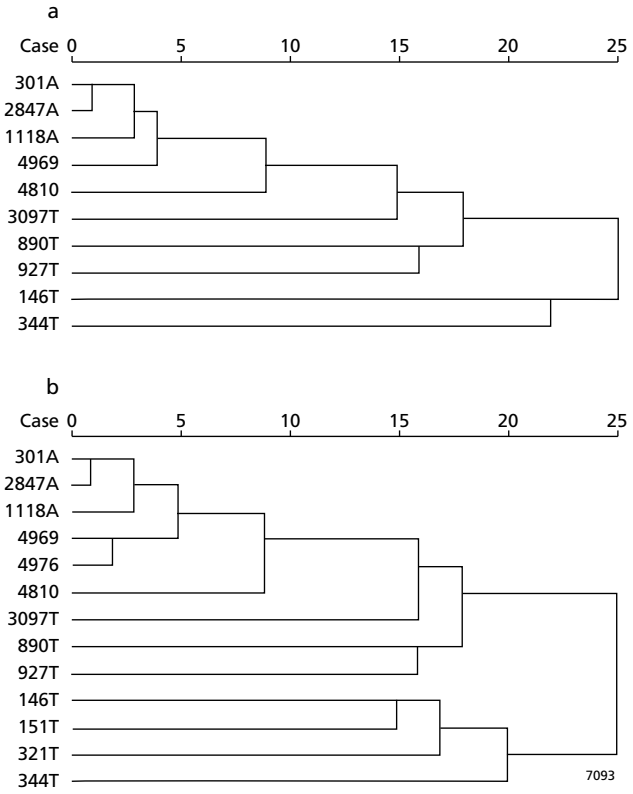


Figure 3.3. Dendrogram obtained by a hierarchical cluster analysis (squared Euclidian distance, average linkage). 3a.) Dendrogram produced using stations sampled in May only. 3b.) Dendrogram comprising all stations including the sites sampled in October 2003. The clustering was based on a presence-absence matrix of the total data set, including the arborescent and tubular foraminifera, and all the rare species. See section 3.3.2. for details.

high current speed may periodically flush away surface material (including fresh organic matter) and fauna. Low numbers of living foraminifera (even barren sites) were also recorded in submarine canyons off New Jersey (Jorissen et. al., 1994). The authors postulated that the downslope sediment transport, small scale mass wasting and/or bottom currents must be responsible for lack of fauna in the canyon sediments, as the sediments appeared neither food nor oxygen limited.

The near absence of relatively fragile tubular and branching arborescent foraminifera may also be attributed to the high degree of physical disturbance. Hess and Kuhnt (1996) found that large arborescent foraminifera are slow and poor recolonisers after environmental disturbance. Therefore, it is unlikely that these species could flourish in unstable environments.

Site 1118A

The upper canyon axis station 1118A is of particular interest in the context of the response of benthic foraminifera to sediment disturbance. Despite very high sediment fluxes related to frequent resuspension by tidal currents and sediment gravity flows (a maximum of 788.3 g/m^2·d was recorded by De Stigter et al. (in press) in a sediment trap placed near the bottom), this site had the highest TSS of the canyon axis stations. The assemblage was dominated by a species belonging to the genus *Technitella* (Figure 3.2; Table 3.4; Plate 3.1). *Technitella* spp. are rarely described in the literature. Anschutz et al. (2002) recorded high abundances of *Technitella melo* (an atypical species in their study area) in the Cap Breton Canyon after deposition of a turbidite. The authors interpreted *T. melo* as an opportunistic, first recoloniser species following the turbidite. When the same site was resampled a year later the foraminiferal assemblage was more diverse and dominated by *Bolivina subaenariensis* (Hess et al. 2005). Some *T. melo* were found, but the numbers had declined drastically, while other taxa had increased in abundance and the assemblage was quite similar to the fauna present prior to turbidite deposition. Bernhard (1992) found *Technitella* sp. in organically enriched (3-4 wt % C_{org}) sediments with shallow oxygen penetration depth from the Californian continental slope. Living *Technitella* spp. were also found by Swallow and Culver (1999) in canyons off the continental margin off New Jersey, but the ecological significance of this taxon was not discussed. The picture emerging is that the genus *Technitella* thrives in organically enriched sediments, and is able to quickly colonise new, barren habitats in the aftermath of sediment disturbance. To ascertain that the site was not inhabited by smaller foraminifera, the surficial sediments at this site were qualitatively inspected for smaller (63-150 µm)

146T													
151T	**0.690**												
301A		**0.218**											
321T	**0.364**	**0.492**	**0.634**										
344T	**0.400**	**0.493**	**0.274**	**0.698**									
890T					0.191								
927T	0.194	**0.269**	**0.388**	**0.779**	**0.528**	**0.339**							
1118A							**0.218**						
2847A													
3097T		**0.492**			0.178				**0.467**				
48010													
4696													
4976												**0.977**	
	146T	151T	301A	321T	344T	890T	927T	1118A	2847A	3097T	4810	4969	4976

Table 3.4. Pearson correlation coefficients. Correlation based on absolute counts of all foraminifera, including arborescent and tubular taxa (N=146). For values presented in bold, $p < 0.01$; values presented in standard font, $p < 0.05$.

foraminifera. The sediment, consisting of mica flakes and dark woody particles, looked similar to the larger size fraction (>150 µm) and was (nearly) barren of foraminiferal tests. This implies that the prevailing active sedimentary regime is so distressing for fauna, that *Technitella* spp. are the only foraminifera able to inhabit this environment.

A high degree of disturbance at station 1118A was also evident from the meiofaunal assemblage described by Garcia et al. (2007), dominated by two opportunistic nematode genera, *Sabatieria* sp. and *Metalinhomoeus* sp. These species are common in sediments disturbed by dredging and trawling activities (e.g. Boyd et al. 2000). In addition, they flourish in organic rich sediments and withstand relatively low-oxygen environments (e.g Jensen et al. 1992, Hendelberg and Jensen 1993, Lampadariou et al. 1997). Plate 3.1 and 3.2 somewhere close here.

3.5.3 Foraminifera on the canyon terraces

The highest standing stocks of foraminifera and the most diverse assemblages were found on the upper canyon terraces (Table 3.3), the TSS and the species richness declining with increasing water depth. These stations were predominantly inhabited by species as *Bolivina alata*, *Bulimina inflata*, *Bigenerina cylindrica*, *Melonis barleeanum*, *Globobulimina* spp. and *Chilostomella oolina*, previously referred to as infaunal by several authors (e.g. Corliss 1985, Corliss and Emerson, 1990, Buzas et al, 1993). The relatively shallow ALD5 of these species compared to other areas with deeper oxygen penetration (e.g. Corliss and Emerson, 1990, Corliss 1991, Schmiedl et al. 2000) suggest that their microhabitat is controlled by the prevailing redox conditions, in accordance with the TROX model developed by Jorissen et al. (1995) and amended by Jorissen (1999).

In comparison with the canyon axis however, the microhabitat distribution of foraminifera in the canyon terrace sediments is relatively well developed. This can be related to the prevailing, more stable sedimentary regime, and the concurrent greater stability of the redox zones. In terms of disturbance, the more stable nature of the terrace sites is also evidenced by the presence of several, fragile agglutinated species, including *Crithionina hispida* and another peculiar *Crithionina* species (Plate 3.2, Figure 3.2a, 3.3b) using two mica flakes to build its test.

In view of their frequent use in paleoceanographic studies, the infaunal taxa are of special interest. The occurrence of specific infaunal taxa and their microhabitats has previously been related to dietary requirements and/or to specific redox gradients and the associated bacterial populations. For instance, *M. barleeanum*, a common species on the upper canyon terrace stations 890T and 927T, has been described to occupy organic rich sediments of variable quality, i.e. sediments rich in relatively fresh organic matter (Caralp 1989a) or rich in degraded organic matter (Caralp 1989b). More recently, living *M. barleeanum* was found within the nitrate reduction zone in the sediment, and the dietary preferences of this taxon have been related to the presence of bacteria or degradation products of metabolically nutritious particles produced by bacteria in the sediment (Licari et al. 2003). Fontanier et al. (2005) also reported high numbers of *M. barleeanum* in the dysoxic sediments of Cap Ferret Canyon and hypothesised a relation between this taxon and prokaryotic communities within the sediment redox zones. Most of the stained *M. barleeanum* in our samples were surrounded by a sediment envelope, covering most of the test but especially concentrated near the aperture. This envelope may represent a feeding cyst, used by the foraminifer in gathering sediment particles together with bacteria and other detritus

Globobulimina spp. and *Fursenkoina* spp., relatively abundant in the middle canyon, are considered typical infaunal species and are also linked to high organic carbon loads (e.g. Corliss 1991, Silva et al., 1996, Fontanier et al., 2005). Recently, Risgaard-Petersen et al. (2006) observed respiration of *Globobulimina pseudospinescens* through denitrification of an intracellural nitrate pool under anoxic conditions; a direct observation that these foraminferal species have evolved to live in anoxic sediments. The ALD5 of *Globobulimina* spp. on station 3097T was deeper (2.5 cm depth) than *Fursenkoina bradyi* (1.4 cm) or Fursenkoina sp. (1.6 cm), implying that *Globobulimina* spp. prefers a deeper microhabitat.

3.5.4 Foraminifera in the lower canyon

In general, the foraminiferal assemblages in the lower canyon are more similar to other abyssal communities described in literature. At greater depth a decrease in calcareous foraminifera and an increase in agglutinated taxa is often observed, as well as an increase in the relative abundance of monothalamous taxa (Cornelius and Gooday, 2004). Our observation that the lower canyon stations were populated by relatively high abundances of agglutinated monothalamous species, such as *Lagenammina* spp. and *Psammosphaera fusca*, is in agreement with this. The only calcareous foraminiferal species present in relatively high numbers is *Pullenia simplex*. The deepest stations (4969, 4976) were characterised by very low TSS and assemblages dominated by the arborescent species *Saccorrhiza ramosa*. The measured current velocities in the lower canyon at 4976 m water depth were not observed to exceed 5 cm/s (De Stigter et al., in press), hence particle resuspension and transport of agglutinated fragments is unlikely. Therefore, it may be considered that the fragments of the arborescent fauna at the deepest sites were found in situ.

3.5.5 Arborescent and tubular foraminifera ecology

Several *Bathysiphon* species were found at the upper canyon terrace sites, and their abundance may be related to high organic carbon content and relatively low oxygen penetration depth in the upper canyon sediments. Gooday et al. (1992) found many *B. filiformis* on the continental slope off North Carolina, an area which receives a large input of C_{org} from both terrestrial and marine sources. This is also the case in the upper canyon sediments, which have a high terrigenous organic carbon component with some phytodetritus in surface sediments. Gooday et al. (2000) discovered two small undescribed species of *Bathysiphon* living inside the Oxygen Minimum Zone (OMZ) in the Arabian Sea. In addition, *B. capillare* was named as a dysoxic indicator by Schönfeld (2001), who found a significant correlation between the occurrence of *B. capillare* and dysoxic conditions in the sediments of the western Iberian Margin. All in all, our results agree with previous research and confirm that several *Bathysiphon* species occupy sediments with high organic carbon loads and with a relatively shallow oxygen penetration.

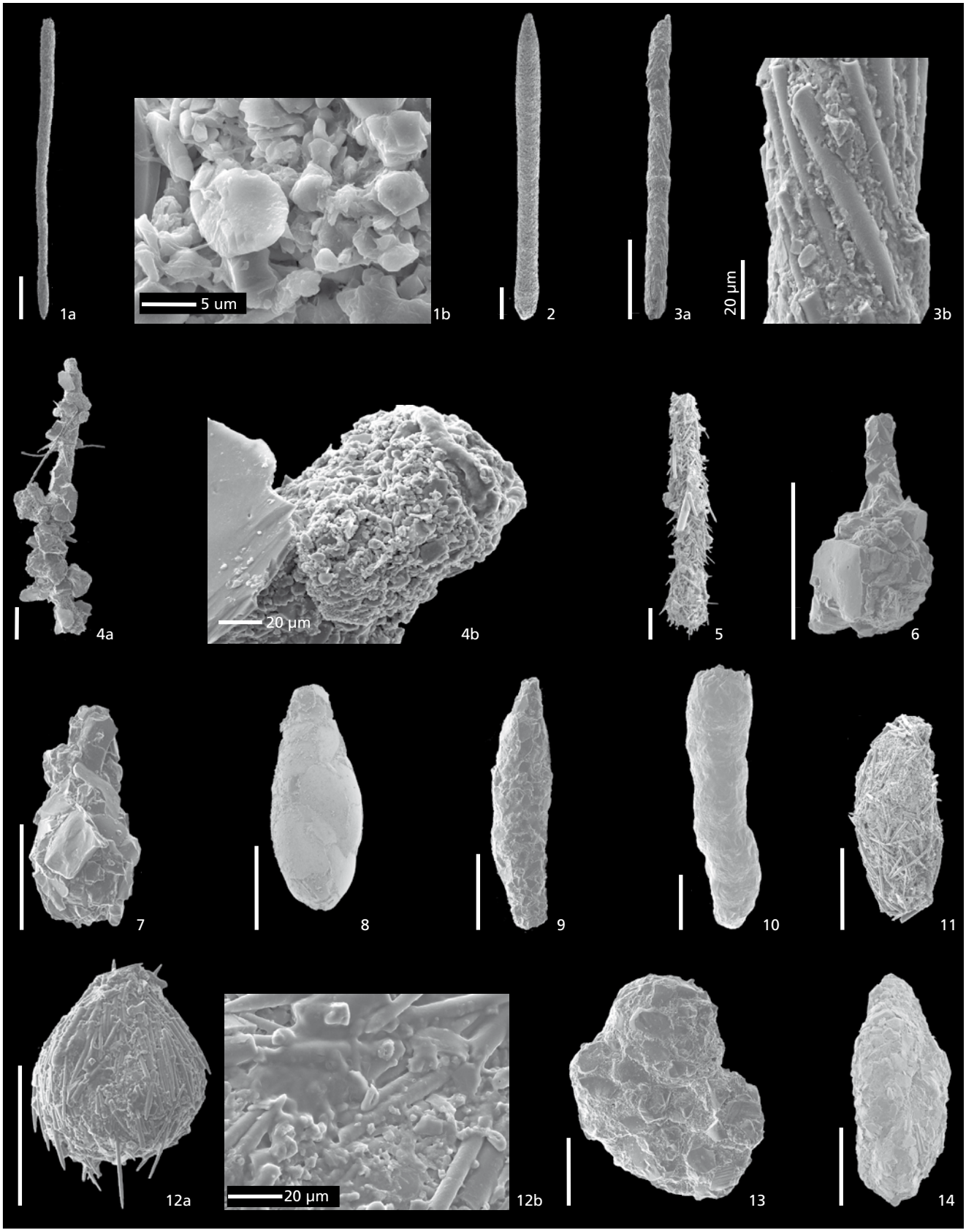


Plate 3.1.
Scale bar 200 µm, unless indicated otherwise.
1a, b. *Bathysiphon* sp.2
2. *Bathysiphon* sp.5
3a, b. *Bathysiphon strictus*
4a, b. *Hyperammina*? sp.
5. *Hyperammina* sp. (very spinous)
6. *Lagenammina* sp.2
7. *Lagenammina* sp.1
8. *Reophax* sp.1
9. *Reophax* sp.2
10. *Bigenerina cylindrica*
11. *Technitella* sp.
12a, b. *Technitella melo*
13. *Discammina compressa*
14. *Nouria polymorphinoides*

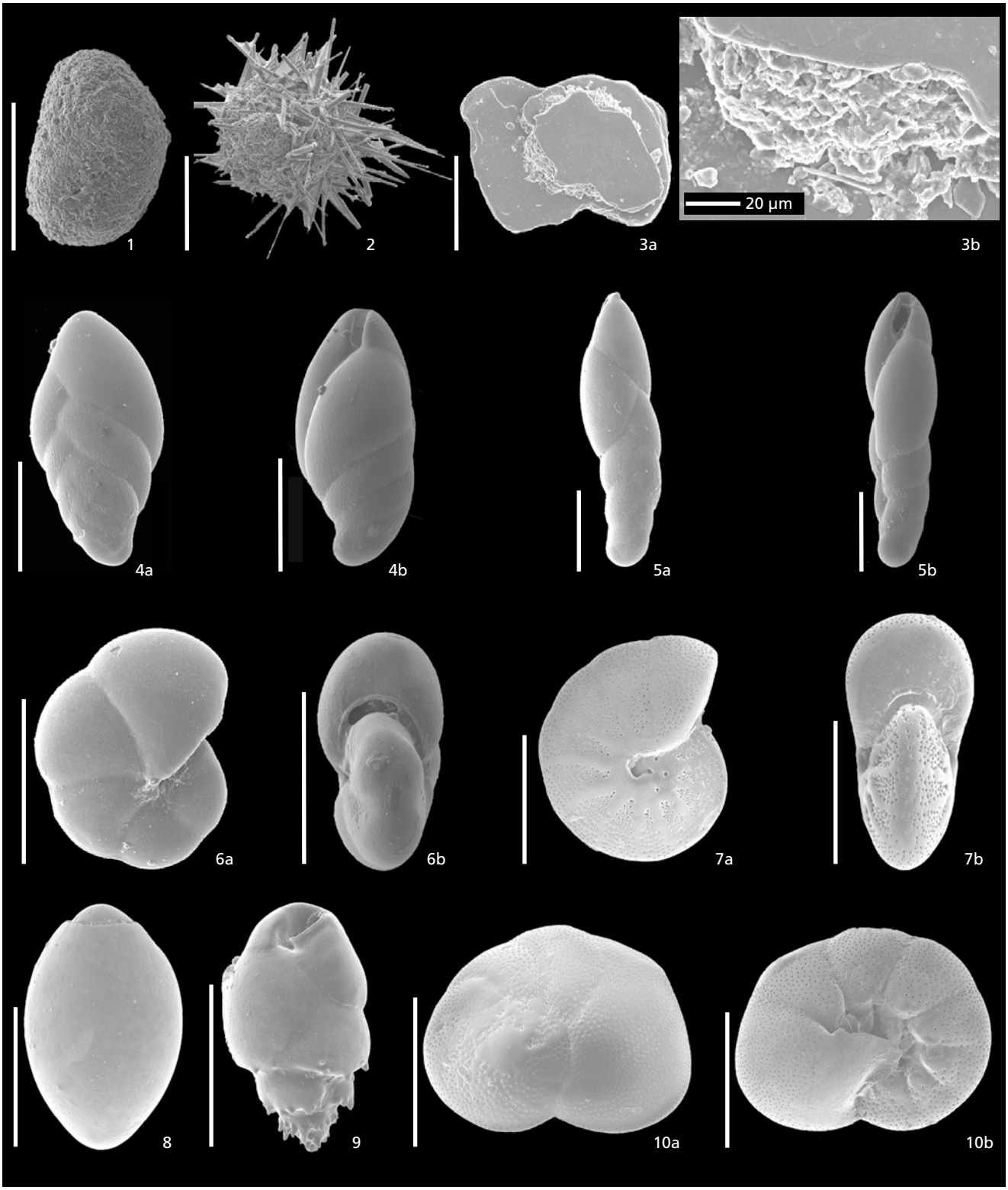


Plate 3.2.
Scale bar 200 µm, unless indicated otherwise.
1. *Saccammina* sp. (fine grained)
2. *Crithionina hispida*
3a, b. *Crithionina* sp. (mica sandwich)
4a, b *Fursenkoina* sp.
5a, b *Fursenkoina bradyi*
6a, b. *Pullenia simplex*
7a, b *Melonis barleeanum*
8 Chilostomella oolina
9. *Bulimina marginata*
10a, b *Valvulineria bradyana*

The near-surface position of the arborescent fauna in the Nazaré Canyon suggests that these large foraminifera consume organic matter either directly from the settling detritus or from the surface sediments. Some specimens of B. filiformis were observed to protrude out of the surface sediments in the collected cores. This living position was previously described by Gooday et al. (1992) for B. filiformis that had only 1 cm of the tube buried in the sediment. In the canyon, fragments of B. filiformis were found somewhat deeper, reaching down to 3 cm depth. However, the deep occurrence may be a sampling artefact, as threads and tubes can be pulled down when the multiple corer penetrates the sediment surface. The high abundance of B. filiformis specimens in the near surface sediments and the visual evidence for an out-projecting living position would imply that these species are suspension feeders, as was suggested for Bathysiphon rusticus and B. folini by Gooday (1983).

Numerous rose Bengal stained fragments of *S. ramosa* were found in the top 1 cm of the lower canyon sediments (stations 4969, 4976), indicating that this species prefers an epifaunal microhabitat and thrives in stable environments, under well-oxygenated bottom waters and low food supply. This is in agreement with observations made by Altenbach et al. (1988). Therefore, the absence of *S. ramosa* in the upper canyon sediments may be related to higher current activity, as this species seems to be highly adapted to low bottom currents around 2 cm/s, high current speeds leading to test breakage

Some arborescent foraminifera, e.g. *Rhabdammina abyssorum*, can survive periods of starvation by consuming their own protoplasm, and when food becomes available they are able to benefit and consume it quickly (Linke, 1992). It may be that *S. ramosa* has adopted a similar life strategy and is able to survive for long periods without any food, benefiting from episodic sedimentation events in the lower canyon. Previously, a concentration of suspension feeders including arborescent foraminifera on the upper continental slope of Goban Spur, NE Atlantic was associated with enhanced current speeds up to 35 cm/s (Flach et al., 1998). The authors reasoned that the suspension feeding fauna benefited from the increased loads of suspended matter and that the flow velocity was an important parameter in structuring the benthic community. In the lower Nazaré Canyon, the flow velocities and the suspended load are relatively lower than in the Goban Spur. Nevertheless, the conditions may still be beneficial for suspension feeders. The sediment trap data from De Stigter et al. (in press) indicates that despite low mass fluxes measured in the lower Nazaré Canyon, the arriving material is relatively organic rich (C_{org} up to 4.2 wt. %). In addition, this material is not diluted by resuspended sediment grains as the flow velocities are not sufficient to do so. Therefore, *S. ramosa* may catch and feed on drifting organic particles, comparable to what *Bathysiphon* does in the upper and middle canyon. A relation between suspended matter load and occurrence of *S. ramosa* in the Gulf of Lions, Western Mediterranean, has also been hypothesised by Schmiedl et al (2000).

Foraminiferal species	Upper canyon												Middle canyon						Lower canyon					
	146T		151T		321T		344T		301A		890T		927T		1118A		2847A		3097T		4810		4969		4976	
	no	ALD	no	ALD	no	ALD	no	ALD	no	ALD	no	ALD	no	ALD	no	ALD	no	ALD	no	ALD	no	ALD	no	ALD	no	ALD
Adercotryma glomeratum	6	0,3					1														2		2			
Bigenerina cylindrica	64	1,2	40	1,3	18	0,5	46	0,8			30	1,5	6	0,9	2				1							
Bigenerina nodosaria	50	1,9	47	1,6	2		3																			
Bolivina alata			1		5	0,8	9	0,6			57	1,6	2													
Bolivina spathulata	1		1				4		1						1				2							
Bulimina inflata	3		2		4		6	0,3			83	0,6	1				1		2							
Bulimina marginata	43	0,4	10	0,9	17	0,7	8	0,8											1							
Chilostomella oolina	39	2,3	51	2,3	277	1,1	94	2	4		14	3	372	1,6					3							
Cibicides pachyderma	1						23	0,4			13	0,9	17	0,5												
Cibicides sp.																						1				
Cribrostomoides subglobosus											1		5	0,3					4		1		3		2	
Crithionina hispida											1		52	0,3												
Discammina compressa											7	1,4	107	0,4												
Eggerella bradyi																					1				2	
Eggerella scabra	37	0,4	9	1,8	2		5	0,3											2							
Epistominella exigua																									4	

Foraminiferal species	Upper canyon																Middle canyon				Lower canyon					
	146T		151T		321T		344T		301A		890T		927T		1118A		2847A		3097T		4810		4969		4976	
	no	ALD	no	ALD	no	ALD	no	ALD	no	ALD	no	ALD	no	ALD	no	ALD	no	ALD	no	ALD	no	ALD	no	ALD	no	ALD
Fursenkoina bradyi																	7	2,0	54	1,4						
Fursenkoina sp.																	6	2,6	4							
Globobulimina spp.	30	1,4	91	2,6	22	1,2	31	2,5			16	2,7	3						69	2,5						
Glomospira sp. (white)									1						1											
Hormosinella distans																							3		6	0,5
Lagenammina sp.1																					14	4,2				
Lagenammina sp.2																							4		3	
Melonis barleeanum			4		1		12	0,5			176	1,3	161	0,6	1											
Neolenticulina variabilis	3		1		2		9	0,3	1										1							
Nouria polymorphinoides	3		13	1,6	69	1,3			7	0,9																
Nuttallides umbonifera																									6	0,7
Psammosphaera fusca																					9	0,8			1	
Pullenia simplex																					21	2,9			1	
Reophax sp.1	63	1,9	45	2,8	24	1,7											2									
Reophax sp.2																					18	1,6	2		1	
Saccammina sp.																							1			
Saccammina sp. (fine grained)	3		1		31	0,3					16	1,6														
Spiroplectammina sp.	22	1,4	12	1,7			1		1																	
Technitella spp.	1										3		99	0,4	44	0,4										
Trochammina globigeriniformis	4		1				1				1								2				2			
Uvigerina peregrina			47	0,6	15	0,4	13	1,2											2							
Valvulineria bradyana	8	1,3	12	1,1	39	0,8	100	0,7			2								3							
Valvulineria rugosa	33	0,3	14	0,3	1		9	0,4											2							
Veleroninoides scitulus			7	0,9			14	0,5			95	0,9	17	0,5												
rest	151		169		98		130		0		49		54		5		0		24		18		0		1	
Total	565		578		627		519		15		564		896		54		16		176		84		18		27	

Appendix 3A: Total number of common foraminifera (per core/below 28.3 cm2, in 141.5 cm3 of sediment) in the canyon. The species listed make up four per cent of the total abundance at least in one of the stations. The average living depth (ALD5) is calculated for every species when five specimens or more are present, down to 5 cm depth in sediment. The highlighted stations are on the canyon axis.

Foraminiferal species		Upper canyon																Middle canyon				Lower canyon					
		146T		151T		301A		321T		344T		890T		927T		1118A		2847A		3097T		4810		4969		4976	
		no	ALD	no	ALD	no	ALD	no	ALD	no	ALD	no	ALD	no	ALD	no	ALD	no	ALD	no	ALD	no	ALD	no	ALD	no	ALD
Arborescent sp.1 (coarse grained)	(w)																			0,3							
	(f)											1								1							
Arborescent sp.2 (very spinous)	(w)																										
	(f)											1															
Arborescent sp.3 (tubular)	(w)																										0,3
	(f)									2												2		2		6	
Arborescent sp.4	(w)																										
	(f)															2											
Arborescent sp.5	(w)																										
	(f)															1											
Arborescent sp.6 (tubular, white)	(w)																										0,8
	(f)																									1	
Bathysiphon capillare	(w)	1	0,4							1	0,5																
	(f)	7								6																1	
Bathysiphon filiformis	(w)									1	0,9			8	0,8					5	0,3						
	(f)									6				8						1							
Bathysiphon rufus	(w)																										
	(f)																										
Bathysiphon sp.2	(w)											1		3	0,3												
	(f)	1												2													
Bathysiphon sp.?	(w)																										
	(f)															1											
Bathysiphon sp.5	(w)													2	0,3												
	(f)																										
Bathysiphon strictus	(w)		1,3		1,1						0,4										0,3						
	(f)	8		6						6										5							
Hyperammina sp.?	(w)			1										26	0,4												
	(f)													48													
Hyperammina sp.2	(w)											5	1,6	3	0,5												
	(f)											4		4													
Rhabdammina discreta	(w)													10	0,5												
	(f)											1		14													
Rhabdammina? sp.	(w)																										
	(f)	3																									
Rhizammina sp.?	(w)																										
	(f)													3													
Saccorhiza ramosa	(w)											1													0,5	1	0,7
	(f)																						29			43	

3.6 CONCLUSIONS

The very low total standing stocks (TSS) of foraminifera recorded on the upper and middle canyon axis can be related to prevailing strong physical disturbance, in the form of fast current speeds, high sedimentation rates and frequent sediment resuspension, leading to an unstable sediment substrate. The *Technitella* sp. occurring in station 1118A can be regarded as a highly opportunistic recoloniser, indicating disturbed environments, high sedimentation rates, resuspension of surface sediments and fast current speeds. In addition, *Technitella* spp. appear to thrive under eutrophic conditions.

Contrary to the axis, high TSSs were recorded in the upper and middle canyon terrace stations, where the sedimentary regime is more stable and fine sediment, together with C_{org}, can accumulate. These stations also had more diverse assemblages and better differentiated microhabitat patterns. The assemblages were dominated by infaunal species, such as *Melonis barleeanum, Chilostomella oolina* and *Globobulimina* spp. The high abundances of infaunal species reflect the low oxygen content and high bio-available carbon loads measured in these stations. The absence of sedimentary disturbance is reflected in the occurrence of fragile agglutinanted taxa (e.g. *Crithionina hispida*).

The benthic fauna of the lower canyon is more similar to open slope abyssal communities and dominated by agglutinated taxa, including species of *Reophax* and *Lagenammina.* The bio-available carbon, measured as chloroplastic pigment equivalents (CPE), is low in the deepest part of the canyon and the bulk C_{org} is composed of refractory material. Some fauna may benefit from episodic sedimentation events that can provide food for benthos.

Several species of *Bathysiphon* were encountered in the surface sediments of the upper canyon terraces, implying that this species prefers eutrophic conditions. *B. filiformis* was observed protruding out of the sediment. This life position may suggest a filterfeeding mode of life. The arborescent community in the lower canyon was dominated by *S. ramosa*. The more oligotrophic nature of the lower canyon suggests that *S. ramosa* can successfully colonise and dominate the foraminiferal assemblage in low-energy, food limited environments.

Acknowledgments.
The authors wish to thank the crews and captains of the R.V. Pelagia, and everyone participating in the Portuguese margin canyon and HERMES cruises for all the efforts and hard work at sea. We are grateful to Erica Koning and Eric Epping for sharing knowledge, data, and for stimulating discussions on the canyon geochemistry, and to Rosa Garcia for providing insight into meiofaunal communities of Nazaré Canyon. A very special thanks goes to Andrew J. Gooday, for help with the arborescent and tubular foraminiferal taxonomy and the counting method, and providing references for the subject. We are thankful to Ymke van den Berg, who picked the samples collected during the cruise 64PE138. Also we would like to thank Gerrit van't Veld and Geert Ittmann for their help with sample preparation. We wish to acknowledge A. Altenbach and an anonymous reviewer for their critical and constructive review of the earlier version of this manuscript. Material for this study was collected within the framework of three projects funded by the European Commission: OMEXII, EC contract MAS3-CT96-0056, EUROSTRATAFORM, EC contract EVK3-CT-2002-00079 and HERMES, EC contract OCE-CT-2005-511234. Shiptime on R.V. Pelagia was provided by Royal NIOZ. This is NSG publication number 20070701

Appendix 3B: Counts of arborescent and tubular foraminifera (per core/below 28.3 cm^2); w= whole specimens, f= fragments. The average living depth (ALD5) is based on the total sum of the whole specimens and fragments and calculated in centimetres. The stations highlighted in grey are located on the canyon axis.

Appendix 3C: Taxonomic notes.
Abundant (≥ 4%) taxa are listed, with references to plates and figures in the literature, or plates presented in this paper.

Adercotryma glomeratum (Brady) = *Lituola glomerata* Brady 1878, Jones (1994), Plate 34, Figures 15-18

Bigenerina cylindrica Cushman, 1922 (Plate 3.1, Figure 10)

Bigenerina nodosaria d'Orbigny 1826, Jones (1994), Plate 44, Figures 14-18

Bolivina alata (Sequenza) = *Vulvulina alata* Sequenza, 1862, Jones (1994), Plate 53, Figures 2-4

Bolivina spathulata (Williamson) = *Textularia variabilis* var. *spathulata* Williamson, 1858, Jones (1994), Plate 52, Figures 20-21

Bulimina inflata Seguenza, 1862, Van Leeuwen (1989), Plate 8, Figure 4

Bulimina marginata d'Orbigny, 1826 (Plate 3.2, Figure 9)

Chilostomella oolina Schwager, 1878 (Plate 3.2, Figure 8)

Cibicides pachyderma (d'Orbigny) = *Truncatulina pachyderma* Rzhehak, 1896, Schweizer (2006), Plate 6, Figures k-p

Cribrostomoides subglobosus (Cushman) = *Haplophragmoides subglobosum* Cushman 1910, Jones (1994), Plate 34, Figures 8-10

Crithionina hispida Flint 1988 (Plate 3.2, Figure 2)

Discammina compressa (Goës) = *Lituola irregularis* var. *compressa* Goës, 1882 (Plate 3.1, Figure 13)

Eggerella bradyi (Cushman) = *Verneuilina bradyi* Cushman 1911, Jones (1994), Plate 47, Figures 4-7

Eggerella scabra (Williamson), = *Bulimina scabra* Williamson 1858, Jones (1994), Plate 47, Figures 15-17

Epistomella exigua (Brady) = *Pulvinulina exigua* Brady 1884, Schiebel (1992), Plate 5, Figure 9

Fursenkoina bradyi (Cushman) = *Virgulina bradyi* Cushman, 1922 (Plate 3.2, Figure 5a, 5b).

Fursenkoina sp. (Plate 3.2, Figure 4a, 4b)

Hormosinella distans (Brady) = *Reophax distans* Brady, 1881, Jones (1994), Plate 31, Figures 18-22

Lagenammina sp.1 (Plate 3.1, Figure 7)

Lagenammina sp.2 (Plate 3.1, Figure 6)

Melonis barleeanum Williamson, 1858 (Plate 3.2, Figure 7a, 7b)

Neolenticulina variabilis (Reuss) = *Cristellaria variabilis*, Reuss 1850, Jones (1994), Plate 68, Figures 11-16

Nouria polymorphinoides Heron-Allen and Earland, 1914 (Plate 3.1, Figure 14)

Nutallides umbonifera (Cushman) = *Pulvinulina umbonifera* Cushman 1933, Van Leeuwen (1986), Plate 15, Figures 11-13; Plate 16, Figures 1-7

Psammosphaera fusca Schultz, 1875, Jones (1994), Plate 18, Figures 1-8

Pullenia simplex Feyling-Hanssen 1954 (Plate 3.2, Figure 6a, 6b)

Reophax sp.1 (Plate 3.1, Figure 8)

Reophax sp.2. (Plate 3.1, Figure 9)

Saccammina sp. (fine grained) (Plate 3.2, Figure 1)

Genus *Technitella* Norman 1878 (Plate 3.1, Figure 11, 12a, 12b)

Trochammina globigeriniformis (Parker and Jones) = *Ammoglobigerina globigeriniforamis* Parker and Jones 1865, De Stigter (1996), Plate 3.1, Figures 5a-c

Uvigerina peregrina Cushman, 1923, Schweizer et al. (2005), Figure 3

Valvulineria bradyana (Fornasini) = *Discorbina bradyana* Fornasini 1900 (Plate 3.2, Figure 10a, 10b)

Valvulineria rugosa (d'Orbigny) = *Rosalina rugosa* d'Orbigny 1839, Jones (1994), Plate 87, Figure 3

Veleroninoides scitulus (Brady) = *Haplophragmium scitulum* Brady 1881, Jones (1994), Plate 34, Figures 11-13

Bathysiphon capillare de Folin, 1886, Gooday (1988a), Figures 2-5

Bathysiphon filiformis Sars, 1872, Gooday (1988b), Figures 1-3

Bathysiphon rufus de Folin, 1886, Gooday (1988a), Figures 12-14

Bathysiphon sp.2 (Plate 3.1, Figure 1a, 1b)

Bathysiphon sp.5 (Plate 3.1, Figure 2)

Bathysiphon strictus de Folin, 1886 (Plate 3.1, Figure 3a, 3b)

Hyperammina? sp. (Plate 3.1, Figure 4a, 4b)

Hyperammina sp.2 (Plate 3.1, Figure 5)

Rhabdammina discreta Brady, 1881, Jones (1994), Plate 22, Figures 7-10

Saccorhiza ramosa (Brady) = *Hyperammina ramosa* Brady, 1879, Jones (1994), Plate 23, Figures 15-19

CHAPTER 4

The influence of a simulated diatom bloom on deep-sea benthic foraminifera and bacteria: a mesocosm study

Together with: A.M. Langezaal, Y.A. van Lith, I.A.P. Duijnstee, G.J van der Zwaan. In revision, Deep Sea Research I

ABSTRACT

Live benthic foraminifera were collected from 900 m water depth on the Portuguese continental margin. A diatom species, *Thalassiosira pseudonana*, was used to create an artificial diatom bloom under controlled laboratory conditions. Two different diatom loads, high (6.8 mg C) and low (2.3 mg C) load, were fed to benthos. The response of the benthic foraminifera, total standing stocks (63-150 µm, >150 µm size fractions) and vertical distribution in the sediment, was monitored at 28 and 56 days following the simulated food pulse. The treated cores, or mesocosms, were compared to controls that were harvested at the experimental setup, prior to the feeding and at the end of the experiment. The bacterial activity was assessed in terms of benthic nitrate and ammonium fluxes across the sediment-water interface.

At the onset of the experiment (prior to the simulated diatom bloom) the total standing stocks of foraminifera declined significantly. The population recovered following the feeding and especially under the higher carbon load the foraminiferal numbers increased in comparison to the control cores. In general, a 'two-phased' response was measured in different size classes of foraminifera. The first phase was an increase in the smaller-sized (63-150 µm) subpopulation followed by an increase in the larger-sized (>150 µm) subpopulation during the second phase of the experiment.

Elevated effluxes of ammonium were measured following the simulated diatom bloom. The highest effluxes were seen in the high load treatment, reflecting the highest remineralised carbon load. The ammonium effluxes normalised to control levels around 25 days after the bloom. In addition, high effluxes of nitrate were measured, indicating enhanced nitrification following the diatom deposition. The nitrate effluxes remained positive longer and normalised to control levels around 40 days after the feeding event.

Several foraminiferal taxa, e.g. *Melonis barleeanum*, *Bigenerina cylindrica*, *Chilostomella oolina*, responded to the diatom bloom (or increased bacterial activity) and increased in numbers. However, the vertical distribution of these infaunal species was not influenced by the added food. Only two species, *Pullenia* sp. and *Trochammina* sp., were observed to change their microhabitat distribution in response to the added diatoms, increasing in numbers in the surficial sediments. These two taxa most likely migrated to the surface to consume the labile organic matter. In contrast, the other infaunal species perhaps benefited from the diatom bloom indirectly e.g. from increased bacterial activity in the sediment.

4.1 INTRODUCTION

Benthic foraminifera are among the most important and common living organisms in modern deep-ocean sediments, constituting a substantial part of the biomass in many locations (e.g. Bernstein et al., 1978, Snider et al., 1984, Gooday, 1986, Gage et al., 1995). Because of their high fossilisation potential they are also extensively used in paleoceanographic studies, for instance to interpret past variations in Earth's climate. But despite their value as proxies, much is still unknown about the ecological functioning of benthic foraminifera. Today, it is largely accepted that foraminiferal occurrence in the deep sea is regulated mainly two, often inversely co-varying, parameters: oxygen and food (Jorissen et al, 1995, van der Zwaan et al., 1999). However, the changes in oxygen concentration and food supply are related to other subsequent changes, such as redox zonation and bacterial activity in sediment. For some time, authors have noted that foraminifera may consume bacteria (mainly aerobic bacteria) selectively (Lee et al., 1966, Lee and Muller 1973, Langezaal et al. 2005) or non-selectively (Gooday et al., 2002, Goldstein and Corliss, 1994, Nomaki et al, 2006). In recent years, it has become more apparent that variations in sediment redox chemistry and specific bacterial populations may play a vital role in explaining the occurrence of foraminiferal species and their microhabitats in the sediment. The correlation between zonation of anaerobic bacteria and foraminiferal depth distribution was first suggested by Jorissen et al. (1998). Later, Fontanier et al. (2005) hypothesised that some deep infaunal species may graze on bacteria selectively or benefit from living in symbiosis with heterotrophic and chemolithoautotrophic bacteria. Recently, nitrate respiration has been found in several foraminiferal species (Risgaard-Petersen et al., 2006), suggesting that availability of inorganic nutrients (e.g. nitrate, NO_3^-) as alternative electron acceptor in respiration may also play a crucial role in foraminiferal depth distribution.

The availability of nutrients in benthic environments is controlled largely by phytodetritus flux to the sea floor, as remineralisation of organic carbon leads to release of inorganic nutrients, such as ammonium (NH_4^+; e.g. Blackburn and Henriksen, 1983, Hammond et al. 1985, Jensen et al., 1990 Dahllöf and Karle 2003). The rate of remineralisation (production of NH_4^+) and subsequent bacterial processes e.g.

nitrification (oxidation of NH_4^+ to NO_3^-) or denitrification (NO_3^- reduction to N_2), will dictate the rate of exchange of NH_4^+ and NO_3^- across the sediment-water interface. Net transfer rates of these nitrogen species are known as 'benthic fluxes' where positive flux measurement indicates an efflux from sediment into the overlying water and negative measurement an influx from the overlying water into the sediment.

In order to confine and better validate benthic foraminifera as a proxy for environmental conditions, a mesocosm study was conducted. In a laboratory, it is possible to individually control and restrict parameters that are strongly correlated in nature, i.e. oxygen and food. The aim of the experiment was to investigate a relatively long-term response by deep-sea benthic foraminifera to different quantities of food (diatoms) supply under controlled, constant oxygen concentrations. The response of the total standing stock was observed. As different size classes of foraminifera were investigated independently (>150 μm fraction and 63-150 μm fraction), inferences about reproduction of some foraminiferal taxa and growth of single species were made possible. In addition, the vertical distribution of foraminifera was related to sediment geochemistry (e.g. oxygen, nitrate and ammonium pore-water content). Further, the experiment was designed to analyse bacterial activity in relation to remineralisation of added food, an important process largely neglected in previous long-term feeding studies. Therefore, the mesocosm study was also designed to provide new insight into the interaction of foraminifera and bacteria.

