Benthic foraminifera of the Portuguese margin : Impact of organic supplies on the density, biodiversity and composition of the faunas

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"No animal series offers more facilities and benefits to the geologist and zoologist: first, to determine the temperature of places and second, by their wonderful diversity. Through the elegance of their forms and the uniqueness of their organization, they play, despite their smallness, a role vast in nature." Alcide d'Orbigny.

Being an English student who is passionate about the study of foraminifera at a French University, I thought it very appropriate to quote a Frenchman famous for his great works and love of foraminifera! I first found out about foraminiferans during a third year undergraduate project at Durham University, in which I developed a fascination for their morphology, diversity and ecology. My interest in foraminifera resulted in a 4th year undergraduate dissertation on British marshland foraminifera, followed by a Masters dissertation on foraminifera of the Marmara Sea during an MSc course at UCL. However, I am indebted to Prof. Frans Jorissen for introducing me to the wonders of deep-sea foraminiferal ecology from the Portuguese margin and giving me the opportunity to continue in their research. The central themes of this thesis, the testing of the TROX model and the importance of organic matter on foraminiferal communities, are concepts that have developed during many years of his research and it has been both a privilege and joyful experience to work under his guidance. I'm very thankful for his dedication in reading and editing the multiple drafts of each chapter! I extend my thanks to Henko de Stigter, Meryem Mojtahid, Edouard Metzger and all the crew of RV Pelagia for the acquisition of samples analysed in this thesis, and to Antonio Pusceddu and Silvia Bianchelli for sharing organic component data. Throughout my study at BIAF, I have had many constructive research conversations with Prof. Ralf Schiebel and Dr. Christophe Fontanier for which their ideas and

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CHAPITRE 1

INTRODUCTION

LES FORAMINIFÈRES BENTHIQUES DE LA MARGE PORTUGAISE: IMPACT DES APPORTS ORGANIQUES SUR LA DENSITÉ, LA BIODIVERSITÉ ET LA COMPOSITION DES FAUNES

Cette thèse est le résultat d'une collaboration internationale, dans le contexte du projet HERMES du septième programme Cadre de la Communauté Européenne. Les travaux présentés dans cette thèse ont été produits au laboratoire UMR 6112 LPGN-BIAF, en collaboration avec l'Institut Royal Néerlandais des Recherches sur la Mer (NIOZ, Texel, Dr. Henko de Stigter), l'Université d'Utrecht, Pays-Bas (Dr. Tanja Kouwenhoven, Dr. Karoliina Koho) et l'Université Polytechnique de Marches, Italie (Pr. Roberto Danovaro, Dr. Antonio Pusceddu).

Les foraminifères benthiques sont des protistes unicellulaires avec une structure cellulaire très similaire à celle des amibes. Les foraminifères sont différents par leurs rhizopodes granulaires et leurs filopodes allongés qui sont projetés du corps cellulaire. Ils disposent d'un test qui peut varier d'une seule loge monothalame avec ouverture principale, à des structures architecturales beaucoup plus complexes avec de multiples loges et/ou apertures. Le test peut être entièrement organique, être couvert de grains sédimentaires (foraminifères agglutinés), ou encore être construit en calcite ou aragonite. Dans le dernier cas, le test peut être perforé ou imperforé.

Les foraminifères, qui font partie de la méiofaune, constituent une composante importante des communautés benthiques marines ; dans les fonds océaniques profonds, ils peuvent représenter plus de la moitié de la biomasse totale (Gooday et autres, 1992). Ils peuvent apparaître avec de fortes densités par unité de surface, et par conséquent, des faunes abondantes peuvent être échantillonnées relativement facilement, et des bases de données statistiquement fiables peuvent être obtenues à partir d'échantillons sédimentaires de petite taille. En raison de leur extraordinaire capacité d'adaptation, les foraminifères benthiques

prolifèrent dans un large éventail d'environnements océaniques. Par conséquent, à toute profondeur et dans chaque zone latitudinale, les foraminifères seront un élément majeur de la faune benthique, ce qui rend ce groupe particulièrement utile pour des études écologiques et paléoécologiques.

En raison de la difficulté d'échantillonner les environnements benthiques en milieu océanique profond, notre compréhension de l'écologie des foraminifères est encore imparfaite. En effet, nous connaissons encore très mal les phénomènes de variabilité spatiale (« patchiness ») et temporelle. Toutefois, des études faites pendant les deux dernières décennies ont eu comme résultat un consensus général sur le fait que la composition des assemblages de foraminifères benthiques est fortement liée à la quantité et la qualité des détritus organiques qui atteignent le fond océanique (par exemple, Altenbach et autres, 1999, 2003; Jorissen et d'autres, 1998, 2007; Fontanier et autres, 2002; Gooday, 2003; Koho et autres, 2008).

Le chapitre 2 de cette thèse décrit les assemblages de foraminifères vivant le long d'un transect bathymétrique sur la marge portugaise, du plateau continental externe jusqu'à la plaine abyssale. Des études antérieures sur la marge portugaise (Schönfeld 2001, Koho et les autres, 2008) suggèrent que le flux de matière organique exportée vers le fond océanique, et plus particulièrement son contenu total en phytopigments, sont les principaux facteurs contrôlant la dynamique des foraminifères benthiques dans les milieux de pente ouverte.

Afin de tester cette hypothèse, huit stations ont été échantillonnées pendant la mission 64PE252 du RV Pelagia, en Septembre 2006. Les huit stations ont été sélectionnées sur la marge portugaise, le long d'un transect bathymétrique et/ou trophique, orienté est-ouest, de la partie externe du plateau continental (profondeur d'eau 282 m) jusqu'au plancher océanique abyssal (4987 m). Le transect se situe au large de Cap Sines, à 37°50'N, et s'étend de 9°05'W à 11°W (Fig. 1). L'étude d'un tel transect garantit que toute la gamme de conditions trophiques est représentée, passant de sites oligotrophes par des milieux mésotrophes, pour finir avec des conditions oligotrophes aux sites les plus profonds. A chaque station une carotte interface, avec un diamètre de 6 cm, a été collectée avec un carottier multitube. Le sédiment supérieur de chaque carotte a été échantillonné, avec des intervalles de 0.5 cm entre 0 et 2 cm, et des tranches de 1 cm d'épaisseur entre 2 et 10 cm de profondeur dans le sédiment. Tous les échantillons ont été stockés dans une solution de Rose Bengale dans 96¨% d'éthanol jusqu'au traitement au laboratoire. Tous les intervalles sont

étudiés pour leur contenu en foraminifères colorés au Rose Bengale, à la fois dans les fractions > 150 µm et 63-150 µm. Les densités totales ont été déterminées pour chaque station en additionnant les nombres de foraminifères vivants trouvés à chaque niveau échantillonné.

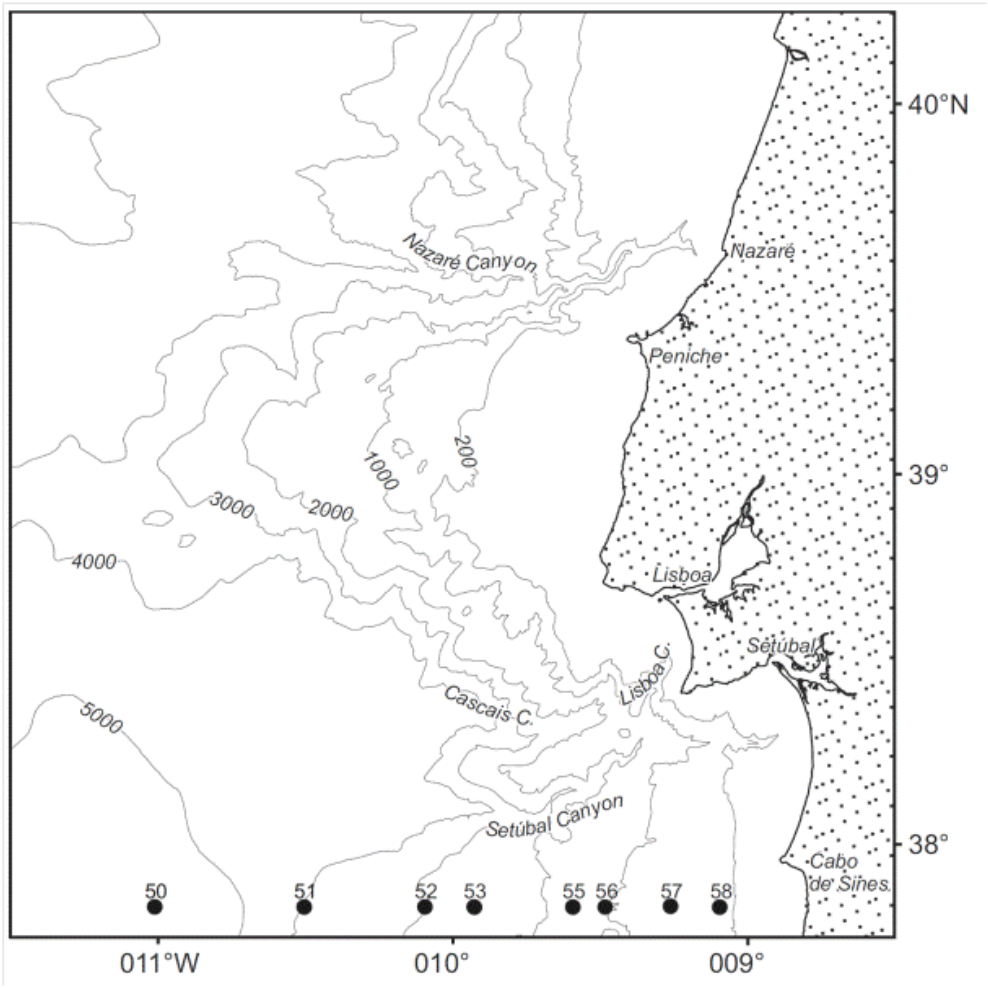

Figure 1. Carte montrant le transect sur la marge océanique au large de Cap Sines. Les huit stations, échantillonnées en septembre 2006, sont indiquées avec des cercles noirs.

L'étude de la fraction fine du sédiment constitue une des particularités de cette thèse. Cette fraction, qui contient entre autre des espèces opportunistes de petite taille, n'est que rarement étudiée, et si c'est le cas, souvent uniquement dans le centimètre supérieur. L'étude de cette fraction 63-150 µm pour tous niveaux sédimentaires jusqu'à 10 cm a été particulièrement chronophage. Cette étude apporte une multitude de nouvelles observations, qui vont permettre de reconsidérer certaines hypothèses concernant l'écologie des

foraminifères et le fonctionnement des écosystèmes benthiques. Ce chapitre a fait l'objet d'une publication dans le journal « Journal of Foraminiferal Research » (Phipps et al., 2012).

Pour ce même transect bathymétrique et trophique, la répartition verticale des foraminifères dans les premiers centimètres du sédiment (les « microhabitats ») a été étudiée en détail. Les résultats de cette étude sont présentés dans le **chapitre 3**. Plus précisément, dans ce chapitre, nous avons voulu tester les idées du modèle conceptuel « TROX » (Jorissen et al., 1995), qui explique que, dans les environnements benthiques de l'océan ouvert, les microhabitats des foraminifères sont contrôlés principalement par la relation inverse entre les apports organiques et la concentration en oxygène des eaux de fond et des eaux interstitielles.

Des additions postérieures au modèle comprennent le rôle de la migration des foraminifères en réponse aux changements des conditions d'oxydoréduction (Jorissen, 1999) et l'effet de la compétition, de la prédation et de la bioturbation sur les microhabitats (Van der Zwaan et al., 1999).

Cette étude fait l'analyse des microhabitats, exprimés par la profondeur de vie moyenne (ALD_x, average living depth), pour différents groupes de foraminifères colorés au Rose Bengale. Plus précisément, nous comparons la répartition verticale pour les deux classes de taille (63-150 µm et > 150 µm), mais également entre les foraminifères à test carbonatés et ceux à test agglutiné. Malheureusement, la méthode de coloration au Rose Bengale pose un problème pour l'inventaire des foraminifères vivant profondément dans le sédiment. La décision si un individu était vivant au moment de l'échantillonnage est quelque peu subjective, parce que le protoplasme des foraminifères peut être préservé dans des conditions anoxiques qui règnent dans les couches plus profondes du sédiment (Corliss et Emerson, 1990). Par conséquent, nous avons appliqué des critères de coloration très stricts, et uniquement des exemplaires qui avaient toutes les loges sauf la dernière colorées rose vif, ont été considérés comme vivants. L'intensité de la coloration des exemplaires douteux trouvés profondément dans le sédiment était systématiquement comparée avec celle des exemplaires trouvés dans les niveaux superficiels. Quand l'intérieur du test n'était pas visible, par exemple dans le cas des espèces agglutinées opaques ou les espèces imperforées, les tests étaient cassés afin d'inspecter le contenu.

Aussi dans ce chapitre, la principale nouveauté est l'étude des foraminifères de petite taille, jusqu'à 10 cm de profondeur. Cela apporte notamment une pléthore de données sur des

petites espèces de foraminifères à test agglutiné. Ces données permettent de proposer des ajustements importants vis-à-vis des stratégies écologiques de ce groupe.

Le **chapitre 4** présente une étude détaillée sur la biodiversité des assemblages de foraminifères. Nous avons examiné en détail les différences en biodiversité entre les différentes classes de taille (c'est à dire les classes 63-150 µm et > 150 µm) et entre les groupes d'espèces avec différents types de test (calcaire ou agglutiné). Un grand nombre d'indices de biodiversité existe. Un des objectifs de ces indices est de corriger pour des différences en richesse de foraminifères des échantillons étudiés. Ces indices ont différentes sensibilités vis-à-vis de l'équitabilité et la dominance des espèces (Gage et May, 1993). Pour ces raisons, cette étude utilise une large gamme d'indices pour décrire la biodiversité et pour mettre en évidence des différences entre les échantillons (e.g., Buzas, 1979; Williamson, 1985; Levin et al., 2001). Ces indices incluent la Richesse Spécifique, Raréfaction (Sanders, 1969; Hayek et Buzas 1997; Gray 2000), Fisher alpha (Fisher et al., 1943; Williams, 1964), Shannon-Weaver (Shannon et Weaver, 1949), Dominance (Simpson 1949; Magurran, 2004) et Equitability (Pielou, 1975).

La nouveauté de ce chapitre est donc de mettre en évidence des différences en biodiversité entre des groupes de foraminifère de différentes tailles, avec différents types de parois.

Le **chapitre 5** présente les résultats d'une étude de la répartition des foraminifères benthiques le long d'un transect latitudinal sur la marge portugaise, en fonction de la profondeur de pénétration de l'oxygène dans le sédiment et de la disponibilité en nourriture. Le transect latitudinal étudié inclut sept stations, toutes aux environs de 1000 m de profondeur, aussi bien de pente ouverte que des environs des canyons sous-marins. Nous avons notamment étudié des échantillons des terrasses du canyon sous-marin de Nazaré, des axes des canyons de Cascais et Setubal, et des pentes ouvertes au large de Mondego, de l'Estremadura et d'Alentejo (Fig. 2). Ces deux types de milieu marin (canyon sous-marin et pente ouverte) sont censés avoir des conditions environnementales très contrastées. Tous nos échantillons sauf un ont été collectés en mai 2007 pendant la mission 64PE269 avec le RV Pelagia, en utilisant un carottier multitube avec un diamètre interne de 9.5 cm. L'échantillon de la pente ouverte de l'Estremadura a été prélevé en Septembre 2006 pendant la mission 64PE252 avec le RV Pelagia, en utilisant un carottier multitube avec un diamètre interne de 6cm. Les faunes de foraminifères vivants (colorés au Rose Bengale) ont été étudiées dans la

fraction supérieure à 150 µm, jusqu'à 10 cm de profondeur. Nous avons limité notre étude aux espèces à test calcaire et à test agglutiné fossilisant, afin de pouvoir comparer nos données à celles des études antérieures portant sur la même zone d'étude.

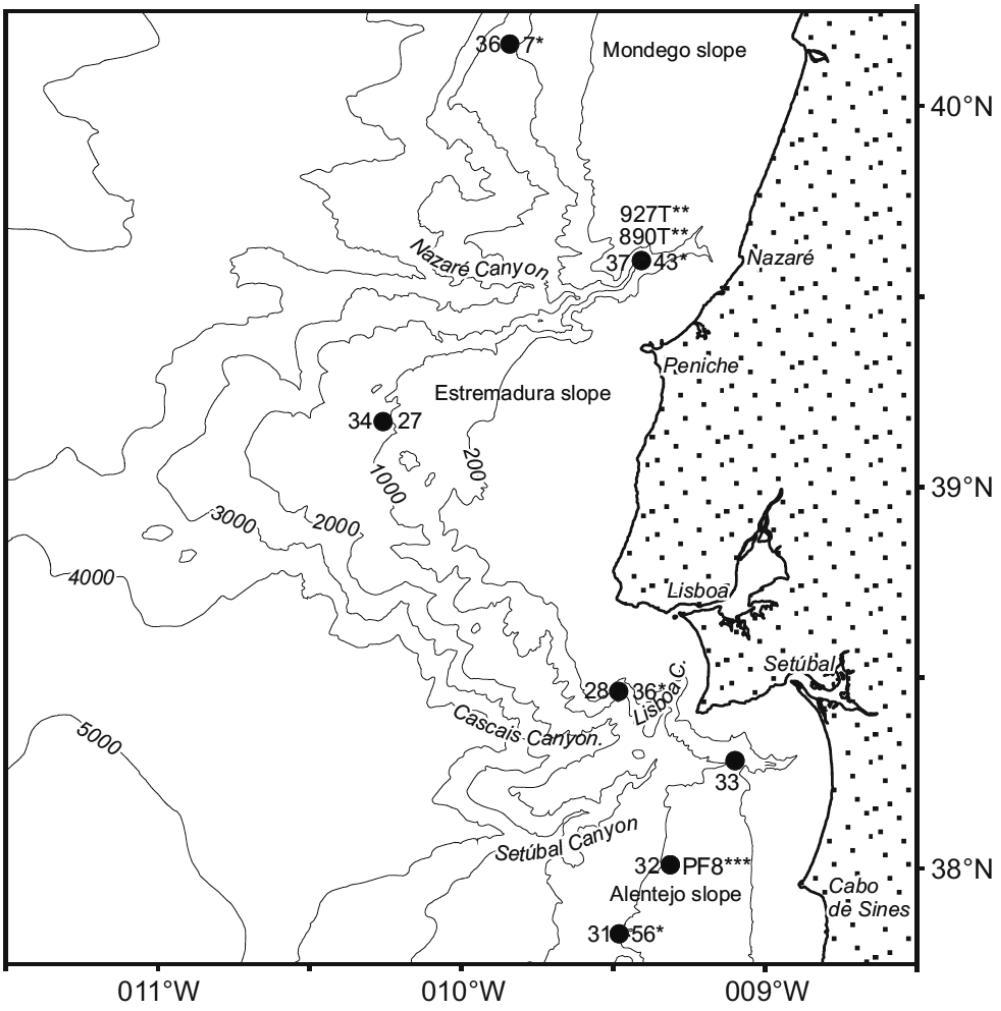

Figure 2. Carte montrant le transect latitudinal sur la marge portugaise. Les stations échantillonnées sont indiquées avec des cercles noirs. Les numéros sans étoile indiquent les échantillons étudiés dans cette étude. Les numéros suivis de 1, 2 ou 3 étoiles indiquent la localisation des échantillons étudiés par Nardelli et al. (2010), Koho et al. (2007) et Griveaud et al. (2010), respectivement.

En effet, la majorité de nos stations a été échantillonnée auparavant, en Mai 1999 et Mai 2005 (résultats décrits par Koho et al., 2007), en Août 2003 (Griveaud et al., 2010) et en Septembre 2006 (Nardelli et al., 2010). Le détail des échantillons considérés est présenté dans

le tableau 1. Tous ces auteurs ont gracieusement mis leurs données détaillées à notre disposition. La comparaison de ces paires d'échantillons pour les mêmes sites nous permet d'obtenir une idée de la variabilité temporelle des faunes.

Le site sur la terrasse du Canyon de Nazaré, situé à 39°35'N et 9°24'W, a précédemment été étudié par Koho et al. (2007) et Nardelli et al. (2010). Les deux études concluent que cet environnement est très enrichi en matière organique labile, ce qui induit une pénétration minimale de l'oxygène dans le sédiment. Néanmoins, les faunes sont caractérisées par de fortes densités d'espèces endopéliques intermédiaires et profondes, telles que *Melonis barleeanus*, *Chilostomella oolina* et *Globobulimina* spp.

Le site dans l'axe du canyon de Cascais, à 38°27'N et 9°28'W, a été étudié dans un premier temps par Nardelli et al. (2010). Ce site était également riche en matière organique labile. Par contre, la densité de la faune était beaucoup moins importante, et les espèces endopéliques superficielles *Cibicidoides pachydermus* et *Uvigerina mediterranea* dominaient la faune. Nardelli et al. (2010) ont suggéré que la faible densité de la faune était due à un récent événement de dépôt sédimentaire en masse. Cette hypothèse est corroborée par les profils de ^{210}Pb, et par la présence d'une faune dominée par des espèces de surface à 1,5-2 cm de profondeur. Cette dernière faune représenterait la faune avant l'événement sédimentaire, tandis que la faune pauvre trouvée à la surface représenterait un premier stade de colonisation. Notre échantillonnage, un an plus tard, permet de vérifier cette hypothèse.

En comparaison à ces sites de canyon, l'ensemble des sites échantillonnés sur la pente de Mondego (40°09'N, 09°49'W) et Alentejo (37°50, 09°28'W), étudiés dans un premier temps par Nardelli et al. (2010) et par Griveaud et al. (2010), respectivement, montrent une beaucoup plus faible quantité de matière organique, d'une qualité nettement inférieure. Des espèces endopéliques superficielles (*Uvigerina mediterranea*) y sont communes, par contre, les espèces endopéliques intermédiaires et profondes sont plutôt rares, ce qui correspond au caractère plus oligotrophique de ces sites.

		CANYONS			OPEN SLOPE			
Author	Date	Nazaré	Cascais	Setúbal	Mondego	Estremadura	Alentejo	
This study	May-07 Sep-06	Core 37	Core 28	Core 33	Core 36	Core 34 Core 27	Core 32	Core 31
Nardelli et al. (2010)	Sep-06	Core 43	Core 36		Core 7			Core 56
Koho et al. (2007)	May-99 May-05	Core 890T Core 927T						
Griveaud et al. (2010)	Aug-03						Station FP8	

Tableau 1. Résumé des carottes considérées dans le chapitre 5, avec leur période d'échantillonnage. Pour chaque secteur, les deux carottes étudiées ont été prélevées exactement au même endroit, à l'exception des carottes de Koho et al. (2007) prélevées à une profondeur légèrement différente que les carottes 37 et 43.

Finalement, le **chapitre 6** présente une synthèse des principaux résultats de cette thèse, fait le bilan des questions non résolues, et propose des perspectives de recherche future.

Les données de comptage des faunes de foraminifères pour le transect bathymétrique (chapitres 2 à 4) et pour le transect latitudinal (chapitre 5) sont présentées dans les **Annexes 1 et 2**, respectivement.

Annexe 3 présente un article intitulé "Live benthic foraminiferal faunas along a bathymetrical transect (282–4987 m) on the Portuguese margin (NE Atlantic)", publié dans le Journal of Foraminiferal Research (Phipps et al., 2012), basé sur le chapitre 2 de cette thèse.

Annexe 4 présente l'article "Calcareous benthic foraminiferal biofacies along a depth transect on the southwestern Marmara shelf (Turkey)", publié en 2010 dans le journal "Micropaleontology" (Phipps et al., 2010). Cet article est basé sur une étude des faunes de foraminifères dans la Mer de Marmara, sujet de la thèse de Master à l'University College de Londres. Dans cette étude, il est expliqué comment la température, la salinité, la teneur en oxygène et les apports de nourriture déterminent les faunes dans la Mer de Marmara. A cause

du sujet très similaire, cet article décrit une étude parfaitement complémentaire à celles qui ont fait l'objet des travaux de thèse.

CHAPITRE 2

LIVE BENTHIC FORAMINIFERAL FAUNAS ALONG A BATHYMETRICAL TRANSECT (282–4987 M) ON THE PORTUGUESE MARGIN (NE ATLANTIC)

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2.1 ABSTRACT

Live benthic foraminifera were studied in eight cores collected along a depth transect ranging 282–4987 m on the Portuguese margin. Total standing stocks (TSS) and species assemblages from both 63–150 and >150 μm fractions are compared between stations along the transect and with previous live foraminiferal studies from the Bay of Biscay and western Iberian margin. Based on the sedimentary organic matter contents and ecological traits of the retrieved foraminifera, three groups of stations are distinguished: (1) eutrophic upper-slope stations (282–1002 m) with faunas dominated by *Uvigerina mediterranea, U. elongatastriata, Melonis barleeanus, Bigenerina nodosaria, Trifarina bradyi, Epistominella vitrea, Cribrostomoides bradyi*, and *Bolivina robusta,* (2) mesotrophic middle- to lower-slope stations (1374–2475 m) with faunas dominated by *Uvigerina peregrina, Globobulimina affinis,* and *Repmanina charoides,* and (3) oligotrophic lower slope and abyssal plain stations (2908–4987 m) with faunas in the larger size fraction dominated by *Cibicides kullenbergi* and agglutinated species such as *Reophax fusiformis* and *Recurvoides* sp. 1. The smaller size fraction is dominated by opportunistic calcareous species such as *Bulimina translucens, Epistominella exigua,* and *Nuttallides pusillus,* along with *Reophax fusiformis,* but most of these species are diminished at 4987 m, where *Reophax fusiformis, Pullenia salisburyi*, and various monothalamous agglutinates are dominant. This succession of assemblages probably reflects the increasing scarcity of trophic resources with water depth. This hypothesis is corroborated by 1) the clear decrease of TSS with increasing water depth, and 2) the decreasing sediment phytopigment concentrations towards deeper sites. Moreover, the decreasing percentage of perforate calcareous foraminifera, and increasing percentage of agglutinated foraminifera with water depth, suggests that, in general, perforate calcareous species have higher trophic requirements than agglutinated ones.

2.2 INTRODUCTION

Benthic foraminifera are an important component of meiofaunal communities in many benthic environments, from intertidal to hadal depths. In the deep sea they may account for >50% of the total benthic biomass (Gooday and others, 1992). Because they often occur in high densities, small sediment volumes typically yield large numbers of specimens, making them particularly useful for ecological as well as paleoecological studies. There is a general consensus that the composition of benthic foraminiferal assemblages is strongly linked to the quantity and nutritive quality of the organic detritus reaching the ocean floor, and to the oxygenation of the interstitial waters (e.g., Jorissen and others, 1998, 2007; Gooday, 2003).

Depending on the traditions and procedures of different laboratories, the study of foraminiferal faunas is mostly based on the >63µm, >125 µm and >150 µm size fractions. In many foraminiferal ecology studies, only the larger size fractions (e.g., >125, >150, or even >250 µm) are considered, as it is sometimes difficult to maintain consistent taxonomic concepts in smaller fractions where most juveniles are concentrated and where the risk of analyzing transported specimens is much higher. Additionally, many authors do not consider working the smaller size fractions (in most cases 63–125 or 63–150 µm) because they can be very tedious and time-consuming. Studies where multiple fractions are analyzed have an additional benefit of allowing direct comparisons with other studies, and can aid the picking process (e.g., the removal of large tubular taxa from smaller fractions). When dealing only with foraminiferal faunas from the large size fraction, many small species are overlooked (Duchemin and others, 2007). Some small-sized foraminifera have an opportunistic behavior characterized by rapid reproduction or growth in response to intermittent food supply at the sediment-water interface (e.g., Gooday, 1988, 1993; Cornelius and Gooday 2004). These small-sized foraminifera are therefore considered to be potential indicators of seasonal

episodes of organic carbon flux in modern and ancient marine environments (Gooday, 1993, 2003; Smart and others, 1994; Duchemin and others, 2007). In fact, the foraminiferal response to phytodetritus deposits appears to be much stronger in the 63–150 μm fraction than in the corresponding >150μm fraction (e.g., Fontanier and others, 2003, 2006; Duchemin and others, 2007; Shepherd and others, 2007).

On the Portuguese margin (northeast Atlantic), the exported organic matter flux is a major factor controlling benthic foraminiferal dynamics in shelf and open-slope environments (Schönfeld 2001, Koho and others, 2008). However, no study on the smaller-sized (63–150 μm) fraction has been carried out in this rather well known area. Therefore we consider the live benthic foraminiferal faunas of the large (>150 μm) as well as small size (63–150 μm) fractions of eight stations along an upper-slope to abyssal plain depth transect (282–4987 m) from the Portuguese margin.

Our main objectives are 1) to analyze benthic foraminiferal assemblage and density variation with increasing water depth and varying sedimentary organic matter contents and biochemical composition, and 2) to compare the foraminiferal response to changing trophic conditions between the 63–150 and >150 μm fractions.

2.3 MATERIAL AND METHODS

2.3.1 STUDY AREA

We studied an east–west transect of stations located at depths ranging 282–4987 m on the open slope off Cape Sines, on the Portuguese Margin at 37°50'N, 9°05'–11°W (Fig. 1). The shelf between the Setúbal Canyon and Cape Sines has a maximum width of 25 km. At

282 m depth, surface sediments consist of fine sands with a unimodal particle size distribution, with a peak at 169 µm. Towards deeper sites, these fine sands progressively become finer, until the modal grain size falls to ~5 µm at 1000 m depth. Still deeper, the modal grain-size distribution remains constant down to the Tagus Abyssal Plain at about 5000 m depth. Full details of materials and methods for grain size analysis are presented in de Stigter and others (2011) and the results of modal grain size distribution are summarized in Table 1. Steep slopes are only found at the intersection with the Setúbal Canyon, which incises the shelf in an E–W orientation. The slope is influenced by seasonally changing hydrodynamics as a result of the wind-driven upwelling system occurring along the western coasts of the Iberian Peninsula and Africa down to 15°N (Wooster and others, 1976). Conditions favorable for upwelling off Cape Sines occur between May and September as a result of strong and steady northerly winds and southward surface currents (Fiúza, 1984; Sousa and Bricaud, 1992; Huthnance and others, 2002).

The water column in this area comprises several water masses (García and others, 2003). Below the seasonally varying thermocline (30–600 m depth), the Eastern North Atlantic Central Water mass (ENACW) can be distinguished by its warm (12–16°C) and salty (≤36) properties (Fig. 2). Mediterranean Outflow Water (MOW) occurs between 600–1600 m and displays a strong salinity peak at 1100 m (>36). Two midwater maxima in temperature and salinity indicate the presence of two components of Mediterranean Water. The Northeast Atlantic Deep Water (NEADW), characterized by a lower temperature (2–10°C) and salinity (~35), forms the main water mass below the MOW. Finally, below ~4000 m is the Lower Deep Water (LDW) of Antarctic origin (Van Aken, 2000), recognizable by its cold (~2°C) and low-saline (<35) properties (Fig. 2).

Station no.	Latitude	Longitude	Depth (m)	Temperature (˚C)	Salinity (psu)	Water mass	Mode (μm)
58	37˚50.00'N	9˚04.99'W	282	12.8	35.8	ENACW	168.9
57	37˚49.80'N	9˚14.95'W	490	11.7	35.8	ENACW	66.4
56	37˚49.99'N	9˚28.48'W	1002	11.7	36.4	MOW	4.9
55	37˚50.00'N	9˚35.00'W	1374	10.7	36.3	MOW	4.9
53	37˚49.98'N	9˚54.97'W	2475	3.2	35.0	NEADW	4.9
52	37˚50.00'N	10˚05.00'W	2908	2.6	35.0	NEADW	5.4
51	37˚50.01'N	10˚30.00'W	3908	2.1	34.9	NEADW	4.9
50	37˚50.01'N	10˚59.99'W	4987	2.1	34.9	LDW	5.4

Table 1. Water depth, geographical position, temperature (°C), salinity, water mass, and modal sediment size of the eight stations analyzed in this chapter.

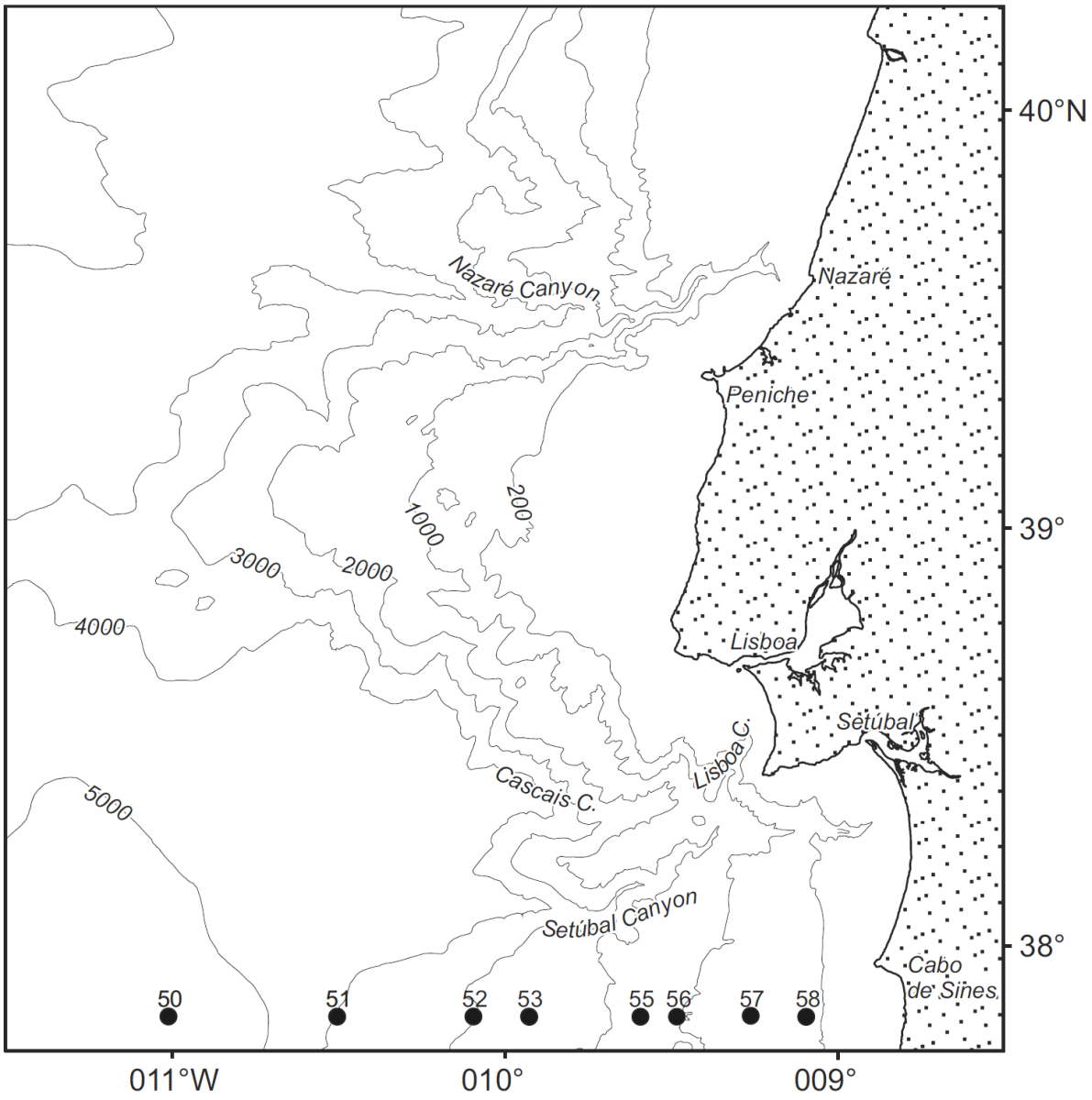

Figure 1. Map of the Cape Sines continental slope transect. All stations, sampled in September 2006, are marked in black circles.

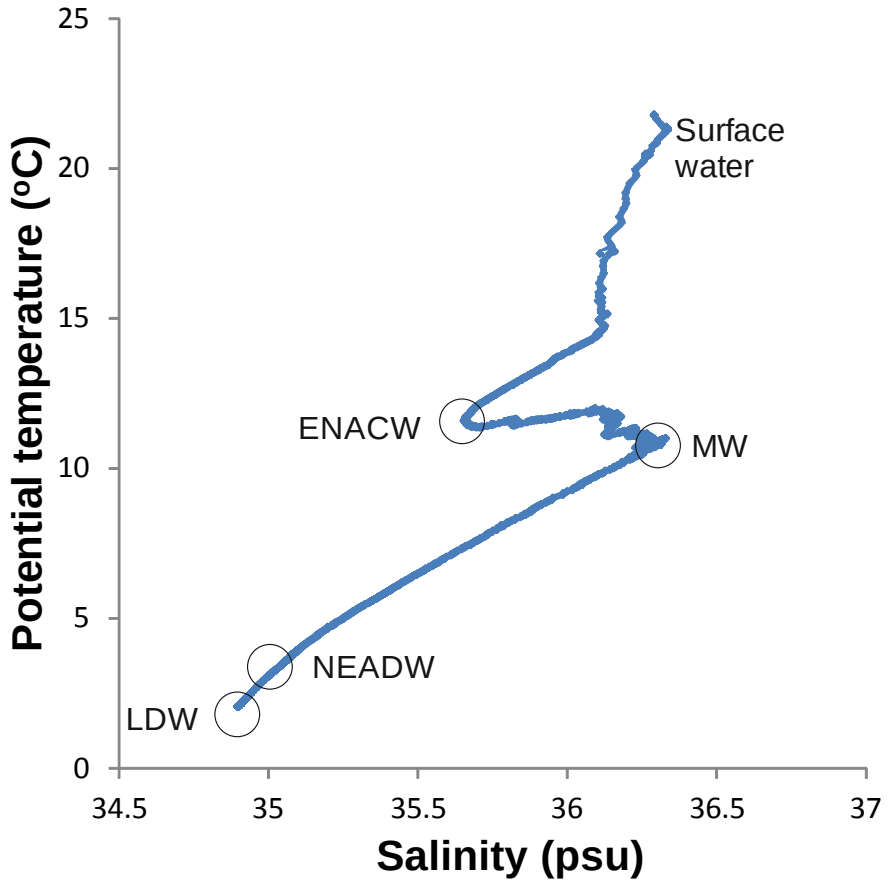

Figure 2. Potential temperature-salinity diagram constructed from CTD measurements along the Cape Sines transect. Temperature and salinity measurements for the Mediterranean Water (MW) at Gibraltar, North East Atlantic Deep Water (NEADW) and Lower Deep Water (LDW) at the western Iberian margin according to Van Aken (2000).

2.3.2 Sample Preparation and Processing of Foraminifera

During Cruise 64PE252 of RV Pelagia, cores with a diameter of 6 cm and consisting of undisturbed sediment surfaces were collected using a MUC multicorer in September 2006. At each sampling site (Table 1, Fig. 1), a single corer was sliced at 0.5 cm intervals from 0–2

cm depth, and 1 cm intervals from 2–10 cm depth. All slices were subsequently stored in a solution of rose Bengal in 96% ethanol until further treatment in the laboratory. These samples were gently shaken for several minutes to disaggregate the sediment and ensure staining of all live foraminifera. In the laboratory, each sediment layer was carefully washed with tap water through sieves with 63 and 150 μm meshes, and residues were subsequently stored in 96% ethanol.

Stained foraminifera from both the 63–150 and >150 μm fractions were sorted from wet samples and placed onto Chapman slides. The decision whether or not a stained specimen was alive at the time of collection remains slightly subjective, particularly as the protoplasm of dead foraminifera may be relatively well-preserved under anoxic conditions deeper in the sediment (Corliss and Emerson, 1990). As a result, a strict staining criterion was applied, where only specimens that were stained brightly pink in all chambers except the last one were counted as alive; the staining of doubtful foraminifera from deeper in the sediment was compared with stained individuals of the same species from more superficial levels. When the interior of a specimen was not visible, opaque agglutinated and miliolid tests were broken in order to confirm if there was stained material inside. Another difficulty concerns the counting of fragmentary tests, particularly in the case of arborescent forms, such as the large tubular species of the genus *Rhizammina*. We decided to inventory only stained protochambers, which were considered to represent a single individual; all other fragments were counted separately and not included in the faunal description. Soft-walled monothalamous taxa were also excluded from this study. The total densities of the live foraminiferal fauna, expressed as the number of live foraminifera found in and below a 28 cm^2 surface area (and standardized to 50 cm^2), were determined by integrating the numbers of live individuals picked from all levels sampled in the upper 10 cm of the core. Descriptions of foraminiferal microhabitats are not included in this study due to the large size

of the dataset. We calculated species richness (S), which is a count of living foraminiferal species for each station, and Fisher's α index (Fisher and others, 1943), a diversity index defined implicitly by the formula:

$$S = \alpha * 1n(1 + n / \alpha)$$

where, *S* is number of taxa, *n* is number of individuals and α is the index value.

Picking and identifying foraminiferal species in finer size fractions (<150 µm) is extremely time-consuming; hence; no replicate samples were studied at any of the eight stations.

2.3.3 PHYTOPIGMENT CONTENTS

Chlorophyll-a and phaeopigment analyses were carried out according to Lorenzen and Jeffrey (1980). Pigments were extracted (12 h at 4°C in the dark) from triplicate sediment core samples (about 1 g) at 0–1, 1–3, 3–5, and 5–10 cm intervals, obtained from independent deployments of the multicorer, using 3–5 ml of 90% acetone as the extractant. Extracts were analyzed fluorometrically to estimate chlorophyll-a, and, after acidification with 200 µl 0.1N HCl, to estimate phaeopigments. We avoided the use of fluorometric chlorophyll-a estimates as the unique tracer of organic C associated with algal material and instead summed the values of chlorophyll-a and phaeopigment concentrations (i.e., total phytopigments).

Concentrations of total phytopigments, once converted into C equivalents using 40 as a conversion factor (Pusceddu and others, 1999), are reported in μg g^{-1} DW.

2.3.4 Quantity and Biochemical Composition of Sediment Organic Matter

Protein, carbohydrate, and lipid sediment contents were analyzed spectrophotometrically in accordance with Pusceddu and others (2004) and their concentrations were expressed as bovine serum albumin, glucose, and tripalmitine equivalents, respectively. For each biochemical assay, blanks were obtained using pre-combusted sediments (450°C for 4 h). For all stations, the analyses were performed on triplicate sediment core samples (~0.5 g) at 0–1, 1–3, 3–5, and 5–10 cm intervals, obtained from independent deployments of a multiple or box corer. Carbohydrate, protein and lipid sediment contents were converted into carbon equivalents using the conversion factors of 0.40, 0.49, and 0.75 mg C mg^{-1}, respectively, and their sum defined as the biopolymeric organic carbon (Fabiano and others, 1995).

2.4 RESULTS

2.4.1 ORGANIC MATTER COMPONENTS

All components have maximum values at the shallowest station for which we have data (1002 m) and generally decrease with increasing depth (Fig. 3). However, total phytopigment and protein contents have slightly raised values at the deepest station (6.9±2.2 μg g^{-1} and 1.0±0.1 mg g^{-1} at 4987 m respectively) in comparison to our 3908 m station (2.8±0.6 μg g^{-1} and 0.9±0.3 mg g^{-1} respectively). Conversely, carbohydrates, lipids, and biopolymeric carbon all have minimal values at our deepest station (1.0±0.4, 0.2±0.03, and 1.1±0.2 mg g^{-1} respectively). Total phytopigment contents show clear decreases towards deeper intervals in each of the four cores. However, all other measures of organic matter show rather stable values downcore, or even slight increases (Fig. 3).

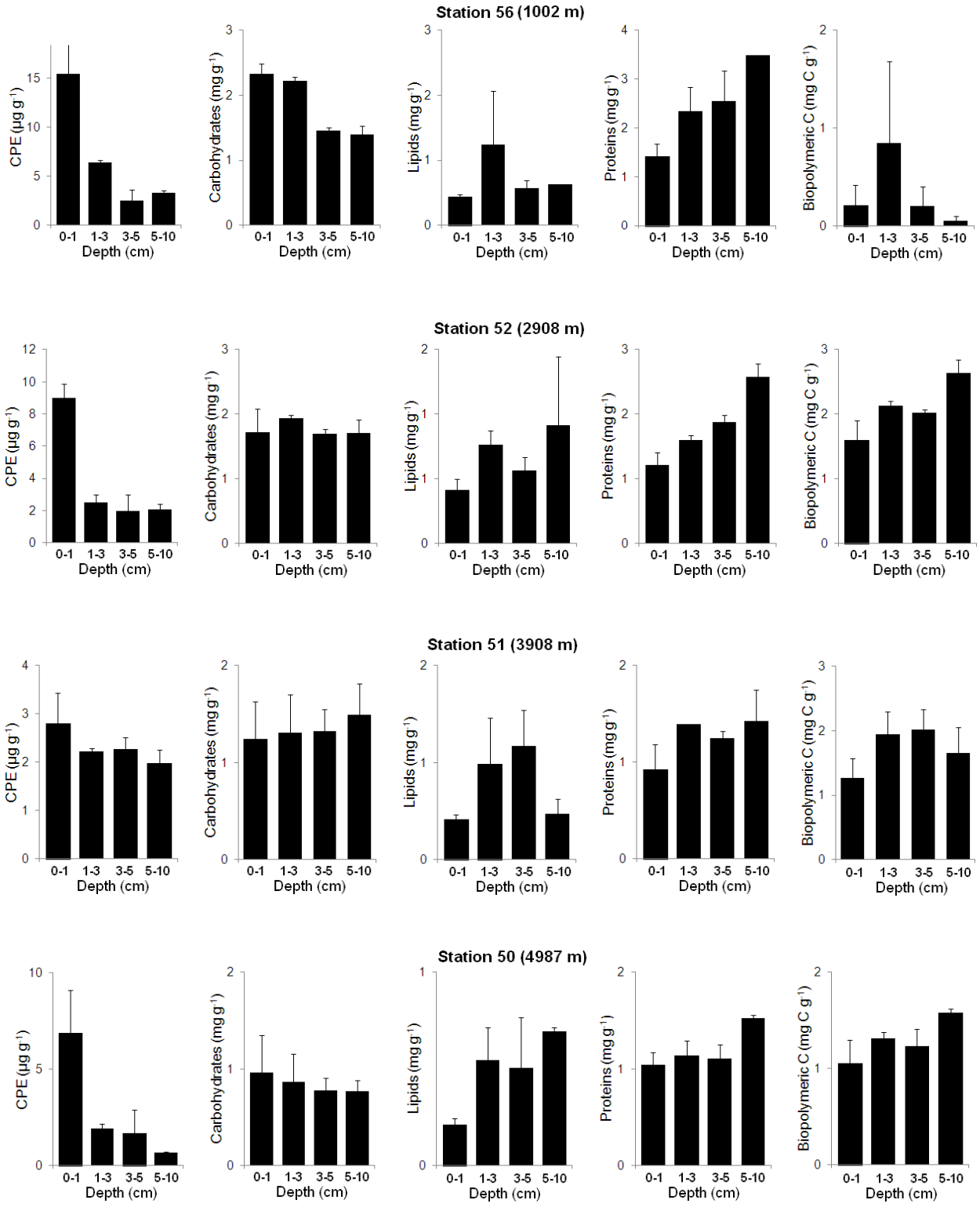

Figure 3. Components of organic carbon measured at 0–1, 1–3, 3–5, and 5–10 cm intervals downcore for four stations in this study.

2.4.2 TOTAL FORAMINIFERAL DENSITIES

There was a general decrease in foraminiferal densities with increasing water depth for both the >150 µm and 63–150 µm fractions (Fig. 4). For the >150 µm fraction, our shallowest station at 282 m presented a maximum density of ~1200 specimens/50 cm^2. Towards ~1000 m water depth, density drops to ~200 specimens/50 cm^2. Standing stocks then increased slightly to ~300 specimens/50 cm^2 at 2475 m, then decreased until a minimum value of <80 individuals/50 cm^2 at 3908 m. For all stations, densities of the 63–150 µm fraction were more than two times higher than those of the >150 µm fraction. The depth pattern mimics that of the >150 µm fraction: the highest densities were recorded at 282 m and 490 m with ~2400 live individuals per 50 cm^2, whereas our deepest stations at 4987 and 3908 m were much poorer with ~740 and ~580 live specimens per 50 cm^2, respectively. The relative importance of the 63–150 µm fraction (with respect to the >150 µm fraction) increased with water depth, from 67% at 282 m to as much as 88% at 3908 m. (Fig. 4).

2.4.3 SPECIES DIVERSITY

Species richness varies considerably between the stations, for both size fractions (Fig 5). In the >150 µm fraction the highest species numbers were found at the shallowest stations (79 at 282 m and 74 at 490 m). The deepest stations at 3908 and 4987 m have the lowest numbers of species (27 and 28 respectively). At 1002 m, species richness is also comparatively low (31 species). Generally, the species number shows the same trends as the foraminiferal density; apart from the minimum at 1002 m, there is a decrease in species

richness with increasing depth. Surprisingly, Fisher's α values for the >150 µm fraction show a different pattern (Fig. 5): after a sudden fall from 27 at 490 m to 14 at 1002 m, there is a subsequent rise on the middle to lower slope with a maximum value of 31 at 3908 m. This is followed by a steep drop to a minimum value of 13 at 4987 m (Fig. 5).

In the 63–150 µm fraction, changes in species richness with depth basically mirror those of the >150 µm fraction by clearly decreasing with greater water depth. However, at all stations species richness is much higher in the 63–150 µm fraction than in the >150 µm fraction. Highest species richness is found at 282 m (115 species), whereas our deepest stations at 3908 and 4987 m have the lowest species richness with 53 and 54 species respectively. Unlike the >150 µm fraction, Fisher's α values for the 63–150 µm fraction show an overall decrease with water depth.

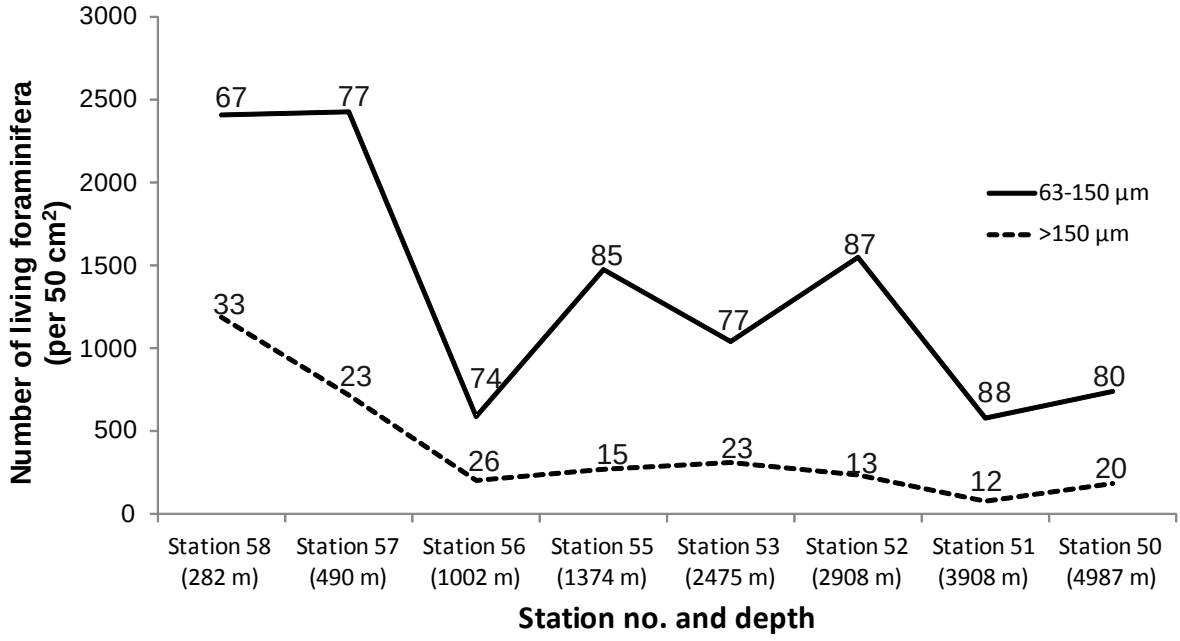

Figure 4. Density of foraminiferal faunas (total number of stained foraminifera per 50 cm^2) for >150 µm and 63–150 µm fractions along the bathymetrical transect. Percentage relative abundances of the total fauna (>63 µm) are provided for each data point.

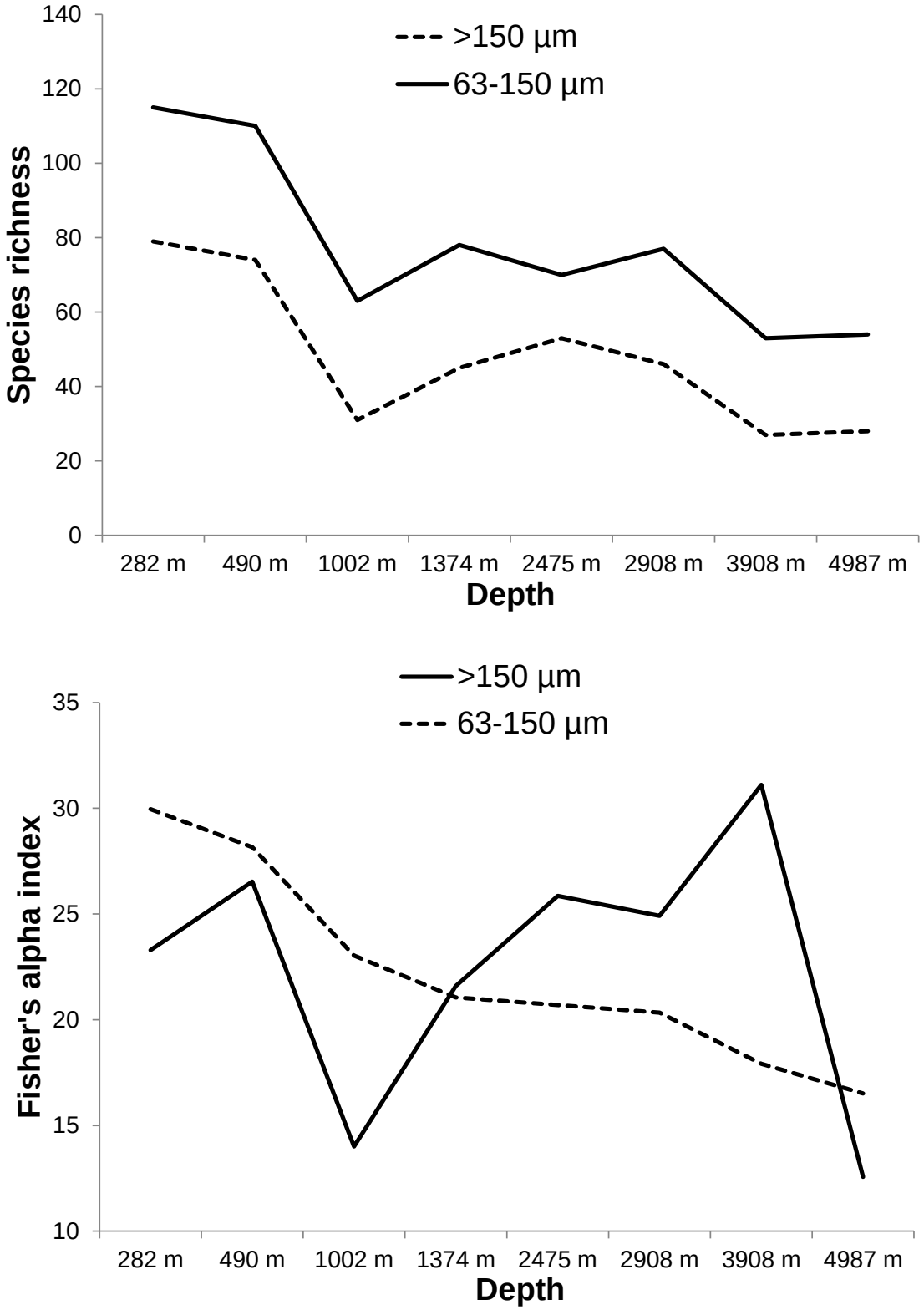

Figure 5. Species richness and Fisher's α index values of foraminiferal assemblages for >150 µm and 63–150 µm fractions along the bathymetrical transect.

2.4.4 BATHYMETRICAL TRENDS OF MAIN FORAMINIFERAL GROUPS

The foraminiferal assemblages comprise a mixture of perforate, porcellaneous and agglutinated forms, with the relative proportions changing with water depth (Fig. 6). In the >150 μm fraction, perforate and agglutinated foraminifera form the main component of the assemblage, with a more-or-less equal contribution at 282 and 490 m. Slightly deeper, at 1002 m, perforate foraminifera dominate the assemblage (68%). At much deeper stations, there is a strong increase in the relative abundance of agglutinated foraminifera (91% at 4987 m), and a corresponding decrease in perforate foraminifera (6% at 4987 m). Porcelaneous foraminifera are rare at all stations (≤6%) with the exception at 3908 m, where they account for 12% of the assemblage. The 63–150 μm fraction shows a rather similar pattern. From 282 –1374 m water depth, there is an increase in perforate species (~53% to ~66%) at the expense of the agglutinated taxa (~44% to 33%). Below 1374 m, perforate foraminifera decrease to ~21% of the total fauna at 4987 m, where agglutinates make up ~77% of the total assemblage. Similarly to the >150 μm fraction, porcelaneous foraminifera are rare, always accounting for <4%. Although the two size fractions show similar trends, it should be noted that at deeper stations, perforate foraminifera have a much higher relative abundance in the 63–150 μm than in the >150 μm fraction.