4.2 MATERIALS AND METHODS

4.2.1 Sediment collection

Sediment was collected during cruise 64PE236 of RV "Pelagia" on 14 May 2005. The sample site was located on a terrace in the Nazaré Canyon (station 64PE236-13: 39°60' N, 9°40'E), at 900 m water depth (Figure 4.1). Eighteen cores were collected using a MUC 8+4 multiple-corer developed by Octopus GmbH, equipped with eight tubes with an internal diameter of 6 cm and four tubes with a diameter of 10 cm. The smaller 6 cm cores were used for direct sample collection, while the larger 10 cm cores were sub-sampled with 6 cm tubes. The cores were kept intact, stored at in-situ temperature in the dark and transported to Utrecht in cool boxes within four days after sediment recovery. For transport purposes and in order to prevent development of anoxia, the cores were drained and only a thin overlying water column of about 1-2 cm was left on top of the sediment. The overlying water from the collected cores was saved and additional bottom water from the sample site was collected using a CTD rosette sampler. Seawater was filtered (through a 0.4 μm a polycarbonate filter) and stored under in-situ temperature and in darkness until use in the laboratory.

4.2.2 Experimental setup

In the laboratory the cores were immediately processed for experiment use at time (t) = 0 (Table 4.1). All cores were sliced into three depth intervals: 0-2 cm, 2-5 cm and 5-10 cm. Sediment samples from each depth interval were placed into separate buckets. Some collected sea water was added into the buckets to allow gentle mixing and homogenisation of sediment in composition. The produced slurries were left to settle over night after which forty millilitres of the homogenised

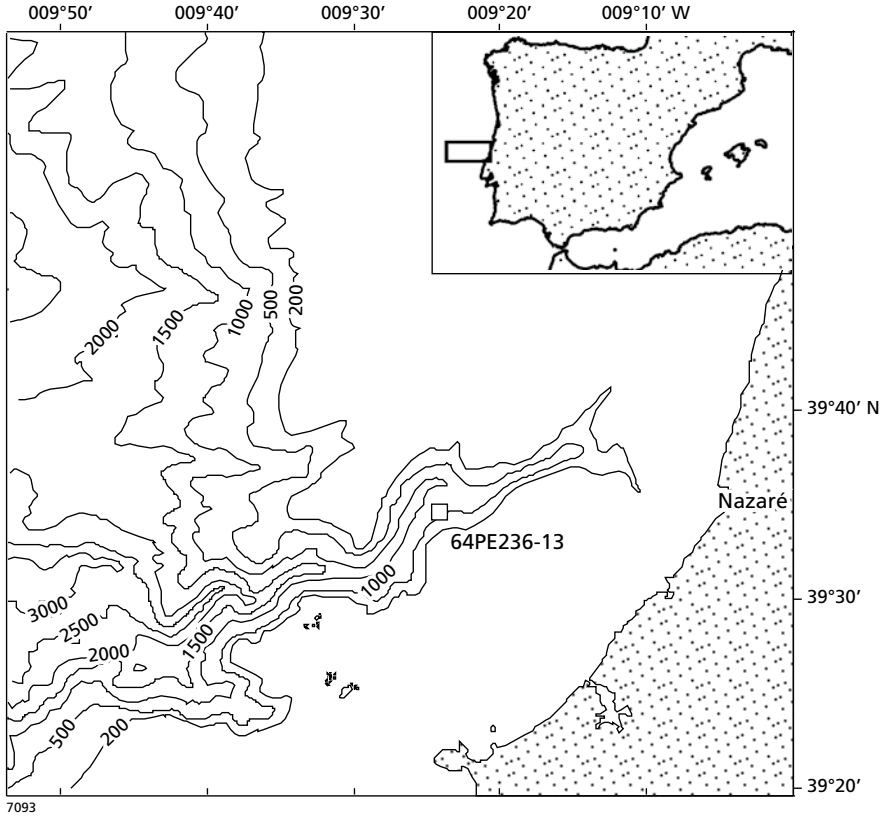


Figure 4.1. Map of the Nazaré Canyon indicating the sediment sampling site. Inset shows the Iberian Peninsula and the location of the Nazaré Canyon. Figure modified from De Stigter et al. (in press).

Sampling time	t=0, day 1	cores settling	t=1, day 48	t=2, day 76	t=3, day 104
Experiment set up	Sediment homogenised, experiment cores filled				
Feeding			12 cores fed: 6 with high load (HL) = 6.8 mg C, and 6 with low load (LL) = 2.3 mg C. Three cores left as blank (no load, NL)		
Sampling	40 ml of sediment sampled from each homogenised depth interval (0-2; 2-5; 5-10)		3 cores sampled and sliced as starting values (2 foraminifera, 1 geochemistry)	6 cores sampled: 3 HL, 3 LL (in each case: 2 foraminifera, 1 geochemistry)	9 cores sampled: 3 HL, 3 LL, 3 NL (in each case: 2 foraminifera and 1 geochemistry)
Oxygen	Pore-water oxygen (O_2) measured periodically through out the experiment				
Fluxes			Nitrate (NO_3^-) and ammonium (NH_4^+) measured periodically in the overlaying water column		

Table 4.1. Experiment summary and time scale.

Core inventory																		
Core no	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Treatment	NL	NL	NL	HL	HL	HL	HL	HL	HL	LL	LL	LL	LL	LL	LL	NL	NL	NL
Analysis	F	F	G	F	F	G	F	F	G	F	F	G	F	F	G	F	F	G
Sampling time	1	1	1	2	2	2	3	3	3	2	2	2	3	3	3	3	3	3

Table 4.2. Core inventory: summary of the eighteen cores and their treatments (food load), analysis and sample moment in time. NL, no load; HL, high load; LL, low load. F, foraminifera; G, geochemistry.

sediment of each depth interval was sampled for living foraminifera.

Eighteen cylindrical mesocosms with a diameter of 6 cm (henceforth referred to as cores) were filled with 300 ml of homogenised sediment, in the correct stratigraphic order. Thus, each core was filled with 175 ml of sediment from the 5-10 cm section, 75 ml from the 2-5 cm section and 50 ml from the 0-2 cm section. The aim of the homogenisation was to create identical starting conditions for all cores, ideally containing the same number of living fauna and having similar geochemical conditions. The homogenisation may have affected the sediment porosity and volume.

The cores were placed in an aquarium filled with the overlying water from the cores and additional filtered seawater from the sample site, and left to settle for 48 days. The aquarium was kept in the dark and at constant in situ temperature (10°C). The water was well-aerated using aquarium pumps. Evaporation was prevented by sealing the aquarium with Parafilm®. The water level in the aquarium was monitored periodically. No great loss occurred during the experiment; hence salinity remained stable.

At t=1 (48 days after t=0) prior to the simulated diatom bloom deposition, or feeding, three cores were sampled: two for foraminifera, and one for pore-water and solid phase geochemistry (Tables 4.1, 4.2). Twelve cores were fed with 39 mg of diatoms; of these six cores were fed with high load diatoms (equal to 6.8 mg carbon) and six with low load diatoms (equal to 2.3 mg carbon). The organic carbon enrichment in the high load (HL) setting represented the average C_{org} flux over 56-day period (duration of the experiment following the feeding) at the study site (Epping et al., 2002); the LL C_{org} enrichment was about one third of this. The preparation of the diatoms is described in detail in section 2.3. Three cores were kept as controls and are referred to as "no load" (NL) cores.

Prior to the bloom deposition all remaining 15 cores were taken out of the aquarium and the overlying water level in each core was adjusted such that it contained exactly 100 ml. This was done in order to measure nitrate (NO_3^-) and ammonium (NH_4^+) fluxes from the sediment during the experiment (methods section "Water sampling and benthic fluxes"). The 1000 ml comprised 5 ml 'diatom suspension' and 95 ml filtered seawater collected from the experiment site. For NL cores 1000 ml of filtered seawater was used.

A single aquarium pump outlet was placed into each of the cores to keep them well aerated. Evaporation was prevented by sealing each individual core with Parafilm®; the water level was monitored periodically and remained stable throughout the experiment.

At t=2 (76 days after t=0, 28 days after t=1), six cores were processed: three HL cores and three LL cores. In each case, two cores were used for foraminiferal analyses, and one for solid phase and pore-water geochemistry. At the end of the experiment, at t=3 (104 days after t=0, 56 days after feeding or t=1), the remaining nine cores were treated in a similar manner: three HL cores, three LL cores and three blank NL cores were sampled, in each case two for foraminiferal analyses and one for solid phase and pore-water geochemistry.

4.2.3 Diatoms

An axenic culture of diatoms, *Thalassiosira pseudonana,* was ordered from the Provasoli-Guillard National Center for Culture of Marine Phytoplankton (CCMP), Bigelow Laboratory for Ocean Sciences, U.S.A. The diatoms were cultured at room temperature in sterile f/2 medium (after Guillard and Ryther, 1962; Guillard 1975) in 1L Erlenmeyer flasks under a natural

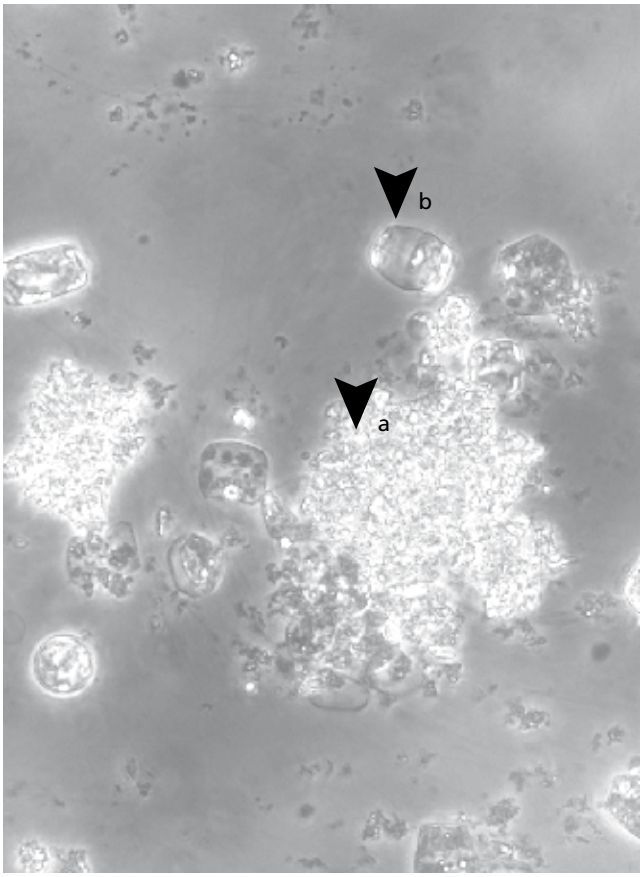


Figure 4.2. A microscope image of the dissociation of diatoms, *Thalassiosira pseudonana*, used in the high load (HL) treatment. Arrow (a): a burst diatom cell. Arrow (b): a complete diatom test. Cell width approximately 5 µm.

day-night light cycle. To maintain the exponential growth of the *T. pseudonana*, fresh culture medium was inoculated every three weeks or when the culture visually appeared to have a maximum density.

From the *T. pseudonana* culture two food loads were prepared. For the organic carbon measurements of the diatoms, see section 4.2.4. Both food loads were concentrated by centrifugation for 15 minutes at 1814 x *g* and freeze dried for preservation. The low load food (LL) was made of complete, freeze dried diatoms, with a C_{org} content of 5.8 wt %. The high load (HL) diatoms were produced by an osmotic shock, a process that encourages cell wall breakage (e.g. Sullivan and Volcani 1974, Middelberg 1995, Scawen and Hammond 2000). The osmotic shock treatment was conducted as follows: concentrated algae were exposed to 25 ml of ultra-high quality (UHQ) water, leading to a sudden change in salinity, and subsequently rupture of the diatom tests. A visual inspection of dissociation of the diatoms was carried out with the use of Zeiss Axioskop phase-contrast microscope (Figure 4.2). The osmotic shock led to a threefold enrichment of weight percent organic carbon in the HL diatoms in comparison to the LL diatoms, most likely due to removal of the silicate tests and breakdown of the cell wall. The C_{org} content of the HL diatoms was 17.5 wt %.

The bio-availability of the shocked and non-shocked diatoms was investigated independently by inoculating 1.2 mg of shocked and 3.6 mg of non-shocked diatoms (both equal to 0.2 mg of carbon) in 7 ml of oxygenated UHQ water, containing a wide variety of bacteria. The incubation was carried out at room temperature, and the diatoms were kept in continuous suspension by a shaker. After an incubation period of 20 days with bacteria, the water was sampled for dissolved inorganic carbon (DIC) produced by the bacteria respiring the diatoms. The bio-availability of both diatom types was equal, as indicated by the similar DIC contents (Table 4.3). Filtered (through 0.2 µm GHP Acrodisc from PALL) water samples were measured using Shimadzu Total Organic Carbon Analyser (Model TOC-5050A) following acidification of samples with phosphoric acid, H_3PO_4 (25%).

4.2.4 Geochemistry

Oxygen measurements

Pore-water oxygen content and overlying water were measured periodically during the experiment. A calibrated OXO10 Unisense Clark-type microelectrode attached to a micromanipulator was used to obtain the measurements at millimetre intervals.

Water sampling and benthic fluxes

Four millilitres of overlying water from the experiment cores was sampled prior to the feeding (t=1) and from then on periodically to monitor changes in the concentration of nitrate and ammonium in the overlying water of each core. The flux values were based on linear regression of concentration of nutrients as a function of time and multiplication of the slope by a specific volume/area (volume of overlying water/core area) ratio for each core (Lohse et al, 1998).

To measure pore-water profiles of dissolved nitrate (NO_3^-) and ammonium (NH_4^+) the sediment was first pushed out of the core and sectioned into intervals of 0.5 cm (for the top 2 cm) and 1 cm intervals (for 2-6 cm depth). The samples were then weighed and centrifuged for 15 minutes at 1814 x *g*, after which the pore-water was collected and filtered through 0.2 µm (GHP Acrodisc from PALL).

	DIC (mg C/L)	DIC (mg C/L)	DIC (mg C/L)	DIC (mg C/L)	Average	STDEV
High load diatoms	4.6	4.3	4.9	5.3	4.8	0.41
Low load diatoms	5.0	4.8	4.8	5.0	4.9	0.14
Blank	1.5	1.1	2.0	1.3	1.5	0.36

Table 4.3. The dissolved inorganic carbon (DIC) measured as a respiration product of remineralised diatoms. High load (HL) diatoms produced by the osmotic shock treatment. Low load (LL) diatoms are complete, freeze-dried diatoms. A blank (demineralised water incubated with wide variety of bacteria) measured as a standard. Each treatment was carried out in quadruplicate.

All water samples were frozen immediately after sampling and stored at -20 °C until analyses. The dissolved nitrate was measured on an AA3 autoanalyzer (Bran-Luebbe) and ammonium by spectrophotometry using phenol-hypochlorite (Helder and De Vries, 1979).

Sedimentary carbon and nitrogen

After pore-water extraction, the samples were oven dried, weighed and ground. Carbonate was removed and quantified by treatment with 1M HCl, and aliquots of the remaining sediment were measured for organic carbon and nitrogen using an NCS analyzer (Fisons NA 1500). A standard procedure described by Reichart et al. (2002) was used for sample preparation. International and in-house standards were used to assess the analytical precision, which was always within 1%.

The organic carbon content of the freeze dried diatom samples was measured in the same manner, with the exception of the decarbonation, which was considered unnecessary as diatoms have a silicate test.

4.2.5 Foraminifera

The cores used for foraminiferal analyses were sliced down to 6 cm depth (the experimental cores were around 6-7 cm long following the compaction of sediment). The top 2 cm of the cores was sliced every 0.5 cm. The remaining 4 cm was sliced every 1 cm. Immediately after slicing, the samples were stored in a solution of 1g/L rose Bengal and 96% ethanol.

The samples were washed with water and sieved into >150 μm and 63-150 μm size fractions. For the smaller size fraction, samples were examined down to 2 cm depth and no replicates were analysed. The cores analysed for the 63-150 μm fractions were chosen randomly. However, in some of the cores (t=2 HL/4 and t=3 HL/7) there was an obvious dissolution of calcareous foraminifera, and thus these cores were excluded from the 63-150 μm counts. The samples were kept wet at all times and picked as soon as possible after the washing procedure. Strict rules were applied to the identification of living individuals. Only the well-stained specimens were regarded as living, and any patchiness of the stained protoplasm was regarded as an indication of dead material. In case of doubt, tests were broken and the protoplasm remains were inspected in more detail.

The rose Bengal stain

The rose Bengal staining method is frequently used in ecological studies to distinguish living or recently living benthic foraminifera. Nevertheless, this technique has disadvantages and, in exceptional cases, some specimens may stain several months after the death of an organism under anoxic conditions (Bernhard, 1988, Hannah and Rogerson, 1997). Despite this, Murray and Bowser (2000) argue that where bottom-water is well oxygenated, the problem of staining of dead specimens is negligible as tests that contributed to the sediment are emptied of protoplasm due to reproduction, growth stages, or predation. Further, comparative studies using different techniques with rose Bengal stain (e.g. Bernhard et al., 1997; Lutze and Altenbach, 1991) have yielded comparable results and suggest that if rose Bengal is used with care, results can be 96 % correct.

In our experiment, the overlying water column and the top sediments of the experiment cores remained well oxygenated at all times. Therefore, it is unlikely that significant bias would result from anoxia. In addition, the sediments used in the study were not sieved and the meiofauna or other fauna was not removed. Therefore, natural predators and bacteria should have been present during the experiment. In addition, the sampling interval for foraminiferal analyses was on the order of a month, thus allowing time for possible remineralisation. Most importantly, the living foraminifera were strictly identified and only the well-stained specimens were counted. Many agglutinated specimens were broken to examine the protoplasm in detail.

Statistical analyses

The Principal Response Curve (PRC) analysis is a multivariate method designed for mesocosm experiments to test and display time-dependent treatment effects at a community level. The technique is based on a reduced rank regression that is adjusted for temporal changes in the control treatment (Van den Brink and Ter Braak 1998, Ernst et al. 2005), thus allowing focus on time-dependent treatment effects. The principal component is plotted against time in the PRC diagram.

In addition to the species data as used in common ordination techniques (such as PCA), in PRC analysis several dummy variables (or products thereof) are included. A separate variable is created for each sampling time or treatment. Samples belonging to that specific sampling time or treatment have the value one; a zero is assigned to all the others. In our case, two different data designs were used: one to summarise the effects at the community level of the two treatments compared with the control situation, and the other to compare both treatments (LL and HL). In case of the first, the product of the dummy variables for sampling time and those for both treatments (so excluding the control) were included as variables in the analysis. The variables indicating to which sampling time a sample belongs served as covariables. For the latter analyses (HL versus LL), LL samples were treated as the control samples in the first analyses. Thus, in this case the LL situation served as a baseline, while the true control samples were disregarded. All PRC and RDA analyses were carried out in CANOCO (Ter Braak and Šmilauer 1998).

The data sets were used in Redundancy Analyses (RDA, Rao 1964), i.e., the canonical form of Principal Component Analysis (PCA). Just as in PCA, in RDA samples are spaced along axes to maximize changes in species composition. The difference is that in RDA the positions of the samples on the axes are constrained to being linear combinations of the environmental variables included in the analysis. For the construction of PRC diagrams, the canonical coefficients for each standardized environmental variable in the RDA (i.e., each time*treatment product variable) are multiplied by the total standard deviation of the species data, and divided by the standard deviation of that particular environmental variable (Ter Braak and Šmilauer, 1998). These so-called treatment scores or regression coefficients (C_{dt}) are then plotted against time. The RDA species scores are plotted next to the PRC. These species scores can be interpreted as a species' affinity for the PRCs. Estimates of the changes in a species' abundance relative to the control can be inferred by multiplying the treatment score and species score. Hence,

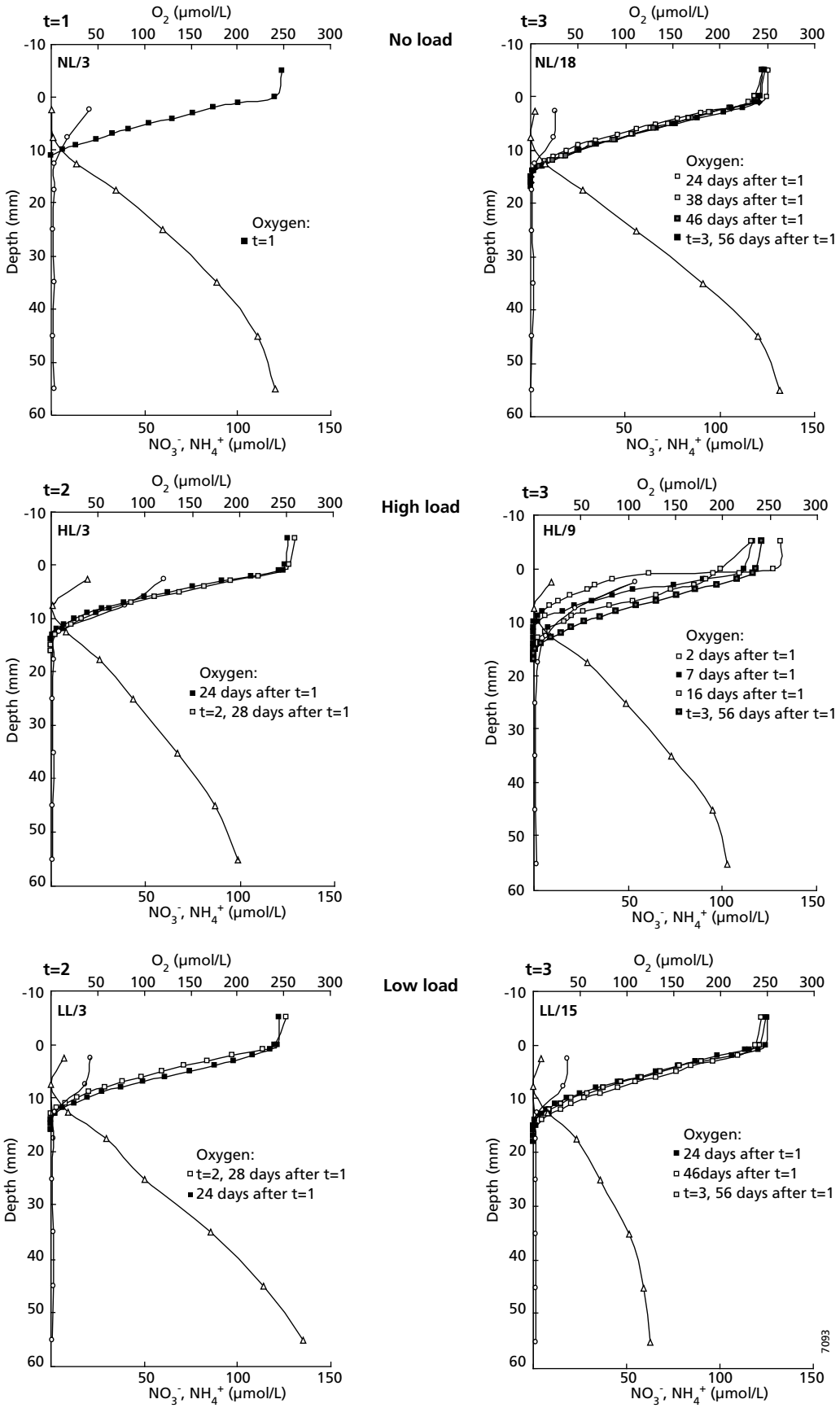


Figure 4.3. Oxygen, nitrate and ammonium pore-water profiles measured in the cores used for geochemistry only. Top row: non fed, control cores (no load, NL), time (t) = 1 right hand side, t = 3 left hand side. Middle row: High load (HL) treatment, t = 2 left hand side, t = 3 right hand side. Bottom row: low load (LL) treatment, t = 2 left hand side, t = 3 right hand side. O_2 profiles are marked with the square symbols. The date of the O_2 measurements is indicated adjacent to each figure. NO_3^- profiles marked with open circles and NH_4^+ profiles with open triangles.

species scores close to zero indicate a low affinity, whereas values much higher or lower than zero indicate that a species' abundance increased relative to the control situation when the PRC is on the same side of zero, or it decreased when the sign of the PRC is opposite that of the species score.

The analyses were carried out for three different data sets: firstly, the summed abundances >63 µm in the upper 2 cm of the cores; secondly, the summed abundances 63-150 µm also in 0-2 cm; and thirdly, the summed abundances >150 µm in the upper 6 cm. In each of the data sets the only species included were those that had an average relative abundance in all cores larger than 1%.

4.3 RESULTS

4.3.1 Geochemistry

Pore-water profiles: oxygen, nitrate and ammonium

The pore-water profiles of O_2, NO_3^- and NH_4^+ (Figure 4.3) indicate that the pore-waters remained well-oxygenated throughout the experiment. In general, the oxygen content of the overlying water was 250 µmol/L, and the oxygen penetration depth was 1.5 cm. A slight upward migration of the O_2 front was measured two days after the feeding in the HL cores (HL/9, Figure 4.3). The fluctuation most likely resulted from the relatively large load of added organic material and subsequent enhanced O_2 consumption. This should not lead to bias in the foraminiferal counts as the oxygen migration is within the sample interval for the faunal analyses (0.5 cm), and by the time the foraminifera were sampled, the O_2 profile had normalised to a depth of 1.5.

The O_2 measurements at foraminiferal sampling time are shown in Figure 4.8a and 4.8b (together with the vertical distribution of single species of foraminifera in the sediment). In general, the profiles are consistent. The only exception was observed at t=1 in core NL/1 where the O_2 penetration depth was shallower, despite the fact that all cores were equally oxygenated at all times. However, the O_2 content of the overlying water was similar to that of the other cores. The shallower oxygen penetration depth in this core may have resulted from decay of dead meio- or macrofauna in the sediment right at the spot were O_2 was measured.

In general, the nitrate (NO_3^-) pore-water concentration decreased with depth in the sediment. Prior to the feeding at t=1, the surface values in the top 0.5 cm slice of sediment were 20 µmol/L, decreasing slightly to 13 µmol/L in the blank no load core by the end of the experiment (t=3). The highest

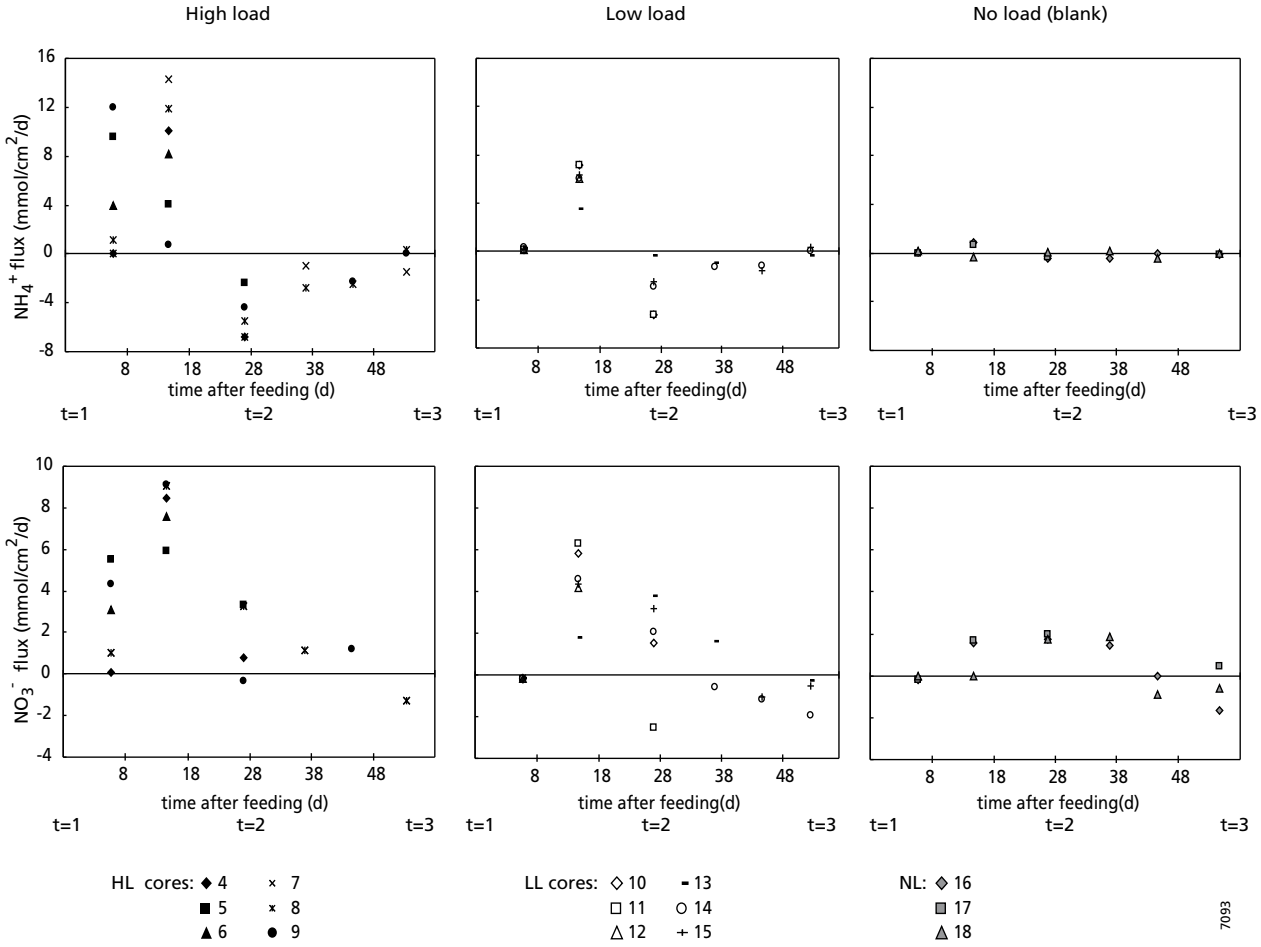


Figure 4.4. Ammonium and nitrate fluxes measured in the experiment cores. The left-hand column shows the measurements in the high load (HL) treatment. The middle column displays the low load (LL) measurements and the right-hand column the non-fed, no load (NL) measurements. In all figures, time is indicated as days following the feeding (t=1). In addition, times t=1, 2 and 3 are indicated.

Sample moment		t=1	t=2		t=3		
food load/core no		NL/3	HL/6	LL/12	HL/9	LL/15	NL/18
C_{org} (molar wt %)	top 0.5 cm	2.4	2.5	2.5	2.4	2.5	2.5
	ave./core	2.4	2.3	2.4	2.3	2.4	2.3
C/N (molar)	top 0.5 cm	12.7	13.5	14	11.9	12.4	11.7
	ave./core	13.7	11.3	13.2	12.4	11.8	12.2

Table 4.4. Solid phase geochemistry measured in experiment cores at t = 1, t = 2 and t = 3. Organic carbon (C_{org}) and C_{org}/Nitrate (C/N; molar) measured for each treatment (NL, no load; HL, high load; LL, low load) in the top 0.5 cm of sediment and average (ave.) for the complete core (0-6 cm).

		% of total variance accounted for by time	% of total variance accounted for by treatment regime	% of variance explained by treatment regime captured by first PRC
>63 µm, 0-2 cm	Treatment effect	-	100	98.3
	HL versus LL	42.5	57.5	95.8
63-150 µm, 0-2 cm	Treatment effect	-	100	94.9
	HL versus LL	17.2	82.8	87.8
>150 µm, 0-6cm	Treatment effect	-	100	97.6
	HL versus LL	60.6	39.4	96.2

Table 4.5. The amount of variance accounted for by time and treatment regime (i.e. the remaining time*treatment interaction) of the Principal Response Curves (PRCs) shown in Figure 4.6

concentration was detected in the high load treatment cores at t=2 (60 µmol/L), and at t=3 the values were still high (55 µmol/L). Constant values of 18 µmol/L were measured in the low load treatment at t=2 and t=3.

Ammonium (NH_4^+) increased with sediment depth in the sub- to anoxic part of the cores (from 1.0 cm depth downwards). In the fed cores a NH_4^+ peak was also measured at the surface. The highest surface value (19 µmol/L) was recorded at t=2 in the high load treatment. In the low load treatment, a surface value of 7 µmol/L was measured at t=2 and 4.5 µmol/L at t=3.

Benthic NH_4^+ and NO_3^- fluxes (bacterial activity)

In general, for both NH_4^+ and NO_3^-, the highest effluxes were measured in the high load treatment (Figure 4.4a). The effluxes peaked around 17 days after the feeding in both HL and LL treatments. The NH_4^+ fluxes switched to negative (an influx) around 25 days after the feeding, becoming similar to the measurement in the NL cores. The NO_3^- fluxes remained positive longer and standardised to control (NL) levels around 40 days after the feeding. The NH_4^+ and NO_3^- fluxes in the NL cores remained relatively stable throughout the experiment.

Solid phase analyses

The organic carbon content in top sediments (0-0.5 cm) was similar for all cores (Table 4.4). Further, the average values for complete cores were alike. Molar C/N ratios varied slightly between cores, ranging from 11.3 to 14.

4.3.2 Foraminifera

The total standing stocks

A clear decline was observed in the total standing stocks (TSS) between t=0 and t=1, in both size fractions (Figure 4.5). Following the feeding, both low load (LL) and high load (HL) food, some increase was observed in the TSS of foraminifera >150 µm. However, differences were seen between the replicate cores. Some increase was also observed in the blank, no load (NL) core, from t=1 to t=3. The highest TSS in the >150 µm size fraction, measuring 454 individuals, was recorded in core HL/8 at t=3.

In the smaller 63-150 µm size class, a clear decrease was seen in the TSS of foraminifera in the NL cores from t=1 to t=3 (from 205 individuals/core to 88 individuals/core), (Figure 4.5b). An increase was observed in the HL cores, where foraminiferal numbers rose from 205 (t=1) to 320 (t=3) individuals/core. In the LL cores the TSS remained relatively constant.

Discrepancies were measured in the TSS of the replicate cores despite the sediment homogenisation at the beginning of the experiment (Figure 4.5). For instance, at t=1 in the >150 µm fraction, 209 individuals were found in core NL/1 and 129 individuals in core NL/2. Dissolution of well-stained foraminiferal tests was observed in cores that corresponded with the lower TSS values (t=2 HL/4, LL/10 and t=3 HL/7). Therefore, the dissolution may be partly responsible for the observed differences. In addition, some sediment was lost from core LL/14 (sampled at t=3) during the washing and sieving procedure. The lost sediment was from the 1.0-1.5 cm depth interval, the section where in the majority of the experiment cores most foraminifera were encountered.

Community response

The majority of the foraminiferal species increased in abundance with increasing food load (Figure 4.6; see Table 4.5 for level of variance explained by PRCs). *Melonis baleeanum*, the most common species in the experiment, was most affected by the added food (species always showing the highest affinity for the Principle Response Curves, PRC). Other relatively abundant species displaying a positive response to the added food included *Pullenia* spp., *Adercotryma glomeratum*, *Bigenerina cylindrica* and *Chilostomella oolina*. Only a few taxa appeared negatively affected

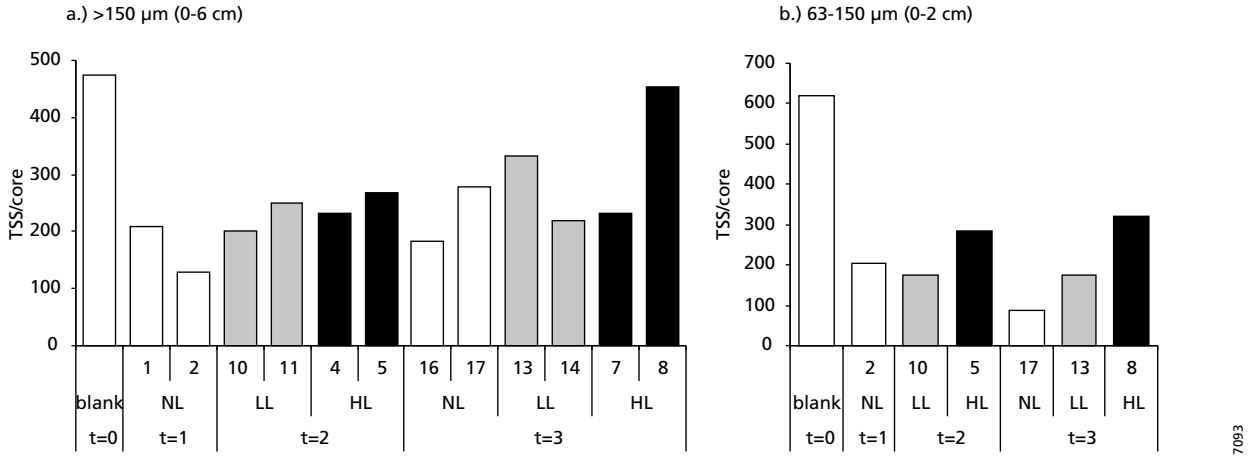


Figure 4.5. a) The total standing stock of foraminifera in the >150 µm fraction. No replicate core was processed at t=0. b) Total standing stock of foraminifera in the 63-150 µm fractions. The counts at the t=0 were standardised to equal the volume of the other experiment cores. Dissolution observed in cores HL/4, HL/7 and some in LL/10. Some sediment lost from the core LL/14 (1.0-1.5 depth interval).

by the added food e.g. *Bolivina alata*, *Bolivina spathualata*, *Globobulimina* spp. and *Valvulineria* spp. Some differences were observed in the response of the larger (>150 µm) and smaller (63-150 µm) foraminifera. Response was stronger in the smaller than in the larger size fraction. Where the smaller-sized foraminifera in the HL cores were more abundant (relative to LL) at t=2 and t=3, the larger-sized foraminiferal subpopulation did not seem to benefit from the extra amount of C_{org} in the HL cores until t=3.

Foraminiferal species response

The numbers of *Adercotryma glomeratum* increased most in the fed treatments (both HL and LL; Figure 4.7). The largest increase was generally seen in the small size fraction (63-150 µm) and the highest TSS was recorded at t=3 in core HL/8. In this size fraction, a marked increase was also observed in the NL core from t=1 to t=3; however, in the larger fraction (>150 µm) well-stained specimens were found only in the fed cores.

Bigenerina cylindrica and *Chilostomella oolina* were present mainly in the >150 µm fraction. The highest TSS for both species was recorded in the HL cores; however, large discrepancies were seen in the abundance of *C. oolina* between the replicate cores. Most *B. cylindrica* were found in the top 2 cm whereas relatively more *C. oolina* individuals were present deeper in the sediment (depth interval 2-6 cm). Only a few specimens were encountered in the smaller (63-150 µm) size class of the fed cores.

Melonis barleeanum, the most common species in the experiment, was found in both size classes, and some individuals were present deeper in the sediment. A clear increase in the abundance of this taxon (>63 µm, 0-2 cm) was observed with increasing food load. In the NL cores, the TTS of smaller individuals (63-150 µm) declined significantly whereas the larger-sized (>150 µm) subpopulation almost doubled.

Trochammina sp., *Pullenia* sp. and *Cassidulina* sp. were found only in the smaller 63-150 µm size class and declined in abundance in the NL cores. *Trochammina* sp. population responded to both HL and LL treatments, whereas *Cassidulina* sp. responded only to the HL treatment, increasing in abundance. A small increase was observed in the TSS of *Pullenia* sp. in the HL setting; however, the numbers remained relatively stable in the NL and LL cores.

Vertical distribution of individual species

The only species in the > 150 µm fraction displaying epifaunal behaviour or preference for a near-sediment-surface habitat was *Adercotryma glomeratum* (Figure 4.8a). This species increased in abundance in the fed cores only.

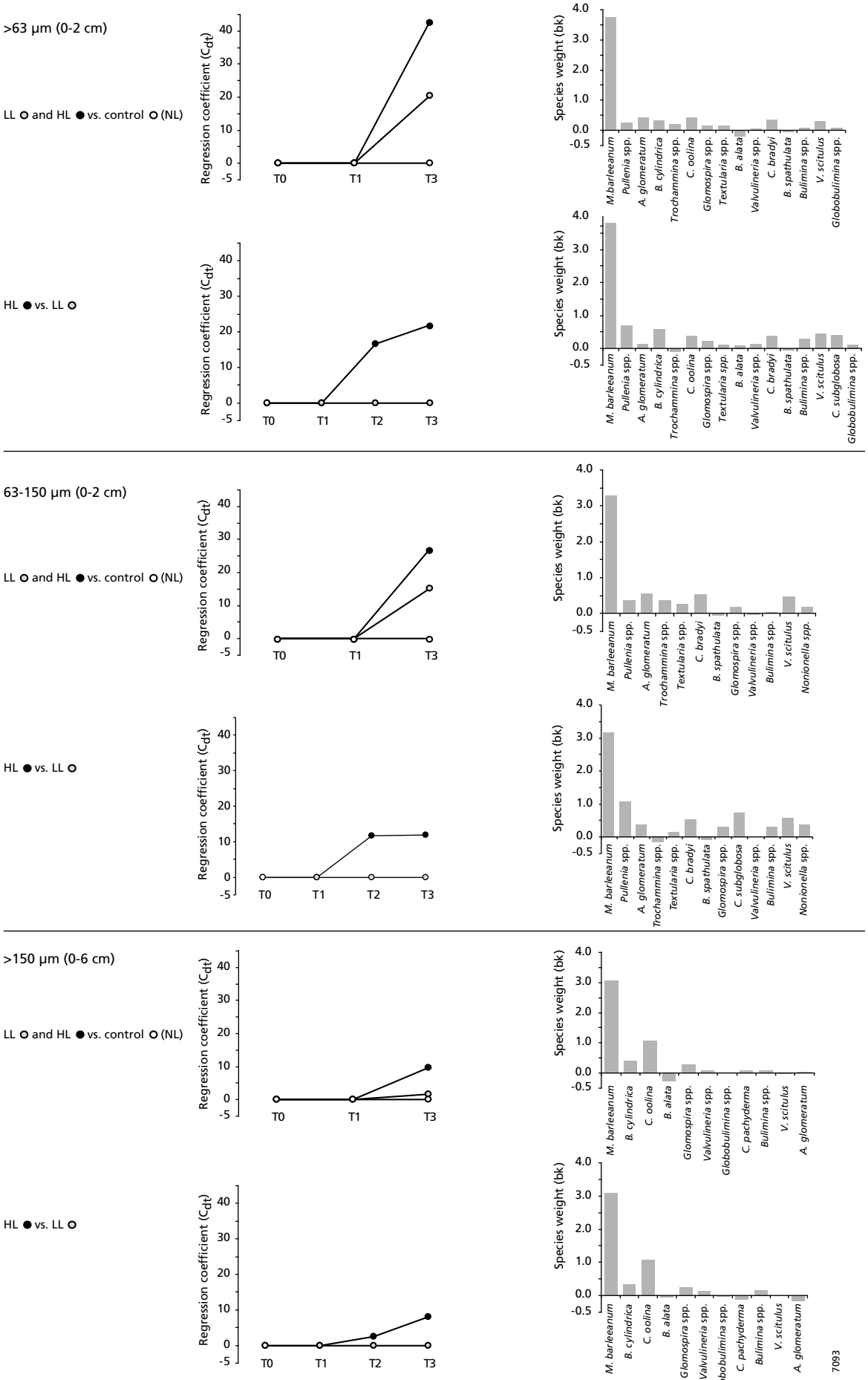
Bigenerina cylindrica, *Melonis barleeanum*, and *Chilostomella oolina* preferred an infaunal microhabitat, having a subsurface maximum close to 1.0 cm or 1.5 cm depth in sediment (Figure 4.8a). The only exception was recorded at t=1 in core NL/1 where an abundance peaked at the sediment surface (0-0.5 cm layer).

Of the small (63-150 µm) foraminifera two species, *A. glomeratum* and *Trochammina* sp., were found mainly in the surface sediments (Figure 4.8b). In contrast, *M. barleeanum* and *Cassidulina* sp. showed a clear infaunal microhabitat throughout the experiment (Figure 4.8b). The microhabitat of *Pullenia* sp. varied depending on the treatment. In the NL and LL treatments a shallow infaunal microhabitat was found whereas in the HL treatment specimens were also found in the surficial sediments.

4.4 DISCUSSION

4.4.1 Bacterial activity and organic matter remineralisation

Bacteria play an important role in the carbon consumption and remineralisation of C_{org} on the sea floor, responding rapidly to food supply (e.g. Rowe and Deming 1985). The significance of bacteria in the initial consumption of phytoplankton was also demonstrated by Moodley et al. (2000), who observed fast uptake of algae, 4.0 ± 0.4 % of algal carbon, into bacterial biomass within 12 hours. During remineralisation, bacteria break down organic matter utilising electron acceptors in order of decreasing free energy yield (O_2, NO_3^-, MnO_2, FeOOH, SO^{2-}_4; Froelich et al 1979). The respiration of organic matter


>63 µm (0-2 cm)
LL ○ and HL ● vs. control ○ (NL)
HL ● vs. LL ○
63-150 µm (0-2 cm)
LL ○ and HL ● vs. control ○ (NL)
HL ● vs. LL ○
>150 µm (0-6 cm)
LL ○ and HL ● vs. control ○ (NL)
HL ● vs. LL ○
Regression coefficient (Cdt)
Species weight (bk)
T0
T1
T2
T3
M.barleeanum
Pullenia spp.
A. glomeratum
B. cylindrica
Trochammina spp.
C. oolina
Glomospira spp.
Textularia spp.
B. alata
Valvulineria spp.
C. bradyi
B. spathulata
Bulimina spp.
V. scitulus
Globobulimina spp.
C. subglobosa
Nonionella spp.
C. pachyderma
7093

releases ammonium (NH_4^+) (e.g. Blackburn and Henriksen 1983, Hammond et al. 1985, Jensen et al. 1990, Dahllöf and Karle 2003), which under oxic conditions can be converted into nitrate (NO_3^-) through nitrification. However, under suboxic conditions denitrification becomes the dominant process where NO_3^- is consumed and processed into dinitrogen (N_2) gas (e.g. Herbert 1999 and references therein). Thus, the benthic fluxes of NH_4^+ and NO_3^- can be regarded as an indication of organic matter remineralisation rate and specific bacterial activities

A schematic representation of processes taking place during the experiment is shown in Figure 4.9. The remineralisation of the added diatoms in the high load (HL) and low load (LL) treatments was clearly indicated by elevated effluxes of NH_4^+ in comparison with the measurements in the no load (NL) treatment. Similar rapid release of NH_4^+ has been observed both in laboratory experiments (Hansen and Blackburn 1992, Enoksson 1993) and in field studies (Hammond et al., 1985, Jensen et al., 1990) following phytodetritus deposition. The highest NH_4^+effluxes were seen in the HL cores, reflecting the highest carbon load. The effluxes of NH_4^+peaked around 17 days after the feeding, when the bacterial degradation (ammonification) was most active. A change into an influx was observed around 25 days, indicating that the labile material had been remineralised. These results fall between the estimates of Hansen and Blackburn (1992) and Enoksson (1993). The time frame is also consistent with observations of Harvey et al. (1995), who noted that phytoplankton degradation in oxic conditions slows down rapidly after ~20 days and ceases in ~ 40 days.

An elevated efflux of NO_3^- was observed following the feeding, indicating enhanced nitrification. This is in contrast with the experiments of Hansen and Blackburn (1992) and Enoksson (1993), who observed a large influx of NO_3^-, indicating denitrification following feeding. Phytodetritus input on the seafloor typically leads to enhanced O_2 consumption rates, leading to a limited benthic O_2 supply. Hence in oxygen-limited environments denitrifying bacteria, which utilise NO_3^- as a terminal electron acceptor, can be activated. In our experiment however, the overlying water was continuously and vigorously aerated, thus preventing the development of anoxia. This prohibited oxygen depletion and was likely to encourage nitrification over denitrification.

Some scatter was detected in the flux measurements at any specific time, both in LL and HL settings. The scatter may be explained by slightly varying initial conditions in different cores e.g. bacterial activity or number of other living fauna. Langezaal et al. (2004) observed pronounced disturbance in the bacterial populations and foraminiferal abundances due to sieving at experiment setup. In our experiment, sediment was not sieved; nevertheless some degree of disturbance may be expected from homogenisation of the sediment at t=0.

The enhanced remineralisation and bacterial activity (nitrification) were also apparent from the elevated pore-water profiles of NO_3^- and NH_4^+ measured in LL and HL cores, in relation to the significantly lower measurements of the blank NL cores. As was shown for the flux data, these profiles also indicated the highest activity in the HL cores, resulting from the highest added carbon load.

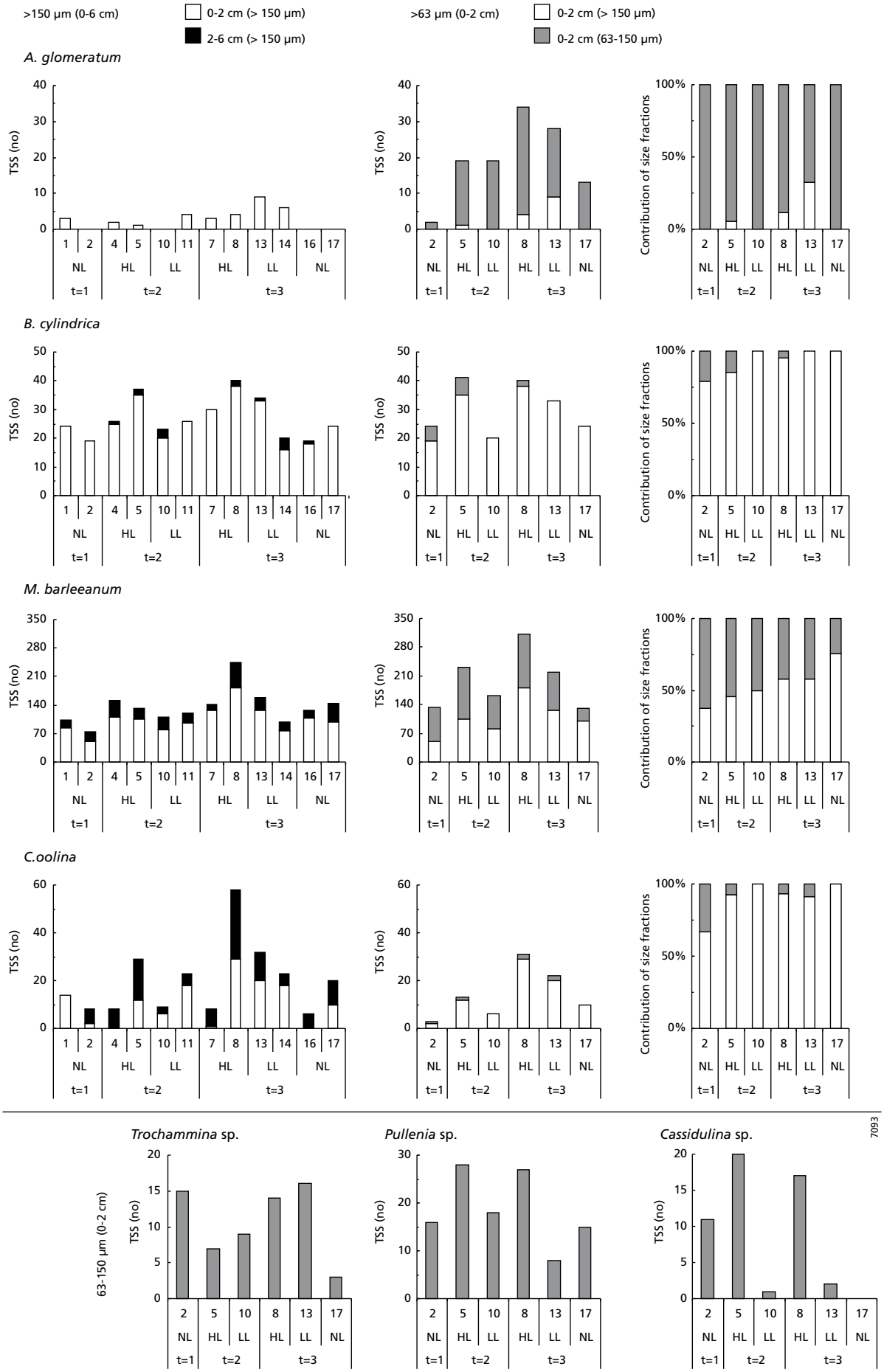
4.4.2 Foraminifera

Total community response

A clear response to the added diatoms or the associated increased bacterial activity was observed in the total standing stocks (TSS) of foraminifera (see Figure 4.6 and Figure 4.9 for an overview). The most pronounced increase in the numbers of foraminifera took place in the HL setting, where the TSS continued to increase until t=3. However, the rate of increase was greatest during the first four weeks following the feeding. In the NL cores a slight increase was observed in the larger foraminiferal subpopulation (>150 μm fraction) from t=1 to t=3; however, a clear decline was seen in the numbers of small sized (63-150μm) foraminifera.

Previously, an increase in the number of foraminifera following a phytoplankton deposition has been observed, both in the field (e.g. Gooday 1988c, Gooday and Turley 1990 and Drazen et al. 1998) and in the laboratory (Heinz et al. 2001, Heinz et al. 2002, Ernst et al. 2005). However, a decline was seen in the feeding experiment of Nomaki et al. (2005). The authors speculated that the decrease in the number of foraminifera was due to the low quantity of food (0.9 μg or 19 μg C cm^{-2}) used in the study. Alternatively, it may be that the feeding experiment was initiated too soon (three weeks) after the sediment recovery, and therefore the foraminiferal population did not have adequate time to readjust to the laboratory conditions. The number of well-stained foraminifera declined significantly at the onset of our experiment (from t=0 to t=1, Figure 4.5), indicating that a large proportion of foraminifera died either during the core recovery and transport of sediment or during the experiment setup. Evidence for mortality was observed a few days after the experiment setup, when dark rings were seen inside some of the cores, along with dead meiofauna on the sediment surface. Mortality at the beginning of an experiment is common, especially with deep-sea foraminifera. Other culture studies have reported a decline in the number of living organisms in a laboratory in relation to the field densities (Ernst et al. 2002, Duijnstee et al. 2003, Langezaal et al. 2004; Nomaki et al. 2005). A seven-week period prior to the feeding in our experiment was thought to be sufficient for the foraminiferal population to re-stabilise in numbers and re-establish their preferred microhabitat in the experiment cores in relation to new geochemical gradients.

Figure 4.6. Principal Response Curves (PRCs) summarising the response of the foraminiferal community to the experimental treatments across time. Only the first PRC is shown. Three different data sets were analysed: >63 μm, 0-2 cm; 63-150 μm, 0-2 cm; and >150 μm, 0-6 cm. Only species with an average relative abundance over 1% were included. The top panels of each data set summarise the community effect of the two treatments (LL and HL) relative to the control situation; the bottom panels compare both treatments (LL versus HL). Species weights can be interpreted as the species' affinities with the PRC. See section 4.2.5 *Statistical analyses* for further explanation. The amount of variance explained and displayed is listed in Table 4.5.


>150 µm (0-6 cm)
0-2 cm (> 150 µm)
2-6 cm (> 150 µm)
>63 µm (0-2 cm)
0-2 cm (> 150 µm)
0-2 cm (63-150 µm)
A. glomeratum
B. cylindrica
M. barleeanum
C.oolina
TSS (no)
Contribution of size fractions
0%
50%
100%
1 2 4 5 10 11 7 8 13 14 16 17
2 5 10 8 13 17
NL HL LL HL LL NL
t=1 t=2 t=3
Trochammina sp.
Pullenia sp.
Cassidulina sp.
63-150 µm (0-2 cm)
7093

In general, the community response to the added food supply can be described as 'two-phased' and it was measured as an increase in different size classes of the population (Figure 4.6). The first response (between t=1 and t=2) was a rise in the number of small-sized (>63-150 μm) foraminifera. This increase can be interpreted either as growth of foraminifera from the <63 μm fraction or as reproduction. We believe that the increase in the 63-150 μm class, at least in part, represents reproduction. The dominant species in the experiment was *Melonis barleeanum*, which is a relatively large species, found only in low numbers in the <63 μm size class (Ernst et al., 2004) because it rapidly grows into the >63 μm class. In addition, preliminary data from culture experiments indicate that following the birth of a foraminifer (in this case *Bulimina marginata*) calcification is relatively quick, two to three chambers in a few days (C. Barras, pers. com.). Therefore specimens reach ~90 μm in size within a few days of birth, after which the rate of calcification decreases. This suggest that a large addition in numbers of *M. barleeanum* in the 63-150 fraction is a result of reproduction, as opposed to growth from a pool of tinier individuals.

The second response phase was an increase in the numbers >150 μm, at least partly caused by growth of the initially smaller individuals. The response of growth was observed on a longer time frame, from the start (t=1) to the end of the experiment (t=3); however, a slight increase in the growth rate was observed during the second phase of the experiment (from t=2 to t=3). It is possible that the larger-sized (>150 μm) foraminiferal subpopulation was still growing at the end of the experiment, at least in the HL setting.

Discrepancies were measured in the TSS of foraminifera between the replicate cores, and there may have been several factors contributing to this. For instance, the intial sediment homogenisation was not thorough enough and hence different numbers of foraminifera were present in the cores to begin with. Alternatively, the discrepancies may have been caused by a sum of random factors e.g. an accidental presence of one "pregnant" individual ready to "give birth" to fifty little ones. Nevertheless, some deviation in the TSS may be due to dissolution. Highly dissolved, well-stained specimens were found in a few of the cores (t=2 HL core 4, LL core 10 and t=3 HL core 7), which yielded fewer foraminifera. Carbonate undersaturation is known to cause dissolution and increased mortality of living shallow-water foraminifera (Green et al. 1998). Hence, in some of the cores dissolution may have caused additional stress restricting the growth of the calcareous foraminiferal population. The origin of the dissolution is not known, although it may be related to oxidation of sulphur species in the sediment, causing acidification.

Figure 4.7. Total standing stocks (TSS) of selected common foraminifera. Left hand panel: TSS (>150 μm) in the complete core. White bars indicate foraminifera found in the top 2 cm of sediment and black between 2 and 6 cm depth. The middle panel: TSS in the top 2 cm (>63 μm). The light grey bars indicate smaller-sized foraminifera (>63-150μm) and white bars the larger-sized foraminifera (>150 μm). The right-hand panel: relative abundance of larger (>150 μm) and smaller (>63-150μm) foraminifera.

Species responses

Several species responded to the phytodetritus deposition and increased in numbers (Figures 4.6 and 4.7). For instance, the total standing stocks of *Adercotryma glomeratum* and *Trochammina* sp. increased under both LL and HL food supply and declined in the blank NL cores. For *A. glomeratum* the increase was greatest in the smaller size class (63-150 μm), especially in the HL cores. Other feeding studies have noted similar increase in the number of *A. glomeratum* after addition of food (Heinz et al., 2001, Heinz et al., 2002, Ernst and van der Zwaan 2004). Further, *A. glomeratum* has been named as one of the 'phytodetritus' species in the fields studies of Gooday (1988c) and Cornelius and Gooday (2004) where it was found in the phytodetrital aggregates. In our experiment, foraminifera were not separately counted from the phytodetritus aggregates; however, the near surface preference of *A. glomeratum* supports the 'phytodetrital' species description given by Cornelius and Gooday (2004).

An increase was also recorded for several infaunal taxa. For instance, *Melonis barleeanum* increased especially in the HL fed cores in both size fractions and some increase was also seen in the LL fed cores. In contrast, a decline in abundance was observed from t=1 to t=3 in the small size fraction (63-150 μm) of the blank NL core. Therefore, significant growth (or reproduction) occurred only in the fed cores. The increase also appeared to be related to the quantity of added carbon (i.e more carbon higher the standing stock); hence the abundance of *M. barleeanum* reflects the trophic state of the sediment in this experimental setup.

A response of *M. barleeanum* was observed also in the feeding experiment of Heinz et al. (2002), which recorded a clear increase in the total number (>30 μm) of *M. barleeanum* 21 days after the feeding; a small increase in the numbers was also observed for 42 days (the end date of the experiment). In our experiment the larger-sized subpopulation (>150 μm) of *M. barleeanum* in the HL fed cores continued to increase until 56 days (t=3) after the feeding, whereas the small-sized subpopulation remained more constant after 28 days (t=2). This implies that the initial increase in the abundance occurred before t=2, however, the growth into the larger size hardly occurred until t=3. Therefore, potential reproduction of this species seems most likely linked to the presence of the actual added organic matter or the associated bacterial activity. The relation with the bacterial activity appears more likely as in the experiment *M. barleeanum* did not migrate to the surface to feed on the fresh phytodetritus but remained in the sediment, exhibiting a subsurface maximum close to the oxygen penetration depth in sediment between 1.0 and 1.5 cm. Previously, Fontanier et al. (2005) hypothesised a relation between occurrence of *M. barleeanum* and bacterial activity, suggesting that some infaunal species (including *M. barleeanum*) may be highly specialised and either feed on or live in symbiosis with heterotrophic and chemolithotrophic bacteria.

In our experiment an increase in abundance was detected for the deeper infaunal species (*Chilostomella oolina*). In contrast, in a feeding study of Nomaki et al. (2005), a response of deep infaunal species was slow or non-existent. Especially, *C. ovoidea* did not show any reaction to the deposited food. As mentioned earlier, in the experiment of Nomaki et al. (2005), the quantity

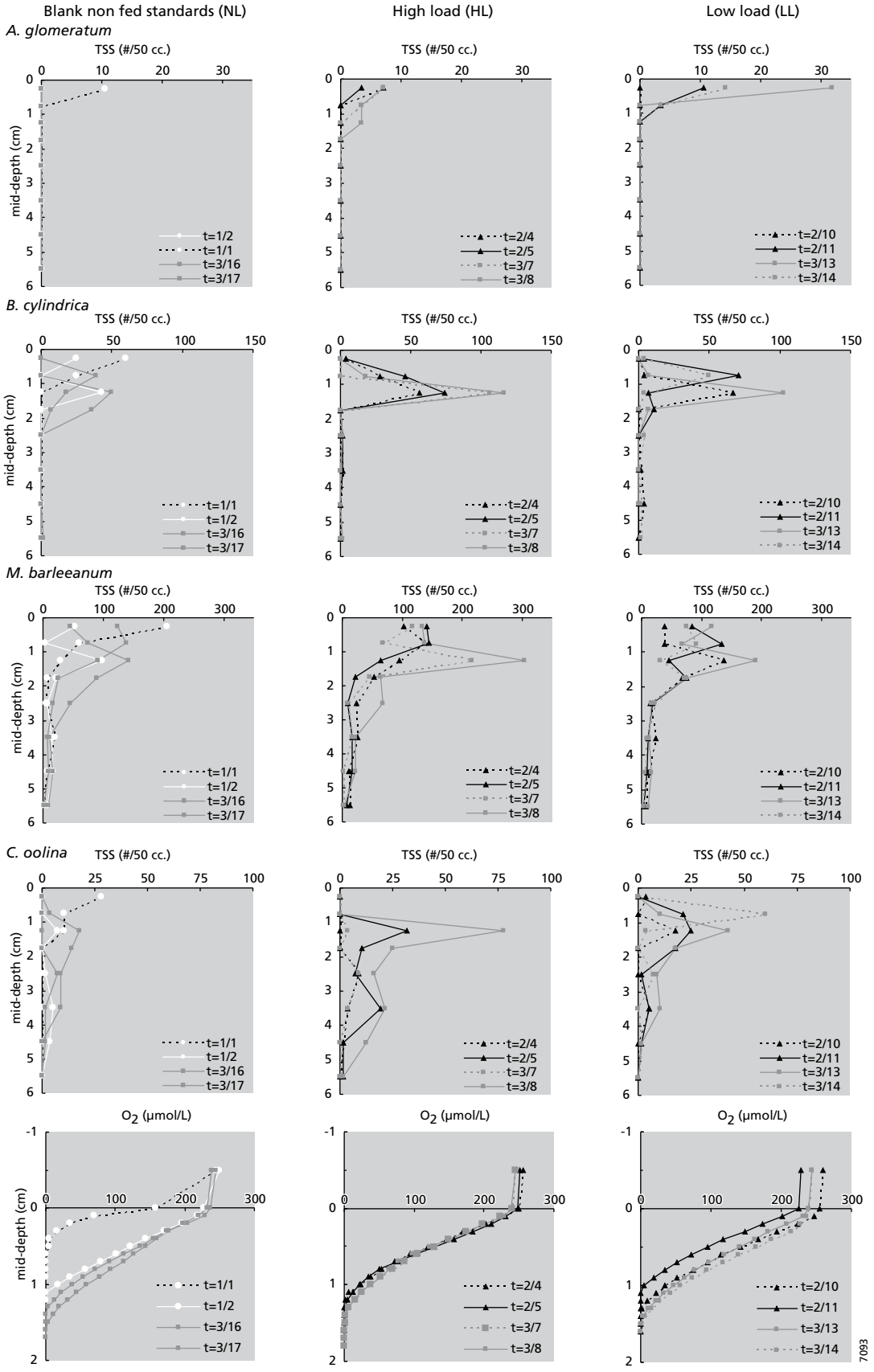


Figure 4.8. a.) The vertical distribution of selected common foraminifera (> 150µm) in sediment. Left-hand column, the non-fed (no load, NL) standards sampled at t = 1 and t =3; the time label (t) is followed by the designated core number. Middle column, the high load (HL) treatment sampled at t = 2 and t = 3. Right hand column, low load treatment (LL) sampled at t = 2 and t = 3. Replicate cores processed only for the larger size fraction. The pore-water oxygen profiles measured briefly prior to the foraminiferal sampling displayed below the species vertical distribution plots.

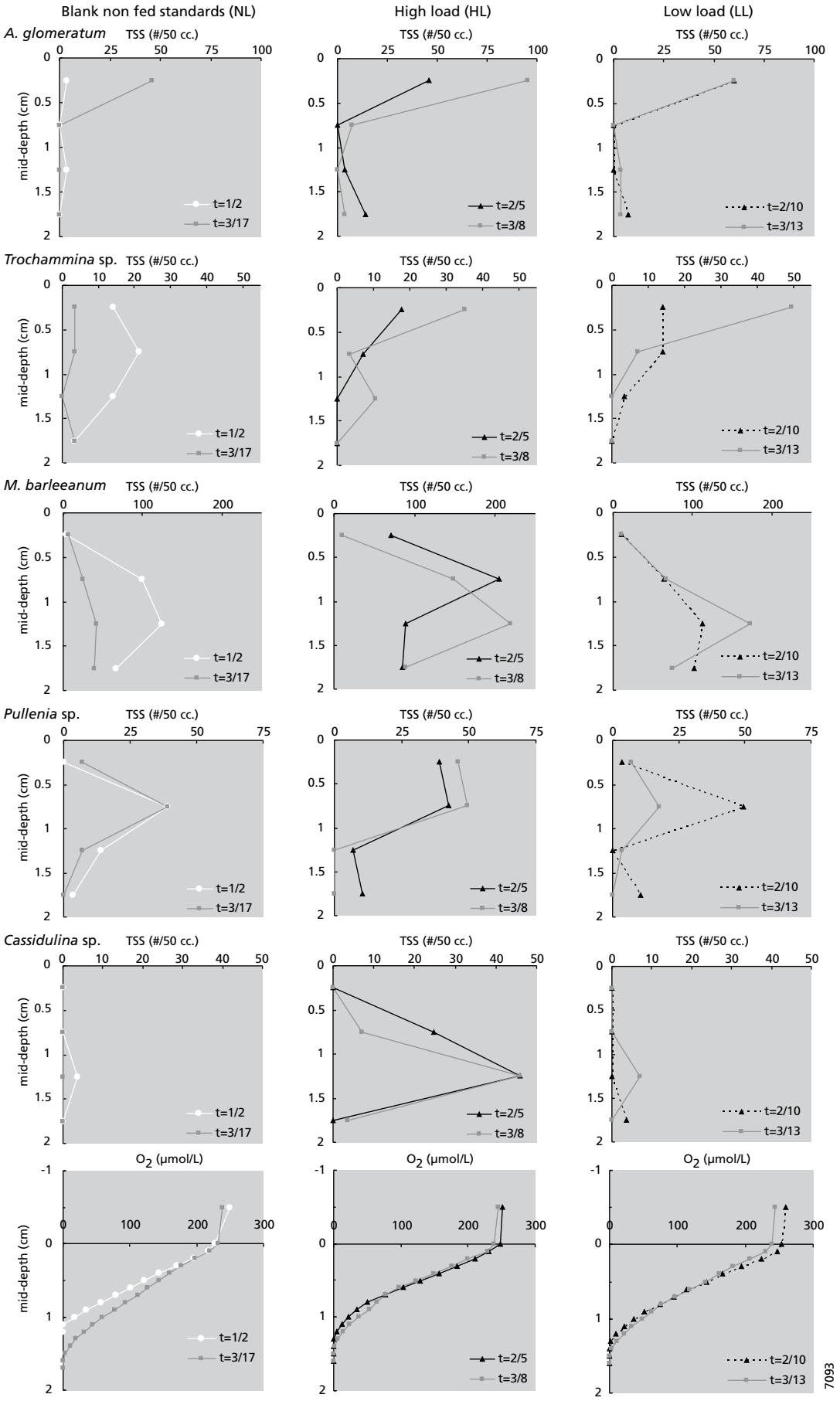
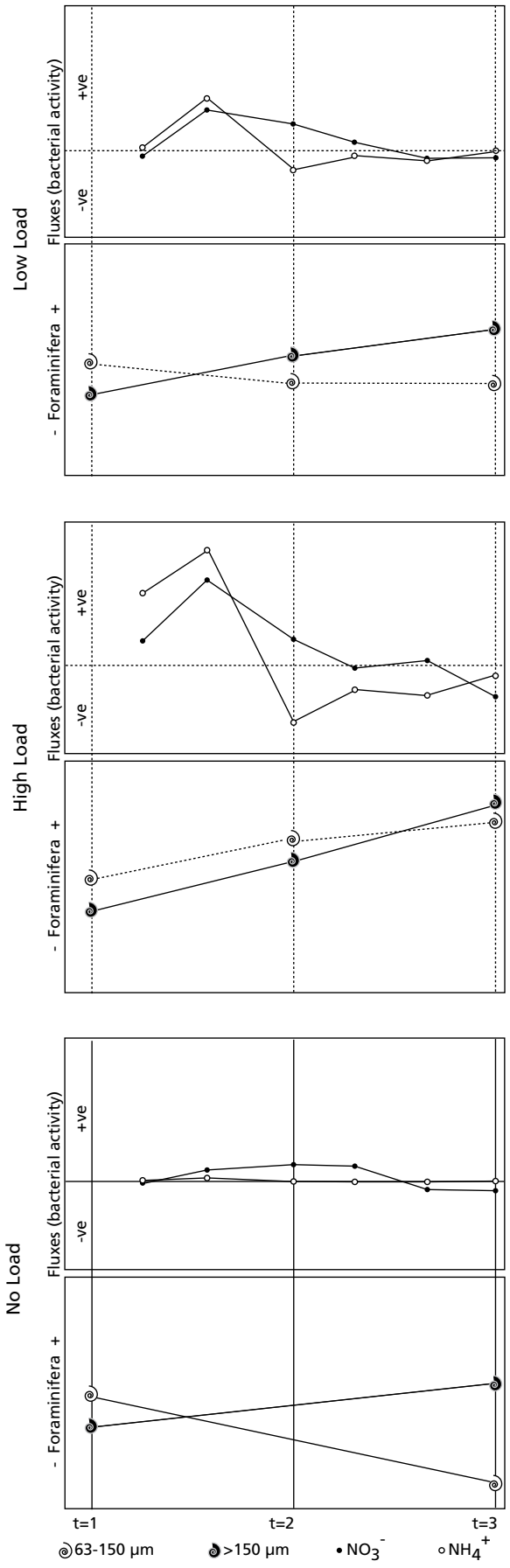


Figure 4.8. b.) The vertical distribution of selected foraminifera (63-150 µm) in sediment.



of added food was relatively low (0.9 µg or 19 µg C cm^{-2}). Therefore, the response by infaunal foraminifera may have been restricted as the added phytodetritus was consumed quickly by epifaunal or shallow infaunal species on the sediment surface. Further, Nomaki et al. (2005) did observe some increase in the movements of *Globobulimina affinis* and ingestion of algae under slightly higher food supply (19 µg C cm^{-2}), implying that a deep infaunal response was related to the quantity of added food.

The vertical distribution of foraminifera

The distribution of foraminifera in sediment or the species-specific microhabitat appears to be related to geochemical gradients or food supply (e.g. Corliss 1985, Corliss 1991, Corliss and Emerson 1990, Jorissen et al 1995) and is therefore reflected in the trophic state of the environment. This relationship was described by Jorissen et al. (1995) in terms of the conceptual TROX model.

In our experiment two species, *Pullenia* sp. and *Trochammina* sp., changed their vertical distribution in response to food supply. In the HL cores *Pullenia* sp. was found throughout the top 1 cm of sediment in an equal abundance. In contrast, a clear subsurface maximum, located between 0.5 and 1.0 cm depth in sediment, was recorded in the blank NL cores and in the LL cores. This implies that following a relatively high C_{org} flux to the sediment surface, migration, growth or reproduction of *Pullenia* sp. takes place in the surface sediments, where it benefits directly from the added food. In contrast, at times of lower food supply, *Pullenia* sp. resides slightly deeper in sediment. As an increase in abundance was only observed in the HL cores, it can be inferred that *Pullenia* sp. requires a relatively high food input to trigger measurable change in the distribution of the population in the sediment. On the other hand, *Trochammina* sp. increased in the surficial sediments of the HL and LL treatment, thus implying that even a smaller food input was enough to initiate changes in the vertical distribution.

The vertical distribution of infaunal species in the sediment appears not to be controlled by algal food (phytodetritus) but more related to sediment redox chemistry or the associated bacterial processes. None of the infaunal species, such as *M. barleeanum*, *B. cylindrica*, *C. oolina*, were observed to move closer to the surface or increase in abundance in the surficial sediment after the phytodetritus deposition. The close association between the redox gradients and infauna becomes evident when the pore-water oxygen profiles and the vertical distribution plots of infauna, e.g. *M. barleeanum*, *B. cylindrica*, *C. oolina* (Figure 4.8), are compared. All these species displayed their subsurface maximum around the oxygen penetration depth in sediment.

Figure 4.9. A schematic overview of processes measured during the experiment. The foraminiferal numbers presented in the >150 µm fraction are the average values measured in the replicate cores. The flux measurements (an efflux, +ve); influx, -ve) for single treatment (no load, NL; high load, HL; low load, LD) are based on average values measured in all the cores of the same treatment at one time. All representations of a single parameter (e.g. foraminifera) are on scale with each other but not on scale with different parameters (e.g. scale of foraminifera ≠ scale of flux measurements).

The distribution profile of infauna in the core t=1/1 (sampled prior to the feeding) was significantly different from the rest, with infauna displaying maximum abundances at the sediment surface. However, this core showed a relatively shallow pore-water oxygen penetration depth (~ 0.5 cm), thus causing infauna to migrate closer to the surface. This observation is in accordance with previous laboratory studies (Alve and Bernhard 1995, Moodley et al. 1998b, Duijnstee et al. 2003, Geslin et al. 2004, Ernst et al., 2005) that observed migration of foraminifera as a result of changing pore-water oxygen concentrations. The reason for low pore-water oxygen content in this particular core is unknown; however, it may have been due to dead meio- or macrofauna in the sediment, thus leading enhanced oxygen consumption in the sediment. The oxygen content of the overlying water in the core t=1/1 (~ 250 µmol) was similar to that in the other cores.

4.5 CONCLUSIONS

A clear disturbance of the foraminiferal population was demonstrated at the start of our experiment between t=0 and t=1, when a significant decline in the total standing stocks was observed. In our experiment, where the recovery depth was 900 m, seven weeks appeared to be sufficient for foraminiferal communities to reach stability. However, samples that originate from deeper waters may require even longer to readjust. Therefore, in future laboratory studies with deep-sea organisms, it is important to allow enough time for fauna to re-establish prior to the start of the actual experiment.

Benthic fluxes of ammonium and nitrate were used to assess bacterial activity, which increased after the diatom deposition. Effluxes of ammonium and nitrate were measured in the treated cores, indicating organic matter remineralisation. The highest fluxes were recorded in the high load (HL) treatment, coinciding with the highest C_{org} load. The ammonium fluxes dropped to the levels of the control cores around 25 days after diatom addition, indicating that the labile material had been remineralised. The nitrate fluxes remained positive longer, suggesting that nitrification continued even after remineralisation had slowed down.

Foraminifera showed a 'two-phased' response to feeding, which was noted as an increase of different size classes of foraminifera. The first phase was an increase in the smaller-sized (63-150 µm) subpopulation followed by an increase in the larger-sized (>150 µm) subpopulation during the second phase of the experiment. Most foraminifera were found in the high load treatment; hence with increasing food load a larger response was observed. In the control (no load; NL) cores, a slight increase was observed in the larger foraminiferal population (>150 µm fraction); however, a clear decline was seen in the number of small sized (63-150µm) foraminifera. These results imply that growth or reproduction of foraminifera is directly or indirectly (via enhanced bacterial activity) dependent on food supply and can be triggered by a phytoplankton bloom and inhibited by low nutritional state of the sediment.

Several taxa, including infaunal species such as *Chilostomella oolina* and *Melonis barleeanum*, increased in numbers, thus indicating a positive response to the added food. At the same time the microhabitat of most infaunal species did not seem to be affected by the food pulse. Only two species, *Pullenia* sp. and *Trochammina* sp., were observed to alter their microhabitat and increase in abundance in the top 0.5 cm of sediment.

Acknowledgements.
The authors are grateful to Tanja Kouwenhoven for help with the sediment sampling, transportation and initial experiment setup In addition, her comments improved the manuscript. Henko de Stigter is thanked for the opportunity of sampling and his support throughout the experiment. Eric Epping provided information on the osmotic shock procedure. The bio-availability analyses of the diatoms were carried out with help of

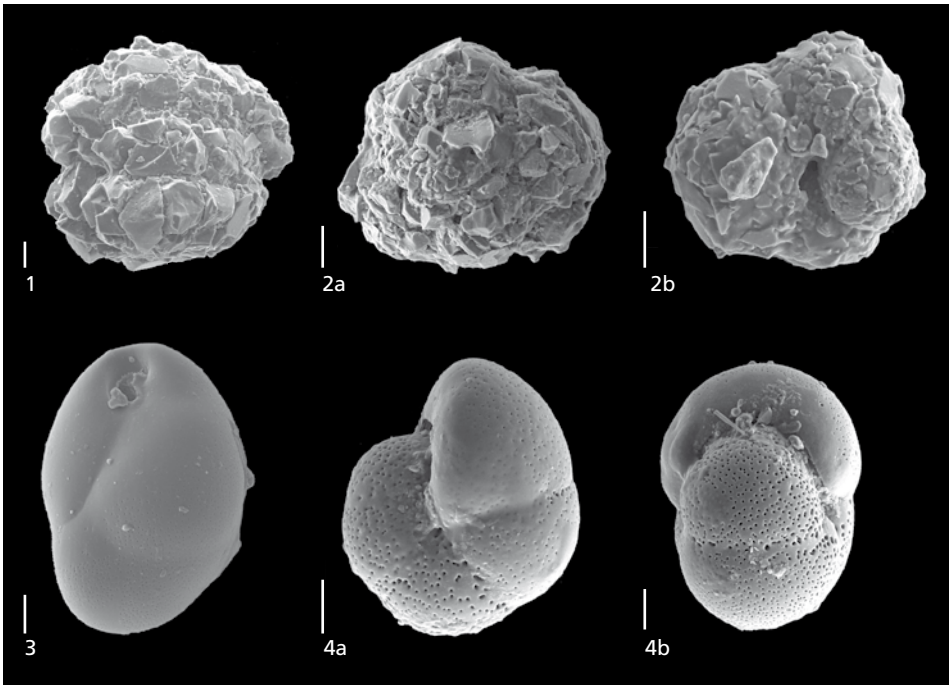


Plate 4.1. Scale bar 20 µm.
1. *Adercotryma glomeratum*
2a. *Trochammina* sp. spiral view
2b. *Trochammina* sp. umbilical view
3. *Cassidulina* sp.
4a. *Pullenia* sp. side view. Note the enlarged pores as a result of dissolution.
4b. *Pullenia* sp. apertural view. Note the enlarged pores as a result of dissolution.

Gert-Jan Reichart. Geert Ittmann is thanked for the preparation of foraminiferal samples and Dineke van de Meent-Olieman for the analyses of the water samples. Interesting discussions with Frans Jorissen, Christine Barras and Emmanuelle Geslin provided new insight into the foraminiferal data. A special thank you goes to the crew and captain of the R.V. Pelagia and everyone participating in the CANYONS cruise 64PE236. Shiptime was provided by Royal NIOZ. This research was supported by Netherlands Organization for Scientific Research (N*W*O).

Appendix 4.1. Taxonomic notes. The common and associated species appearing in this paper are listed with the original genus designation. Reference to plates and figures in this paper or others are given.

Adercotryma glomeratum (Brady) = *Lituola glomerata* Brady 1878; Plate 4.1, Figure 1.

Bigenerina cylindrica Cushman 1922; Koho et al. (2007), Plate 1, Figure 10.

Bolivina alata (Sequenza) = *Vulvulina alata* Sequenza 1862; Jones (1994), Plate 53, Figures 2-4.

Bolivina spathulata (Williamson) = *Textularia variabilis* var. *spathulata* Williamson 1858; Jones (1994), Plate 52, Figures 20-21.

Cassidulina sp.; Plate 4.1, Figure 3.

Cassidulina subglobosa Brady 1881; Jones (1994) Plate 54, Figure 17.

Cassidulinoides bradyi (Norman 1881) = *Cassidulina bradyi* Norman 1881; Jones (1994) Plate 54, Figures 6-9.

Chilostomella oolina Schwager 1878; Koho et al. (2007), Plate 2, Figure 8.

Cibicides pachyderma (d'Orbigny) = *Truncatulina pachyderma* Rzhehak 1896; Schweizer (2006), Plate 6, Figures k-p.

Cribrostomoides subglobosus (Cushman) = *Haplophragmoides subglobosum* Cushman 1910; Jones (1994), Plate 34, Figures 8-10.

Melonis barleeanum Williamson 1858; Koho et al. (2007), Plate 2, Figure 7a-b.

Neolenticulina variabilis (Reuss) = *Cristellaria variabilis* Reuss 1850; Jones (1994), Plate 68, Figures 11-16.

Pullenia sp.; Plate 4.1, Figures 4a-b.

Trochammina sp.; Plate 4.1, Figures 2a-b.

Veleroninoides scitulus (Brady) = *Haplophragmium scitulum* Brady 1881; Jones (1994), Plate 34, Figures 11-13.