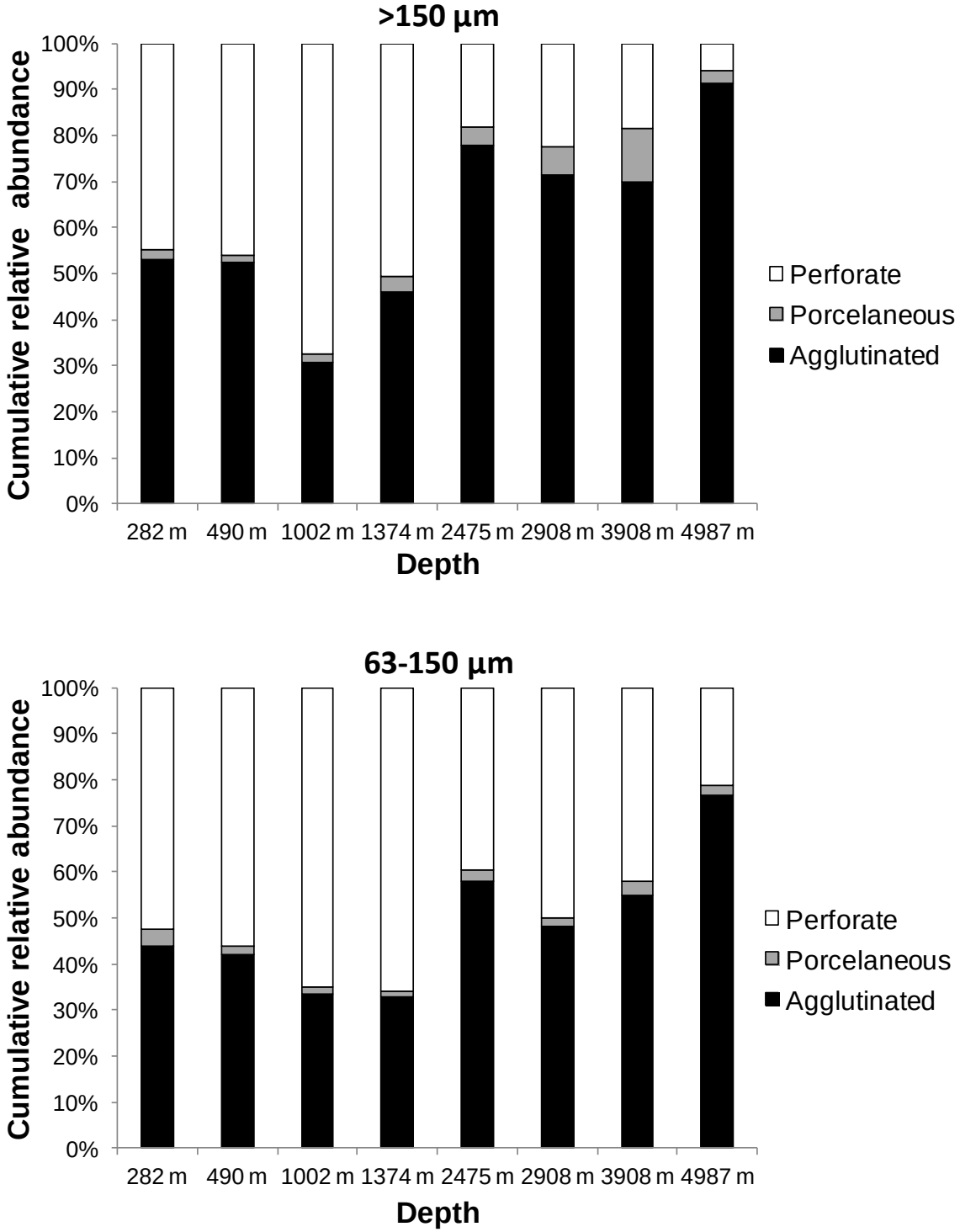

Figure 6. Relative percentage abundances of perforate, porcellaneous and agglutinated foraminiferal groups for both >150 µm and 63–150 µm fractions along the bathymetrical transect.

2.4.5 FAUNAL COMPOSITION

In both size fractions, the presence/absence as well as relative abundances of the dominant species show some remarkable patterns along the transect. Appendix 1 is the taxonomic list of species; Figures 7 and 8 show some common agglutinated and calcareous species, respectively.

>150 μm Fraction

Figure 9 presents the percentages of all species that are >5% of the >150 μm fraction from at least one station; it also suggests the presence of two main faunal boundaries, between stations 56 and 55 (between 1002–1374 m) and stations 53 and 52 (2475–2908 m depth). At 1002 m and shallower, *Uvigerina mediterranea* is a dominant species. Between 1374 and 2475 m, faunas are dominated by *Globobulimina affinis*, *Thurammina papillata*, and *Uvigerina peregrina*. At 2908 m and deeper, *Recurvoides* sp. 1, *Reophax fusiformis, Cibicides kullenbergi*, and *Epistominella exigua* are prominent.

At our shallowest station (282 m), the >150-μm faunas are dominated by *Reophax helenae* (~12%), which is accompanied by *Melonis barleeanus, Bigenerina nodosaria*, and *Uvigerina elongatastriata*, each accounting for ~8%, while *U. mediterranea, Textularia sagittula*, and *Buzasina ringens* each represent ~6% of the fauna. At 490 m, *U. mediterranea* increases to 27%, whereas *U. elongatastriata, M. barleeanus*, and the agglutinated species have much lower percentages (*B. nodosaria*, *T. sagittula*) or are even absent (*R. helenae, B. ringens*); other agglutinated species, such as *Reophax spiculifer, Psammosphaera fusca*, and *Ammodiscus anguillae*, show increased frequencies (5–7% each). At 1002 m, *U. mediterranea* (25%) remains strongly dominant and *Nuttallides convexus* (8%) appears. In

the agglutinated assemblage, the previously dominant species (*R. spiculifer*, *P. fusca*, and *A. anguillae*) are much less abundant, and *Cyclammina trullissata* dominates (18%).

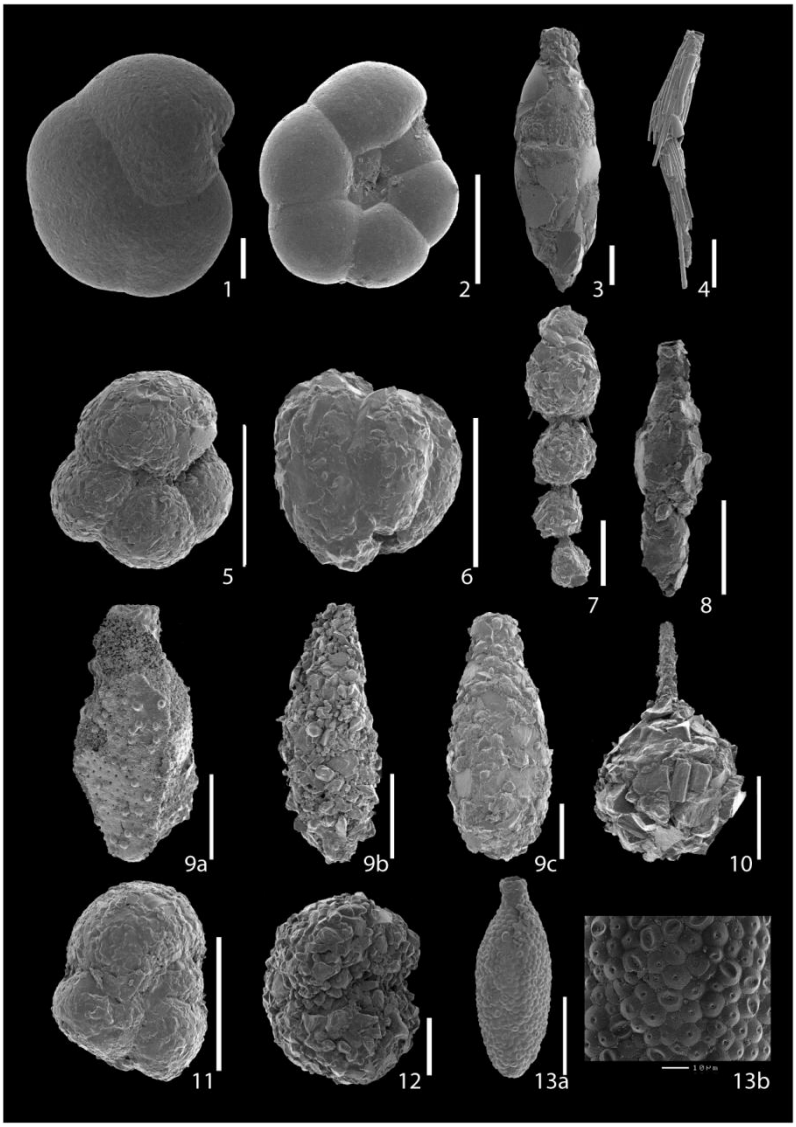

Figure 7. Some agglutinated foraminifera observed from both size fractions in this study. Scale bar = 100 µm unless stated otherwise. 1 Buzasina ringens, station 58, 282 m (0.5–1 cm). 2 Cribrostomoides bradyi, station 58, 282 m (0–0.5 cm). 3 Reophax helenae, station 58, 282 m (0.5–1 cm). 4 Reophax spiculifer, station 57, 490 m (0–0.5 cm). 5 Ammoglobigerina globigeriniformis, station 57, 490 m (0–0.5 cm). 6 Adercotryma glomerata, station 55, 1374 m (0–0.5 cm). 7 Hormosinella guttifera, station 55, 1374 m (0–0.5 cm). 8 Reophax sp. 1, station 51, 3908 m (0–0.5 cm). 9 Reophax fusiformis: a,

calcareous morphotype, station 51, 3908 m (0–0.5 cm); b, rough-quartz morphotype, station 50, 4987 m (0–0.5 cm); c, smooth-quartz morphotype), station 50, 4987 m (0–0.5 cm). 10 Lagenammina tubulata, station 50, 4987 m (0–0.5 cm). 11 Haplophragmoides sphaeriloculum, station 50, 4987 m (0–0.5 cm). 12 Recurvoides sp. 1, station 50, 4987 m (0–0.5 cm). 13 Spirolocammina sp. 1, station 50, 4987 m (0–0.5 cm); b, close-up of coccolith wall texture made up of Calcidiscus quadripeforatus.

Between 1002 and 1374 m, there is a major faunal change. At 1374 m, *U. mediterranea* is virtually absent and *Globobulimina affinis* (19%), *Bulimina inflata* (13%), and *U. peregrina* (7%) dominate the calcareous assemblage. The previously dominant agglutinated species *C. trullissata* has strongly diminished, whereas *Thurammina papillata* accounts for 20% of the fauna. At 2475 m the perforate fauna is strongly diminished, and agglutinated species, such as *Karrerulina apicularis* (12%), *Repmanina charoides* (11%), and *Hormosina globulifera* (6%) dominate. *Uvigerina peregrina* (9%) is the most frequent perforate species.

At 2908 m, *Cibicides kullenbergi* (8%) is the dominant calcareous species. Among the agglutinants, *Recurvoides* sp. 1 (9%) *Cribrostomoides bradyi* (8%), and *Reophax fusiformis* (8%) dominate while *K. apicularis* has a lower percentage (5%), and *R. charoides* is absent. The standing stock at 3908 m is particularly poor and no species is represented by more than five individuals. The main species here include *R. fusiformis, Psammosphaera testacea, Epistominella exigua*, and *Pyrgo elongata*. The 4987 m station is dominated by agglutinated taxa. *Reophax fusiformis* (25%) is at its maximum relative abundance here. *Hormosina globulifera* (15%), after being absent at 3908 m, returns as a subdominant species. Other notable species include *Recurvoides* sp. 1 and *Thurammina papillata* (both 6%).

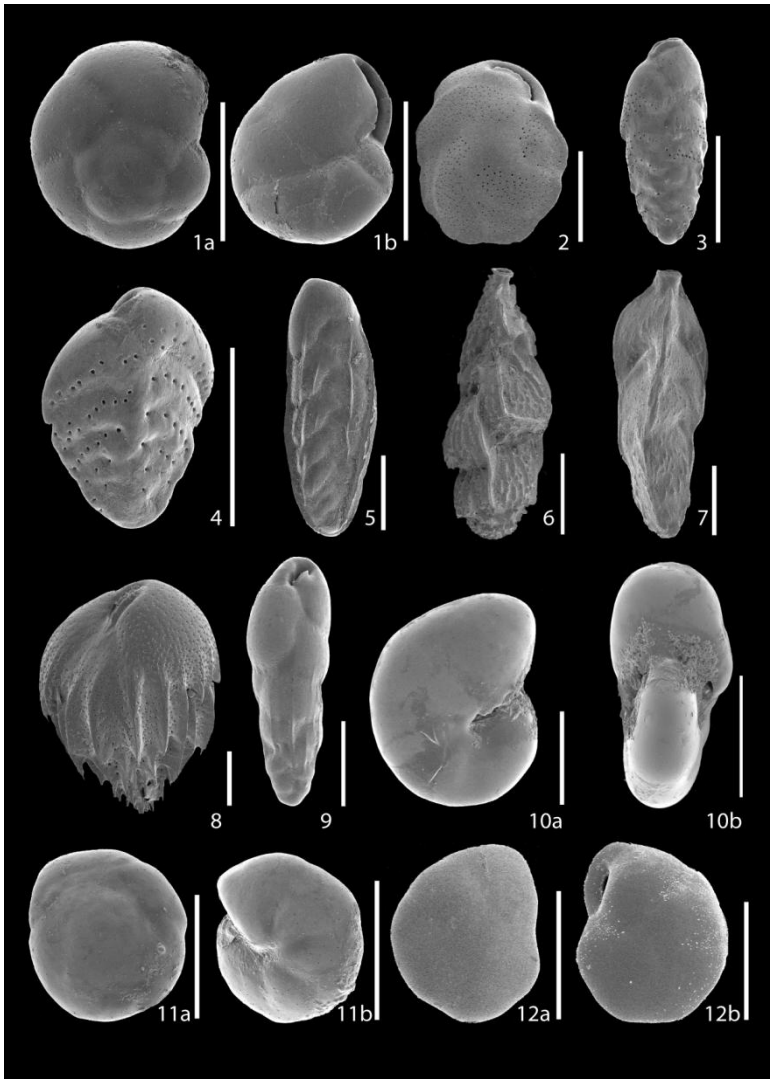

Figure 8. Common calcareous foraminifera found in this study. Scale bar = 100 µm. 1 Epistominella vitrea, station 58, 282 m (0–0.5 cm). 2 Cassidulina carinata, station 58, 282 m (0.5–1 cm). 3 Bolivina dilatata, station 58, 282 m (0.5–1 cm). 4 Bolivina robusta, station 58, 282 m (0-0.5 cm). 5 Bolivina tongi, station 58, 282 m (0–0.5 cm). 6 Trifauna pauperata, station 56, 1006 m (0–0.5 cm). 7 Trifauna bradyi, station 56, 1006 m (0–0.5 cm). 8 Bulimina inflata, station 55, 1374 m (0–0.5 cm). 9 Buliminia translucens, station 52, 2908 m (0–0.5 cm). 10 Pullenia salisburyi, station 50, 4987 m (1.5–2 cm). 11 Nuttallides pusillus, station 50, 4987 m (0–0.5 cm). 12 Epistominella exigua, station 50, 4987 m (0–0.5 cm).

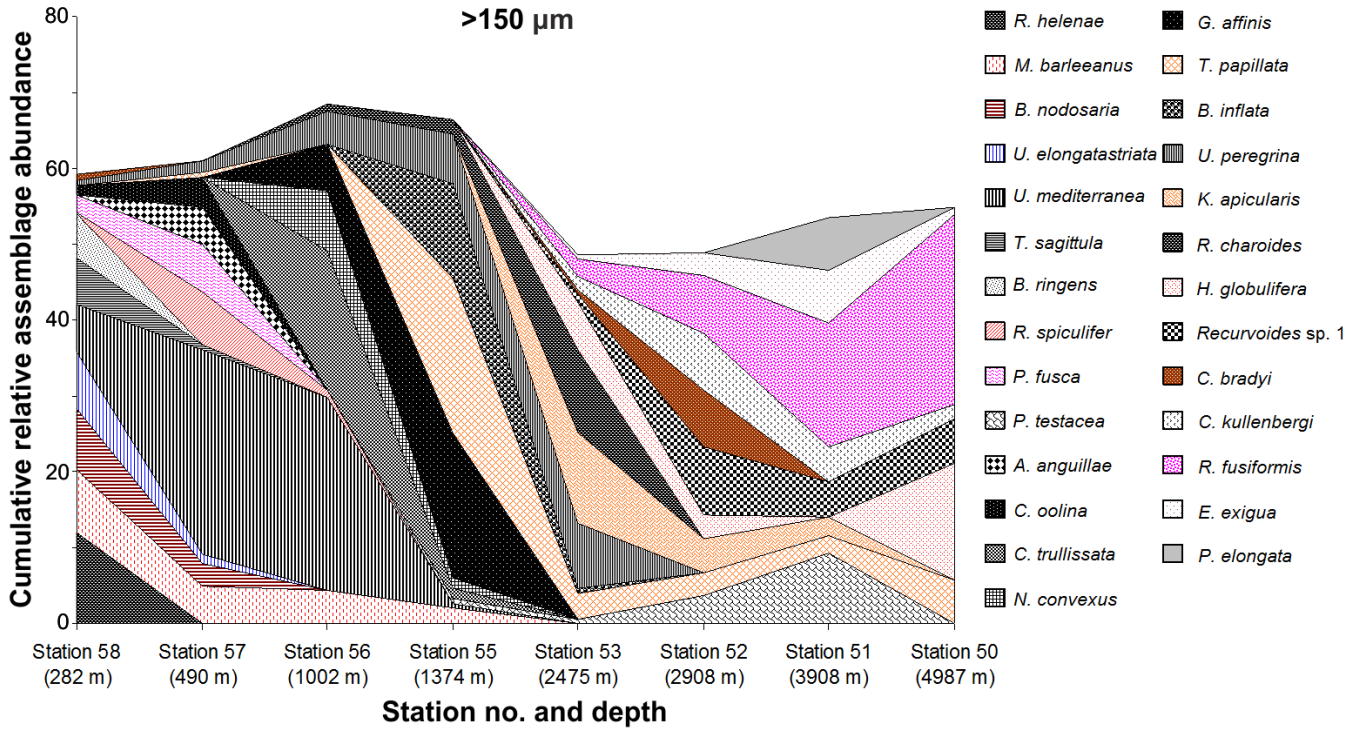

Figure 9. Composition of the live benthic live foraminiferal faunas (in % of the total faunas) of the >150 µm fraction. All species with a relative abundance >5% at any one station are presented.

63–150 µm Fraction

For the 63–150 µm fraction, all species that account for >5% in any of the stations are presented in Figure 10. It is important to note that many of the species that dominate this fraction are not also present in the >150 µm fraction, particularly most representatives of *Bolivina* and *Epistominella*. Faunal changes appear to be more gradual in the 63–150 µm fraction, although large faunal differences occur between stations 55 and 53 (1374–2475 m) and stations 53 and 52 (2475–2908 m). At 1374 m and shallower, *Trifarina bradyi* and *Melonis barleeanus* are conspicuous elements. The 2475 m station is dominated by *Repmanina charoides* and *Pullenia salisburyi*, whereas at 2908 m and deeper, *Reophax fusiformis* and *Nuttallides pusillus* are dominant elements.

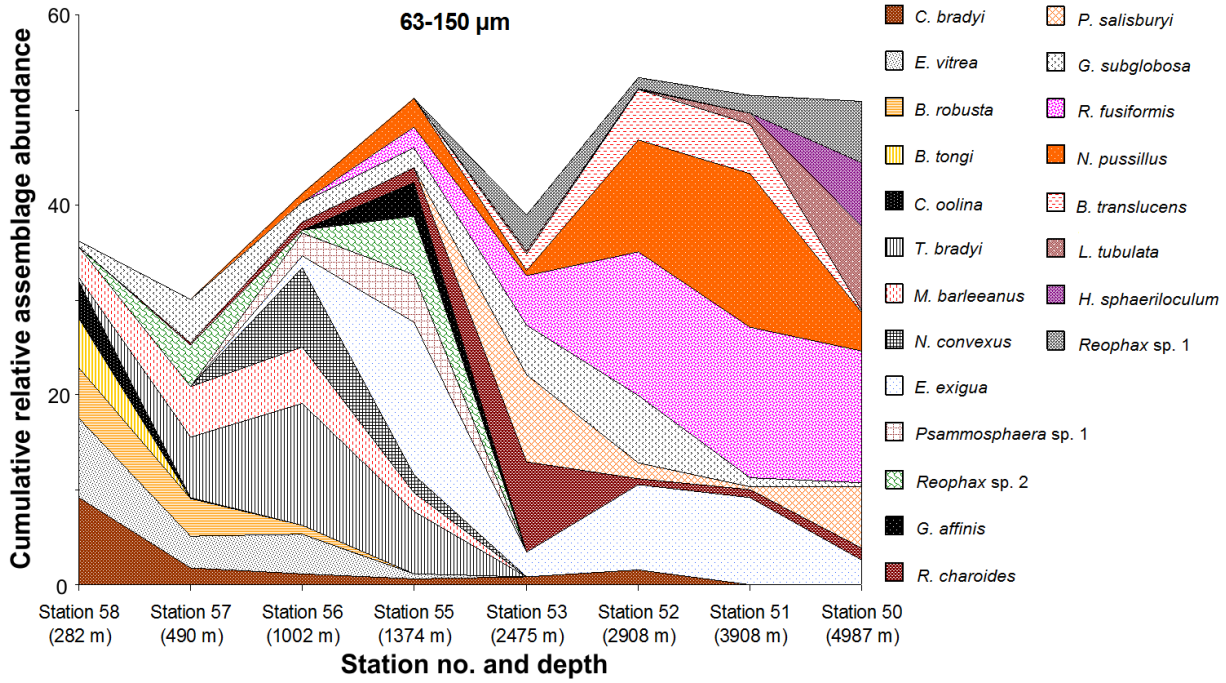

Figure 10. Composition of the live benthic live foraminiferal faunas (in % of the total faunas) of the 63–150 µm fraction. All species with a relative abundance >5% at any one station are presented.

The shallowest station at 282 m is dominated by *Cribrostomoides bradyi* (10%), followed by *Epistominella vitrea* (8%), *Bolivina robusta* (5%), and *B. tongi* (5%). At 490 m, the most abundant species are *Trifarina bradyi* (6%), *Melonis barleeanus* (5%), *Globocassidulina subglobosa* (5%), and *B. robusta* (4%). Several *Reophax* species together account for 14% of the assemblage. At 1002 m, there is a higher percentage of *T. bradyi* (13%), *Nuttallides convexus* (8%) appears, and the relative abundance of *M. barleeanus* (6%) also increases, whereas bolivinids are no longer present. At 1374 m, *Epistominella exigua* (16%) replaces *E. vitrea* as the dominant *Epistominella* species. In addition, two agglutinated species that construct their tests with calcareous particles, *Psammosphaera* sp. 1 and *Reophax*

sp. 2, each account for 6% and 5% respectively. *T. bradyi* (7%) remains a key component of the assemblage.

At 2475 m, *Trifarina* species are no longer present, and *E. exigua* (3%) has decreased significantly. Instead, there is an increase in *G. subglobosa* (5%) and juveniles of *Repmanina charoides* (10%) and *Pullenia salisburyi* (9%) are dominant elements.

The 2908 m station is dominated by *Reophax fusiformis* (15%). Also *Nuttallides pusillus* (12%), *Epistominella exigua* (9%), *Globocassidulina subglobosa* (7%), and *Bulimina translucens* (5%) show increased percentages. The fauna at 3908 m continues to be dominated by *N. pusillus* (16%), *R. fusiformis* (16%), *E. exigua* (9%), and *B. translucens* (5%). Conversely, *Pullenia salisburyi* and *G. subglobosa* are almost absent at this station. At our deepest station (4987 m), *E. exigua*, *N. pusillus*, and *Bulimina translucens* all fall below 5%. Instead, agglutinated taxa such as *R. fusiformis* (14%), *Lagenammina tubulata* (9%), *Haplophragmoides sphaeriloculum* (7%), and *Reophax* sp. 1 (7%) dominate. *Pullenia salisburyi* (7%)is the only calcareous species >5% at this station.

2.5 DISCUSSION

2.5.1 DENSITY AND DIVERSITY

It is generally accepted that foraminiferal standing stocks vary as a function of the amount of labile organic carbon arriving at the sea floor (e.g., Thiel, 1983; Berger and Diester Haas, 1988; Altenbach and Sarnthein, 1989; Koho and others, 2008; Mojtahid and others, 2010). Some species specialize on particular foods, such as diatoms, bacteria, or specific components of phytodetritus (e.g., Bertram and Cowen, 1999; Moodley and others, 2000; Suhr and others, 2003; Suhr and Pond 2006; Nomaki and others, 2006). Our samples from the shallowest stations at 282 and 490 m contain around five times more stained foraminifera than those of the deeper stations at 3908 and 4987 m. This general decrease of faunal density with increasing water depth corresponds to the expected decreasing flux of labile organic matter, as underlined by total phytopigment contents (Fig. 3). When we compare the faunal densities with total phytopigment contents of surface and deeper sediment levels (Fig. 11), it appears that the calcareous fauna of the >150 µm fraction strongly correlates with total phytopigment content (r = 0.96, p < 0.001), while this correlation is much weaker for the calcareous fauna of the 63–150 µm fraction (r = 0.069, p = 0.0023). Agglutinated taxa from both size fractions show no significant correlation with total phytopigment content (r <0.4, p >0.05). In other continental shelf to abyssal plain transects, agglutinated foraminifera replace calcareous ones as the dominant foraminiferal group at deep-sea sites (e.g., Cornelius and Gooday, 2004; Koho and others, 2008). This is usually attributed to increasingly oligotrophic conditions. Consequently, it has been suggested that agglutinated foraminifera are generally less dependent upon labile organic matter availability, in particular the total phytopigment

content of the sediment, than calcareous forms (Koho and others, 2008); an observation that is repeated in our study. Our study found no relation between foraminiferal standing stocks and the contents of other organic compounds. Species richness shows a pattern similar to standing stocks: by far the highest numbers of species found in both fractions are 138 at 282 m on the outer shelf and 139 at 490 m on the upper slope, while stations at 3908 and 4987 m have only half as many species (66 and 70 respectively). It appears therefore that both foraminiferal standing stocks and species richness are directly related to the phytopigment component of the labile organic matter analyzed in this study. The comparatively poor total fauna at 1002 m is surprising in view of the high total phytopigment content at this site. Two other studies of Portuguese margin open-slope sites from similar water depths (Griveaud and others, 2010; Nardelli and others, 2010) show comparably low densities. However, Griveaud (2010) showed very high spatial patchiness at a site 980 m deep at 37°31'N, 9°45'W. It is evident that single time samplings without replicates may yield unrepresentative densities in a context of important spatial and temporal faunal variability.

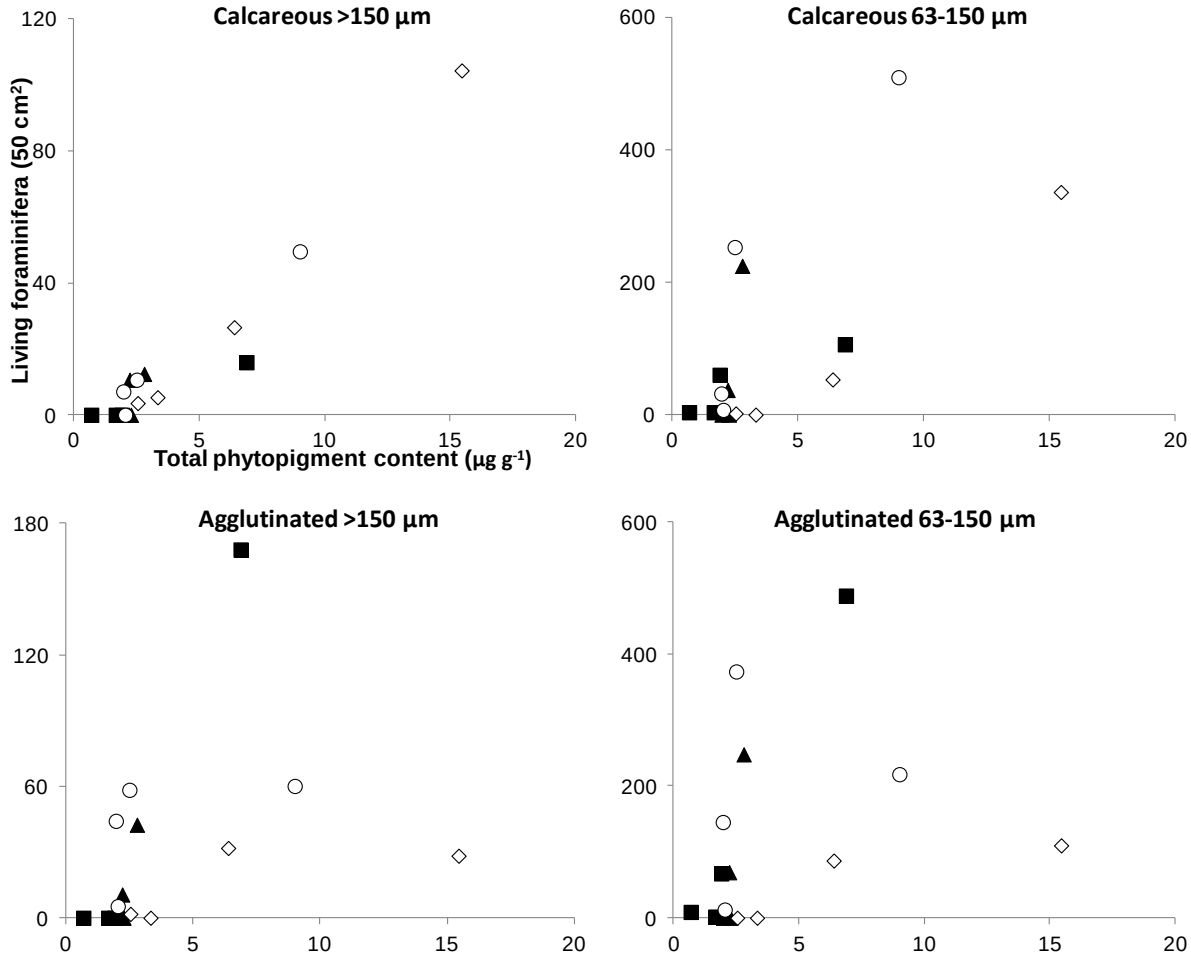

Figure 11. Density of living (Rose Bengal stained) calcareous and agglutinated foraminifera of both >150 µm and 63–150 µm fractions from four stations relative to total phytopigment contents from their relative sediment levels. Filled squares and triangles, and unfilled circles and diamonds represent samples from 4987 m, 3908 m, 2908 m and 1002 m respectively. Calcareous foraminifera >150 µm: r = 0.96, p = 0.00001; Calcareous foraminifera 63–150 µm: r = 0.69, p = 0.002; Agglutinated foraminifera >150 µm: r = 0.38, p = 0.070; Agglutinated foraminifera 63–150 µm: r = 0.31, p = 0.120.

2.5.2 CHANGES IN TEST SIZE WITH WATER DEPTH

The increase of the relative proportion of the 63–150 µm fraction with increasing water depth (Fig. 4) suggests that foraminiferal species with a small test size may be favored at greater water depth, where there is less organic matter available. A recent study by Geslin and others (2011) confirmed a strong positive relationship between estimated biovolume (test size) and respiration rates in benthic foraminifera. The results of this study also suggest that compared to other benthic meiofaunal groups, foraminifera have lower metabolic rates. Nevertheless, smaller life forms such as prokaryotes and protists (including foraminifera) contribute to 70% of the total benthic carbon respiration in lower-slope and abyssal environments, whereas their contribution is much less (~23%) on the upper slope and shelf (Heip and others, 2001). We suggest that this pattern can be explained by the fact that foraminifera with greater biovolumes necessarily have more elevated trophic requirements (even if their metabolic rates would be lower, as is suggested by Giere, 2009), and consequently cannot survive below critical threshold values of C_{org} availability. Therefore, we think the observed trend towards smaller benthic foraminifera at greater water depth may be an adaptation to food-limited environments in the deep sea. Additionally when we consider calcareous and agglutinated foraminifera groups separately (Fig. 12), with increasing water depth calcareous foraminifera become more strongly concentrated in the 63–150 µm fraction (r = 0.83, p = 0.006) than agglutinated ones (r = 0.60, p = 0.05). This suggests that calcareous species are more impacted by increasingly oligotrophic conditions and show a stronger response by having smaller test sizes overall when compared to agglutinated species. The greater importance of smaller organisms relative-to larger ones with increasing water depth is documented as a general phenomenon of the deep sea and commonly attributed to declining food resources (e.g., Thiel, 1975; Rex and others, 2006);

our study suggests this also applies to foraminifera when studied as an individual group. However, trophic resources may not influence all meiofaunal groups in the same way, such as in the case of nematode faunas that have overall reduced body size in organically enriched deep-sea sites (Danovaro and others, 2002).

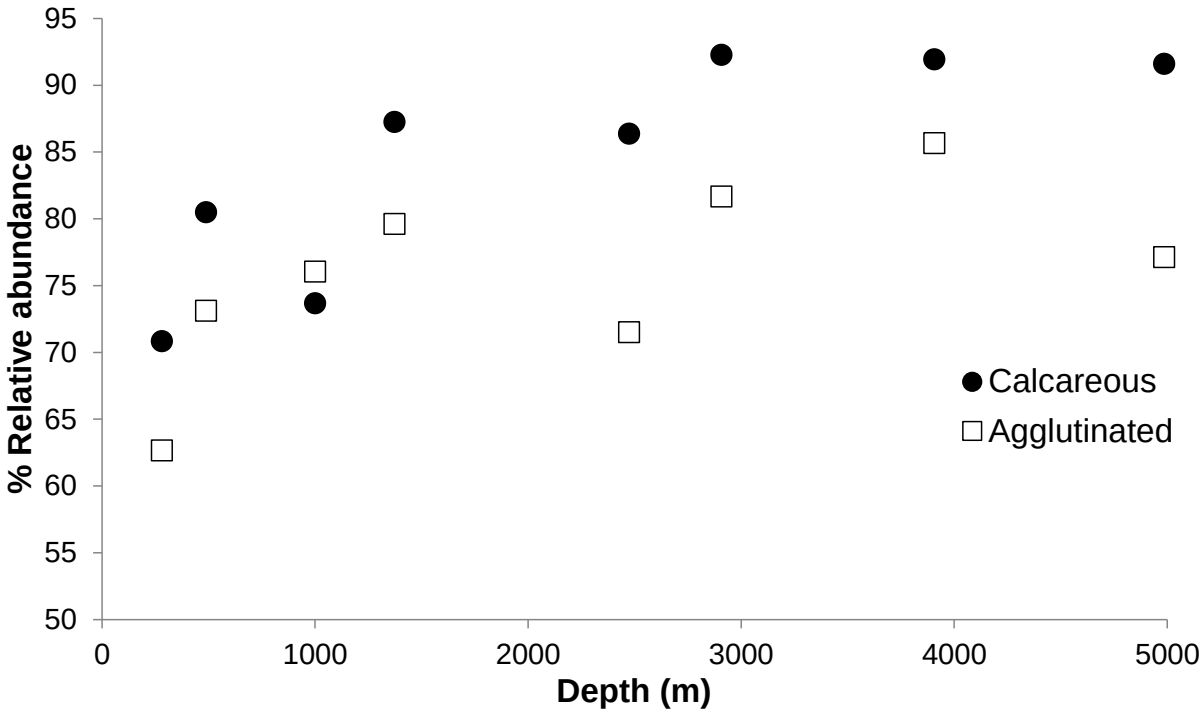

Figure 12. Percentage relative proportion of the 63–150 µm fraction (versus total faunas, 63–150 plus >150 fractions) for calcareous and agglutinated foraminifera. Calcareous fauna: r = 0.83, p = 0.0006; Agglutinated fauna: r = 0.60, p = 0.05.

2.5.3 FAUNAL TRENDS WITH DEPTH

During the 1970s, bathymetric distributions of benthic foraminifera were thought to mainly reflect the water mass characteristics (e.g., Pujos-Lamy, 1973; Streeter, 1973; Schnitker, 1974; Streeter and Shackleton, 1979). More recent studies tend to discredit this concept (e.g., Mackensen and others, 1990; Schmiedl and others, 1997; Jorissen and others, 2007; Koho and others, 2008; Mojtahid and others, 2010), mainly because important water mass boundaries do not systematically coincide with the boundaries of the main faunal components. Also in our data, species occurrences do not seem to be related to water masses. In fact, none of the dominant species appear to be restricted to a single water mass, and also our main faunal changes (between 1000–1300 m and between 2500–2900 m, respectively) do not coincide with water mass boundaries. Several authors have suggested that many foraminiferal species have critical thresholds of organic flux, which delimit the range in which they are most competitive. Therefore, at present, organic flux is generally supposed to be the main factor responsible for bathymetrical species successions (e.g., Altenbach and others, 1999, 2003; de Rijk and others, 2000; Fontanier and others, 2002; Morigi and others, 2001; Eberwein and Mackensen 2006; Koho and others, 2008; Mojtahid and others, 2010). On the continental slope, with increasing water depth, the majority of "eutrophic" species disappear and the assemblages become progressively dominated by other species more adapted to mesotrophic or oligotrophic conditions. In Figures 13 and 14, we plotted the depth distribution of the main (≥5%) species encountered along our bathymetrical transect in the >150 µm and 63–150 µm fractions respectively, together with total phytopigment sediment contents measured at four of our stations. The changes in species composition of the foraminiferal are consistent with a general decrease in organic fluxes from the outer continental shelf to the abyssal plain on the Portuguese margin. We observe high densities of

species that have previously been considered typical of eutrophic conditions at our shallower stations, which gradually disappear with increasing depth and decreasing trophic level. In turn, species better adapted to lower trophic levels appear. On the basis of the information summarized in these figures, we can separate our stations, as well as the dominant species at these stations, into three categories: eutrophic, mesotrophic, and oligotrophic (Figs. 13, 14).

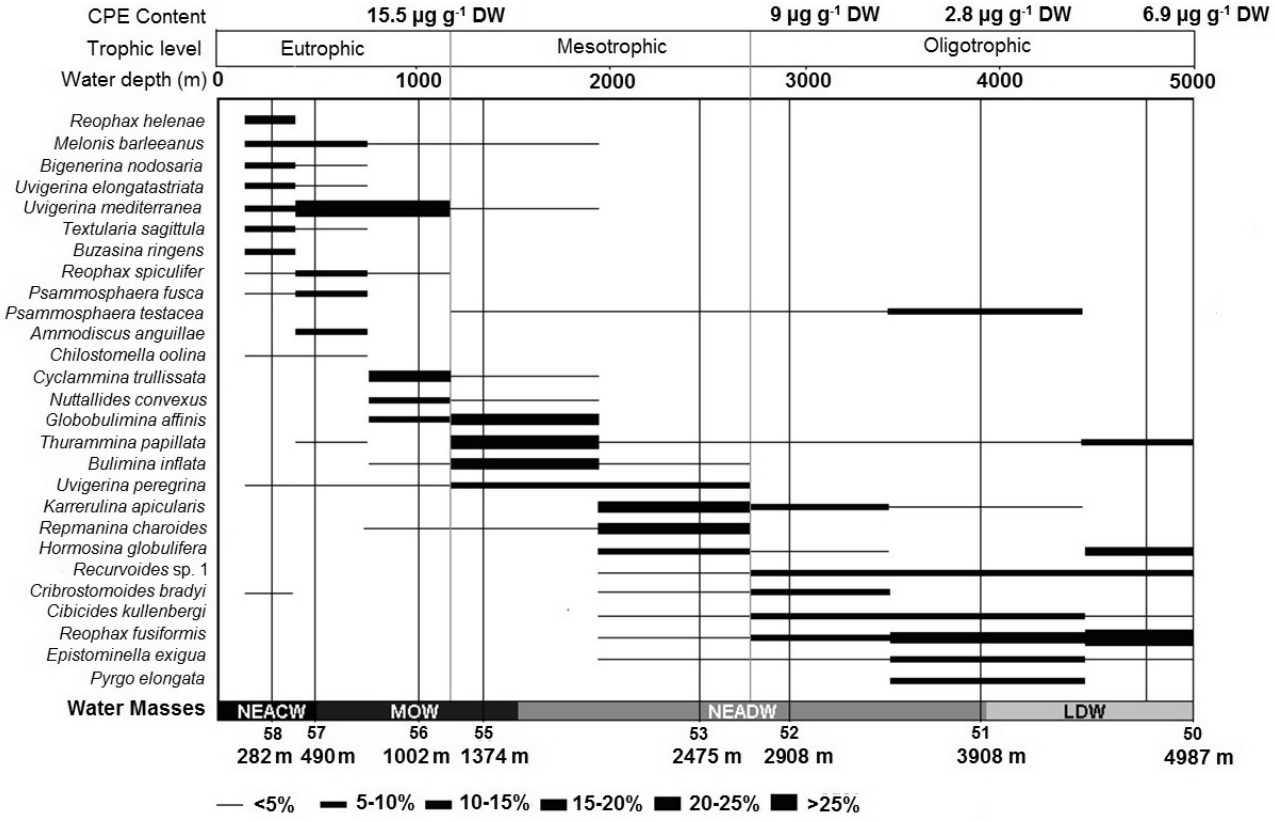

Figure 13. Relative densities (>150 µm) of live foraminifera species (present with percentage higher than 5% in at least one station) along the eight-station bathymetric transect.

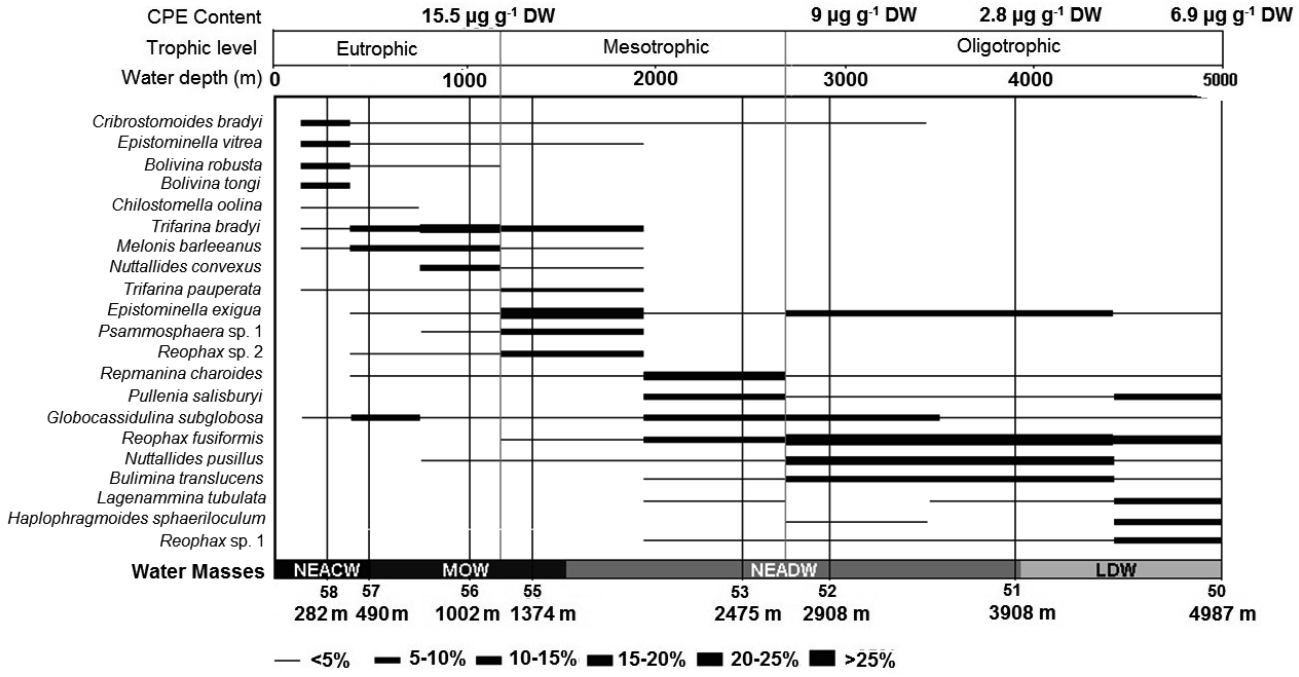

Figure 14. Relative densities (63–150 µm) of the important live foraminifera species (present at >5% in at least one station) along the eight-station bathymetric transect.

2.5.4 COMPARISON WITH PREVIOUS STUDIES

Similar studies have been performed in nearby areas of the Portuguese margin around Nazaré and Setúbal canyons (Koho and others, 2007, 2008) and in the Bay of Biscay (Fontanier and others, 2002, 2003, 2006; Duchemin and others, 2007; Mojtahid and others, 2010). With the exception of Duchemin and others (2007), all were concerned with the fraction >150 µm.

Under eutrophic conditions (>15 µg g^{-1} DW), found at our shallow stations (<1200 m), a high annual organic carbon flux promotes rich and ecologically diverse calcareous and

agglutinated faunas, including surface-dwelling, infaunal, and opportunistic species. The dominant species of the >150 μm fraction, the opportunistic surface-dweller *Uvigerina mediterranea*, and the infaunal *Melonis barleeanus* and *Uvigerina elongatastriata* are also key elements of the relatively eutrophic and shallower assemblages (<1000 m) in the Bay of Biscay (Fontanier and others, 2002, 2003; Mojtahid and others, 2010) and on the Portuguese margin, where they thrive in sediments with total phytopigment contents ≥10μg cm^{-3} (Koho and others, 2008). However, the dominant eutrophic agglutinated species observed in our study area do not occur consistently in the other two areas, except for *Bigenerina nodosaria*. For instance, *Reophax helenae* is not recorded in the Bay of Biscay, but has been documented (as *Reophax* sp. 1) at eutrophic shallow stations (≤500 m) at both canyon and open-slope locations on the Portuguese margin (Koho and others, 2007, 2008). Also, *Cyclammina trullissata*, a dominant infaunal species at our 1002 m site, is not recorded in either of the other two areas. In the 63–150 μm fraction, *Trifarina bradyi* is strongly dominant between 490–1374 m depth, with a maximum relative abundance at 1002 m. *Trifarina pauperata* occurs in association with *T. bradyi* and shows an identical distribution but with somewhat smaller populations. In the Bay of Biscay, *T. bradyi* occurs only as a minor component at 550 m (Fontanier and others, 2003), whereas *Trifarina pauperata* is supposed to be related to seasonally eutrophic environments in the Bay of Biscay at 1000 m (Duchemin and others, 2007). Our 282 m station also shows elevated numbers of *Cribrostomoides bradyi* (*Haplophragmoides bradyi* in Duchemin and others, 2007), *Epistominella vitrea*, and *Bolivina robusta* (*B. spathulata* in Duchemin and others, 2007), all of which diminish in abundance with increasing depth. In the Bay of Biscay, these three species occur at the most eutrophic environments, between 90–140 m.

The onset of relatively mesotrophic conditions (total phytopigment contents ranging 10–15 μg g^{-1} DW) at mid-depths (1374–2475 m) is marked by a reduced number of

calcareous species, particularly in the >150 μm fraction (Fig. 6). However, the shallow infaunal species *Uvigerina peregrina* and *Bulimina inflata* are still dominant at 2475 m. On the open Setúbal slope, *U. peregrina* occupies a relatively broad range of trophic conditions, from sediments containing total phytopigment contents ranging >18 g cm^{-3}, where *U. peregrina* var. *celtica* morphotypes dominate, to ~5 μg cm^{-3}, which favors the true *U. peregrina* morphotype (Koho and others, 2008). Because there is a continuous morphological transition between the two morphogroups, we decided not to split them in our study. Nonetheless, *U. peregrina* var. *celtica* morphotypes tend to dominate at 1374 m, whereas at the morphotypes at 2475 m are predominantly *U. peregrina*. In the Bay of Biscay, Fontanier and others (2003, 2006) suggested that, among species in the >150 μm fraction, *U. peregrina* has the strongest response to surface water phytoplankton blooms and associated phytodetritus deposits at 550 and 1000 m. In the smaller size fraction, small calcareous opportunistic species known to exploit phytodetritus (e.g., *Epistominella exigua*) start to increase. Among the calcareous deep and intermediate infauna, only *Globobulimina affinis* occurs in significant numbers (at 1374 m), while infaunal agglutinants remain relatively rich. At 1000 m in the Bay of Biscay, *G. affinis* dominates a deep infaunal assemblage (Fontanier and others, 2002), while *Globobulimina* spp. occur from 300–1760 m on the Setúbal open slope, in sediments ranging from relatively rich to poor in phytopigments (Koho and others, 2008). Along our transect, *G. affinis* is absent deeper than 1374 m depth, and agglutinated species such as *Karrerulina apicularis* and *Repmanina charoides* dominate the infauna at 2475 m. This transition may reflect a further decrease in trophic level.

Under oligotrophic conditions (total phytopigment content <10 μg g^{-1} DW) on the lower slope and abyssal plain (2908–4987 m depth), small, opportunistic, calcareous species attain their maximum relative abundance, whereas infaunal agglutinated species become less common. *Bulimina translucens*, *Epistominella exigua*, and *Nuttallides pusillus* have elevated

relative abundances at 2908 and 3908 m depth. These three small species are mostly restricted to the 63–150 μm fraction, have thin-walled tests, and occupy shallow-infaunal niches. A similar *E. exigua-N. pusillus* association was recorded in the Bay of Biscay at 1000 m by Duchemin and others (2007), who interpreted their high abundances as a response to spring phytodetritus deposits. *Reophax fusiformis* is a dominant element of the agglutinant assemblages in both size fractions. In the Setúbal open-slope and canyon environments on the Portuguese margin, Koho and others, (2008) recorded *Reophax fusiformis* (as *Lagenammina* sp.) under strongly oligotrophic conditions, with total sediment phytopigment contents ≤2 μg cm^{-3}. Gooday and others (2010) suggested that similar morphotypes (assigned to *Lagenammina*) in the Porcupine Abyssal Plain may be connected with phytodetritus deposits. Below the critical organic flux threshold between 4000–5000 m, seasonal phytodetritus may become too rare to sustain a significant number of opportunistic calcareous species. Nonetheless, small opportunistic agglutinants, as well as agglutinants with less-opportunistic life strategies, thrive at this depth and exploit eutrophic microenvironments created by phytodetritus falls in otherwise oligotrophic settings.

2.6 CONCLUSIONS

We have investigated the distributional patterns of live (rose Bengal-stained), small (63–150 μm) and large-sized (>150 μm) benthic foraminifera along a bathymetric transect from outer shelf (282 m) to abyssal plain (4987 m) environments on the Portuguese margin. The results of our study show that with increasing depth and declining availability of food particles in the sediments (i.e., trophic conditions), there is a succession of different groups of foraminifera characterized by different test sizes, wall types, and life-histories. Calcareous foraminifera are more strongly impacted by increasingly oligotrophic conditions than agglutinated ones, as indicated by the decreased proportion of perforate calcareous foraminifera, and the increased proportion of agglutinated foraminifera, between 1374–4987 m, overall suggesting that calcareous foraminifera have more elevated trophic requirements. These findings could have important implications for our understanding of different foraminiferal groups and their relative contributions to carbon cycling in deep sea.

2.7 APPENDIX 1

TAXONOMIC REFERENCE LIST. FOR ALL SPECIES (>5%) DETERMINED TO SPECIES LEVEL, A MODERN REFERENCE IS GIVEN, IN WHICH THE SPECIES IS CORRECTLY FIGURED.

Ammodiscus anguillae Høgland, 1947—Jones (1994), pl. 38, figs. 1–3.

Bigenerina nodosaria (d'Orbigny, 1826) —Jones (1994), pl. 44, figs. 19–24.

Bolivina robusta Brady, 1881—Jones (1994), pl. 53, figs. 7–9.

Bolivina tongi Cushman, 1929—Schiebel (1992), pl 1. figs 10a–10b.

Bulimina inflata (Seguenza, 1862) —Van Leeuwen (1989), pl. 8, fig. 4.

Bulimina translucens Parker, 1953—Van Leeuwen (1989), pl. 8, fig. 7.

Buzasina ringens (Brady, 1879)—Jones (1994), pl. 40, figs. 17, 18.

Chilostomella oolina (Schwager, 1878) —Jones (1994), pl. 55, figs. 12–14.

Cibicidoides kullenbergi (Parker, 1953)—Koho and others, (2008), pl. 1, fig. 1.

Cribrostomoides bradyi (Robertson, 1891)—Timm (1992), pl. 3, fig. 13.

Cyclammina trullissata (Brady, 1879)—Jones (1994), pl. 40, figs. 13.

Epistominella exigua (Brady, 1884)—Duchemin and others, (2007), pl. 2, figs. 1, 2.

Globobulimina affinis (d'Orbigny, 1839)—Hess (1998), pl. 10, fig. 13.

Globocassidulina subglobosa (Brady, 1881)—Van Leeuwen (1989), pl. 8, fig. 11.

Haplophragmoides sphaeriloculum Cushman, 1910—Hess (1998), pl. 6, fig. 10.

Hormosina globulifera Brady, 1879—Jones (1994), pl. 39, figs. 1–4, 6.

Karrerulina apicularis (Cushman, 1911)—Murray & Alve (1994), fig. 19.

Lagenammina tubulata (Rhumbler, 1931)—Hess (1998), pl .2, fig. 10.

Melonis barleeanus (Williamson, 1858) —Van Leeuwen (1989), pl. 13, figs. 1, 2.

Nuttallides convexus (Parker, 1958) —Van Leeuwen (1989), pl. 15, figs. 5–10.

Nuttallides pusillus (Parr, 1950)—Van Leeuwen (1989), pl. 14, figs. 4–12.

Psammosphaera fusca Schulze, 1875—Jones (1994), pl. 18, figs. 1–8.

Psammophaera testacea Flint, 1899—Hofker (1972), pl. 7 figs. 6–7.

Pullenia salisburyi Stewart and Stewart, 1930—Stewart and Stewart (1930), pl. 8, fig. 2.

Reophax fusiformis (Williamson, 1858) —Wollenburg and Mackensen (1998) pl. 1, fig. 12.

Reophax helenae (Rhumbler, 1913)—Hess (1998), pl. 3, fig. 9.

Reophax spiculifer Montfort, 1879—Jones (1994), pl. 31, figs. 16, 17.

Repmanina charoides (Jones & Parker, 1860)—Cimerman and Langer (1991), pl. 3,

figs. 6–9.

Textularia sagittula Defrance, 1824—Jorissen (1988), pl. 3 fig. 12.

Thurammina papillata Brady, 1879—Jones (1994), pl. 36, figs. 7–18.

Trifarina bradyi (Cushman, 1923)—Jones (1994), pl. 67, figs. 1–3.

Trifarina pauperata (Heron-Allen & Earland, 1932)—Duchemin and others, (2007), pl. 3, figs 14–15.

Uvigerina elongatastriata (Colom, 1952)—Koho and others, (2008), pl. 1, fig. 5.

Uvigerina mediterranea (Hofker, 1932)—Koho and others, (2008), pl. 1, fig. 6.

Uvigerina peregrina (Cushman, 1923)—Hess (1998), pl. 11, figs. 2, 3.

CHAPITRE 3

BENTHIC FORAMINIFERAL MICROHABITATS ALONG A 280 TO 5000 M DEPTH TRANSECT ON THE PORTUGUESE MARGIN

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Ce chapitre correspond à un article en preparation pour soumission

3.1 ABSTRACT

The microhabitats of live benthic foraminifera were studied in 8 cores collected in May 2007 along a depth transect on the Portuguese margin from 282 to 4987 m. The transect allowed a test of the TROX model of Jorissen and others, (1995) for calcareous and agglutinated foraminifera from both the >150 µm and 63-150 µm fractions. At some stations, the presence of large amounts of rose Bengal stained specimens in deeper sediment layers largely obscures the usual vertical succession of shallow, intermediate and deep infaunal species. This phenomenon was particularly evident at bathyal depths, where the Average Living Depth (ALD_{10}), inferred oxygen penetration and sediment mixed layers were deepest. We do not think that our observations can be explained by active colonisation of bio-irrigation structures, but rather suggest that these irregular infaunal presences are the result of passive transport by macrofaunal bioturbation, and a limited capacity of many species to "migrate" back to their preferred microhabitats close to the sediment water interface. In general, agglutinated foraminifera appear more affected by this phenomenon than calcareous ones, suggesting they are less successful in readjusting to their preferred microhabitat after displacement. We hypothesise that there is a link between the greater readjustment capacity of perforate shallow infaunal species and their generally higher trophic requirements, which can only be fulfilled close to the sediment surface, where the concentration of labile food components (phytopigments) is maximal. Average Living Depth (ALD_{10}) patterns for calcareous and agglutinant species of the >150 µm fitted well with the predictions of the TROX model. Surprisingly, in the >150 µm fraction, maximal depth in the sediment for calcareous taxa is reached at 1374 m, whereas this is much deeper for agglutinated species at 2908 m depth (2475 m in the 63-150 µm). This large difference strengthens the idea that larger calcareous species have higher trophic requirements than agglutinated ones. The much shallower microhabitats of most small-sized (63-150 µm) calcareous species suggests that

they depend on the more labile food particles, and may have an overall more opportunistic life strategy.

3.2 INTRODUCTION

Benthic foraminifera are generally concentrated at the sediment-interface, although they can be found alive at considerable depth in the sediment, sometimes down to 10 cm (Corliss, 1985; Mackensen and Douglas, 1989; Fontanier and others, 2002, Phipps and others, in prep). The conceptual TROX-Model of Jorissen and others, (1995) explains how in deep sea environments, benthic foraminiferal communities and microhabitat selection are controlled primarily by a negative relationship between exported organic matter flux and the oxygenation of the bottom and interstitial waters. Later modifications to the model include the role of migrational behaviour of foraminifera during changing redox regimes (Van der Zwaan and others, 1999) and the consideration of competition, predation and bioturbation affects on microhabitats (Jorissen and others, 1999). Standing stocks are generally high in relatively eutrophic shelf and upper open slope environments where foraminifera may be restricted to the uppermost millimetres or centimetres due to a shallowing of redox fronts and anoxia in deeper sediment layers (Murray, 2001; Fontanier and others, 2002; Jorissen and others, 2007). In relatively oligotrophic lower slope environments, foraminiferal standing stocks are much poorer and tend to be concentrated at the sediment surface as well (Fontanier and others, 2002). Conversely, in mesotrophic settings, where oxygen penetration is relatively deep, and more or less labile food particles are introduced deeper into sediment by bioturbating macrofauna, faunal penetration will be maximal (Jorissen, 1999; Fontanier and others, 2002). Many studies of larger sized fractions (e.g., >125 μm, >150 μm) confirm a vertical succession of preferred microhabitats among calcareous species, apparently related to some important redox boundaries. For example, in relatively eutrophic slope and shelf

environments, *Melonis barleeanus* is a well known intermediate infaunal species which preferentially lives in dysoxic sediments where nitrates are present with maximal concentrations, while *Globobulimina* spp. generally occur as deep infauna around the zero oxygen layer (Jorissen and others, 1998; Schönfeld, 2001; Fontanier and others, 2002, 2003, 2005; Koho and others, 2008; Mojtahid and others, 2010).