Appendix 4.2. Census data, total number of foraminifera (>150 μm) per sediment sample. At time (t)=0 sample volume is 40 ml. Volume of a 0.5 cm thick slice is 14.1 cm^3.Volume of a 1 cm thick slice is 28.3 cm^3.

t=0 (40 ml sediment)	0-2.0	2.0-5.0	5.0-10.0
agglutinated (single chambered, soft)	2		
Ammobaculites sp.	2		
Ammolagena clavata	1		
Bigenerina cylindrica	18	10	
Bolivina alata	5	2	
Bulimina inflata	3		
Chilostomella oolina	8	3	
Cibicides pachyderma	3	5	4
Cribrostomoides subglobosus	4	2	
Dentalina sp.	1		
Discammina compressa		2	
Eggerella spp.	1		
Glomospira charoides	12	8	2
Globobulimina spp.		3	
Haplophragmoides sp.			1
Hormosinella sp.		1	
Hyalinea balthica		1	1
Melonis barleeanum	72	60	12
Reophax sp. (mica)		1	
Reophax spiculifer	1		
Saccammina spp.	2		
Spirillina spp.	1		
Technitella sp.	4		1
Trochammina spp.	1		
Valvulineria bradyana	3	2	1
Veleroninoides scitulus		6	

Appendix 4.2. (Continued)

Core 1/NL	0.0-0.5	0.5-1.0	1.0-1.5	1.5-2.0	2.0-3.0	3.0-4.0	4.0-5.0
Adercotryma glomeratum	3						
agglutinated (spherical)				1			
Bigenerina cylindrica	17	7					
Bolivina alata	14	5					
Bolivina subaenariensis	1						
Bulimina inflata	6						
Chilostomella oolina	8	3	3				
Cibicides ungerianus						2	
Cibicides wuellerstorfi		1					
Cribrostomoides subglobosus	2						
Cyclammina cancellata	1						
Discammina compressa	1						
Evolvocassidulina orientalis	1						
Fissurina spp.					1		
Globobulimina spp.		2					
Glomospira charoides	2		4	2	2	3	
Hyalinea balthica	2						
Melonis barleeanum	58	17	8	2	3	11	4
Nonionella spp.	1						
Technitella sp.	1						
Trochammina spp.	1						
Uvigerina mediterranea	1						
Valvulineria bradyana		8					

Core 2/NL	0.0-0.5	0.5-1.0	1.0-1.5	1.5-2.0	2.0-3.0	3.0-4.0	4.0-5.0
Bigenerina cylindrica	7		12				
Bolivina alata	1						
Bulimina inflata	1				1		1
Chilostomella oolina			2		1	3	2
Cibicides pachyderma	1					1	1
Cribrostomoides subglobosus	2						
Globobulimina spp.	2		1				1
Glomospira charoides	1		1			1	3
Hyalinea balthica				1			
Melonis barleeanum	15	1	28	6	4	8	9
Sphaeroidina bulloides	1						
Valvulineria bradyana	1						
Veleroninoides scitulus					1		

Core 4/HL	0.0-0.5	0.5-1.0	1.0-1.5	1.5-2.0	2.0-3.0	3.0-4.0	4.0-5.0
Adercotryma glomeratum	2						
Bigenerina cylindrica	1	8	16			1	
Bolivina alata			2				
Bulimina inflata	3	2					
Buzasina sp.?		1					
Chilostomella oolina					5	2	1
Cibicides pachyderma			3		2	1	
Cibicides sp. (encrusting)	1						
Cribrostomoides subglobosus	1		1				
Eggerella spp.		1					
Globobulimina spp.					2		
Glomospira charoides		2	1	1	2	1	
Haplohragmoides sp. (coarse grained)					1		
Hyalinea balthica	2		1				
Melonis barleeanum	29	39	27	15	13	15	6
Nodosaria spp.		1					
Psammosphaera sp.					1		
Reophax spiculifer		1					
Uvigerina mediterranea	2						
Valvulineria bradyana		1	3				1
Veleroninoides scitulus		2					

Appendix 4.2. (Continued)

Core 5/HL	0.0-0.5	0.5-1.0	1.0-1.5	1.5-2.0	2.0-3.0	3.0-4.0	4.0-5.0
Adercotryma glomeratum	1						
Astrononion sp.				1			
Bigenerina cylindrica	1	13	21		1	1	
Bolivina alata		6	4				
Bolivinita quadrilatera	1						
Bulimina inflata	2					2	
Chilostomella oolina			9	3	4	11	1
Cibicides lobatulus						1	
Cibicides pachyderma	2						
Cibicides ungerianus			1			1	
Cribrostomoides subglobosus	2						
Evolvocassidulina orientalis		1	1				
Globobulimina spp.			1	1		1	6
Glomospira charoides	3	5	1	2	3		
Haplophragmoides sp.	1						
Hyalinea balthica	1						
Marginulina obesa		1					
Melonis barleeanum	40	41	18	6	5	9	9
Pyrgo spp.	1						
Rosalina sp.	1						
Saccammina spp.	1	1		1			
Textularia spp.	1		1				
Uvigerina mediterranea	2						
Valvulineria bradyana			5				
Valvulineria rugosa?	1						

Core 7/HL	0.0-0.5	0.5-1.0	1.0-1.5	1.5-2.0	2.0-3.0	3.0-4.0	4.0-5.0
Adercotryma glomeratum	2	1					
agglutinated (spherical)			1				
Bigenerina cylindrica			30				
Bolivina alata			8				
Bulimina inflata	1						
Chilostomella oolina			1		5	2	
Cibicides lobatulus							1
Cibicides pachyderma	1				1	1	1
Cibicides ungerianus				1			
Eggerella spp.		2					
Globobulimina spp.			2	2			
Glomospira charoides	1	3	3	1	4		
Hyalinea balthica	1						
Melonis barleeanum	33	19	61	13	5	9	1
Reophax spiculifer		1					
Saccammina spp.		1					
Uvigerina mediterranea	1						
Valvulineria bradyana			4	1			
Valvulineria rugosa	1						
Velorinoides scitulus	1	2	2				

Appendix 4.2. (Continued)

Core 8/HL	0.0-0.5	0.5-1.0	1.0-1.5	1.5-2.0	2.0-3.0	3.0-4.0	4.0-5.0
Adercotryma glomeratum	2	1	1				
agglutinated (spherical, spinous, white)	1	2	2				
agglutinated (spherical, white)	2						
Bigenerina cylindrica		5	33		1		
Bolivina alata		1	15				
Bolivinita quadrilatera	2						
Bulimina elongata			1				
Bulimina inflata	3		1	1			
Bulimina marginata	1						
Cassidulinoides bradyi			1				
Chilostomella oolina			22	7	9	12	7
Cibicides pachyderma	7	1					
Discorbina sp.		1	1				
Eggerella spp.	1						
encrusting 1/2 sphere		3					
Glandulina sp.		1					
Globobulimina spp.		3	1	1	1	1	2
Glomospira charoides		4		4	1	3	4
Glomospira sp. (white)			1				
Hyalinea balthica	1						
Lagena spp.				1			
Melonis barleeanum	38	39	86	18	38	12	12
Neolenticulina variabilis		1					
Reophax spiculifer		1					
Uvigerina elongatastriata			1				
Uvigerina mediterranea	2	1		1			
Valvulineria bradyana			13	1			
Veleroninoides scitulus	2	3	1				
Veleroninoides wiesneri		1	1				

Core 10/LL	0.0-0.5	0.5-1.0	1.0-1.5	1.5-2.0	2.0-3.0	3.0-4.0	4.0-5.0
Bigenerina cylindrica		1	19			1	2
Bigenerina nodosaria	1						
Bolivina alata			10			1	
Bulimina inflata							1
Chilostomella oolina	1		5			3	
Cibicides pachyderma	2		1	5	1	1	
Cribrostomoides subglobosus	2	1	1	1			
Eggerella spp.	1						
Globobulimina spp.		1				5	1
Glomospira charoides	1	3	2	1	2	1	
Hyalinea balthica	1						
Melonis barleeanum	11	11	39	19	8	13	6
Psammosphaera sp. (white)	1						
Pyrgo spp.	1						
Reophax scorpiurus	1						
Technitella sp.	1						
Uvigerina mediterranea							
Valvulineria bradyana			4		1		

Appendix 4.2. (Continued)

Core 11/LL	0.0-0.5	0.5-1.0	1.0-1.5	1.5-2.0	2.0-3.0	3.0-4.0	4.0-5.0
Adercotryma glomeratum	3	1					
agglutinated, (spherical)		2					
agglutinated (3 spheres)		1					
Ammodiscus sp.				1			
Bigenerina cylindrica	1	20	2	3			
Bolivina alata		12		6			
Bulimina inflata	2						
Buzasina sp.?		2					
Chilostomella oolina		6	7	5	1	3	1
Cibicides pachyderma	1	1					1
Cibicides ungerianus		1		2			
Cyclammina cancellata	1						
Discammina compressa	1						
Globobulimina spp.				1	1	2	2
Glomospira charoides		5	2	1	1		
Hyalinea balthica	2						
Melonis barleeanum	24	38	13	21	10	6	5
Textularia spp.	1						
Valvulineria bradyana		6		8		1	
Veleroninoides scitulus	1	2		6			

Core 13/LL	0.0-0.5	0.5-1.0	1.0-1.5	1.5-2.0	2.0-3.0	3.0-4.0	4.0-5.0
Adercotryma glomeratum	9						
agglutinated (spherical, mica)	2			1			
Bigenerina cylindrica		2	29	2			
Bolivina alata			17				
Bulimina inflata	1						
Bulimina marginata	1						
Bulimina sp.	1						
Chilostomella oolina		3	12	5	5	6	1
Cibicides pachyderma	5	1		1			
Cibicides ungerianus				1			
Cribrostomoides subglobosus	1						
Discorbina sp.			1				
Fissurina ssp.		1					
Globobulimina spp.		1			3		3
Glomospira charoides	2	3	6				
Hyalinea balthica	1			1			
Lagenammina difflugiformis	2						
Melonis barleeanum	33	19	54	21	9	7	9
Reophax sp. (mica)				1			
Reophax spiculifer	3						
Tritaxia spp.		1					
Uvigerina mediterranea	1					1	
Valvulineria bradyana			9	1			
Veleroninoides scitulus	4				2		
Veleroninoides wiesneri		1					

Core 14/LL (sediment lost from 1.0-1.5 cm depth interval)	0.0-0.5	0.5-1.0	1.0-1.5	1.5-2.0	2.0-3.0	3.0-4.0	4.0-5.0
Adercotryma glomeratum	4	1		1			
agglutinated (spherical)	2						
Bigenerina cylindrica	1	14	1		2		1
Bolivina alata	1	11	1		1		
Bolivinita quadrilatera	1	1					
Buzasina sp.?		4					
Cassidulina crassa		1					
Chilostomella oolina		17	1		4		1
Cibicides pachyderma		1	1	4		1	
Cibicides ungerianus				1			

Appendix 4.2. (Continued)

Globobulimina spp.	1	1				1	1
Glomospira charoides	3	4	2			1	3
Melonis barleeanum	21	26	9	20	12	5	3
Neolenticulina variabilis	1						
Pullenia bulloides	3						
Reophax sp.		1					
Reophax spiculifer	1	1					
Uvigerina mediterranea	1			1			
Vaginulina sp.		1					
Valvulineria bradyana		7					
Valvulineria rugosa							1
Veleroninoides scitulus	2	2					
Core 16/NL	0.0-0.5	0.5-1.0	1.0-1.5	1.5-2.0	2.0-3.0	3.0-4.0	4.0-5.0
Bigenerina cylindrica		11	5	2			
Bolivina alata		3					
Bulimina inflata	1						
Chilostomella oolina					4	1	1
Cibicides pachyderma			1				
Cibicides ungerianus	1						
Fissurina spp.						1	
Globobulimina spp.		1			1		
Glomospira charoides	1	5	4	1	2	1	1
Hyalinea balthica	1						
Melonis barleeanum	35	39	26	7	9	4	5
Valvulineria bradyana			1				
Veleroninoides scitulus		6	1				
Core 17/NL	0.0-0.5	0.5-1.0	1.0-1.5	1.5-2.0	2.0-3.0	3.0-4.0	4.0-5.0
agglutinated (spherical, mica)		1					
Bigenerina cylindrica			14	10			
Bolivina alata			19	9			
Bolivinita quadrilatera		1					
Bulimina inflata	2	2			1		
Chilostomella oolina		1	5	4	5	5	
Cibicides pachyderma					1		2
Cyclammina cancellata		1					
encrusting 1/2 sphere		1					
Globobulimina spp.			1		1	5	2
Glomospira charoides		5	1	2			
Haplophragmoides sp.		3					
Lenticulina sp.	1						
Melonis barleeanum	13	21	40	25	26	6	9
Pyrgo spp.		1					
Reophax spiculifer		1					
Sphaeroidina bulloides	1						
Trochammina spp.				1			
Uvigerina mediterranea	3						
Vaginulinopsis sp.			1				
Valvulineria bradyana			8	3			1
Valvulineria rugosa						1	
Veleroninoides scitulus		5	2				

Appendix 4.3. Census data, total number of foraminifera (63-150 µm) per sediment sample. At time (t)=0 sample volume is 40 ml. All other samples are 14.1 cm^3 in volume.

t=0 (40 ml)	0-2
agglutinated (round; transparent; thin long neck)	3
agglutinated (single chambered, quartz)	1
agglutinated (spherical)	6
agglutinated (spherical; thin walled;white; non-spinous)	15
Bigenerina cylindrica	14
Bolivina sp.	5
Bolivina alata	22
Bolivina spathulata	3
Bolivina subaenariensis	2
Bulimina aculeata	3
Bulimina inflata	2
Cassidulina sp.	14
Cassidulinoides bradyi	1
Chilostomella oolina	25
Cibicides pachyderma	1
Cibicides sp. (juvenile)	4
Cibicides sp.?	1
Eggerella spp.	1
Fursenkoina spp.	16
Glomospira charoides	4
Glomospira sp. (white)	1
Grigelis sp.	2
Gyroidina spp.	1
Haplophragmoides sp.	7
Heterostegina sp.?	1
Hormosinella guttifera	4
Hyalinea balthica	2
Lagena spp.	1
Lagenammina spp.	1
Lenticulina sp.	1
Leptohalysis catella	8
Marsipella sp.	1
Melonis barleeanum	186
Nonion sp. (juvenile)	2
Nonionella spp.	6
Pullenia sp.	43
Reophax spiculifer	3
Rotalid sp.	1
Spirillina spp.	1
Trochammina sp.	11
Valvulineria bradyana	2
Veleroninoides wiesneri	8
indet.	2

Core 2/NL	0.0-0.5	0.5-1.0	1.0-1.5	1.5-2.0
Adercotryma glomeratum	1		1	
agglutinated (spherical, thin wall)	1			
Bigenerina cylindrica			4	1
Bolivina alata		2	2	
Bolivina spathulata	1	11		
Bolivina subaenariensis		1		
Bulimina aculeata		2	1	
Bulimina marginata			1	
Bulimina sp.				1
Cassidulina sp.		1	10	
Cassidulina subglobosa			1	
Chilostomella oolina			1	
Cibicides sp. (juvenile)		1	2	2

Appendix 4.3 (Continued)

Cibicides sp.			1	
Eggerella spp.			1	
Fursenkoina spp.		1	1	
Glomospira charoides			2	3
Glomospira sp. (white)	1			
Lagena spp.		1		
Lagenammina spp.			1	
Leptohalysis catella	1	1	2	1
Melonis barleeanum	1	28	35	19
Nonion sp. (juvenile)		1		
Pullenia sp.		11	4	1
Textularia spp.		15	3	
Trifarina bradyi		1		
Trochammina sp.	4	6	4	1
Veleroninoides wiesneri		5	1	
Core 5/HL	0.0-0.5	0.5-1.0	1.0-1.5	1.5-2.0
Adercotryma glomeratum	13		1	4
agglutinated (round; transparent; thin long neck)			2	
agglutinated (spherical)	1			1
agglutinated (spherical, thin wall)	2			
Astrononion spp.	1			
Bigenerina cylindrica		2	3	1
Bolivina alata			4	
Bolivina spathulata	6	1		
Bolivina subaenariensis	1			
Bolivinella sp.?	6			
Bolivinita quadrilatera	1			
Bulimina aculeata	4		1	
Bulimina marginata	1			
Bulimina sp.	2			
Cassidulina sp.		7	13	
Chilostomella oolina				1
Cibicides sp. (juvenile)	3	1		
Crithionina sp. (mica sandwich)				1
Discorbina sp.	1			
Eggerella spp.	3			
Epistominella sp.				1
Fursenkoina spp.	1			2
Glomospira charoides	2			
Hormosinella guttifera			1	
Hyalinea balthica	1			
Lenticulina sp.		1		
Leptohalysis catella			2	2
Melonis barleeanum	20	58	25	24
Nonion sp. (juvenile)	1	2	1	
Nonionella spp.		1	2	
Pullenia sp.	11	12	2	3
Reophax spiculifer			1	
Saidovina karreriana	1			
Textularia spp.	5			
Trifarina bradyi				1
Trochammina sp.	5	2		
Valvulineria bradyana			2	
Veleroninoides wiesneri	2			
indet.	1			

Appendix 4.3 (Continued)

Core 8/HL	0.0-0.5	0.5-1.0	1.0-1.5	1.5-2.0
Adercotryma glomeratum	27	2		1
Bigenerina cylindrica		2		
Bolivina alata		1	1	
Bolivina sp.	3	2	2	3
Bolivina subaenariensis	1	2	1	
Bulimina inflata	2			
Cassidulina cf. *laevigata*				1
Cassidulina sp.		2	13	1
Chilostomella oolina			2	
Cibicides sp.	1	1	1	
Discorbina sp.	1			
Eggerella spp.			1	
Fissurina spp.				1
Glomospira charoides		7	2	1
Glomospira gordialis	1			
Gyroidina spp.	1			
Leptohalysis catella	4	3		
Melonis barleeanum	3	42	62	25
Nonion sp.	2			
Nonionella spp.	4	3	1	
Pullenia sp.	13	14		
Reophax sp.	1			
Reophax sp. (mica)				1
Reophax spiculifer			1	
Rotalid sp.		2		
Saccammina (clear, long thin neck)	1	1		
Saidovina karreriana		1		
Sigmoilopsis schlumbergeri	2			
Textularia spp.	9			
Trifarina angulosa	1			
Trochammina sp.	10	1	3	
Valvulineria bradyana			4	
Valvulineria sp.	1			
Veleroninoides scitulus			2	
Veleroninoides sp. (bright orange, smooth wall)	5	7	3	
indet.	1			

Core 10/LL	0.0-0.5	0.5-1.0	1.0-1.5	1.5-2.0
agglutinated (spherical, thin wall)		1	1	
agglutinated (round; transparent; thin long neck)	1			1
Adercotryma glomeratum	17			2
Bolivina spathulata	2	6		
Bolivina subaenariensis		1		
Bolivinita quadrilatera		1		
Bulimina aculeata				1
Bulimina marginata	1			
Cassidulina sp.				1
Cibicides pachyderma	1			
Cibicides sp. (juvenile)			1	
Cibicides kullenbergi				2
Crithionina sp. (mica sandwich)		1		
Discorbina sp.			1	
Fursenkoina spp.	1		1	1
Glaphyrammina sp.				1
Glomospira charoides			1	
Glomospira sp. (white)		2		
Heterostegina sp.?			1	
Hyalinea balthica	2			
Melonis barleeanum	3	18	32	29

Appendix 4.3 (Continued)

Nonion sp. (juvenile)		3		
Pullenia sp.	1	14		3
Leptohalysis catella		1	1	
Saidovina karreriana		3		
Textularia spp.	1	1		
Trifarina angulosa	1			
Trochammina sp.	4	4	1	
Uvigerina mediterranea	1			
indet.		1	1	
Core 13/LL	0.0-0.5	0.5-1.0	1.0-1.5	1.5-2.0
Adercotryma glomeratum	17		1	1
Bolivina spathulata		1		
Bolivina sp.			1	
Bolivinita quadrilatera	3			
Cassidulina sp.			2	
Chilostomella oolina			1	1
Cibicides pachyderma				1
Discammina compressa			1	
Eggerella spp.		1		
Glomospira charoides		2		
Gyroidina spp.	1			
Hyalinea balthica			1	
Nodosaria sp.	1			
Melonis barleeanum	3	19	49	21
Nonionella spp.			1	
Pullenia sp.	2	5	1	
Rotalid sp.				1
Saccammina sp.	1		1	
Saidovina karreriana	1	1		
Textularia spp.	20	4		
Valvulineria bradyana			6	
Valvulineria rugosa	1			
Veleroninoides wiesneri	1	1		
Core 17/NL	0.0-0.5	0.5-1.0	1.0-1.5	1.5-2.0
Adercotryma glomeratum	13			
agglutinated (round, transparent, thin long neck)	1			
Bolivina spathulata	1	1		
Bolivina subaenariensis		1		
Bulimina inflata			1	
Glomospira charoides		4	1	
Gyroidina spp.		1		
Hyalinea balthica	2			
Melonis barleeanum	2	7	12	11
Nonionella spp.			2	
Pullenia sp.	2	11	2	
Saidovina karreriana		1		
Textularia spp.	1			
Trifarina bradyi		1	1	
Trochammina sp.	1	1		1
Valvulineria bradyana			3	3

CHAPTER 5

Sedimentary labile organic carbon and pore water redox control on species distribution of benthic foraminifera: A case study from Lisbon Setúbal Canyon

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ABSTRACT

Rose Bengal stained benthic foraminifera were studied from 11 cores collected along two depth transects: one in the Lisbon-Setúbal Canyon and the other on the adjacent continental slope. The total standing stocks and distribution of foraminifera were investigated in relation to sediment and pore water geochemistry. Nitrate was used as a redox indicator, sedimentary chlorophyll *a* and CPE (chloroplastic pigment equivalents) contents as a measure of labile organic matter, and total organic carbon as a measure of bulk organic matter availability.

The canyon sediments were enriched in organic carbon and phytopigments at all water depths in comparison with the open slope. Water depth seemed to control sedimentary phytopigment content, but not total organic carbon. No significant correlation was seen between pigment and total organic carbon content.

The abundance of calcareous foraminifera correlated with the labile organic matter content, whereas a weaker correlation was observed for the agglutinated taxa. Therefore, calcareous foraminifera appear to require a fresher food input than agglutinated taxa. The foraminiferal species composition also varied with pigment content and nitrate penetration depth in the sediment, in line with the TROX concept. Phytopigment-rich (surficial CPE content > 20g/cm^3) sediments with a shallow nitrate penetration depth (~ 1cm depth) were inhabited by infaunal species such as *Chilostomella oolina*, *Melonis barleeanum* and *Globobulimina* spp. As the nitrate penetration increased to ~ 2 cm depth in sediment and the pigment content remained relatively high (> 15 g/cm^3), *Uvigerina mediterranea* and *U. elongatastriata* became dominant species in the surface sediments. With declining CPE content and increasing nitrate penetration depth, the foraminiferal assemblages changed from the mesotrophic *Cibicides kullenbergi- U. peregrina* assemblage to the oligotrophic abyssal assemblage, mainly consisting of agglutinated taxa.

5.1 INTRODUCTION

Organic carbon flux is an important parameter structuring deep sea benthic ecosystems (Rowe, 1983; Gage and Tyler, 1991; Schaff et al., 1992; Altenbach and Struck, 2001). In accordance, the taxonomical composition of benthic foraminiferal communities (e.g. Schmiedl et al., 1997, de Stigter et al., 1998, Jorissen et al., 1998, Licari et al., 2003) and the depth distribution of foraminifera in sediment (microhabitat) is related to quantity and quality of the available food flux (e.g. Corliss and Silva 1993, Licari et al. 2003, Schmiedl et al. 2000).

Redox zonation in the sediment is associated with organic matter remineralisation, which is largely mediated by microorganisms. Microbial communities actively break down organic carbon (C_{org}), typically utilising electron acceptors in the order of decreasing free energy yield (i.e. O_2, NO_3^-, MnO_2, FeOOH, SO^{2-}_4; Froelich et al 1979). In oligotrophic regions where the organic matter flux and sedimentary C_{org} content are low, almost all carbon is remineralised through oxic respiration (e.g. Jahnke et al., 1982, Goloway and Bender 1982), resulting in deep redox zonation. With increasing carbon load and enhanced oxidation rates alternative electron acceptors become important in the bacterial remineralisation of C_{org} (Canfield 1993), leading to the development of vertically compressed and shallower redox zonation.

The relationship between labile (i.e. bio-available) organic matter, redox zonation and microhabitat of benthic foraminifera was described by Jorissen et al. (1995) in terms of the conceptual TROX (TRophic OXygen) model. According to this model, in food-limited and well-oxygenated environments, the foraminiferal community is restricted to the surficial sediments due to low food supply, and consists of epifaunal taxa specialised to live in oligotrophic regions. In eutrophic environments, where food is plentiful and the pore water oxygen content is often reduced, the foraminiferal assemblage is dominated by infaunal taxa. In these environments, the depth distribution is controlled by the sediment redox zonation; prolonged exposure to hydrogen sulphide being toxic for foraminifera (Moodley et al. 1998a). In the intermediate situation, where food is relatively abundant and the oxygen penetration depth is moderate, a well developed vertical species distribution can be expected, consisting of both epifaunal and infaunal taxa.

In this study we propose to evaluate the TROX concept by investigating the distribution of benthic foraminifera, using pore water nitrate profiles as indicator of redox zonation and sedimentary chlorophyll *a* and CPE (chloroplastic pigment equivalents) content as a measure of the labile organic matter availability. We feel it is vital to improve our understanding of, and to begin to quantify, the influence of these parameters on the distribution of benthic foraminifera as this would

increase the potential of benthic foraminifera as proxies in paleoenvironmetal studies.

To this aim 11 stations, seven located in the Lisbon-Setúbal submarine canyon and four on the adjacent continental slope, were sampled for living benthic foraminifera, and sediment and pore water geochemistry. The studied settings, canyon and slope, provide an environmental range in the parameters of interest. In general, submarine canyons can act as sedimentary traps where material, including organic carbon, from the surrounding shelf is advected into (Van Weering et al., 2002). Higher organic carbon concentrations have been reported from several canyons in comparison to the adjacent open slope environments (e.g. Schmiedl et al. 2000, Duineveld et al., 2001, Epping et al. 2002, de Stigter et al. in press, Garcia et al. 2007), thus leading to enhanced oxygen consumption rates and relatively sharp redox clines in the canyon sediments (Epping et al., 2002). Therefore, the canyon sediments were expected to provide an ideal study region for the organic rich sediments, whereas the adjacent slope should offer the opposite, more oligotrophic setting. In addition, changes in all parameters (e.g. foraminifera, organic matter and redox zonation), were expected to covary with water depth.

5.2 MATERIALS AND METHODS

5.2.1 Study region

The Lisbon-Setúbal Canyon is located on the Portuguese continental margin around 38º 00'-38° 24' N; 009°-010° 30' W (Figure 5.1). The water column in the study area consists of several water masses (Fiuza et al. 1998, Garcia et al., 2003). At the surface, below the seasonally varying thermocline, a light (warm and salty, ≤36.0 psu) body of subtropical Eastern North Atlantic Central Water (ENACW) can be distinguished. Below ENACW, between 600-1600m water depth, relatively warm (~10 °C) and saline (>36.0 psu) Mediterranean Outflow Water (MOW) is found, its salinity peak centred at 1100 m depth. North Atlantic Deep Water (NADW) dominates below the MOW, having a cooler (6-2 °C) and less salty (~35.0 psu) nature.

The Portuguese margin is influenced by complex, seasonally changing hydrodynamics. Winters (typically December-January) are characterised by prevailing southerly winds leading to downwelling events and offshore bottom water Ekman transport (Vitorino et al. 2002 a). In addition, winters are marked by intense storms capable of eroding sediments at mid-shelf depths, and hence leading to offshore transport of fine grained sediments in the form of nepheloid layers (Vitorino et al., 2002 a,b). During summer the wind direction is reversed (Vitorino et al. 2002a) followed by the development of an upwelling regime, which is most active between the months of June and September (Huthnance et al. 2002). The upwelling results in a clear increase in the primary productivity in surface waters during summer (Joint et al 2001).

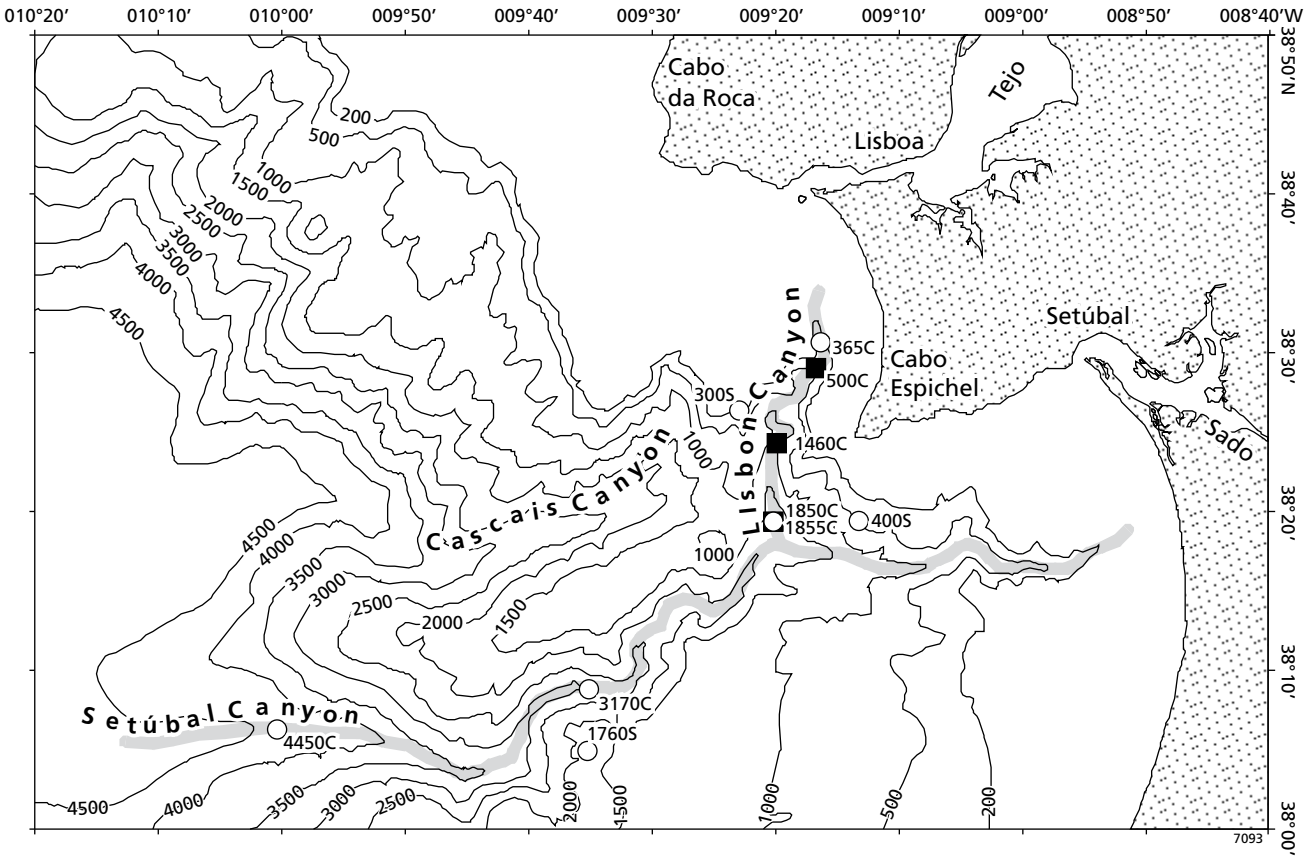


Figure 5.1. Map of the Lisbon-Setúbal Canyon and the adjacent continental slope. The stations sampled in October 2003 and May 2004 marked with, respectively, black squares and white circles.

Original station name	Sample moment	Depth (m)	New station name	Longitude (°W)	Latitude (°N)	Chl *a* µg/cm³	CPE µg/cm³	Chla: phaeo	C_{org} (wt. %)	C/N (molar)	NO_3^- penetration depth (cm)*
Canyon											
225-01	May 04	365	365C	9°16.42′	38°31.07′	0.91	21.71	0.044	1.0	9.3	1.25
225-03	May 04	1855	1855C	9°19.60′	38°19.96′	0.23	8.56	0.028	1.6	8.0	3.5
225-05	May 04	3170	3170C	9°35.00′	38°09.43′	0.08	3.12	0.026	1.1	7.6	4.5
225-07	May 04	4450	4450C	10°00.26′	38°6.38′	0.02	1.18	0.017	0.9	8.2	8.0
218-21	Oct 03	500	500C	9°16.03′	38°29.99′						
218-22	Oct 03	1460	1460C	9°19.77′	38°24.78′						
218-23	Oct 03	1850	1850C	9°19.59′	38°19.97′						
Open slope											
225-02	May 04	300	300S	9°23.06′	38°25.98′	0.62	16.09	0.040			
225-46	May 04	400	400S	9°12.50′	38°19.50′				0.6	8.2	2.75
225-21	May 04	1760	1760S	9°34.85′	38°04.99′	0.14	4.24	0.034	1.1	8.1	5
225-06	May 04	2945	2945S	9°58.51′	38°00.46′	0.04	1.95	0.021	1.0	7.6	8

*NO_3^- penetration depth (cm); considered once the pore water concentrations stabilised to ~2-3 µmol/L.

Table 5.1. Station locations (water depth, latitude, longitude), sample moment and characteristics of the surface sediments (average of top 1 cm): Chlorophyll *a* (Chl *a*) and concentrations of chloroplastic pigments equivalents (CPE), chlorophyll *a*: phaeopigment ratio (Chla:phaeo), and organic carbon (C_{org}), organic carbon to total nitrogen molar ratio (C:N) and nitrate (NO_3^-) penetration depth in sediment.

5.2.2 Samples and analyses

Surface sediment cores used for this study were collected using a MUC 8+4 multiple corer developed by Oktopus GmbH (equipped with eight 6 cm and four 10 cm diameter coring tubes) during cruises 64PE218 (October 2003) and 64PE225 (May 2004) of RV "Pelagia" of Royal NIOZ. Altogether, 11 stations were measured for this study, of which seven were located in the Lisbon-Setúbal Canyon and four on the adjacent slope; see Figure 5.1 and Table 5.1 for sample sites. From here on the stations will be referred to by their water depth and a distinction is made between stations in the canyon (marked by C) and on the open slope (marked by S).

Geochemical and sedimentological analyses

The geochemical analyses were performed on material collected in May 2004. To obtain pore water profiles of dissolved nitrate (NO_3^-) and ammonium (NH_4^+) in the sediment, the cores were immediately sectioned upon arrival on board, at in situ temperature, using a hydraulic slicer. The top centimetre of the sediment was sectioned into 0.25 cm slices, from 1 to 3 cm the slices were 0.5 cm, from 3 to 7 cm the slices were 1.0 cm, below 7 cm slices were 2 cm. The sediment was centrifuged at 3000 rpm for 10 min. The supernatant was filtered (0.45 µm, Acrodisc filters) and analysed on board for nitrate (following methods outlined in Grashoff et al. 1983) and ammonia (Helder, 1989) on a TRAACS-800+ autoanalyser. Sediment pellets were stored frozen at -20°C for solid phase analyses. Sedimentary carbon, total nitrogen and organic carbon were measured with a Thermo Finnigan flash element analyser following the procedures described by Lohse et al. (2000).

The concentrations of sediment-bound chlorophyll *a* (chl *a*) and phaeopigment (phaeo, degradation product of chl *a*) were quantified following Yentsch and Menzel (1963) in order to evaluate recent input of fresh organic matter as a high quality food source for benthic organisms. Cores were subsectioned at 0.5 cm intervals down to 1 cm and at 1 cm intervals down to 5 cm. The samples were stored at -20°C until analysis. In the laboratory, the sediment samples were first freeze-dried and homogenised in a mortar. Subsequently pigments were extracted in 10 ml 90% acetone solution and measured in a Turner TD 700 fluorometer following Shuman and Lorenzen (1975). The bulk of pigments measured with this method (chl a + phaeo) were termed "chloroplastic pigment equivalents", CPE (Thiel 1978). The ratio of chla:phaeo was used for assessment of phytodetritus quality.

Foraminifera

Foraminifera were analysed from cores with an internal diameter of 6 cm. On board the sediment cores were sliced: the top 2 cm was cut in slices of 0.5 cm thick and the remaining sediment in 1 cm thick slices. Immediately after slicing the samples were stored in a solution of rose Bengal in 96% ethanol (1 g/L) until further treatment in the laboratory. The rose Bengal stain is extensively used in ecological studies to distinguish foraminifera living at the time of sample collection. This technique has some limitations because in anoxic conditions specimens may stain several months after the death of the organism (Bernhard 1988, Hannah and Rogerson 1997). Nevertheless, if rose Bengal is used with care this problem is negligible (Murray and Bowser, 2000).

Samples were wet-sieved into >150 and 63-150 µm size fractions and kept wet at all times. As soon as possible after the washing procedure, the rose Bengal stained foraminifera were hand-picked and sorted on Chapman slides. Only the well-stained specimens were regarded as living and any patchy colouring was interpreted to indicate material that was already dead at the moment of sampling. In case of doubt, tests were broken and the protoplasm was inspected in more detail.

The results are presented of the >150 µm fraction in the top 5cm of the sediment. Total standing stocks (TSS), the number of living foraminifera (excluding branching/tubular agglutinated foraminifera) per core (under 28.3 cm^2), were calculated by

summation of the number of stained foraminifera in depth intervals 0 to 5 cm. The numbers per core slice were converted to densities by standardising the number of individuals to 50 cm^3. The numbers of arborescent and tubular foraminifera are reported separately, because of limitations of the counting method. Arborescent/tubular foraminifera break apart easily and therefore it may be difficult to distinguish single individuals. In this paper numbers of these foraminifera are counted as whole specimens if an aperture, a middle bulge (e.g. in *Rhabdammina* spp.) or terminal bulb is present (e.g in *Saccorhiza ramosa*); otherwise they are counted as fragments.

The average living depth (ALD) can be used as an indication of the vertical distribution of the total foraminiferal standing stock or of individual species, and is calculated following Jorissen et al. (1995) as:

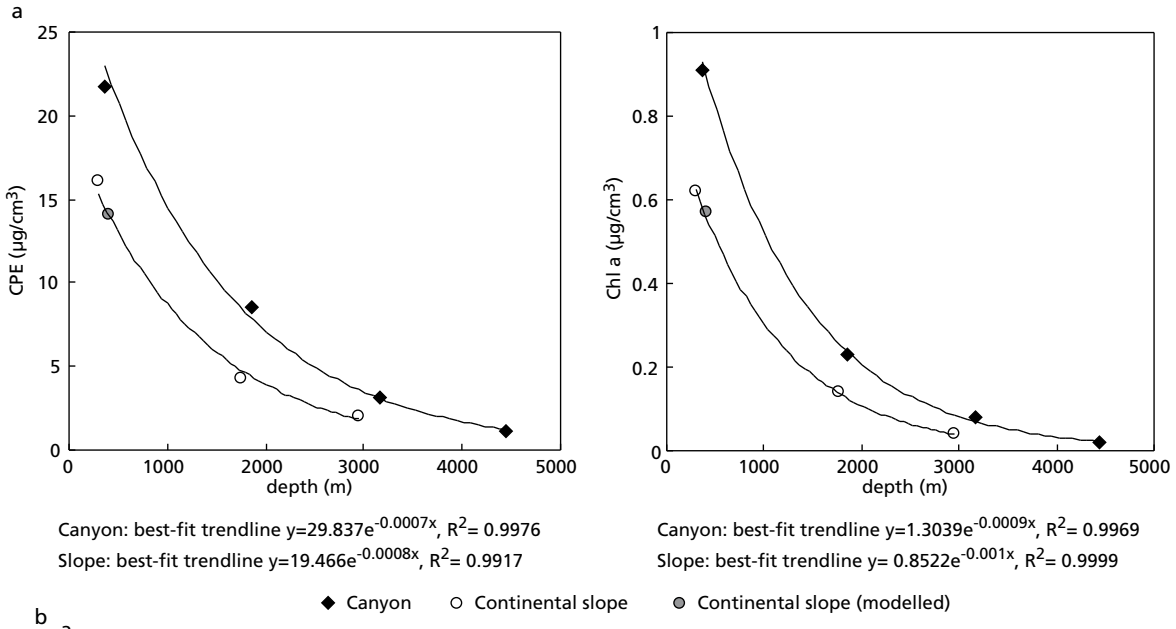
$$ALD_x = \sum_{i=0,x} (n_i D_i)/N,$$

where x describes the lower boundary of the deepest sample, n_i is the number of foraminifera in the interval i, D_i is mid-depth of the sample interval i, and N is the total standing stock for all levels. In this study we report the living depth for the top 5 cm in sediment, ALD_5, for species represented by five or more specimens at one site.

Species richness (S), a count of living foraminiferal species per station, the Shannon-Wiener Index H(S) (Shannon and Weaver, 1949; a diversity index) and equitability E(S) (Buzas and Gibson 1969; a measure of the evenness of species distribution) were calculated for foraminiferal assemblages from each site.

Statistical analyses

A hierarchical cluster analysis (squared Euclidean distance, average linkage: within group) was performed using statistical software SPSS 11.0 for Windows. The analysis was based on a presence-absence matrix of all counts, a value of 1 given to a taxon if present and 0 if absent. Arborescent and tubular species were included in the analysis. In order to evaluate effects caused by different sampling moments, such as seasonality and interannual variability, clustering was first performed on the stations sampled in May 2004; later the stations sampled in October 2003 were included in the analysis. The cluster analysis was also used to examine the similarities between stations located in the canyon and on the slope.



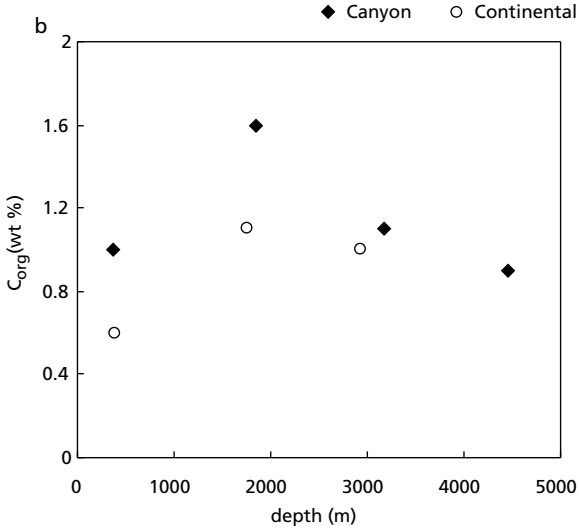


Figure 5.2a. Chlorophyll *a* and CPE (chloroplastic pigment equivalents) concentrations measured in the top 1 cm of the sediment. No pigments were measured in station 400S (May 2004). Interpolated pigment concentrations were calculated for station 400S, using the best fit exponential decline curves as shown in the figure. The pigments are reported in cubic centimetre wet sediment. 2b. The organic carbon (wt %) measured in the top 1 cm of the sediment.

Further, the relationship between the standing stocks of foraminifera (total, calcareous, agglutinated, and arborescent and tubular species studied separately) and environmental parameters were investigated using Pearson correlation. The analyses were performed using May 2004 data only as no pore water nitrate and phytopigment analyses were made in October 2003.

5.3 RESULTS

5.3.1 Sedimentary carbon and pigment contents

The downcore profiles of organic carbon were relatively uniform (Figure 5.3a, b), and no systematic trend was observed with increasing sediment depth. Only at two stations, 1760S and 2945S, was a slight surface maximum measured. Hence, considering the C_{org} values in the top centimetre representative, the C_{org} content was generally higher in the canyon than on the open slope, ranging from a maximum of 1.6 wt % in the canyon at 1855 m water depth to a minimum of 0.6 wt % in the open slope at 400 m water depth (Figure 5.2b; Table 5.1). No correlation was observed of C_{org} with water depth (Table 5.3); however, both for the open slope and the canyon, the maximum C_{org} concentrations were measured in sediments from around 1800 m water depth (Figure 5.2a).

The surficial C/N ratios showed no systematic trend with water depth either (Table 5.1 and 2). The lowest values (7.6) were measured in the open slope station 2945S and canyon station 3170C, and the highest ratio (9.3) was measured in canyon site 365C.

In contrast with C_{org} content and C/N ratios, the concentrations of chlorophyll *a* (chl *a*) and chloroplastic pigment equivalents (CPE) in the top centimetre of sediment did correlate with water depth, showing an exponential decline (Figure 5.2a). At equivalent water depths, higher concentrations were measured in the canyon than on the open slope, however, the difference diminished towards the deeper sites. In the canyon the chl *a* values ranged from 0.91 μg/cm^3 at 365 m water depth to 0.02 μg/cm^3 at 4450 m water depth and the CPEs from 21.71 μg/cm^3 to 1.18μg/cm^3, respectively. The chl *a* values measured in the open slope sediments ranged from 0.62 μg/cm^3 at 300 m water depth to 0.04 μg/cm^3 at 2945 m water depth and CPEs from 16.09 μg/cm^3 to 1.95 μg/cm^3. The Chl *a*:phaeo ratios declined with increasing water depth, both in the canyon and on the open slope (Table 5.1).

Only the downcore profiles of CPEs are presented (Figure 5.3a and 5.3b) as the sediment distribution profiles for chl *a* and CPE were always similar in shape. In general, the highest CPE concentrations were recorded at the sediment surface. However, in the canyon cores 365C and 3710C a subsurface maximum was present between 0.5 and 1 cm depth in sediment. Additionally, if the surficial CPE concentrations were low (< 3 μg/cm^3; stations 2945S, 4450C) no clear relationship was observed between the pigment content and the sediment depth.

5.3.2 Pore water profiles: nitrate and ammonium

The penetration depth of NO_3^- in the sediment was always shallower in the canyon than in the open slope sediments at comparable water depths (Figures 5.3a, b). The shallowest NO_3^- penetration depth (1.2 cm) was measured in the canyon station 365C, from where the penetration depth increased with water depth. At the deepest canyon site (4450C) relatively high NO_3^- concentrations (13.5 μmol/L) were still measured at 4.5 cm depth in sediment. In the open slope sediments an increase in NO_3^- penetration with increasing water depth was also observed. The penetration depth was shallowest (2.75 cm) at site 400S; in the deepest site (2945S) 21.9 μmol/L of NO_3^- was still measured at 4.5 cm depth in sediment.

In all cores the surficial NH_4^+ concentrations were relatively low and ranged from 1.3 μmol/L (station 400S) to 5.4 μmol/L (station 2945S). A clear build up of NH_4^+ with depth in sediment was observed in three of the cores, 365C, 1855C and 400S.

5.3.3 Foraminifera

Abundance and in- sediment distribution: relation to environmental parameters

Included in Figure 5.3(a, b) is the vertical distribution of the standing stocks of foraminifera sampled in May 2004. Most foraminifera were located relatively close to the sediment surface and in every station, including the sites sampled in October 2003, 90 per cent or more of the foraminifera were located in the top 3 cm of the sediment column. Five out of eight stations (365C, 1855C, 400S, 1760S and 2945S) showed a clear surface maximum in the foraminiferal abundance, and an approximately exponential decline in the standing stocks with increasing sediment depth. A subsurface maximum, located between 0.5-1.0 cm depth in sediment, was observed in the remaining three cores (300S, 3170C, 4450C).

Total standing stocks declined with water depth (Table 5.2, Figure 5.4a) in the canyon as well as in the slope stations at both sampling moments (October 2003 and May 2004). The highest numbers were recorded in the upper canyon and slope stations

	Station	TSS	S	H(S)	E	Arborescent/ tubular taxa	
						Whole	fragment
Canyon							
May 2004	365C	766	46	3.1	0.5	0	10
	1855C	165	28	2.2	0.3	2	3
	3170C	157	31	2.8	0.5	10	85
	4450C	155	29	2.9	0.6	0	8
Oct 2003	500C	341	45	3.1	0.5	0	14
	1460C	202	29	2.5	0.4	3	70
	1850C	21	11	2.2	0.8	0	0
Open slope							
May 2004	300S	620	72	3.1	0.3	3	33
	400S	430	46	3.0	0.4	1	168
	1760S	183	38	3.2	0.6	3	62
	2945S	163	51	3.5	0.7	15	132

Table 5.2 Total standing stock (TSS, number below 28.3 cm^2 surface area, down 5 cm) of foraminifera (excluding arborescent/tubular foraminifera); and counts of arborescent/ tubular foraminifera, whole specimens and fragments. Species richness (S), Shannon-Wiener Index H(S) and equitability E.

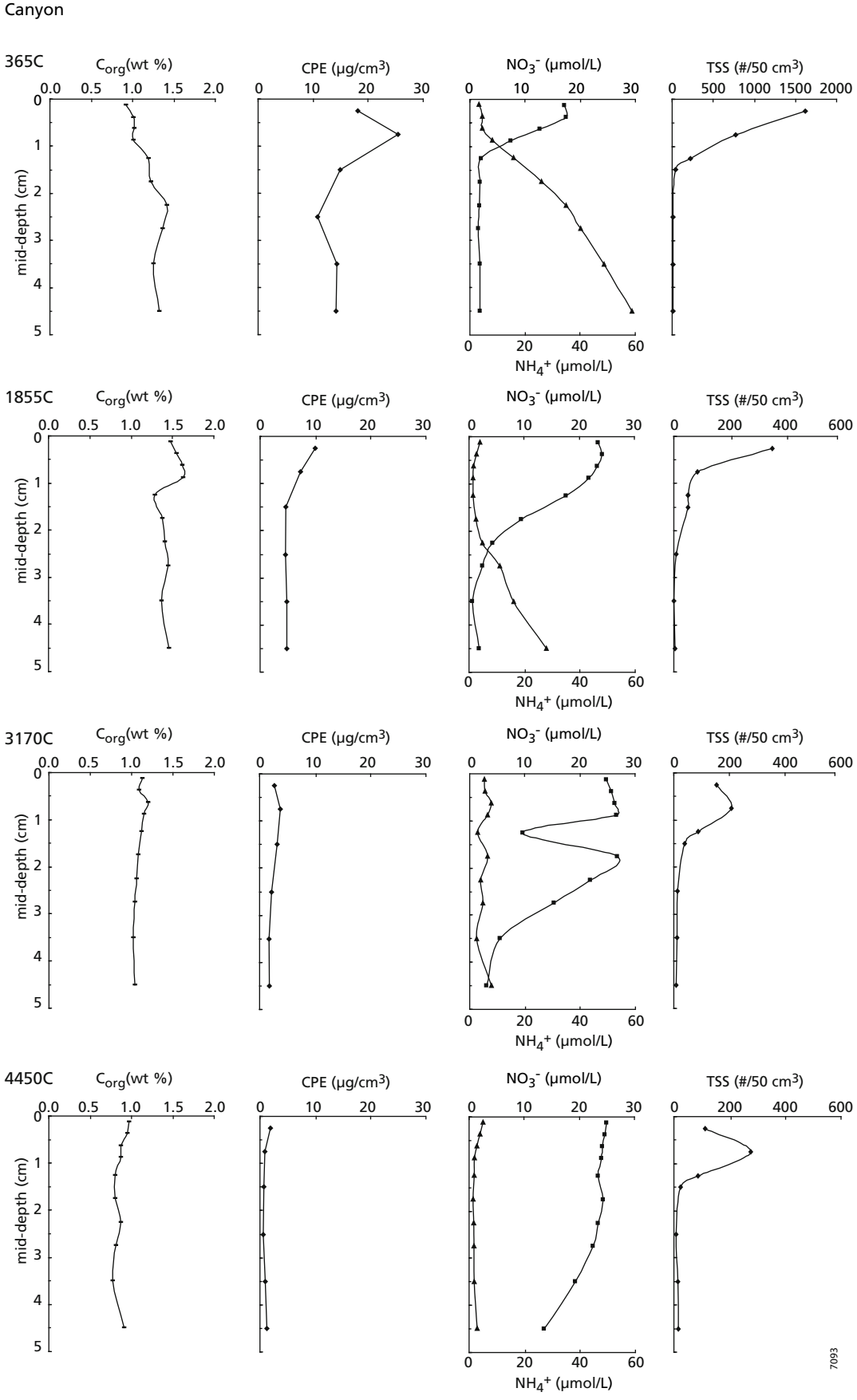
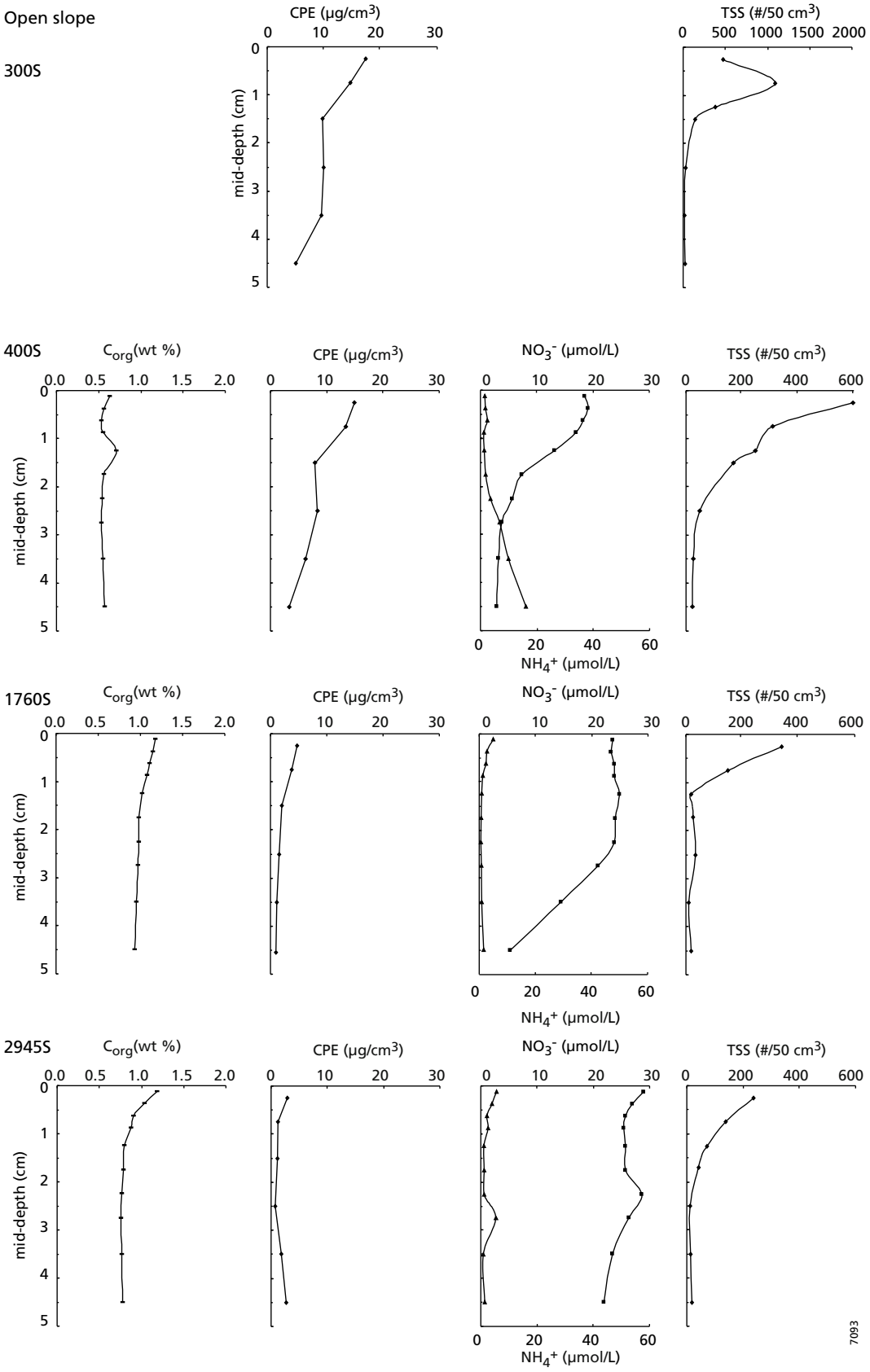


Figure 5.3. From left: the downcore profiles of organic carbon (C_{org}), CPE* (chloroplastic pigment equivalents), nitrate (NO_3^-; square symbol) and ammonium (NH_4^+; triangle symbol) pore water profiles, and foraminiferal standing stocks. a.) Canyon stations. b.) Continental slope stations. *The CPE profile for station 400S was obtained by exponential interpolation of CPE



profiles in Stations 300S, 1760S and 2945S in relation to water depth. Concentrations were interpolated separately for each sediment depth interval (equations for each depth interval not shown separately).

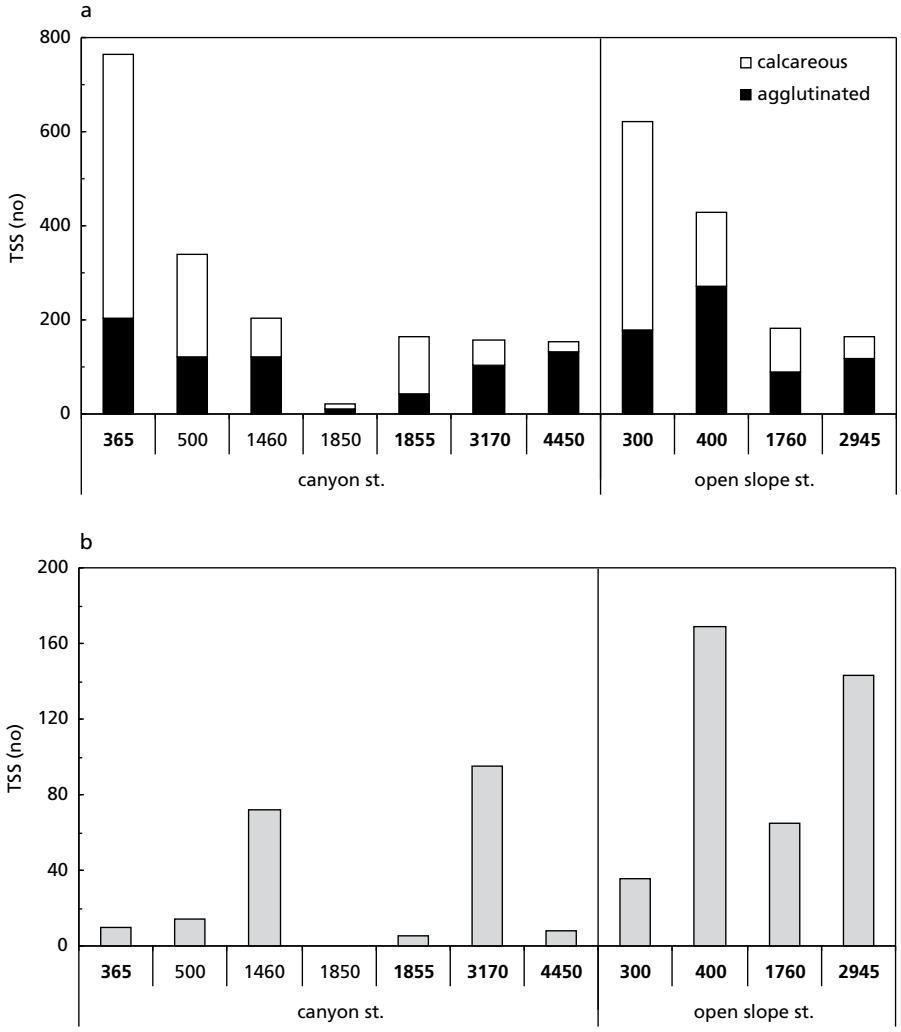


Figure 5.4 Total standing stocks of foraminifera per core (below 28.3 cm^2 surface area, down 5 cm depth). Stations sampled in May 2004 in bold, and stations sampled in October 2003 in normal font. a.) Calcareous and agglutinated foraminifera, excluding arborescent/tubular foraminifera b.) arborescent/tubular foraminifera, fragments and whole individuals.

with a maximum in station 365C sampled in May 2004 (766 individuals/core). A positive and statistically significant ($p<0.05$) relationship was observed between the TSS of foraminifera and water depth (Table 5.3). In addition, the TSS correlated with the sedimentary pigment content (Chl *a*, CPE, Chla:phaeo) and sedimentary C/N ratios. In more detail, the correlation with sedimentary pigment content was especially significant for the calcareous foraminifera. The agglutinated population showed a weaker correlation with Chl *a* content than the calcareous fauna and no relation was observed with sedimentary CPE content. In contrast, the organic carbon content showed no correlation with water depth, whereas a negative correlation was found between agglutinated foraminifera and the sedimentary organic carbon and nitrogen content.

Overall higher diversities were recorded on the open slope than in the canyon (Table 5.2). The species richness was largest in the shallower sites, both in the canyon and on the open slope, where up to 72 living species with a diversity value H(S)=3.1 were recorded in station 300S. However, station 300S had the lowest equitability value (E=0.3), indicating low evenness in the abundance of species. The highest diversity (H(S)=3.5) together with the highest equitability (E=0.7) was found at site 2945S.

Higher abundances of arborescent and tubular foraminifera were found on the continental slope than in the canyon (Table 5.2, Figure 5.4b). The maximum total abundance (168 specimens) was recorded in station 400S. The most complete individuals (15 specimens) were found in station 2945S. In the canyon, the highest abundances of arborescent/tubular taxa occurred in the lower canyon, at station 3170 C, where 85 fragments and 10 whole individuals were found. No correlations were observed between the abundance of arborescent and tubular taxa and any of the measured geochemical parameters.

Foraminiferal communities

In general, the foraminiferal communities changed with water depth (Appendix 5.2). The upper canyon station (365C) was dominated by species like *Chilostomella oolina*, *Globobulimina* spp., *Bigenerina cylindrica* and *Melonis barleeanum*. A similar species assemblage was seen in station 500C sampled in October 2003. On the adjacent slope either *Uvigerina elongatastriata* (300S) or *U. mediterranea* (400S) were the most abundant species, however deep infaunal taxa were also present although in lower abundances

Cibicides kullenbergi was in May 2004 the most abundant species both in the middle canyon station 1855C and the middle continental slope station 1760S; however the absolute and relative abundance was far greater in the canyon station (83 specimens; 50%) than on the open slope site (24 specimens; 13%). In station 1850C, sampled in October 2003 only 2 live specimens (~10%) of *C. kullenbergi* were found. Other common

and relatively abundant taxa in the middle canyon included *Cribrostomoides subglobosus*, *Globobulimina* spp. and on the slope *Uvigerina peregrina*.

The lower canyon and lower continental slope were dominated by agglutinated species, including *Lagenammin*a spp., *Reophax* spp. and various single chambered spherical taxa. In the canyon relatively common calcareous species were *Hoeglundina elegans* (3170C) and *Nuttallides umbonifera* (4450C).

The arborescent/tubular communities also changed with water depth (Appendix 5.3). In the upper canyon and upper continental slope stations several *Bathysiphon* species were found. In the upper slope stations, however, the most abundant tubular foraminiferal species were *Rhabdammina linearis* (300S) or *Marsipella* spp. (400S). The middle continental slope (1760S) was dominated by *Saccorhiza ramosa*, *Marsipella* spp. and *Rhizammina algaeformis*, whereas in the canyon only few specimens of *Rhabdammina abyssorum* were found. The lower continental slope and lower canyon assemblages were dominated by *Rhizammina* spp. and *S. ramosa*.

The relationships between foraminiferal assemblages sampled from the canyon and open slope were investigated by hierarchical cluster analysis (Figure 5.5a, b). A separate cluster was formed by the shallow canyon and shallow open slope sites, indicating that taxa from these water depths differ from the remaining deeper stations. Addition of stations sampled in October 2003 did not change the main subdivision of the clusters (Figure 5.5b). Generally, in Figure 5.5b, the stations appeared to be arranged in order of declining sedimentary pigment content, except for the very deep stations 4450C and 2945S.

Species specific distribution in the sediment

The formation of mixed clusters (Figure 5.5), containing both canyon and open slope stations, indicates that the foraminiferal faunas in these two settings are fundamentally similar, differences mainly consisting of variations in TSS and relative abundance of species. Also independent of the setting (canyon or open slope), is the consistent relationship with labile organic matter, which is demonstrated by the near perfect correlation between the CPE and Chl *a* inventory and TSS (Table 5.3). According to the TROX concept, the vertical distribution of foraminifera in sediment is principally controlled by availability of labile organic matter and redox zonation in the sediment. To test this concept we have plotted the distribution of a number of common foraminiferal species relative to lateral and vertical trends (Figure 5.6) in phytopigment and pore water nitrate. Firstly, the CPE and NO_3^- profiles of canyon and slope stations were arranged in order of decreasing CPE inventory in the top 5 cm of sediment, and contoured (Figure 5.7). Subsequently the main features of the resulting graph were redrawn and

	Water depth	TSS	$TSS_{calcareous}$	$TSS_{agglutinated}$	$TSS_{arb.+tubular\ taxa}$	S	H(S)	E	C_{org}	C/N (molar)	CPE	Chl *a*	chla:phaeo
TSS	-0.80												
N	8												
$TSS_{calcareous}$	-0.77	**0.97**											
N	8												
$TSS_{agglutinated}$													
N													
$TSS_{arb.+tubular\ taxa}$													
N													
S													
N													
S (H)													
N													
E													
N													
C_{org}				-0.86									
N													
C/N (molar)		**0.90**	**0.91**										
N		7	7										
CPE	**-0.89**	**0.95**	**0.93**							0.84			
N		8	8							7			
Chl a	**-0.88**	**0.96**	**0.92**	0.74						0.83	**0.99**		
N	8	8	8							7	8		
chla:phaeo	**-0.96**	0.86	**0.90**	7							**0.90**	**0.90**	
N	7	7									7	7	
NO_3^- penetration depth	0.87		-0.75								**-0.88**	-0.85	-0.89
	7		7								**7**	7	7

Table 5.3. Pearson correlation coefficients for environmental parameters specified in Table 5.1 vs. totals standing stocks of calcareous, agglutinated and arborescent/tubular foraminifera, and diversity indices (S = Species Richness, S(H) = Shannon-Wiener, E = evenness). Only statistically significant correlations are shown: in bold $p < 0.01$, in normal font $p < 0.05$.

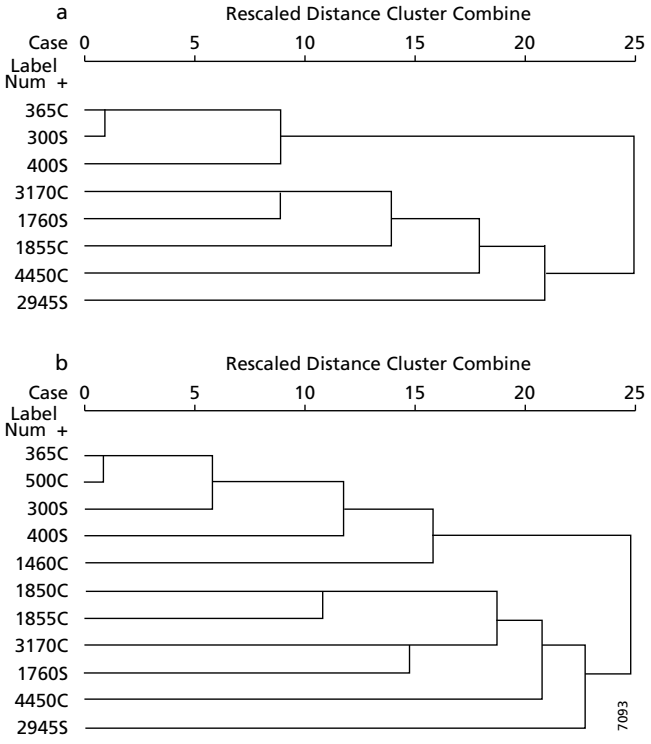


Figure 5.5. Dendrograms obtained by hierarchical cluster analyses (squared Euclidean distance, average linkage: within group). Clustering based on a presence-absence matrix of all counts including arborescent and tubular species, see section 5.2.2. (Statistical analysis) for more details. a.) Stations sampled in May 2004. b.) Stations sampled in October 2003 included.

abundance contours of foraminiferal species were added (Figure 5.8).

Deep infaunal foraminifera *Globobulimina* spp. and *Chilostomella oolina* showed similar distribution profiles, both occupying sediment depths where the pore water nitrate content declined sharply, but *C. oolina* was restricted to sediment with CPE content higher than 5 g/cm^3 whereas *Globobulimina* was also present in sediment with lower CPE content.

The occurrence of *Melonis barleeanum* seemed to co-vary with the pore water NO_3^- content, maximum abundance corresponding to a depth interval in the sediment where NO_3^- declined rapidly. Only few specimens were found below NO_3^- penetration depth in sediment and no specimens were present once the CPE content was < 5 µg/cm^3.

The distribution of *Uvigerina elongatastriata* and *Bigenerina cylindrica* were alike, both species mainly present in the top 2 cm of sediment, with a shallow subsurface maximum. In contrast, a surface maximum was always recorded for *U. mediterranea* and *U. peregrina*, where free NO_3^- was present in the pore waters. The occurrence of U. *mediterranea* was limited in the sediments rich in CPE, whereas *U. peregrina* occupied relatively broader range of trophic conditions, sediments measuring high (>18 µg/cm^3) and relatively low (~ 5 µg/cm^3) CPE concentrations.

The occurrence of *Cibicides kullenbergi* and *Hoeglundina elegans* was limited to the top 1.0 cm, and generally to sediments where the pore water NO_3^- content was higher than 20 µmol/L. Both taxa were mainly present in sediments with intermediate (< 10 µg/cm^3) to low (~ 2 µg/cm^3) CPE content, except for a few specimens of *H. elegans* in station 300S. Once the CPE content dropped below 2 µg/cm^3, the only abundant calcareous species was *Nuttallides umbonifera*.

5.4 DISCUSSION

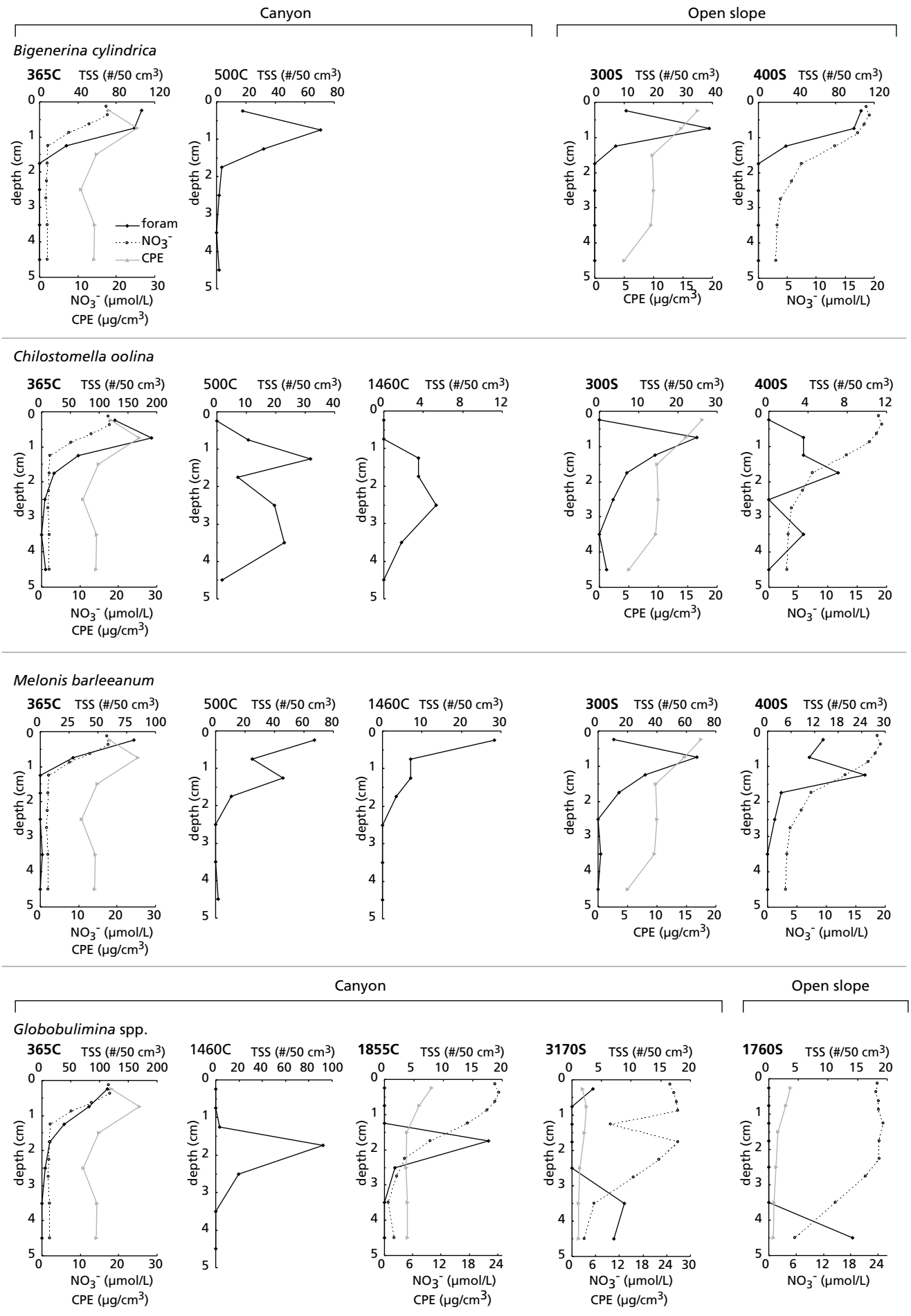
Benthic communities in canyons may be adversely affected by sedimentary disturbance (e.g. Jorissen et al., 1994), and this is also true for Nazaré Canyon, the other large canyon system on the central Portuguese margin (García et al., 2007, Koho et al., 2007). In the upper Nazaré Canyon, foraminiferal numbers were suppressed in the canyon axis even though Chl *a* and CPE content were high. Only the opportunistic taxon *Technitella* spp. was encountered in significant numbers. The active sedimentary regime in this part of the canyon was evident from frequent resuspension of sediment from the seabed, resulting in high turbidity in the bottom water, and common occurrence of fine-medium sand below the surficial mud layer, indicating relatively frequent sediment mass transport (De Stigter et al., in press). Sedimentary disturbance appears to be less common in the Lisbon-Setúbal Canyon axis, as indicated by time series observations of near-bottom hydrodynamics and turbidity with benthic landers (De Stigter and shipboard party 64PE218, 2004). The more stable environment is also clearly reflected in the abundant and relatively diverse foraminiferal communities.

Based on these observations, we do not believe that sedimentary disturbance is to be considered a major parameter shaping the ecosystems in this particular canyon at the time we sampled; but rather the interplay between food and redox zonation, as will be discussed below.

5.4.1 Foraminiferal distribution and relation to quality of sedimentary organic matter

Few earlier studies have directly compared the abundances of deep sea benthic foraminifera and sedimentary pigment content (Altenbach 1985, Altenbach and Sarnthein 1989, Ahrens et al, 1995, Schönfeld 2001, García et al. 2007), whereas this is common practise in marine biology studies of metazoan meiobenthos (Soltwedel 2000 and references therein). Generally, a positive correlation has been observed between the benthic biomass and/or abundance, and the pigment content of the sediment, a trend also observed in our study. This relationship was especially strong for calcareous taxa and weaker for agglutinated taxa suggeting that calcareous foraminifera are more sensitive to labile organic matter input and require a high quality food source to survive. The reproduction of calcareous foraminifera may also be related to availability of fresh organic

Figure 5.6. The vertical distribution of selected species in sediment (black line). The counts for each sediment slice standardised to 50 cm^3. When available, the downcore profile of CPE (chloroplastic pigment equivalents; light grey line) concentrations per cubic centimetre wet sediment and pore water nitrate (NO_3^-; dashed line) content are shown. Stations in bold font sampled in May 2004 and in standard font sampled in October 2003.


Canyon
Open slope
Bigenerina cylindrica
365C TSS (#/50 cm3)
500C TSS (#/50 cm3)
300S TSS (#/50 cm3)
400S TSS (#/50 cm3)
depth (cm)
foram
NO3-
CPE
NO3- (µmol/L)
CPE (µg/cm3)
Chilostomella oolina
365C TSS (#/50 cm3)
500C TSS (#/50 cm3)
1460C TSS (#/50 cm3)
300S TSS (#/50 cm3)
400S TSS (#/50 cm3)
Melonis barleeanum
365C TSS (#/50 cm3)
500C TSS (#/50 cm3)
1460C TSS (#/50 cm3)
300S TSS (#/50 cm3)
400S TSS (#/50 cm3)
Canyon
Open slope
Globobulimina spp.
365C TSS (#/50 cm3)
1460C TSS (#/50 cm3)
1855C TSS (#/50 cm3)
3170S TSS (#/50 cm3)
1760S TSS (#/50 cm3)

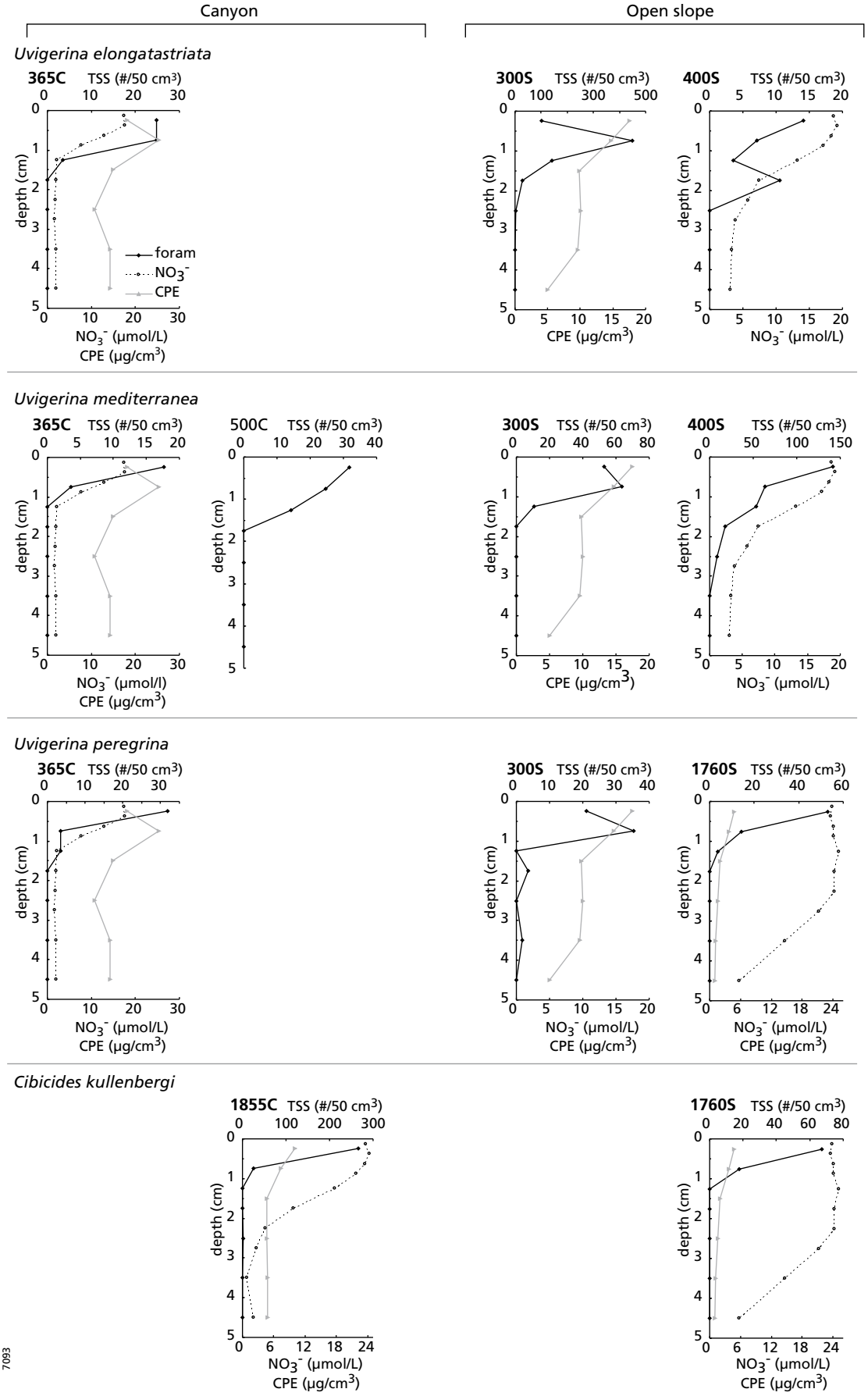


Figure 5.6. (Continued)

matter as field observations suggest that total standing stock of calcareous foraminifera increases following the deposition of a phytoplankton spring bloom (Shepherd et al., 2007), and only some agglutinated taxa (e.g. *Textularia kattegatensis*) appear to respond to organic carbon flux (Ohga and Kitazato, 1997). Therefore, agglutinated species appear to be less influenced by the lability of phytodetritus, and have developed other feeding habits. Linke (1992) suggested that some agglutinated species (e.g. *Cribrostomoides subglobosus* and *Rhabdammina abyssorum)* are able to survive long periods without regular fresh food input, while feeding on their own protoplasm. Some agglutinated deep sea foraminifera, such as *Crithionina* spp., have also been described as deposit feeders (Gooday et al., 1996), and are thus able to ingest bulk sediment and extract organic compounds from it.

Overall, the quality of the sedimentary organic matter seems to play an important role in structuring deep sea benthic ecosystems, as was demonstrated by a positive correlation of foraminiferal numbers and phytopigment content, and a lack of correlation with the bulk organic carbon content in sediment. In the deep sea environment, the organic detritus deposited on the sediments surface may be extensively degraded due to mineralisation in the water column, or it may be laterally transported and redeposited, hence leaving the sedimentary C_{org} unreactive and poor food in quality for benthic organisms. The implication is that sedimentary C_{org} content alone is not a good measure for benthic food availability but should be used with care and preferentially replaced by other indexes such as phytopigments.

5.4.2 Foraminiferal communities and the TROX concept

The relation with food supply was recently demonstrated again by Eberwein and Mackensen (2006) who identified five foraminiferal assemblages on the continental slope off NW Africa, reflecting the different productivity regimes. In the Lisbon-Setúbal Canyon and on the adjacent open slope, laterally corresponding changes were also observed in the foraminiferal abundance and species composition, and food availability (or sedimentary CPE). Additionally, an inverse relationship was seen with the pore water NO_3^- content (Figure 5.7); a shallow NO_3^- penetration coincides with high CPE concentrations and vice versa. The relation between the CPE and pore water NO_3^- could be expected as increasing labile carbon load will lead to higher bacterial remineralisation rates and enhanced benthic oxygen consumption rates (Canfield 1993). Therefore, in eutrophic conditions low oxygen concentrations may limit the occurrence of some fauna.

In the next sections the species specific changes with food supply and redox chemistry (Figure 5.6 and 5.8; pore water nitrate content used as an indicator) are discussed, in

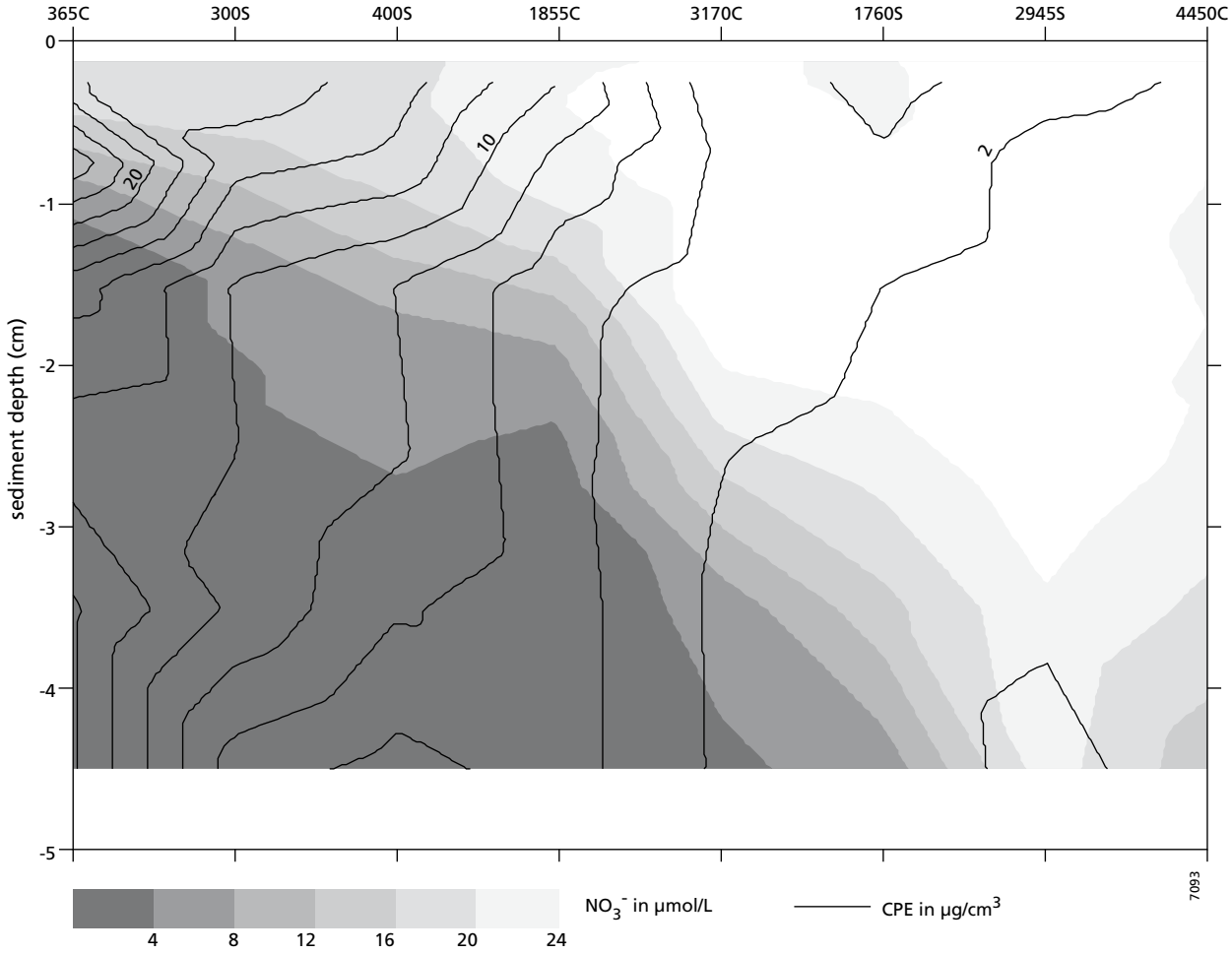
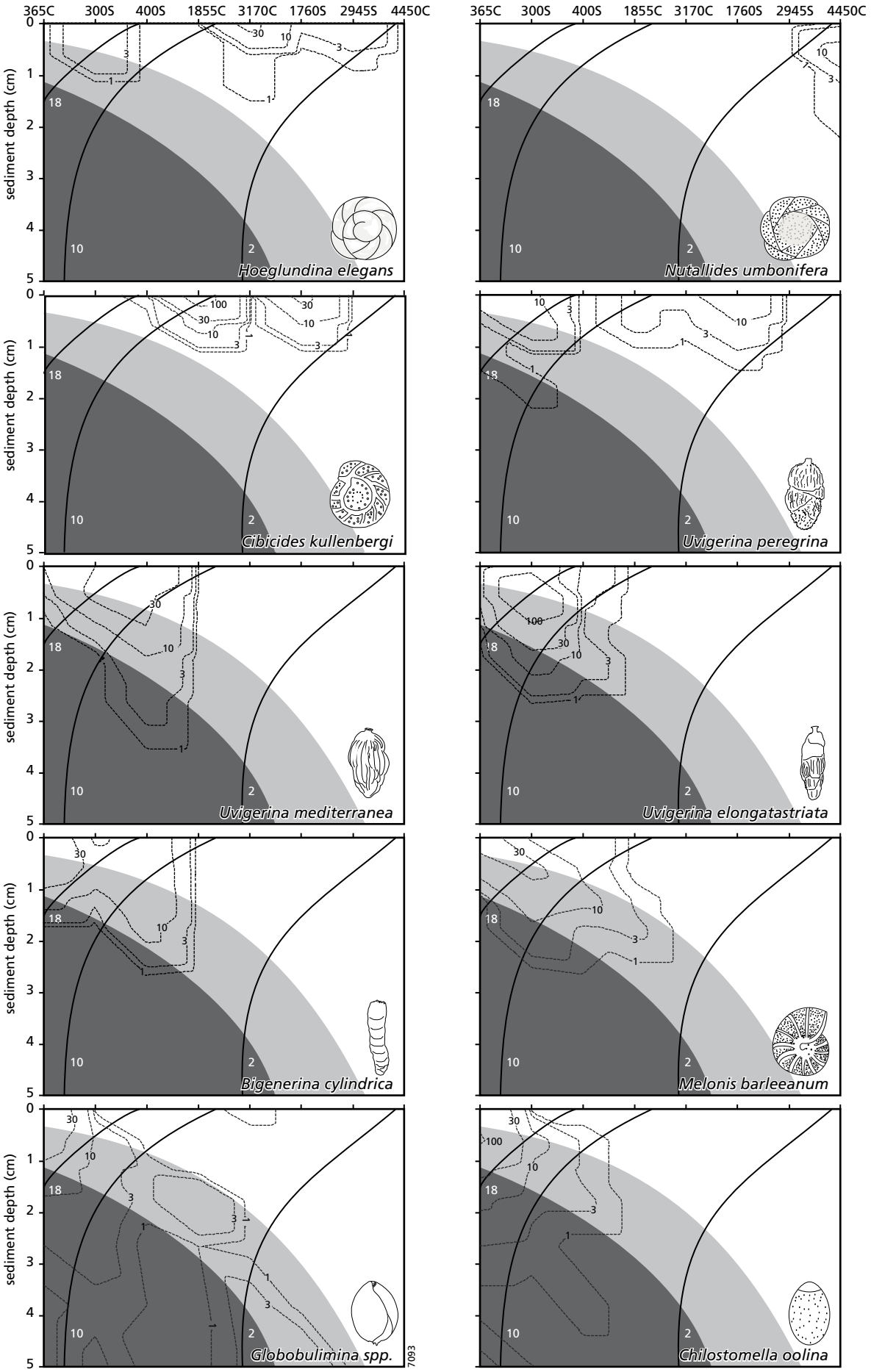


Figure 5.7. Map of variation of CPE (µg/cm³) and pore water nitrate (µmol/L) along a gradient of decreasing CPE inventory in top 5 cm of sediment.