In contrast, a recent study by Loubere and others (2011) suggests an alternative hypothesis to the TROX model, in which subsurface distributions of calcareous foraminifera do not adhere to a simplistic vertical stratification. Instead, infaunal foraminifera supposedly colonise bio-irrigation systems, regardless of vertical microhabitat preference (i.e. shallow, intermediate or deep infaunal), where they may benefit from labile organic carbon and oxygen introduced deeper into the sediment. An important argument in favour of this hypothesis is the geochemical composition of the tests of calcareous species, especially the carbon stable isotopes and Cd/Ca ratios (Loubere and others, 2011). It has been suggested earlier that the presence of macrofaunal burrows may provide microhabitats for some specialised, normally shallow infaunal taxa, such as *Bulimina marginata* and *Eggerelloides scabra* (Jorissen and others, 1999; Hess and Jorissen, 2009). However, the presence of clear vertical species successions observed in numerous studies from a wide range of deep sea environments suggests that such a colonisation of macrofaunal bio-irrigation systems is not a dominant mechanism explaining foraminiferal microhabitats, and will probably not apply to all infaunal taxa.

However, it is true that in many described cores where clear vertical microhabitat successions are present, not all individuals follow the expected vertical microhabitat succession. We think that this could also be due to the fact that macrofaunal bioturbation has actively displaced foraminifera from their preferred microhabitat to a deeper sediment layer (Buzas, 1977; Collison, 1980; Langer and others, 1989; Moodley, 1990, 1998, Boucher and

others, 2009). Logically, such displaced foraminifera will either survive under the conditions they are displaced into, or will attempt to move back to their preferred microhabitat closer to the sediment surface. Unfortunately, Loubere and others (2011) did not consider agglutinated species in their study, for which there is only limited information available from previous studies (Mackensen and Douglas, 1989; Fontanier and others, 2002, 2003, 2005; Koho and others, 2008; Mojtahid and others, 2010). For small-sized taxa (<150 µm or <125 µm), even less information is available (e.g. Gooday, 1986; de Stigter and others, 1998). Information on both groups is important, because foraminifera with different test structures and from different size groups may behave differently for a number of reasons. Firstly, it has been suggested that calcareous foraminifera are more sensitive to labile organic matter input than agglutinated ones and require a high quality food source to survive (Koho and others, 2008; Alve, 2010; Phipps and others, 2012). Conversely, agglutinated and softshelled foraminifera, which are perhaps less competitive for the most labile food particles, may have adopted different life strategies in order to survive with lower quality organic matter particles. Examples are gigantism in large agglutinated suspension feeders such as *Astrorhiza limicola*, *Pelosina arborescens* (Cedhagen, 1988, 1993) and *Saccorhiza ramosa* (Altenbach and others, 1988), osmotrophy in *Notodendrodes antarkticos* (DeLaca and others,. 1981, DeLaca, 1982), spherical passive deposit feeders (Saccamminidae and Psammosphaeridae) in oligotrophic strong bottom currents (Kaminski, 1985, Fontanier and others, 2008, Goineau and others, 2011) and autophagy in species such as *Cribrostomoides subglobosus* and *Rhabdammina abyssorum* (Linke 1992). In particular, some abyssal monothalamous species accumulate stercomata (waste pellets composed of fine sediment particles) as a bulk ingestion feeding strategy that would allow digestion of associated bacteria and more refractory organic matter (Tendal, 1979, Gooday and others 2002, 2006; Gooday, 2008). This could suggest that such species have lower metabolic rates than the predominantly calcareous foraminifera that are

observed to exploit labile organic matter deposits (Gooday 1988, 1993, 2008; Gooday and Lambshead, 1989; Gooday and others., 2001; Gooday and Hughes, 2002; Fontanier and others, 2003; Cornelius and Gooday 2004; Nomaki and others, 2005, 2006). However, foraminiferal mobility studies have so far not revealed significant differences between the mobility of calcareous and agglutinated foraminifera, suggesting that both groups may have similar metabolic rates (e.g. Kitazato 1988; Geslin, 2004). Further, agglutinated species such as *Adercotryma glomerata*, some species of *Lagenammina* and *Reophax*, and some saccamminids have also been observed to profit from phytodetritus deposits (Gooday and Hughes, 2002; Cornelius and Gooday, 2004; Gooday and others, 2010), while large tubular forms (e.g. *Pelosina* sp., *Hyperammina* spp. and *Bathysiphon rufum*) have been recorded to rapidly ingest ^{13}C-labelled diatoms (Levin and others, 1999). Nonetheless, agglutinated faunas increase in relative percentage abundance in the deep sea where conditions become progressively oligotrophic, suggesting their tolerance for less abundant and/or lower quality food supplies (Cornelius and Gooday and others, 2004; Gooday and others, 2008; Koho and others, 2008; Phipps and others, 2012). Finally, it has also been observed that many species with opportunistic tendencies have small tests (Gooday, 1993, 1996; Gooday and Rathburn, 1999; Gooday and Hughes, 2002; Cornelius and Gooday, 2004). Such small species typically occupy shallow infaunal habitats where they may take full advantage of high quality C_{org} in the form of phytodetritus at the sediment surface (Gooday, 1996). The eventual dominance of phytodetritus exploiting species could lead to a strong predominance of surface dwellers in the 63-150 μm fraction.

This study focuses on the vertical distribution of benthic foraminifera from a depth transect of 8 stations (282 to 4987m) along the Portuguese margin. An earlier paper, Phipps et al., (2012) described the overall faunal trends along the same transect. This dataset on the vertical distribution along the transect allows us to examine whether the downcore

distribution of foraminifera exhibits a prominently vertical microhabitat succession (i.e. shallow, intermediate and deep infaunal), as depicted by the TROX model (Jorissen and others, 1995). Next, we will consider the relative importance of the individuals which do not follow such a vertical microhabitat succession, either because they have colonised macrofaunal burrows (as suggested by Loubere and others 2011), or because they have been transported there accidentally by macrofaunal bioturbation. Finally, we will determine whether the TROX model is also valid for explaining microhabitat selection among agglutinated foraminifera >150 µm and smaller sized (63-150 µm) calcareous and agglutinated taxa. If this is the case, we will determine whether their response to the trophic parameters is the same as that of the >150 µm calcareous faunas.

3.3 MATERIAL AND METHODS

3.3.1 STUDY AREA

Our transect study is located on the open slope off Cape Sines, on the Portuguese Margin at 37°50'N, from 9°05'W to 11°W (Fig. 1). The open slope between the Setúbal Canyon and Cape Sines has a maximum width of 25 km. Steep slopes are only found at the intersection with the Setúbal Canyon, which incises the shelf from east to west. At 280 m depth, surface sediments consist of fine sands; towards deeper sites (~1000 m) sediments progressively become finer, consisting of silt and mud. Still deeper, grain size remains constant down to the Tagus Abyssal Plain at about 5000 m depth (de Stigter and others, 2011, Phipps and others, 2012).

The slope is influenced by seasonally changing hydrodynamics as a result of the wind-driven upwelling system occurring along the western coasts of the Iberian Peninsula and Africa down to 15°N (Wooster and others, 1976). Conditions favorable for upwelling off Cape Sines occur between May and September as a result of strong and steady northerly winds and southward surface currents (Fiúza, 1984; Sousa and Bricaud, 1992; Huthnance and others, 2002).

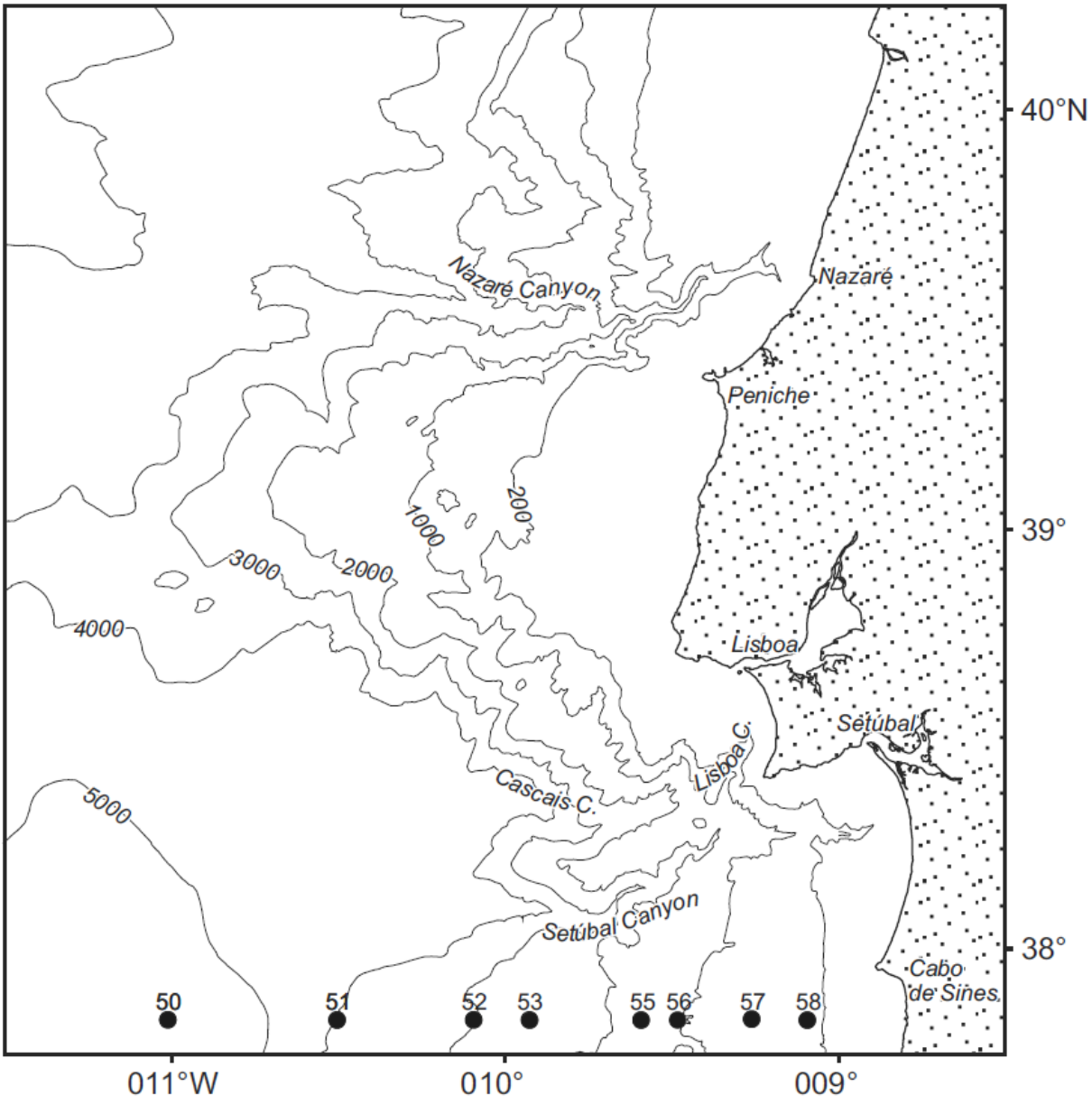


Figure 1. Map of the Cape Sines continental slope transect. All stations sampled in September 2006, are marked in black circles.

Several water masses constitute the water column along the transect (Fiuza and others, 1998; García and others, 2003). Below the surface waters (~30 m) the North Atlantic Central Water mass (ENACW), is characterised by warm (12-16°C) and salty (≤36) properties, down to 600 m depth. Between 600 and 1600 m water depth, the Mediterranean Outflow Water (MOW) is distinguished by a strong salinity peak at 1100 m (>36). The North East Atlantic Deep Water (NEADW) forms the main water mass below the MOW, with relatively lower temperature (2-10°C) and salinity (~35). Below approximately 4000 m, the Lower Deep Water (LDW) of Antarctic origin (Van Aken, 2000) is observed, with cold (~2°C) and low saline (<35) properties.

3.3.2 Sample Preparation and Processing of Foraminifera

All samples were collected using a MUC multicorer in September 2006 on board the RV Pelagia (Fig. 1). For reasons of time limitation, no duplicate samples were studied at any of the 8 stations. Each core had an inner diameter of 6 cm and was sliced at 0.5 cm intervals from 0 to 2 cm depth, and 1 cm intervals from 2 to 10 cm depth. Details of the sample preparation are documented in Phipps and others, (2012). Special care was taken not to break small, fragile agglutinated tests by using a low power showerhead to wash samples. Soft-walled monothalamous taxa and fragments of large tubular taxa were tabulated into an outside count and not included in the sample analysis.

3.3.3 PHYTOPIGMENT CONTENTS

Chlorophyll-a and phaeopigment analyses were carried out for stations 56, 52, 51 and 50 according to the procedure described by Lorenzen and Jeffrey (1980). Pigments were extracted (12 h at 4°C in the dark) from triplicate sediment samples (about 1 g) at 0-1 cm, 1-3 cm, 3-5 cm and 5-10 cm intervals, obtained from independent deployments of the multicorer, using 3-5 ml of 90% acetone as the extractant. Extracts were analyzed fluorometrically to estimate chlorophyll-a, and, after acidification with 200 µl 0.1N HCl, to estimate phaeopigments. We avoided the use of fluorometric chlorophyll-a estimates as the unique tracer of organic C associated with algal material and, instead, summed up chlorophyll-a and phaeopigment concentrations (i.e., total phytopigments). Concentrations of total phytopigments, once converted into C equivalents using a conversion factor of 40 (Pusceddu and others, 1999) are reported in µg g^{-1} DW.

3.3.4 QUANTITY AND BIOCHEMICAL COMPOSITION OF SEDIMENT ORGANIC MATTER

Protein, carbohydrate and lipid sediment contents were analyzed spectrophotometrically according to Pusceddu and others, (2004) and concentrations are expressed as bovine serum albumin, glucose and tripalmitine equivalents, respectively. For each biochemical assay, blanks were obtained using pre-combusted sediments (450°C for 4 h). For all of the stations, all analyses were performed on triplicate sediment samples (about 0.5 g) at 0-1 cm, 1-3 cm, 3-5 cm and 5-10 cm intervals, obtained from independent deployments of a multiple corer. Carbohydrate, protein and lipid sediment contents were converted into carbon equivalents using the conversion factors of 0.40, 0.49 and 0.75 mg C mg-1, respectively, and their sum is defined as the biopolymeric organic carbon (Fabiano and others, 1995).

3.4 RESULTS

3.4.1 ORGANIC MATTER COMPONENTS

Results for the different organic components at the four stations for which we have measurements are presented in Figure 2. All organic components have relatively high concentrations at 1002 m, and show an overall decrease with increasing depth. In detail, total phytopigment and protein contents show slightly higher values at the deepest station (6.9 ± 2.2 μg g^{-1} and 1.0 ± 0.1 mg g^{-1} at 4987 m respectively) in comparison to the 3908 m station (2.8 ± 0.6 μg g^{-1} and 0.9 ± 0.3 mg g^{-1} respectively), while carbohydrates, lipids (and biopolymeric carbon) all have lowest values at the deepest station (1.0 ± 0.4, 0.2 ± 0.03 and 1.1 ± 0.2 mg g^{-1} respectively). At each of the 4 stations, total phytopigment contents show clear decreases from the sediment surface towards deeper intervals. However, this downward decrease is much less evident at station 51 (3908 m), where the surface phytopigment concentrations are minimal. All other measures of organic matter show rather stable values downcore, or even slight increases (Fig. 2).

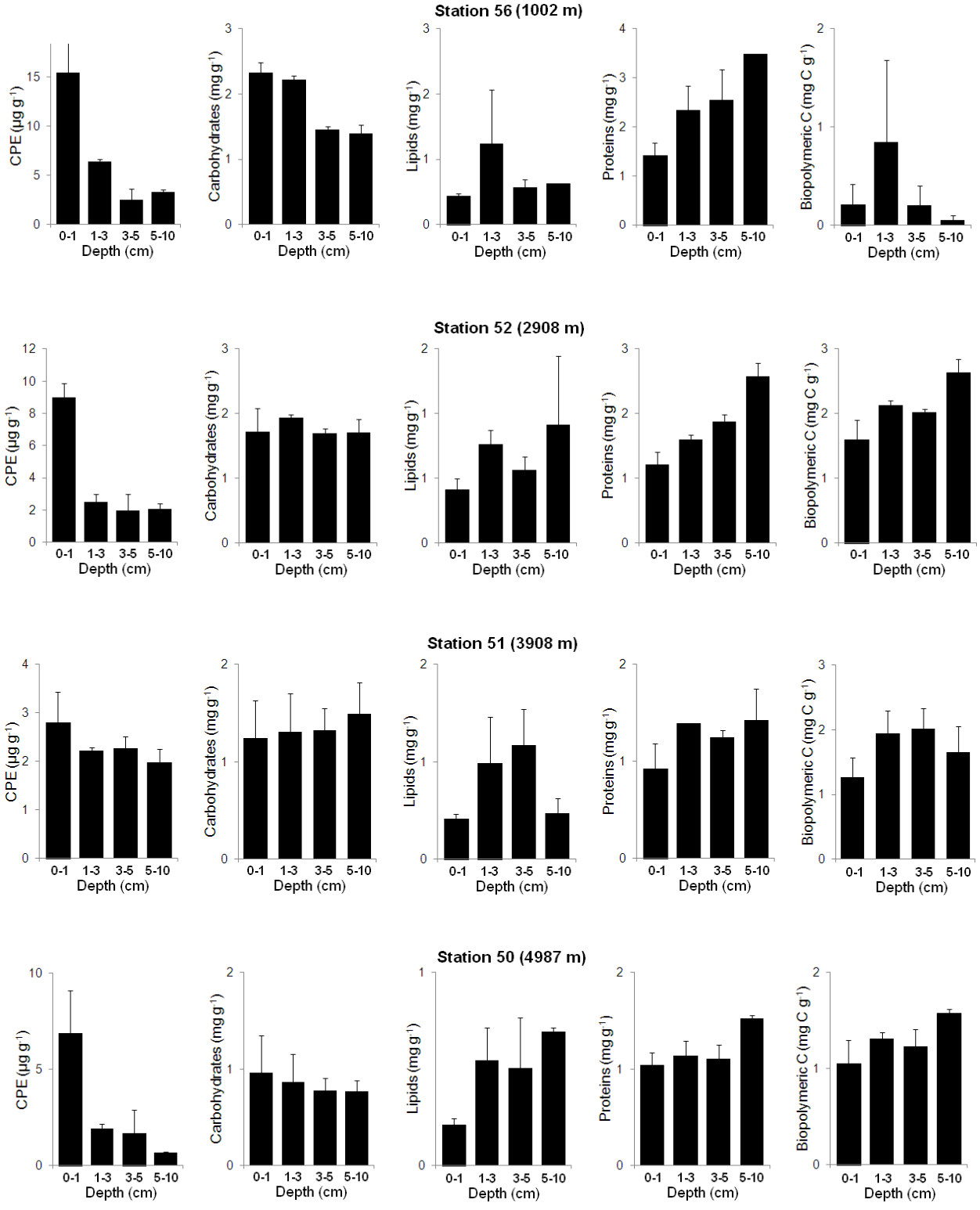


Figure 2. Components of organic carbon measured at 0–1, 1–3, 3–5, and 5–10 cm intervals downcore for four stations in this study.

3.4.2 LEAD PROFILES

Downcore ^{210}Pb profiles for all our stations except 490 m are presented in Figure 3. Macrofaunal bioturbation causes ^{210}Pb values to become homogenised in the topmost levels of the sediment (e.g., Robbins and others, 1977; Rhoads and Boyer, 1982; Stordal and others, 1985; Thomson and others, 1988; Boudreau, 1994; Muñoz and others, 2007). Only below this Surface Mixed Layer (SML) does the normal, radioactive exponential decrease of ^{210}Pb become evident. Stations at 282 m, 1374 m, 3908 m and 4987 m appear to have clear exponential downcore ^{210}Pb profiles starting in the uppermost cm, indicating the absence of a substantial SML at these sites; intensive macrofaunal bioturbation appears to be limited to the upper cm of the sediment here (Fig. 3, Table 1). On the contrary, stations at 1002 m (1.0 cm) and 2475 m (4.5 cm) show varying degrees of sediment mixing, with the deepest mixing being observed at mid depths (2475 m) (Fig. 3, Table 1). A peculiar downcore profile is observed at 2908 m, where a maximum value in the top 0.5 cm is followed by a homogenous layer between 0.5 and 2.5 cm; we interpret this layer to represent the SML.

Water depth (m)	Sediment mixing layer (cm)	Estimated zero oxygen layer (cm)	Estimated maximum nitrate layer (cm)
282	<0.5	1–1.5	0.5–1
490	No Data	3–4	1.5–2
1002	1	3–4	1–1.5
1374	<0.5	3–4	
2475	4.5	4-5	
2908	2.5	4-5	
3908	<0.5		
4987	<0.5		

Table 1. Depth of sediment mixed layer, estimated zero oxygen and maximum nitrate levels of each core according to ^{210}Pb data and distributions of key intermediate and deep infaunal calcareous marker species.

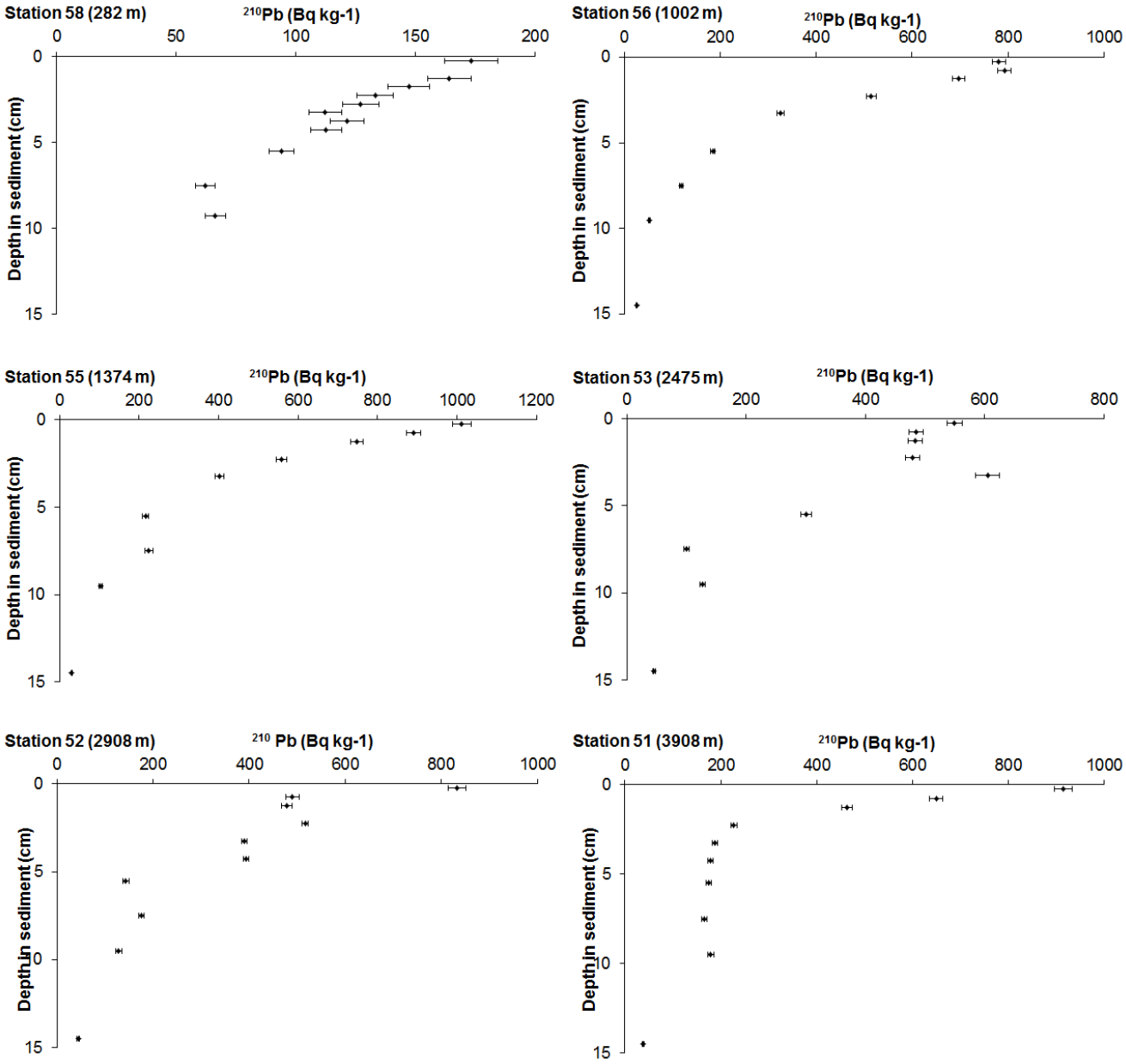


Figure 3. Downcore ^{210}Pb profiles for stations 58, 56, 55, 53, 52, 51 and 50.

3.4.3 VERTICAL DISTRIBUTION OF DOMINANT SPECIES

In the following paragraphs we describe the main microhabitat trends observed for the >150 µm and 63-150 µm fractions at each of our eight stations, from shallowest to deepest. As we lack oxygen penetration profiles, we will first describe the vertical patterns of calcareous species for which the microhabitat characteristics are well known in the literature (i.e. *Chilostomella oolina*, *Globobulimina* spp, *Melonis barleeanus*, *Uvigerina elongatastriata*, see Table 2). On the basis of the vertical distribution of these species we will tentatively determine the depth of major biogeochemical domains (e.g. nitrate maximum, zero oxygen level). This will provide the framework for our interpretations of the microhabitat patterns of less well known calcareous and agglutinated taxa.

Species	Microhabitat	Redox conditions	Oxygen conditions	Authors
Melonis barleeanus	II	Zone of maximum nitrate reduction	Dysoxic	Jorissen et al. 1998, Fontanier et al. 2002, 2003, 2005 Koho et al. 2008, Mojtahid et al. 2010
Chilostomella oolina	II/DI	Fe^{2+} oxidation	Zero oxygen boundary	Gooday and Rathburn 1999, Jorissen 1999 Fontanier et al., 2002, 2003, 2005, 2008
Globobulimina affinis	DI	Fe^{2+} oxidation	Zero oxygen boundary	Fontanier et al. 2002, 2003, 2005, 2008 Koho et al. 2008
Globobulimina pyrula	DI	Fe^{2+} oxidation	Zero oxygen boundary	Jorissen et al. 1998, Fontanier et al. 2002, 2003, 2005 Koho et al. 2008
Uvigerina elongatastriata	II	Zone of maximum nitrate reduction	Dysoxic	Fontanier et al. 2002, 2006 Koho et al. 2008

Table 2. Summary of key intermediate and deep infaunal calcareous species encountered in this study and their corresponding preferred redox/oxygen conditions in the literature.

At 282 m (Figure 4a), the surface fauna of the >150 µm fraction is characterised by the shallow infaunal species *Uvigerina mediterranea* (ALD_{10} = 0.4 cm) which occurs mainly in the first 0.5 cm, where it is accompanied by *Trifarina fornasinii* (ALD_{10} = 0.6 cm) and the agglutinated species *Bigenerina nodosaria* (ALD_{10} = 0.5 cm) and *Textularia sagittula* (ALD_{10} = 0.4 cm). Further, *Epistominella vitrea* (ALD_{10} = 0.4 cm), *Bolivina robusta* (ALD_{10} = 0.5 cm), *Bolivina tongi (*ALD_{10} = 0.7 cm), *Cribrostomoides bradyi* (ALD_{10} = 0.5 cm), *Labrospira jeffreysii* (ALD_{10} = 0.4 cm) and *Pseudobolivina fusiformis* (ALD_{10} = 0.5 cm) all occupy shallow infaunal microhabitats (topmost 0.5 cm) mostly in the 63-150 µm fraction. In the >150µm fraction the classical intermediate infaunal species *Melonis barleeanus* (ALD_{10} = 0.7 cm) and *Uvigerina elongatastriata* (ALD_{10} = 0.8 cm) are found in the topmost 1 cm, both showing a maximum abundance in the 0.5-1.0 cm level, together with the agglutinated species *Buzasina ringens* (ALD_{10} = 1 cm) and *Reophax helenae* (ALD_{10} = 1.3 cm). The deep infaunal species *Globobulimina turgida* (ALD_{10} = 0.7 cm) occurs in low numbers in the first 1.5 cm. Low numbers of *Chilostomella oolina* (ALD_{10} = 1.3 cm) are found down to 3 cm, whereas the richer assemblage observed in the 63-150 µm fraction shows a clear maximum in the 1-1.5 cm level. These distributional data suggests the presence of maximum nitrate concentrations in the 0.5-1 cm level and a position of the zero oxygen level between 1 and 1.5 cm depth.

At 490 m depth (Figure 4b), the >150 µm fraction of the uppermost cm is strongly dominated by *Uvigerina mediterranea* (ALD_{10} = 0.6 cm) along with various *Reophax* species and *Psammosphaera fusca* (ALD_{10} = 0.9 cm). In the 63-150 µm fraction, faunas in the top 1 cm are dominated by *Reophax* sp. 2 (ALD_{10} = 0.5 cm), *Eggerelloides medius* (ALD_{10} = 0.4 cm), *Trifarina bradyi* (ALD_{10} = 0.7 cm), *Bolivina robusta* (ALD_{10} = 0.4 cm), *Globocassidulina subglobosa* (ALD_{10} = 0.5 cm) and *Reophax spiculifer* (ALD_{10} = 0.7 cm). In the >150 µm fraction the calcareous intermediate infaunal species *Melonis barleeanus*

(ALD_{10} = 1.4 cm) and *Uvigerina elongatastriata* (ALD_{10} = 1.8 cm) occur between 0.5 and 3 cm, with a maximum abundance at 1-1.5 cm and 1-2 cm respectively, while the agglutinated species *Ammodiscus anguillae* (ALD_{10} = 2 cm) occurs mostly at 1.5-2 cm. The deep infaunal species *Chilostomella oolina* (ALD_{10} = 3.8 cm) is present in the >150 µm fraction between 2 and 6 cm with a maximum abundance between 3 and 5 cm. These observations suggest maximum nitrate concentrations at about 1.5 cm depth and a zero oxygen depth at about 3-4 cm.

At 1002 m (Fig 4c), *Uvigerina mediterranea* (>150 µm fraction ALD_{10} = 0.6 cm) and *Nuttallides convexus* (>150 µm ALD_{10} = 0.5 cm, 63-150 µm ALD_{10} = 0.3 cm) occupy shallow infaunal microhabitats in the top cm of the core along with *Trifarina bradyi* (ALD_{10} = 0.4 cm) and *Trifarina pauperata* (ALD_{10} = 0.3 cm) in the 63-150 µm. Low numbers of the intermediate infaunal species *Melonis barleeanus* occur in both size fractions down to 3 cm, with a maximum in the 1-1.5 cm interval. Scarce individuals of the deep infaunal species *Globobulimina affinis* (ALD_{10} = 3.9 cm) occur between 1 and 6 cm in the >150 µm fraction. These data suggest a nitrate maximum between 1 and 1.5 cm and a zero oxygen level around 3-4 cm. Oxygen measurements performed at the same site in May 2007 show an oxygen zero level at 3 cm depth (Phipps and others *in prep*). Agglutinated species with a clear preference for a surficial microhabitat are poor at this station. Instead, the agglutinated species *Cyclammina trullissata* (ALD_{10} = 1.4 cm) appears to occupy an intermediate infaunal microhabitat in the >150 µm fraction, occurring mostly between 0.5 to 3 cm.

At 1374 m (Fig 4d), *Bulimina inflata* (ALD_{10} = 0.4 cm) and *Uvigerina peregrina* (ALD_{10} = 0.5 cm) dominate the >150 µm fraction in the top centimetre, accompanied in the 63-150 µm fraction by *Bulimina rostrata* (ALD_{10} = 0.3 cm), *Epistominella exigua* (ALD_{10} = 0.4 cm), *Trifarina bradyi* and *Trifarina pauperata* (both ALD_{10} = 0.3 cm). Here, *Melonis barleeanus* (ALD_{10} = 1.4 cm) only occurs in significant numbers in the smaller fraction

between 0 and 3 cm. *Globobulimina affinis* is present between 3 and 7 cm with a well defined maximum at 3-4 cm (>150 µm fraction ALD_{10} = 4.3 cm, 63-150 µm fraction ALD_{10} = 4 cm). This suggests a zero oxygen level between 3 and 4 cm depth. The agglutinated species *Reophax* sp. 2 (ALD_{10} = 0.3 cm) and *Psammosphaera* sp. 1 (ALD_{10} = 0.3 cm) (mostly in the 63-150 µm fraction) both show a clear maximum in the top half centimetre. *Thurammina papillata* (ALD_{10} = 1 cm) is absent in the uppermost half centimetre, but occurs with maximum concentrations between 0.5 and 1.5 cm in the >150 µm fraction, whereas *T. albicans* (ALD_{10} = 0.9 cm) is already present in the surface level, but extends deeper into the sediment (0-2 cm).

At 2475 m (Fig 4e) *Uvigerina peregrina* (ALD_{10} = 0.4 cm) dominates the calcareous fauna >150 µm in the uppermost centimetre, together with *Globocassidulina subglobosa* (ALD_{10} = 0.5 cm in the 63-150 µm fraction). No typical calcareous intermediate infaunal species of the >150 µm fraction are found in this core. However, in the 63-150 µm fraction *Pullenia salisburyi* (ALD_{10} = 1.6 cm) is present with significant densities between 0.5 and 4 cm depth. Further, *Globobulimina affinis* is represented by only 2 individuals in the 4-5 cm interval. On the basis of this observation, we tentatively position the zero oxygen level at about 4 cm. At this station, many agglutinants and some calcareous species such as *Karrerulina apicularis* (in the >150 µm fraction) and *Reophax fusiformis*, *Gyroidinoides umbonatus* and *Cystammina argentea* (all mostly in the 63-150 µm fraction) show diffuse patterns, with live specimens being present down to a considerable depth in the sediment (down to 4-5 cm), and without a clear density maximum at any specific depth. On the other hand, *Repmanina charoides* (>150 µm fraction ALD_{10} = 3.4 cm, 63-150 µm fraction ALD_{10} = 4.2 cm) shows a clear maximum between 2 and 5 cm depth.

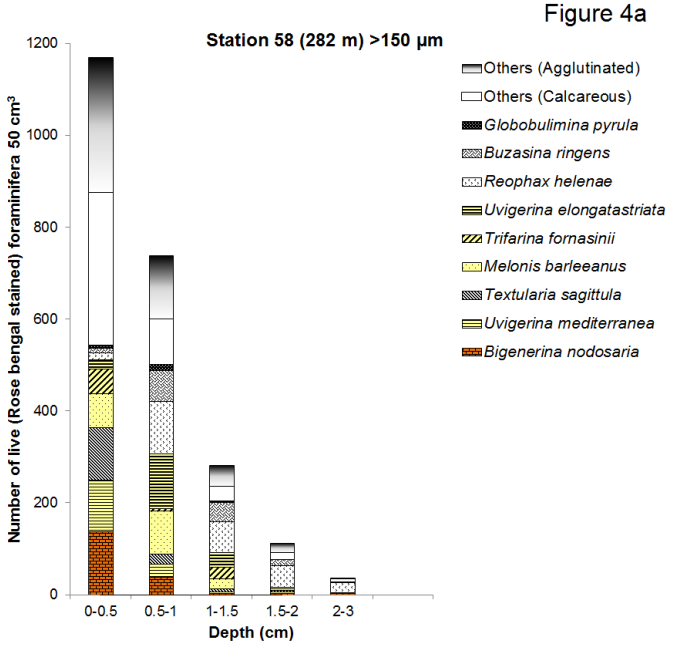
At 2908 m (Fig 4f), *Cibicidoides kullenbergi* (ALD_{10} = 0.3) and *Hoeglundina elegans* (ALD_{10} = 0.7 cm) dominate the uppermost 1 cm of the >150 µm fraction, along with *Nuttallides pusillus* (ALD_{10} = 0.7 cm), *Epistominella exigua* (ALD_{10} = 0.6 cm) and *Bulimina translucens* (ALD_{10} = 0.8 cm) (mostly in the 63-150 µm fraction). Deeper infaunal calcareous species are very rare at this station; the intermediate infaunal species *Pullenia salisburyi* (ALD_{10} = 2.4 cm) shows a rather diffuse distribution at this station, occurring between 0 and 5 cm. Only *Fursenkoina* spp. (ALD_{10} = 3.9 cm) show a clear preference for deeper sediment levels (3-6 cm) in the 63-150 µm fraction. Among the agglutinated faunas, only *Hormosinella guttifera* (ALD_{10} = 0.6 cm) shows a clear preference for the topmost level. Similarly to the 2475 m station, many agglutinated faunas show diffuse distributions here (e.g. *Karrerulina apicularis*, *Reophax fusiformis*, *Recurvoides* sp. 1 and *Globocassidulina subglobosa*) which makes it difficult to describe their microhabitats. However, in the >150 µm fraction *Cribrostomoides bradyi* (ALD_{10} = 4 cm) and *Cystammina pauciloculata* (ALD_{10} = 2.8 cm) both show a clear intermediate to deep infaunal maximum at 2 to 4 cm depth.

At 3908 m (Fig 4g) the faunas in the >150 µm fraction are poor and restricted to the upper 0-1.5 cm, with many species represented by a single individual. The 63-150 µm fraction is much richer, and *Nuttallides pusillus* (ALD_{10} = 0.5 cm), *Epistominella exigua* (ALD_{10} = 0.6 cm), *Bulimina translucens* (ALD_{10} = 0.5 cm) and *Reophax fusiformis* (63-150 µm ALD_{10} = 0.3 cm, >150 µm ALD_{10} = 0.8 cm) all show clear surface maxima. Below the 0-0.5 cm interval, standing stocks fall sharply; no foraminifera were found stained below the 2-3 cm interval.

At our deepest station, at 4987 m (Fig 4h), the extremely poor calcareous fauna of the >150 µm fraction is largely restricted to the uppermost half centimetre. The same is true for the much richer agglutinated fauna, containing *Reophax fusiformis* (ALD_{10} = 0.3 cm) *Hormosina globulifera* (ALD_{10} = 0.3 cm), *Recurvoides* sp, 1 (ALD_{10} = 0.3 cm) and

Thurammina papillata (all ALD_{10} = 0.3 cm). In the 63-150 µm fraction the calcareous species *Nuttallides pusillus* (ALD_{10} = 0.3 cm) and *Epistominella exigua* (ALD_{10} = 0.3 cm) show a clear surface maximum. Also the agglutinated species *Adercotryma glomerata, Reophax fusiformis, Hormosina globulifera, Lagenammina tubulata, Haplophragmoides sphaeriloculum,* various *Thurammina* species (all ALD_{10} = 0.3 cm) and *Reophax* sp. 1 (ALD_{10} = 0.4 cm) (mostly 63-150 µm fraction) show a maximum in the topmost level. There are no agglutinant species with a conspicuous infaunal maximum. However the calcareous species *Pullenia salisburyi* (ALD_{10} = 1.7 cm) shows again a clear infaunal maximum between 1 and 2 cm.

Figure 4a



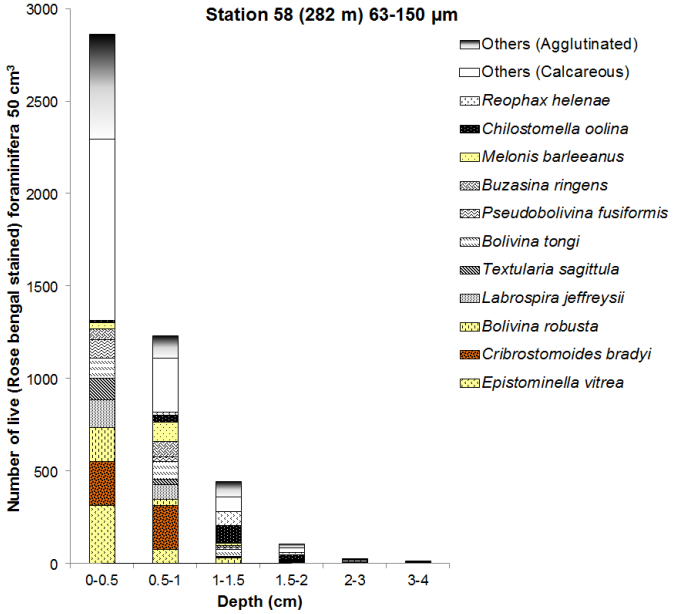
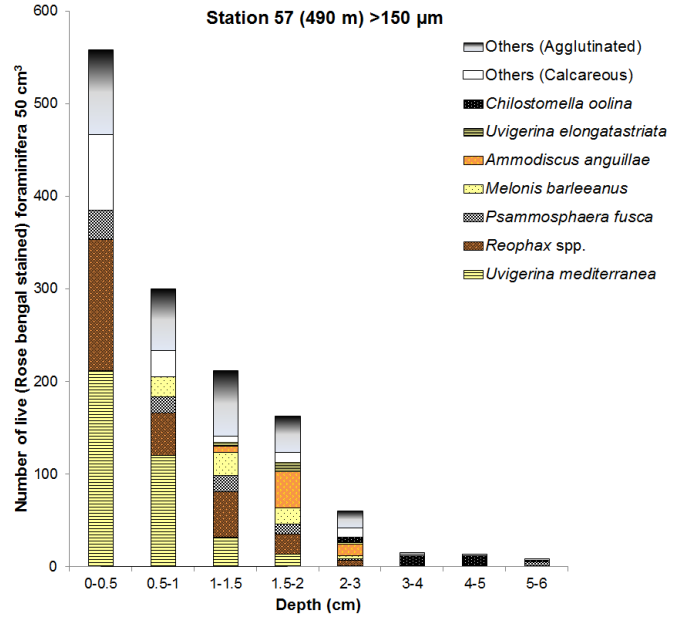


Figure 4b



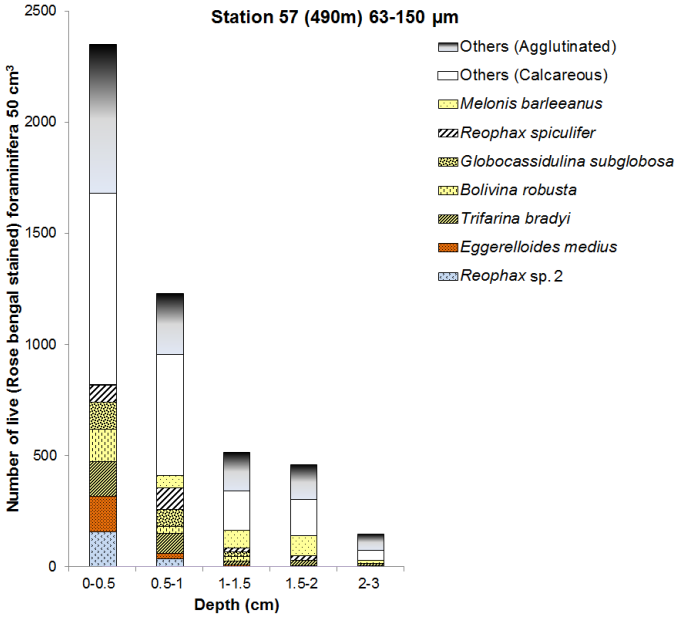
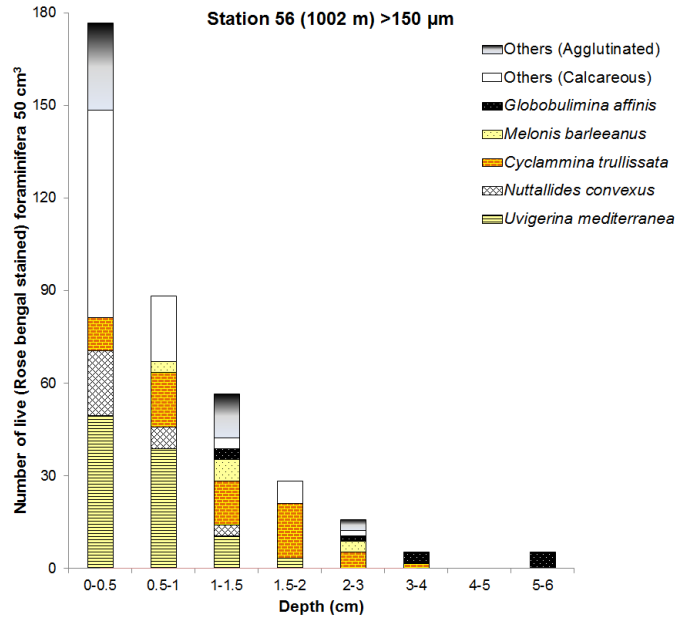


Figure 4c



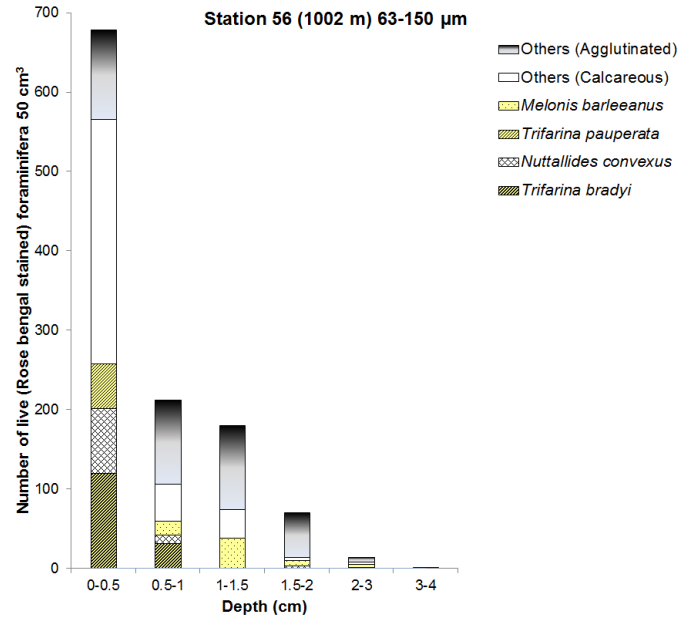
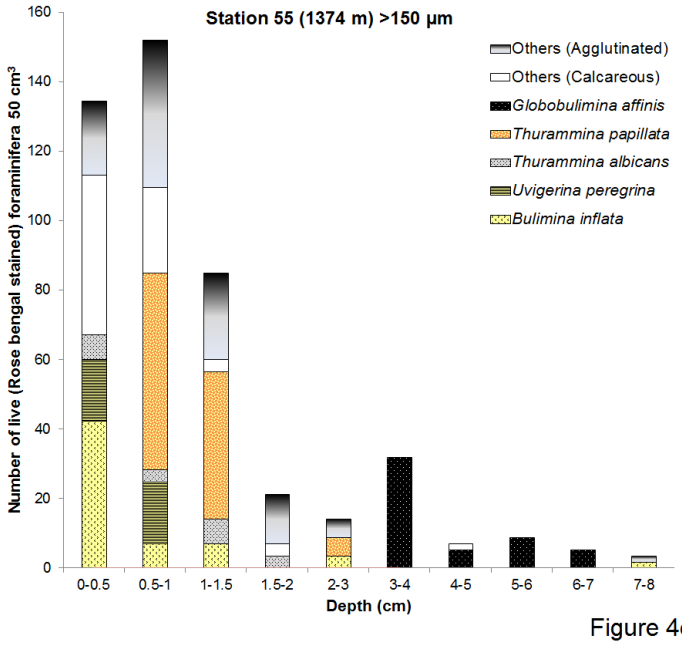


Figure 4d



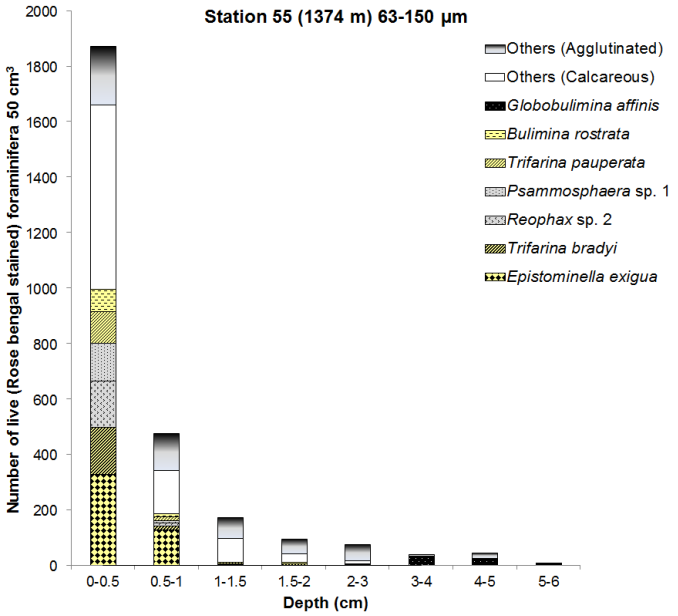
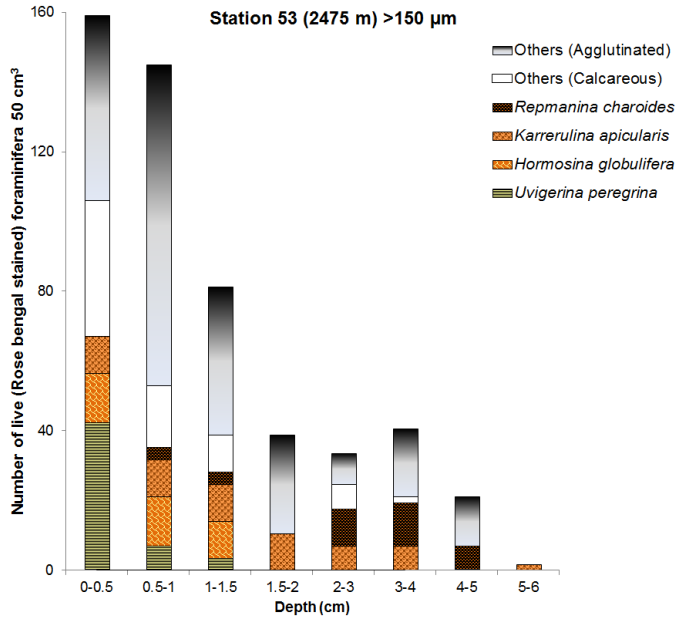


Figure 4e



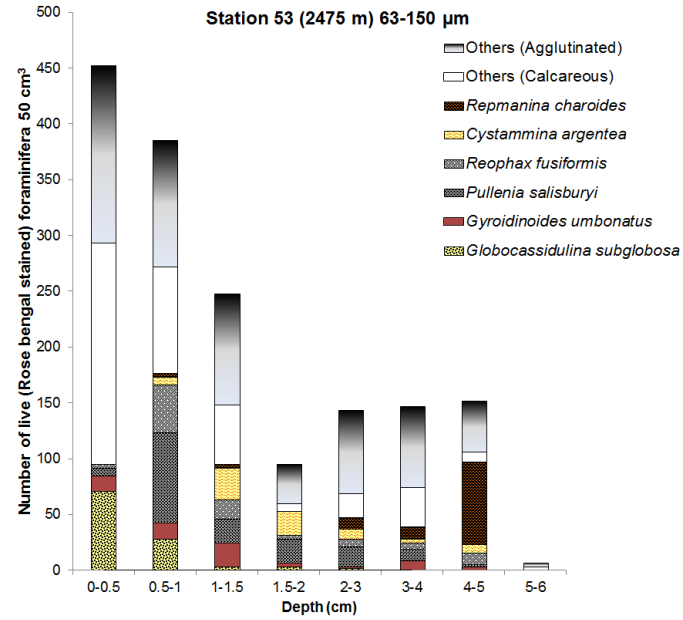
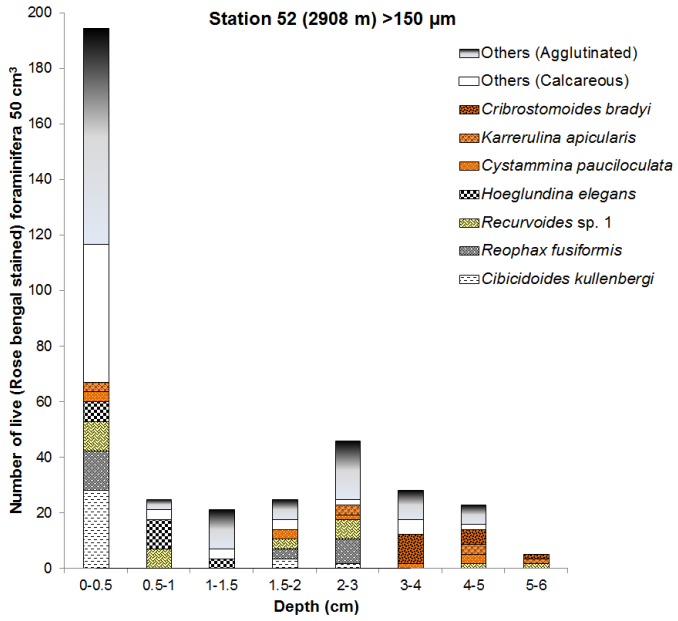


Figure 4e



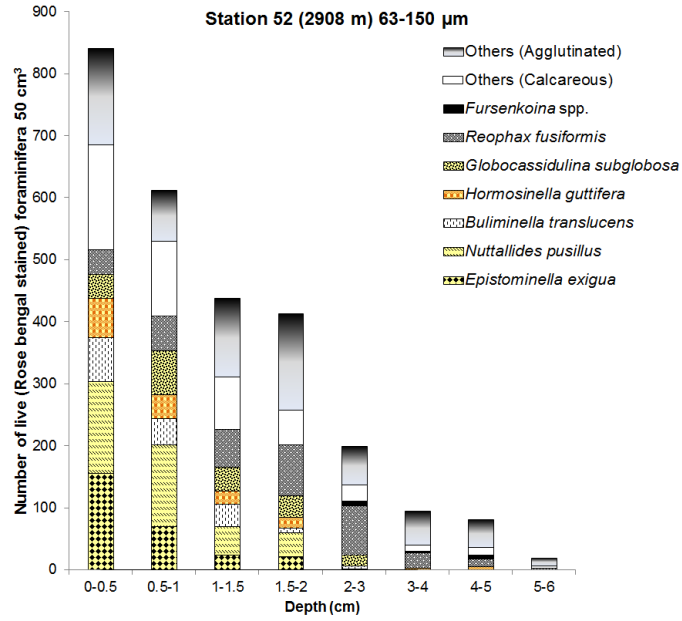
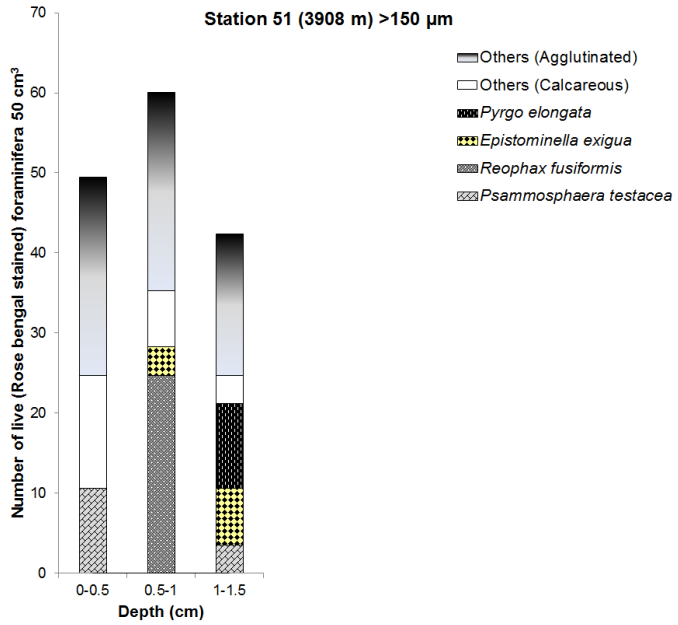


Figure 4g



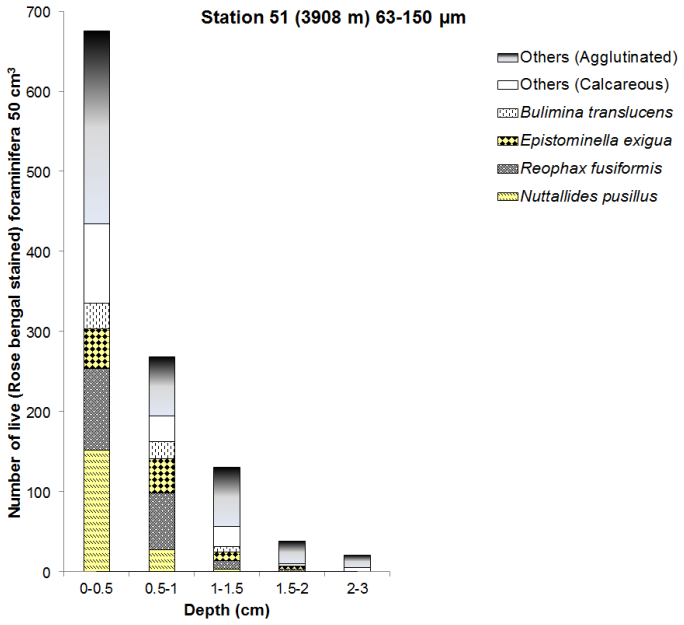
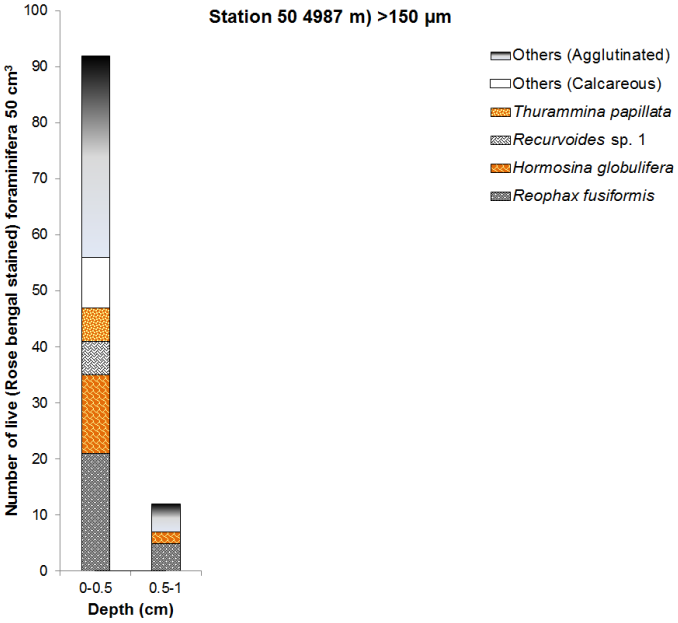


Figure 4h



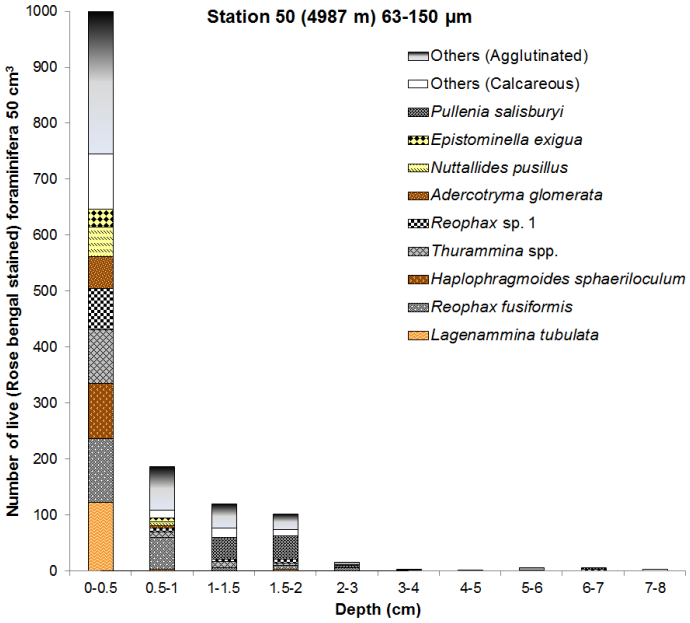


Figure 4a-h. Living foraminiferal downcore distributions (number of individuals found at each sampled level, standardised for 50 cm^3 sediment volume) for all eight stations. For each core, all dominant species discussed in the text are represented.

3.5 DISCUSSION

3.5.1 CALCAREOUS INTERMEDIATE AND DEEP INFAUNAL TAXA (>150 µm)

In almost all cores, an abundance maximum in both the >150 µm and 63-150 µm fractions occurs in the upper first centimetre of the sediment (Figures 4a-h). However, not all cores show the typical exponential decline in standing stocks deeper into the sediment. In particular our mid-depth stations at 2475 m and 2908 m show rather substantial standing stocks at deeper sediment layers in both size fractions, down to 5 cm. Across the transect the total average living depth (ALD_{10}) for the >150 µm increases from 0.7 cm at our shallowest station at 282 m to 1.8 cm at lower bathyal depths (2908 m), followed by a strong decrease towards abyssal depths (0.3 cm at 4987 m) (Fig. 5). For the calcareous part of the fauna, in the >150 µm fraction (Fig. 6 a) the deepening of the ALD_{10} from 0.6 cm at 282 m to 2 cm at 1374 m is largely the result of the increasing ALDs of intermediate (e.g., *Melonis barleeanus* and *Uvigerina elongatastriata*) and deep infaunal species (e.g., *Globobulimina affinis* and *Chilostomella oolina*).

There is a clear bathymetrical succession of intermediate and deep infaunal species: at 290 m, *Melonis barleeanus*, *Globobulimina turgida* and *Uvigerina elongatastriata* all occupy intermediate infaunal microhabitats close to sediment surface, in the 0.5-1cm interval, while *Chilostomella oolina* preferentially lives slightly deeper in the sediment at 1-1.5 cm. Slightly deeper, at 490 m, the maximum occurrence intervals and ALD_{10}'s of *Melonis barleeanus*, *Uvigerina elongatastriata* and *Chilostomella oolina* notably increase, which we interpret as reflecting greater oxygen penetration into the sediment, while the absence of *Globobulimina turgida* may be due to reduced quantities of metabolisable organic compounds. At 1002 m

Uvigerina elongatastriata and *Chilostomella oolina* are absent and *Globobulimina affinis* occupies a deep infaunal microhabitat at 3-4 cm. A similar succession is seen in the Bay of Biscay where *C. oolina* dominates at a 140 m deep outer shelf station, probably in response to abundant labile organic matter input, and *G. affinis* is dominant at deeper sites, supposedly with less important organic supplies (Fontanier and others, 2002; Mojtahid and others, 2010). At 1374 m, *M. barleeanus* diminishes, and *G. affinis* presents a deep infaunal maximum at 4-5 cm. Until 1374 m, intermediate and deep infaunal calcareous species allow us to infer oxygen penetration depths, which suggest that from 282 m to 1374 m oxygen penetration depth increases from 1-1.5 cm to about 3.5 cm (Fig 5). At stations deeper than 1374 m, intermediate and deep infaunal calcareous species are absent in the >150 µm fraction, suggesting that conditions are too oligotrophic to sustain them (Jorissen and others, 1995, Fontanier and others, 2002). Overall, the succession and increasing ALD_{10} of intermediate and deep infaunal species with increasing water depth until 1374 m (bathyal slope) appears to be a response to diminishing organic flux and increasing oxygen penetration, in agreement with the TROX model (Jorissen and others, 1995, Fontanier and others, 2002).

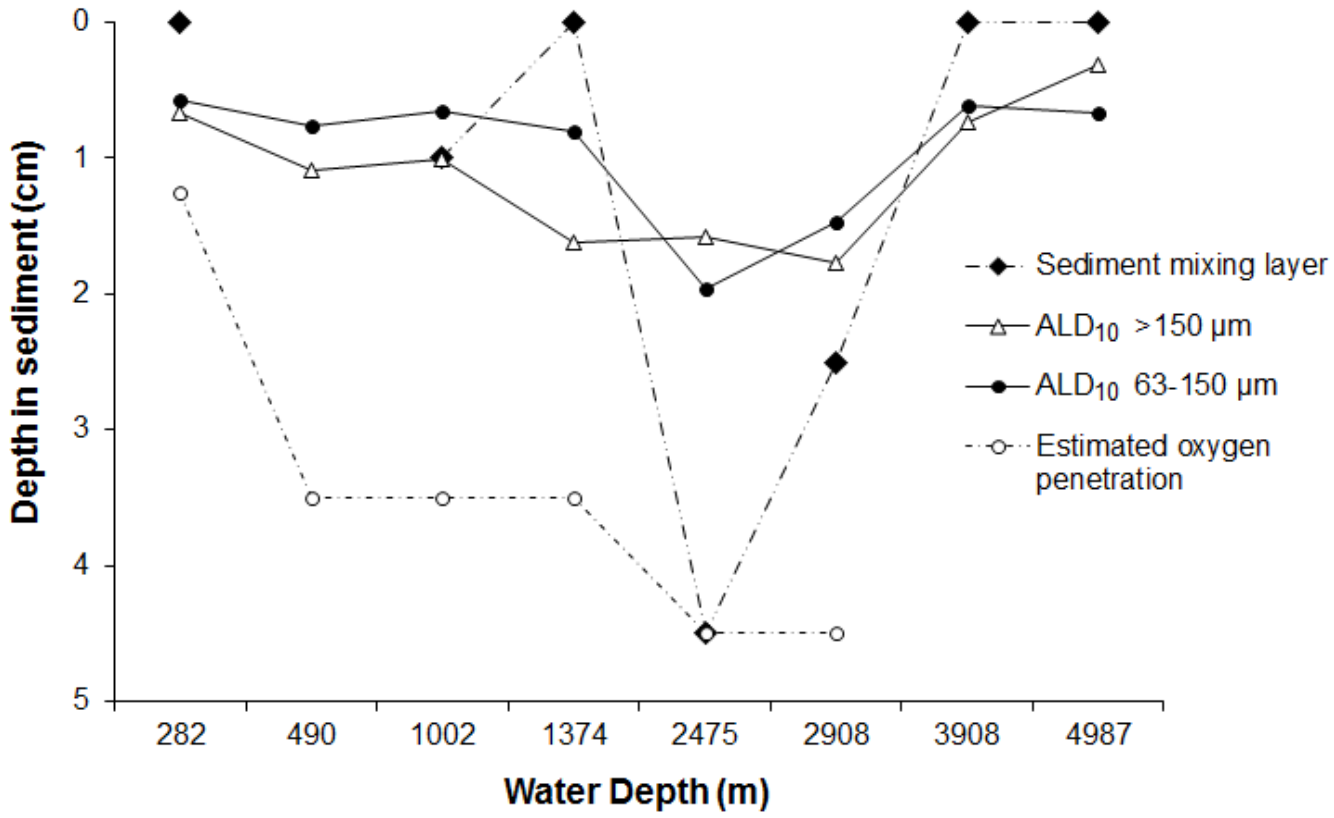


Figure 5. Estimated oxygen penetration, sediment mixing layer and ALD10 of foraminifera from >150 µm and 63-150 µm fractions.

Figure 6a Calcareous >150 µm

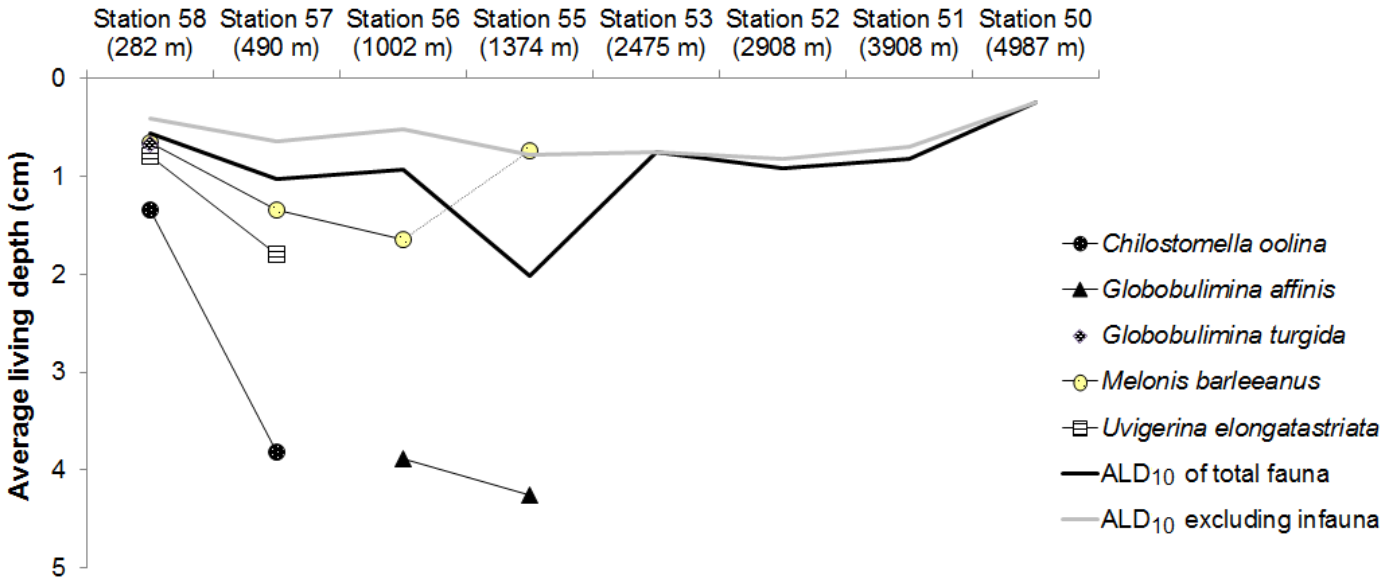
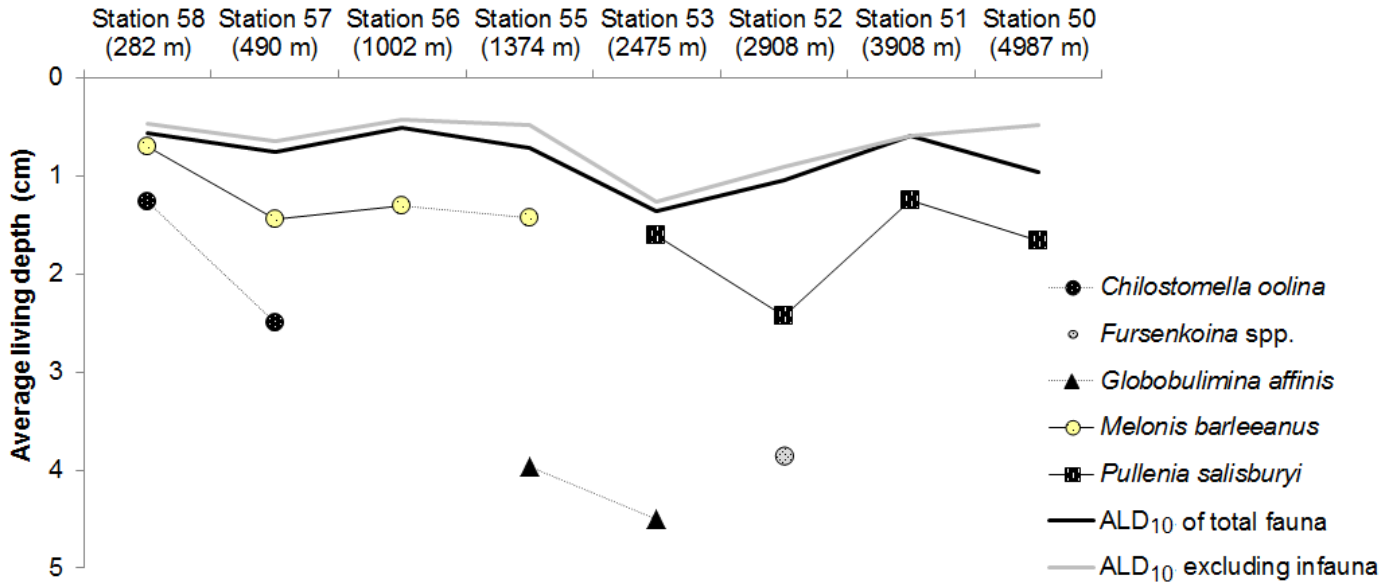
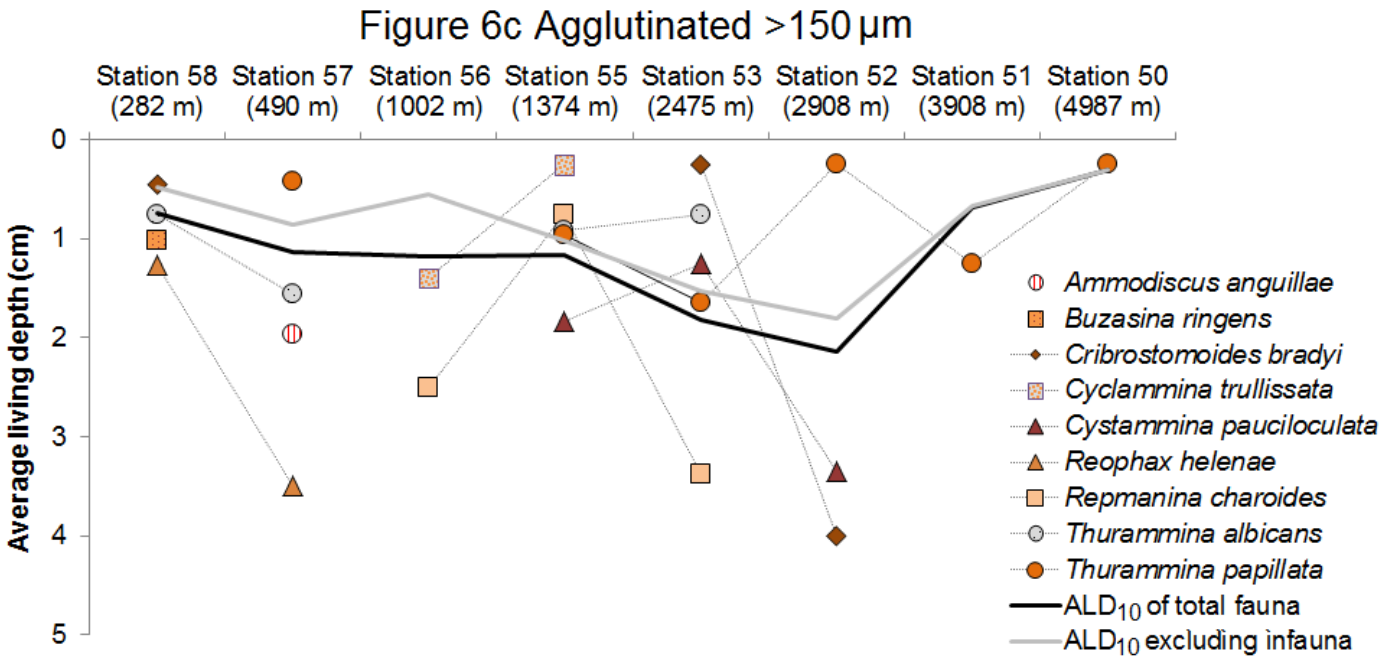


Figure 6b Calcareous 63-150 µm





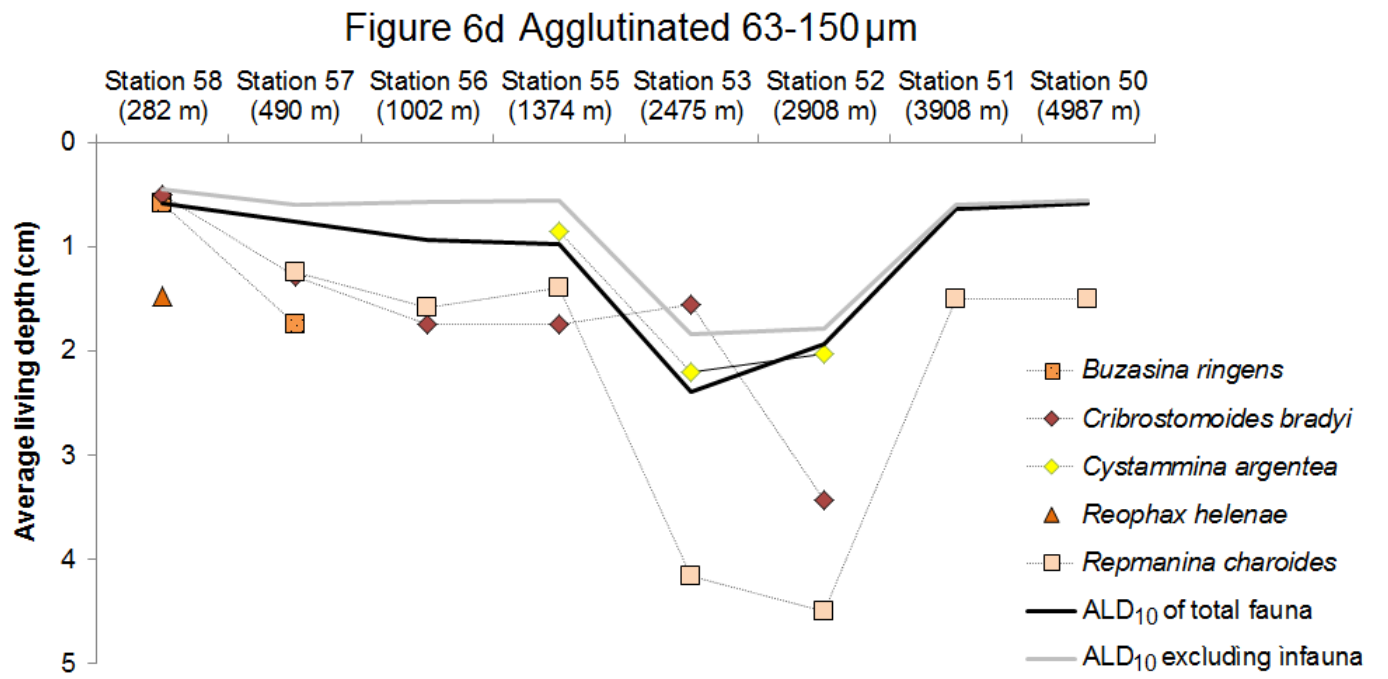


Figure 6 a-d. ALD_{10} values of dominant infaunal species for each wall group from the >150 µm and 63-150 µm fractions at each station.

3.5.2 CALCAREOUS INTERMEDIATE AND DEEP INFAUNAL TAXA (63-150 µm)

Very few studies have discussed the microhabitats of small calcareous faunas in the 63-150 µm fraction (Gooday and others, 1986; de Stigter and others, 1998; Kitazato and others, 2000). Between 282 and 1374 m, many calcareous species which express strictly intermediate and deep infaunal distributions (e.g., *Chilostomella oolina*, *Globobulimina affinis*, *Melonis barleeanus*) are juveniles of those recorded in the >150 µm fraction, and show very similar patterns (Figure 6 b). Similar observations have been recorded for *Chilostomella ovoidea* and *Globobulimina* spp. in Kitazato and others (2000). Despite the lack of intermediate and deep infauna in the >150 µm fraction below 1374 m, there is a continuous presence of such taxa in the 63-150 fraction, for instance *Fursenkoina* spp., appearing between 3 and 5 cm at 2908 m (Fig. 4f; ALD_{10} = 3.9 cm), or *Pullenia salisburyi* which shows an intermediate infaunal distribution between 2475 m (Fig. 4e; ALD_{10} = 1.6 cm) and 4987 m (Fig. 4h; ALD_{10} = 1.7 cm. *Pullenia salisburyi* has earlier been recorded in the zone of nitrate reduction (Jorissen and others, 1998).

3.5.3 AGGLUTINATED INTERMEDIATE AND DEEP INFAUNAL TAXA

(> 150 µm AND 63-150 µm FRACTIONS)

Similarly to the calcareous component of the assemblages, agglutinated foraminifera also show vertical species successions and changes in ALD_{10}. On the shelf where we anticipate a maximum organic carbon flux, *Buzasina ringens* and *Reophax helenae* occupy intermediate and deep infaunal microhabitats, respectively, which are relatively contracted in the

uppermost 1-1.5 cm (Fig. 4a, 6c). Towards progressively deeper stations there is a succession in dominance of infaunal species, with *Ammodiscus anguillae* (490 m), *Cyclammina trullissata* (1002 m) and *Thurammina papillata* (1374 m) all occupying intermediate infaunal microhabitats and finally *Repmanina charoides* (2475 m) and *Cribrostomoides bradyi* (2908 m) occurring still deeper in the sediment (Figs 4b-f, 6c). Below 2908 m on the abyssal plain, agglutinated species from the >150 µm fraction are limited to the uppermost 1 and 1.5 cms, and lack distinctive deep infaunal maxima. Such observations are in line with the TROX model (Jorissen and others, 1995), where the combination of oxygen penetration and nutrient availability is considered as optimal at bathyal depths, while at deeper stations foraminifera become restricted to the uppermost cm because of food scarcity in deeper sediment layers. In our data set, the presence of agglutinated deeper infaunal taxa at 2475 m and 2908 m on the lower bathyal slope is particularly striking, given the absence of calcareous deeper infauna >150 µm at these water depths. These observations suggests that in general, agglutinated deeper infaunal taxa have lower trophic requirements than calcareous ones and can therefore still proliferate in deeper sediment levels at greater water depth.

3.5.4 DIFFUSE VERTICAL PATTERNS

At several of our stations benthic foraminiferal species, which are usually limited to the upper sediment layer, are irregularly distributed over a larger depth range of the sediment column, with no clear microhabitat preference. This phenomenon is especially clear at 2475 m and 2908 m depth, where the total $ALD_{10,}$ inferred oxygen penetration and sediment mixed layers are deepest (Figure 5) Such an erratic distribution has also been observed at some sites in earlier studies (e.g., Gooday and others, 1986, Figs. 7L-O; Licari and others, 2003, Fig. 2;

Fontanier and others, 2005, Fig. 8, 2008, Fig. 3; Tapia and others, 2008, Fig. 2) where foraminifera frequently show presences down to significant depths in the sediment beyond their normal microhabitat ranges. There are a number of possibilities that could explain these observations:

1. Some species may display downward dispersal within the sediment by active locomotion (Gross, 2000). Foraminifera can migrate below the uppermost sediment in response to factors such as predation, changing redox fronts and interspecific competition and at the same time take advantage of organic matter within the sediment. (e.g., Corliss and Chen, 1988; Linke and Lutze, 1993; Rathburn and Corliss, 1994; Rathburn and others, 1996; Jorissen, 1999; Kitazato and others, 2000). Although this may be the case for some species (e.g., *Hippocrepina* sp. in Heinz and others, 2001 and *Quinqueloculina* sp. in Severin and others, 1982, Gross, 2000 and Gooday and others, 2010), this does not explain why some typically shallow infaunal species which tend to have clear maxima in the uppermost cm in most stations have more diffuse downcore distributions at some of our stations. Many of these species e.g. *Epistominella exigua*, *Globocassidulina subglobosa*, *Hormosinella guttifera and Nuttallides pusillus* have been documented to respond positively, either directly or indirectly, to phytodetritus (Fontanier and others, 2003, Gooday 1993, Gooday and Hughes 2004, Gooday and others, 2010) suggesting that they may have a pronounced preference for labile organic matter. However, downcore profiles of organic matter components (Fig. 2) systematically show that deeper sediment layers at 2908 m are very poor in phytopigments. Phytopigments are known to have a positive influence on foraminiferal standing stocks (Koho and others, 2008, Phipps and others, 2012), but these are mostly consumed in the uppermost cm. It is therefore highly unlikely that these species have moved deliberately to the deeper sediment layers where we observe them.

2. Deeper occurring representatives of shallow infaunal species may be living in the vicinity of microhabitats created by macrofaunal burrows in deeper sediment layers where oxygen and labile food particles are introduced (Aller and Aller, 1986; Aller, 1988, 2001; Meyers and others, 1987, 1988; Thomsen and Altenbach, 1993; Loubere and others, 1995; Jorissen, 1999; Murray and others, 2002; Meysman and others, 2006; Hess and Jorissen, 2009, Gooday and others, 2010, Loubere and others, 2011). Previous studies have singled out certain species such as *Bulimina marginata* and *Eggerelloides scabra,* which could preferentially select microhabitats within such burrows (Jorissen and others, 1999; Hess and Jorissen, 2009). This suggestion was based on the appearance of clear maxima of these species in deeper sediment layers, well below the zero oxygen level. The suggestion of Loubere and others (2011) that calcareous foraminifera mainly colonise macrofaunal burrows, and are not organised according to a vertical microhabitat succession, could explain our diffuse patterns with no apparent microhabitat selection at 2475 and 2908 m. However, even at these two stations, where bioturbation is extensive, it is still possible to distinguish a more classical vertical microhabitat succession, particularly with the intermediate/deep infaunal microhabitats of *Fursenkoina* spp. (below 2-3 cm at 2908 m, Fig. 4e) and *Pullenia salisburyi*. The latter species consistently shows a preference for subsurface distributions in both bioturbated and non bioturbated stations between 2475 m and 4908 m (Figs. 4e, 4h). Shallow infaunal species such as *Bulimina translucens, Epistominella exigua, Globocassidulina subglobosa* and *Nuttallides pusillus* which dominate the 63-150 µm calcareous assemblages are also clearly concentrated in the uppermost cm. The specimens occurring in deeper sediment layers do not present clear secondary density maxima, but rather a diffuse downcore distribution. The infaunal individuals represent only a small proportion of their total populations, suggesting that even if they do colonise macrofaunal burrows, these habitats form only a minor part of their total niche. Finally, agglutinated

foraminifera such as *Karrerulina apicularis* and *Reophax fusiformis* express diffuse vertical patterns much more frequently than calcareous foraminifera. Since agglutinated foraminifera are generally more tolerant of low quality food (Cornelius and Gooday and others, 2004; Gooday and others, 2008; Koho and others, 2008; Phipps and others, 2012), this observation is difficult to combine with the idea that foraminifera actively select food-enriched bio-irrigation structures.

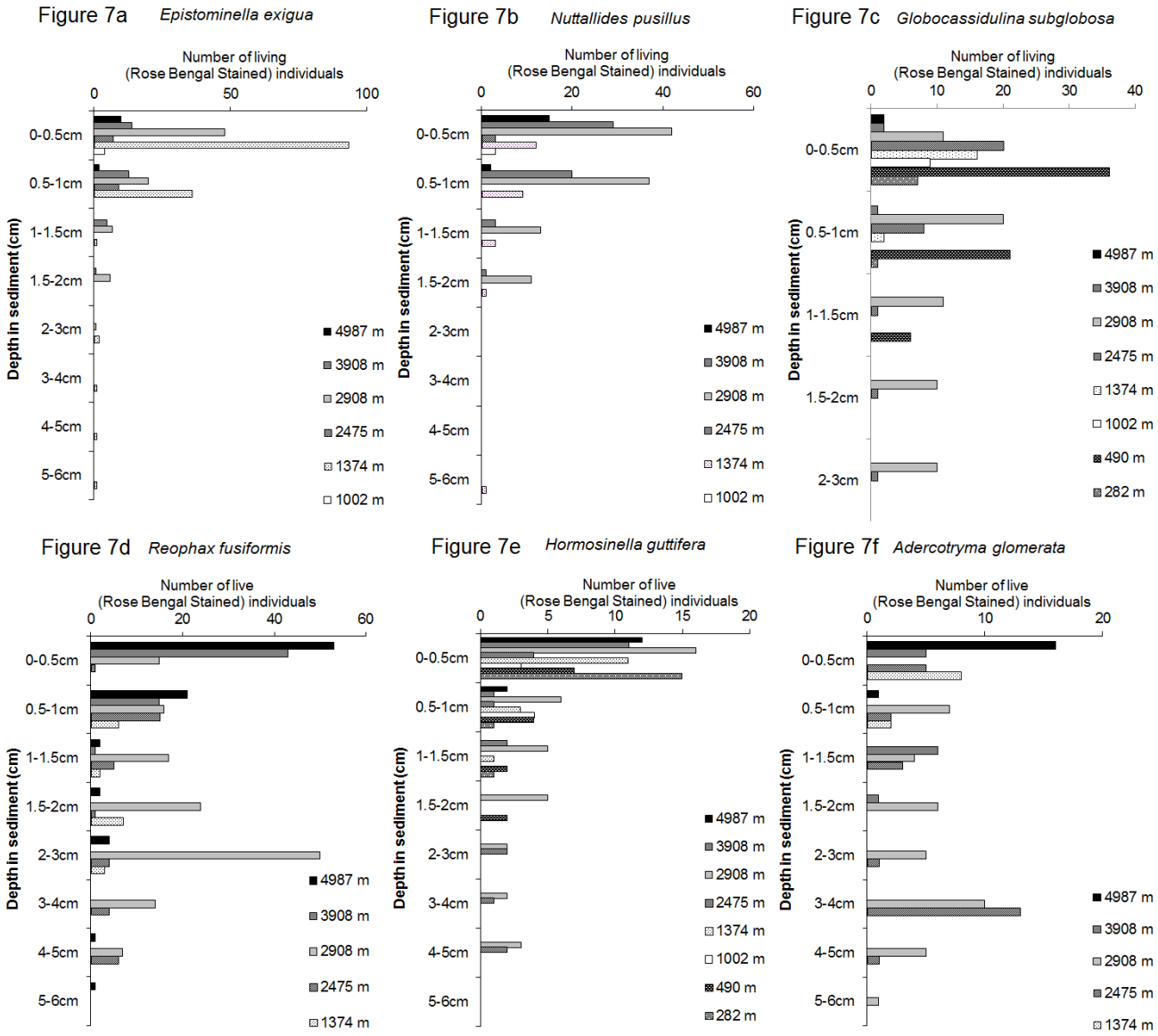
3. Finally, the specimens occurring in deeper sediment layers may have been passively transported to deeper sediment layers by macrofaunal bioturbation. Macrofaunal bioturbation is known to play an important role in displacing foraminifera and modifying their vertical distributions (Buzas, 1977; Collison, 1980; Langer and others, 1989; Moodley, 1990, 1998, Boucher and others, 2009) and are easily moved downwards into the sediment (Lipps, 1983; DePatra and Levin, 1989). In the absence of mixing, shallow infaunal foraminifera are expected to be concentrated in the surface layers of the sediment where nutrient resources and oxygen concentrations are optimal (Moodley, 1990). When displaced, they will either 1) immediately attempt to move back to their preferred microhabitat at the surface, 2) survive under the conditions created by macrofaunal burrows until they become anoxic and then readjust to the surface, or 3) stay trapped in the deeper sediments, being unable to move back to the surface, but able to survive for a period of time.

Summarising, it seems probable that the diffuse distributional patterns of many taxa are a consequence of intensive macrofaunal bioturbation. Although it has been suggested for some species (*Bulimina marginata, Eggerelloides scabra*) that they may actively colonise deeper burrows, the absence of clear infaunal maximum distributions among foraminifera suggests that active colonisation of bio-irrigation structures is not a dominant feature at our stations. Conversely, diffuse patterns suggest that many foraminifera have been transported passively to deeper sediment layers, where they encounter less favourable conditions. It appears

furthermore that for some species, the diffuse patterns are much more developed than for other ones. In fact, calcareous and agglutinated foraminiferal groups show different patterns. Although their vertical ranges are expanded, calcareous foraminifera still show exponential downward decreases in standing stocks (examples in Figures 7a-c). In contrast, agglutinated species show much more random and erratic distributions downcore (examples in Figures 7d-f). This suggests that after being displaced to deeper sediment layers, calcareous faunas have a higher capacity to migrate back to their preferred microhabitats close to the sediment surface than agglutinated ones. In fact, many laboratory experiments which simulate bioturbation of sediments with reduced oxygen and under the absence of food inputs, generated an upward migration of benthic foraminiferal species after they were randomly displaced downward (Alve and Bernhard, 1995; Moodley and others, 1998; Gross, 2000; Duijnstee and others, 2003; Ernst and van der Zwaan, 2004; Geslin and others, 2004; Panchang and others, 2006; Bouchet and others, 2009).

Furthermore, Ernst and others, (2002) found that strictly shallow infaunal opportunistic foraminifera incurred high mortality but re-equilibrated rapidly to their preferred microhabitat at the top 1 cm. Conversely, deeper infaunal taxa did not show any net upward or downward change of their distribution patterns, but survived successfully and in some cases reproduced. Migratory responses to bioturbation may not be uniform between different foraminiferal species as once below the surface layers, survival or success would depend on a range of factors associated with the activity of the individual species. An overview by Geslin and others, (2004) of the minimum speeds of different foraminifera species within the literature range from 0.004 to 0.77 cm h^{-1} in shallow water and from 0.002 to 0.53 cm h^{-1} for deep-sea foraminifera. This suggests that foraminiferal mobility rates may vary between different species as well as within a single species (Wetmore, 1988). However, Gross (2000, 2002) did not determine a difference in speed of migration between epifaunal and infaunal foraminiferal

groups, or any changes linked to water depth, although under oligotrophic conditions foraminifera tended to have higher mobility rates than under more eutrophic conditions.



Figures 7a–f. Downcore distributions of common shallow infaunal calcareous and agglutinated foraminifera.

3.5.5 ESTIMATING THE NUMBER OF FORAMINIFERA NOT FITTING A CLASSICAL VERTICAL MICROHABITAT SUCCESSION

In the absence of direct observations, we cannot determine whether dispersed individuals occurring in deeper sediment layers have been transported there by bioturbation, or have perhaps in some cases actively colonised bio-irrigations structures, as suggested by Loubere and others, (2011). However, we may investigate if there are any differences in the number of foraminifera living outside of their "normal" microhabitat according to their wall structure (calcareous or agglutinated) and size (>150 µm or 63-150 µm). In order to do this it is important to know which species occupy which microhabitats in less bioturbated sediments. Tentatively, for all species with a known shallow faunal microhabitat and those with a clear maximum abundance in the uppermost 0-1 cm, we considered all individuals found at deeper sediment levels (below 1 cm) as "anomalous". We considered the intervals where maximum abundances occur of *Melonis barleeanus* and *Pullenia salisburyi* (where applicable), and *Chilostomella oolina* and *Globobulimina affinis*, to represent the preferred living depth ranges of other intermediate infauna and deep infauna respectively; specimens above or below these sediment intervals were considered as "anomalous". Considering the bathymetrical gradient, there are clearly higher estimated percentages of anomalous foraminifera at 2475 m and 2908 m (>150µm 33-43% and 63-150µm 32-42% respectively). At other depths, their percentage ranges from 6-19%. When agglutinated and calcareous foraminifera are considered separately (Figure 8), there is a clear difference. At all depths with the exception of 282 m, agglutinated foraminifera show higher estimated percentages of "anomalous" foraminifera than calcareous ones. At 2908 m, the difference is particularly evident. Nonetheless, both wall types share the same trends along the depth transect. These

data indicate that the factor causing the atypical appearance of foraminifera below their usual microhabitats affects both calcareous and agglutinated foraminifera. However, calcareous taxa are less prone to this phenomenon than agglutinated taxa. This suggests that after being displaced passively to deeper sediment intervals, calcareous foraminifera are more successful in readjusting to their preferred microhabitat than agglutinated ones. Alternatively, it could also mean that they are less successful colonisers of bio-irrigation structures than agglutinated taxa. Finally, the estimated percentage of "anomalous" foraminifera does not vary much between the two studied size fractions (Figure 8). This suggests that the size of foraminifera is not an important factor in this context.

Summaring, on the basis of our vertical distribution patterns, we have the impression that individuals are found in deeper sediment layers mainly due to macrofaunal bioturbation, by which they have been transported passively below their preferred microhabitat zone. For the calcareous component of the assemblage, we suspect a more rapid return to their preferred shallow infaunal microhabitats immediately following displacement by macrofaunal bioturbation. For agglutinated species, this is much less clear. We suggest that calcareous foraminifera readjust more rapidly due to their higher trophic requirements and migrate along a food gradient (e.g. phytopigment concentrations, Fig. 2). Although no conclusive differences in mobility have been shown between calcareous and agglutinated foraminifera, agglutinated ones may have lower trophic needs and could be able to survive in more food impoverished sediments. This hypothesis is supported by the fact that calcareous foraminifera show a significant positive response to labile phytopigments (Koho and others, 2008; Phipps and others, 2012), and also by the observation that agglutinated foraminifera increase in relative percentage abundance in the deep sea where conditions become progressively oligotrophic (Cornelius and Gooday and others, 2004; Gooday and others, 2008; Koho and others, 2008; Phipps and others, 2012).

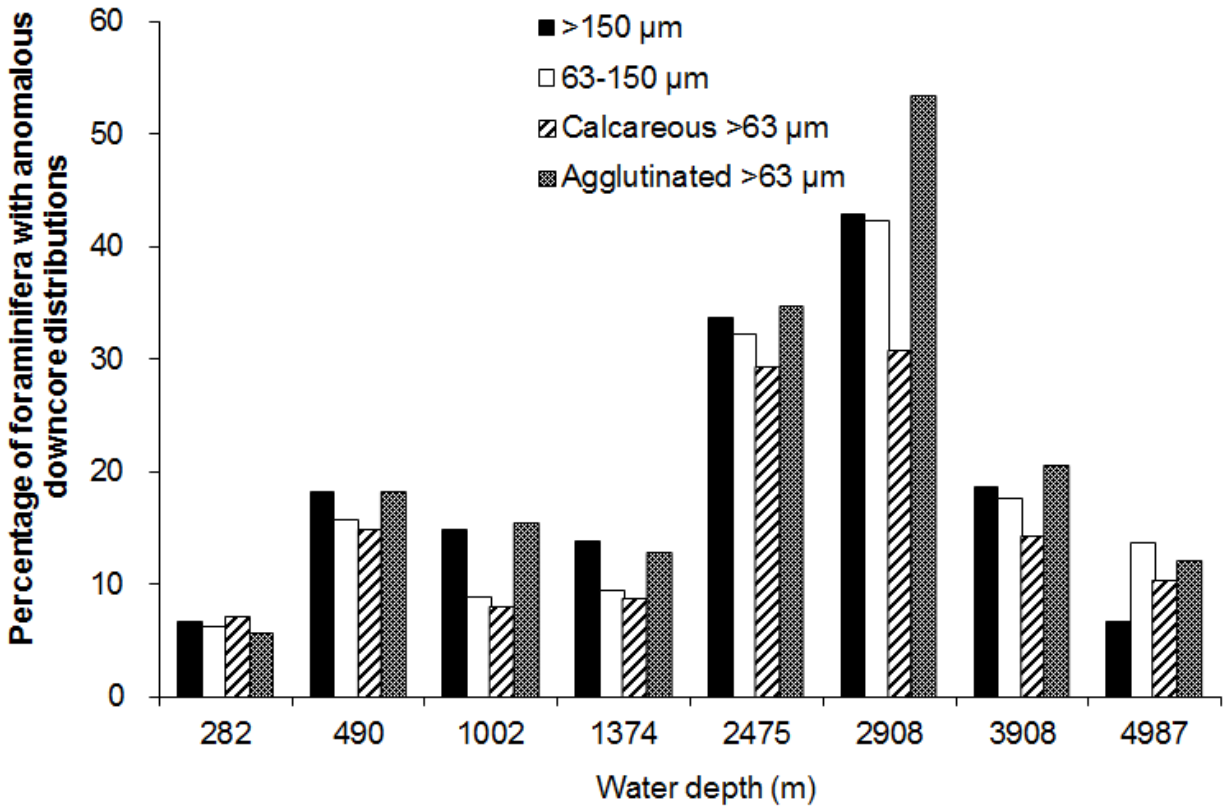


Figure 8. Estimated relative percentages of anomalously distributed foraminifera in >150 µm and 63-150 µm fractions, and in the total (>63 µm) calcareous and agglutinated assemblages.

3.5.6 CORRECTED ALD_{10} PATTERNS FOR SMALL AND LARGE SIZED CALCAREOUS AND AGGLUTINANT TAXA

In Fig. 9 we corrected all our ALD_{10} calculations by not including individuals of shallow infaunal taxa found in deeper sediment layers. When comparing total faunal ALD_{10} values with and without shallow infaunal foraminifera with anomalous distributions downcore for the >150 µm fraction (Fig. 9a) and 63-150 µm fraction (Fig. 9b), the ALD_{10} values from 282-1374 m and 3908-4987 m are fairly similar. The greatest difference between corrected and uncorrected ALD_{10} values occurs at 2475 m and 2908 m. This coincides with the maximum inferred oxygen penetration and maximum extension of the sediment mixed layer (Fig. 5). When corrected ALD_{10} values are considered separately for calcareous and agglutinated groups (Figs. 9c-f), some interesting observations arise:

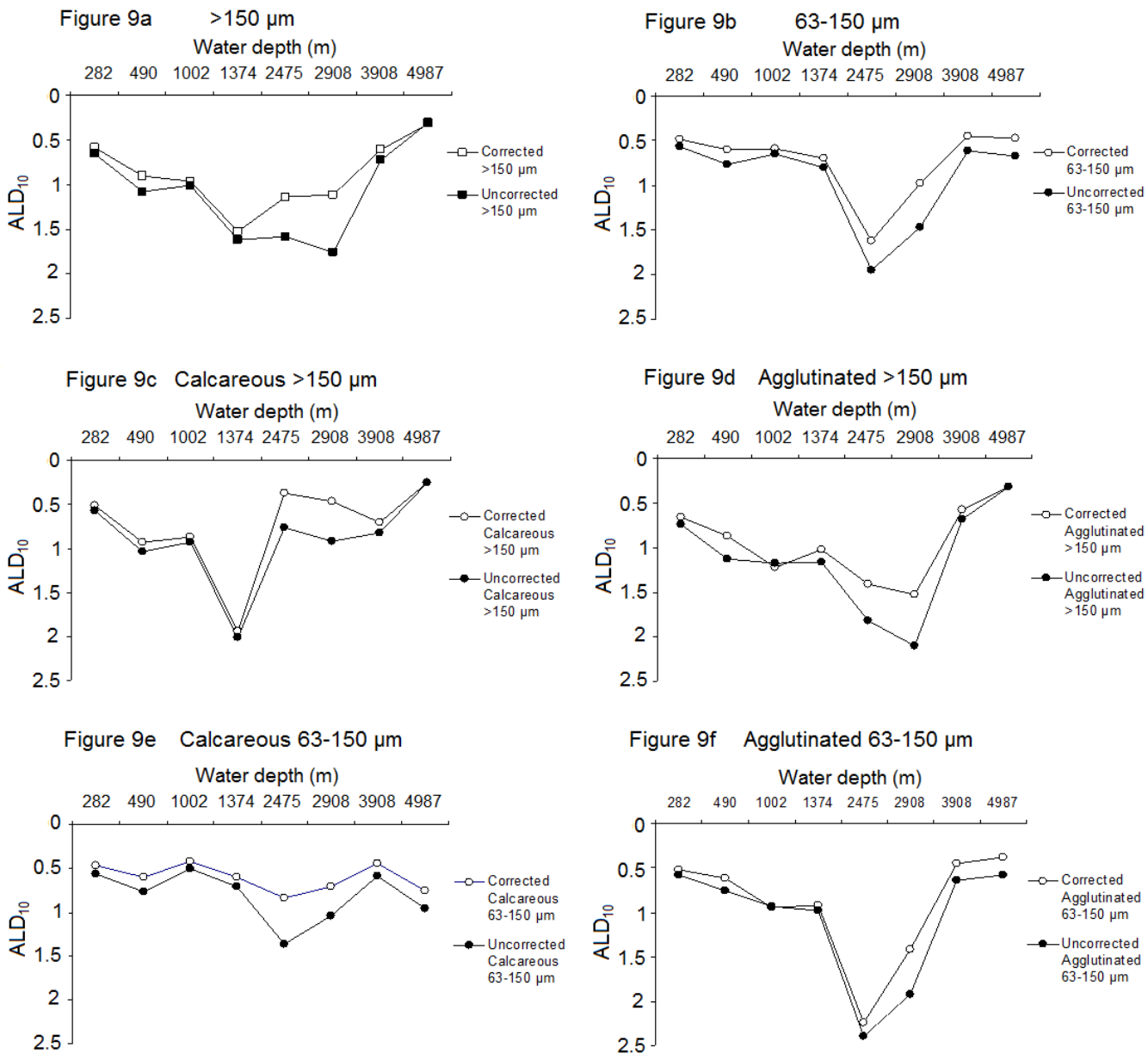
1) Calcareous foraminifera >150 µm (Figure 9c) show an increase in ALD_{10} with increasing water depth, culminating in a strong ALD_{10} peak at 1374 m, which is largely due to the deep microhabitat of *Globobulimina affinis,* which is dominant at this station. At depths greater than 1374 m, corrected ALD_{10} values drop to values around 0.5 cm, reflecting the poverty of intermediate and deep infauna at these stations.

2) Agglutinated taxa >150 µm (Figure 9d) show an increase in ALD_{10} across the depth transect until a peak at 2908 m. This may be attributed to a bathymetric succession of large numbers of intermediate and deep infaunal taxa that occur increasingly deeper within the sediment. At 2475 and 2908 m depth, where calcareous intermediate and deep infaunal species are very rare, agglutinated deeper infaunal species are still common, such as *Repmanina charoides* (2475 m) and *Cribrostomoides bradyi* (2908 m). However at deeper

and shallower sites these agglutinated deeper infaunal species are either absent or occupy shallow infaunal microhabitats. Both corrected ALD_{10} patterns, for calcareous and agglutinant foraminifera are perfectly in line with the TROX model (Jorissen and others, 1995), but maximal depth in the sediment is not attained at the same water depth. The peak in ALD_{10} of the calcareous faunas >150 µm occurs at a shallower depth (1374 m) compared to the peak observed in the >150 µm agglutinated faunas at 2908 m, over 1000 m deeper. This difference strongly suggests that calcareous intermediate and deep infaunal species have higher trophic requirements than agglutinated ones. Below 1374 m calcareous deeper infaunal species are virtually absent, whereas agglutinated infauna are a perspicuous feature of the assemblages until 2908 m.

3) Compared to the other groups, calcareous foraminifera of the 63-150 µm (Fig. 9e) fraction shows relatively little change in corrected ALD_{10}, which is always <1 cm. These shallow microhabitats suggest that most small-sized calcareous foraminifera depend on labile food particles, and may have an opportunistic life strategy. However, a maximum in ALD_{10} occurs at 2475 m, which is partially due to the abundance of *Pullenia salisburyi,* a small intermediate infaunal species which never occurs in the larger size fraction in our transect, and appears to be tolerant to oligotrophic conditions.

4) The agglutinated 63-150 µm fraction (Fig. 9f) shows a general increase in corrected ALD_{10} down to 1374 m, followed by a conspicuous maximum at 2475 m. The high ALD_{10} values at 2475 and 2908 m are due to a large number of intermediate and deep infaunal species at this station (e.g., *Cribrostomoides bradyi*, *Cystammina argentea, Repmanina charoides*). As for the other groups and size fractions, corrected ALD_{10} values are lowest (<0.5 cm) at our deepest stations 3908 m and 4987 m. Apart from the maximal ALD_{10} at 2475 m (rather than 2908 m), the pattern is quite similar to that of agglutinant foraminifera >150 µm .



Figures 9a–f. Average living depths of foraminifera with different wall types and from different size fractions. Both uncorrected (total foraminifera) and corrected (excluding anomalously distributed individuals) ALD_{10} values are presented.

3.6 CONCLUSIONS

In this present study we have tested for the first time the validity of the TROX model for calcareous and agglutinated faunas from both the >150 µm and 63-150 µm fractions. At some of our stations benthic foraminiferal species that are normally limited to the upper sediment layer are irregularly distributed over a larger depth range of the sediment column, with no clear microhabitat preference. This phenomenon is especially clear at 2475 m and 2908 m depth where the ALD_{10}, inferred oxygen penetration and sediment mixed layer are all deepest, and appear to be the result of intensive macrofaunal bioturbation. Although we cannot entirely exclude that some of the specimens occasionally occurring in deeper sediment levels have colonised bio-irrigation structures (Loubere and others, 2011), we think that their presence is due to displacement by macrofaunal bioturbation. Our analyses of estimated percentages of displaced foraminifera (shallow infaunal species living below the top 1cm) show little variation between the two studied size fractions. This suggests that the size of foraminifera is not an important factor in determining whether shallow infauna microhabitats are altered by macrofaunal bioturbation. However, agglutinated foraminifera show systematically higher estimated percentages of anomalously distributed specimens downcore than calcareous ones, suggesting that in strongly bioturbated sediments, calcareous shallow infauna retain their normal superficial distribution in the uppermost cm more successfully than agglutinated ones. We suggest that this is due to the higher trophic requirements of calcareous taxa, and their ability to track a gradient of increasing food particles (e.g., phytopigments) towards the sediment surface. Average Living Depth (ALD_{10}) patterns for calcareous and agglutinant taxa >150 µm, corrected for anomalously distributed specimens, fit well with the predictions of the TROX model. However, maximal depth in the sediment is

not attained at the same water depth for calcareous and agglutinated taxa. The peak in ALD_{10} of calcareous taxa >150 µm occurs at 1374 m, whereas the peak of agglutinated taxa >150 µm occurs at 2908 m, more than 1000 m deeper. This difference suggests that calcareous deeper infaunal taxa have higher trophic requirements than agglutinated ones. Agglutinated faunas of the 63-150 µm fraction show a general increase in corrected ALD_{10} values down to 1374 m, followed by a conspicuous maximum at 2475 m, that is very similar to agglutinated foraminifera >150 µm. Calcareous faunas of the 63-150 µm fraction show relatively little change in corrected ALD_{10} values, which are always below 1 cm. These shallow microhabitats suggest that most small-sized calcareous taxa depend on more labile food particles, and may have a more opportunistic life strategy.

CHAPITRE 4

DIVERSITY TRENDS OF LIVE BENTHIC FORAMINIFERA ALONG A TRANSECT OF THE PORTUGUESE MARGIN OPEN SLOPE.

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4.1 ABSTRACT

We studied a bathymetrical transect of eight stations from 282–4987 m along the Portuguese margin open slope. Our study demonstrates the importance of analysing foraminifera from smaller fractions (e.g., >63 µm), from deeper sediment intervals down to 10 cm, and the consideration of calcareous and agglutinated foraminifera as separate groups when determining the causes of diversity patterns. In the > 63 µm, diversity is highest at the most shallow, eutrophic station (282 m). A general decrease in diversity with increasing depth is observed, as species richness decreases and dominance of certain small species increases in response to greater oligotrophic conditions. Diversity of the >150 µm fraction is also highest at the most shallow station but expresses a bimodal diversity pattern across the transect. Secondary peaks in diversity at 2908–3908 m coincide with high equitability where many species are represented by a single individual. When analysed separately, calcareous foraminifera >63 µm show a very similar diversity pattern to the total foraminifera >63 µm. Highest diversity occurs at our most eutrophic, low-oxygen station (282 m) suggesting that low-oxygen does not limit calcareous foraminiferal diversity. Towards greater depths calcareous foraminifera diversity decreases; they do not exploit intermediate and deep infaunal niches created by macrofaunal bioturbation. These results suggest that the TROX model cannot explain biodiversity patterns in calcareous foraminifera, which instead appear to be exclusively related to the quantity, quality and seasonality of organic carbon flux. In contrast agglutinated foraminifera >63 µm have comparatively low diversity at 282 m. In comparison to calcareous taxa, they appear to be less competitive for food resources in superficial sediment layers. Consequently, they appear to be limited (by competition) to slightly deeper infaunal niches, where at eutrophic sites, shallow oxygen penetration could limit their species richness and increases dominance. Increased oxygen penetration and bioturbation at deeper sites opens up additional niches for intermediate and deep infaunal

agglutinated species, thus increasing their species richness and diversity. Finally at our deepest, most oligotrophic stations, diversity is minimal. Therefore, the TROX-model adequately explains the observed diversity trends of agglutinated foraminifera.

4.2 INTRODUCTION

In the 1960's, a surprisingly large number of species were recorded from the deep sea (Sanders and others, 1965; Hessler and Sanders, 1967; Sanders, 1968), contrary to the then prevailing idea that the deep sea was depauperate of life (Forbes, 1844). This discovery was made possible by advances in sampling technology that allowed the collection of semi-quantitative and quantitative samples of smaller faunas living in deep-sea sediments (Hessler and Sanders, 1967; Grassle and Sanders, 1973; Grassle, 1977; Sanders, 1979). Subsequent observations have confirmed that high species diversity in the deep sea, particularly of the benthic macrofauna and meiofauna, is a global feature (Rowe and others, 1982; Gage, 1996; Gooday and others, 1998, Rex and others, 2005b). In deep-sea samples, there may be as many as 250 species of macro- and meio-benthic invertebrates in a single square meter of sediment (Smith and others, 1998). Certain groups may be particularly rich in species and therefore of special importance in biodiversity research. Estimates of total species diversity in the deep sea suggest that there may be up to 10 million macrobenthic species (Grassle and Maciolek, 1992; Poore and Wilson, 1993). However, these estimates do not take into account the possible cosmopolitan nature of both the deep-sea habitat and the wide bathymetrical and geographic ranges of most species, and therefore is likely to be a gross overestimate (Gray and others, 1997). It has also been suggested that foraminifera may show a high diversity in the deep sea (Gooday, 1999). A recent estimate of foraminiferal diversity suggests that there may be 4280 known modern benthic foraminifera species (Murray, 2007).

Observations have indicated several patterns in the distribution of diversity of deep-sea species. Firstly, the density of all size categories of organisms gradually decreases with increasing distance from the continental shelf, with the exception of bacteria (e.g., Hessler and Sanders, 1967; Rex, 1981; Rex and others, 1990, 2006). Secondly, the diversity within the deep sea is not evenly distributed amongst phyla. For example polychaetes, crustaceans (Peracarida) and molluscs (Bivalvia) contribute most to total macrofauna diversity (Hessler and Sanders, 1967; Grassle and Maciolek, 1992). Finally, most groups of organisms have greatest diversity at intermediate depths (2000-3000 m), and lowest at shallow and abyssal depths (Rex, 1973, 1976, 1981, 1983; Etter and Grassle, 1992; Boucher and Lambshead, 1995; Levington, 1995; Cosson-Sarradin and others, 1998; Levin and others, 2001; Stuart and others, 2003; Rex and others, 2005a,b). However, this unimodal pattern of diversity is not universal (Hessler and Wilson, 1983; Allen and Sanders, 1996; Rex and others, 1997; Levin and others, 2001; Stuart and others, 2001). Diversity studies of some groups, such as polychaetes, have not revealed unimodal patterns with depth (Hessler and Jumars, 1974; Jumars and Hessler, 1976). However it is thought that these observations may have arisen from limited sampling of very low-density communities (Gage and Tyler, 1991).

The first theories explaining the unusually high diversity of deep-sea communities were based on long-term evolutionary processes, particularly extreme niche specialisation in a constant physical environment (the Stability-Time hypothesis: Sanders, 1968; Thistle, 1983). However, hypotheses following this have focused on the causes of the unimodal pattern of diversity with depth, such as gradients of biological and physical parameters. Biological factors that change with depth may include productivity, competitive displacement, predation and bioturbation (e.g., Rex, 1981; Gage and Tyler, 1991, Rex and others, 2005a, b). Physical factors include changes in levels of physical disturbance or in features of the physical environment such as sediment heterogeneity, productivity, bottom-

water oxygenation, deep sea currents and catastrophic disturbances (Etter and Grassle, 1992; Paterson and Lambshead, 1995; Levin and others, 2001). There has been particular emphasis on the processes that may generate patches of different niches over a variety of spatial scales (Grassle and Sanders, 1973; Thistle, 1998). These have included the generation of patch mosaics by disturbance (Grassle and Maciolek, 1992; Lambshead, 1993; Levin and others, 2001) or by the activities of deep-sea organisms that modify the benthic environment (Thistle, 1979; Levin, 1991; Gage, 1996). In the latter case, patches may be extremely small, even down to the magnitude of an individual organism (Levin and Edesa, 1997). Such levels of disturbance may lead to a spatially and temporally random mosaic of patches on the deep-sea bed, at differing stages of recovery from disturbance which can increase diversity (Gage, 1996).