365C 300S 400S 1855C 3170C 1760S 2945S 4450C
sediment depth (cm)
Hoeglundina elegans
Nutallides umbonifera
Cibicides kullenbergi
Uvigerina peregrina
Uvigerina mediterranea
Uvigerina elongatastriata
Bigenerina cylindrica
Melonis barleeanum
Globobulimina spp.
Chilostomella oolina
7093

comparison to the TROX model. Further, the discussion is arranged according to declining CPE content, which appears to control the foraminiferal standing stocks.

"Eutrophic foraminifera"

The canyon site (365C), measuring the highest CPE content and the lower NO_3^- penetration depth, was dominated by intermediate to deep infaunal species such as *Chilostomella oolina*, *Globobulimina* spp., *Bigenerina cylindrica* and *Melonis barleeanum*. Once the nitrate penetration depth increased to ~ 2 cm depth in sediment (stations 300S and 400S) the assemblage became dominated by *Uvigerina mediterranea* and/or *U. elongatastriata* (station 300S).

The occurrence of *Globobulimina* spp. is closely linked to the nitrate reduction zone in sediment, where the maximum abundances were recorded (Figure 5.8), and to a lesser extent by food availability as specimens were found in sediments relatively rich as well as poor in CPEs. The preferential occurrence of *Globobulimina pacifica* in the nitrate reduction zone was also documented by Licari et al. (2003) in the tropical east Atlantic. More recently, it was also discovered that under anoxic condition *G. pseudospinescens* can respire through denitrification of an intracellular nitrate pool (Risgaard-Petersen et al., 2006).

Another deep infaunal taxon, *Chilostomella oolina*, was found to inhabit sediments at and below the nitrate penetration depth. However, the occurrence of *C. oolina* was restricted to sediments with phytopigment content > 5 g/cm^3. This implies that this species must benefit from the labile organic matter either directly by consuming it, or indirectly from the associated bacterial populations and/or bacterial activity. The latter option appears more likely, as in a feeding experiment of Nomaki et al. (2005) *Chilostomella ovoidea* was not observed to ingest any algae, and was later described to consume sedimentary organic matter unselectively (Nomaki et al. 2006). Further, following a simulated diatom deposition under controlled laboratory conditions, the vertical distribution of *C. oolina* did not change and no migration to the upper sediment intervals was observed despite the added food (Koho et al., under review).

The maximum abundance of *M. barleeanum* in sediment appeared to correspond to a maximum in nitrate reduction (depth interval in the sediment where NO_3^- declined most rapidly), as the species was (nearly) absent from sediments where pore water nitrate content was less than ~ 5 µmol/L. A similar distribution pattern was observed by Jorissen et al., (1998) and Licari et al. (2003). Further, the occurrence of *M. barleeanum* coincided with relatively rich labile organic matter only (CPE content ≥10 µg/cm^3). This observation is in contrast with Caralp (1989b), who suggested that *M. barleeanum* preferred to digest more refractory organic matter.

Figure 5.8. Contour plot of foraminiferal distribution in sediment relative to schematised pore water nitrate and sedimentary CPE content. White area represents oxic sediment. Light grey area represents dysoxic sediment where nitrate declines from 20 to 2 µmol/L. Dark grey area represents anoxic sediment below the nitrate reduction zone. Stations arranged in order of declining CPE inventory in top 5 cm.

Uvigerina spp. were found to inhabit (sub)oxic sediment and the maximum numbers were always recorded in the zone where free NO_3^- was present in the pore waters. Therefore, the near absence of *Uvigerina* spp. from the most eutrophic sediments (station 365C) must be related to the shallow redox zonation at these sites. This observation is consistent with Fontanier et al. (2006) who described *U. mediterranea* as shallow infaunal, and *U. elongatastriata* as an intermediate infaunal species. Previously, the occurrence of *Uvigerina* spp. has been associated with sediments rich in organic carbon (e.g. Schmiedl et al., 1997, Schmiedl et al., 2000, Harloff and Mackensen 1997, Fontanier et al., 2006). Our results imply that the sedimentary C_{org} is not the controlling factor, rather the quantity of phytopigments, or labile organic matter, as numbers of *U. mediterranea* and *U. elongatastriata* declined once the CPE content fell below 10 µg/cm^3.

"Mesotrophic foraminifera"

Unlike *U. mediterranea* and *U. elongatastriata*, *U. peregrina* appeared to occupy a relatively broad range of trophic conditions from sediments containing very high (>18 g/cm^3) to relatively low (~ 5 µg/cm^3) CPE concentrations. In addition, the microhabitat of *U. peregrina* was limited to the top 1 cm, despite the changes in the redox zonation and phytopigment content. Previously, *U. peregrina* has been linked to north Atlantic deep water (NADW; Lohmann 1978, Mead 1985, Harloff and Mackensen 1997). However, more recently Schönfeld and Altenbach (2005) argued that maximum abundances of *U. peregrina* are found in regions of extensive lateral sediment advection, with high fluxes of C_{org}, implying these factors to be more important than the water mass in determining the distribution of the taxon. Our data suggest that the occurrence of *U. peregrina* is not limited by water masses, as specimens were found between 365 m and 1760m water depth in different water masses (see section 5.2.1.). Due to lack of C_{org} flux data, we cannot corroborate the observation of Schönfeld and Altenbach (2005); nevertheless the maximum abundances of *U. peregrina* were recorded at an open slope site, with elevated sedimentary C_{org} content.

The distribution of *Cibicides kullenbergi* and *Hoeglundina elegans* in sediment seems to be related to food availability, as the NO_3^- penetration depth in sediment far exceeded the in-sediment distribution of this particular taxon. Previously these taxa have been found in sediments low in organic matter (Lutze and Coulbourn, 1984), and to live under oxic conditions (Schönfeld, 2001). Our results imply that these taxa inhabit sediments low in labile organic matter (phytopigments), not in bulk organic matter which was relatively high at the sites where *C. kullenbergi* was found. An additional observation concerning *C. kullenbergi* was made at station 1855C, where the majority of specimens were found encrusting one end of a worm tube, thus suggesting a facultative elevated habitat. The canyon station 1855C is situated near the intercept of the Lisbon and Setúbal Canyons, where current speed regularly exceeds 30 cm/s (H. de Stigter, unpublished data), beneficial for suspension feeders (Flach et al., 1998). Therefore, *C. kullenbergi* may have adapted to a filter feeding life mode at this site (Linke and Lutze, 1993).

"Oligotrophic foraminifera"
The assemblages living under oligotrophic conditions (CPE ≤ 2 μg/cm^3, NO_3^- penetration depth ≥ 5 cm) appear to be food controlled as the majority of the foraminifera was found close to the sediment surface, where slightly higher pigment content, which declined with sediment depth, was measured (Figure 5.3). These stations (2945S, 4450C) were dominated by agglutinated taxa, especially monothalamous species; a trend typically seen with increasing water depth and lower food availability (Cornelius and Gooday, 2004). In the open slope site 2945S all relatively abundant taxa were agglutinated. The assemblages found in the deepest canyon station (4450C) resemble abyssal communities described by Schmiedl et al. (1997), consisting of *Nuttallides umbonifera* and agglutinated taxa. In addition, the foraminiferal community at site 4450C was similar to one found in the lower Nazaré Canyon from similar water depths (Koho et al., 2007), common species including *N. umbonifera*, *Reophax* sp. 2 and *Lagenammina* spp.

5.4.3 The arborescent and tubular foraminifera

The occurrence of large agglutinated taxa has been related to several factors. Altenbach et al. (1988) observed *Saccorhiza ramosa* to inhabit quiescent, low energy environments where current speeds did not exceed 2 cm/s, enhanced current speeds leading to test breakage. Similarly, Gage et al (1995) recorded higher abundances of arborescent/tubular taxa in the low energy abyssal plain than in Setúbal Canyon where current ripples on a seabed at 3400 m water depth indicated higher current speeds. In the axis of the upper Nazaré Canyon on the Portuguese margin (Koho et al., 2007), the low abundances of large agglutinated taxa was related to frequent gravity flows and poor recolonising capabilities of arborescent foraminifera (Hess and Kuhnt, 1996). Flach et al. (1998), however, suggested that the large agglutinated foraminifera, of which many species are believed to be filter feeders, may benefit from elevated suspended matter loads associated with enhanced current speeds. Food availability was also considered by Gooday et al. (1997) to be an important parameter in determining the occurrence of larger agglutinated foraminifera; tubular taxa inhabiting oligotrophic continental margin sediments which experience fluctuating pulsed food inputs.

Our data suggest there is a combination of parameters involved in structuring arborescent/tubular foraminiferal communities and that different species prefer, or can tolerate, different environmental conditions. The upper canyon and upper continental slope sediments, rich in phytopigments, were inhabited by many *Bathysiphon* species. Several *Bathysiphon* taxa were also found living in the organic rich sediments in the upper Nazaré Canyon (Koho et al., 2007). However, the specimens were only found on the relatively stable canyon terraces and not on the axis, thus indicating that this species does not tolerate disturbance. Gooday et al. (1992) described *Bathysiphon filiformis* from the continental slope off North Carolina; a region influenced by relatively high organic carbon fluxes. Living *Bathysiphon* spp. were also found in the oxygen minimum zone in the Arabian Sea (Gooday et al., 2000) and *B. capillare* has been named as a dysoxic indicator by Schönfeld (2001). Therefore, the observations suggest that this species thrives in organic rich sediments and may be able to tolerate low oxygen conditions.

The tubular taxon *Rhizammina algaeformis* was found to inhabit sediments of the middle continental slope (1760S), and lower slope (2945S) and canyon (3170C). The microhabitat of this species appears infaunal, having its ALD_5 ranging between 1.0 and 2.5 cm depth in sediment. Previously however, *R. algaeformis* has been found to inhabit the upper most sediment layers (Cartwright et al., 1989 and Gooday et al., 1997)

Saccorhiza ramosa was another relatively common species in the middle continental slope, and lower slope and canyon. This species seems to prefer a low energy regime (Altenbach et al. 1988) and relatively oligotrophic conditions (Koho et al. 2007). These observations appear consistent with this study as the sedimentary pigment contents were relatively low at these sites and the chla:phaeo ratios indicated that the detritus was refractory.

5.5 CONCLUSIONS

Total standing stocks of benthic foraminifera were higher in the canyon than at equivalent depth on the open slope, and decreased exponentially with increasing water depth. The trend in foraminiferal abundance seems to match closely with the trend of decreasing phytopigment concentration and inventory with water depth, suggesting that foraminiferal stocks were primarily controlled by availability of labile organic matter. This seems especially the case for the calcareous foraminifera.

The foraminiferal assemblage composition changed with water depth, NO_3^- penetration depth and the phytopigment content, and differences were found in assemblage composition between canyon and slope at equivalent water depths. In the eutrophic upper canyon sites deep infaunal species dominated the assemblages and were present in the surficial sediments. With increasing water depth and declining phytopigment content the assemblages changed via a *Cibicides kullenbergi-Uvigerina peregrina* assemblage at mid-depths to the oligotrophic deep-water assemblage mainly consisting of agglutinated monothalamous species. *Hoeglundina elegans* (3170S) and *Nuttallides umbonifera* (4450C) were the only relatively abundant calcareous species found in the lower canyon.

The vertical distribution of some infaunal taxa, *Melonis barleeanum, Chilostomella oolina* and *Globobulimina* spp., appeared to track redox fronts, as their in-sediment profile covaried with the pore water NO_3^- content. *M. barleeanum* was found in the sediment where NO_3^- begins to decline rapidly and no specimens were found once the concentrations fell below 5 μmol/L. *Globobulimina* spp. was found somewhat deeper, showing a peak in abundance at the maximum NO_3^- penetration depth in sediment.

The arborescent/tubular foraminiferal assemblages also changed with water depth, but no relation was found with sedimentary pigment content. For evaluation food supply to those foraminifera, one should begin to evaluate the concentration of suspended organic matter in combination with currents dynamics.

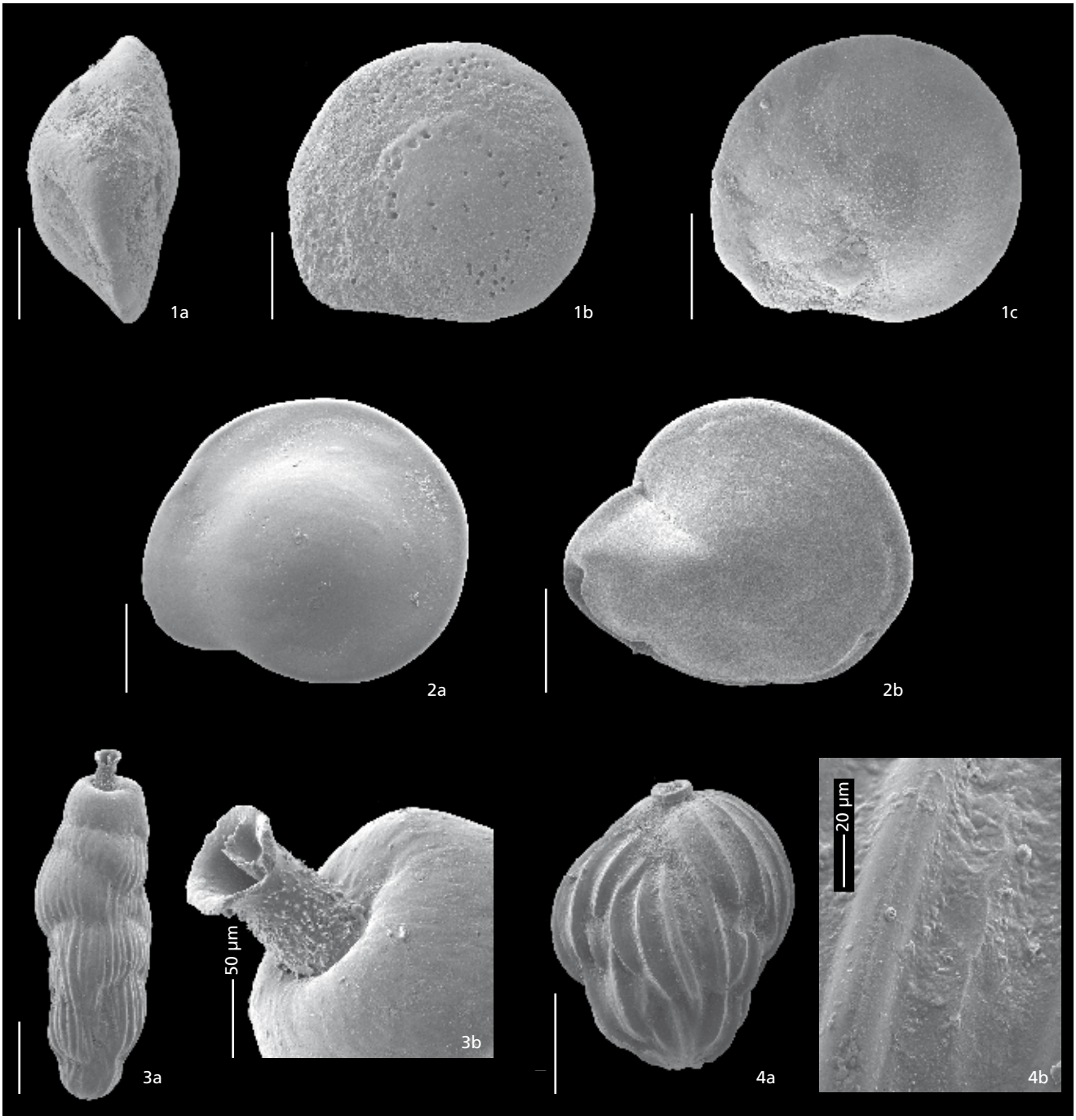


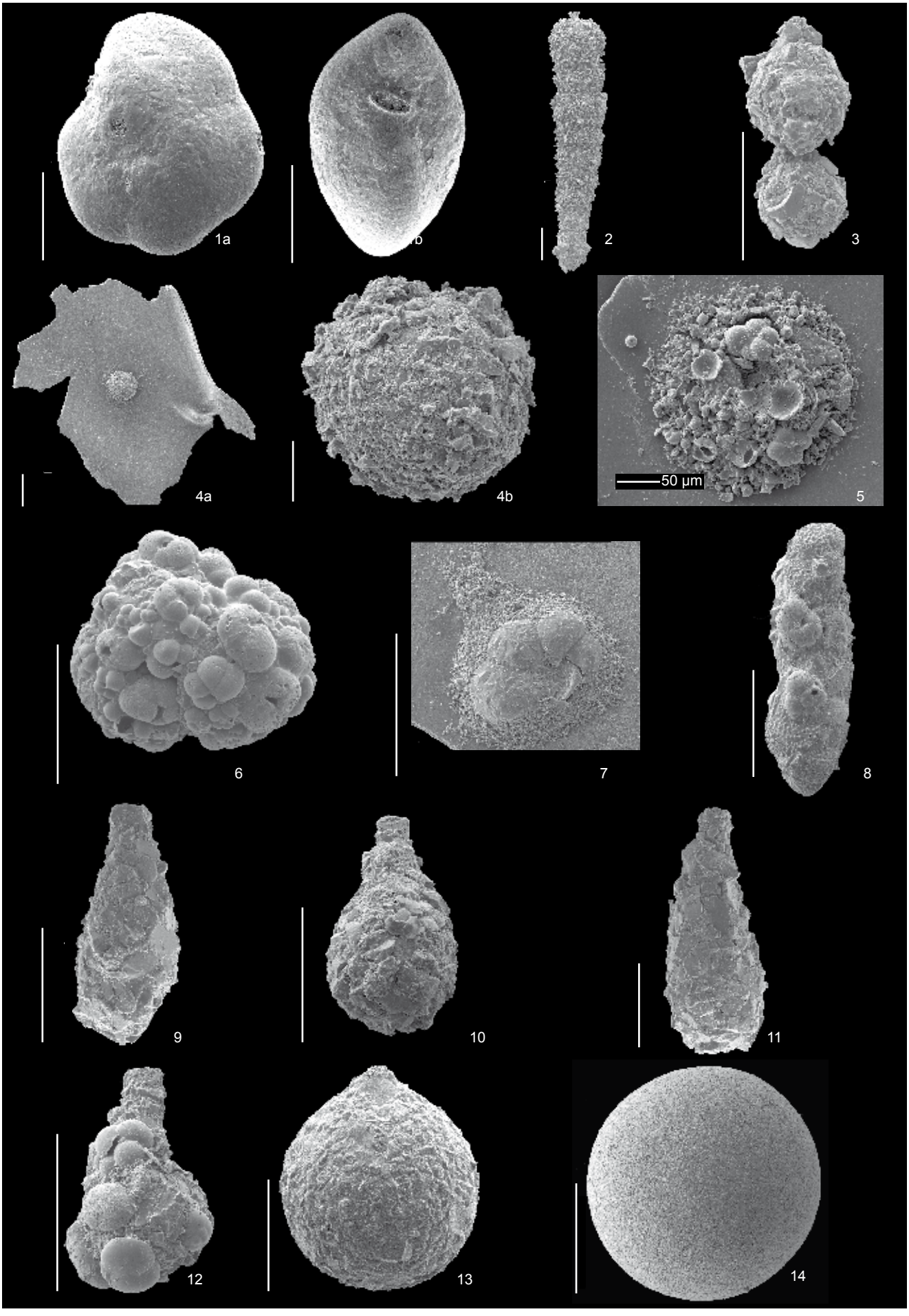
Plate 5.1. Common calcareous taxa discussed in the text. Scale bar 200 µm unless specified otherwise. 1. *Cibicides kullenbergi*. a.) Axial profile, b.) Spiral side, c.) Umbilical side. Station 1855C (0-0.5 cm). 2. *Hoeglundina elegans* a.) Spiral side, b.) Umbilical side. Station 3170C (0-0.5 cm). 3a.) *Uvigerina elongatastriata* b.) Close up of the neck, note the numerous small spines. Station 400S (0.5-1.0 cm). 4a.) *Uvigerina mediterranea* b.) Close up of the sutures; note the diatom frustules on top of the test. Station 400S (0.0-0.5 cm).

Acknowledgements.
The authors wish to thank the crews and captains of the R.V. Pelagia, and everyone participating in the Portuguese margin Canyons cruises for all the efforts and hard work at sea. Also we would like to thank Gerrit van't Veld and Geert Ittmann for their help with foraminiferal sample preparation. Stimulating discussions with Sander Ernst and Ivo Duijnstee concerning ecology of benthic foraminifera provided interesting ideas. Material for this study was collected within the framework of the EUROSTRATAFORM project funded by the European Commission, contract EVK3-CT-2002-00079. The 2nd, 3rd, 4th and 5th author acknowledge funding from EUROSTRATAFORM as well as the European project HERMES, EC contract OCE-CT-2005-511234. Shiptime on R.V. Pelagia was provided by Royal NIOZ.

Appendix 5.1.

Taxonomic notes. Foraminiferal species discussed in the text are listed only.

Bigenerina cylindrica Cushman, 1922. Koho et al. (2007), Plate 1, Figure 10.


1a
2
3
4a
4b
50 µm
5
6
7
8
9
10
11
12
13
14

Cibicides kullenbergi Parker, 1953. Plate 5.1, Figures 1a-c.

Chilostomella oolina Schwager, 1878. Koho et al. (2007), Plate 2, Figure 8.

Cribrostomoides subglobosus (Cushman) = *Haplophragmoides subglobosum* Cushman 1910. Jones (1994), Plate 34, Figures 8-10.

Globobulimina spp.

Hoeglundina elegans (d'Orbigny 1826) = *Rotalia (Turbinuline) elegans* d'Orbigny, 1826. Plate 5.1, Figures 3a-b.

*Lagenammin*a spp.

Melonis barleeanum Williamson, 1858. Koho et al. (2007), Plate 2, Figure 7a-b.

Nuttallides umbonifera (Cushman) = *Pulvinulina umbonifera* Cushman 1933. Van Leeuwen (1989), Plate 15, Figures. 11-13; Plate 16, Figures 1-7.

Reophax spp.

Uvigerina mediterranea Hofker 1932. Plate 5.1, Figures 4a-b.

Uvigerina elongatastriata (Colom 1952) = *Angulogerina elongatastriata* Colom, 1952. Plate 5.1, Figures 4a-b.

Uvigerina peregrina Cushman, 1923, Schweizer et al. (2005), Figure 3.

Bathysiphon filiformis Sars, 1872, Gooday (1988b), Figures 1-3

Bathysiphon capillare de Folin, 1886, Gooday (1988a), Figures 2-5

Marsipella spp.

Rhabdammina linearis Brady 1879, Jones (1994), Plate 22, Figures 1-3, 5-6

Rhabdammina abyssorum M. Sars 1869, Jones (1994), Plate 21, Figures 1-8, 10-13

Rhizammina algaeformis Bradyi 1879, Jones (1994), Plate 28, Figures 1-11

Saccorhiza ramosa (Brady) = *Hyperammina ramosa* Brady, 1879, Jones (1994), Plate 23, Figures 15-19

Plate 5.2. Some unfamiliar agglutinated taxa detailed in Appendix 5.2. Scale bar 200 μm unless specified otherwise.

1. *Buzasina* cf. *ringens* a.) Side view. b.) Axial view. Station 365C (0-0.5 cm); tests are white, unlike in *Buzasina ringens* in Jones (1994) Plate 40, Figures 17-18.
2. *Hormisina bacillaris*. Station 1760S (0-0.5 cm).
3. *Hormosina* cf. *pilulifera*. Station 2945S (0.5-1.0 cm).
4. *Tholosina* cf. *bulla* a.) Encrusting on a pteropod shell. b.) Close up. Station 2945S (0-0.5 cm).
5. Encrusting foraminifera on top of a pteropod test; the specimen is white and very flat. Station 24945S (0-0.5 cm).
6. *Trochammina* sp. (plankton), spiral view. Station 2945S (0-0.5 cm).
7. *Trochammina* sp. (encrusting). Station 400S (0-0.5 cm).
8. *Reophax* cf. *calcareous*. Station 400S (0-0.5 cm).
9. *Lagenammina* sp. (mica; white cement). Station 4450C (1-1.5 cm).
10. *Lagenammina* sp. (yellow; Fe-cement). Station 1760S (0-0.5 cm).
11. *Lagenammina* sp. (opaque, clear cement). Station 400S (0.5-1.0 cm).
12. *Lagenammina* sp. (plankton). Station 2945S (0.5-1.0 cm).
13. *Saccammina sphaerica*. Station 2945S (1-1.5 cm).
14. White ball (snowball); *Psammosphaera*? Station 2945S (0.5-1.0 cm).

Appendix 5.2. Total number of common foraminifera (below 28.3 cm^2 surface area, down to 5 cm depth). The species listed make up three percent of the total abundance at least in one of the stations. The average living depth (ALD_5) is calculated for every species when five specimens or more are present. The stations written in bold were sampled in May 2004; stations written in standard font were sampled in October 2003.

	Canyon														Open slope							
	365C		500C		1460C		1850C		**1855C**		**3170C**		**4450C**		**300S**		**400S**		**1760S**		**2945S**	
	n	**ALD_5**	**n**	**ALD_5**	**n**	**ALD_5**	**n**	**ALD_5**	**n**	**ALD_5**	**n**	**ALD_5**	**n**	**ALD_5**	**n**	**ALD_5**	**n**	**ALD_5**	**n**	**ALD_5**	**n**	**ALD_5**
Ammobaculites villosus					22	0,3																
Ammodiscus sp.											7	1,4										
Bigeneria cylindrica	66	0,6	37	1											16	0,7	41	1				
Bolivina alata	8	0,7	11	1,5											10	1						
Bulimina marginata	64	0,4	6	1											14	1,3	1					
Buzasina cf. *ringens*	40	0,6	32	0,9											5	0,8	1					
Calcareous trochospiral, encrusting																					6	0,4
Chilostomella oolina	121	0,9	39	2,4	6	2,3									16	1,5	6	2,1				
Cibicides bradyi																			7	0,6	3	
Cibicides dutemplei									6	0,5									6	0,4		
Cibicides kullenbergi					3	0,3	2		83	0,3							1		24	0,4		
Cibicides cf. *pachyderma*															3				3			
Cribrostomoides subglobosus					1		2		17	1	16	0,9	5	1,4			1		10	1,5		
Eggerella bradyi					1						1		6	0,8					4			
Eggerella scarba	25	0,3	16	0,3											17	0,8						
Encrusting, flat, white stuff																					5	1,2
Fursenkoina sp. (Nazarè)					4		4															
Gavelinopsis sp.																			6	0,3		
Globobulimina spp.	73	0,7	28	2,4	38	2	1		6	1,9	10	3,6			20	2,4	3		8	4,5		
Glomospira charoides					8	0,6					8	0,8			1		10	0,5	16	2,2	2	
Gyroidina soldanii							1		3													
Hoeglundina elegans							1				21	0,3			9	0,7			2		6	0,3
Hormosinella distans													26	0,7								
Hormosina bacillaris											34	0,8									1	
Hormosina cf. *pilulifera*																					5	0,9
Karreriella apicularis									1				1								5	1
Lagenammina sp (yellowish)																			6	0,4		
Lagenammina sp.							4		1													
Lagenammina sp. (mica)													17	1,1								
Lagenammina sp. (plankton)																					8	0,5
Lagenammina sp.(opaque)													12	0,5								
Lenticulina thalmanni							1															
Melonis barleeanum	32	0,5	43	0,8	13	0,6			3						36	1	16	1				
Nutallides umbonifera													11	0,8								
Psammosphaera fusca													13	0,8	2							
Quinqueloculina spp.	1		2				1		1		1				5	0,7	10	0,5	1		6	0,6

	Canyon														Open slope							
	365C		500C		1460C		1850C		1855C		3170C		4450C		300S		400S		1760S		2945S	
	n	ALD_5	n	ALD_5	n	ALD_5	n	ALD_5	n	ALD_5	n	ALD_5	n	ALD_5	n	ALD_5	n	ALD_5	n	ALD_5	n	ALD_5
Reophax cf. *calcareous*									2		5	0,7			2		22	0,4	4	0,4		
Reophax dentaliniformis									2		4				2				5	2,6	6	2,1
Reophax difflugiformis	7	0,3	11	0,5	6	0,4									4		59	1				
Reophax sp.							1															
Reophax sp. (rough surface)											7	0,7										
Reophax sp.2 (Nazarè)											3		10	1,8								
Reophax sp.1	7	1,4	10	1,7											14	1,1	49	2,9				
Saccammina sphaerica									3		5	1	1						1		6	1,3
Tholosina cf. *bulla*																	3				14	0,5
Tritaxis spp.											1				1		5	0,7	10	0,6		
Trochammina globigeriniformis					10	0,4			4				8	0,8	4		2					
Trochammina sp.							3															
Trochammina sp. (plankton)													6	0,6							12	0,4
Trochammina sp. (small)					9	0,3			2								3					
Trochamminid (encrusting)																	13	0,4				
Uvigerina elongatastriata	15	0,6	1												205	0,8	10	0,9				
Uvigerina mediterranea	6	0,3	20	0,6	10	0,5									36	0,6	83	0,8				
Uvigerina peregrina	11	0,4	2		2				4		4				18	0,8			20	0,4		
Valvulineria bradyana	47	0,6	15	1,4											3							
Veleroninoides scitulus			2		51	0,4					1				15	0,9			1			
Veleroninoides sp.																					5	2,7
Veleroninoides wiesneri													5	3,8					1			
White balls (snow balls)													3	0,8							16	1
TSS	766		341		202		21		165		157		155		620		430		183		163	

Appendix 5.3. Counts of arborescent and tubular foraminifera (per core/below 28.3 cm2); w= whole specimens, f= fragments. The average living depth (ALD_5) is based on the total sum of the whole specimens and fragments and is calculated for every species when five specimens or more are present. The stations written in bold were sampled in May 2004; stations written in standard font were sampled in October 2003.

		Canyon														Open slope							
		365C		500C		1460C		1850C		**1855C**		**3170C**		**4450C**		**300S**		**400S**		**1760S**		**2945S**	
		n	**ALD_5**	**n**	**ALD_5**	**n**	**ALD_5**	**n**	**ALD_5**	**n**	**ALD_5**	**n**	**ALD_5**	**n**	**ALD_5**	**n**	**ALD_5**	**n**	**ALD_5**	**n**	**ALD_5**	**n**	**ALD_5**
Arborescent (grainy,transparent)	f													4									
	w													0									
Astrorhiza arenonia	f																	10	0,8				
	w																	0					
Bathysiphon capillare	f					3	1,3									4	0,6	11	0,9	6	3,5		
	w					3										1		1		0			
Bathysiphon filiformis	f					4																	
	w					0																	
Bathysiphon sp. (orange)	f																			2			
	w																			0			
Bathysiphon sp. (long, thin)	f	10	0,4													7	0,5	5	0,5				
	w	0														0		0					
Bathysiphon sp. (fat)	f																					3	
	w																					0	
Bathysiphon sp. (white, fat)	f																			3			
	w																			0			
Bathysiphon strictus	f			3		1												17	1				
	w			0		0												0					
Hyperammina? sp. (white, spines)	f																	3					
	w																	0					
Marsipella spp.	f																	109	0,7	14	2,1		
	w																	0		0			
Rhabdammina abyssorum	f					50	0,6			3	0,3												
	w					0				2													
Rhabdammina linearis	f			11	0,3							1		3		19	0,5	4					
	w			0								0		0		2		0					
Rhanbdammina sp. (fine grained)	f																			2	2,9		
	w																			3			
Rhizammina algeaformis	f											18	2,5							9	2,1	9	1
	w											0								0		5	
Rhizammina sp.	f																					105	0,9
	w																					7	
Saccorhiza ramosa	f					7	0,6					66	1,5	1				9	0,5	22	1,9	11	1,2
	w					0						10		0				0		0		3	

		Canyon														Open slope							
		365C		500C		1460C		1850C		**1855C**		**3170C**		**4450C**		**300S**		**400S**		**1760S**		**2945S**	
		n	**ALD_5**	**n**	**ALD_5**	**n**	**ALD_5**	**n**	**ALD_5**	**n**	**ALD_5**	**n**	**ALD_5**	**n**	**ALD_5**	**n**	**ALD_5**	**n**	**ALD_5**	**n**	**ALD_5**	**n**	**ALD_5**
Talypammina vagans	f																			4			
	w																			0			
Tubular (orange, plankton)	f																					4	
	w																					0	
Tubular (flexible, opaque)	f															3							
	w															0							
Tubular (quartz and shell parts)	f					5	0,3																
	w					0																	

CHAPTER 6

The response of benthic foraminifera to differential sedimentary regimes in the lower Nazaré Canyon since the last deglaciation

Together with: H.C. de Stigter, T.J. Kouwenhoven, M. Ruhl, A. Kuijpers, G.J. van der Zwaan

ABSTRACT

Two piston cores were recovered from the northern and southern bank of the lower Nazaré Canyon (Portuguese margin). Preferential deposition on the northern bank of sediments supplied via the canyon, as revealed by bathymetric data and seismic sections, was confirmed by sedimentological and geochemical analysis of the cores. The different sedimentation on the northern and southern bank was expected to influence benthic foraminiferal communities living at these sites

Pre-Holocene sedimentation rates were found to be a factor four higher on the northern levee as compared to the southern bank, the difference being less but still present in the Holocene. Transported shallow water benthic foraminifera constituted a considerably larger percentage of the assemblages on the northern levee, in agreement with the greater sediment supply from the canyon.

In both cores a faunal shift was observed over time, from dominance of infaunal taxa in the late glacial to dominance of epifaunal taxa in the Holocene. This shift may be related to the overall changing sediment supply and productivity on the Portuguese margin related to sealevel rise and climate change. Comparing equivalent time intervals in both cores, however, the assemblages in core 06 generally showed a stronger prevalence of infaunal taxa, and those of core 08 higher relative abundances of epifaunal taxa. This systematic difference between the two sites can be attributed to the relative enrichment of the northern bank with organic matter supplied by the canyon. In addition, dynamic, turbidite-dominated sedimentation occurring on the northern bank around termination 1a may also have affected the foraminiferal communities by intermittently disturbing their habitat.

6.1 INTRODUCTION

Geological and physical oceanographic investigation of the Nazaré submarine canyon on the Portuguese Atlantic continental margin, performed in the framework of the European EUROSTRATAFORM programme, indicates the importance of this canyon for the transport of sedimentary material from the shallow coastal sea to the deep ocean. The down-canyon sediment transport occurs primarily in the form of gravity flows, however, in the upper and middle canyon tidal currents play an important role in the sediment resuspension and transport (De Stigter et al., in press). In the present day Nazaré Canyon, major turbidite activity reaching the lower canyon is intermittent (centennial scale events) whereas events on annual or shorter scales are restricted to the upper and middle part of the canyon (De Stigter et al., in press). Nevertheless, cores collected from the lower canyon reveal that in the past larger turbidity events were capable of transporting coarse sand and even coarser material to abyssal depths. For example, sediment transport to the lower Nazaré Canyon is expected to have been greater during the last glacial period as a result of the lower sea level: regression of the coastline exposed the continental shelf, and the proximity of the canyon to the coastline was conducive to efficient transport of material to the deep ocean.

The finer sediment fraction transported by turbidity currents appears to accumulate on the sides of the Nazaré canyon. Deflection of turbidity currents to north under influence of Coriolis force and residual currents on the slope has resulted in formation of an impressive sedimentary levee on the northern side of the canyon, whereas pelagic sedimentation dominates on the structurally elevated southern bank.

The contrasting sedimentary regimes, and especially the associated differences in the organic matter supply, may be expected to influence benthic faunal communities at these sites. In addition, highly active sedimentary regimes have been shown to play a role in controlling benthic foraminiferal assemblages in submarine canyons (Jorissen et al., 1994; Anschutz et al., 2002; Hess et al., 2005; Garcia et al., 2007, Koho et al., 2007).

For this study, two piston cores from the crest of the southern and northern bank were investigated (Figure 6.1). The aim was to characterise the sedimentation patterns noted on the southern and northern banks from the seismic section, their impact on benthic foraminiferal assemblages and the changes in both parameters across the Pleistocene-Holocene transition. Specifically, we investigated the hypothesis that a greater supply of terrigenous material reaches the northern bank, whereas sedimentation is predominantly hemipelagic on the southern site, and that this contrast is reflected in benthic foraminiferal assemblages. Especially the higher supply of organic matter associated with fine-grained terrigenous sediment on the northern bank was expected to have an impact on foraminiferal communities, by affecting both the trophic regime and the redox conditions in the sediment.

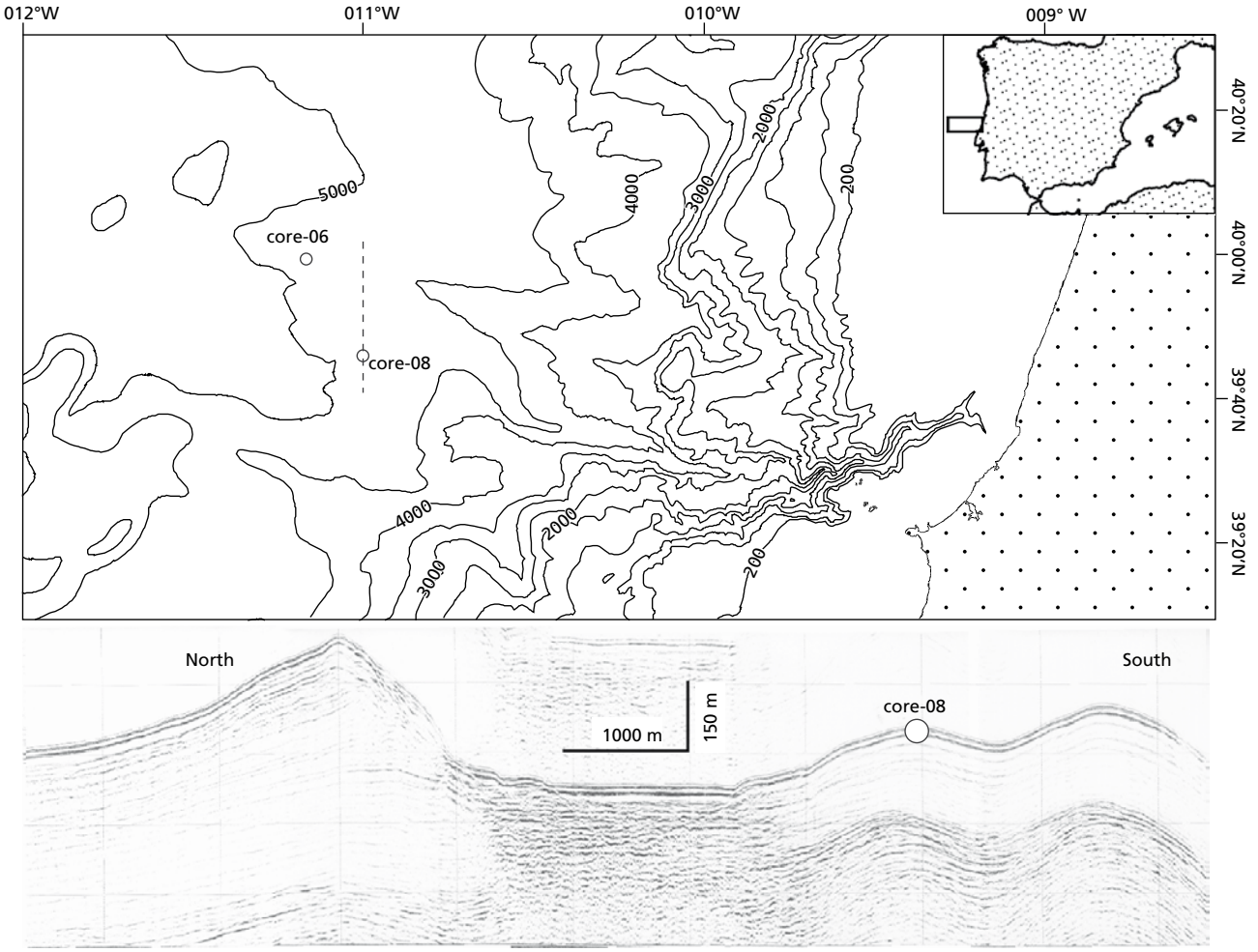


Figure 6.1. Map indicating the coring locations and the position of the seismic line (dashed line); presented below.