Foraminifera are an important component of the meiofaunal community in many benthic marine environments. In the deep sea they may account for more than 50% of the total biomass (Gooday and others, 1992). They express high densities for very low surface areas, meaning that they can be sampled relatively easily. Because of their extraordinary ability to adapt to extreme as well as more stable ecosystems, benthic foraminifera proliferate in a wide range of environments. Therefore at any depth and in every latitudinal zone, foraminifera will be a common element of the faunas, making them particularly useful for ecological (as well as paleoecological) studies. In order to adapt to such a wide range of environments, foraminifera have evolved many morphological characteristics and hence exhibit an extraordinary amount of morphological variation (Culver and Buzas, 2000). Furthermore, benthic foraminifera have a fully operational and relatively complete existing taxonomical framework, so that different sites may be compared easily. Many benthic foraminiferal tests are resistant to taphonomic processes, meaning that they have relatively high preservation potential. Their high abundances in the fossil record means that benthic

foraminifera are of great value in palaeoenvironmental and palaeoceanographic studies. However, little is still known of deep sea foraminifera, particularly abyssal plain foraminifera in which many undescribed soft-shelled forms have been found, which are not preserved in the fossil record (Gooday and others, 1999). Nonetheless, unlike many other groups, most foraminifera can be identified to species level, and the vast majority to generic level.

Diversity expresses the relationship between the number of species present (species richness) and the number of individuals of each of these species (evenness, dominance). Different diversity indices have been used in foraminiferal ecological studies. One of the aims of these indices is to correct for different sample sizes. These indices have a different sensitivity with respect to species equitability (Gage and May, 1993). Therefore it is preferable to use and compare several indices to describe and measure differences in diversity between samples (e.g., Buzas, 1979; Williamson, 1985; Levin and others, 2001). Such indices may include Species richness, Rarefaction (Sanders, 1969; Hayek and Buzas 1997; Gray, 2000), Fisher alpha (Fisher and others, 1943; Williams, 1964), Shannon-Weaver (Shannon and Weaver, 1949), Dominance (Simpson, 1949; Magurran, 2004) and Equitability (Pielou, 1975).

Foraminiferal diversity gradients have been observed for both latitude and bathymetry. For example some studies have recorded an overall decline in diversity of calcareous benthic foraminifera from the equator towards higher latitudes (Culver and Buzas, 2000; Corlis and others, 2009). This decrease in diversity is attributed to increased seasonality and the episodic presence of of pulsed organic carbon flux at higher latitudes. The phytodetritus which arrives at the seafloor during such events is consumed by only a few species of dominant, opportunistic calcareous foraminifera such as *Epistominella exigua* and *Nuttallides pusillus*. Although these species may temporarily raise species richness slightly, they occur in much higher numbers than other species which normally inhabit sediments

below phytodetrital layers. Consequently blooms of these species lead to lower evenness, and therefore lower diversity. This interpretation is consistent with research by Thomas and Gooday (1996) on ODP sites, where they suggested increased seasonality and strongly pulsed organic matter input as a mechanism for explaining reduced latitudinal diversity towards the pole. In contrast, regions with lower seasonality and more stable food input are characterised by a more even distribution of species, slightly higher species richness and therefore higher diversity (Corliss and others, 2009).

With increasing depth benthic foraminiferal diversity has been observed to decrease, attributed to declining food resources (Wollenburg and Mackensen, 1998; Wollenburg and Kuhnt, 2000; Fontanier and others, 2002, 2008). However higher foraminiferal diversities have been recorded at abyssal depths (>3000 m) than at shallow depths on continental slopes under the influence of Oxygen Minimum Zones (Gooday, 1999; Gooday and others, 2000). Recent work by Koho and others, (2008) on benthic foraminiferal distributions on the Portuguese continental margin has yielded some interesting results. A fundamental outcome of this study is the observation of different faunal assemblages and higher diversity (highest Shannon index and equitability values) on open slope compared to canyon environments. The authors suggest these differences are a response to changes in the quantity and quality of the organic material, which seem to be the main parameters influencing the distribution, standing stock and diversity of benthic foraminifera (Altenbach, 1985; Altenbach and Sarnthein, 1989; Ahrens and others, 1995; Schönfeld, 2001; Garcia and others, 2007; Jorissen and others, 2007). Many foraminifera workers use the TROX model (Jorissen and others, 1995) as a conceptual approach to explain the vertical distribution of foraminifera, in function of changing dissolved oxygen values and organic carbon flux at the sea floor with depth. The organic carbon supply is highest at shallow depths and decreases towards the abyssal plain, while oxygen penetration into the sediment follows the opposite trend. In mesotrophic, mid

bathyal settings, where oxygen penetration and organic carbon flux both reach high values, optimal conditions are created for maximum microhabitat differentiation, potentially causing higher diversity. Conversely at shallow depths and abyssal depths, microhabitats are limited to the uppermost centimetres or even millimetres, potentially causing a lower biodiversity.

In many deep-sea benthic foraminiferal studies, soft-bodied forms account for much of the diversity at lower bathyal and abyssal sites (Gooday and others, 1999, 2001). These forms still remain very poorly studied. Due to their lack of preservation in the fossil record, they are of little to no use in paleo-environmental studies. In fact, also many of the hard shelled agglutinating forms are very fragile and do not fossilize, leading some foraminifera workers to ignore them, even in modern ecological studies (Culver and Buzas, 2000; Corliss and others, 2009). Therefore, in order to compile meaningful data for the study of recent diversity trends of foraminifera with bathymetry and to permit comparisons with other deep sea metazoans, it is essential that total live assemblages are studied, including the non-fossilising taxa.

In order to obtain a better idea of bathymetrical trends of foraminiferal diversity, this paper reviews the diversity of benthic foraminifera from a single transect of open slope stations of the South Western Portuguese margin. All our data refer to live (i.e. Rose Bengal stained) foraminiferal faunas. Details on taxonomic and bathymetric ranges of foraminifera from the same transect are presented in Phipps and others, (2012) and their microhabitats are detailed in Phipps and others, (*in prep*)

4.3 MATERIAL AND METHODS

4.3.1 STUDY AREA

We studied the diversity of live benthic foraminifera > 63 µm from a westward oriented transect of stations located at depths ranging from 282 to 4987 m on the open slope off Cape Sines, on the Portuguese Margin at 37°50'N, from 9°05'W to 11°W (Fig. 1). The water column in this area is made up of a composite of water masses (García and others, 2003). Below the surficial waters (~30 m) the North Atlantic Central Water mass (ENACW) can be distinguished by its warm (12-16°C) and salty (≤36) properties, down to 600 m depth. Between 600 and 1600 m water depth, the Mediterranean Outflow Water (MOW) is distinguished by a strong salinity peak at 1100 m (>36). The North East Atlantic Deep Water (NEADW) forms the main water mass below the MOW, characterised by cooler temperature (2-10°C) and lower salinity (~35). Below approximately 4000 m, the Lower Deep Water (LDW) of Antarctic origin (Van Aken, 1999) is observed, with cold (~2°C) and low saline (<35) properties.

4.3.2 SAMPLE PREPARATION AND PROCESSING OF FORAMINIFERA

All samples were collected using a MUC multicorer in September 2006 on board the RV Pelagia (Fig. 1). Each core had an inner diameter of 6 cm and was sliced at 0.5 cm intervals from 0 to 2 cm depth, and 1 cm intervals from 2 to 10 cm depth. Details of the sample preparation are documented in Phipps and others, (2012). Special care was taken not to break small, fragile agglutinated tests by using a low power showerhead to wash samples. Organic-shelled monothalamous foraminifera and fragments of large tubular taxa were tabulated into an outside count and not included in diversity measurements. It should be noted that for reasons of time limitation, no replicate samples were studied at any of the eight

stations. The picking and determination of foraminiferal faunas in the finer size classes (below 100 μm) is particularly extremely time consuming. For this reason, in other deep-sea foraminiferal studies, the use of replicates has been limited to the top centimetre (e.g. Cornelius and Gooday, 2004), or the fine fraction (63-150 μm) is only studied in the topmost cm, without replicates (Wollenburg and Kuhnt, 2000; Duchemin and others, 2007). Alternatively, Mackensen and Douglas (1989) and Fontanier (2002) only analyse the >125 μm and >150 μm fractions respectively, down to 10 cm, but do not analyse the >63 μm fraction and did not study replicate samples.

Diversity indices were calculated using PAST software (Hammer and others, 2001). When counting species richness (*S*), we also implemented the rarefaction analysis (Sanders, 1969) to compare samples of different sizes (Hayek and Buzas, 1997; Gray, 2000). We use both the Fisher alpha diversity index (Fisher and others,, 1943; Williams, 1964) and the Shannon-Weaver heterogeneity index, H(S) (Shannon and Weaver, 1949) to measure assemblage diversity. Finally we use Dominance (D) (Simpson, 1949; Magurran, 2004) and Equitability (J) (Pielou, 1975) values to provide information on the evenness of the species abundance structure.

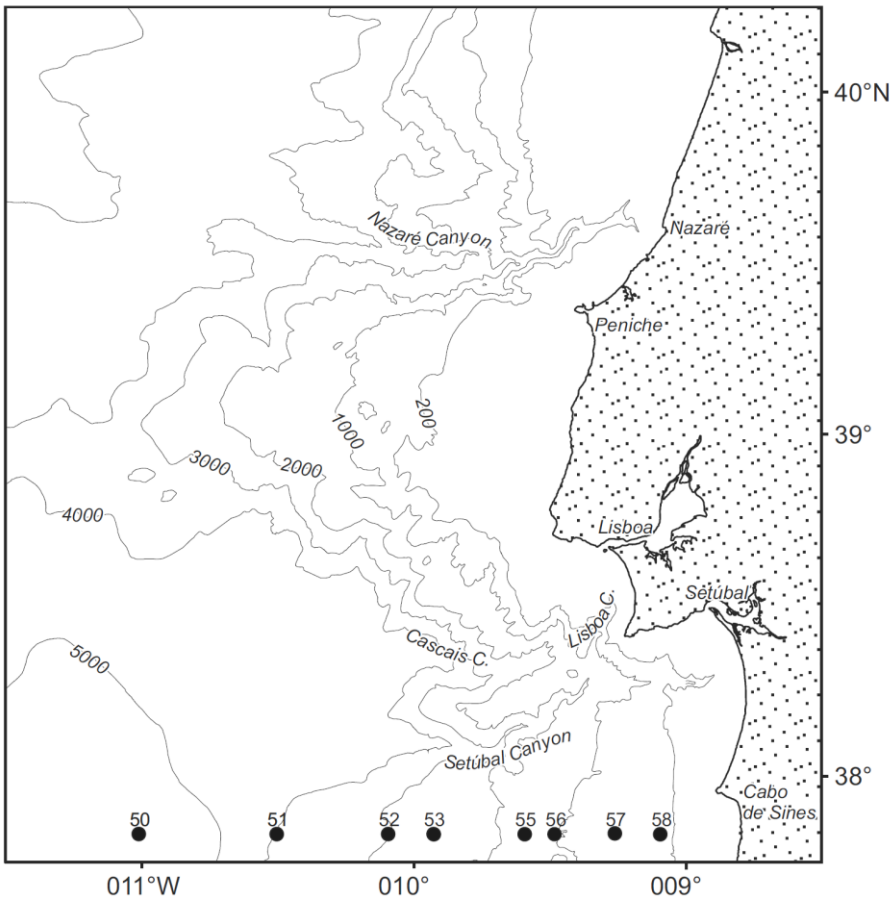

Figure 1. Study area of the Portuguese margin open slope transect. Black circles represent the position of each station.

4.4 RESULTS

4.4.1 >63 µm FRACTION (63-150 µm + >150 µm FRACTIONS)

Total foraminiferal densities, species richness and diversity indices for the > 63 µm µm fraction of the eight stations are recorded in Table 1 and diversity indices are illustrated in Figure 2. There is an overall trend of decreasing standing stocks with increasing depth. Foraminiferal density is highest at 282 m (~3600 specimens/50 cm^2). Towards ~1000 m

water depth, density drops to ~790 specimens/50 cm^2. Standing stocks then increase to ~1800 specimens/50 cm^2 at 2908 m, and then finally decrease to ~650 specimens/50 cm^2 at 3908 m. Similarly to standing stocks, species richness and diversity indices generally decrease with increasing water depth. In detail, species richness is highest at 282–490 m (both 138 species) and lowest at 3908 m (66 species) while species richness calculated by rarefaction ($S(E_{300})$) also shows a highest value at 282 m (78.5) and lowest value at 4987 m (58.5). Fisher alpha and Shannon indices are both highest at 282–490 m (33.5–35.0 and 4.1 respectively), whereas lowest Fisher alpha (21.8) and Shannon (3.4) index values occur at 4987 m and 3908 m respectively. In contrast to the other diversity indices, dominance shows a clear positive relationship with increasing depth. It is lowest at 280–490 m (0.03), and greatest at 3908 m (0.07). Finally, equitability values range from 0.85 (2475 m) to 0.78 (2908 m) and show no clear pattern with depth.

Station	Depth (m)	TSS (50 cm^2)	S	S (E_{300})	Fisher α	*H′*	*J′*	D
58	282	3595	138	78.5	33.5	4.1	0.82	0.03
57	490	3142	138	76.3	35.0	4.1	0.82	0.03
56	1002	789	82	69.5	29.5	3.7	0.84	0.04
55	1374	1744	104	66.7	29.4	3.7	0.81	0.04
53	2475	1349	98	71.3	29.9	3.9	0.85	0.03
52	2908	1784	104	66.9	29.1	3.6	0.78	0.05
51	3908	654	66	60.8	23.4	3.4	0.80	0.07
50	4987	923	70	58.5	21.8	3.5	0.83	0.05

Table 1. Diversity parameters of the >63 µm fraction

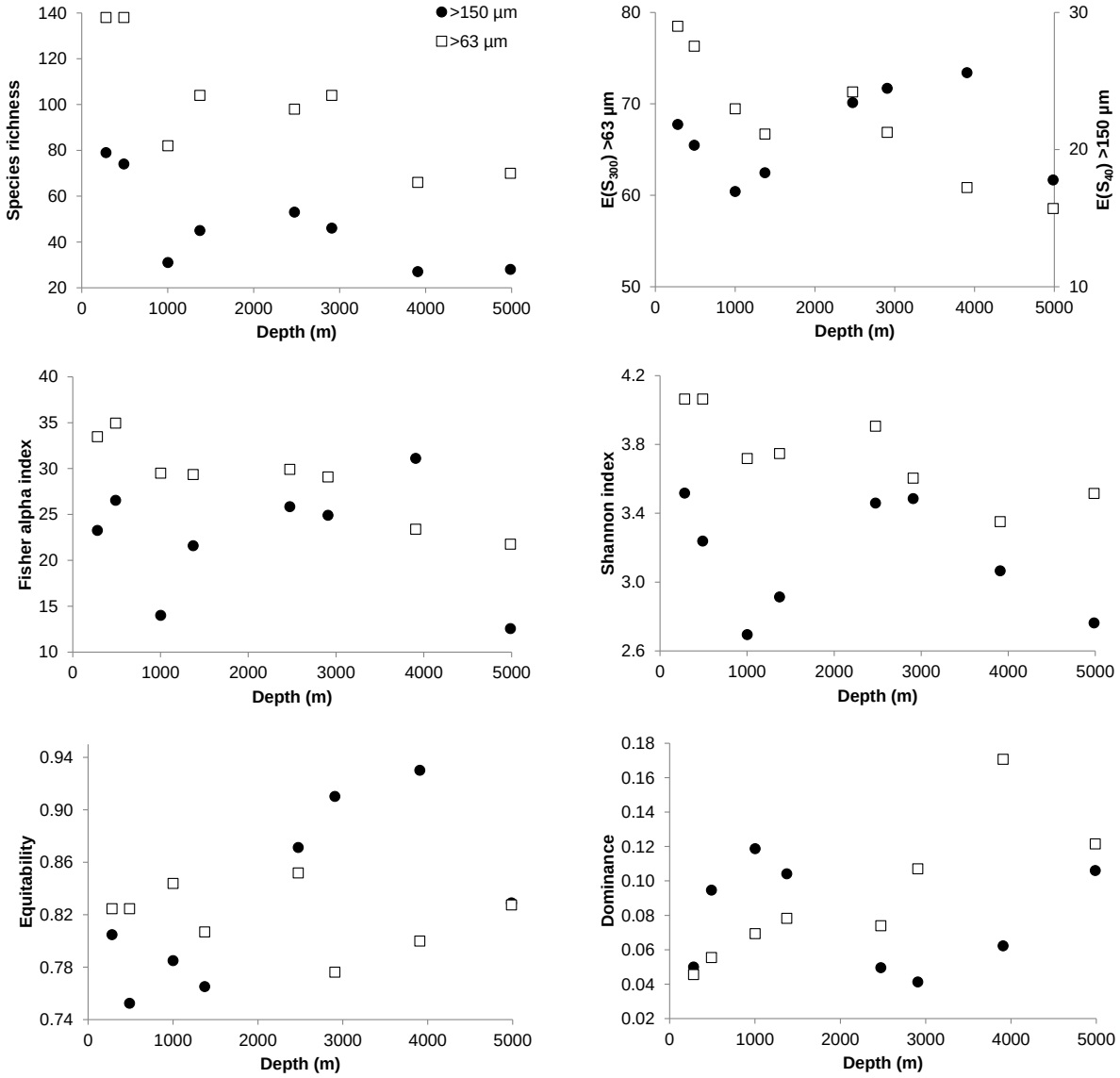

Figure 2. Diversity parameters of 150 and 63-150 µm fractions for each station. Black circles represent values for the >150 µm fraction and squares represent values for the >63 µm fraction.

4.4.2 >150 μm FRACTION

Densities, species richness and diversity indices of live foraminifera recorded in the > 150 μm fraction of the eight stations are shown in Table 2 and diversity indices are illustrated in Figure 2. The decrease with increasing depth revealed in the >63 μm standing stocks (Figure 2) is also shown in the >150 μm. A peak in standing stock is recorded at 282 m (~1200 specimens/50 cm^2) with a corresponding fall with increasing depth at 1002 m (~200 specimens/50 cm^2). Standing stocks show a small increase at 2475 m (~300 specimens/50 cm^2) but then fall to a minimum at 3908 m (~75 specimens/50 cm^2). Generally, species richness shows the same decrease with increasing water depth observed for the >63 μm fraction. Species richness is highest at 282 m (79 species) and lowest at 3908–4987 m (27 and 28 species respectively). In contrast, species richness measured by rarefraction ($E_{(40)}$) is highest at 282 m (21.8) and 3908 m (25.6) whereas the lowest can be found at 1002 m ($E_{(40)}$ = 16.9) and 4987 m (17.8). Generally rarefaction, Fisher alpha and Shannon indices show similar bimodal distributions with increasing depth. Fisher α index values are highest at 490 m (26.5) and 3908 m (31.1), and lowest at 1002 m and 4987 m (14.0 and 12.6 respectively). The Shannon index (Fig. 3 c) is highest at 282 m, 2475 m and 2908 m (all 3.5), and lowest at 1002 m (2.7) and 4987 m (2.8). While rarefaction, Fisher alpha and Shannon index values are lowest at 1002 m, dominance at this water depth is greatest (0.12). Lowest dominance values are recorded at 2908 m (0.04). Finally, equitability which shows no conceivable change in the > 63 fraction shows a clear increase with increasing depth in the > 150 μm fraction (Fig. 3f). Lowest equitability values are found at 490 m (0.75), whereas highest values are found at 3908 m (0.93).

Station	Depth (m)	TSS (50 cm^2)	S	S (E_{40})	Fisher α	*H'*	*J'*	D
58	282	1187	79	21.8	23.3	3.5	0.80	0.05
57	490	716	74	20.3	26.5	3.2	0.75	0.09
56	1002	202	31	16.9	14.0	2.7	0.78	0.12
55	1374	269	45	18.3	21.6	2.9	0.77	0.10
53	2475	309	53	23.4	25.9	3.5	0.87	0.05
52	2908	235	46	24.5	24.9	3.5	0.91	0.04
51	3908	76	27	25.6	31.1	3.1	0.93	0.06
50	4987	184	28	17.8	12.6	2.8	0.83	0.11

Table 2. Diversity parameters of the >150 µm fraction

4.4.3 CALCAREOUS FORAMINIFERA >63 µm

When analysed separately, calcareous foraminifera (sum of perforates and porcellaneous species) and agglutinated foraminifera show different characteristics; the differences in diversity indices between these two groups can be seen in Figure 3. Table 3 represents a summary of calcareous foraminiferal diversity measures and standing stocks for the >63 µm fraction. Calcareous foraminiferal standing stocks are highest at 280 m (~1900 specimens/50 cm^2) and generally decrease with increasing depth until our deepest station at 4987 m (~190 specimens/50 cm^2). Species richness is also highest at 280 m (82 species) and lowest at 4987 m (21 species). Species richness measured by rarefaction ($E(S_{100})$) confirms the general decline in species richness with increasing depth between 280 m (36.0) and 3908–4987 m (both 20.5). Similarly both the Fisher alpha and Shannon indices are highest at 280 m (20.6 and 3.5 respectively), and lowest at 3908–4987 m (7.8 and 2.3–2.4 respectively). Conversely, dominance values clearly rise with increasing depth; dominance is lowest at 280 m (0.05) and

maximal at 3908 m (0.17). Equitability values show no overall trend with increasing water depth. However while at other depths equitability values range from 0.82–0.78, they are particularly low (0.72–0.73) at 2908–3908 m.

Station	Depth	TSS (50 cm^2)	S	S (E100)	Fisher alpha	*H′*	*J′*	D
58	282	1910	82	36.0	20.6	3.5	0.80	0.05
57	490	1747	70	30.4	17.2	3.3	0.78	0.06
56	1002	531	46	28.9	15.2	3.1	0.81	0.07
55	1374	1137	55	28.3	14.4	3.1	0.77	0.08
53	2475	506	41	27.8	13.1	3.0	0.82	0.07
52	2908	868	46	24.4	12.4	2.8	0.72	0.11
51	3908	285	24	20.5	7.8	2.3	0.73	0.17
50	4987	189	21	20.5	7.8	2.5	0.82	0.12

Table 3. Diversity parameters of calcareous foraminifera >63 µm

4.4.4 AGGLUTINATED FORAMINIFERA >63 µm

Standing stocks and diversity indices for agglutinated foraminifera > 63 µm are summarised in Table 4. Total standing stocks are highest (1685 specimens/50 cm^2) at 280 m and lowest at ~1000 m (~260 specimens/50 cm^2). However below ~1000 m standing stocks increase to ~900 specimens/50 cm^2 at 2908 m before decreasing again to 370 specimens/50 cm^2 at 3908 m. Species richness is also lowest at ~1000 m (36 species) but highest at 490 m

(68 species). Similarly to standing stocks, species richness increases below ~1000 m to 58 species at 2908 m and decreases at 3908 m (42 species). However, species richness measured by rarefaction ($E(S_{100})$) suggests a bimodal distribution of species richness with increasing depth; two peaks are observed at 490 m (34.3) and 2475 m (33.4), while lowest species richness occurs at 282 m, 1374 m (both 29.7) and 3908–4987 m (both 30.0). Shannon index values also show a bimodal distribution with increasing depth, with two peaks at 490 m (3.5) and 2475 (3.4) and a lowest value at 3908 m (2.9). Fisher alpha index values are also highest at 490 m (17.8) and 2475 m (16.9), but lowest at 282 m (13.0). In contrast, dominance values are lowest at 490 m and 2475 m (both 0.05); highest dominance values occurs at 2908–3908 m (both 0.10) for which the lowest value, 13.7, is recorded at this station. This value is lower than that recorded on the abyssal plain (14.7 at 4806 m). Finally, equitability values show no particular trend with increasing depth. However equitability values are highest at 1002 m (0.86) and lowest at 2908 m (0.75).

Station	Depth	TSS (50 cm^2)	S	S (E100)	Fisher alpha	*H′*	*J′*	D
58	282	1685	56	29.7	13.0	3.2	0.79	0.07
57	490	1395	68	34.3	17.8	3.5	0.82	0.05
56	1002	258	36	30.5	15.3	3.1	0.86	0.07
55	1374	607	49	29.7	15.6	3.1	0.80	0.07
53	2475	844	57	33.4	16.9	3.4	0.83	0.05
52	2908	916	58	31.0	16.8	3.1	0.75	0.10
51	3908	370	42	30.0	15.8	2.9	0.79	0.11
50	4987	734	49	30.1	14.5	3.1	0.81	0.07

Table 4. Diversity parameters of agglutinated foraminifera >63 µm

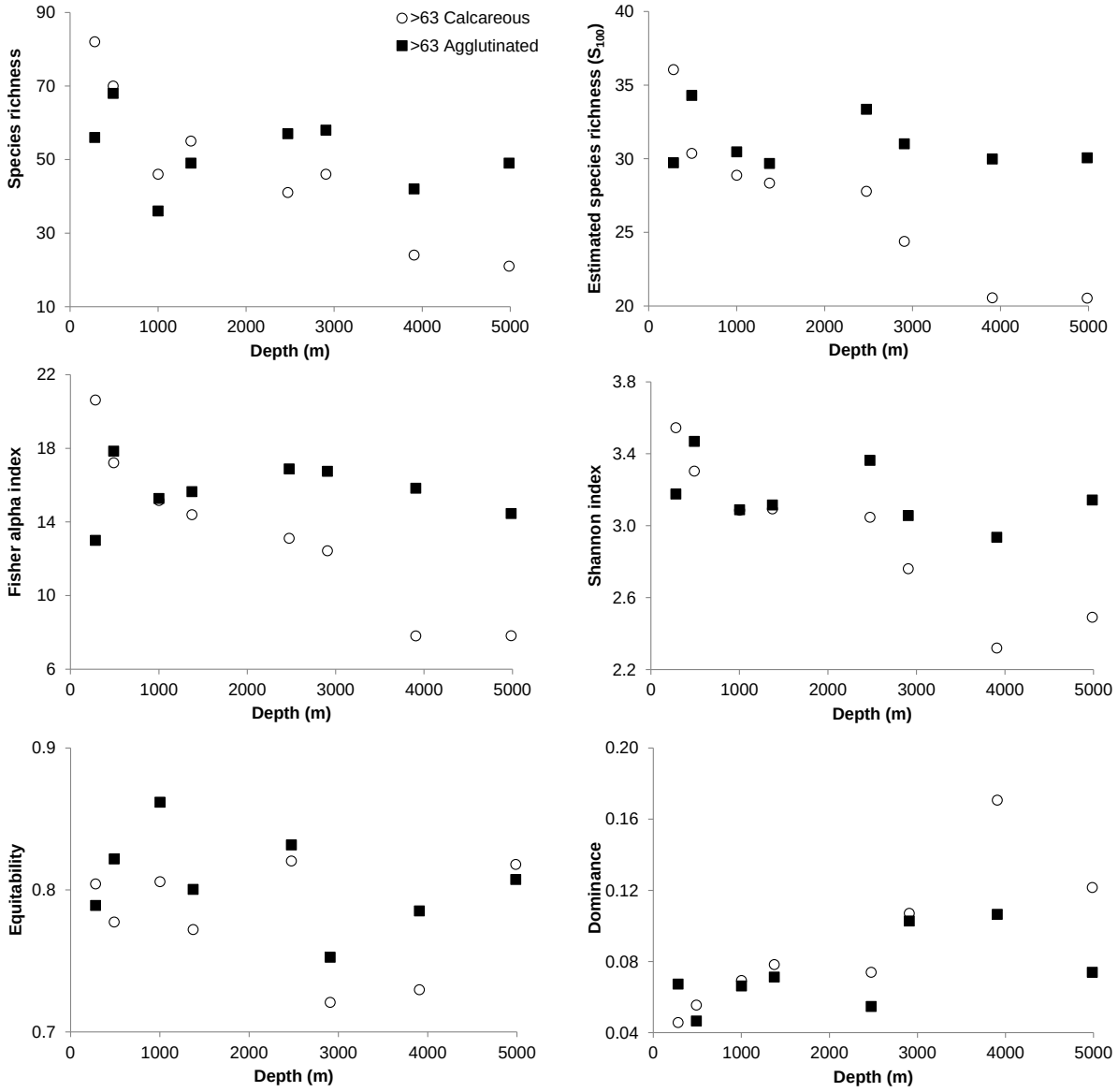

Figure 3. Diversity parameters measured for each station. White circles represent values for the calcareous foraminifera >63 µm and black squares represent values for agglutinated foraminifera >63 µm.

4.5 DISCUSSION

4.5.1 OVERALL TRENDS

In the >63 µm fraction (63-150 µm plus >150 µm fractions), species richness (both raw and measured by rarefaction), Fisher alpha and Shannon indices suggest maximum foraminiferal diversities at 282–490 m. These indices, which decrease with increasing water depth, indicate lowest diversity at our deepest stations (3908–4987 m). Dominance values, which show the inverse trend, are lowest at 282–490 m and highest at 3908 m. Higher dominance at the deeper stations suggests that foraminiferal communities there are strongly dominated by a limited number of species. Further, equitability is particularly low at 2908 – 3908 m which also suggests that these two stations in particular are dominated by a few species.

Species richness in the >150 µm fraction, which only takes into account the larger species, shows a more or less similar pattern as the >63 µm fraction which suggests diversity is highest at 282 m, and lowest at 3908–4987 m. However species richness measured by rarefaction, Fisher alpha and Shannon indices have bimodal distributions along the depth transect. Species rarefaction and Fisher alpha index values that suggest diversity is highest at 282 m and 3908 m and lowest at 1002 m and 4987 m. Shannon index values also indicate that diversity is lowest at 1002 m and 4987 m but highest at 282 m and 2475–2908 m. On the other hand, Dominance values are greatest at 1002 m and 4987 m suggesting that at these depths foraminiferal faunas are dominated by only a few species. In contrast to the other diversity indices, equitability values show a general increase with increasing depth, with a peak at 3908 m. The high equitability at 3908 m suggests a very even foraminiferal fauna,

with most species represented by a limited number of individuals. In fact, many foraminiferal species are represented by only 1 individual.

Diversity indices calculated for calcareous foraminifera >63 µm show a very similar pattern to those expressed in the total fauna >63 µm. Highest species richness and diversity is recorded at 282–490 m, which decrease with increasing depth until 3908–4987 m. Dominance, which becomes greater with water depth, suggests that calcareous foraminiferal faunas at deeper water depths are increasingly dominated by a limited number of species. This is particularly true at 2908–3908 m, where very low equitability values suggest very uneven calcareous foraminiferal faunas at these depths.

Species richness and diversity indices for agglutinated foraminifera suggest that diversity has a bimodal distribution with increasing water depth. Diversity is highest at 490 m and 2475 m, and lowest at 282 m and 3908 m respectively. Dominance values are lowest at 490 m and 2475 m suggesting relatively even foraminiferal assemblages at these depths. However, similarly to calcareous foraminifera > 63 µm, high dominance and low evenness at 2908–3908 m indicate very uneven foraminiferal faunas at these depths.

4.5.2 WHY DOES DIVERSITY CHANGE WITH DEPTH?

A COMPARISON WITH OTHER BENTHIC COMMUNITIES

Several papers describing the diversity of metazoan macrofauna and megafauna, such as nematodes, polychaetes, molluscs and fish (Etter and Grassle, 1992; Boucher and Lambshead, 1995; Paterson and Lambshead, 1995; Rex, 1981, 1983; Rex and others, 1997; Rex and others, 2005b), record highest diversity at bathyal depths (~2000-3000 m) and

lowest diversity at shallow (continental shelf) and abyssal depths. It is generally accepted that lower diversity on the abyssal plain is related to extremely low rates of organic carbon flux. Causes of lower diversity on the continental shelf are much less clear, but it has been suggested that competition, predation and oxygen deficiency may reduce diversity under high organic flux conditions (Stuart and others, 2003; Rex and others, 2005a; Rex and others, 2005b; Rex and Etter, 2010; Tittensor and others, 2011).

The role of organic carbon flux to the sea floor as a mechanism in driving deep sea diversity has been incorporated into a number of recent hypotheses for the diversity patterns observed for deep-sea taxa. The source sink hypothesis (Rex and others, 2005a), suggests that populations on the abyssal plain are too low to be reproductively self-sustaining and are instead maintained by larval dispersal from established bathyal communities. Central to this hypothesis is the assumption that the organic carbon flux decreases exponentially with increasing depth and distance from the more productive coastal (Rex and others, 2005a,b; Rex and others, 2006). Consequently, the biomass of megafauna, macrofauna and meiofauna decrease with increasing depth (Hessler and Sanders, 1967; Rex, 1981; Rex and others, 1990; Rex and others, 2006). This decrease is more rapid for megafauna and macrofauna than for meiofauna (Rex and others, 2006). At abyssal depths, extremely low standing stocks and biomass on the abyssal plain may limit the potential for evolutionary diversification in larger size groups (Etter and others, 2005). However, foraminifera, which can reproduce asexually and are generally in the meiofaunal size class (but may also express gigantism, see Gooday and others, 1997) can maintain higher diversity at abyssal depths. A reduced abundance of macrofauna and megafauna at greater depth may allow more nutrients to be available for meiofaunal foraminifera, and may also decrease predation pressure (Rex and Etter, 2010). Further, many studies that investigate foraminifera along bathymetric transects (Altenbach *et al*.,and others, 1999, 2003; de Rijk *et al*.,and others,, 2000; Morigi and others, 2001;

Fontanier and others, 2002; Eberwein and Mackensen, 2006; Koho and others, 2008; Mojtahid and others, 2010; Phipps and others, 2012) show fundamentally different foraminiferal species assemblages between mid to upper bathyal depths and lower bathyal and abyssal depths. For example on our Portuguese margin transect, "oligotrophic" species such as *Cibicides kullenbergi*, *Reophax fusiformis* and *Recurvoides* sp. 1 dominate lower bathyal and abyssal depths greater than 2500 m. At upper to mid-bathyal depths "mesotrophic" depths species such as *Globobulimina affinis*, *Repmanina charoides* and *Uvigerina peregrina* dominate (Phipps and others, 2012).

Another hypothesis, the patch-mosaic model proposed by Grassle and Sanders (1973), predicts that temporal and spatial patchiness of organic enrichment (Grassle and Morse-Porteous, 1987; Grassle and Maciolek, 1992) and biological disturbances by bioturbating macrofauna (Dayton and Hessler, 1972; Snelgrove and Smith, 2002) would contribute to heterogeneity in deep sea environments. In particular, seasonal phytodetrital deposits are of great importance as a food resource in deep-sea environments (Gooday, 1988, 1993; Gooday and Lambshead, 1989; Thomas and Gooday, 1996; Gooday and others, 1998; Gooday and Rathburn, 1999). The patch-mosaic model suggests higher diversity would be associated with these organic enrichments, which have patchy distributions that change over time. However, such a higher diversity is not seen in calcareous benthic foraminifera from North Atlantic lower bathyal and abyssal sites (Gooday, 1988, 1993; Gooday and Lambshead, 1989; Thomas and Gooday, 1996; Gooday and others, 1998; Gooday and Rathburn, 1999; Gooday and Hughes, 2002; Corliss and others, 2009; Gooday and others, 2010). Instead, opportunistic species tend to dominate the foraminiferal faunas colonizing the phytodetritus, which in turn lowers evenness, and therefore diversity (Sun and others, 2006; Corlis and others, 2009). In spite of the vast areal extent of the deep sea, recent genetic tests on these opportunistic species, such as *Epistominella exigua* from different ocean basins (e.g., Brandt and others,

2007; Pawlowski and others, 2007; Lecroq and others, 2009) express very high genetic similarities with global distributions. It has also been suggested that as a group, foraminifera are more opportunistic than metazoans and have population dynamics that are more closely coupled with organic matter inputs (Gooday and others, 2001).

4.5.3 CAN THE TROX CONCEPTUAL MODEL EXPLAIN BENTHIC FORAMINIFERAL DIVERSITY PATTERNS IN THE DEEP SEA?

The interaction between food and oxygen availability on foraminiferal ecology is a well studied concept (Jorissen and others, 1995; de Stigter, 1996). According to the so-called TROX model (Jorissen and others, 1995), benthic foraminiferal communities and microhabitat selection are controlled primarily by a negative relationship between exported organic matter flux and the oxygenation of the bottom and interstitial waters. The model predicts a succession of foraminiferal assemblages in response to declining food resources and increasing oxygenation with increasing water depth. At relatively eutrophic shelf and upper open slope environments, foraminiferal standing stocks are high but may be restricted to the uppermost millimetres or centimetres due to a shallowing of redox fronts and anoxia in deeper sediment layers (Murray, 2001; Fontanier and others, 2002; Jorissen and others, 2007). In relatively oligotrophic lower slope and abyssal environments, foraminiferal standing stocks are much poorer, but also tend to be concentrated at the sediment surface due to scarce food resources (Fontanier and others, 2002). Conversely in mesotrophic, bathyal settings, where oxygen penetration is relatively deep, and more or less labile food particles are introduced deeper into sediment by bioturbating macrofauna, foraminifera may colonise

deeper sediment intervals (Jorissen, 1999; Fontanier and others, 2002). Following this, one would expect a peak in diversity where the number of niches available to foraminifera is greatest i.e. in mesotrophic regions. There, organic carbon flux and dissolved oxygen concentrations would be optimal, and a maximum number of species could occupy a complete series of shallow, intermediate and deep infaunal niches (Gooday, 1986; Jorissen, 1999). At the eutrophic and oligotrophic extremes, diversity is expected to be lower, reflecting the descending (eutrophic) and ascending (oligtrophic) sides of the unimodal diversity curve described by Levin and others, (2001). In fact, Carney (2005) and Rex and Etter (2010) have suggested that the TROX model could also partly explain unimodal bathymetric diversity distributions observed in macrofauna.

4.5.4 CONTRASTING DIVERSITY PATTERNS FOR DIFFERENT FORAMINIFERAL SIZE FRACTIONS

As previously demonstrated, the diversity of foraminifera from different size fractions (>63 µm, >150 µm) and with different wall structures (calcareous and agglutinated) show different patterns. However, none of these groups show a strictly unimodal diversity curve with maximum diversity at mid bathyal sites. Instead, the clear decrease in diversity with increasing water depth expressed by the total foraminifera > 63 µm probably reflects increasingly oligotrophic conditions, as predicted by the TROX model. In previous bathymetrical studies, foraminiferal standing stocks and diversity are generally observed to be highest on the upper slope where organic-matter flux is high (Corliss, 1991; Jorissen and others, 1998; Fontanier and others, 2002, 2008; Licari and others, 2003; Eberwein and Mackensen, 2006; Mojtahid and others, 2010). On more oligotrophic lower-slope and abyssal

plain environments, foraminiferal standing stocks and diversity are lower. This has led many authors to suggest a positive correlation between foraminiferal density/diversity and organic matter. Some authors have even identified specific labile organic compounds such as lipids (Fontanier and others, 2008) and phytopigments (Koho and others, 2008; Phipps and others, 2012) to be responsible for higher foraminiferal standing stocks and diversity. Also along our transect, components of labile organic matter (phytopigments, proteins, lipids, carbohydrates and biopolymeric carbon) diminish with depth (Phipps and others, 2012).

In contrast to the >63 μm, foraminifera >150 μm express a bimodal diversity distribution with increasing depth. The differences in diversity parameters between foraminifera > 150 μm and foraminifera > 63 μm may be partially due to the relative concentrations of "phytodetritus species" in each of the fractions at various water depths. Several small opportunistic benthic foraminiferal species (e.g., *Epistominella exigua*, *Nuttallides pusillus* and *Globocassidulina subglobosa*) have been shown to preferentially colonize phytodetritus. They multiply their standing stock very rapidly in the short periods following phytodetritus deposition in deep sea environments (Gooday, 1988; Gooday and Turley, 1990; Gooday and Hughes, 2002; Moodley and others,, 2002; Corliss and others,, 2009; Gooday and others,, 2010). We did not have visual confirmation of phytodetritus deposits in any of our samples at the time of their collection. However, foraminiferal faunas dominated by small calcareous species associated with phytodetritus layers are marked with low diversity and high dominance (Sun and others, 2006; Corlis and others, 2009). These species are often missed in studies of foraminifera >150 μm because of their small size (Jorissen and others, 2007). For example, at 2908–3908 m species such as *Epistominella exigua* and *Nuttallides pusillus* are dominant elements (>20% combined) in the 63–150 μm but occur only in low numbers or are absent in the > 150 μm fraction (Phipps and others, 2012). These species cause high dominance (0.05–0.07) and low evenness (0.78–0.80) in the

>63 μm fraction. In the >150 μm where "phytodetritus" species are mostly absent, and standing stocks are much lower, dominance is lower (0.04–0.06) and evenness is higher (>0.9). This coincides with the secondary peak observed in some diversity parameters at 2908 m (Shannon index) and 3908 m (Fisher alpha index and rarefaction) for the >150 μm fraction. Nonetheless, species such as *Uvigerina peregrina*, *Uvigerina mediterranea* and *Epistominella vitrea*, which are also thought to profit from phytodetritus input, occur in relatively shallow eutrophic and mesotrophic settings (Fontanier and others, 2003, 2006; Duchemin and others, 2007). Further, *Uvigerina* spp., are commonly retained in the >150 μm fraction. A strong dominance of *Uvigerina mediterranea* (25%) in the >150 μm fraction at 1002 m (Phipps and others, 2012) coincides with high dominance (0.12) and low equitability (0.78), Shannon index (2.7), Fisher alpha (14.0) and rarefaction (16.9) values at this depth. Smaller phytodetritus species from the 63-150 μm fraction are relatively minor components of foraminiferal assemblages at depths less than 1374 m (Phipps and others, 2012). Summarising, it appears that small phytodetritus exploiting species generally increase in relative number with increasing depth (Phipps and others, 2012). Such species are at least partially responsible for increasing dominance and lowering diversity at greater depths along our transect in the >63 μm. Conversely, larger opportunistic species that have been related to phytodetritus falls such as *Uvigerina* spp. are absent at depths >2475 m (Phipps and others, 2012). They are most abundant towards shallower sites (i.e. ~1000 m) where dominance values are greatest in the >150 μm.

4.5.5 CONTRASTING DIVERSITY PATTERNS FOR DIFFERENT WALL TYPES

Similarly to total foraminifera >63 µm, calcareous foraminifera >63 µm show a linear decrease in diversity with increasing depth and a corresponding increase in dominance. On the other hand diversity of agglutinated foraminifera >63 µm shows a bimodal distribution. The differences in diversity between the two groups could reflect differences in their relative trophic requirements. The low species richness, high dominance assemblages predicted by the TROX model in eutrophic, low oxygen settings are not observed for calcareous foraminifera > 63 µm at shallow depths along our transect, probably because oxygen concentrations at the sediment surface are never low enough to inhibit the development of calcareous species. Some authors have suggested that for many calcareous species, oxygen concentration is not a major limiting factor (Phleger and others, 1973; Bernhard, 1989, 1992, 1993; Rathburn and Corliss, 1994; Morigi and others, 2001); some species are known to be capable to shift to an anaerobic metabolism by respiring nitrates (Risgaard-Petersen and others, 2006; Pucci and others, 2009; Piña-Ochoa and others, 2010). However, agglutinated foraminifera > 63 µm have markedly lower species richness and higher dominance at 282 m than calcareous ones. Though we have no direct oxygen measurements for our stations, the rather shallow average living depths of intermediate infaunal (*Melonis barleeanus, Globobulimina pyrula, Uvigerina elongatastriata*) and deep infaunal (*Chilostomella oolina*) calcareous foraminifera at 282 m suggest a relatively shallow oxygen penetration depth (1-1.5 cm, Phipps and others, *in prep*). Some previous studies have suggested that as a group, agglutinated foraminifera are much less tolerant of low-oxygen conditions than calcareous foraminifera (Moodley and others, 1997; Gooday and others, 2000, 2001, 2009; Neira and others, 2001, Levin and others, 2002). Under eutrophic, low-oxygen conditions, less tolerant species will be eliminated, particularly those which are adapted to epifaunal/shallow infaunal niches (de Stigter, 1996). However, it is interesting to note that many dominant agglutinated

species at 282 m (e.g., *Buzasina ringens*, *Cribrostomoides bradyi*, *Reophax helenae*) occupy intermediate and deep infaunal niches suggesting these species are tolerant to low-oxygen (Phipps and others, *in prep*). We think that these low-oxygen tolerant agglutinated species may prefer living deeper within the sediment to avoid competition with the calcareous species living in the better oxygenated sediments closer to the surface (Buzas and others, 1989; Van der Zwaan and others, 1999; Gooday, 2003). If true, at 282 m, agglutinated foraminifera species would be more or less outcompeted in the superficial niches by the calcareous foraminifera, which are more competitive under eutrophic conditions (Cornelius and Gooday and others, 2004; Gooday and others, 2008; Koho and others, 2008; Phipps and others, 2012). As a result, the less competitive agglutinated foraminifera would occupy deeper infaunal niches where competition is reduced. At 490 m oxygen penetration is greater (~3-4 cm) as is evidenced by the deeper average living depths of intermediate infaunal (*Melonis barleeanus*, *Uvigerina elongatastriata*) and deep infaunal (*Chilostomella oolina*) calcareous foraminifera (Phipps and others, *in prep*). Conditions are still relatively eutrophic at this water depth and competition with the more eutrophic calcareous foraminifera will probably still be high. However increased niche space created by greater oxygen penetration can allow more agglutinated species to occupy infaunal habitats. This could account for the peak observed in agglutinated foraminiferal diversity at 490 m.

The number of foraminifera species occupying intermediate and deep infaunal microhabitats between the stations along our transect for the different wall groups are presented in Figure 4a-b. Agglutinated foraminifera >63 µm have a greater number of intermediate and infaunal species (11 species) at 490 m compared to only 6 at 282 m (Figure 4a). Towards deeper settings along our transect at depths below 2475 m, agglutinated foraminiferal species richness and diversity indices do not decline as rapidly as calcareous foraminifera (Figure 3). A large number of agglutinated foraminifera species (9–10 species)

still occupy intermediate and deep infaunal microhabitats at 2475–2908 m (Figure 4a). Therefore, the two peaks in diversity of agglutinated foraminifera along our transect at 490 m and 2475–2908 m appear to broadly relate to the presence of greater number of intermediate and deep infaunal species at these depths. The secondary peak in agglutinated diversity at 2475–2908 m directly coincides with a putative maximum of macrofaunal bioturbation along our transect (Phipps and others, *in prep*). Bioturbation can introduce oxygen and labile food particles into deeper sediment layers which foraminifera may exploit (e.g., Aller and Aller, 1986; Meyers and others, 1987, 1988; Aller, 1988, 2001; Thomsen and Altenbach, 1993; Loubere and others, 1995; Jorissen, 1999; Murray and others, 2002; Meysman and others, 2006; Hess and Jorissen,

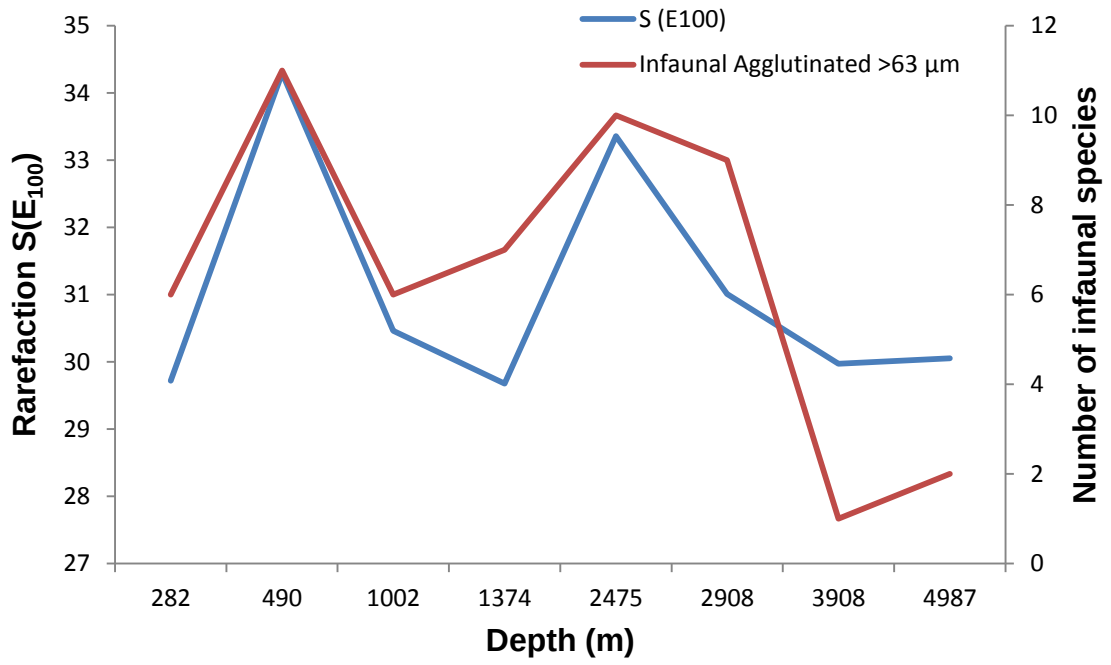

Figure 4a. Number of agglutinated species vs agglutinated species richness measured by rarefaction for every 100 individuals ($S(E_{100})$)

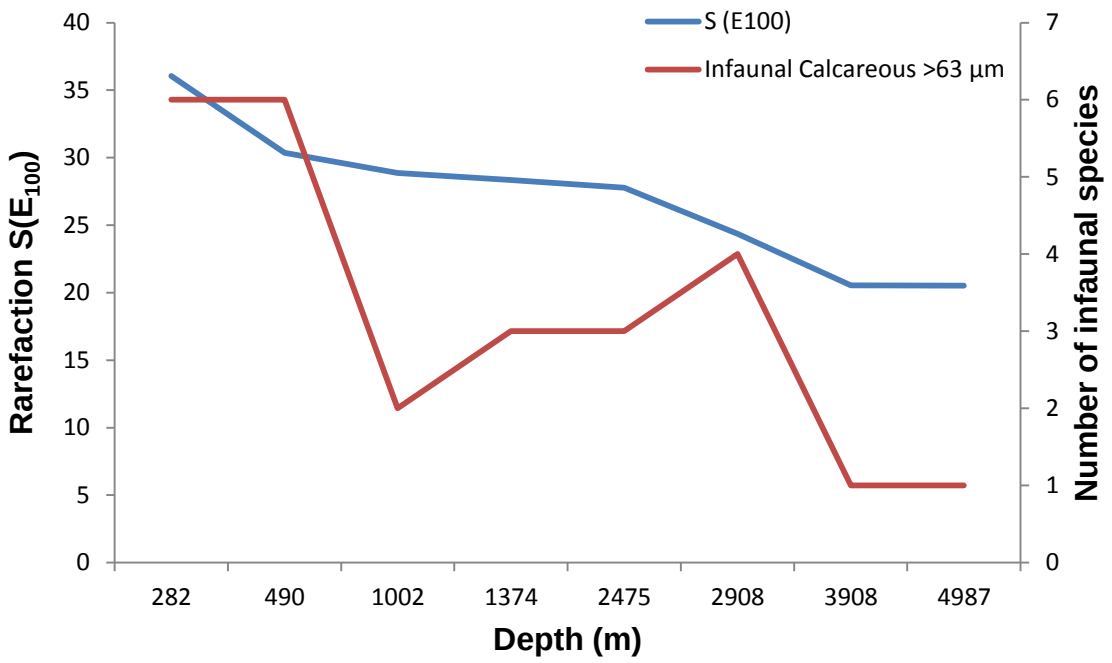

Figure 4b. Number of calcareous species vs calcareous species richness measured by rarefaction for every 100 individuals ($S(E_{100})$)

2009; Loubere and others, 2011) In contrast, there are comparatively few intermediate and deep infaunal calcareous foraminifera occuring at depths >500 m (Figure 4b). In fact, it appears that calcareous foraminifera generally adopt a more opportunistic mode of life, which explains why calcareous foraminifera are more competitive than agglutinated ones at the sediment surface of shallow sites, where labile food particles are abundant (Phipps and others, 2012). This leads to a general increase in dominance values and decrease in diversity parameters for calcareous foraminifera along the transect. Finally, at our deepest stations (3908–4987 m) even agglutinated foraminifera are restricted to the uppermost 0–1 cm (Phipps and others, *in prep*). Under the most oligotrophic conditions, bioturbation is more or less absent and the more rapid decline of calcareous foraminiferal standing stocks (and

diversity) explains why agglutinated foraminifera can compete for resources close to the sediment-water interface here.

Summarising, it seems that calcareous foraminifera, which as a group have higher trophic requirements than agglutinated foraminifera, show a more rapid decrease in diversity across our transect. This is because towards deeper sites they rapidly become restricted to the shallow infaunal food-rich habitats close to the sediment surface, even in the presence of macrofaunal bioturbation. Contrary to the TROX model, calcareous foraminiferal diversity is not depressed at shallow depths that are under eutrophic and low oxygen conditions. In contrast, agglutinated foraminifera diversity is supressed at our most shallow station. However, the dominance of a limited number of agglutinated species in deeper sediment layers suggests that their low diversity is caused by intense competition with calcareous foraminifera rather than by low-oxygen conditions. Where oxygen penetration is greater, but competition with calcareous foraminifera is still high, agglutinating foraminiferal diversity increases because of an increased availability of infaunal niches. Because of their lower trophic requirements, agglutinated foraminifera are able to survive in intermediate and deep infaunal niches created by macrofauna under mesotrophic conditions on the bathyal slope, in accordance with the TROX-model. At the deepest, oligotrophic settings along our transect both calcareous and agglutinated foraminifera are mostly restricted to the uppermost cm, also in agreement with the TROX-model.

4.6 CONCLUSIONS

The diversity patterns of living benthic foraminifera located between 282–4987 m along the Portuguese margin suggest that the TROX-model only partially explains some elements of foraminiferal diversity trends with depth. Different foraminifera groups determined by size (>150 µm, >63 µm) and wall texture (calcareous and agglutinated) show different diversity patterns. Each group can be characterised as follows:

- Total foraminifera >63 µm have highest diversity at 282 m, and decrease with increasing depth, in probable response to increasing oligotrophic conditions along our transect. Low-oxygen conditions at more eutrophic, shallow depths do not seem to have any negative effect on diversity. Evenness is low and dominance is high at greater depths, particularly at 2908–3908 m. This is because at these depths, opportunistic species which are characteristic of phytodetritus deposits increase in dominance with increasing depth.
- Total foraminifera >150 µm show different diversity trends than the >63 µm fraction. Highest diversity is also found at 282 m, and low-oxygen conditions there do not appear to depress foraminiferal diversity. However, there are secondary diversity peaks at 3908 m (Fisher alpha index) and 2908 m (Shannon index) respectively. Higher diversity at these depths coincides with high equitability where many species are represented by a single individual. Low diversity at 1002 m coincides with a strong dominance of the opportunistic species *Uvigerina mediterranea*. However, most opportunistic species, particularly calcareous ones, are too small to be recorded in the >150 µm fraction at depths >1000 m.

- Calcareous foraminifera >63 µm have highest diversity at 282 m, and decrease with increasing depth in response to increasing oligotrophic conditions. Intermediate and deep infaunal species are relatively abundant at 282–494 m but are infrequent at greater depths. Low-oxygen conditions at relatively eutrophic, shallow depths do not have a negative impact on calcareous foraminiferal diversity. With increasing water depth, dominance increases and species richness and evenness decreases, as small opportunistic ‘‘phytodetritus’’ species become increasingly dominant components of the calcareous assemblages. Contrary to the TROX-Model, mesotrophic conditions coupled with bioturbation do not encourage higher diversity in calcareous foraminifera. Instead they are mostly limited to the topmost sediment level due to their high trophic requirements.
- Agglutinated foraminifera >63 µm shows a bimodal diversity distribution with highest diversity at 490 m, and 2475–2908 m respectively. Low diversity at 282 m is caused by low species richness and high dominance of some deep infaunal agglutinated species. At the sediment surface, agglutinated taxa may be outcompeted by more opportunistic calcareous foraminifera. The peak in diversity at 490 m could be caused by a combination of greater oxygen penetration, leading to a greater availability of infaunal niches (TROX-Model). This would allow more intermediate and deep agglutinated infaunal taxa to colonise deeper sediment intervals, thus increasing diversity. At mesotrophic, bathyal depths (2475–2908), more intermediate and deep infaunal niches are also made available to agglutinated foraminifera by macrofaunal bioturbation, which again raises diversity. Finally at 3908-4987 m, diversity is low as oligotrophic conditions limit agglutinated foraminifera to the sediment surface.

CHAPITRE 5

SPATIAL AND TEMPORAL VARIABILITY OF LIVING BENTHIC FORAMINIFERA ALONG A LATITUDINAL TRANSECT AT 1000M DEPTH ON THE PORTUGUESE MARGIN (NE ATLANTIC)

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Ce chapitre correspond à un article en preparation pour soumission

5.1 ABSTRACT

Live benthic foraminifera were studied from eight cores collected along a latitudinal transect from both canyon and open slope sites at ~1000 m depth. Total standing stocks, diversity and species assemblages from the >150 μm fraction are analysed for the topmost 10 cm in each core and compared with previous live foraminiferal studies taken from the same sites. Cores from the Nazaré canyon terrace and axes of the Cascais and Setúbal canyons are characterized by a high quantity and quality of organic matter, high foraminiferal densities and relatively shallow oxygen penetration depths. All three canyons have high numbers of *Melonis barleeanus, Chilostomella oolina* and *Globobulimina turgida* although they occur in higher densities and relative abundances in the Nazaré canyon which has the lowest diversity among the three canyons. In contrast Cascais and Setubal canyons have much higher diversities because of the relative contribution of abundant shallow infaunal species. Diversity indices and ALD_{10} values of dominant species on the Nazaré canyon terrace show clear differences between May 1999 and May 2007. These differences probably relate to variations in oxygen penetration depth and associated redox fronts in response to significant organic carbon loads. In the Cascais canyon, standing stocks and colonisation of deeper intervals were much greater in May 2007 than in September 2006, some time after a recent mass depositional event. Generally cores from the open slope are characterized by a low quantity and quality of organic matter and low foraminiferal densities together with a fairly deep oxygen penetration depth. Open slope cores typically have a high dominance of *Uvigerina mediterranea* in the uppermost cm, followed by lower numbers of *Melonis barleeanus* at intermediate intervals and *Globobulimina affinis* at and around the $O_2 = 0$ boundary. On the Mondego slope (Northern open slope), standing stocks are generally lower and diversity is higher, associated with relative oligotrophy and lower dominance. The

presence of *Hoeglundina elegans* and absence of deep infauna such as *G. affinis* attests to a lower trophic level. Further south, standing stocks generally increase, while the appearance of species associated with higher trophic levels such as *Uvigerina peregrina* and *Bulimina inflata*, together with deeper microhabitat development, reflects more eutrophic conditions. However, apart from the greater abundance of *B. inflata* in 2007 on the Alentejo slope, temporal variability on the open slope seems to be much less significant than in canyon environments.