6.2 MATERIALS AND METHODS

6.2.1 Samples and analyses

Two piston cores, 64PE218-06 (39° 59.50' N, 011°10.00' W; length 310 cm) and 64PE218-08 (39°46.50' N, 011°00.00' W; length 860 cm), were collected from the northern and southern bank of the lower Nazaré Canyon at 4800 m water depth with R/V Pelagia in October 2003 (Figure 6.1). Magnetic susceptibility was measured on board at 5 cm intervals. The cores were opened and described at Royal NIOZ. X-ray photographs of the core sections were taken in Utrecht at TNO-NITG.

The core taken at the northern bank (64PE218-06, from now on referred to as core 06) was characterised by a brownish red, oxidised Mn-Fe rich sediment surface unit measuring ~8 cm in thickness. A clear Fe-oxide enriched horizon was seen at 8 cm depth in the core, implying that relatively recent sediments were recovered. Between 10 and 160 cm depth in core the sediments were relatively homogeneous and brownish-grey in colour. Below 160 cm depth in core, the sediments became darker in colour and banded, consisting of alternating dark-grey/black and lighter brownish-grey intervals. Frequent thin turbidites, consisting of silt and sand rich in lithic grains, were recognised.

The southern core (64PE218-08, from now on referred to as core 08) was characterised by a fine grained reddish-brown top sediment unit measuring 70 cm. At the surface of this core, several fragments of tubular and arborescent foraminifera were found. The presence of these poorly-fossilising foraminifera indicates that surface sediment was recovered in the core top. Down to 300 cm depth in core, the sediment was relatively homogenous carbonate-rich silty clay, grey/brown in colour. Occasional slightly darker grey horizons were documented. No turbidites were observed. Below 300 cm depth, the sediments became more banded, consisting of irregular alternations of dark grey/brown and lighter coloured sediment intervals. These units became increasingly more frequent with increasing depth in core. Ice rafted debris levels (IRD) can be recognised in the magnetic susceptibility record of the core and on the X-ray photographs at 85 cm and 190 cm depth in the core.

Sampling for micropaleontological, sedimentological and geochemical analysis was carried out in general at 5 cm intervals; however benthic foraminifera were examined on average at 10 cm intervals. Micropaleontological samples for foraminifera and stable isotope analysis were only taken from the homogenous, relatively fine grained sediment units. Turbidite sequences were avoided with the aid of the X-ray photographs. The samples were freeze dried and the water content was determined from the weight loss of fixed volume samples.

6.2.2 Micropaleontological analyses

The freeze dried sediment samples were washed over 63, 150 and 595 μm mesh sieves. For this study the 150-595 μm size

fraction was analysed. From each sample, up to 260 benthic foraminiferal tests were hand picked and counted. In most cases, a complete sample was picked. In a few instances, a sample was split using an Otto micro-splitter. Relative abundance of benthic foraminiferal species was calculated.

Stable oxygen isotopes ($\delta^{18}O$) of the planktonic foraminifer *Globigerina bulloides* were measured on a VG SIRA 24 mass spectrometer at Utrecht University. An average of 40 tests was used for a measurement. Values are reported relative to the Pee-Dee Belemnite in standard "δ" notation.

Sinistral and dextral forms of the planktonic foraminifera *Neogloboquadrina* spp., *Globorotalia truncatulinoides* and *G. hirsuta* were counted to determine the coiling ratio of these species. Specimens were counted until 50 individuals of the more prevalent coiling direction had been collected. If this was insufficient for an accurate estimate, a further 50 specimens were counted. At some depth levels, however, the amount of 50 specimens was not reached.

AMS ^{14}C ages for monospecific samples of *G. bulloides* were determined at Christian-Albrechts-Iniversität Kiel. A reservoir age of 400 years as applicable for the region (Waelbroeck et al. 2001, Bard et al. 2004) was made, and calibration to calendar ages was made using the online radiocarbon calibration program CalPal developed by Weninger, Jöris and Danzeglocke (http://www.calpal-online.de/index.html).

6.2.3 Sediment texture and composition

The grain size distribution of bulk sediment was determined with a Coulter LS230 laser particle sizer. The sediment was dispersed by ultrasonication (Branson 5510) without use of a chemical dispergent. $CaCO_3$ was not removed prior to the analysis.

The sediment bound inorganic and organic carbon and total nitrogen were measured on a Thermo Elemental Analyser Flash EA 1112, following the methods described in Verardo et al. (1990). For organic carbon analyses, sediment was decalcified using 1 M hydrochloric acid.

6.3. RESULTS AND DISCUSSION

6.3.1 Age model and sediment accumulation rates

Age model

With the two AMS ^{14}C dates of core 08 as tie points, the oxygen isotope curves of both cores, 08 and 06, were correlated and linearly interpolated with the $\delta^{18}O$ record of *G. bulloides* of core MD95-2042 (Shackleton et al. 2000). This core was recovered at the Iberian margin, and correlated in turn with the GRIP (the Greenland Ice Core Project) timescale (Figure 6.2).

Onboard analysed magnetic susceptibility data in combination with visual inspection of X-ray photographs were used to define the depths of Heinrich Layers (e.g. Heinrich, 1988, Broecker et al, 1992). Two peaks in the magnetic susceptibility record of core 08 at depths of 90 cm and 200 cm, corresponded with coarser sediment as revealed by the X-ray photographs. The stratigraphic position of the units suggests that this could be ice rafted debris associated with Heinrich Events 1 and 2, dated at ~16-17 cal ka BP and ~23.5-26 cal ka BP respectively (e.g. Cortijo et al. 1997,Vidal et al. 1997, Grousset et al. 2001). In core 06, no ice rafted debris was found to be associated with the magnetic susceptibility peak. Instead, the sieved coarse sediment fraction from 165 cm depth contained abundant Mn-oxide casts of worm burrows. Therefore, it seems that no Heinrich events were recorded in this core. It is possible that the sedimentary signal of H1 was lost due to the active nature of this site.

From the $\delta^{18}O$ curves of both cores on which the age determinations were based, the Holocene, Younger Dryas (YD) and Bölling-Allerød (B-A) were identified. The coiling ratios of planktonic foraminifera *G. truncatulinoides* and *G. hirsuta* were used to further correlate the early Holocene period between the two cores. A maximum dominance of the sinistral variant of *G. truncatulinoides* was noted at 90 cm depth in core 06 and 40 cm depth in core 08. This maximum was radiocarbon dated by Duprat (1983) at 7-8 ka BP and 8-9 ka BP in cores from the central and southern Portuguese margin, respectively. We have adopted to use a date of ~8 ka BP, an average estimate.

Based on the available evidence, the Last Glacial maximum (LGM) was only identified in core 08, coinciding with the heaviest $\delta^{18}O$ values at 115 cm depth. Just after the isotope excursion, the coiling ratio of *Neogloboquadrina* spp. was found to be 100% sinistral. Today, the occurrence of *Neogloboquadrina* spp. (sinistral) is restricted to polar waters (Ericson, 1959), however during the glacial period and Younger Dryas (YD), sinistral forms were abundant (at the LGM typically 100% sinistral) in the Iberian margin and Gulf of Cadiz (e.g. Pujol 1980, Duprat 1983, Sierro et al., 1999). In core 06, the LGM could not be located with certainty. The $\delta^{18}O$ record indicates relatively constant heavy values below 180 cm depth, with a maximum $\delta^{18}O$ of 3.0 per mil at 270 cm. However, sinistrally coiled *Neogloboquadrina* spp. remain low (≤ 25 %), suggesting that the LGM is not present in this core.

Sedimentation rates

The linear sedimentation rates (Figure 6.3) were always higher in core 06 than in core 08. However, in both cores a decline in the sedimentation rates was observed from the termination of Pleistocene to Holocene time period. In core 06 the absence of the LGM implies that the sedimentation rate were in excess of 55 cm/ka during deglaciation. The sedimentation rates in core 08 at the corresponding time period were 14 cm/ka. The sedimentation rates during the late Holocene were in a range of 11 cm/ka in core 06 and 5 cm/ka in core 08.

6.3.2 Sediment composition and foraminifera

Sedimentological data

The contrasting sedimentary regimes of the northern and southern banks of the lower Nazaré Canyon are clearly visible from the sedimentological analyses (Figure 6.4). To begin with, the sediment grain size was considerably coarser in core 06 than in core 08; the sand fraction measuring around 20 % in core 06 and typically less than 5 % in core 08, respectively.

Further, $CaCO_3$ content in core 06 was only about half that of core 08, despite the similar position of the cores with respect to distance to land, water depth, and the lysocline. The largest discrepancies between the carbonate records were observed

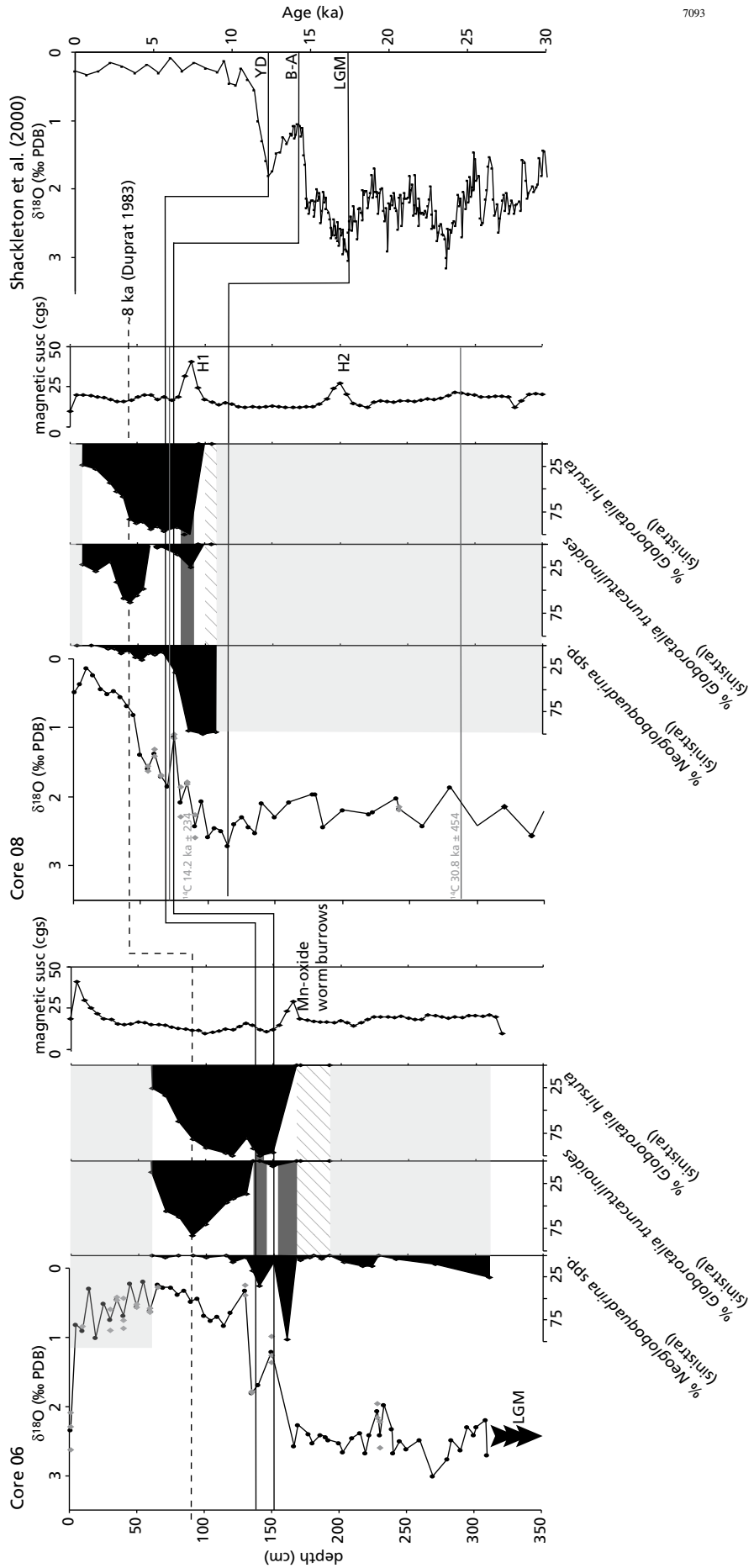


Figure 6.2. Age model. Black lines indicate the correlation with the isotope record of Shackleton et al. (2000). The dashed line is based on changes in the planktonic coiling ratio. Area shaded in light gray, no foraminiferal data gathered. Area shaded in dark gray, foraminiferal data based on ten specimens or less. The hatched area, no specimens found. YD = Younger Dryas, B-A = Bölling–Allerød, LGM = Last Glacial Maximum, H1 and H2 = Heinrich event 1 and 2

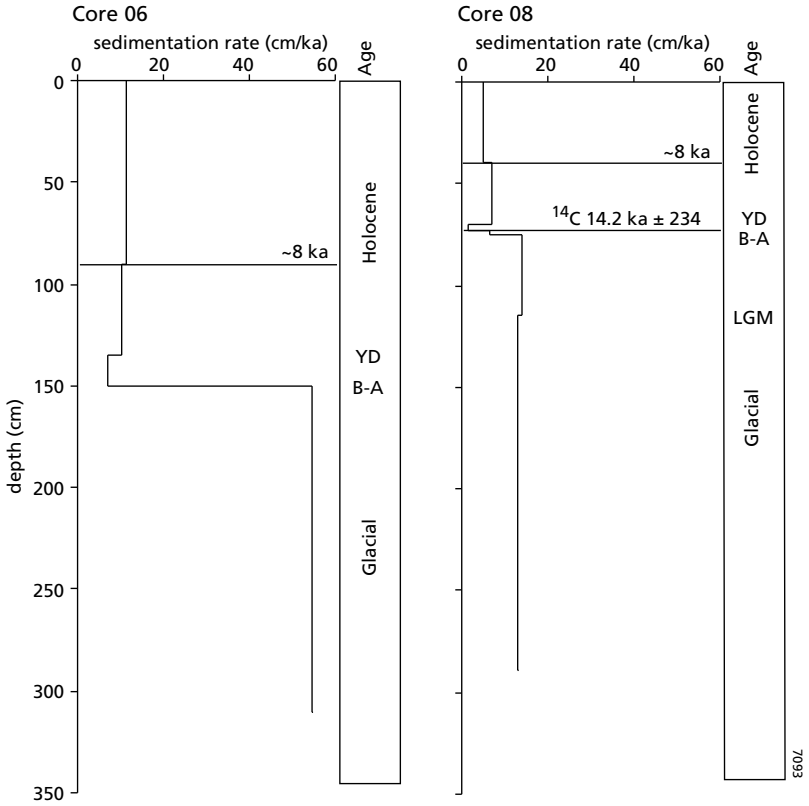


Figure 6.3. The linear sedimentation rates for core 06 and 08 calculated on the basis of the age model presented in Figure 6.2.

during the late Holocene when the $CaCO_3$ content in core 08 was around 50% and in core 06 between 20% and 35%.

The higher contribution of terrigenous material to sediment deposited on the northern bank was also indicated by the differing C/N ratios in core 06 and 08, which can be used to identify the source of organic matter, marine organic matter having higher protein and thus nitrogen content than terrigenous plant material (e.g. Bordovskiy 1965, Hedges et al. 1988, Thornton and McManus 1994). Nevertheless, the C/N ratio must be used with caution as it may be significantly modified by post-depositional processes. A systematic decrease (from >14 to ~8) was observed in the C/N ratios in core 06 from the glacial period up to the B-A and YD, indicating enhanced terrigenous input at this site during the pre-Holocene period. For the Holocene the C/N ratio fluctuated between 8 and 10. In contrast, in core 08 the C/N ratios remained more stable and closer to the marine end member (C/N ratio 6-8, Hedges et al., 1988).

Generally higher concentrations of C_{org} were measured in core 06 than in core 08. In core 06, a peak in the C_{org} content was measured during B-A and YD, corresponding with an increase in the C/N ratios and a relative minimum in the $CaCO_3$ content. At some of these depth levels, foraminifera were scarce or absent. The absence may be associated with dissolution of foraminiferal tests as a result of the higher organic matter input. Pore water acidification may occur as a result of intense oxic decomposition of organic matter, which will release CO_2, causing supralysoclinal $CaCO_3$ dissolution (Morse and Mackenzie, 1990), provided that bioturbation prevents the build-up of HCO_3^-. Nevertheless, some of the low foraminiferal abundances occurred in sandy intervals, and a lack of foraminiferal tests is likely due to dilution with terrigenous material.

In both cores, a C_{org} minimum (corresponding to a high in $CaCO_3$ record) was measured during the early-mid-Holocene time period, dating close to ~8 ka. This time period is likely to represent the Holocene Climatic Optimum (HCO) dated around 8000-6800 cal. year BP (Ran et al., 2006). During HCO the climate in the Iberian Peninsula was relatively warmer and more humid (e.g. Dorado Valiño et al. 2002, Zazo et al.2005), thus changes may be expected in fluxes of eroded material. Our grainsize data suggests a shift towards a more 'distal' clay rich composition, implying a reduction in these fluxes, probably related to the rising sea level (Cremer et a., 1992). It is therefore possible that the C_{org} minimum represents the corresponding low-point in transport of terrestrial organic matter. However, upwelling and hence the productivity regime may also have been affected by the prevailing synoptic conditions of the HCO, during which the ITCZ occupied a more northerly position (Haug et al. 2001). Consequently, the possibility cannot be excluded that our C_{org} minimum represents a decrease in productivity on the Iberian margin during the HCO.

The C_{org} content and C/N ratios in core 08 co-vary throughout the record. At several levels, among others the C_{org} minimum during the early Holocene between 40 and 60 cm depth in core, the C/N ratios were peculiarly low, measuring close to 4. Commonly, during oxic degradation marine sedimentary organic matter may lose its original C/N signature by preferential loss of nitrogen, thus resulting in higher C/N ratios (e.g. Hamilton and Hedges 1988; Hedges et al., 1988). However, in this core the co-variance between the sedimentary C_{org} content and C/N ratio implies that some carbon instead of nitrogen may have been lost during remineralisation, leading to selective preservation of N. Previously, similar observation was reported of organic-poor pelagic sediments (Suess and Müller, 1980) and across a relict turbidite (Cowie et al. 1995), which

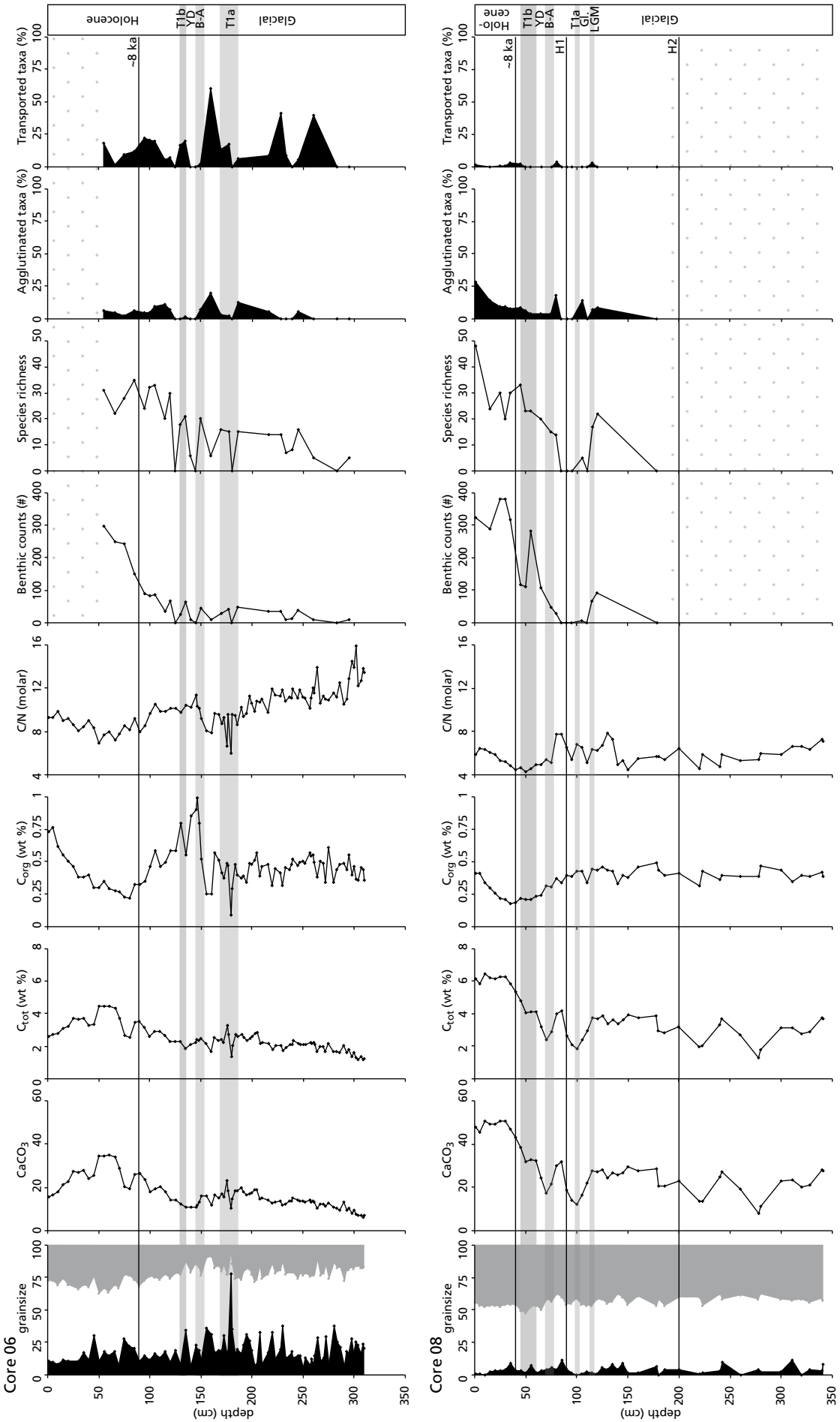


Figure 6.4. Downcore changes in sedimentological parameters and total foraminiferal numbers. Foraminiferal numbers standardised to sample size. All foraminiferal samples were taken with a 10 cm^3 syringe. For description of transported taxa, see Table 6.1. The age model is indicated on the right hand side T1a, b = Termination 1a, b (abrupt change in the isotope ratios indicating termination of glacial period (T1a) and deglaciation or start of Holocene (T1b)), YD = Younger Dryas, B-A = Bölling-Allerød, LGM = Last Glacial Maximum, H1 and H2 = Heinrich event 1 and 2. Grainsize fractions: black is sand, white is silt and light grey is clay.

Foraminiferal species	Habitat	References (e.g.):
Ammonia spp.	Shelf	Jorissen 1988, Mendes et al. 2004; De Nooijer 2007
Bolivina spathulata	Upper outer shelf	Mendes et al. 2004
Bolivina subaenariensis	Upper outer shelf	Mendes et al. 2004
Cassidulina laevigata	Upper outer shelf	Mendes et al. 2004
Cibicides lobatula	Shelf	Murray, 2003
Elphidium spp.	Shelf	Jorissen 1988, Murray 2003, Mendes et al. 2004
Hyalinea balthica	Shelf	Murray, 2003
Planoglabratella opercularis	Inner shelf	Preobrazhenskaya and Tarasova 2004
Planorbulina mediterranensis	Shelf species	Murray 2003
Rosalina sp.	Shelf	Murray, 2003; Langer and Lipps, 2006

Table 6.1. Taxa classified as shallow water foraminifera; indicating transported taxa.

suggested preferential preservation of N-rich organic matter on clay mineral particles.

Foraminiferal data

Benthic foraminiferal numbers and species richness increased from the glacial towards the Holocene in both cores (Figure 6.4). Barren samples or very low abundances were found until the start of the Holocene in core 06 and around T1a and following T1b in core 08. A parallel trend was observed between the benthic counts and sedimentary carbonate content in both cores, thus suggesting that both pelagic $CaCO_3$ and benthic foraminiferal test are equally diluted with lithic material. The lower foraminiferal abundances during the deglacial period can be related to dissolution and/or dilution with terrigenous material. In both cores, samples barren of benthic foraminifera were characterised by poorly preserved and often fragmented planktonic foraminiferal tests. Terrigenous material, such as woody particles, mica and quartz, was found only in core 06. The only exception in core 08 was at the depth level 85 cm, located near Heinrich Event 1, where lithic fragments were encountered in the >150 µm fraction.

Agglutinated foraminifera generally made up less than ten per cent of the counts. In core 08 an increase in the percentage agglutinated foraminifera was recorded from the start of the Holocene towards the present day. However, this is most likely a taphonomic effect reflecting the poor fossilisation potential of arenaceous species, which leads to a downcore decline in abundance. A loss of species using Fe-cement was especially noted. A few abundance peaks of agglutinated species were also observed prior to and after T1a, however these peaks must be considered with care as at these depth levels the total benthic numbers were very low.

Significantly higher percentages of transported taxa (Table 6.1, Figure 6.4) were found in sediment originating from the northern bank (core 06) than from the southern bank; the most common shallow water foraminifera being *Elphidium* spp. In core 06 several sharp peaks were recorded in the abundance of transported taxa prior to T1 and during the deglaciation, suggesting enhanced sediment transport from the shallow seas at the time. The relative abundance of transported taxa was lower during the Holocene.

Species distribution

The downcore relative abundance data of common foraminifera species are shown in Figure 6.5 (for complete assemblage data see Appendix 6.2). Many of the species present are typically found in modern deep sea environments (see Table 6.2 for references). Due to the low abundance of foraminifera in the samples of glacial age, the confidence with which conclusions can be drawn about relative species abundances is limited and statistical analyses were not carried out. However, based on the available information some interpretations appear reasonable.

The similarity of foraminiferal assemblages in both cores suggests that the faunal composition was at least in part controlled by similar parameters. During the glacial period both cores recorded relatively high abundances of *Pullenia* spp. (especially *P. simplex*). In literature, both *P. simplex* and *P. bulloides* have been described as infaunal taxa (Corliss 1991, Mackensen et al. 1993, Koho et al. 2007; Table 6.2) and *P. bulloides* has been reported to live in relatively organic rich sediments (Mackensen et al. 1993; Table 6.2). The dominance of infaunal taxa suggests higher organic carbon fluxes, and/or shallowing of the redox zonation, during the glacial period. A higher primary productivity off the Iberian Peninsula has been reconstructed for glacial times (Cachão and Moita 2000, Thomson et al. 2000, Pailler and Bard 2002). Alternatively, a relatively eutrophic regime during the glacial may have also resulted from greater terrigenous C_{org} supply due to enhanced canyon activity. However, the C/N ratios indicate significantly higher terrestrial fluxes to site 06 only. Core 06 does contain *Fursenkoina* spp., a species that was only occasionally found in core 08. Further, frequent episodic sedimentation events, as noted in the sedimentological observations, may have also influenced foraminiferal populations at the time.

During B-A and YD the foraminiferal assemblages differed in core 06 and 08. The northern levee was still dominated by infauna, now including *Chilostomella* spp., whereas the assemblages on the southern bank had changed, consisting of more oligotrophic species e.g. *Nuttallides umbonifera*. The higher abundance of the infaunal taxa in core 06 may be related to an increase in the down canyon transport of organic material at the time. A clear peak in the organic carbon record with relatively high C/N ratios was measured. However, this is not supported by the calculated sedimentation rates, which were lower at the time.

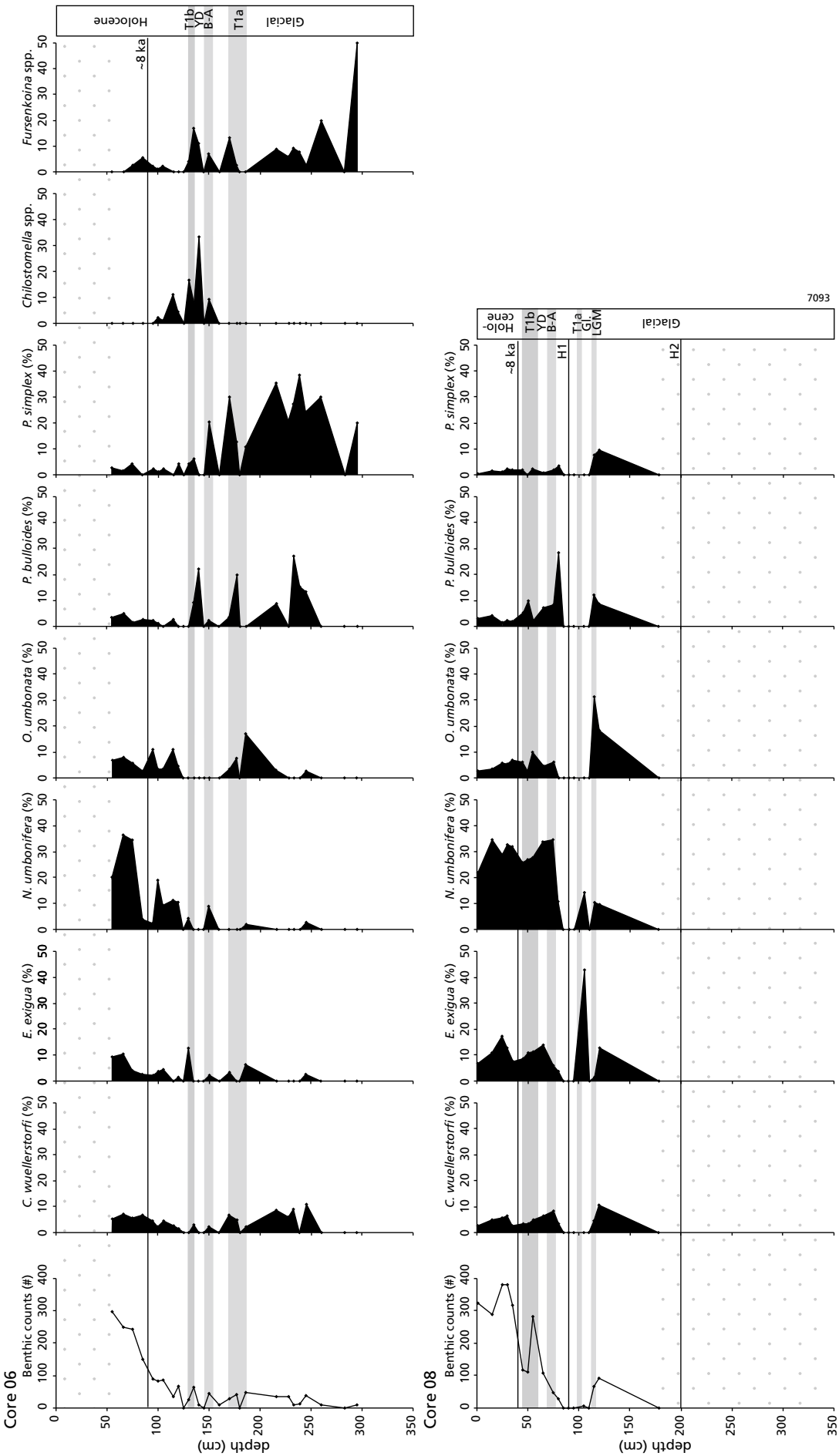


Figure 6.5. Relative abundance changes in the distribution of common deep sea foraminifera in core 06 and 08. *Chilostomella* spp. and *Fursenkoina* spp. are shown in core 06 only, as the abundance was always less than four percent in core 08.

Foraminiferal species	Habitat	Ecological implication	References (e.g.):
Cibicides wuellerstorfi	(i) Lower slope - Abyssal (ii)Epifauna	(i) Low C_{org} flux	(i) Gooday 2003 and refs. there in (ii) Corliss 1991
Chilostomella spp.	(i), (ii) (iii) Deep infauna	(i), (ii) C_{org} rich sediments, (ii), (iii) Low oxygen	(i) Koho et al (2007) (ii) Koho et al. (in prep) (iii) Gooday 2003 and refs. there in
Epistominella exigua	(i) Slope-Abyssal	(i), (ii) Seasonal phytodetritus species	(i) Gooday 2003 and refs. there in (ii) Gooday and Hughes 2002
Fursenkoina spp.	(i) Infauna	(i), (ii) C_{org} rich sediments	(i) Koho et al. 2007 (ii) Gooday 2003 and refs. there in
Nuttallides umbonifera	(i) Abyssal	(i),(ii) Carbonate corrosiveness, (i),(iii) Oligotrophic conditions	(i) Gooday 2003 and refs. there in (ii) Mackensen et al. 1995 (iii) Loubere 1991
Oridorsalis umbonata	(i) Abyssal; (ii) Microhabitat "transitional (0-4 cm)	(iii) Low C_{org} flux	(i) Gooday 2003 and refs. there in (ii) Rathburn et al. 1996 (iii) Loubere 1991
Pullenia bulloides	(i) Shallow infauna (iii) infauna	(ii) C_{org} rich sediments, (iii) High productivity	(i) Corliss 1991, Mackensen 1985 (ii), (iii) Mackensen et al. 1993
Pullenia simplex	(i) (ii) Intermediate infauna		(i) Corliss 1991 (ii) Koho et al. 2007

Table 6.2. Common deep sea foraminifera found in cores 06 and 08. Habitat characteristics and ecological implications are detailed.

At the start of the Holocene the infaunal species also declined in core 06, and the abundance of *N. umbonifera* increased, thus assemblages on both sides of the lower Nazaré Canyon became more alike, now suggesting a more oligotrophic regime. Due to lack of data for the uppermost part of core 06, the influence of different sedimentary regimes can not be ascertained for the later part of the Holocene.

No clear trends were observed in the abundance patterns of other common foraminiferal fauna, *Cibicides wuellerstorfi*, *Oridorsalis umbonata* and *Epistominella exigua.* A large peak in the relative abundance of *E. exigua* recorded at 105 cm depth in core 08 must be considered an artefact as only seven specimens were found in the sample. Further, this species is commonly present in the < 150μm fraction (Gooday 1993), thus our results may not reflect the real abundance of the taxon.

6.4 CONCLUSIONS

The larger input of terrigenous sediments on the northern bank of the lower Nazaré Canyon was confirmed by the sedimentological analyses, which showed higher sand fraction, lower carbonate content and higher C/N ratios in core 06 than in core 08. Further, the sedimentation rates on the northern bank always exceeded the rates calculated for the southern bank. The greater sediment supply at site 06 was also evident from the higher quantity of transported shallow water benthic foraminifera.

Low numbers of benthic foraminifera were present in both cores in the (post)glacial sediments, either due to dissolution or to dilution by sediment supply or both, so the patterns must be interpreted with caution. The numbers of foraminifera were considerably higher in the Holocene sections of the cores.

The faunal shift observed in both cores from late glacial to Holocene is probably related to overall changes in sediment supply and productivity on the Portuguese margin. However, foraminiferal assemblages on the northern levee were also influenced by sediment supply from the canyon, leading to higher abundances of infaunal taxa (*Chilostomella* spp., *Fursenkoina* spp. and *Pullenia* spp.).

Acknowledgements.
The authors wish to thank the crews and captains of the R.V. Pelagia, and everyone participating in the Portuguese margin Canyon cruise 64PE218. Also we would like to thank Gerrit van't Veld and Geert Ittmann for their help with foraminiferal sample preparation. Thomas Richter is thanked for discussions about the Heinrich events, and providing relevant references on the subject. Material for this study was collected within the framework of the EUROSTRATAFORM project funded by the European Commission, contract EVK3-CT-2002-00079. De Stigter acknowledges funding from EUROSTRATAFORM as well as the European project HERMES, EC contract OCE-CT-2005-511234. Shiptime on R.V. Pelagia was provided by Royal NIOZ

Appendix 6.1: Taxonomic notes

Taxonomic notes on benthic foraminiferal species discussed in this paper are detailed.

Bolivina spathulata (Williamson) = *Textularia variabilis var. spathulata* Williamson, 1858, Jones (1994), Plate 52, Figures 20-21.

Bolivina subaenariensis Cushman, 1922 Phleger et al. (1953), Plate 7, Figures 24 and 25

Cassidulina laevigata d' Orbigny, 1826, Mendes et al. (2004), Plate 2, Figure 11

Cibicides lobatulus (Walker and Jacob 1798) = *Nautilus lobatulus* Walker and Jacob 1798, Schweizer (2006), Plate 5, Figures a-l.

Cibicides wuellerstorfi (Schwager), 1866 Van Leeuwen (1989), Plate 10, Figures. 1-9

Elphidium spp.

Epistominella exigua (Brady)= *Pulvinulina exigua* Brady 1884, Schiebel (1992), Plate 5, Figures 9

(Continue on page 105)

Appendix 6.2. Counts of benthic foraminifera. Barren intervals highlighted in grey.

Core 06																												
Depth (cm) in core	**55**	**66**	**75**	**85**	**95**	**100**	**105**	**115**	**120**	**125**	**130**	**135**	**140**	**145**	**150**	**160**	**170**	**177**	**180**	**186**	**216**	**228**	**233**	**239**	**245**	**260**	**283**	**295**
split	**1/2**	**1/2**	**1/2**	**1/2**	**1/2**																							
Ammonia sp.			1	1		2																1						
Arborescent fragment																		1										
Astrononion spp.									1			1			1		1											
Bolivina alata	1																											
Bolivina earlundi									1																			
Bolivina sp.					1																							
Bolivina spathualata	2		1	2	1	1	1									1		3				2						
Bolivina subareansis			2	2		1	1		1								1											
Bulimina aculeata	2		1	1			1																					
Bulimina elongata	3	1	4	1	2	2					1							1										
Bulimina marginata							1														1				1			
Bulimina? sp.												5												1				
Calcereous spiral	2	2	2	1	2	3	2	1																				
Cassidulina laevigata	3	2	3	4	2	1	2		3		1					1	2	4				11			2	2		
Cassidulina sp.			1	1					1																			
Cassidulinoides bradyi						1	1															1						
Chilostomella oolina								1																				
Chilostomella ovoidea						2	1	3	3		4	5	3		4													
Cibicides bradyi		1	1	6		4	4	2			1	1																
Cibicides lobatula	6		4	2	7	7	11	1			1									3		1						
Cibicides sp. (juvenile)	2	1			2		1					1																
Cibicides wuellerstrofi	8	9	7	5	2	2	4	1	1			2			1		2	2		1	3	2	1		4			
Crystalleria spp.					1		1																					
Cushmanina stelligera							1																					
Dentalina spp.					1															1		2						
Eggerella bradyi	3	4	2	3	1		1	3	2						1		1			3					2			
Elphidium spp.	17		4	1	1	7	4	1	2		2	13			1	4	2	3			3	1	1			2		
Epistominella exigua	14	13	5	2	1	3	4		1		3				1		1			3					1			
Fissurina spp.	1		1									1			1													
Francesita advena											1																	
Fursenkoina rotunda			2									1									1							
Fursenkoina sp.				1																								
Fursenkoina sp. (thin)			1	3	1	1	1				1	9	1		2		1	1							1			
Fursenkoina spp.							1					1			1		3				2	2	1	1		2		5
Glandulina ovula?																												1
Globobulimina spp.					1	1			1		1																	
Globocassidulina subglobosa	8	4	4	1		1	2		1		1									1								

Core 06																												
Depth (cm) in core	**55**	**66**	**75**	**85**	**95**	**100**	**105**	**115**	**120**	**125**	**130**	**135**	**140**	**145**	**150**	**160**	**170**	**177**	**180**	**186**	**216**	**228**	**233**	**239**	**245**	**260**	**283**	**295**
split	**1/2**	**1/2**	**1/2**	**1/2**	**1/2**																							
Gyroidina altiformis	1	1			1			1			1									1		1						
Gyroidina cf. parva	1	1	2	1			1	1			1																	
Gyroidinoides spp.	3	1			1	1	2	1	1																			
Hyalinea balthica	1			1																								
Karreriella cf. *bradyi*	1					2	1					1			2					3	2							
Lagena spp.		1				2			1		1	1			1		2	1		2	1		1		4			
Lagenammina spp.							4		3																			
Marginulina obesa	1																1	2										
Miliolinella sp.									1																			
Nodosaria spp.																									1			
Nonion soldanii					4	4	1	1	3			4	1		1						1				1			
Nonion sp. (cf. *zaandama*?)		2	3	2		1	3	2				1											1	1				
Nonion spp.	3			1		3	3		1		1	1	1		3			3		4	1				2			
Nonionella turgida				2				2	2			3																
Nuttalides umbonifera	30	45	42	3	1	16	8	4	7		1				4					1					1			
Oolina spp.	5	5		1		1			2								1					1			1			
Oridorsalis umbonata	10	10	7	2	5	3	3	4	3								1	3		8	1				1			
Planoglabratella opercularis																1					1			1				1
Planorbulina mediterranea																1												
Praeglobobulimina sp.																				6								
Pullenia bulloides	5	6	2	2	1	1		1				6	2		1		1	8			3		3	2	5			
Pullenia simplex	4	2	5		1	1	2		3		1	4			9		9	5		5	12	7	3	5	9	3		2
Pyrgo murrhina	3	10	11	11	4	5	11	4	15			3	1		5		1	2		5	2			1	1			
Quinqueloculina spp.	2	1	1	2		2			2		1				2							1						1
Reophax sp.						1	1											1										
Rosalina spp.				1																								
Sphaeroidina bulloides									1			1			2													
spherical agglutinated																2												
Spiroloculina spp.				1					1													1		1				
Textularia sp.	4	2	1	2	1	1																						
Texturaria sp. (v fat)	1						1	1																				
Triferina spp.			2	1		1																						
Triloculina spp.				3					1																			
Unknown calc	1			1				1	1						1											1		
Uvigerina mediterranea (fragment)				1																								
Valvulineria? sp.									2																			

Appendix 6.2. (Continued)

Core 08																		
Depth (cm) in core	**1**	**15**	**25**	**30**	**35**	**45**	**50**	**55**	**65**	**75**	**80**	**85**	**90**	**95**	**105**	**110**	**115**	**120**	**178**
split		**1/2**	**1/2**	**1/4**	**1/2**			**1/2**											
Ammodiscus sp.	2					1													
Ammonia sp.			1																
Arborescent fragment	13		1																
Bulimina aculeata			1		1														
Bulimina elongata					1	1													
Bulimina marginata				1															
Calcereous spiral	1	2	3	3	5	2	2	1	2										
Cassidulina laevigata					2	2													
Chilostomella ovoidea						1	1				1								
Cibicides bradyi	1	1	3	5	9	1	3	5	5	1								1	
Cibicides lobatula	5		1		2						1						2		
Cibicides sp.						1													
Cibicides sp. (juvenile)		1																	
Cibicides wuellerstrofi	9	7	11	6	4	4	4	7	7	4	1						3	10	
Cibicides?										1									
Cribrostomoides subglobosus	4	1																	
Crystalleria spp.							1	1											
Cushmanina stelligera			2			1													
Cyclammina sp	1																		
Cystammina sp.			1																
Dentalina spp.		1				1				1									
Eggerella bradyi	29	12	14	6	7	7	7	4	2	2	3						4	4	
Elphidium spp.				1		1													
Epistominella exigua	22	16	33	12	12	10	12	16	15	3	1				3		1	12	
Epistominella sp.	1																	1	
Fissurina spp.	3	2	3	3	2	1	3	4	1									2	
Francesita advena						2	1	1	2									1	
Fursenkoina spp.							1			1							1	2	
Globocassidulina subglobosa	14	7	7	3	11	7	2	7	4	1							3	1	
Glomospira spp.	4																		
Gyroidina altiformis	12	3	1	2	1	2		2										1	
Gyroidina cf. *parva*	3				1				1										
Gyroidina cf. *soldanii*	3	2		1	1	2	2												
Gyroidinoides spp.	1				1	1													
Haplophragmoides spp.	2	1																	
Hormosinella distans	12																		
Hyalinea balthica					1														
Karreriella cf. *bradyi*	4		1	1	2	2		1	2		1						1	3	
Karreriella sp. (orange)	3	1																	
Lagena spp.	2		2		2	2		3	2									3	
Lagenammina spp.	2																		
Lenticulina sp.	1																		
Marginulina obesa				1															
Nodosaria spp.											1				1			1	
Nonion soldanii	3		1		2	2	7	5	1	1	1						2		
Nonion sp. (cf. *zaandama*?)	4	2	2		4	2	1	1	1									2	
Nonion spp.							2	1									1		
Nonionella sp.	1																		
Nuttalides umbonifera	71	50	55	31	51	30	30	39	37	17	3				1		7	9	
Oolina spp.	1	5	1	2	3	2	3	3		1	1							1	
Oridorsalis umbonata	9	5	11	5	11	7	3	14	5	3							21	17	
Parafissurina spp.									1										
Praeglobobulimina? Fragment	1																		
Pullenia bulloides	10	6	3	2	3	6	11	3	8	4	8						8	8	
Pullenia simplex	1	2	2	2	3	2		3	1	1	1						5	9	
Pyrgo murrhina	11	8	18	6	9	9	13	16	10	8	4						4	3	
Pyrgo sp.																	1		

Appendix 6.2. (Continued)

Core 08																			
Depth (cm) in core	**1**	**15**	**25**	**30**	**35**	**45**	**50**	**55**	**65**	**75**	**80**	**85**	**90**	**95**	**105**	**110**	**115**	**120**	**178**
split		**1/2**	**1/2**	**1/4**	**1/2**			**1/2**											
Quinqueloculina spp.	6	4	6		3	1	1											1	
Reophax sp.	1																		
Reophax sp.											1							1	
Reophax sp. (spinous)	5																		
Rhizammina algaeformis	3																		
Rimulina gladra																	1		
Rosalina spp.	1		1																
Saccammina sp. (v thin neck)	1																		
Sphaeroidina bulloides	10	1	1		1	1	1	2	2										
spherical agglutinated	4																		
Spiroloculina spp.															1				
Subreophax sp.	7																		
Textularia sp.	14	5	2	2	3														
Triferina bradyi			1				1												
Triloculina sp.	1					1		2											
Trochammina globigeriniformis	1																		
Trochammina spp.	5																		
Unknown calc			1		1										1		2		
Uvigerina canariensis						1													

Appendix 6.1. (Continued)

Hyalinea balthica (Schroeter) = *Nautilus balthicus* Schroeter, 1782, Den Dulk et al. 1998, Plate I, 10a, b

Planoglabratella opercularis (d'orbigny 1839) = *Rosalina opercularis* d'orbigny 1839, Jones (1994), Plate 89, Figures 8-9.

Planorbulina mediterranensis d' Orbigny 1826, Mendes et al. 2004, Plate 1, Figures 5a, b

Pullenia bulloides (d'Orbigny) = *Nonionina bulloides* d'Orbigny, 1846; Jones (1994), Plate 84, Figures 12-13

Pullenia simplex Feyling-Hanssen 1954, Koho et al. (2007), Plate 2, Figures 6a, b

Nuttallides umbonifera (Cushman) = *Pulvinulina umbonifera* Cushman 1933, Van Leeuwen (1989), Plate 15, Figures. 11-13; Plate 16, Figures 1-7.

Oridorsalis umbonata (Reuss) = *Rotalina umbonata* Reuss, 1851, Jones (1994), Plate 95, Figure 11.

Rosalina sp.

CHAPTER 7

Synopsis: "The dynamic balance between food abundance and habitat instability: benthic foraminifera of Portuguese margin canyons"

In this chapter the main findings of the PhD project entitled "*The dynamic balance between food abundance and habitat instability: benthic foraminifera of Portuguese margin canyons*" are summarised. In general, the aim of the project was to further our understanding of the ecology of modern benthic foraminifera and to improve their usefulness as proxies of past sedimentary environments. In particular, it was of interest to understand how foraminiferal ecosystems are affected by both sedimentary disturbance within canyons (e.g. sudden sedimentation events and gravity flows) and changes in food availability. Therefore, the major part of the project focussed on investigating living (rose Bengal stained) foraminifera and their response to changes in these two parameters. In this study, living benthic foraminiferal assemblages were picked and identified from 27 multi- and boxcores from the Portuguese margin canyons (Figure 7.1, Table 7.1) and cross-correlated with a host of physical and chemical parameters (e.g. current speed, sedimentation rate, frequency of disturbance, pore water and sediment geochemistry). Eventually this information was used to investigate temporal changes in sedimentation processes in a lower canyon (deep sea) record dating back to the last glacial period. The detailed survey of modern foraminiferal assemblages assisted the interpretation of this record. For example, anomalous occurrences of species known to be occurring in shallow waters could be used to indicate increased canyon activity or sediment transport.

7.1 SUBMARINE CANYONS

Submarine canyons are important sediment conduits (van Weering et al., 2002), with sediment transport primarily occurring in the form of gravity flows, a turbulent process causing sediment reworking and re-deposition. Additional parameters such as the magnitude of tidal currents in combination with internal waves (Gardner et al. 1989), downwelling (Palanques et al. 2006) and dense cascading shelf water (Canals et al. 2006) also contribute to the activity of modern canyons.

Canyon activity differs from one canyon to the next. For example on the Portuguese margin, generally higher sedimentation rates and more frequent sedimentary disturbance were observed in Nazaré Canyon than in Lisbon- Setúbal Canyon (Table 7.1). The disturbance was greatest in the axis of Nazaré Canyon, decreasing in intensity towards the canyon terraces and with increasing water depth (De Stigter et al. in press). The more dynamic nature of the Nazaré Canyon axis was also evident from the sediment grain size distribution (Figure 7.2; core 225-26); with medium-fine sand commonly found underlying a surficial mud-drape. In contrast, no sand was found in multicores collected from the Nazaré terraces or Lisbon-Setúbal Canyon, indicating a lower energy regime.

Canyon activity can also vary in time. During glacial periods, higher sediment transport may be expected due to lowering of the sea level and subsequent exposure of the continental shelf. Much of the material discharged by canyons derives from the adjacent continents, so a narrow shelf is conducive to efficient transport of this material to the deep ocean. Four-fold higher sedimentation rates were measured in the lower Nazaré Canyon during the last deglaciation with respect to the modern values (Chapter 6).

In addition to higher sedimentation rates, elevated sedimentary organic carbon concentrations are observed in Nazaré and Lisbon-Setúbal Canyons relative to the adjacent open slope environments (Table 7.1). However, much of the organic detritus in canyon sediments is laterally advected and refractory in composition (Epping et al. 2002), resulting in an enrichment of old, non-reactive carbon. Therefore, high organic matter content may not always indicate high benthic food availability, as shown in Chapter 5. In this study, the sedimentary phytopigment content was shown to be a better indicator of benthic food availability, and recorded a clear exponential decline with increasing water depth and an inverse relationship with pore water nitrate content.

7.2 THE INFLUENCE OF SEDIMENTARY DISTURBANCE ON BENTHIC FORAMINIFERA

Significantly lower benthic foraminiferal standing stocks were recorded in the Nazaré Canyon axis than in the Nazaré terrace stations (Chapter 3) and in the Lisbon-Setúbal Canyon (Chapter 5). The low foraminiferal abundances along the Nazaré axis were related to frequent gravity flows in the upper Nazaré Canyon axis and the associated high sediment fluxes and resuspension of surface sediments, disturbing foraminiferal populations and hindering the ecosystem development. Substrate (or habitat) stability appears to be an important factor in controlling the foraminiferal populations. Further, the frequency of the disturbance must play a role, determining whether repopulation is possible. Experimental results indicate that following physical disturbance (i.e. sediment mixing), the recovery of benthic foraminiferal microhabitats in sediment takes considerable time (over 22 days; Ernst et al. 2002).

Map #	Station	sample	depth m	Latitude °N	Longitude °W	C_{org}[b] wt %	O^2 depth*[b] cm	C_{org}/N[b] molar	CPE[c] µg/cm³	Chl *a*: phaeo[c]	Mode[a] µm	SAR[a] g/m²·d	v5[a] cm/s	v50[a] cm/s	v95[a] cm/s	Mass flux$_{max}$ g/m²·d
	Nazare Canyon															
1	64PE225-42	bc	146	39° 38.48′	009° 16.99′											
2	64PE218-57	bc	151	39° 38.50′	009° 16.99′	1,5					14,3	2,9				
3	64PE225-41	mc	301	39° 34.71′	009° 09.18′	2	~0.1	9	27,1	0,15	12,1	46,2				
4	64PE218-05	mc	321	39° 38.80′	009° 14.50′	1,7					10,3	14,6				
5	64PE204-56	L	338	39° 38.90′	009° 14.69′	1,6					16,4	1,8	3	13	25	69,5
6	64PE138-12	mc	344	39° 38.87′	009° 14.72′	3,3	0,5	9,9			13,6	2,2				
7	64PE138-16	mc	890	39° 35.72′	009° 24.24′	3		10			14,9	12,9				
8	64PE236-13	mc	927	39° 35.87′	009° 24.26′				15,2	0,04	16,4					
9	64PE225-26	mc	1118	39° 35.97′	009° 24.00′	1,8	~0.5	10,9	18,6	0,07	13					
10	64PE236-07	L	1126	39° 36.00′	009° 24.05′								1	6	13	788,3
11	64PE225-34	mc	2847	39° 30.05′	009° 45.00′	1,6	~1.25	10,9	13,1	0,02						
12	64PE208-01	L	3010	39° 31.52′	009° 49.00′								1	6	15	46,5
13	64PE138-14	mc	3097	39° 30.76′	009° 51.05′	3,8	1,5	11,1			30,1	32,6				
14	64PE218-55	L	4298	39° 35.06′	010° 17.33′								<1	3	7	46,7
15	64PE218-06	pc	4806	39° 59.50′	011° 10.00′											
16	64PE218-08	pc	4806	39° 46.50′	011° 00.00′											
17	64PE225-24	mc	4810	39° 48.04′	010° 37.98′	1,5	~4.5	12,1	2,5	0,02						
18	64PE225-22	mc/L	4969	39° 54.99′	011° 09.95′	1,8	~5.0	12,5	1,2	0,02	6,5	0,8	<1	<1	3	0,2
19	64PE218-07	bc	4976	39° 54.00′	011° 10.00′	1,5					105,9	0,9				
	Lisbon-Setubal Canyon															
20	64PE225-01	mc	365	38° 31.07′	009° 16.42′	1,0	~0.75	9,3	21,7	0,04	13,0					
21	64PE269-02	L	497	38° 30.00′	009° 16.01′								4	16	31	
22	64PE218-21	mc	500	38° 29.99′	009° 16.03′						59,2					
23	64PE252-34	L	1070	38° 26.36′	009° 20.38′								1	7	19	
24	64PE218-22	mc	1463	38° 24.78′	009° 19.77′	1,2		9,8			8,6					
25	64PE218-23	mc	1850	38° 19.97′	009° 19.59′						14,9					
26	64PE225-03	mc/L	1855	38° 19.96′	009° 19.60′	1,6	~1.5	8,0	8,6	0,03	9,0		2	10	21	
27	64PE204-33	bc	2233	38° 14.00′	009° 24.00′	1,4		8,9			7,8	2,1				
28	64PE204-35	L	2716	38° 12.00′	009° 31.37′								<1	5	13	
29	64PE225-05	mc	3170	38° 09.43′	009° 35.00′	1,1	~4.5	7,6	3,1	0,03						
30	64PE225-07	mc	4450	38° 06.38′	010° 00.26′	0,9	~8.0	8,2	1,2	0,02	5,1	0,8	<1	5	27	

Map #	Station	sample	depth m	Latitude °N	Longitude °W	C_{org}[b] wt %	O^2 depth*[b] cm	C_{org}/N[b] molar	CPE[c] µg/cm³	Chl *a*: phaeo[c]	Mode[a] µm	SAR[a] g/m²·d	v5[a] cm/s	v50[a] cm/s	v95[a] cm/s	Mass $flux_{max}$ g/m²·d
	Open Slope (Nazare)															
31	64PE225-39	mc	300	39° 39.99′	009° 36.00′	0,3	~1.0	7,2	6,5	0,02	96,5					
32	64PE225-27	mc	1000	39° 33.94′	009° 40.96′	1	~2.5	8,3	3,11	0,03	6,8					
33	64PE236-12	L	1796	39° 34.52′	009° 44.40′								5	23	44	40,1
34	64PE225-25	mc	4798	39° 46.49′	011° 00.00′	0,6	>10	8,6	0,81	0,02						
	Open Slope (Lisbon-Setubal)															
35	64PE225-02	mc	301	38° 25.98′	009° 23.06′	0,9		10,2	16,1	0,04	14,9					
36	64PE225-46	bc	400	38° 19.50′	009° 12.50′	0,6	~2.75	8,2			101,2					
37	64PE225-21	mc	1742	38° 04.99′	009° 34.85′	1,1	~5.0	8,1	4,2	0,03	5,4	1,1				
38	64PE225-06	mc	2939	38° 00.46′	009° 58.51′	1,0	~8.0	7,6	2,0	0,02						

* O_2 penetration depth = Nitrate (NO_3^-) declines sharply at this depth in the pore waters and ammonium (NH_4^+) begins to build up.
data from: [a]De Stigter [b]Epping and Koning [c]Garcia

Table 7.1. Stations used in this study, and shown in Figure 7.1. Sample description: bc = box core, mc = multicore, L = lander station and pc = piston core. Environmental data used in this study (measured in top 1 cm of sediment). Organic carbon content (C_{org}), oxygen pentration depth (O_2 depth), molar C_{org} total nitrogen ration (C_{org}/N), chloroplastic pigment equivalents (CPE), chlorophyll *a*: phaeopigment ration (Chla:phaeo), Modal grain size (Mode), Sediment accumulation rate (SAR), current speed (v5, v50 and v95, where v5 is the lower value below which current speed is during 5% of the time, v50 is the mean, and v95 is the upper value below which current speed is 95% of the time); maximum mass flux of sediment recorded in benthic lander sediment traps ($Mass\ flux_{max}$).

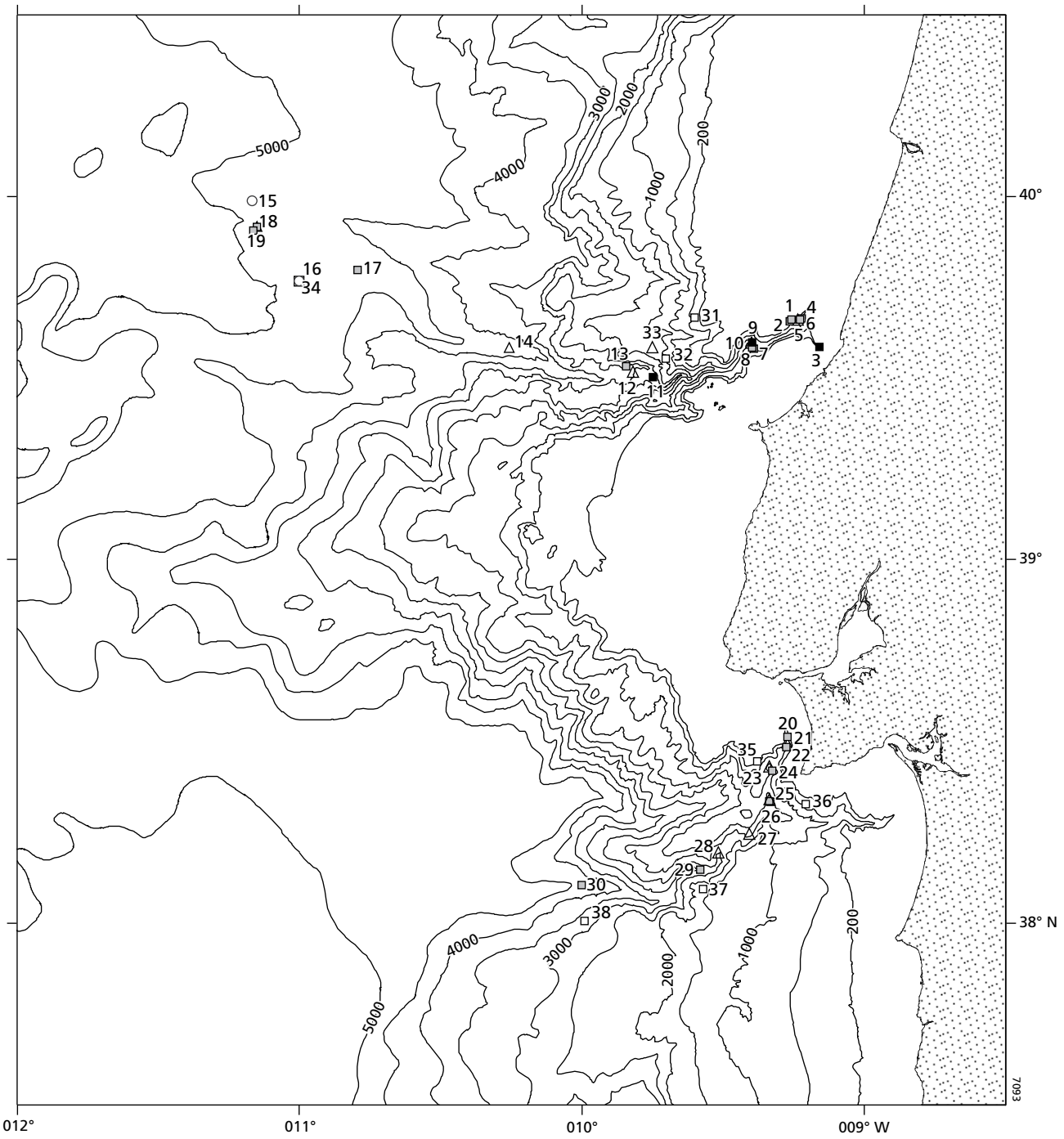


Figure 7.1. Map of stations used in this study. For station names and more details, see Table 7.1. Stations for living rose Bengal foraminiferal analyses and geochemical data are marked with a square (grey square = canyon station; black square = Nazaré Canyon axis; white square = open slope station); lander stations (used for environmental data) indicated with a triangle; piston core stations (paleo study, Chapter 6) marked with a white circle.

In addition, the disturbance may be lethal for some species, epifaunal species generally suffering more from sudden changes in redox chemistry than infaunal species. In Chapter 4 sediment collected from the upper Nazaré Canyon terrace was subject to disturbance (sediment homogenisation/mixing) as a result of experiment setup. The results indicate that seven weeks after the disturbance, foraminifera had migrated into their preferred microhabitat and the population seemed to have stabilised. Considerable mortality was observed following the disturbance. In addition, as noted by Ernst et al. (2002), infaunal foraminifera were more successful in the experiment than epifaunal taxa, which apart from *Adercotryma glomeratum* nearly disappeared in this experiment. All in all, it appears that if the frequency of disturbance along the Nazaré Canyon axis is very high (resuspension of surface sediments occurring at every tidal cycle in the upper canyon), it is unlikely that foraminiferal communities are able to exist under these conditions, as repopulation and microhabitat stabilisation take a long time.

Nevertheless, a unique foraminiferal assemblage, dominated by *Technitella* spp. was found in the upper Nazaré axis at 1118

m water depth; a station experiencing very high sediment fluxes (a maximum of 788.3 g/m^2·d; De Stigter et al. in press) due to frequent resuspension by tidal currents and sediment gravity flows. Therefore, the dominance of this taxon at this particular site indicates that *Technitella* spp. can be regarded as highly opportunistic recolonisers of newly exposed habitats, or may be able to tolerate high sedimentation rates, frequent resuspension of surface sediments and severe turbulence. Previously, *Technitella melo* was described as a recoloniser following a turbidite event in the Cap Breton canyon (Anschutz et al. 2002), supporting the first interpretation. The dynamic nature of the station in the upper Nazaré axis was also recorded in the meiofaunal community (Chapter 2), which was dominated by two opportunistic nematode genera, *Sabatieria* sp. and *Metalinhomoeus* sp., commonly found in dredged sediments (e.g. Boyd et al. 2000).

7.3 THE INFLUENCE OF LABILE ORGANIC MATTER ON BENTHIC FORAMINIFERA

Generally, a positive correlation has been observed between benthic meiofaunal biomass and the sedimentary CPE (chloroplastic pigment equivalents, the sum of chlorophyll *a* and its breakdown products) (Soltwedel, 2000 and references therein). Likewise, a positive correlation has been found for the benthic foraminiferal biomass and the CPE content in sediment (Altenbach 1985, Altenbach and Sarnthein, 1989). This relationship was further confirmed by our field studies. In all study environments, both in canyons and on the adjacent open slope, a strong positive correlation was found between the total standings stocks of calcareous foraminifera and the sedimentary CPE content (Figure 7.3a). The only exceptions were the frequently disturbed stations located on the Nazaré axis, which clearly plot as outliers. A weaker correlation was observed for the agglutinated taxa (Figure 7.3b). It appears that the distribution of agglutinated foraminifera is less confined by the availability of labile organic carbon, and relatively high abundances of agglutinated species (132 specimens/core) were found even at an abyssal site in the Setúbal Canyon where the sedimentary CPE content was extremely low (1.2 µg/cm^3). In addition, the majority of the agglutinated taxa found at these sites had a relatively fragile test, hence low potential for fossilisation. Therefore, the trend observed for the calcareous taxa generally appears more important in terms of the proxy-value of foraminifera for paleoceanographic studies. Figure 7.3 close here

A positive response of foraminiferal abundance was also observed after addition of algae in a laboratory study (Chapter 4). In the experiment foraminifera were separately quantified from two different size classes (63-150 µm and >150 µm), thus allowing an independent estimation of the reproduction and growth of foraminifera. In general, a 'two-phased' response was observed. The first phase, occurring during the first four weeks following addition of algae, was an increase in the smaller sized (63-150 µm) sub-population. The second phase, an increase in the larger sized (>150 µm) sub-population, continued longer, probably until after the end of the experiment (eight weeks after the feeding). In control cores, where no algae were added,

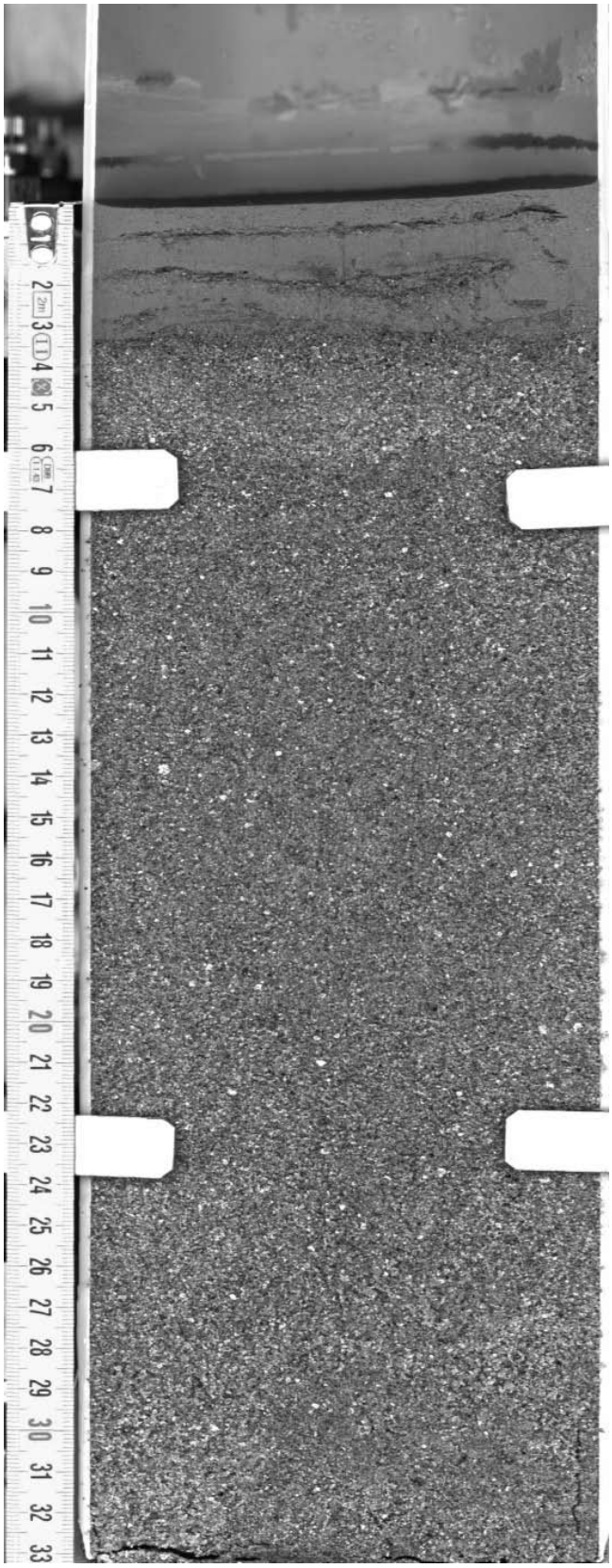


Figure 7.2. A cross section through the core 64PE225-26 located on the upper Nazaré Canyon axis. Note the surficial mud-drape underlain by medium sand. *(Photo taken by Henko de Stigter)*

a decline in the small sized sub-population was measured. Therefore, the results indicate that foraminiferal reproduction, at least in part, can be triggered by deposition of fresh marine algae or ceased by low food availability.

In short, the quality of organic matter seems to play an important role in foraminiferal standings stocks and reproduction. Generally our results indicate that foraminifera benefit from the presence of relatively fresh organic matter in the sediment, rather than simply an abundance of total organic matter. The organic-rich lower Nazaré sediments recorded only very low foraminiferal abundances due to the largely refractory (low phytodetritus) nature of the carbon they contain. Further, foraminifera were only abundant deeper in the sediment units if the phytodetritus content (CPE) was relatively high. Therefore, we question the suggestion made by some authors e.g. Caralp (1989), that some taxa specialise to live on refractory organic matter.

Foraminiferal species distribution in the sediment appears to be mainly related to two, often inversely co-varying parameters in nature: oxygen and food, as summarised in the TROX model (Jorissen et al, 1995, van der Zwaan et al., 1999). In the laboratory, it was possible to separate the two parameters by adding algae while aerating the aquarium vigorously; hence providing enough oxygen for aerobic remineralisation and preventing major changes in the redox zones (Chapter 4). The experimental results imply that the vertical distribution of most infaunal taxa (e.g. *Melonis barleeanum* and *Bigenerina cylindrica*) is mainly regulated by, or related to, sediment redox conditions as no measurable changes were observed in the microhabitat of these species following the addition of food. Only two taxa, *Pullenia* sp. and *Trochammina* sp., were observed to change their microhabitat after the addition of food and migrate to the surface (presumably to feed on the algae). However, in nature the two parameters food and oxygen are usually inseparable, as an increase in labile organic matter will lead to enhanced oxygen consumption and changes in the redox zonation, these factors working together to shape and structure the foraminiferal community.

This relationship was further evaluated in Chapter 5, in which the benthic foraminiferal distribution was related to redox conditions and food availability, using pore water nitrate profiles and sedimentary chlorophyll *a* and CPE contents, respectively. Our results are in line with the TROX model and further identified the optimum conditions for several foraminiferal taxa in terms of food availability and pore water nitrate content. For example, phytopigment-rich (surficial CPE content > 20g/cm^3) sediments with a shallow nitrate penetration depth (~ 1cm depth) were inhabited by infaunal species such as *Chilostomella oolina*, *Melonis barleeanum* and *Globobulimina* spp. As the nitrate penetration increased to ~ 2 cm depth and the pigment content remained relatively high (> 15 g/cm^3), *Uvigerina mediterranea* and *U. elongatastriata* became dominant species in the surface sediments. With declining CPE content and increasing nitrate penetration depth, the foraminiferal assemblages changed from the mesotrophic *Cibicides kullenbergi – U. peregrina* assemblage to the oligotrophic abyssal assemblage, mainly consisting of agglutinated taxa.

7.4 ARBORESCENT AND TUBULAR FORAMINIFERA

Large agglutinated foraminifera are often not included in ecological studies of benthic foraminifera due to difficulties in the counting methods. However, in our study area these taxa contributed significantly to the living standing stock, hence leaving them out of the analyses seemed unjustified.

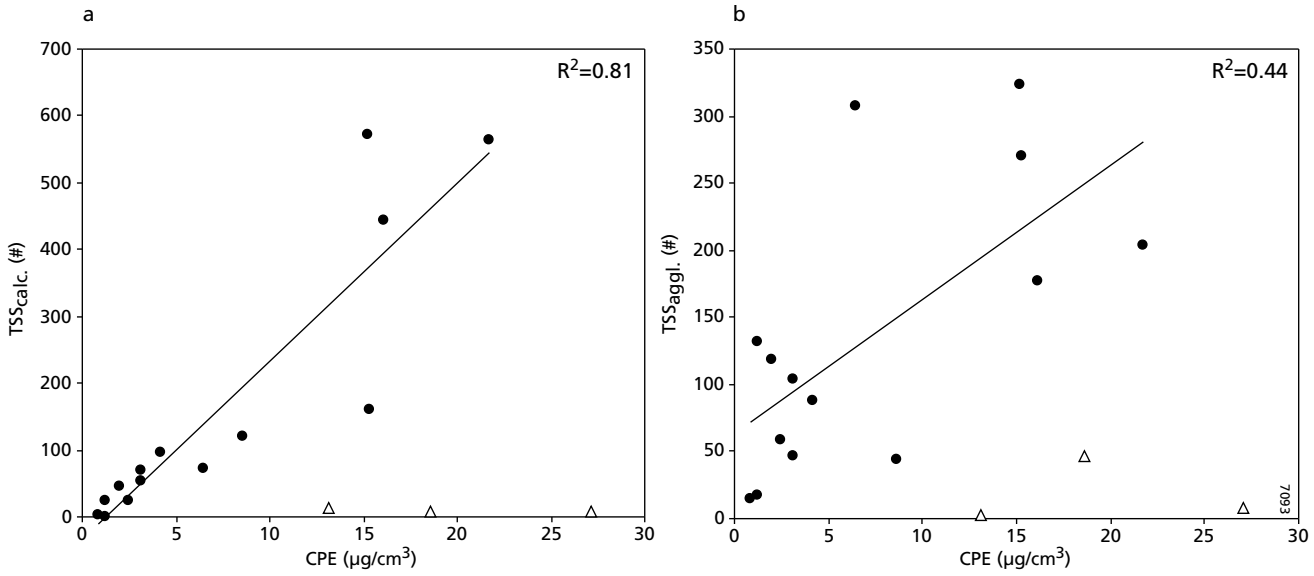
No correlation was observed between the total number of the arborescent and tubular taxa and measured environmental parameters (i.e. sedimentary C_{org} and pigment content, water depth, nitrate penetration depth; Chapter 5). However, sedimentary disturbance appears to limit the occurrence of these large agglutinated foraminifera (Chapter 2 & 3).

The species composition of the arborescent and tubular community did appear to reflect environmental conditions, e.g. food supply. Several *Bathysiphon* species were found in Nazaré terraces, upper Lisbon-Setúbal Canyon and on the adjacent open slope stations. All these sites were rich in phytopigments, therefore implying that the occurrence of *Bathysiphon* spp. is restricted to sediments rich in labile marine organic carbon. Previously, *Bathysiphon filiformis* has been described from organic-rich sediments off the continental slope of North Carolina (Gooday et al. 1992). In addition, living *Bathysiphon* spp. were found inside the oxygen minimum zone in the Arabian Sea (Gooday et al., 2000) and *B. capillare* has been named as a dysoxic indicator by Schönfeld (2001). In our study some Bathysiphon spp., including *B. filiformis,* were observed to protrude out of the sediment, therefore suggesting that these tubular taxa consume organic matter directly from the settling detritus. The suspension feeding mode has been previously suggested for *Bathysiphon rusticus* and *B. folini* by Gooday (1983).

Saccorhiza ramosa was a common arborescent species in stations located on the mid-lower continental slope and lower Lisbon-Setúbal and Nazaré Canyons. Therefore, it seems that this species thrives in relatively stable environments characterised by low current velocities, well-oxygenated bottom waters and oligotrophic conditions. Previously, the preference of this species for a low energy environment was observed by Altenbach (1988) who found that enhanced current activity led to test breakage.

7.5 CANYON FORAMINIFERA: WHAT IS LEFT IN THE FOSSIL RECORD

A relatively large proportion of foraminiferal assemblages living in the Nazaré and Lisbon-Setúbal Canyons is made of agglutinated taxa; their abundance generally increasing with water depth. Further, the ecologically interesting taxon *Technitella* spp., which occurs in (recently) disturbed environments, is also agglutinated. The preservation potential of these foraminiferal species is low, as was demonstrated by a clear downcore decline in the abundance of agglutinated foraminifera in core 08 (Chapter 6). Therefore, a lot of ecological information may be lost due to taphonomic processes. However, it seems that calcareous foraminifera, in addition to having a higher preservation potential, may be better tracers of climatic signals



Fig*ure 7.3.* Total standing stocks of a.) calcareous and b.) agglutinated foraminifera vs. sedimentary CPE content. Foraminiferal samples collected during cruise of 64PE225 from both Nazaré and Lisbon-Setúbal Canyons, and from the adjacent open slope. In addition, station 64PE236-13 included. Stations sampled from the Nazaré canyon axis are labelled with an open triangle. These sites are not included in the linear regression.

such as productivity, as was demonstrated in Chapter 5 by their good correlation with the pigment content of the sediments.

High resolution environmental reconstructions in canyons can be problematic due to downslope transport and reworking of sediments, leading to difficulties in stratigraphic interpretations. Further, the numbers of benthic foraminifera in canyon sediments may be diluted due to locally high sedimentation rates, thus leading to extremely low numbers of foraminifera per sample and uncertainties in the significance of the results. These often "undesirable" processes, however, can also provide us with clues of past sedimentary regimes and environmental conditions. Generally, low foraminiferal abundances were found to coincide with enhanced sediment transport (Chapter 6), or disturbance as described in Chapter 3. The occurrence of shallow-water benthic foraminifera in deep-sea sediment also serves as an indicator of enhanced transport of material from the continental shelf. In any case, regardless of the problems these processes present for short-timescale reconstructions, lower resolution climate signals such as the glacial-Holocene transition are visible in time series of foraminiferal abundances and assemblages.

Away from heavily disturbed locations, and during less active periods, recognisable foraminiferal assemblages develop in response to the balance between pore-water redox state and food supply (Chapter 5). Our field validation and quantification of the TROX model. is thus a major value of the thesis in terms of palaeoceanographic proxy development: The assemblages predicted by the model are shown to be robust across the studied range of environmental conditions, and are readily fossilised, therefore corroborating their value as proxies of past conditions.

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Summary

Submarine canyons are dynamic sedimentary environments influenced by sediment transport, erosion and deposition. Gravity flows can scour and erode the canyon floor, thus redistributing sediment to distal locations. In addition, submarine canyons can act as sedimentary traps where sediment transported laterally across the continental shelf and slope is advected into. Hence, elevated sedimentation rates and high organic carbon content are often found in submarine canyons in comparison with the adjacent open slope.

Such dynamic processes must affect the ecosystems inhabiting these exceptional environments. To investigate and quantify this relationship, living benthic foraminifera were sampled from Nazaré and Lisbon-Setúbal submarine canyons located on the Portuguese continental margin. The foraminiferal abundances and species distribution were correlated with a host of geochemical (e.g. organic carbon, phytopigment content, redox chemistry) and physical/sedimentological parameters (e.g. current speed, sedimentation rate, frequency of gravity flows). Eventually this information was used to reconstruct temporal variations in sedimentation processes and associated changes in foraminiferal community structure in two piston cores derived from the lower canyon.

The results of these studies highlight the importance of habitat instability and food abundance in structuring the foraminiferal communities in canyons. Food, quantified in terms of the sedimentary phytopigment content, was readily available in the studied canyons, declining in abundance with increasing water depth. Food abundance was also reflected in the pore water chemistry (nitrate penetration depth used as a redox indicator), higher pigment content coinciding with shallower nitrate penetration depth in sediment. The standing stocks of foraminifera and community structure changed with these parameters, and a positive correlation was observed between foraminiferal numbers and the sedimentary pigment content and a negative with the nitrate penetration depth. Stations recording the highest pigment loads (> 15μg/cm^3) and the shallowest redox zones (nitrate penetration depth < 1cm) were inhabited by infaunal taxa e.g. *Chilostomella oolina, Melonis barleeanum, Bigenerina cylindrica and Globobulimina* spp. At the deepest sites, where the pigment concentrations were very low (≤ 2 μg/ cm^3) and the redox zonation deep (nitrate penetration depth exceeding 5 cm depth in sediment) communities were dominated by agglutinated taxa and only few calcareous species were present, including Nuttallides umbonifera. Despite the high pigment concentrations however, foraminiferal numbers were low in the upper and middle Nazaré canyon axis. At these sites the development of stable ecosystems appeared to be hindered by sedimentary disturbance. Distinct agglutinated foraminifera, *Technitella* spp., were found to inhabit the unstable environment. This species can be regarded as a highly opportunistic recoloniser of newly exposed habitats, and/or may be able to tolerate high sedimentation rates and frequent sedimentary disturbance (i.e. gravity flows).

In the paleostudy, a postglacial increase in the sediment transport was clearly reflected in the foraminiferal record as an increase in the relative abundance of shallow water taxa. Further, a shift in faunal composition was observed as a response to changing sedimentary regime; higher sediment and organic carbon supply from the canyon leading to a development of an infaunal *Pullenia* spp. assemblage and decreasing activity to the hemipelagic *Nutallides umbonifera* assemblage.

Acknowledgments

This book would never have been completed without the support and help of many friends, colleagues and family.

First of all I would like to thank my promoter Bert van der Zwaan and my supervisor Tanja Kouwenhoven, who just over four years ago gave me the opportunity to do my PhD here in Utrecht. During the past years both Tanja and Bert have always supported my work and answered any of my questions. In addition to helping me in the office and in the lab, Tanja has been at sea with me and helped me with the intensive task of sediment sampling. This would also have been impossible without the help of my other supervisor, Henko de Stigter, who co-ordinated the cruises on during which the material was recovered. Further, Henko's great eye for detail, and his "endless" comments have improved my work and the manuscripts in this thesis a great deal. I have learned a lot from these three people!

The next person I want to thank is Tom Jilbert, who has always been there for me. In addition to being my "walking dictionary and proof reader", he has supported me emotionally, both at home and work. Tom you are my rock!

I must acknowledge the (ex)co-workers who have all taught me something new and contributed towards the pleasant and friendly working environment in Utrecht. Therefore, in no particular order I would like to thank Anja Mourik (also my paranymph), Mariëtte Wolthers, Sandra Langezaal, Yvonne van Lith, Ivo Duijnstee, Lennart de Nooijer, Sander Ernst, Natasja Jannink, Magali Schweizer, Frits Hilgen, Luc Lourens, Hemmo Abels, Kees Hordijk, Lucy Stap, Wilma Wessels, Martin Ziegler, Mike Rogerson, Shauna Ní Fhlaithearta, Adriana Dueñas-Bohórquez and Gert Jan Reichart, and everyone else from the Start/Pal group.

I would also like to thank Rosa García, Eric Epping and Erica Koning, who all contributed data towards my chapters. In addition, these people were a pleasure to work with at sea.

Many thanks go to the technical staff in Utrecht University, especially Geert Ittmann, Gerrit van't Veld, Dineke van de Meent-Olieman, Arnold van Dijk and Gijs Nobbe.

I would also like to thank the reading committee, Prof. Dr. A.J. Gooday, Prof. Dr. F.J. Jorissen, Prof. Dr. A.F. Lotter, Prof. Dr. G. Schmiedl and Prof. Dr. T.C.E. van Weering, for reading and accepting my thesis.

I wish to thank my family, my mother Anja, my father Kari and my brother Jussi Koho, for their loving support. Despite living in separate countries for the past eight years, I always feel close to you all.

Last but not least, I would like to thank all of my friends here in Utrecht, without whom the past four years would not have been the same! So big thanks (and a hug) to Maron de Groot (you are a star girl; and thanks for being my other paranymph), Brigit van Kuyk, Elise Vikander, Anna Niemi and many more…..