5.2 INTRODUCTION

In deep-sea environments, the quantity and quality of exported organic matter flux, oxygenation of bottom and interstitial waters and associated redox conditions together constitute major controls on the density, composition and microhabitats of benthic foraminiferal faunas (e.g., Altenbach 1988; Altenbach and Sarnthein,1989; Lutze and Thiel, 1989; Jorissen and others, 1998, 2007; Licari and others, 2003; Gooday, 2003; Fontanier and others, 2002, 2003, 2005; Koho and others, 2007, 2008a). The conceptual TROX-Model of Jorissen and others, (1995) describes the negative relationship between exported organic matter flux and the oxygenation of the bottom and interstitial waters, and the impact of these interdependent parameters on the benthic foraminiferal microhabitats. Further modifications to the model include the role of migrational behaviour of foraminifera during changing redox regimes (Van der Zwaan and others, 1999) and the consideration of competition, predation and bioturbation effects on microhabitats (Jorissen and others, 1999).

In general, submarine canyons behave as sediment traps, functioning as conduits for transporting sediment originating from the continental shelf to the deep sea (e.g. Shepard, 1963; Weaver and others, 2000, Van Weering and others, 2002). As a result, canyons tend to have elevated organic carbon concentrations in comparison to the adjacent slope environments (e.g. Vetter and Dayton, 1998; Schmiedl and others, 2000; Duineveld and others, 2001; Epping and others, 2002; Garcia and others, 2003; Fontanier and others, 2005; de Stigter and others, 2007; García and others, 2007; Bianchelli and others, 2008; Pusceddu and others, 2009) which leads to enhanced biological productivity and oxygen consumption rates, and a condensed succession of relatively sharp redox clines in the superficial sediment (Epping and others, 2002). This is reflected in benthic foraminiferal communities exhibiting higher densities in canyons compared to the adjacent open slope at equivalent water depths and also show very different species compositions (e.g., Schmiedl and others, 2000; Fontanier and others, 2005; Nardelli and others, 2010; Duros and others, 2011). For instance, intermediate and deep infaunal taxa (e.g. *Melonis, Globobulimina* and *Chilostomella*) which are commonly associated with eutrophic and low oxygen upper slope and shelf environments, tend to dominate canyon faunas, even at much greater water depths (e.g. Schmiedl and others, 2000; Fontanier and others, 2005; Koho and others, 2008a; Nardelli and others, 2010). Conversely, on the open slope at an equivalent water depth (which is generally more oligotrophic) shallow infaunal and surface dwelling foraminifera (e.g. *Uvigerina*, *Hoeglundina*, *Cibicidoides*) dominate the assemblages and intermediate and deep infaunal taxa constitute only a minor component or are absent from the assemblage. Also, on the Portuguese margin foraminiferal assemblages from different canyons of equivalent water depths are by no means homogenous, as demonstrated by the recent paper by Nardelli and others, (2010), which shows very different species compositions and vertical distributions between stations from the Nazaré canyon terrace and Cascais canyon axis (both ~1000 m).

Studies by Koho and others, in 2007 and 2008a also recorded a suppressed foraminiferal community (almost exclusively dominated by *Technitella* spp.) in the Nazaré Canyon axis, and a much richer and diverse foraminiferal assemblage in the Lisbon-Setúbal Canyon axis. Foraminiferal assemblages from canyon sites may also express significant temporal variability, especially in light of the high sedimentation rates and higher frequency of turbidites and gravity flows that occur in canyons. For example, Hess and others, (2005) described the succession of foraminiferal assemblages following a recent turbidite deposit in the Cape Breton Canyon (Bay of Biscay). Consequently, each sampling may show foraminiferal assemblages in different stages of sediment re-colonisation. Spatial variability has also been documented from environments along the Portuguese margin open slope. For example, Nardelli and others, (2011) described notable differences between stations from the north (core 7, Mondego slope) and south (core 56, Alentejo slope) of the margin, particularly the higher abundance of foraminifera (170 individuals per 50 cm^2) in core 56 which remained high down to 1.5 cm depth in the sediment. Conversely, at core 7 (120 individuals per 50 cm^2) foraminifera were more concentrated in the uppermost 0-0.5 cm. This was attributed to higher availability of metabolisable organic matter on the southern Portuguese margin, particularly the higher quantity of biopolymeric carbon. Further, Griveaud and others, (2010) investigated the effect of localised spatial variability otherwise known as "patchiness" (Diggle 1983) on foraminifera extracted from 6 cores taken from the Alentejo slope (station FP8). They noted a relatively high abundance of 400 specimens per 50 cm^2 in one of the cores, while the other five expressed lower, more consistent densities of ~100 specimens per 50 cm^2 which are more comparable to the densities observed by Nardelli and others, (2010). Nonetheless the cores investigated in both studies are all characterised by similar foraminiferal assemblages, particularly the high dominance of *Uvigerina mediterranea* and the presence of *Melonis barleeanus* and *Globubulimina affinis* in intermediate and deep

infaunal microhabitats. Despite the effects of spatial variability, other foraminiferal studies from different continental margins consider seasonal and interannual variability to have a greater influence on foraminiferal assemblages (Silva and others, 1996, Fontanier and others, 2005, Barras and others, 2010), and consequently most temporal records should not be obscured significantly by spatial variability.

In the present study we analyse living benthic foraminifera from eight cores taken from stations located along the Portuguese continental margin at approximately 1000 m depth. Three of the cores are from canyon environments (Nazaré, Cascais and Setúbal canyons) and five are from open slope environments (Mondego, Estremadura and Alentejo slope). The aims of our study are 1) to increase our knowledge of the spatial variability of densities, species compositions and diversities of living benthic foraminifera assemblages from the topmost 10 cm in three submarine canyons (Nazaré, Cascais and Setúbal canyons) and from four open slope sites collected from the 64PE269 Cruise (May 2007), 2) to improve our understanding of the temporal variability (density, composition and diversity) of living foraminifera from canyons by comparing our cores from the Nazaré and Cascais canyons with those studied by Nardelli and others, (2011), and Koho and others, (2007) and 3) to improve our understanding of the temporal variability (density, composition and diversity) of living benthic foraminiferal assemblages from the open slope by comparing our cores from the Mondego, Estremadura and Alentejo slope with those studied by Nardelli and others, (2011) and Griveaud and others, (2010), and with an additional core analysed in this study (core 27) from Cruise 64PE252.

5.3 MATERIAL AND METHODS

5.3.1 STUDY AREA

The Portuguese margin (Fig. 1) is characterized by a relatively narrow shelf and steep irregular slope, dissected by a number of deep canyons. The margin is influenced by seasonally changing hydrodynamics as a result of the wind-driven upwelling system occurring along the western coasts of the Iberian Peninsula and Africa down to 15°N (Wooster and others, 1976). Conditions favorable for upwelling occur between June and September as a result of strong and steady northerly winds and southward surface currents (Fiúza, 1984; Sousa and Bricaud, 1992; Huthnance and others, 2002; Vitorino and others, 2002). Primary productivity along the Portuguese margin is fairly high (~230 to ~360 $gCm^{-2}y^{-1}$; Epping and others, 2002). The water column in this area is made up of a composite of water masses (García and others, 2003). The Mediterranea Outflow water (MOW) occurs between 600 and 1600 m with a strong salinity peak at 1100 m (>36). The eight cores of our study area, located at ~1000 water depth (Table 1, Figure 1), are bathed by the MOW which has a temperature between 11-12 ^{o}C and salinity of ≥36.0 (Fiúza and others, 1998). Core 37 (968 m) was taken from the Nazaré canyon terrace, while cores 28 (1059 m) and 33 (969 m) were collected from the axes of the Cascais and Setúbal canyons respectively. The largest of

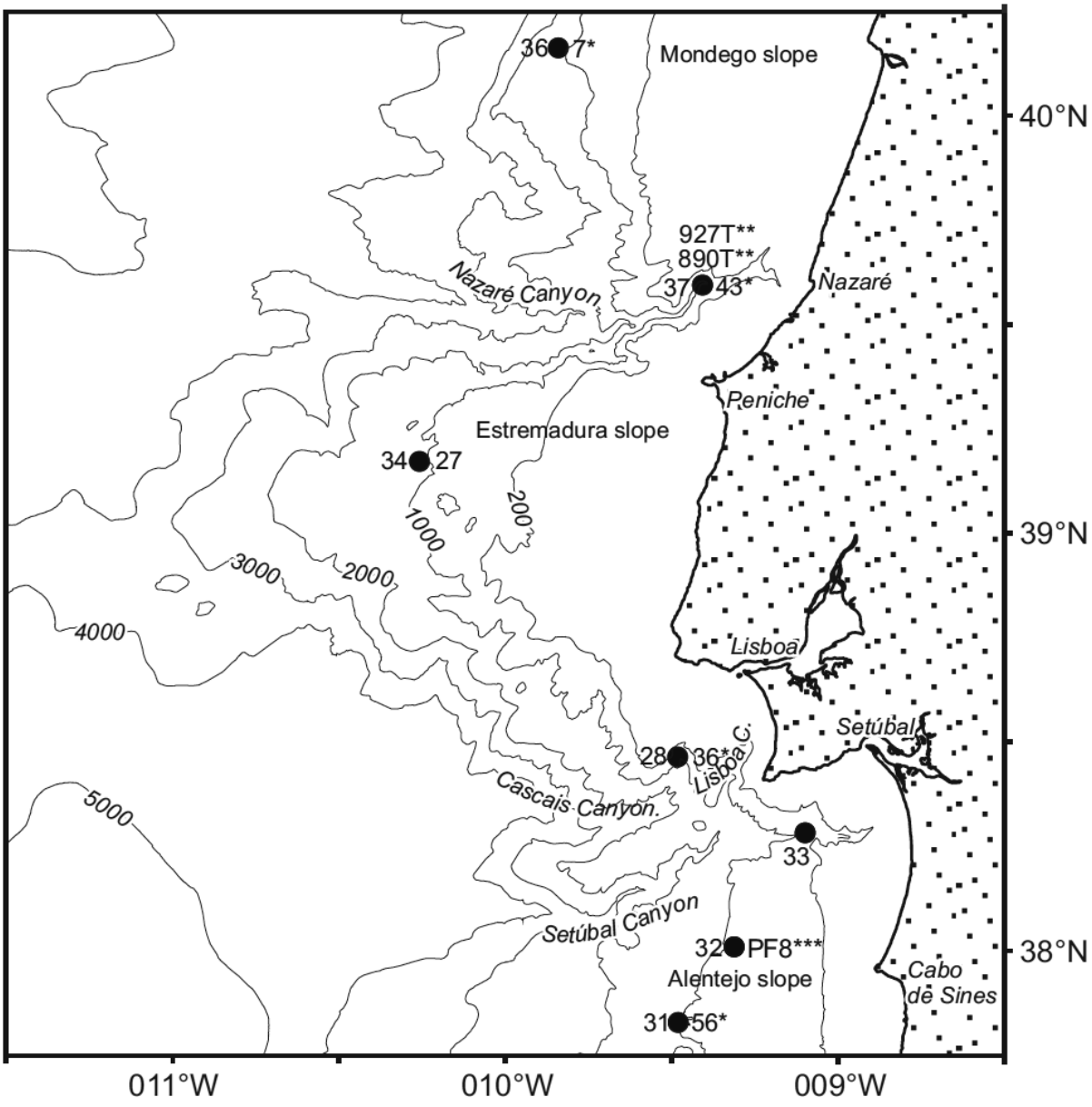


Figure 1. Map of the Portuguese margin latitudinal transect. Sample locations are marked in black circles. Samples without * are analysed from this study. Samples with *,** and *** are studied in Nardelli and others (2010), Koho and others (2008) and Griveaud and others (2010) respectively.

Core	Date	Cruise	Latitude	Longitude	Depth (m)	Temp (°C)	Salinity (psu)
36	May-07	64PE269	40°09.98'N	009°49.99'W	962	11.6	36.2
37	May-07	64PE269	39°35.81'N	009°24.22'W	968	11.8	36.2
34	May-07	64PE269	39°10.36'N	010°15.24'W	1039	11.3	36.2
27	Sep-06	64PE252	39°10.36'N	010°15.23'W	1034	N/A	N/A
28	May-07	64PE269	38°27.90'N	009°28.50'W	1059	11.6	36.3
33	May-07	64PE269	38°17.10'N	009°06.00'W	969	11.8	36.2
32	May-07	64PE269	38°01.50'N	009°20.40'W	974	11.5	36.1
31	May-07	64PE269	37°50.00'N	009°28.50'W	1000	11.8	36.4

Table 1. Sampling moment, geographical position, water depth, temperature (°C and salinity of the eight cores analyzed in this chapter.

these canyons is the Nazaré canyon (more than 230 km long), characterized by the rapid accumulation of non-cohesive, predominantly terrigenous silts and clays that enter the canyon from the adjacent open slopes through tidal currents and discontinuous advected fluxes (Schmidt and others, 2001), and via long-shore transport (de Stigter and others, 2007, 2011). The Nazaré canyon is particularly prone to sediment resuspension and gravity flows, making it an effective conduit for transport of sediments from coastal waters to the deep sea, and is considered an "active" canyon (de Stigter and others, 2007, 2011). In contrast, sediment accumulation in the Setúbal and Cascais canyons is controlled primarily by bottom nepheloid layers that detach from the adjacent shelf, and are inactive in terms of down-canyon sediment dispersal (Jouanneau and others, 1998; Jesus and others, 2010; de Stigter and others, 2011). Core 36 (962 m), cores 34 (1039 m) and 27 (1034 m) and cores 32 (974 m) and 31 (1000 m) are located on the Mondego, Estremadura and Alentejo slopes respectively. The Mondego shelf lies north of the the Nazaré canyon, with a maximum width of about 60 km and gently slopes into the Iberia Abyssal Plain. The Duoro and Mondego rivers are important sources of terrigenous sediment here. The Estremadura slope separates the Nazaré canyon to the north from the Cascais canyon to the south and is incised by numerous deep valleys of which some

act as tributaries to these canyons. Finally, the Alentejo slope lies south of the Setúbal canyon and extends as far south as Cabo São Vicente.

5.3.2 Sample Preparation and Processing of Foraminifera

During Cruise 64PE252 with RV Pelagia, seven cores with an inner diameter of 9.5 cm (corresponding to a surface area of 70.9 cm^2), with undisturbed sediment surfaces were collected using a MUC multicorer in May 2007. Immediately after retrieval the cores were taken to a temperature controlled container in order to perform oxygen profiles of the sediment. Oxygen profiles were measured twice for each core using a 500 μm tip Clark's electrode connected to a Unisense© picoamperometer allowing a submillimeter spatial resolution. The top 10 cm of the sediment cores were then extruded and sliced at 0.5 cm intervals from 0 to 2 cm depth, and 1 cm intervals from 2 to 10 cm depth. All slices were subsequently stored in a solution of 1g/l Rose Bengal in 96% ethanol until further treatment in the laboratory. Once in the laboratory, each sediment layer was carefully washed, using tap water, through sieves with 63 and 150 μm meshes and residues were subsequently stored in 96% ethanol. Core 27, acquired from the 64PE252 cruise in September 2006 follows the same collection procedure as Phipps and others, (2012).

Stained foraminifera from the >150 μm fractions were sorted from wet samples and placed onto Chapman slides. As we intend to compare the foraminifera from our cores with those from other studies (Table 2) we decided to compare only the perforate, porcellaneous and fossilising agglutinated foraminifera and inventoried the non-fossilising agglutinated foraminifera separately. Fossilising agglutinating taxa are characterised by having a calcitic

matrix that makes them more resistant to mechanical and chemical degradation. In contrast to calcareous and fossilising agglutinated faunas, non-fossilising agglutinated foraminifera are usually very weakly cemented, difficult to identify and often have an orange-reddish colour that makes it difficult to assess staining, and were therefore removed from comparative analyses to avoid sampling bias. The densities of the live foraminiferal fauna from each investigated sediment layer are expressed as the number of live foraminifera found in and below a 70.9 cm^2 surface area (the surface of a single core) and standardized to 50 cm^2. The Average Living Depth (ALD_{10}) of each foraminiferal species, and of the total fauna at each station, was calculated in order to describe the vertical distribution of benthic foraminifera in the sediment, using the equation proposed by Jorissen and others, (1995):

$$ALDx = \Sigma\ ni \times Di$$

Where x is the deepest studied level of the core (cm), ni the numbers of individuals in the interval I, D, the average depth of the interval I and N the total number of individuals in the whole core. Isolated individuals separated by more than one centimeter from the main population of the taxon were considered to have been accidentally transported by bioturbation and therefore were not considered in the ALD_{10} calculation. Diversity indexes were calculated using PAST software (Hammer and others, 2001). As well as counting species richness (*S*), we implemented rarefaction analysis (Sanders, 1969) to compare samples of different sizes (Hayek & Buzas 1997, Gray 2000). The diversities of the assemblages are expressed by the Fisher alpha diversity index (Fisher and others, 1943; Williams, 1964) and the Shannon-Weaver heterogeneity index, H(S) (Shannon and Weaver, 1949). Dominance

(D) (Simpson 1949; Magurran, 2004) and Equitability (J) (Pielou, 1975) values are included to provide information on the evenness of the species abundance structure.

		CANYONS			OPEN SLOPE			
Author	Date	Nazaré	Cascais	Setúbal	Mondego	Estremadura	Alentejo	
This study	May-07 Sep-06	Core 37	Core 28	Core 33	Core 36	Core 34 Core 27	Core 32	Core 31
Nardelli et al. (2010)	Sep-06	Core 43	Core 36		Core 7			Core 56
Koho et al. (2007)	May-99 May-05	Core 890T Core 927T						
Griveaud et al. (2010)	Aug-03						Station FP8	

Table 2. Summary of core sampling moments taken from this study and those from other studies taken from the same locality.

5.3.3 PHYTOPIGMENT CONTENTS

Chlorophyll-a and phaeopigment analyses were carried out on cores 37, 36, 34, 31 and 28, according to Lorenzen and Jeffrey (1980). For the five cores analyzed, pigments were extracted (12 h at 4°C in the dark) from triplicate sediment samples (about 1 g) at 0-1, 1-3, 3-5 and 5-10 cm sediment intervals obtained from independent deployments of the multicorer, using 3-5 ml of 90% acetone as the extractant. Extracts were analyzed fluorometrically to estimate chlorophyll-a, and, after acidification with 200 µl 0.1N HCl, to estimate phaeopigments. We avoided the use of fluorometric chlorophyll-a estimates as the unique tracer of organic C associated with algal material and, instead, summed up chlorophyll-a and

phaeopigment concentrations (i.e., total phytopigments). Concentrations of total phytopigments, once converted into C equivalents using 40 as a conversion factor (Pusceddu and others, 1999) are reported in μg C g^{-1}.

5.3.4 Quantity and biochemical composition of sedimentary organic matter

Protein, carbohydrate and lipid sediment contents were analyzed spectrophotometrically according to Pusceddu and others, (2004) and concentrations expressed as bovine serum albumin, glucose and tripalmitine equivalents, respectively. For each biochemical assay, blanks were obtained using pre-combusted sediments (450°C for 4 h). For all of the stations, all analyses were performed on triplicate sediment samples (about 0.5 g) at 0-1, 1-3, 3-5 and 5-10 cm sediment intervals obtained from independent deployments of a multiple or box corer. Carbohydrate, protein and lipid sediment contents were converted into carbon equivalents using the conversion factors of 0.40, 0.49 and 0.75 mg C mg^{-1}, respectively, and their sum defined as the biopolymeric organic carbon (Fabiano and others, 1995).

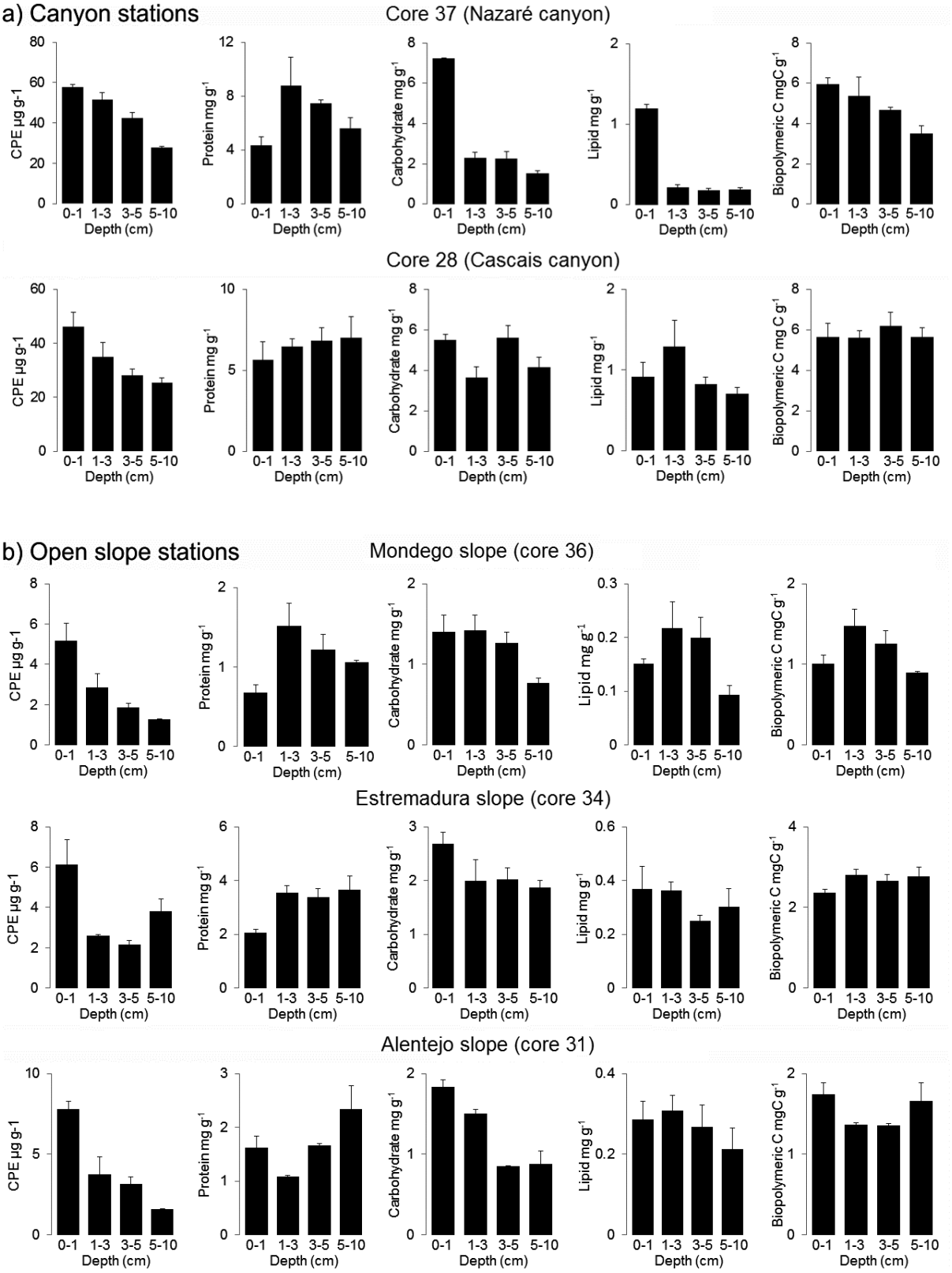
5.4 Results

5.4.1 Quantity and biochemical composition of sediment organic matter

Phytopigment, protein, carbohydrate, lipid and biopolymeric C concentrations in the sediment of canyon cores 37 and 28, and open slope cores 36, 34 and 31 are presented in

Figures 2a-b respectively. Generally, organic matter measurements in the top 1 cm are comparable between the Nazaré (core 37) and Cascais (core 28) canyons (Figure 2a). However, phytopigment (57.9 ± 1.2 μg g^{-1}), carbohydrate (7.2 ± 0.01 mg g^{-1}), lipid (1.2 ± 0.05 mg g^{-1}) and biopolymeric C (5.9 ± 0.3 mg g^{-1}) concentrations are slightly higher in the Nazaré canyon than in the Cascais canyon (46.1 ± 5.2 μg g^{-1}, 5.5 ± 0.3 mg g^{-1}, 0.9 ± 0.2 mg $g^{-1}$and 5.6 ± 0.7 mg g^{-1} respectively). Protein content is higher in the Cascais canyon (5.6 ± 1.1 mg g^{-1}) than in the Nazaré canyon (4.4 ± 0.6 mg g^{-1}) and therefore the protein to carbohydrate ratio is higher in the Cascais canyon (1.0) than in the Nazaré canyon (0.6) (Figure 2a.) Total phytopigment contents show clear decreases towards deeper intervals at both stations, whereas carbohydrates, lipids and biopolymeric C show clear decreases only in the Nazaré canyon. Protein content decreases downcore after a subsurface peak at the 1-3 cm interval in the Nazaré canyon, while it shows increased concentrations downcore in the Cascais canyon.

In comparison to the canyon cores, organic matter measurements from the open slope cores are five to ten times lower (Figure 2b). At core 36 (Mondego slope) phytopigment (5.2 ± 0.9 μg g^{-1}), protein (0.7 ± 0.1 mg g^{-1}), carbohydrate (1.4 ± 0.2 mg g^{-1}), lipid (0.2 ± 0.01 mg g^{-1}) and biopolymeric C (1.0 ± 0.1 mg g^{-1}) contents are lowest among the three cores in the uppermost 1 cm. Core 31 (Alentejo slope) has the highest phytopigment contents (7.8 ± 0.5 μg g^{-1}), while core 34 (Estremadura slope) has the highest protein (2.1 ± 0.1 mg g^{-1}), carbohydrate (2.7 ± 0.2 mg g^{-1}), lipid (0.4 ± 0.08 mg g^{-1}) and biopolymeric C (2.3± 0.09 mg g^{-1}). The protein to carbohydrate ratio is higher in core 31 (0.9) than in cores 34 (0.8) and 36 (0.5). Downcore, phytopigment and carbohydrate contents generally decrease, while protein contents show slight increases in all three cores. Lipid and biopolymeric contents are comparatively stable downcore in cores 31 and 34 while both show a bimodal distribution downcore in core 36.



Figures 2a-b. Components of organic carbon measured at 0–1, 1–3, 3–5, and 5–10 cm intervals downcore for two canyon cores (2a) and three open slope cores (2b) in this study.

5.4.2 OXYGENATION OF BOTTOM AND PORE WATERS

Bottom water oxygen concentrations for the seven cores collected from 64PE269 vary between 215.5 µmol/kg (core 31) and 170.1 µmol/kg (core 37) (Figure 3). The penetration of free oxygen into the sediment varies from 14 mm in core 28, to 32 mm in core 31. Oxygen penetration is shallower in the canyons (14 mm in core 28 to 18 mm in cores 33 and 37) than cores from the open slope (25 mm in core 36 to 32 mm in core 31, see Figure 3), suggesting that the oxygen gradients within interstitial waters are more strongly influenced by the rate of organic matter degradation in the three canyons, compared to the open slope stations.

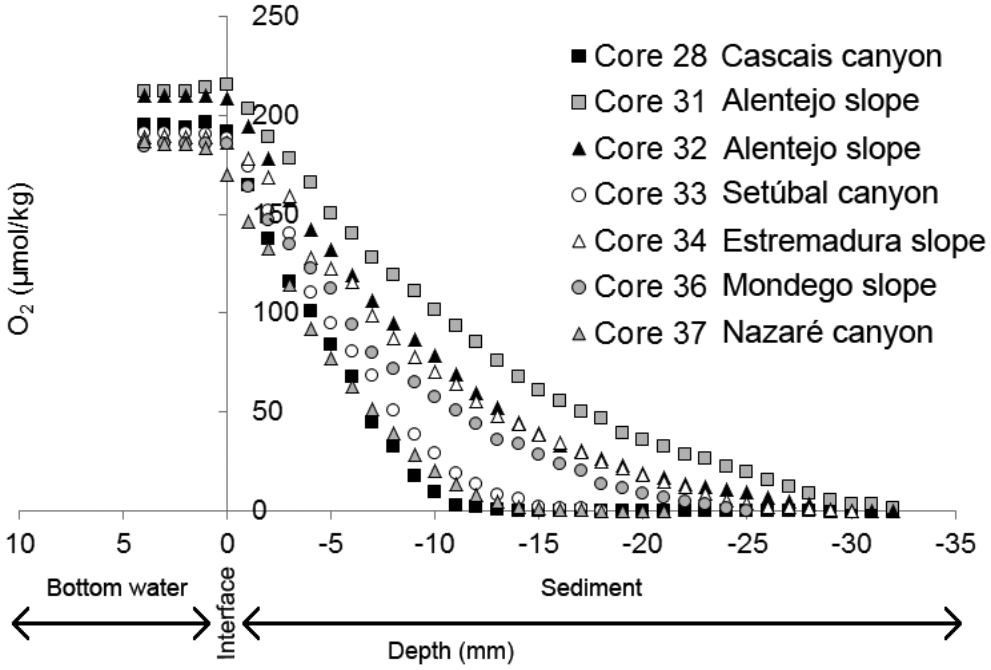


Figure 3. Downcore oxygen measurements for seven cores in this study.

5.4.3 FORAMINIFERAL ABUNDANCE AND COMMUNITY STRUCTURE

The following paragraphs describe foraminiferal abundance, species richness and diversity indices for each core studied along the latitudinal transect. Cores 37, 33 and 28 (canyon sites) and cores 36, 34, 32 and 31 (open slope sites) were all collected during cruise 64PE269 in May 2007. Core 27 was collected during cruise 64PE252 in September 2006, and is from the same open slope locality as core 34 (Tables 1 and 2).

Total foraminiferal abundance, species richness and diversity indices for each core are recorded in Table 3. On the Nazaré canyon terrace (core 37), foraminiferal density (~1600 individuals per 50 cm^2) is more than double that of the Cascais (core 28) and Setúbal (core 33) canyon axes which have rather similar densities of ~650 and ~450 individuals per 50 cm^2 respectively. Species richness ranges from only 29 species on the Nazaré canyon terrace, to ~50 species on the Setúbal and Cascais canyon axes; species richness measured by rarefaction ($E(S_{50})$) is also lowest on the Nazaré canyon terrace (9 species) and much higher on the Cascais (17) and Setúbal (18) canyon axes. The Nazaré canyon terrace has lowest Fisher-α, Shannon (*H'*) and equitability (*J*) index values (4.7, 1.63 and 0.49 respectively), whereas these are highest on the Cascais and Setúbal canyon axes (11.1-12.1, 2.68-2.87 and 0.69-0.74 respectively). Conversely, dominance (D) is greatest on the Nazaré canyon terrace (0.34) and lower on the Cascais (0.13) and Setúbal (0.09) canyon axes. There are also many notable differences between the faunal compositions of the three canyon stations (Table 4). In fact, *Melonis barleeanus* is present in significant numbers in all three cores (though its relative abundance varies considerably), while other species such as *Valvulineria bradyana* and *Globobulimina affinis* dominate only one of the canyon sites. In more detail, the Nazaré

Area	Core	N	TSS (50 cm2)	S	S(E_{50})	Fisher alpha	H'	J	D	ALD_{10}
Nazaré	37	2242	1581	29	9.1	4.7	1.63	0.49	0.34	2.2
	43	676	1195	20	7.0	3.9	0.97	0.32	0.62	1.1
	890T	393	695	17	9.2	3.6	1.71	0.60	0.27	1.9
	927T	572	1012	13	4.9	2.4	0.95	0.37	0.50	1.3
Setúbal	33	634	447	48	17.7	12.1	2.87	0.74	0.09	1.2
Cascais	28	912	643	49	16.7	11.1	2.68	0.69	0.13	1.7
	36	84	149	23	17.2	9.0	2.38	0.78	0.14	1.1
Mondego	36	139	98	41	21.6	19.6	2.79	0.75	0.15	0.6
	7	57	101	23	21.4	14.3	2.66	0.85	0.12	0.9
Estremadura	34	197	139	36	17.8	12.4	2.34	0.66	0.22	1.0
	27	102	180	28	19.6	12.7	2.75	0.82	0.11	0.9
Alentejo	32	195	138	28	16.2	9.0	2.47	0.74	0.14	1.0
	31	333	235	40	16.5	11.9	2.44	0.66	0.17	0.8
	56	79	140	19	16.4	7.9	2.29	0.78	0.17	0.9

Table 3. Total standing stocks, species richness, diversity parameters and total Average living depths (ALD_{10}), of the cores compared in this study.

canyon terrace assemblage is strongly dominated by *Melonis barleeanus* (56%), followed by *Valvulineria bradyana* (11%), *Chilostomella oolina* (10%), *Globobulimina turgida* (6%), *Bulimina inflata* (6%) and *Bolivina alata* (4%). The fauna of the Cascais canyon axis (core 28) is characterized by the dominance of *Melonis barleeanus (*26%), *Cibicidoides pachydermus* (19%), *Chilostomella oolina* (11%), *Uvigerina mediterranea* (6%) and *Globobulimina turgida* (5%). On the Setúbal canyon axis (core 33) the faunas are dominated by *Melonis barleeanus* (18%), *Uvigerina mediterranea* (16%), and *Globobulimina affinis* (10%), followed by *Uvigerina peregrina* (8%), *Bigenerina nodosaria* (7%), *Chilostomella oolina* (5%), *Cibicidoides pachydermus* (5%) and *Hanzawaia boueana* (4%). Total foraminiferal densities of our four open slope cores taken from cruise 64PE269 (May 2007) range from ~100 (core 36, Mondego slope), to 235 (core 31, Alentejo slope) individuals per 50 cm^2. The number of species between the four open slope cores varies from 41 (Core 36, Mondego slope), to 28 (Core 32, Alentejo slope), while species richness calculated by rarefaction ($E(S_{50})$) also shows a highest value in core 36 (21.6) and lowest value in core 32 (15.3). Fisher alpha, Shannon and Equitability index values are also highest at core 36 (19.6,

2.79 and 0.75 respectively); lowest values for these indices are found in core 32 (9.0), core 34 (2.34) and cores 34 and 31 (both 0.66) respectively. Finally, dominance is greatest in core 34 (0.22) and lowest in core 32. Similarly to the canyon assemblages, there are many notable similarities and differences between the open slope foraminiferal assemblages (Table 5). For instance *Uvigerina mediterranea* is a dominant species in all cores, while *Hoeglundina elegans* and *Bulimina inflata* attain substantial densities in only one or two of the cores. In more detail core 36 (Mondego slope) is strongly dominated by *Uvigerina mediterranea* (35%), followed by *Melonis barleeanus* (9%), *Bigenerina nodosaria* (7%) and *Hoeglundina elegans* (4%). Core 34 (Estremadura slope) is strongly dominated by *U. mediterranea* (45%) followed by *Globobulimina affinis* (11%), *Cibicidoides pachydermus* (6%), *M. barleeanus* and *Hanzawaia boueana* (both 5%). Core 32 (Alentejo slope) is dominated by *Bulimina inflata* (28%) and *U. mediterranea* (19%), followed by *G. affinis* (10%), *M. barleeanus* (8%), *Uvigerina peregrina* and *B. nodosaria* (both 5%) and *Siphotextularia heterostoma* (4%). Finally core 31 (Alentejo slope) is dominated by *U. mediterranea* (36%) and *B. inflata* (17%) followed by *M. barleeanus* and *U. peregrina* (both 6%) and *B. nodosaria* (5%).

Finally, core 27 (Estremadura slope), which was taken from a different season to core 34, but from the same locality, has a foraminiferal density of 180 individuals per 50 cm^2 and a species richness of 28 (Table 3). Species richness measured by rarefaction is 19.6 ($E(S_{50})$), while values for Fisher alpha, Shannon, Equitability and Dominance indices are 12.7, 2.75, 0.82 and 0.11 respectively. The foraminiferal assemblage is dominated by *Uvigerina mediterranea* (27%), *Bulimina inflata* and *Cibicidoides pachydermus* (both 10%), followed by *Uvigerina auberiana* (6%), *Globobulimina affinis*, *Melonis barleeanus* and *Nuttallides convexus* (each 5%).

	Core 37	Nazaré	Core 28	Cascais	Core 33	Setúbal	
Species	ALD_{10}	R%A	ALD_{10}	R%A	ALD_{10}	R%A	Microhabitat
Calcareous foraminifera							
Bolivina alata	**1.8 (92)**	**4.1**	0.8 (23)	2.5	0.25 (1)	0.2	
Bulimina inflata	**1.1 (124)**	**5.6**	0.31 (8)	2.1	0.25 (3)	0.6	SI/II
Chilostomella oolina	**4.6 (215)**	**9.6**	**2.5 (103)**	**11.3**	**3.3 (33)**	**5.2**	DI
Cibicidoides pachydermus	0.9 (66)	3.0	**0.34 (117)**	**18.6**	**0.45 (30)**	**4.7**	SI
Globobulimina affinis	-	-	3.5 (2)	0.2	**2.27 (62)**	**9.8**	DI
Globobulimina turgida	**5.3 (132)**	**5.9**	**3.9 (47)**	**5.2**	2.9 (22)	3.5	DI
Hanzawaia boueana	1.2 (5)	0.2	0.3 (4)	0.8	**0.38 (27)**	**4.4**	SI
Melonis barleeanus	**1.7 (1245)**	**55.5**	**1.1 (235)**	**25.8**	**1.1 (111)**	**17.7**	II
Uvigerina mediterranea	0.8 (6)	0.3	**0.5 (36)**	**5.8**	**0.4 (90)**	**15.6**	SI
Uvigerina peregrina	1.3 (1)	0.04	0.4 (22)	3.5	**0.6 (53)**	**8.40**	SI
Valvulineria bradyana	**2.4 (249)**	**11.2**	-	-	-	-	II
Fossilising agglutinates							
Bigenerina nodosaria	-	-	0.3 (1)	0.2	**0.54 (42)**	**6.6**	SI
ALD_{10} of the core	**2.2 (2242)**		**1.7 (912)**		**1.2 (634)**		

Table 4. Average living depths (ALD_{10}), relative percentage abundances and microhabitat descriptions of dominant species from canyon cores. SI = shallow infaunal, II = intermediate infaunal, DI = deep infaunal.

	Core 36	Mondego	Core 34	Estremadura	Core 32	Alentejo	Core 31	Alentejo	Core 27	Estremadura	
Species	ALD_{10}	%	ALD_{10}	%	ALD_{10}	%		%		%	Microhabitat
Calcareous foraminifera											
Bolivina alata											
Bulimina inflata	0.75 (1)	0.7	0.25 (2)	2.0	**0.45 (55)**	**28.2**	**0.4 (50)**	**16.8**	**0.3 (10)**	**9.8**	SI
Cibicidoides pachydermus	0.25 (2)	1.4	**0.48 (11)**	**6.1**	0.25 (2)	1.0	0.4 (7)	2.1	**0.4 (10**	**9.8**	SI
Globobulimina affinis	-	-	**4.7 (21)**	**10.7**	**3.6 (18)**	**9.7**	3.9 (12)	3.6	**4.3 (5)**	**4.9**	DI
Hanzawaia boueana	0.25 (4)	2.9	**0.25 (9)**	**5.1**	0.45 (5)	3.1	0.30 (12)	3.6	0.25 (4)	3.9	SI
Hoeglundina elegans	**0.25 (6)**	**4.3**	0.25 (2)	1.0	-	-	0.3 (1)	0.3	-	-	SI
Melonis barleeanus	**1.31 (12)**	**8.6**	**1.8 (10)**	**5.1**	**1.6 (15)**	**7.7**	**1.3 (21)**	**6.3**	**1.9 (5)**	**4.9**	II
Nuttallides convexus	1.25 (1)	0.7	0.5 (2)	1.0	0.25 (1)	0.5	0.3 (10)	3.3	**0.55 (5)**	**4.9**	SI
Uvigerina auberiana	0.75 (2)	1.4	0.25 (2)	1.0	0.25 (1)	0.5	0.3 (3)	0.9	**0.42 (6)**	**5.9**	SI
Uvigerina mediterranea	**0.35 (48)**	**35.3**	**0.32 (87)**	**44.7**	**0.27 (31)**	**18.5**	**0.7 (119)**	**35.7**	**0.56 (27)**	**26.5**	SI
Uvigerina peregrina	-	-	0.5 (6)	3.0	**0.38 (8)**	**5.1**	**0.6 (21)**	**6.3**	0.75 (3)	2.9	SI
Fossilising agglutinates											
Bigenerina nodosaria	**0.64 (9)**	**6.5**	0.75 (2)	1.0	**0.25 (8)**	**5.1**	**0.5 (14)**	**4.8**	0.25 (2)	2.0	SI
Siphotextularia heterostoma	0.25 (1)	0.7	0.25 (1)	0.5	**0.25 (8)**	**4.1**	0.4 (3)	0.9	-	-	SI
ALD_{10} of the core	**0.6 (139)**		**1.0 (197)**		**1.0 (195)**		**0.8 (333)**		**0.9 (102)**		

Table 5. Average living depths (ALD_{10}), relative percentage abundances and microhabitat descriptions of dominant species from open slope cores. SI = shallow infaunal, II = intermediate infaunal, DI = deep infaunal.

5.4.4 VERTICAL DISTRIBUTION OF CANYON LIVING FAUNA AND MICROHABITATS

The vertical distributions of the "live" canyon foraminifera in the topmost 10 cm of the sediment are shown in figures (4a-c) along with downcore oxygen measurements. On the Nazaré canyon terrace (core 37), there is a peak in foraminiferal density in the 1-1.5 cm layer, followed by a clear density decrease down to the bottom of the core; this is in contrast to oxygen concentrations which decline exponentially downcore throughout, to attain zero value at 1.8 cm. Conversely, on the Cascais and Setúbal canyon axes (cores 28 and 33 respectively), maximum densities of live foraminifera are found in the uppermost 0-0.5 cm. Densities decrease with sediment depth and broadly correspond with decreasing oxygen concentrations. Total ALD_{10} of each core and ALD_{10} values for the main species >4% in any one of the three stations are shown in Table 4. Total ALD_{10} values are shallowest in core 33 (1.2 cm), and deepest in core 37 (2.2 cm). *Cibicidoides pachydermus* and *Uvigerina mediterranea* have clear preferences for the topmost 0-0.5 cm interval in all stations. *Melonis barleeanus* which occupies a superficial niche in core 28, has maximum abundances at intermediate depths in the other two cores, while *Bolivina alata*, *Bulimina inflata* and *Valvulineria bradyana* occur at intermediate depths in core 37. Finally *Chilostomella oolina*, *Globobulimina affinis* and *Globobulimina turgida* occupy deep infaunal niches in all three stations.

In more detail, in the Nazaré canyon (Core 37, Figure 4 a), *Bulimina inflata* (ALD_{10} = 1.1 cm), *Bolivina alata* (ALD_{10} = 1.8 cm), *Melonis barleeanus* (ALD_{10} = 1. 7 cm), and *Valvulineria bradyana* (ALD_{10} = 2.4 cm) all show intermediate infaunal tendencies with subsurface infaunal maxima in the 1-1.5 cm interval (*B. inflata B. alata* and *M. barleeanus*) and 2-3 cm interval (*V. bradyana*) respectively. Deeper still, *Chilostomella oolina* (ALD_{10} = 4.6 cm) and *Globobulimina turgida* (ALD_{10} = 5.3 cm) occupy deep infaunal habitats with infaunal maxima at 2-5 cm and 4-5 cm respectively. *Cibicidoides pachydermus* which is

dominant in the other two canyon cores, but only constitutes 3% of the fauna here, is the only species to show a clear shallow infaunal microhabitat with a surficial maximum in the 0-0.5 cm interval.

In the Cascais canyon (core 28, Figure 4 b), *C. pachydermus* (ALD_{10} = 0.3 cm) and *Uvigerina mediterranea* (ALD_{10} = 0.5 cm) show shallow infaunal distributions in the uppermost cm, but substantial numbers occur downcore as well. *M. barleeanus* (ALD_{10} = 1.1 cm) is also mostly present in the uppermost 0-0.5 cm and declines exponentially down to 8 cm. The deep infaunal species, *C. oolina* (ALD_{10} = 2.5 cm), has a bimodal distribution, with maximum abundances in the top 0.5 cm and 4-5 cm interval, while *G. turgida* (ALD_{10} = 3.9 cm) has a deep infaunal maximum between 4-6 cm.

At station 33 (Setúbal canyon, Figure 4 c), *U. mediterranea* and *Hanzawaia boueana* (both ALD_{10} = 0.4 cm), *C. pachydermus* and *Bigenerina nodosaria* (both ALD_{10} = 0.5 cm) and *Uvigerina peregrina* (ALD_{10} = 0.6 cm) all occupy a shallow infaunal habitat in the uppermost 0-0.5 cm, with exponential decreases downcore. *Melonis barleeanus* (ALD_{10} = 1.1 cm) has an intermediate infaunal tendency with maximum abundance in the 0.5-1 cm interval. The deep infaunal species *Globobulimina affinis* (ALD_{10} = 2.3 cm) and *C. oolina* (ALD_{10} = 3.3 cm) occur somewhat deeper with maximum abundances at 2-3 cm and 3-4 cm respectively.

Figure 4 a)

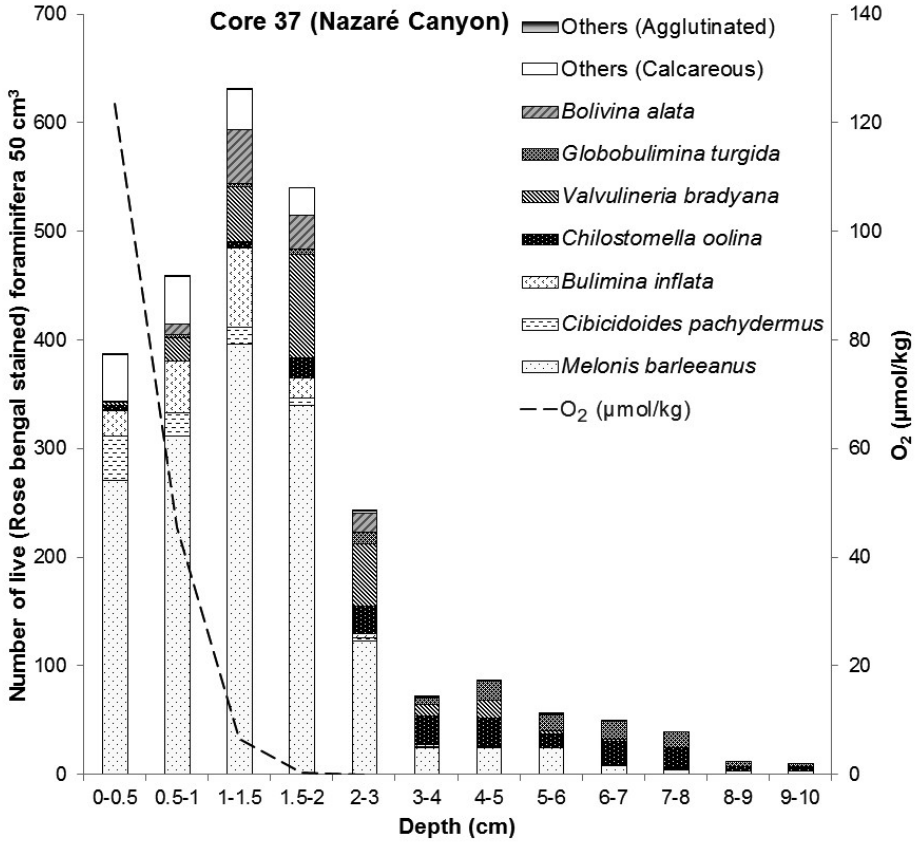


Figure 4 b)

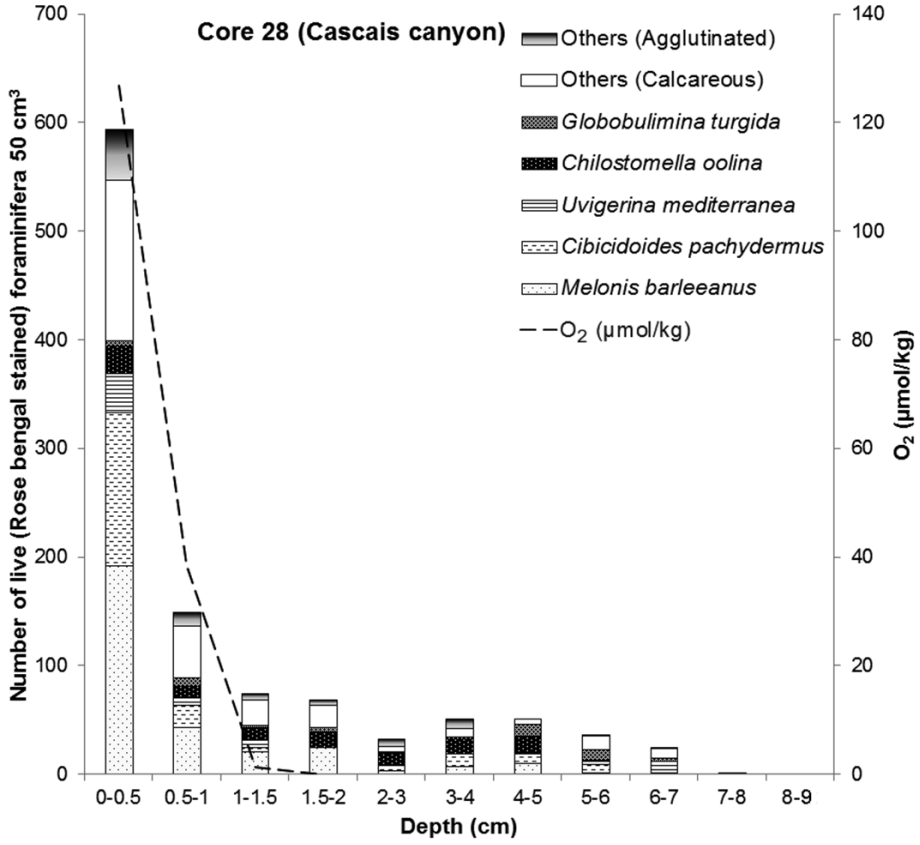
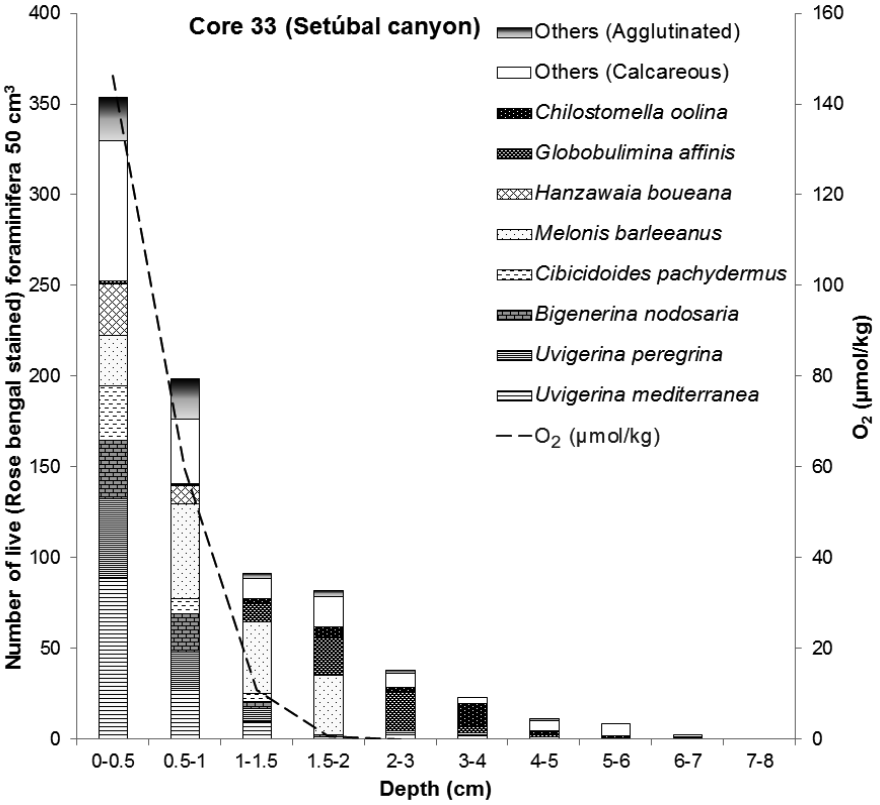


Figure 4 c)



Figures 4a-c. Living foraminiferal downcore distributions (standardised for 50 cm^3 sediment volume) for the three canyon cores. For each core, all species >4% are represented.

5.4.5 VERTICAL DISTRIBUTION OF OPEN SLOPE LIVING FAUNA AND MICROHABITATS

All four open slope cores taken from the 64PE269 cruise, and core 27 collected from the 64PE269 cruise have maximum densities of live foraminifera in the uppermost 0-0.5 cm, which decrease with sediment depth and broadly correspond with decreasing oxygen concentrations and decreasing phytopigment content (Figures 4d-h, Figure 2b). Total ALD_{10} values of each core and ALD_{10} values for the main species >4% in any one of the five cores are shown in Table 5. Total ALD_{10} values are shallowest in core 36 (0.6 cm), and deepest in

Figure 4 d)

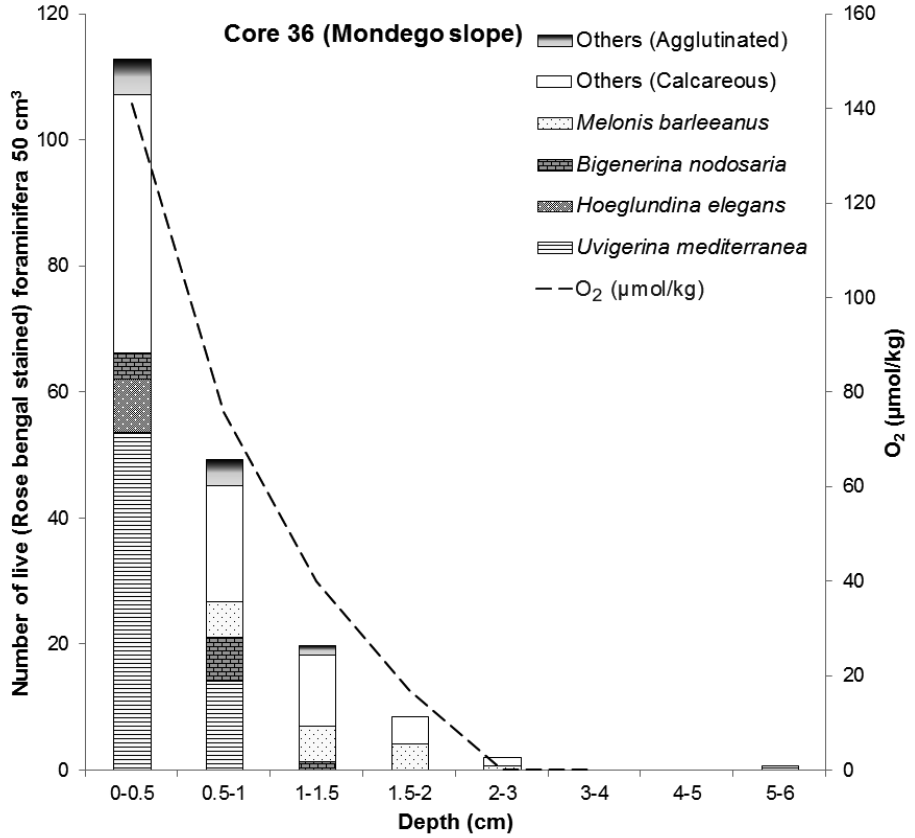


Figure 4 e)

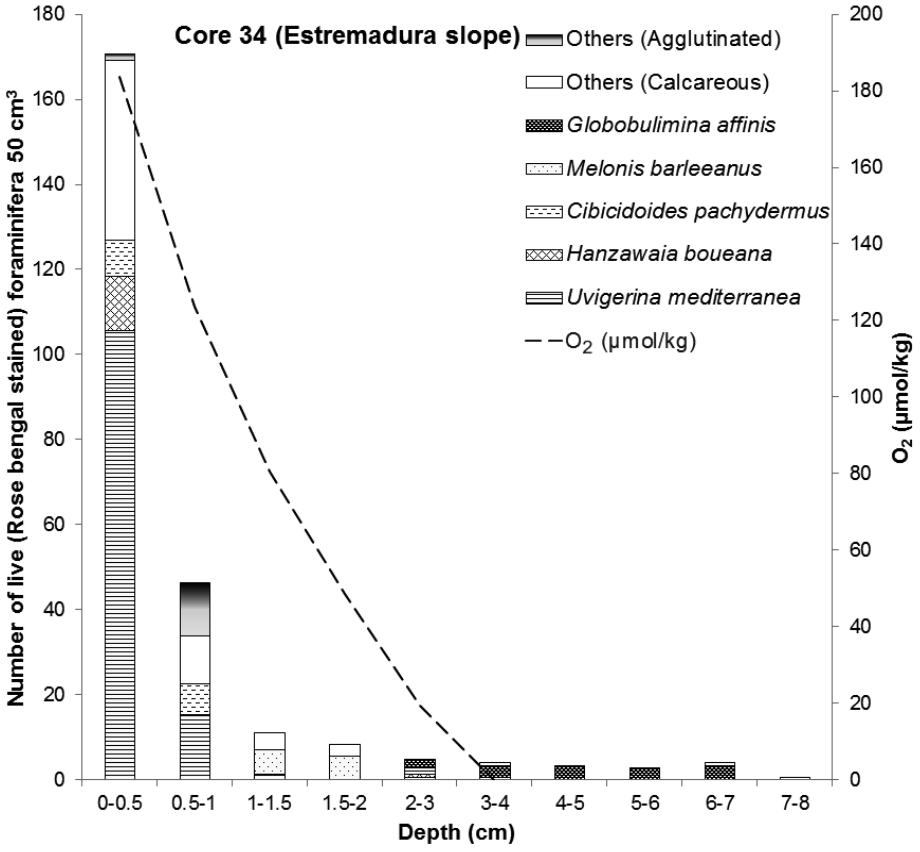


Figure 4 f)

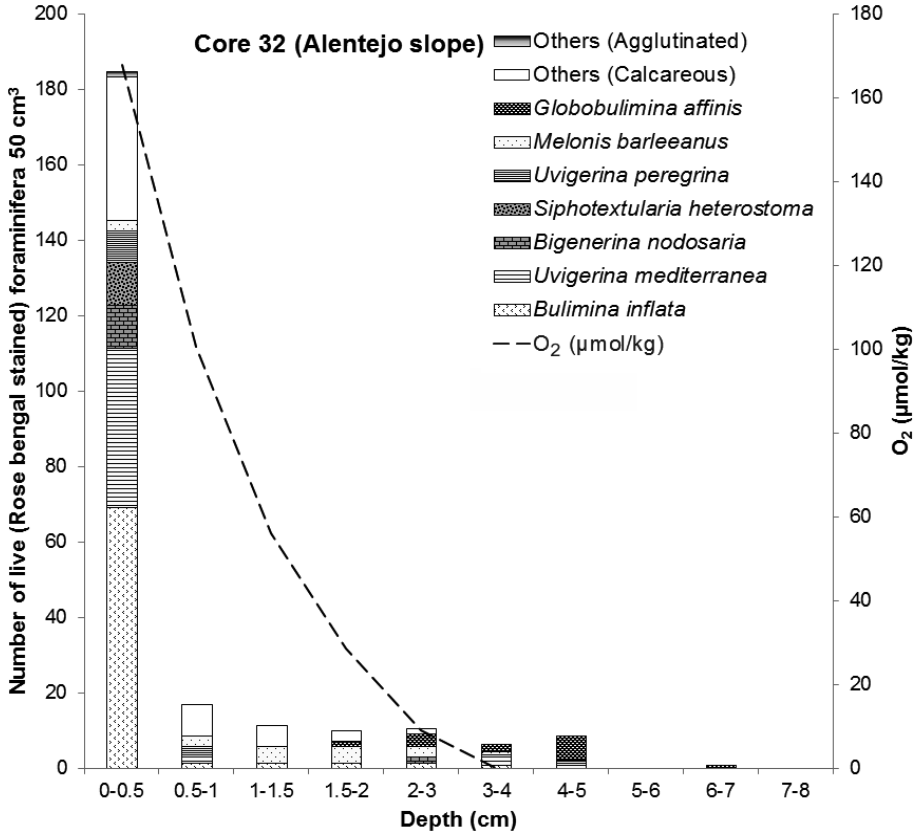


Figure 4 g)

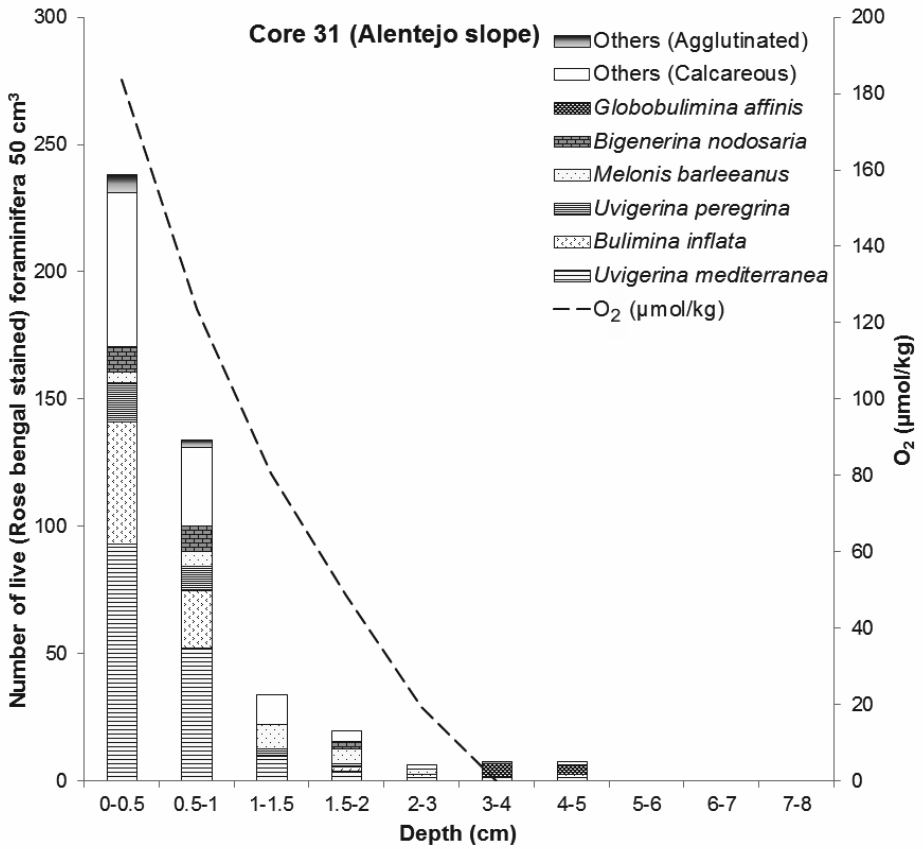
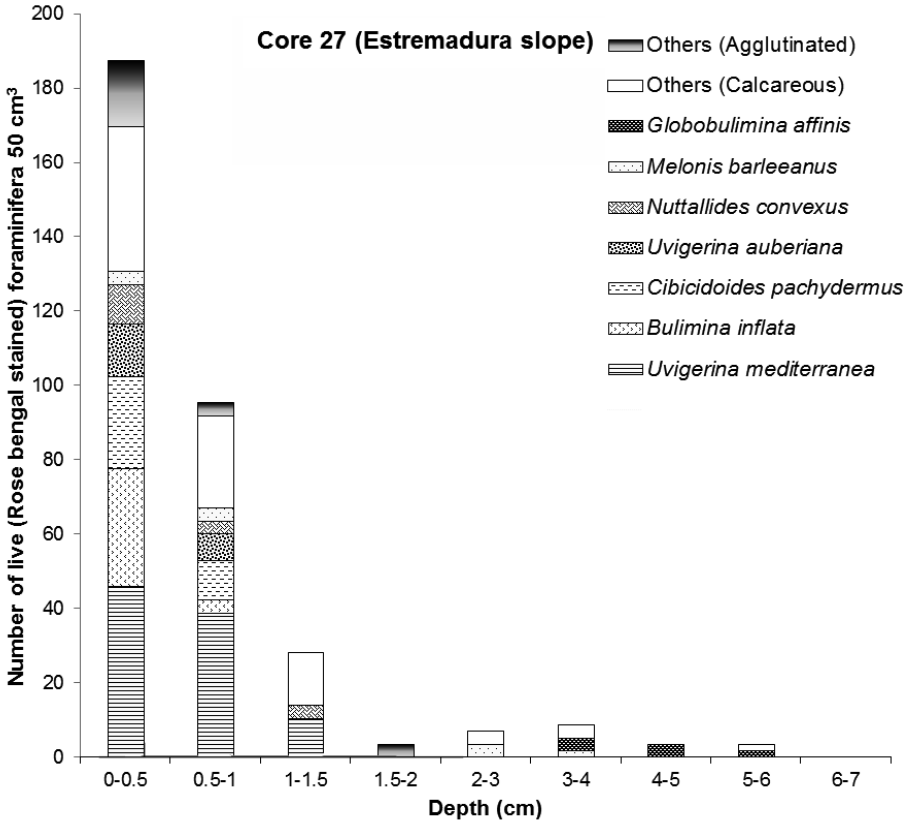


Figure 4 h)



Figures 4d-h. Living foraminiferal downcore distributions (standardised for 50 cm^3 sediment volume) for the five open slope cores. For each core, all species >4% are represented.

cores 34 and 32 (both 1.0 cm). *Bulimina inflata*, *Cibicidoides pachydermus*, *Hoeglundina elegans*, *Uvigerina mediterranea* and *Bigenerina nodosaria* have clear preferences for the topmost 0-0.5 cm interval, *Melonis barleeanus* preferentially occurs at intermediate depths (i.e. 0.5-3 cm) and *Globobulimina affinis* selects sediment intervals ≥2 cm.

In detail, on the Mondego slope (core 36, Figure 4d), *Hoeglundina elegans* (ALD_{10} = 0.3 cm), *Uvigerina mediterranea* (ALD_{10} = 0.4 cm) and *Bigenerina nodosaria* (ALD_{10} = 0.6 cm)

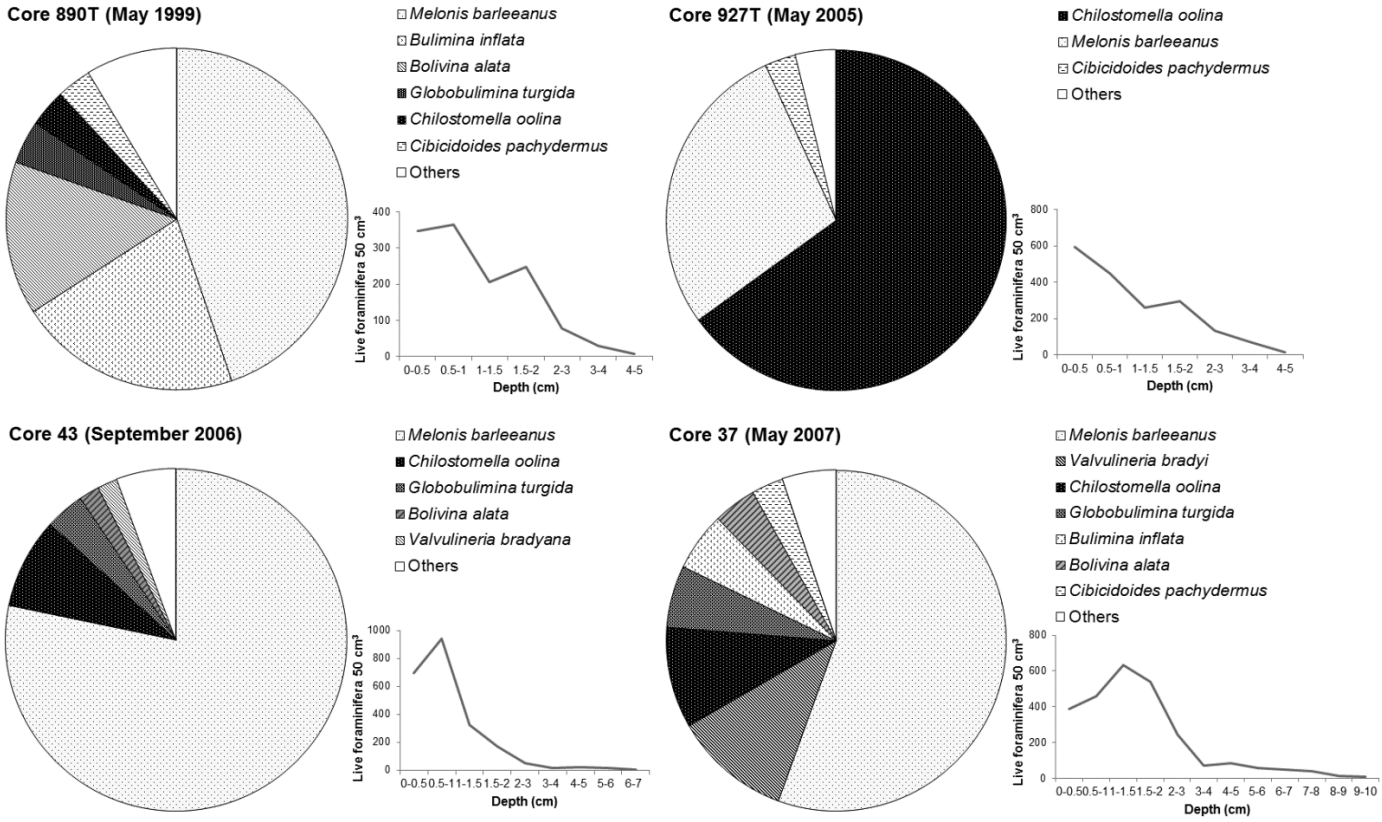
occupy shallow infaunal niches concentrated in the 0-0.5 cm interval, while *Melonis barleeanus* (ALD_{10} = 1.3 cm) occupies a strictly intermediate infaunal habitat that is mostly concentrated between 0.5-2 cm; there are no species with deep infaunal distributions in this core. On the Estremadura slope (core 34, Figure 4e), *U. mediterranea* and *Hanzawaia boueana* (both ALD_{10} = 0.3 cm) and *Cibicidoides pachydermus* (ALD_{10} = 0.5 cm) all occupy shallow infaunal microhabitats. *M. barleeanus* (ALD_{10} = 1.8 cm) shows a strictly intermediate infaunal distribution with a maximum between 1-2 cm, while *Globobulimina affinis* (ALD_{10} = 4.7 cm) occupies a distinctly deep infaunal niche between 3-7 cm. On the Alentejo slope (core 32, Figure 4f), *U. mediterranea*, *B. nodosaria* and *Siphotextularia heterostoma* (each ALD_{10} = 0.3 cm), *Uvigerina peregrina* (ALD_{10} = 0.4 cm) and *Bulimina inflata* (ALD_{10} = 0.5 cm) all occupy shallow infaunal niches in the uppermost cm. *Melonis barleeanus* (ALD_{10} = 1.6 cm) shows an intermediate infaunal distribution with a maximum between 1-3 cm. Still deeper, *Globobulimina affinis* (ALD_{10} = 3.6 cm) occupies a distinctly deep infaunal niche between 2-5 cm. Core 31 (Figure 4g) which is also from the Alentejo slope has a very similar vertical foraminiferal distribution to core 32, with *B. inflata* (ALD_{10} = 0.4 cm), *B. nodosaria* (ALD_{10} = 0.5 cm), *U. peregrina* (ALD_{10} = 0.6 cm) and *U. mediterranea* (ALD_{10} = 0.7 cm) all concentrated in the uppermost cm. *M. barleeanus* (ALD_{10} = 1.3 cm) and *Globobulimina affinis* (ALD_{10} = 3.9 cm) also show intermediate (maximum 1-1.5 cm) and deep infaunal (maximum 3-5 cm) distributions respectively. Finally, in core 27 (Estremadura slope, Figure 4h) taken from the 64PE252 cruise, *B. inflata* (ALD_{10} = 0.3 cm), *C. pachydermus* and *Uvigerina auberiana* (both ALD_{10} = 0.4 cm), *Nuttallides convexus* and *U. mediterranea* (both ALD_{10} = 0.6 cm) are all concentrated in the uppermost cm. *M. barleeanus* (ALD_{10} = 1.9 cm) shows a rather scattered distribution, with 2 specimens present at 2-3 cm. However, *G. affinis* (ALD_{10} = 4.3 cm) shows a distinctly deep infaunal distribution between 3-6 cm.

5.5 DISCUSSION

5.5.1 NAZARÉ CANYON; CORES TAKEN FROM THE CANYON TERRACE AT ~1000 M DEPTH

Here we compare four cores from four different cruises collected in close geographical proximity to each other along the Nazaré canyon terrace (Figure 1, Table 2). High speed currents, high sedimentation rates and frequent sediment resuspension on active canyon axes create a very unstable sediment substrate for most benthic foraminifera. Foraminiferal assemblages in such environments are characterised by a poor pioneer fauna dominated by *Technitella* spp. (Koho and others, 2007; Hess and Jorissen, 2009). However, a first investigation of the Nazaré canyon terrace by Koho and others, 2007 revealed that in contrast to the Nazaré canyon axis, the adjacent canyon terrace has much higher standing stocks. This results from a more stable sediment regime where fine sediment and C_{org} can accumulate. Consequently, cores from the canyon terraces have more diverse assemblages and well developed and differentiated microhabitat patterns in relation to stations from the canyon axis. In particular, core 890T from the May 1999 cruise showed a unimodal subsurface maximum (at 1.5-2 cm) which was attributed to the prevailing stable redox zones (Figure 5). When we compare this core to those from other cruises, this unimodal distribution is also a prevalent feature in cores 37 (this study) and 43 (Nardelli and others, 2010) from the May 2007 and September 2006 cruises respectively. However this pattern is not seen in core 927T (May 2005) where standing stocks show an exponential decline with increasing sediment depth (Figure 5). Nonetheless, the four cores share many species in common, although the relative abundance of these species varies considerably (Figure 5). All have strikingly high numbers of *Melonis barleeanus* (28-79%). In addition, *Chilostomella oolina* and *Cibicidoides pachydermus* both make >3% in all stations. *C. oolina* is particularly dominant in core 927T (65%). *Bolivina alata*, *Bulimina inflata* and *Globobulimina turgida* are also present in all

stations, but are virtually absent at core 927T; *B. alata* and *B. inflata* both have maximum relative abundances in core 890T (15% and 21% respectively), while *G. turgida* is greatest (6%) in core 37. Finally, *Valvulinaria bradyana* is dominant in core 37 (11%), but absent in core 927T. When the ALD_{10} of each of these species is compared between cores (Figure 6), it is clear that all have maximum (deepest) ALD_{10} values in core 37. Conversely, the shallowest ALD_{10} values (with the exception of *G. turgida*) are observed at station 927T, while ALD_{10} values for species in cores 890T and 43 are somewhat between the two. The fact that all dominant species show similar trends in ALD_{10} between the cores suggests that their microhabitat distributions are controlled by the same environmental variable(s). Further, there seems to be a general positive relationship between deeper total ALD_{10} and greater diversity index values (Table 3). For example, highest values for rarefaction are found in both cores 37 ($E(S_{50})$ = 9.2) and 890T ($E(S_{50})$ = 9.1), highest Fisher alpha index values (4.7) are recorded in core 37 and the highest Shannon index (1.71), Equitability (0.60) and lowest Dominance (0.27) values are recorded in core 890T (Table 3). At these two cores, total ALD_{10} values are greatest and dominant species have, relative to the other two stations, deeper ALD_{10} values (Figure 6). In contrast, the lowest rarefaction ($E(S_{50})$ = 4.9), Fisher alpha index (2.4) and Shannon-Wiener index (0.95) values are recorded in core 927T, while lowest Equitability (0.32) and highest Dominance (0.62) are recorded at core 43. Dominant species, particularly *Melonis barleeanus* and *Chilostomella oolina*, have much shallower ALD_{10} values at these two cores compared to cores 37 and 890T. Interestingly, many of the dominant species (e.g. *B. alata, C. oolina, M. barleeanus, G. turgida, V. bradyana*) are recorded to store nitrate, while both *G. turgida* and *V. bradyana* have also been recorded to respire nitrate (Høgslund and others, 2008, Risgaard-Petersen and others, 2006, Piña-Ochoa and others, 2010a, 2010b). Further, these species are typically found to occupy intermediate and deep infaunal microhabitats which track important redox fronts within the sediment.



Figures 5. Pie charts of live foraminifera from cores taken from the Nazaré canyon terrace site from different sampling moments. All species >4% are represented.

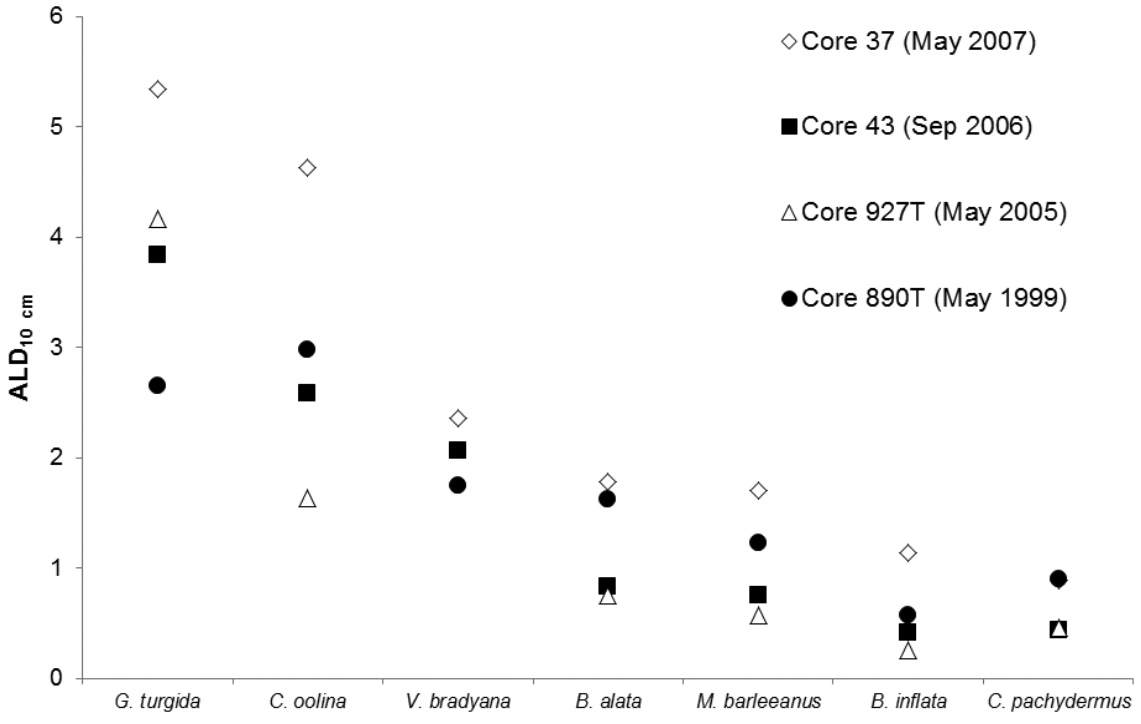


Figure 6. ALD_{10} of dominant species from four cores taken from the Nazaré canyon terrace site.

In particular, *M. barleeanus* is known to preferentially live within the nitrate reduction zone in the sediment, with its dietary preferences related to the presence of bacteria or degradation products of metabolically nutritious particles produced by bacteria in the sediment (Jorissen and others, 1995, 1998, Licari and others, 2003, Fontanier and others, 2002, 2003, 2005, Koho and others, 2007, 2008a). *Globobulimina turgida* is also known to thrive in oxygen-free sediment environments where it can carry out complete denitrification of nitrate to N_2 (Høgslund and others, 2008; Risgaard-Peterson and others, 2006; Piña-Ochoa and others, 2010b). In the Lisbon-Setúbal canyon, *Chilostomella oolina* was recorded to inhabit sediments at and below the nitrate penetration depth where phytopigment content >5 μg/cm^3, suggesting that this species may benefit from the labile organic matter either directly by consuming it or indirectly from associated bacterial populations and/or bacterial activity. The latter option appears to be more likely as in a feeding experiment of Nomaki and others, 2005, *Chilostomella ovoidea* (a species which may be synonymous with *C. oolina*) was not observed to ingest any algae, and was later described to consume sedimentary organic matter unselectively (Nomaki and others, 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 added food (Koho and others, 2008b). It has been suggested by some authors that species such as *M. barleeanus*, *C. oolina* and *G. turgida* occupy sediments rich in refractory organic matter (Caralp, 1989; Fontanier and others, 2002, 2003, 2005). However this suggestion is in contrast with observations by Fontanier and others (2008), Koho and others (2008a) and Nardelli and others (2010), which document *M. barleeanus* occupying sediments rich in labile organic matter. This is also the case for core 37, where phytopigments are rich throughout the core (Figure 2a). As previously discussed, some of the dominant species (*G, turgida* and *V. bradyana*) encountered are known to be facultative anaerobes (see recent review by Piña-

Ochoa et al. 2010). Given the fact that aerobic respiration provides >3 times higher energy yields than nitrate respiration (Piña-Ochoa and others, 2010a), it is likely that denitrification is an auxiliary method of metabolism during conditions of anoxia. Unfortunately in our comparison study, oxygen penetration data is only available for core 37. In this core, oxygen penetrates down to 1.8 cm, which broadly coincides with where the maximum numbers of stained *M. barleeanus* are found (1-1.5 cm). *Bolivina alata* and *Bulimina inflata* show similar downcore distributions as *M. barleeanus*, suggesting these two species may share a similar microhabitat under the same environmental conditions, perhaps benefiting from the zone of nitrate reduction. Further, *C. oolina* and *G. turgida* are most abundant in the anoxic zone between 2-10 cm (ALD_{10} = 4.6 and 5.3 respectively), while *V. bradyana* and *C. cylindrica* seem to peak at the dysoxic-anoxic boundary at 1.5-2 cm. In cores 890T and 43, *M. barleeanus* peaks at the 0.5-1 cm interval, which suggests a shallower oxygen penetration depth. The shallower ALD_{10} values of *C. oolina* and *G. turgida* and other species at these stations support this idea. Finally in core 927T, *M. barleeanus* shows a maximum abundance in the top 0-0.5 cm interval of the core, along with a high abundance of *C. oolina*. The very skewed distribution, without an infaunal maximum of *M. barleeanus*, coupled with the presence of a large number of *C. oolina* at the sediment surface suggests a very shallow oxygen penetration depth of <0.5 cm. It is interesting to note the surprising poverty of species at this site that are dominant in the other cores (e.g., *B. alata, B. inflata, G. turgida, V. bradyana)*. It appears therefore that *M. barleeanus* and *C. oolina* are more tolerant with respect to prolonged anoxia or hypoxia by using efficient denitrification metabolic pathways, and/or are able to utilise nitrates or bacteria related products for longer periods of time.

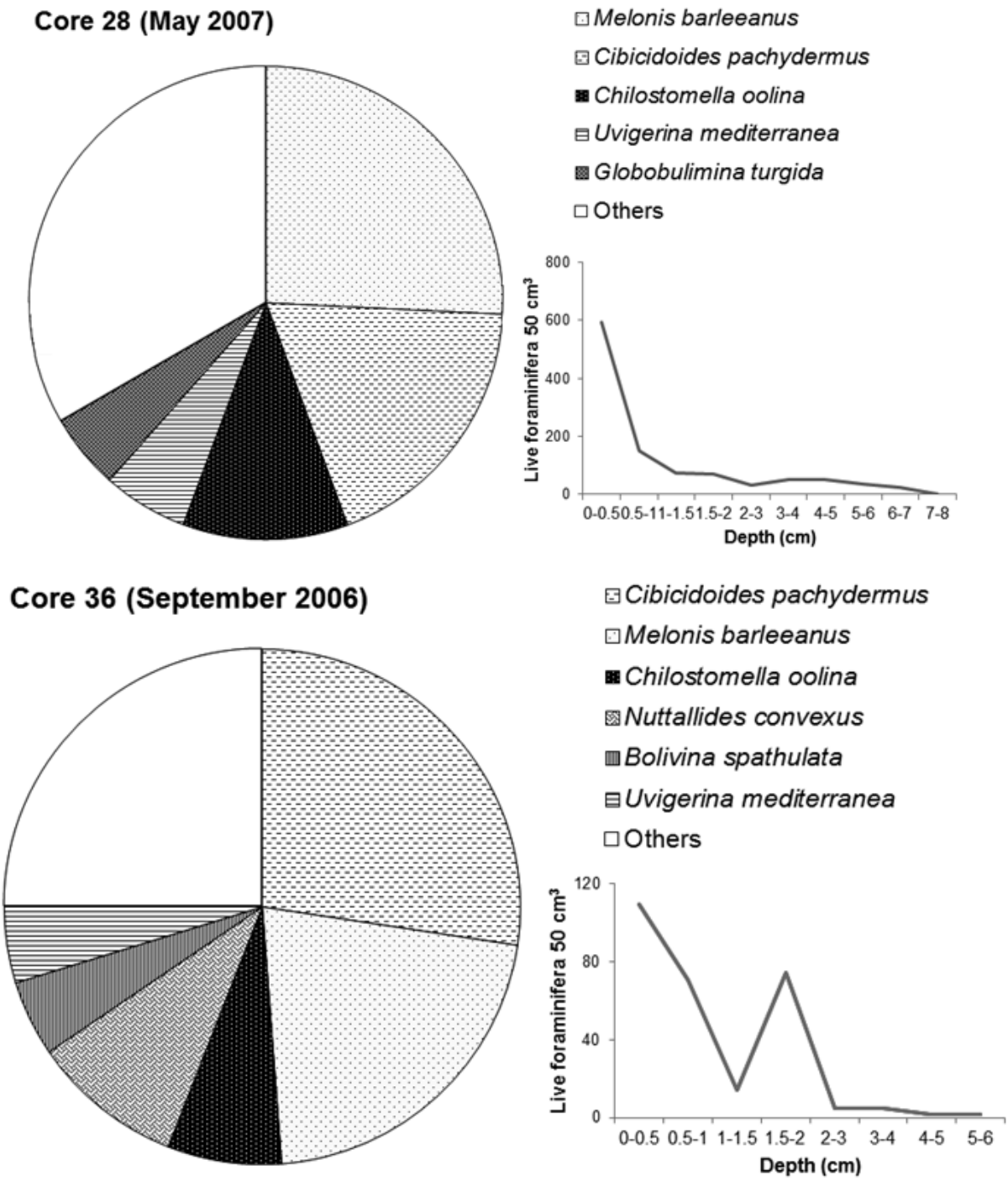
Summarising, the four cores described from the Nazaré canyon terrace appear to represent states of comparable canyon terrace environments. The foraminiferal assemblage in core 927T (Koho and others, 2007) reflects conditions with minimal oxygen penetration that

is a probable response to a maximum flux of labile organic matter. The faunas are strongly dominated by the most anoxic-tolerant taxa. Core 43 (Nardelli and others, 2010) reflects a slightly better oxygenated ecosystem, where intermediate and deep infaunal taxa are living somewhat deeper in the sediment, but where faunal diversity is still low. This core could reflect conditions at a slightly longer period (several weeks-month(s)) after a substantial enrichment in organic matter supply. Finally core 890T (Koho and others, 2007) and core 37 (this study), present more diverse faunas with deeper sediment penetration in response to more stable redox conditions not affected by significant organic matter supplies in the recent past. It appears therefore that in this eutrophic canyon terrace context, the intermittent nature of organic matter supplies is responsible for considerable temporal variability of the main redox boundaries, which in turn controls the composition and microhabitats of the benthic foraminiferal faunas.

5.5.2 CASCAIS CANYON AXIS

In contrast to the Nazaré canyon terrace cores our core from the Cascais canyon axis show a very contrasting foraminiferal assemblage. A first study by Nardelli and others (2010) of the same site (core 36, September 2006) of the Cascais Canyon as the one studied in this chapter (sampled in May 2007), showed a rather poor assemblage (150 individuals per 50 cm^2) with a bimodal downcore distribution despite high concentrations of phytopigments in the upper cm (Figure 7). The two peaks at 0-0.5 cm and 1.5-2 cm, and sediment levels in-between show different foraminiferal assemblages; *Nuttallides convexus*, normally a surface dweller (e.g. Fontanier and others, 2002 ; Mojtahid and others, 2010; Phipps and others, in prep) does not occur at the surface but shows a maximum concentration at 1.5-2 cm, while *Uvigerina mediterranea* and *Melonis barleeanus*, both present at the top 0-0.5 cm interval diminish at 0.5-1cm and 1-1.5 cm respectively, but re-emerge at 1.5-2 cm. *Cibicidoides pachydermus* and *Chilostomella oolina* on the other hand are recorded between 0-1.5 cm, but not at 1.5-2 cm.

Further, a ^{210}Pb profile of the core shows a homogenised surface layer 1.5 cm thick. Nardelli and others (2010) suggested that these distributions were caused by a recent turbidite event that covered the 1.5-2 cm interval (which represented the sediment-water interface before deposition of the turbidite) and subsequently slowed the degradation of protoplasm of the former surface dwellers, which were buried at 1.5 cm depth. Our core 28, which was taken at the same site 8 months after core 36 (Table 2) shows a comparatively well developed fauna with 4 times greater faunal concentrations (~640 individuals per 50 cm^2). Relative abundances of dominant species (*M. barleeanus*, *C. pachyderma*, *C. oolina*, *U. mediterranea*) show little variance between the two cores (Figure 7). Some species such as *Globobulimina turgid*, are present in the May 2007 sampling (core 28), but not in September 2006 (core 36). We think that these data confirm the interpretation of Nardelli and others, (2010). The greater presence of deep infaunal taxa reflects a more developed colonisation a further 8 months after the turbidite deposition. Also, the ALD_{10} values of many species and indeed the total ALD_{10} of the core are deeper in core 28 (1.7 cm) than in core 36 (Figure 7, Table 3) further reflecting the progression of recolonisation and microhabitat partitioning. A more advanced stage of recolonisation may lead to higher diversity as conditions become more stable. However, diversities vary little between the two cores. In particular, species richness (measured by the rarefaction method) shows that for 50 individuals there are 16.7 and 16.0 species in cores 36 and 28 respectively. Nonetheless, the Fisher alpha (11.1) and Shannon indices (2.68) are slightly higher in core 28 than in core 36 (9.0 and 2.38 respectively). These rather comparable biodiversity values between the two cores are probably explained by the fact that diversity indices where artificially high in core 36, because the fauna preserved below 1.5 cm, representing pre-turbidite fauna, was added to the post-turbidite fauna found between 0 and 1.5 cm depth.



Figures 7. Pie charts of live foraminifera from cores taken from the Cascais canyon terrace site from different sampling moments. All species >4% are represented.

5.5.3 INTERCANYON VARIABILITY

In the Setúbal canyon axis, core 33 has an assemblage that resembles more closely that found in the Cascais canyon axis. In particular, the top cm of this core is rich in *Cibicidoides pachydermus. Uvigerina mediterranea*, *Uvigerina peregrina* and *Bigenerina nodosaria* (Figure 4b). These species are well documented to occupy shallow infaunal microhabitats (e.g., Fontanier and others, 2002, 2003, 2008; Barras and others, 2010). In particular, *U. mediterranea* and *U. peregrina* are described as opportunistic species that grow and reproduce in sediments where fresh phytodetritus is available (Fontanier and others, 2003), and thrive in canyon environments rich in labile organic matter (Fontanier and others, 2008). These assemblages are in sharp contrast to those found in the Nazaré canyon axis, where continuous resuspension of surface sediments and intermittent gravity flows create a very stressed environment dominated by one genus (*Technitella* spp.) even with the availability of large quantities of labile organic matter (Koho and others, 2007). However, despite more quiescent conditions on the Nazaré canyon terraces, shallow infaunal species seem to be repressed somewhat; *C. pachydermus* is the only species with a relative percentage abundance greater than 2% that shows a clear shallow infaunal distribution (Figure 4a) This is surprising when we consider that labile organic matter contents recorded at cores 37 and 43 are comparable in quantity to cores 28 and 36 (Figure 2a). Nardelli and others, (2010) attributed the absence of shallow infaunal species such as *Uvigerina mediterranea* to a low oxygen penetration into the sediment. However the oxygen penetration depth at core 37 is 1.8 cm which is comparable to the Setúbal canyon and deeper than in the Cascais canyon where it is 1.4 cm. This suggests that although oxygen concentration may be a limiting factor for these taxa directly after massive organic matter deposits (the conditions represented by Nazaré cores 43 and 927T), it was no longer the limiting factor when our core 37 was sampled. We think that the still low densities of many shallow infaunal taxa in this

core can be explained by competition with the more low oxygen resistant taxa. Their colonisation of shallow infaunal niches, and the competitive replacement of the more low oxygen resistant taxa already present there, needs a longer period of time, suggesting core 37 still represents an intermediate stage of ecological succession, and not the final climax association.

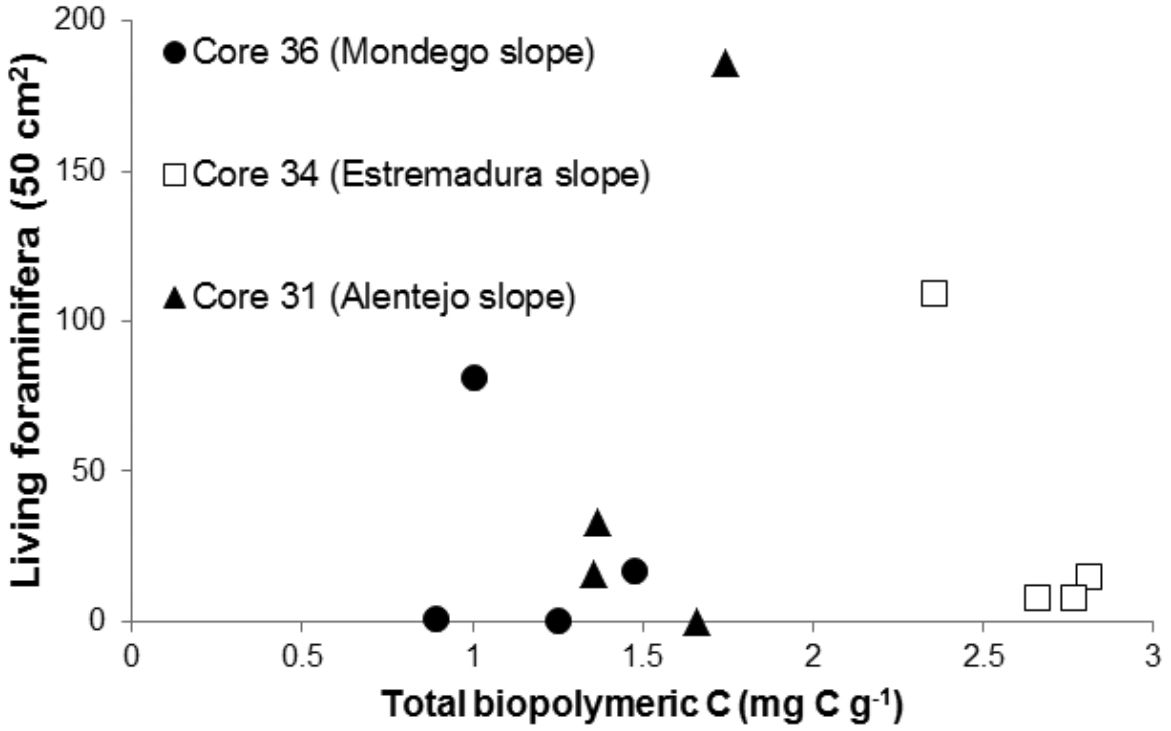
Species such as *Melonis barleeanus*, *Chilostomella oolina* and *Globobulimina turgida* are ubiquitous among the different canyons, although they occur in higher densities and relative abundances in the Nazaré canyon. These faunas have been described as typical "canyon faunas" in canyons where large quantities of degraded (Schmiedl and others, 2000; Fontanier and others, 2005) and fresh organic matter (Koho and others, 2008a ; Nardelli and others, 2010) are transported. As discussed previously, these species are known to sequester nitrate and may also consume bacteria stocks associated with important redox fronts and so labile organic matter may play only a minor role, if any, in their distributions. The dominance of these species in the Nazaré canyon clearly influences diversity parameters, where dominance values are high, ranging between 0.27 and 0.62. In the Cascais and Setúbal canyons, dominance values are much lower, ranging between 0.09 and 0.14 (Table 3). In turn, equitability, species richness (measured via the rarefaction method), Fisher alpha index and Shannon index values are highest in the Setúbal and Cascais canyon stations and lowest in the Nazaré canyon stations (Table 3). These differences are probably related to the relative contributions of shallow infaunal foraminifera to the overall foraminiferal community structure, where their presence raises the diversity indices in the Cascais and Setubal canyons relative to the Nazaré canyon.

It is not immediately clear why the Nazaré assemblages and Cascais/Setúbal assemblages are so different. However the Nazaré canyon, being the most active of the three

canyons (de Stigter and others, 2007, 2011; Koho and and others, 2007, 2008a), has a higher sediment accumulation rate on its terraces at ~1000 m (12.9 ±1.3 g m^{-2} d^{-1}, de Stigter and others, 2007) than in the axes of the Cascais and Setúbal canyons (5.1± 0.1 and 6.3 ±0.1 g m^{-2} d^{-1} respectively, de Stigter and others, 2011). Our faunal data strongly suggest that these higher sedimentation rates are accompanied by more frequent and/or more intense organic matter supplies. Such massive organic matter supplies appear to cause short term decreases of sediment surface oxygen concentrations and oxygen penetration into the sediment. These events favour the low oxygen tolerant intermediate and deep infaunal taxa, which take over the more superficial niches from less resistant shallow infaunal taxa. The return to equilibrium conditions, with sediment surface faunas dominated by shallow infaunal taxa, seems to take a considerable amount of time, and in case of repetitive organic supply events (such as in Nazaré canyon), the time between successive organic matter supply events may be too short to develop such equilibrium faunas.

5.5.4 SPATIAL VARIABILITY ON THE OPEN SLOPE – 64PE269 CRUISE

Compared to the canyon faunas, the faunas from our four open slope stations sampled in May 2007 (Table 3) have considerably lower standing stocks. However it is also clear that standing stocks are lowest on the Mondego slope in the north of our transect (~100 individuals per 50 cm^2) and highest on the Alentejo slope to the south (235 individuals per 50 cm^2). Similarly, Nardelli and others, (2010) found greater abundances on the Alentejo slope (core 56) and lowest on the Mondego slope (core 7). They attributed these differences in abundance to the higher trophic status on the southern slope, particularly the higher quantity of biopolymeric C found in core 56. When we compare downcore foraminiferal densities with sedimentary biopolymeric C for each sediment interval, there is no significant relationship (Figure 8). However there is a very strong relationship between sedimentary phytopigment content and the foraminiferal density in each sediment layer (r = 0.95, p < 0.0001), suggesting that phytopigments may control foraminiferal standing stocks in our open slope cores. The relationship between phytopigments and foraminiferal standing stocks has been demonstrated in a number of recent publications (Koho and others, 2007 ; Barras and others, 2010 ; Duros and others, 2011 ; Phipps and others, 2012) Further, phytopigment contents in the uppermost cm of our cores is slightly higher in the south of our transect (CPE = 7.8 µg g^{-1}, Core 31) and lowest in the north (CPE = 5.2 µg g^{-1}, Core 36), agreeing with the conclusion of Nardelli and others (2010) that the Alentejo slope is more organically enriched. Interestingly core 36 exhibits the greatest diversity among the four cores despite having the lowest organic matter values (Figures 2b, Table 3). An explanation for this could be that the lower amount of bioavailable organic matter at core 36 inhibits more opportunistic shallow infaunal species such as *Uvigerina mediterranea* from dominating the assemblage, allowing less common species to compete for resources in the uppermost cm.


Core 36 (Mondego slope)
Core 34 (Estremadura slope)
Core 31 (Alentejo slope)
Living foraminifera (50 cm²)
Total biopolymeric C (mg C g⁻¹)
0
50
100
150
200
0
0.5
1
1.5
2
2.5
3

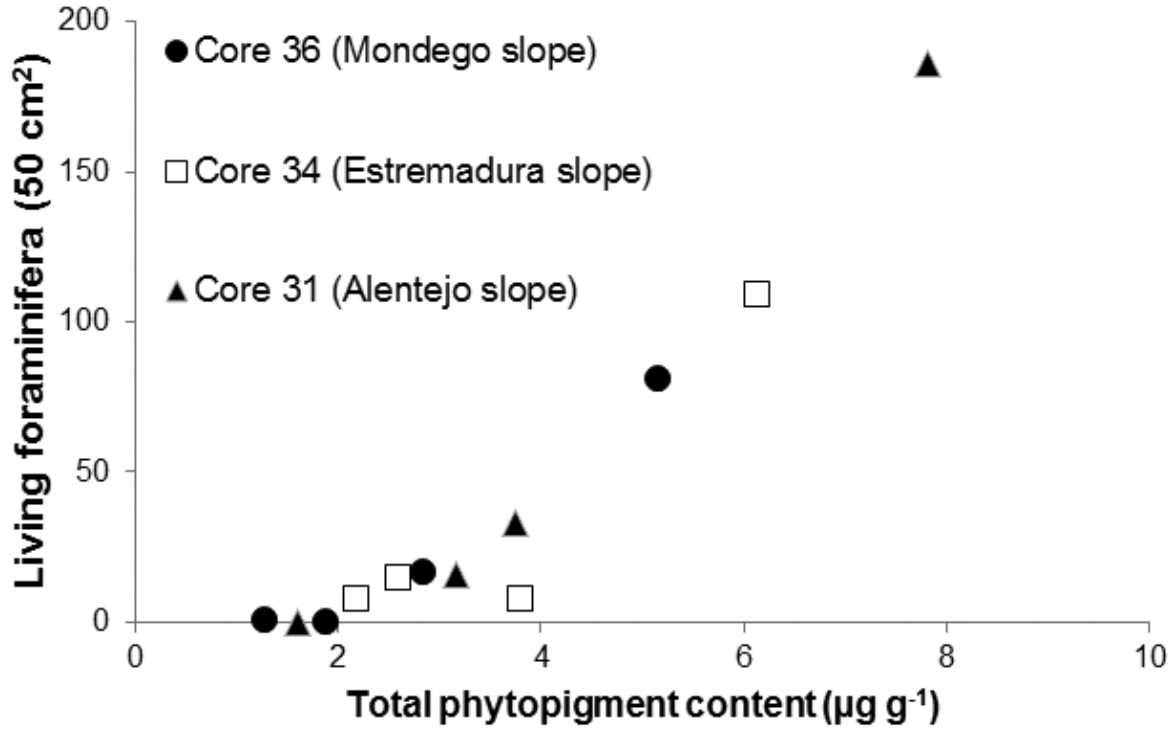

Core 36 (Mondego slope)
Core 34 (Estremadura slope)
Core 31 (Alentejo slope)
Living foraminifera (50 cm²)
Total phytopigment content (µg g⁻¹)
0
50
100
150
200
0
2
4
6
8
10

Figure 8. Density of living foraminifera from open slope cores (this study) relative to total biopolymeric C and phytopigment contents from their relative sediment levels (0-1, 1-3, 3-5 and 5-10 cm)

The faunas of all four of our open slope cores are characterised by a high dominance of *Uvigerina mediterranea* in the uppermost cm, followed by lower numbers of *Melonis barleeanus* between 0.5-3 cm and (with the exception of core 36) *Globobulimina affinis* below 2 cm. This foraminiferal association has been observed both in previous studies of the Portuguese margin (i.e. Schönfeld 2001; Koho and others, 2007, 2008a; Griveaud and others, 2010; Nardelli and others, 2010) and in other open-slope settings from equivalent water depths, particularly in the Bay of Biscay (Fontanier and others, 2002, 2006, 2008 ; Mojtahid and others, 2010) and Mediterranean Sea (Schmiedl and others, 2000). As previously discussed, *U. mediterranea* typically selects a shallow infaunal niche in the uppermost cm, while *M. barleeanus* and *G. affinis* occupy intermediate and deep infaunal niches respectively. This niche selection is remarkably consistent across our transect; *U. mediterranea* is always most abundant in the uppermost cm, with an ALD_{10} varying between 0.3-0.7, *M. barleeanus* is most abundant between 0.5 and 3 cm (ALD_{10}= 1.3-1.8) just before conditions become anoxic while *G. affinis* only occurs around or just below the maximum oxygen penetration depth (ALD_{10} of 3.6-4.7). However, the faunal compositions of our cores are by no means identical and there are some quite distinct differences that probably reflect the different trophic levels along the transect (Figure 9). On the Mondego slope (core 36), there is a notable absence of deep infaunal species (i.e. *G. affinis*) which attests to the comparatively oligotrophic conditions there, as most bioavailable organic matter is consumed within the uppermost cm. Though rare in the other cores, *Hoeglundina elegans* is a dominant species in core 36. In the literature this species is often described to inhabit a shallow infaunal habitat associated with sediments low in organic matter (Lutze and Coulbourn, 1984; Corliss

and Emerson, 1990; Corliss, 1985, 1991; Schmiedl and others, 1997; Fontanier and others, 2002, 2006; Mojtahid and others, 2010; Griveaud and others, 2010). On the Estremadura slope, core 34 has a well developed succession of shallow, intermediate and deep infaunal microhabitats where *G. affinis* is a dominant species. The presence of *G. affinis* in high numbers here probably reflects the comparatively greater amount of bioavailable organic matter reaching deeper sediment intervals. In addition, *U. peregrina* which is absent in core 36, is present in low numbers in core 34; specimens of *U. peregrina* in our cores correspond to the *U. peregrina* var. *celtica* described by Schönfeld (2006) which is more slender and relative smooth compared to the typical *U. peregrina* morphotype which is more spinose. Koho and others, (2008a) found *U. peregrina* var. *celtica* to inhabit relatively shallow water sediments with relatively high phytopigment contents (>10 μg/cm^3) while the typical morphotype constituted the "mesotrophic" foraminifera in sediments with lower (<10 μg/cm^3) phytopigment contents. We interpret the occurrence of the *U. peregrina* var. *celtica* morphotype in core 34 to reflect the more eutrophic environment on the Estremadura slope. Finally, cores 32 and 31 on the Alentejo slope have very similar assemblages, with a marked increase in both the concentrations and relative percentage abundances of *U. peregrina* and *Bulimina inflata. B. inflata* has been recorded by many authors to select a shallow infaunal microhabitat (Corliss, 1985, 1991; Corlis and Emerson, 1990; Fontanier and others, 2002, 2008, Mojtahid and others, 2010; Duros and others, 2011; Phipps and others, in prep). However, as pointed out by Mojtahid and others, (2010), the fact that *B. inflata* has been found in both relative eutrophic conditions (Jorissen and others, 1998; Morigi and others, 2001) and meso-oligotrophic settings (Duros and others, 2011; Phipps and others, 2012). The contrasting intermediate infaunal distribution observed in the Nazaré canyon (Koho and others, 2007; this study), could even suggest that specimens assigned to *B. inflata* may actually represent more than one species. Nonetheless, the increased presence of *B. inflata* in

the two cores, alongside *U. peregrina* appears to coincide with an elevated trophic level on the Alentejo slope.

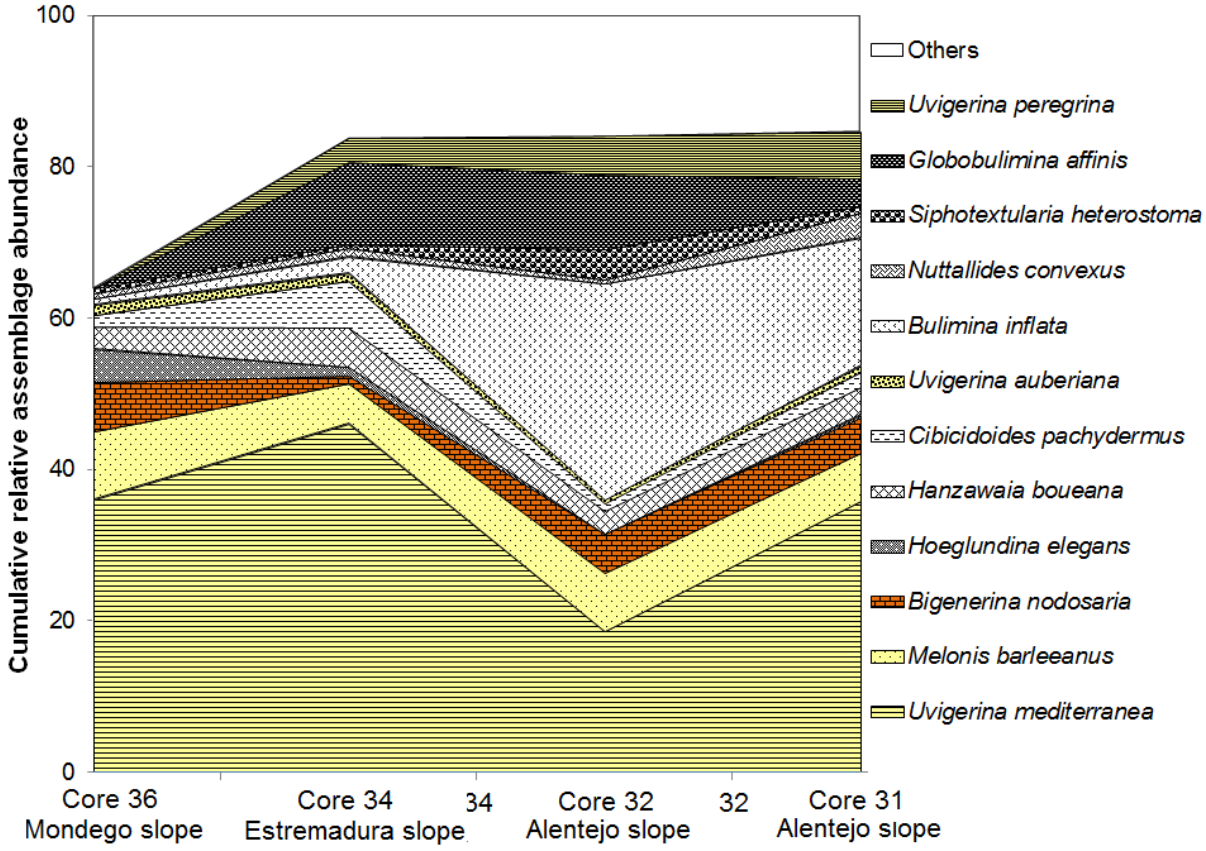


Figure 9. Composition of the live benthic foraminiferal faunas from open slope environments across the latitudinal transect. All species with relative abundance >4% are presented.

5.5.5 TEMPORAL VARIABILITY OF OPEN SLOPE FAUNAS

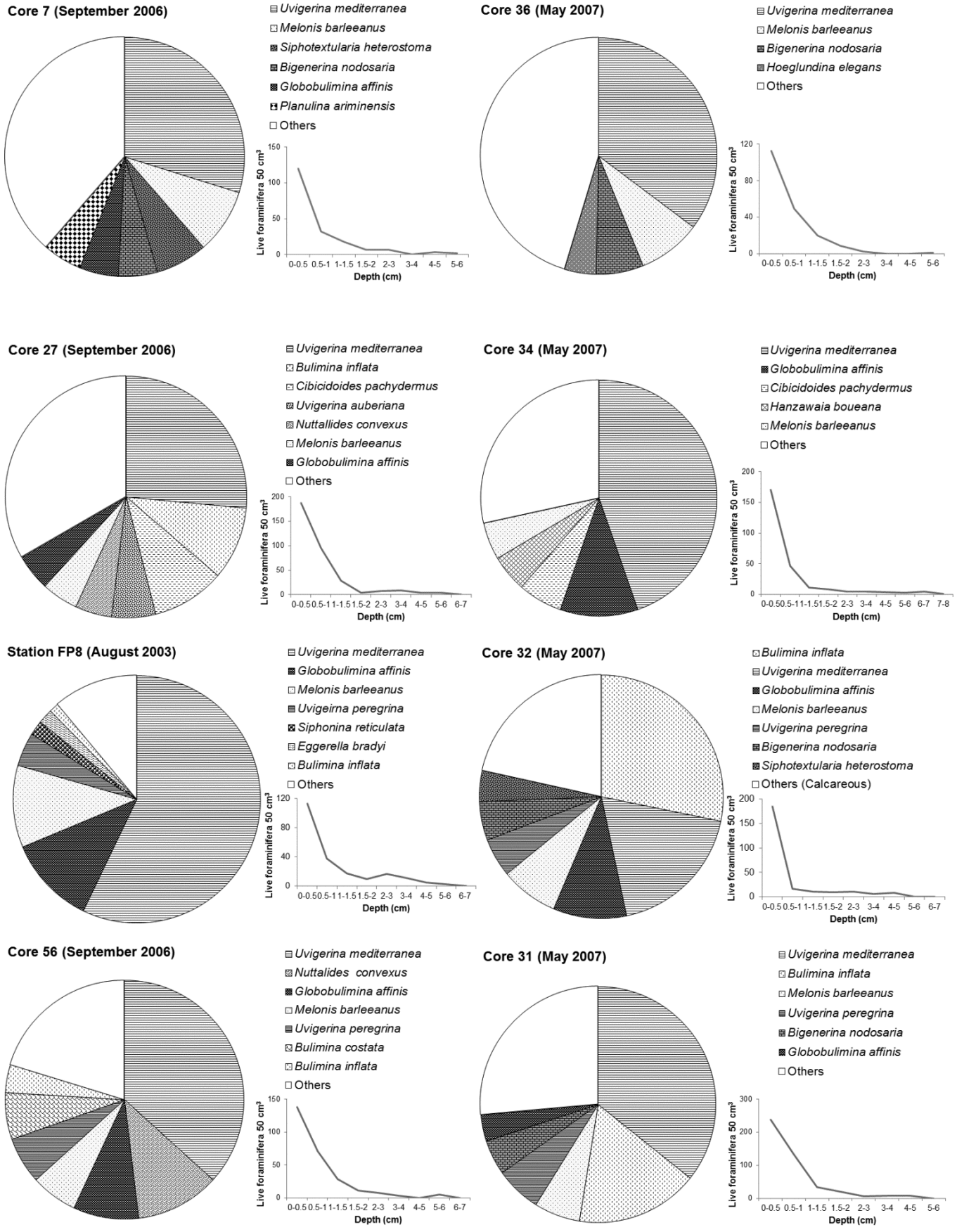
The Portuguese margin is characterised by enhanced productivity in early spring and early autumn. As we compare samples from different months (May, August and September) each sampling moment may represent fundamentally different trophic conditions and therefore exhibit different foraminiferal assemblages. In the early spring (March-April), nutrient rich surface waters trigger phytoplankton to bloom, form aggregates and sink to the sea floor (Griveaud and others, 2010). Given the time delay for aggregates to reach the sea-

floor, foraminifera from cores 36, 34, 32 and 31 (this study), which were collected in May 2007 (a month or so after the spring bloom) would have had time to utilise organic enrichment just before and up to the point they were sampled. Seasonal upwelling conditions reach their maximum in June –September, causing a second bloom in the late summer/early autumn (Fiúza, 1984; Sousa and Bricaud, 1992; Huthnance and others, 2002; Vitorino and others, 2002; Griveaud and others, 2010). However any organic enrichment in cores 56, 27 and 7 (collected in September 2006) may be too recent for shallow infaunal opportunists >150 μm to fully exploit it before the time of sample collection (Fontanier and others, 2003). In contrast cores from station FP8 were collected in August 2003 (Table 2); during this month exported organic matter flux is thought to be comparatively low (Griveaud and others, 2010).

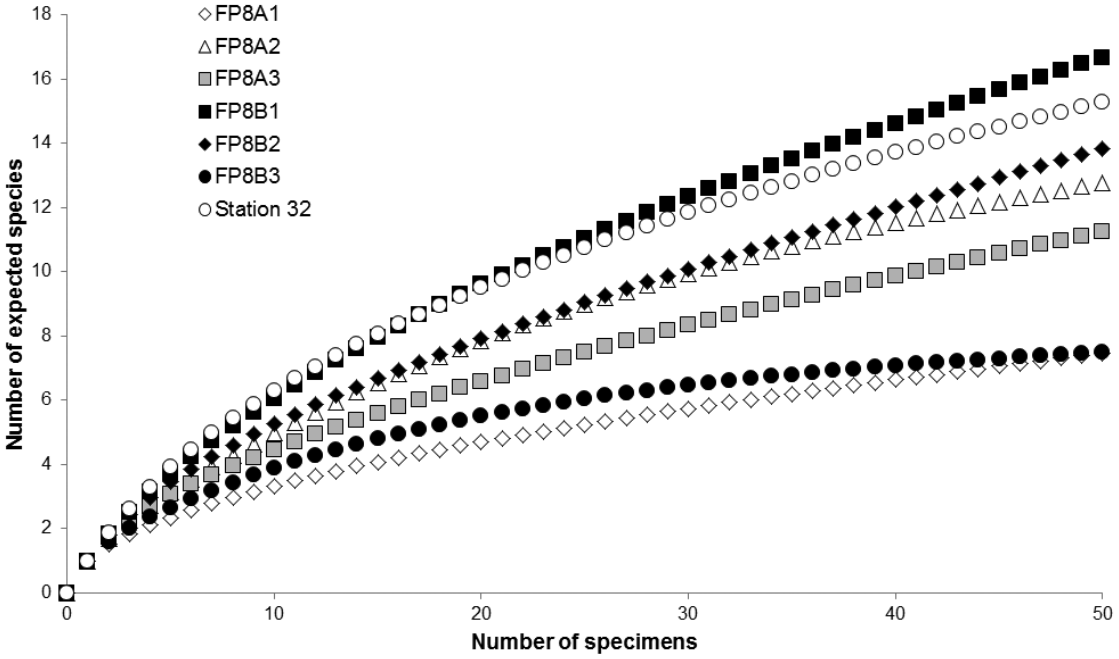
Generally, cores collected from different months share similar foraminiferal assemblages (Figure 10). They are dominated by *Uvigerina mediterranea*, *Melonis barleeanus* and *Globobulimina affinis*. On the Mondego slope, core 7 (September 2006) has similar numbers of *U. mediterranea*, *M. barleeanus* and *Bigenerina nodosaria*, standing stocks (100 individuals per 50 cm^3) and species rarefaction (21.4) to core 36 (May 2007, see Figure 10 and Table 3), suggesting environmental conditions are very comparable between the two samplings. However, core 7 has low numbers of *Globobulimina affinis* present below 4 cm, and a deeper ALD_{10} of 0.9 (Table 3), in comparison to core 36 (Total ALD_{10} = 0.6) where deep infauna are absent. This suggests there is a greater penetration of bioavailable organic matter to deeper intervals during September 2006 than in May 2007. Nonetheless, the conditions in which core 7 was collected still appear more oligotrophic than on the Estremadura slope, as indicated by the lack of *Uvigerina peregrina*, relatively low phytopigment content in the uppermost cm (3.8 μg g^{-1}, Nardelli and others, 2010) and generally higher diversities (Table 3). On the Estremadura slope, core 27 collected in

September 2006 (Table 2, Figure 10) has a similar relative percentage abundance of *Cibicidoides pachydermus*, *M. barleeanus* and *G. affinis* to core 34 (May 2007), but much less *U. mediterranea* (27% compared to 45%) and a greater contribution of *Bulimina inflata* (10% compared to 2%). Standing stocks (180 compared to ~140 individuals per 50 cm^3 in core 34) and diversity indices, particularly rarefaction ($E(S_{50})$ = 19.6 to 16.4) and Equitability (0.82 to 0.66) are also notably higher, probably due to the lower dominance of *U. mediterranea*. Unfortunately no organic matter data is available for core 27 to allow a comparison of trophic level. Nonetheless, the presence of *U. peregrina*, and higher standing stocks in core 27 in relation to core 7 suggests a higher trophic level than the Mondego slope in both May 2007 and September 2006. On the Alentejo slope, Griveaud and others, (2010) analysed 6 replicate cores from station FP8 in August 2003, for which we show an average of the combined foraminiferal assemblages in Figure 10. Foraminiferal assemblages of cores from station FP8 and core 32 (May 2007) have similar relative abundances of *M. barleeanus*, *G. affinis* and *U. peregrina* but *U. mediterranea* is considerably more dominant in station FP8 (57% compared to 18%) while *B. inflata* is only a minor component (1% compared to 28% in core 32). Griveaud and others, (2010) noted that 5 of the cores at station FP8 have ~100 individuals per 50 cm^3 while core FP8A1 had an exceptionally high density of ~400 individuals per 50 cm^3. They suggest the high density in core A1 could be a result of patchiness at the site, hypothesising a localised depression rich in labile organic matter which promoted increased standing stocks. If we compare core 32 with the other 5 cores from station FP8, standing stocks are slightly higher in core 32 (138 individuals per 50 cm^3) while cores at station FP8 range from 80-120 individuals per 50 cm^3. Interestingly, when we compare all the cores using the rarefaction method (Figure 11), species richness values for the FP8 cores range quite considerably ($E(S_{50})$ = 7.5-16.7), while core 32 has a value high within this range of 15.3, suggesting that spatial variability on the Alentejo slope may mask

any subtle changes in temporal variability. Also on the Alentejo slope, core 56 (September 2006, see Figure 10) has a very similar relative abundance of *U. mediterranea*, *M. barleeanus* and *U. peregrina* to core 31, but has considerably less *B. inflata* (4% compared to 17%) and much lower standing stocks (140 compared to 234 individuals per 50 cm^3) despite having a comparatively high concentration of phytopigments (15.5 µg g^{-1}). As previously described, seasonal upwelling conditions reach their maximum in June –September (Fiúza, 1984; Sousa and Bricaud, 1992; Huthnance *and othersand others* 2002; Vitorino and others 2002). As core 56 was collected in September 2006, it is plausible that the enrichment of phytopigments was from a recent autumn bloom, where not enough time had elapsed for shallow infaunal opportunists >150 µm to fully exploit it before the time of collection. Further cores from station FP8 were collected in August 2003 when conditions are comparatively much more oligotrophic (Griveaud and others, 2010). The foraminiferal assemblages in cores 31 and 32 which were taken in May 2007, a month or so after the spring bloom (Griveaud and others, 2010) would have had more time to utilise organic enrichment just before and up to the point they were sampled. We speculate that the elevated relative abundances of *B. inflata* in both cores 31 and 32 (May 2007), and their relatively low abundances in core 56 (Sept 2006) and station FP8 (August 2003), could be related to an opportunistic response to increased organic matter flux after enhanced productivity in the early spring. Summarising, it seems that the temporal variability of foraminifera between September 2006 and May 2007 on the Mondego (cores 7 and 36) and Estremadura (cores 27 and 34) slopes is relatively minor compared to the spatial variability observed in May 2007. However, the greater foraminiferal standing stocks and abundance of *Bulimina inflata* on the Alentejo slope in May 2007 (cores 31 and 32) relative to samplings from August 2003 (station FP8) and September 2006 (core 56) could be a putative response to a spring bloom.



Figures 10. Pie charts of live foraminifera from cores taken from open slope sites from different sampling moments. All species >4% are represented.



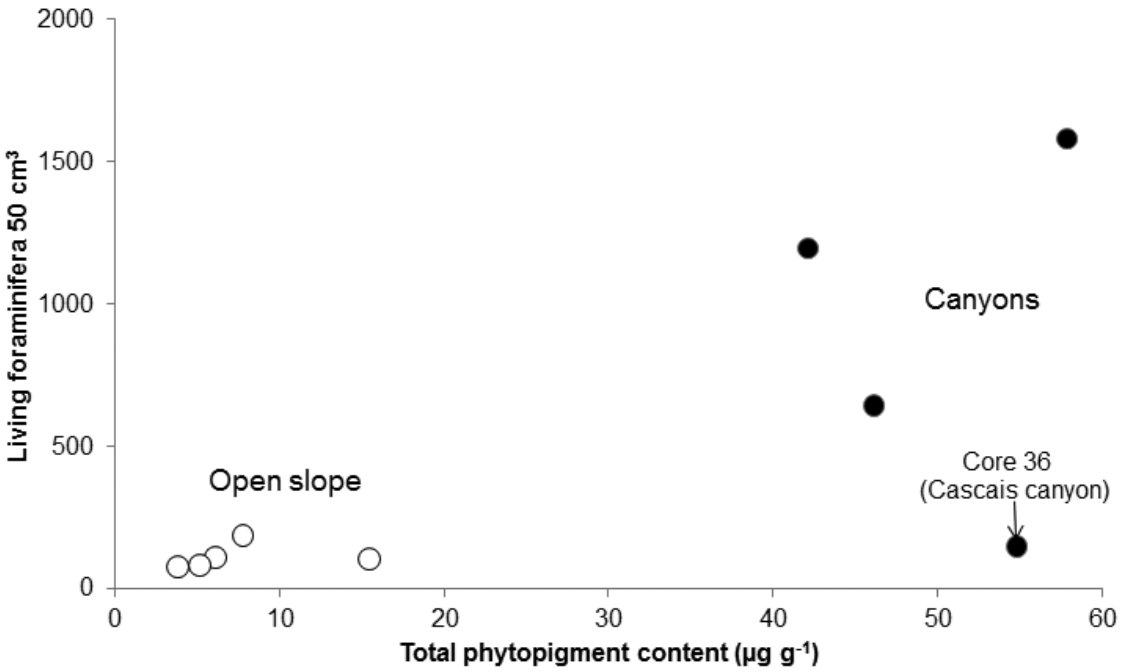
Figures 11. Rarefaction curves for cores taken from station FP8 (Griveaud and others 2010) and core 32 taken from the same locality (Alentejo slope). FP8 cores were collected in August 2003 while core 32 was taken in May 2007.

5.5.6 COMPARISON BETWEEN OPEN SLOPE AND CANYON FAUNAS.

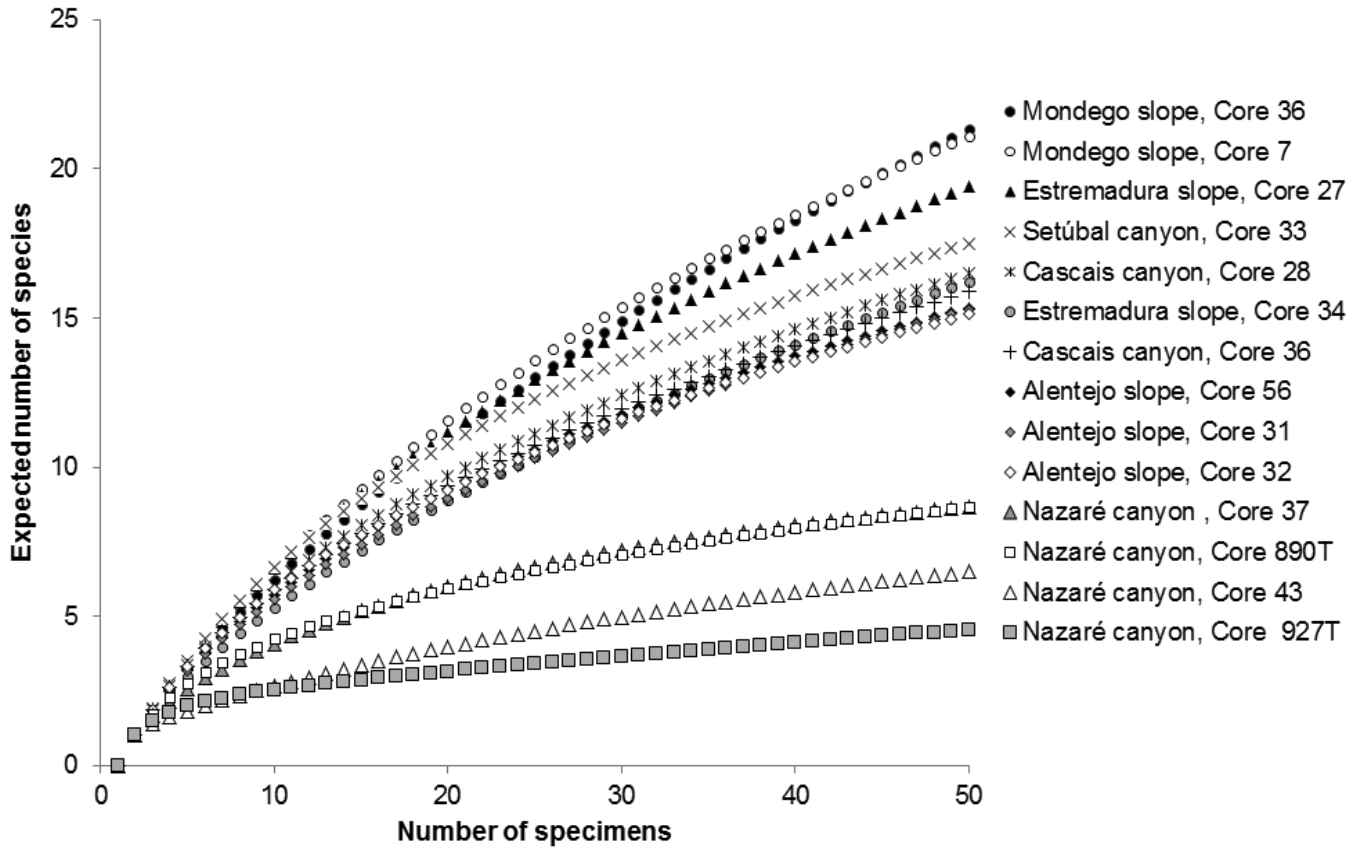
Canyons and open slope settings from ~1000 m along the Portuguese margin are very contrasting environments, particularly with respect to the quantity and quality of labile organic matter and the positioning of important redox fronts in the interstitial waters. Open slope environments are characterised by low quantity and quality of organic matter (i.e., phytopigments <16 μg g^{-1}) and relatively low foraminiferal standing stocks (~100-250 individuals per 50 cm^3), while canyon environments typically have a higher quantity and quality of organic matter with phytopigments

>40 µg g^{-1} and standing stocks of ~650 to ~1500 individuals per 50 cm^3 (Figure 12). The unusually low foraminiferal density in core 36 (September 2006) from the Cascais canyon is highlighted; the low density can be explained by a recent mass depositional event at the time of collection (Nardelli and others, 2010) while core 28 which was taken 8 months later has a greater density that better reflects the high amount of phytopigments in the canyon. The community structure of foraminiferal assemblages as well as their composition also shows remarkable differences. As previously dicussed the open slope cores compared in this study and those analysed from ~1000 m in other open slope studies are generally characterised by a high dominance of *Uvigerina mediterranea* in the uppermost cm, with subordinate *Melonis barleeanus* and *Globobulimina affinis* occupying deeper microhabitats (i.e. Schönfeld 2001; Fontanier and others, 2002, 2006, 2008; Koho and others, 2007, 2008a; Griveaud and others, 2010; Mojtahid and others, 2010; Nardelli and others, 2010). This association is generally connected with well oxygenated, mesotrophic environments (Fontanier and others, 2002, 2006 Mojtahid and others, 2010) in line with the TROX model where a full suite of shallow, intermediate and deep infaunal niches are realised (Jorissen and others, 1995). In contrast the canyon cores exhibit a much greater dominance of the typical "canyon faunas" e.g., *Melonis barleeanus, Chilostomella oolina* and *Globobulimina turgid* which are associated with greater availability of organic matter (e.g., Schmiedl and others, 2000, Fontanier and others, 2005; Koho and others, 2007, 2008a; Nardelli and others, 2010; Duros and others, 2011). These species typically occupy intermediate and deep infaunal microhabitats but are also present in the uppermost cm which according to the TROX model suggests highly eutrophic and potentially a shallow oxygen penetration depth (Jorissen and others, 1995). When we compare diversities for all the canyon and open slope cores using the rarefaction method (Figure 13), it is clear that species richness is systematically much lower on the Nazaré canyon terrace, while the axes of the

Cascais and Setúbal canyons have species richness more akin to those measured on the Estremadura slope. This further adds to the evidence that suggests the Cascais and Setúbal canyons are inactive relative to the Nazaré canyon (Jouanneau and others, 1998; Jesus and others, 2010; de Stigter and others, 2011) and therefore exhibit foraminiferal assemblages that more closely resemble enriched open slope sites found shallower than 1000 m e.g., core FP13 (320 m) in the Bay of Biscay (Mojtahid and others, 2010). The higher diversity in the Cascais and Setúbal canyons reflects the greater presence of shallow infaunal foraminifera in these canyons that are otherwise deficient in the Nazaré canyon, suggesting that the periods between organic matter deposition events in the Nazaré canyon are too short to allow these taxa to recolonise the ecosystem.



Figures 12. Total density of living foraminifera from open slope and canyon cores relative to total phytopigment contents.



Figures 13. Rarefaction curves for all cores compared in this study.

5.6 CONCLUSIONS

We have investigated the spatial and temporal variability of live (rose Bengal-stained) foraminiferal assemblages > 150 µm from a latitudinal transect along the Portuguese margin from both canyon and open slope sites of ~1000 m. The results of our study show considerable spatial variability between the Nazaré canyon terrace and the Cascais/Setúbal canyon axes, particularly

the relative poverty of shallow infauna in the Nazaré canyon. Diversity indices and ALD_{10} values of dominant species on the Nazaré canyon terrace show clear differences between May 1999 and May 2007, which probably relate to variations in oxygen penetration depth and associated redox fronts. Our sample from the Cascais canyon (May 2007) taken an additional 8 month after a supposed mass depositional event shows far greater standing stocks and a more developed colonisation of deeper sediment intervals by *Globobulimina turgida* than a sampling from the same site in September 2006. In May 2007, open slope cores taken from the north of the transect typically exhibit lower standing stocks but greater diversity, associated with relative oligotrophy and lower dominance. Towards the south of the the transect, standing stocks generally increase along with subtle changes in species assemblages and microhabitat development that reflects more eutrophic conditions. Generally temporal variability of the cores between August 2003 and May 2007 (station FP8/core 32) and September 2006 and May 2007 (core 7/core 36, core 27/core 34 and core 56/core 31) does not seem to have a greater influence on benthic communities than the spatial variability observed in May 2007. However the greater abundance of *Bulimina inflata* on the Alentejo slope in May 2007 could be a putative response to a spring bloom. Finally, open slope faunas are characterised by low density/high diversity assemblages associated with lower quantities of bioavailable organic matter where phytopigments are <16 µg g^{-1}, while canyon faunas have considerably greater densities in sediments with phytopigments >40 µg g^{-1}. Though diversity is very low in the Nazaré canyon, the Cascais and Setubal canyons have diversities similar to those on the open slope because of the relative contribution of shallow infaunal species. The different assemblages found in canyons and open slope sites from the same water depth could have important implications for palaeoenvironment and palaeodepth studies of continental margins.

SYNTHÈSE ET PERSPECTIVES

SYNTHÈSE ET PERSPECTIVES

Ce chapitre résume les principales conclusions de la thèse de doctorat **« Les foraminifères benthiques de la marge portugaise : Impact des apports organiques sur la densité, la biodiversité et la composition des faunes»**

Les objectifs généraux de la thèse sont d'examiner la relation entre le niveau trophique et l'oxygène sur les faunes de foraminifères, avec une attention particulière au rôle de la matière organique labile sur leurs densités, diversités et compositions. Dans cette étude, des foraminifères benthiques vivants (colorés au Rose Bengale) ont été prélevés et identifiés dans 16 carottes « multicores » de la pente ouverte et des canyons sous-marins de la marge portugaise. Dans les chapitres 2, 3 et 4 nous présentons les résultats d'une étude des faunes de foraminifères benthiques le long d'un transect bathymétrique de huit stations, sur la pente ouverte, de 282 à 4987 mètres de profondeur. Le chapitre 2 présente la composition des assemblages de foraminifères > 63 μm, le chapitre 3 discute la répartition verticale des faunes dans les premiers centimètres du sédiment superficiel, tandis que le chapitre 4 a comme sujet la diversité des faunes le long du transect. Le chapitre 5 présente les résultats d'une étude sur la variabilité spatiale et temporelle des faunes de foraminifères benthiques le long d'un transect latitudinal sur la marge portugaise, de sept stations, à environ 1000 m de profondeur. Ce transect inclus à la fois des stations de pente ouverte et des stations situées dans des canyons sous-marins.

TRANSECT BATHYMETRIQUE DE LA PENTE DE LA MARGE PORTUGAISE OUVERTE: CONCLUSIONS

Le chapitre 2 présente l'étude des faunes vivantes de foraminifères benthiques, pour les fractions >150 µm et 63-150 µm, le long du transect bathymétrique de la pente portugaise ouverte (282 à 4987 m). L'ensemble des données faunistiques est comparé à des données sur les composantes labiles de la matière organique.

Nos résultats suggèrent que sur la pente continentale, vers une plus grande profondeur d'eau, la majorité des espèces eutrophes (par exemple *Uvigerina mediterranea, Melonis barleeanus, Epistominella vitrea*) diminue en densité, et les assemblages deviennent progressivement dominés par d'autres espèces, mieux adaptées à des conditions mésotrophes (par exemple *Uvigerina peregrina, Globobulimina affinis, Repmanina charoides*). Dans les eaux encore plus profondes, ces espèces mésotrophes sont finalement remplacées par des espèces qui sont caractéristiques des conditions oligotrophes (par exemple *Cibicides kullenbergi, Epistominella exigua, Nuttalides pusillus, Reophax fusiformis*). Cette succession bathymétrique des faunes de foraminifères coïncide avec une diminution des concentrations des phytopigments dans le sédiment. Finalement, la baisse du pourcentage de foraminifères à test carbonaté perforé, et la hausse simultanée de la contribution des espèces à test agglutiné, suggèrent que, de façon générale, les espèces à test carbonaté ont des exigences trophiques plus élevées que les espèces à test agglutinés.

Les microhabitats des foraminifères du même transect bathymétrique sont présentés dans le chapitre 3. Nos résultats montrent des changements suivant la bathymétrie (et donc probablement

les apports organiques), avec un développement d'occupation des microhabitats déterminée par les exigences tropiques des différentes espèces, et leur tolérance vis-à-vis de la sous-oxygénation, en accord avec le modèle conceptuel TROX. Nous avons néanmoins observé des différences substantielles entre les deux classes granulométriques étudiées (>150 µm, 63-150 µm,) et entre les groupes de foraminifères à test carbonaté et à test agglutiné.

Notre étude montre d'abord que les valeurs moyennes de la profondeur de vie (ALD_{10}) des espèces à test perforé et à test agglutiné correspondent parfaitement aux prédictions du modèle TROX. Par contre, à quelques stations, de grandes quantités de spécimens colorés au Rose de Bengale ont été observées dans des couches sédimentaires profondes (>1 cm). Ces exemplaires colorés masquent de façon significative la succession verticale habituelle, avec des espèces endopéliques superficielles, intermédiaires et profondes. Ce phénomène est particulièrement évident aux stations de profondeur bathyale (2475–2908 m), où la profondeur de vie moyenne (ALD_{10}), la profondeur estimée de pénétration de l'oxygène et l'épaisseur de la zone de mélange (« sediment mixed layer) sont toutes maximales. Nous supposons que cette distribution erratique des foraminifères est due aux déplacements passifs des foraminifères causés par la bioturbation de la macrofaune. Les foraminifères à test agglutiné semblent davantage touchés par ce phénomène que les foraminifères à test carbonaté. Selon nous, cela suggère que les foraminifères à test agglutiné sont moins aptes à regagner leur microhabitat préféré (près de l'interface eau-sédiment) après avoir été déplacés par les activités de bioturbation de la macrofaune. Par contre, les espèces endopéliques superficielles paraissent capables, après un déplacement, de regagner très vite les niches écologiques proches de la surface du sédiment, où la concentration des composantes alimentaires labiles (phytopigments) est maximale.

Dans le chapitre 4, nous montrons des résultats très contrastés entre 1) la diversité des assemblages totaux de foraminifères >63 μm et >150 μm, 2) les assemblages de foraminifères à test carbonaté > 63 μm et 3) les assemblages de foraminifères à test agglutiné >63 μm. La faune totale >63 μm et le groupe des foraminifères à test carbonaté >63 μm montrent tous les deux une diminution de la diversité vers une plus grande profondeur. Par contre, la diversité dans la faune totale >150 μm et des foraminifères à test carbonaté >63 μm décrivent une répartition plus ou moins bimodale, avec maxima à 282 m et 2908–3908 m, et à 490 m et 2475–2908 m respectivement, sans aucune tendance générale en fonction de la profondeur. La baisse générale de la diversité avec la profondeur croissante observée pour les faunes totales >63 μm coïncide avec une diminution de la richesse spécifique et une augmentation de la dominance de certaines espèces de petite taille (par exemple, *Epistominella exigua* et *Nuttallides pussilus*). Nous suggérons qu'il s'agit d'une réponse à des conditions oligotrophes à de grandes profondeurs, et à l'importance croissante des apports saisonniers de phytodétritus, qui favorisent les espèces opportunistes, causant une augmentation de la dominance. Ces espèces opportunistes sont pour la plupart trop petites pour être retenues sur un tamis >150 μm. En revanche, la diversité dans la fraction >150 μm, qui montre une tendance bimodale le long du transect, est maximale à la station la plus profonde. Des maxima secondaires de diversité, à 2908 (Shannon index) et 3908 m (Rarefaction, Fisher alpha) de profondeur, sont caractérisés par une équitabilité élevée, avec de nombreuses espèces qui sont représentées par un seul exemplaire. Apparemment, du phytodétritus déposé dans les semaines ou mois avant l'échantillonnage, n'a pas eu un impact sur la diversité des faunes de foraminifères >150 μm.

Quand la diversité des foraminifères >63 μm à test carbonaté est analysée indépendamment, les résultats sont très similaires à ceux des faunes totales >63 μm. La diversité

maximale est trouvée à la station la plus eutrophe (282 m), où la pénétration d'oxygène est minimale. Ceci suggère que la faible teneur en oxygène dans le sédiment ne limite pas la diversité des foraminifères à test carbonaté. Vers les stations plus profondes, la diversité des foraminifères à test carbonaté diminue. Les espèces de ce groupe n'exploitent pas les niches endopéliques intermédiaires et profondes créées par la bio-irrigation, les activités de bioturbation de la macrofaune. Ces résultats suggèrent que le modèle TROX ne peut pas expliquer l'évolution bathymétrique de la biodiversité des foraminifères à test carbonaté, qui semble plutôt être exclusivement liée à la quantité, la qualité et la saisonnalité des apports organiques.

En revanche, les foraminifères >63 µm à test agglutiné ont une diversité relativement faible à 282 m. Il s'avère que ces espèces sont moins compétitives pour les ressources alimentaires dans les niches du sédiment superficiel que les espèces à test carbonaté. Dans les sédiments plus profonds, la faible concentration d'oxygène limite leur richesse spécifique et augmente la dominance d'une espèce. Aux sites à profondeur d'eau plus importante, l'augmentation de la pénétration d'oxygène dans le sédiment et de la bioturbation ouvre des niches supplémentaires pour des espèces endopéliques intermédiaires et profondes à test agglutiné, faisant croître ainsi leur richesse spécifique et leur diversité. Enfin, aux stations les plus profondes, avec les conditions les plus oligotrophes, la diversité des foraminifères à test agglutiné est minimale. A ces égards, le modèle TROX est adéquat pour expliquer les tendances de diversité observées pour les espèces de foraminifères à test agglutiné.

TRANSECT LATITUDINAL DE LA MARGE PORTUGAISE, COMPARAISON DES STATIONS DE PENTE OUVERTE ET DES CANYONS SOUS MARINS : CONCLUSIONS

L'étude des faunes de foraminifères benthiques (>150 μm) de sept stations d'un transect latitudinal, à environ 1000 m de profondeur, est décrite en chapitre 5. Dans ce chapitre, nous nous concentrons sur les différences entre les faunes dans le pente ouverte et celles de canyons sous-marins, sur variabilité temporelle de ces 2 types de faunes.

Il apparait qu'en accord avec le modèle TROX, la densité et la distribution verticale des faunes de foraminifères sont principalement contrôlées par la disponibilité de phytopigments et par la profondeur de pénétration de l'oxygène dans le sédiment. Les stations de canyons sous-marins sont caractérisées par une grande quantité et une meilleure qualité de la matière organique, une pénétration d'oxygène faible, et, au niveau de la faune des foraminifères, par des densités plus élevées. Les assemblages y sont dominés par des espèces typiques des milieux de canyon, telles que *Melonis barleeanus, Chilostomella oolina* et *Globobulimina turgida*. Toutefois, les indices de biodiversité sont beaucoup plus élevés dans les canyons de Cascais et de Setúbal que dans le canyon de Nazaré, en raison des forts pourcentages dans le canyon de Nazaré de quelques espèces épipéliques superficielles (par exemple *Uvigerina mediterranea, Uvigerina peregrina, Bigenerina nodosaria*). En revanche, les milieux benthiques de la pente ouverte sont caractérisés par de faibles quantité et qualité de la matière organique, qui se traduisent par une profondeur de pénétration de l'oxygène assez profonde et une faible densité des faunes de foraminifères. Ces milieux montrent généralement une forte dominance d'*Uvigerina mediterranea* dans le premier centimètre, suivi par un intervalle intermédiaire dominé par

Melonis barleeanus, et une zone encore plus profonde dominée par l'espèce *Globobulimina affinis,* qui a sa niche préférée autour du principal front rédox (le niveau à zéro oxygène). Sur la pente du Mondego (pente ouverte dans le Nord de la zone d'étude), les densités des faunes de foraminifères sont généralement plus faibles et la biodiversité est plus élevée, avec une assez faible dominance. Ceci s'explique par la relative oligotrophie de ce secteur. La présence de *Hoeglundina elegans* et l'absence d'espèces endopéliques profondes, telles que *Globobulimina affinis,* confirment un niveau trophique relativement bas. Plus au sud, les densités de la faune augmentent, et des espèces typiques d'un niveau trophique plus élevé, telles que *Uvigerina peregrina* et *Bulimina inflata*, apparaissent. Ce changement vers un niveau trophique plus élevé est confirmé par le développement des microhabitats plus profonds, autour du principal front rédox.

Les faunes des foraminifères de la fraction >150 µm montrent une variabilité temporelle importante, en particulier aux sites dans les canyons sous-marins. Dans une station aux environs du canyon de Nazaré, les indices de diversité et les valeurs d'ALD_{10} des espèces dominantes sont très différentes entre Mai 1999 et Mai 2007, ce qui est probablement lié à une variabilité importante de la profondeur de pénétration d'oxygène et des principaux fronts rédox dans le sédiment. Dans le canyon de Cascais, les densités des foraminifères et la colonisation des intervalles plus profonds du sédiment étaient beaucoup plus importantes en Mai 2007 qu'en Septembre 2006, quand les échantillons ont été collectés peu de temps après un événement de dépôt sédimentaire. La variabilité temporelle est beaucoup moins évidente pour les environnements de la pente ouverte. Toutefois, la plus grande abondance de *Bulimina inflata* dans les échantillons collectés en Mai 2007 sur la pente Alentejo, en comparaison avec ceux prélevés en Septembre 2006 et Août 2003, suggère une réponse de la faune de foraminifères à

une floraison printanière. Cependant, à l'exception de cette observation, la variabilité temporelle semble être beaucoup moins importante sur la pente ouverte que dans les environnements du canyon.

CONCLUSIONS GÉNÉRALES

Cette thèse présente, pour la première fois, l'étude détaillée des faunes de foraminifères benthiques le long d'un transect bathymétrique (282-4987 m) sur la marge portugaise, à la fois pour les fractions 63-150 µm et >150 µm. Des données supplémentaires, pour les faunes >150 µm, à partir de l'étude d'un transect latitudinal, permet de mieux comprendre la variabilité spatiale et temporelle des faunes. Notre étude confirme que les faunes de foraminifères benthiques sont régies principalement par la quantité et qualité de la matière organique disponible, et dans une moindre mesure, par l'oxygénation de l'eau de fond. Une succession d'assemblages de foraminifères peut être observée avec la profondeur, en fonction du niveau trophique de l'environnement, qui passe d'eutrophe en haut de pente, à mésotrophe en milieu bathyal, pour finir oligotrophe aux sites les plus profonds. Inversement, des limites d'autres facteurs, longtemps considérés importants, tels que les masses d'eau, caractérisées par leur température et salinité, ne correspondent pas aux limites entre ces assemblages fauniques.

Les densités, les microhabitats et la diversité des faunes de foraminifères à test carbonaté sont fortement dépendants des apports de matière organique labile, en particulier de la disponibilité des matières CPE (Chloroplastic Phytopigment Equivalents). Avec l'augmentation de la profondeur et une oligotrophie de plus et plus importante, la densité des espèces à test carbonaté diminue d'une façon linéaire, beaucoup plus vite que celle des espèces à test agglutiné. Des espèces endopéliques intermédiaires et profondes à test carbonaté sont beaucoup plus

abondantes dans les sites eutrophes. Même si à ces sites, la pénétration d'oxygène peut limiter leur profondeur de vie, elle ne semble pas limiter la diversité des foraminifères à test carbonaté. L'exigence trophique plus importante des foraminifères à test carbonaté (en comparaison avec les foraminifères à test agglutiné) explique pourquoi ils sont généralement limités au centimètre supérieur du sédiment aux sites mésotrophes et oligotrophes. Le modèle conceptuel TROX explique donc bien les profondeurs de vie des foraminifères à test carbonaté, mais ne peut pas expliquer leurs caractéristiques en termes de biodiversité.

Les foraminifères à test agglutiné semblent être moins dépendants des apports de matière organique labile que les foraminifères à test carbonaté. Aux sites les plus eutrophes, leur diversité est limitée par la faible pénétration d'oxygène, qui contraint leur microhabitat potentiel à la couche superficielle du sédiment. Dans cette couche superficielle, ils apparaissent moins compétitifs que les foraminifères à test carbonaté, ces derniers étant plus opportunistes. Par conséquent, leur biodiversité est basse dans les milieux eutrophes. Vers de plus grandes profondeurs, en milieu mésotrophe, les profondeurs de vie, et la diversité des foraminifères à test agglutiné augmentent, probablement grâce à une pénétration d'oxygène et une bioturbation macrofaunique plus importantes. Uniquement aux sites oligotrophes, les foraminifères à test agglutiné sont limités à des microhabitats peu profonds, et par conséquent, leur diversité y est faible. A tous ces égards, le modèle TROX prédit bien les microhabitats ainsi que la diversité des foraminifères à test agglutiné.

Les données provenant du transect latitudinal (profondeur ~ 1000 m) présentent des arguments complémentaires pour la conclusion de Koho et al., (2007, 2008) que les foraminifères à test carbonaté ont des exigences trophiques plus élevées, ils dépendent notamment de la disponibilité en matière organique labile. Sur la pente ouverte, des conditions relativement oligotrophes règnent dans le nord du transect latitudinal, où les sédiments ont de faibles teneurs

en CPE, et les faunes sont marquées par des faibles densités et la quasi absence d'espèces endopéliques intermédiaires et profondes. Vers le sud du transect, le contenu en CPE du sédiment, et les densités des faunes de foraminifères augmentent. On note l'apparition d'espèces endopéliques superficielles plus eutrophes, et la présence d'espèces endopéliques intermédiaires et profondes.

Les densités des faunes sont beaucoup plus élevées dans les axes des canyons de Cascais et Setúbal, ainsi que sur les terrasses du canyon de Nazaré, en accord avec des concentrations élevées des CPE dans le sédiment. Dans ces trois milieux de canyon, les faunes de foraminifères montrent des densités d'espèces endopéliques (intermédiaire et profonde) beaucoup plus élevées que sur la pente ouverte, à des profondeurs d'eau comparables. Par contre, l'ALD_{10} affiche des valeurs minimales, indiquant que la succession des microhabitats est fortement comprimée, souvent dans le centimètre supérieur du sédiment.

Dans ce contexte, l'environnement rencontré sur la terrasse du canyon de Nazaré est unique, à cause d'une très forte dominance d'espèces endopéliques intermédiaires et profondes dès le premier demi centimètre, et une quasi-absence d'espèces endopéliques superficielles dans le sédiment de surface. Cette situation particulière est probablement due aux fréquents événements de dépôt sédimentaire en masse. A cause de la richesse en matière organique labile du sédiment déposé, ces dépôts pourraient réduire d'une façon significative la profondeur de pénétration d'oxygène dans le sédiment. A ce titre, le canyon de Nazaré apparait être le seul environnement étudié sur la marge portugaise où les conditions de sous-oxygénation influencent le développement de la faune de façon importante, en limitant fortement la diversité, et en augmentant la dominance de quelques espèces résistantes à ces conditions extrêmes. Par contre, les axes des canyons de Cascais et Setúbal, sont caractérisés par des faunes plus riches en espèces endopéliques superficielles, et des diversités beaucoup plus élevées, comparées à celles trouvées

aux stations de la pente ouverte. Finalement, la variabilité temporelle semble être beaucoup plus grande dans les milieux de canyon, où les perturbations sédimentaires et les apports organiques sont plus importants. En revanche, les conditions dans les environnements de pente ouverte sont plutôt invariables, et la variabilité temporelle est largement causée par des alternances plus subtiles du flux de carbone des eaux superficielles vers le fond marin.

PERSPECTIVES

Les faunes de foraminifères benthiques vivantes sont rarement étudiées en dessous de 5 centimètres de profondeur, encore moins les foraminifères de la fraction 63-150 µm. Pour la grande majorité, les études se limitent au centimètre supérieur. Dans cette thèse nous avons essayé de déterminer s'il y a des différences entre les espèces de grandes (> 150 µm) et de petites (63-150 µm) tailles, et entre les espèces à test carbonaté et à test agglutiné. Une étude plus approfondie est nécessaire, en particulier sur les exigences trophiques de ces deux derniers groupes. Plus spécifiquement, une étude sur les taux métaboliques et des vitesses de bioturbation de diverses espèces de foraminifères agglutinés provenant de différents microhabitats (endopélique superficiel, intermédiaire et profond) pourrait répondre à de nombreuses questions vis-à-vis des stratégies alimentaires de ce groupe de foraminifères. Cela pourrait être réalisé par une expérimentation en laboratoire, par un suivi minutieux des foraminifères vivants dans des conditions strictement contrôlées.

Par rapport aux espèces à test carbonaté, la récente suggestion que l'exploitation des terriers de la macrofaune serait la principale méthode de colonisation des niveaux plus profonds dans le sédiment (Loubere et al., 2010) est totalement contraire aux résultats de notre étude. Nos

recherches suggèrent plutôt que les espèces agglutinées trouvent une niche écologique exploitable dans ces terriers. Nous avons proposé que ces espèces survivent dans ces niches, à cause d'une capacité limitée de migrer vers les niches plus eutrophes près de la surface, et du fait qu'elles sont moins compétitives que les espèces à test carbonaté qui dominent ces milieux. Néanmoins, des études expérimentales en laboratoire sont nécessaires pour confirmer ou affirmer notre hypothèse.

Une limitation de nos recherches est le manque de répliqua, qui s'explique par l'aspect très chronophage de l'étude des foraminifères vivants. Ce point concerne principalement les données pour notre transect bathymétrique. Il est probable que la variabilité spatiale à échelle centimétrique à décimétrique, aussi connue comme "patchiness" joue un rôle important dans la composition et la densité des faunes, en particulier pour la fraction 63 à 150 µm. Ce phénomène peut uniquement être éclairci par l'étude de plusieurs répliqua par station.

Comme nous avons pu montrer, des échantillons prélevés à différents moments donnent des résultats différents. Les échantillons de notre transect bathymétrique ont été prélevés en fin d'été, voir début de l'automne, quelques mois après les conditions les plus eutrophes liées à la floraison algale de printemps. Ces conditions oligotrophes, surtout dans les milieux abyssaux peuvent en partie expliquer pourquoi les espèces à test carbonaté ont tendance à être de petites tailles et de se comporter comme opportunistes. Les espèces *Epistominella exigua* et *Nuttallides pussilus* sont des exemples typiques. En général, ces espèces ne sont pas particulièrement abondantes en milieu bathyal, mais deviennent des éléments dominants aux stations abyssales. Néanmoins, leurs abondances pourraient être beaucoup moins importantes pendant les périodes plus oligotrophes de l'année. Par conséquent, il serait judicieux et nécessaire de prévoir l'étude des faunes le long de notre transect pendant l'automne, l'hiver, et la période de la fleuraison printanier.

En raison de contraintes de temps et pour des raisons de cohérence avec d'autres études, seuls les foraminifères de la fraction > 150 µm ont été analysés pour le transect latitudinal. Une étude plus approfondie, incluant un inventaire de la fraction (63 - 150 µm) et des faunes mortes permettrait d'accroître notre compréhension de la variabilité temporelle et spatiale des faunes. Par rapport à la variabilité temporelle, il serait particulièrement intéressant de voir comment les espèces endopéliques superficielles de la fraction 63-150 µm répondent aux conditions d'oxydo-réduction très instables des terrasses du canyon de Nazaré. Une comparaison des espèces agglutinées et carbonatées serait également très utile. Il semble donc très judicieux d'étudier les foraminifères de la fraction 63-150 µm pour ces sites très particuliers.

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ANNEXE 1

ANNEXE 1

Station 58 (282 m). Counts of live (stained) benthic foraminifera >150 µm in 0-10 cm core (not normalised).

- -	0-0.5	0.5-1	1-1.5	1.5-2	2-3	3-4	4-5	Total	%	ALD_{10} (cm)
Perforates										
Alliatina primitiva		1						**1**	**0.1**	**0.8**
Amphicoryna scalaris	5							**5**	**0.7**	**0.3**
Bolivina robusta	4							**4**	**0.6**	**0.3**
Bolivina tongi			1					**1**	**0.1**	**1.3**
Bulimina costata	6							**6**	**0.9**	**0.3**
Bulimina marginata		1						**1**	**0.1**	**0.8**
Cancris auriculus	3	8	3	1				**15**	**2.2**	**0.8**
Cassidulina carinata	6	1	1					**8**	**1.2**	**0.4**
Cassidulina obtusa	3							**3**	**0.4**	**0.3**
Cassidulinoides bradyi	1							**1**	**0.1**	**0.3**
Chilostomella oolina	1	2	1	3	1			**8**	**1.2**	**1.3**
Cibicides lobatulus		1						**1**	**0.1**	**0.8**
Cibicides refulgens	1							**1**	**0.1**	**0.3**
Cibicides ungerianus	1							**1**	**0.1**	**0.3**
Cibicidoides pachydermus	1	1						**2**	**0.3**	**0.5**
Dentalina communis		1						**1**	**0.1**	**0.8**
Dentalina leguminiformis	1							**1**	**0.1**	**0.3**
Fissurina orbignyana	1							**1**	**0.1**	**0.3**
Fissurina radiata	1							**1**	**0.1**	**0.3**
Gavelinopsis praegeri	4							**4**	**0.6**	**0.3**
Globobulimina turgida	2	4	1					**7**	**1.0**	**0.7**
Gyroidina neosoldanii	9	1						**10**	**1.5**	**0.3**
Hanzawaia boueana	1							**1**	**0.1**	**0.3**
Hoeglundina elegans	6							**6**	**0.9**	**0.3**
Lagena nebulosa	1							**1**	**0.1**	**0.3**
Lagena striata	2							**2**	**0.3**	**0.3**
Lenticulina cultrata			1					**1**	**0.1**	**1.3**
Lenticulina gibba	1	1						**2**	**0.3**	**0.5**
Lenticulina peregrina	2	1						**3**	**0.4**	**0.4**
Melonis barleeanus	21	27	6	1	1			**56**	**8.3**	**0.7**
Oolina acuticostata	2							**2**	**0.3**	**0.3**
Pullenia quinqueloba			2					**2**	**0.3**	**1.3**
Robertina translucens	3	1						**4**	**0.6**	**0.4**

Rosalina globularis	7	4				**11**	**1.6**	**0.4**
Trifarina angulosa	3	2			1	**6**	**0.9**	**0.5**
Trifarina fornasinii	15	1	7			**23**	**3.4**	**0.6**
Uvigerina elongatastriata	6	34	9	1		**50**	**7.5**	**0.8**
Uvigerina mediterranea	32	8	1	1		**42**	**6.3**	**0.4**
Uvigerina peregrina	3	2				**5**	**0.7**	**0.5**
Miliolids								
Biloculinella globula	1					**1**	**0.1**	**0.3**
Biloculinella labiata var. *elongata*	5					**5**	**0.7**	**0.3**
Miliolinella subrotunda	4					**4**	**0.6**	**0.3**
Quinqueloculina seminula	1					**1**	**0.1**	**0.3**
Triloculina tricarinata	4					**4**	**0.6**	**0.3**
Agglutinates								
Ammolagena clavata	1	1				**2**	**0.3**	**0.5**
Bathysiphon filiformis	1					**1**	**0.1**	**0.3**
Bigenerina nodosaria	39	11	1	1	2	**54**	**8.0**	**0.5**
Buzasina ringens	3	19	12	4	1	**39**	**5.8**	**1.0**
Clavulina cylindrica		4	3			**7**	**1.0**	**1.0**
Cribrostomoides bradyi	3	2				**5**	**0.7**	**0.5**
Cribrostomoides subglobosum		1		1		**2**	**0.3**	**1.3**
Deuterammina grisea		1				**1**	**0.1**	**0.8**
Eggerella polita	4					**4**	**0.6**	**0.3**
Eggerelloides medius	5	5	4			**14**	**2.1**	**0.7**
Haplophragmoides sphaeriloculum	4					**4**	**0.6**	**0.3**
Hippocrepinella flexibilis	2	3				**5**	**0.7**	**0.6**
Hyperammina laevigata		2	1			**3**	**0.4**	**0.9**
Labrospira jeffreysii	1					**1**	**0.1**	**0.3**
Lagenammina arenulata	2	5		1		**8**	**1.2**	**0.6**
Nouria harrisii	1					**1**	**0.1**	**0.3**
Nouria polymorphinoides	1					**1**	**0.1**	**0.3**
Paratrochammina madeirae	2					**2**	**0.3**	**0.3**
Psammosphaera asperrima	11	4		1		**16**	**2.4**	**0.4**
Recurvoides contortus	6	1				**7**	**1.0**	**0.3**
Reophax agglutinans	4					**4**	**0.6**	**0.3**
Reophax helenae	4	32	19	13	12	**80**	**11.9**	**1.3**
Reophax micaceus		1				**1**	**0.1**	**0.8**
Reophax scorpiurus		2	1	1		**4**	**0.6**	**1.1**
Reophax spiculifer		2	1			**3**	**0.4**	**0.9**
Reophax subdentaliniformis	5		2	1		**8**	**1.2**	**0.7**
Reophax subfusiformis	6	1		1	1	**9**	**1.3**	**0.3**
Siphotextularia concava	9	2				**11**	**1.6**	**0.3**

Siphotextularia heterostoma	7		1					**8**	**1.2**	**0.3**
Textularia bocki	4							**4**	**0.6**	**0.3**
Textularia conica	2							**2**	**0.3**	**0.3**
Textularia sagittula	32	6	2	1				**41**	**6.1**	**0.4**
Tholosina cf. *vesicularis*	1							**1**	**0.1**	**0.3**
Tholosina sp.1	1	1						**2**	**0.3**	**0.5**
Thurammina albicans		1						**1**	**0.1**	**0.8**
Totals	**331**	**209**	**80**	**32**	**19**	**0**	**0**	**671**		**0.7**

Station 58 (282 m). Counts of live (stained) benthic foraminifera 63-150 µm in 0-10 cm core (not noramlised).

-	**0-0.5**	**0.5-1**	**1-1.5**	**1.5-2**	**2-3**	**3-4**	**4-5**	**Total**	**%**	**ALD_{10} (cm)**
Perforates										
Alliatina primitiva	9	1	4	1	6			**21**	**1.5**	**1.2**
Anomalinoides minimus	9	1	1					**11**	**0.8**	**0.4**
Bolivina albatrossi	3		1					**4**	**0.3**	**0.5**
Bolivina dilatata	17	2						**19**	**1.4**	**0.3**
Bolivina pseudoplicata	1							**1**	**0.1**	**0.3**
Bolivina robusta	52	10	8	1	2			**73**	**5.4**	**0.5**
Bolivina spathulata	1							**1**	**0.1**	**0.3**
Bolivina spinescens	1							**1**	**0.1**	**0.3**
Bolivina striatula	7	23	7	1				**38**	**2.8**	**0.8**
Bolivina subspinescens						1		**1**	**0.1**	**3.5**
Bolivina tongi	30	27	10	2	2			**71**	**5.2**	**0.7**
Bolivina variabilis		1						**1**	**0.1**	**0.8**
Bulimina costata	8	1						**9**	**0.7**	**0.3**
Bulimina marginata	4							**4**	**0.3**	**0.3**
Cancris auriculus	2	12	1					**15**	**1.1**	**0.7**
Cassidulina carinata	26	1	1					**28**	**2.1**	**0.3**
Cassidulina minuta	5	1	1					**7**	**0.5**	**0.5**
Cassidulina obtusa	10	1						**11**	**0.8**	**0.3**
Cassidulinoides bradyi	6	3						**9**	**0.7**	**0.4**
Chilostomella oolina	3	10	28	8	2	1		**52**	**3.8**	**1.3**
Cibicides refulgens	1	1						**2**	**0.1**	**0.5**
Dentalina ariena	1							**1**	**0.1**	**0.3**
Dentalina communis	1							**1**	**0.1**	**0.3**

Dentalina leguminiforis		1					**1**	**0.1**	**0.8**
Dentalina sp.1			1				**1**	**0.1**	**1.3**
Epistominella vitrea	89	22		1	1	1	**114**	**8.4**	**0.3**
Eponides tuberculata	2				1		**3**	**0.2**	**1.0**
Fissurina eburnea	1						**1**	**0.1**	**0.3**
Fissurina fimbriata	1						**1**	**0.1**	**0.3**
Fissurina cf. *lucida*	1						**1**	**0.1**	**0.3**
Gavelinopsis praegeri	3		1				**4**	**0.3**	**0.5**
Glandulonodosaria calomorpha		1					**1**	**0.1**	**0.8**
Globocassidulina subglobosa	7	1					**8**	**0.6**	**0.3**
Guttulina communis	1						**1**	**0.1**	**0.3**
Gyroidinoides umbonatus	5	1					**6**	**0.4**	**0.3**
Hanzawaia boueana	8						**8**	**0.6**	**0.3**
Hoeglundina elegans	3						**3**	**0.2**	**0.3**
Lagena nebulosa		1					**1**	**0.1**	**0.8**
Lagena striata	1						**1**	**0.1**	**0.3**
Lagena sulcata		1					**1**	**0.1**	**0.8**
Lenticulina gibba	2						**2**	**0.1**	**0.3**
Lenticulina peregrina	4						**4**	**0.3**	**0.3**
Melonis barleeanus	10	30	3	1			**44**	**3.2**	**0.7**
Nonionella iridea	7						**7**	**0.5**	**0.3**
Nonionella stella			1				**1**	**0.1**	**1.3**
Nonionella turgida	1	1	2	1			**5**	**0.4**	**1.1**
Paumotua terebra	7	4	1	1			**13**	**1.0**	**0.6**
Planularia patens	1						**1**	**0.1**	**0.3**
Pseudononion granuloumbilicatum	1						**1**	**0.1**	**0.3**
Pullenia quinqueloba	3	1	1	1			**6**	**0.4**	**0.8**
Pyrulina angusta	7	1					**8**	**0.6**	**0.3**
Robertina translucens	8	2					**10**	**0.7**	**0.4**
Rosalina globularis	1						**1**	**0.1**	**0.3**
Seabrookia earlandi	5						**5**	**0.4**	**0.3**
Sphaeroidina bulloides	2	2					**4**	**0.3**	**0.5**
Stainforthia complanata	1						**1**	**0.1**	**0.3**
Trifarina angulosa	10	3		1			**14**	**1.0**	**0.4**
Trifarina bradyi	5			1			**6**	**0.4**	**0.3**
Trifarina pauperata	1						**1**	**0.1**	**0.3**
Trifarina fornasinii	4	2					**6**	**0.4**	**0.4**
Uvigerina elongatastriata	2	8	3				**13**	**1.0**	**0.8**
Uvigerina mediterranea	2						**2**	**0.1**	**0.3**
Uvigerina peregrina	23	1					**24**	**1.8**	**0.3**
Miliolids									
Biloculinella labiata var. *elongata*	11	3					**14**	**1.0**	**0.4**

Cornuspira involvens	1						**1**	**0.1**	**0.3**
Miliolinella subrotunda	7						**7**	**0.5**	**0.3**
Quinqueloculina pygmaea	1						**1**	**0.1**	**0.3**
Quinqueloculina seminula	1					1	**2**	**0.1**	**1.9**
Quinqueloculina stalkeri	15						**15**	**1.1**	**0.3**
Spiropthalmidium concavum	2						**2**	**0.1**	**0.3**
Triloculina tricarinata	6	1					**7**	**0.5**	**0.3**
Agglutinates									
Adercotryma wrighti	5	1					**6**	**0.4**	**0.3**
Ammoglobigerina globigeriniformis	24	1	1		1		**27**	**2.0**	**0.3**
Bigenerina nodosaria	1						**1**	**0.1**	**0.3**
Buzasina ringens	16	23	2				**41**	**3.0**	**0.6**
Cribrostomoides bradyi	67	67	1				**135**	**9.9**	**0.5**
Eggerella advena	1						**1**	**0.1**	**0.3**
Eggerella polita	2						**2**	**0.1**	**0.3**
Eggerelloides medius	11		1				**12**	**0.9**	**0.3**
Eratidus foliaceus	4						**4**	**0.3**	**0.3**
Eratidus foliaceus var. *recurvus*					1		**1**	**0.1**	**2.5**
Glomospira glomerata	2						**2**	**0.1**	**0.3**
Glomospira gordialis	4	2					**6**	**0.4**	**0.4**
Hippocrepinella alba	1	2	3				**6**	**0.4**	**0.9**
Hippocrepinella flexibilis	1		1	1			**3**	**0.2**	**1.1**
Hormosinella guttifera	15	1	1				**17**	**1.2**	**0.3**
Hyperammina laevigata	1	1					**2**	**0.1**	**0.5**
Hyperammina spiculifera		1					**1**	**0.1**	**0.8**
Labrospira jeffreysii	43	22	1				**66**	**4.8**	**0.4**
Lagenammina arenulata	1		1	1			**3**	**0.2**	**1.1**
Morulaeplecta tenuissima	4						**4**	**0.3**	**0.3**
Nouria harrisii	6	2	1				**9**	**0.7**	**0.5**
Paratrochammina kelakasensis			1	1		1	**3**	**0.2**	**2.2**
Paratrochammina madeirae	2	2					**4**	**0.3**	**0.5**
Prolixoplecta earlandi	1						**1**	**0.1**	**0.3**
Psammosphaera hadai	2						**2**	**0.1**	**0.3**
Pseudobolivina antarctica	2	1					**3**	**0.2**	**0.4**
Pseudobolivina fusiformis	29	8	4			1	**42**	**3.1**	**0.4**
Recurvoides contortus	1						**1**	**0.1**	**0.3**
Reophax agglutinans	19	2	1				**22**	**1.6**	**0.3**
Reophax gracilis			10	2	1		**13**	**1.0**	**1.4**
Reophax helenae		5	21	4	5	1	**36**	**2.6**	**1.5**
Reophax micaceus	12	6					**18**	**1.3**	**0.4**
Reophax nana	1						**1**	**0.1**	**0.3**
Reophax scorpiurus var. *testacea*						1	**1**	**0.1**	**3.5**

Reophax spiculifer	13	2						**15**	**1.1**	**0.3**
Reophax subdentaliniformis	3	2						**5**	**0.4**	**0.5**
Siphotextularia concava	2							**2**	**0.1**	**0.3**
Textularia bocki	1							**1**	**0.1**	**0.3**
Textularia sagittula	33	8	2	1				**44**	**3.2**	**0.4**
Tholosina cf. *vesicularis*			1			2		**3**	**0.2**	**2.8**
Thurammina albicans		3						**3**	**0.2**	**0.8**
Tritaxis cf. *britannica*	3	1						**4**	**0.3**	**0.4**
Trochammina grisea	15	1						**16**	**1.2**	**0.3**
Trochamminacean sp.1		4	2	1	1			**8**	**0.6**	**1.2**
Totals	**818**	**350**	**130**	**31**	**23**	**10**	**0**	**1362**		**0.6**

Station 57 (490 m). Counts of live (stained) benthic foraminifera >150 μm in 0-10 cm core (not normalised).

- -	**0-0.5**	**0.5-1**	**1-1.5**	**1.5-2**	**2-3**	**3-4**	**4-5**	**5-6**	**6-7**	**Total**	**%**	**ALD_{10} (cm)**
Perforates												
Amphicoryna scalaris	1									**1**	**0.2**	**0.3**
Astacolus crepidulus					1					**1**	**0.2**	**2.5**
Cassidulina carinata	1	1								**2**	**0.5**	**0.5**
Cassidulinoides bradyi				1						**1**	**0.2**	**1.8**
Chilostomella oolina					3	6	6	1		**16**	**4.0**	**3.8**
Cibicides lobatulus	1									**1**	**0.2**	**0.3**
Cibicidoides pachyderma	3									**3**	**0.7**	**0.3**
Dentalina communis			1							**1**	**0.2**	**1.3**
Fissurina radiata					1					**1**	**0.2**	**2.5**
Glandulonodosaria calomorpha					1					**1**	**0.2**	**2.5**
Globocassidulina subglobosa	1									**1**	**0.2**	**0.3**
Gyroidina altiformis	1									**1**	**0.2**	**0.3**
Hanzawaia boueana	2			1	1					**4**	**1.0**	**1.2**
Hyalina balthica	1					1				**2**	**0.5**	**1.9**
Lenticulina peregrina	1									**1**	**0.2**	**0.3**
Melonis barleeanum		6	7	5	2					**20**	**4.9**	**1.4**
Planulina ariminensis		1								**1**	**0.2**	**0.8**
Pullenia quinqueloba		1								**1**	**0.2**	**0.8**
Rotamorphina involuta				1	1					**2**	**0.5**	**2.1**
Trifarina bradyi	2	1								**3**	**0.7**	**0.4**

Trifarina fornasinii		1						**1**	**0.2**	**0.8**
Uvigerina bononiensis					1			**1**	**0.2**	**2.5**
Uvigerina elongatastriata			1	3	1			**5**	**1.2**	**1.8**
Uvigerina mediterranea	60	34	9	4	1	1		**109**	**26.9**	**0.6**
Uvigerina peregrina	3	2	1					**6**	**1.5**	**0.6**
Miliolids										
Biloculinella labiata	1	1						**2**	**0.5**	**0.5**
Cornuspira foliacea	1							**1**	**0.2**	**0.3**
Cornuspira involvens	1							**1**	**0.2**	**0.3**
Sigmoilopsis schlumbergeri	1							**1**	**0.2**	**0.3**
Spiroloculina excavata	1							**1**	**0.2**	**0.3**
Spiropthalmidiumconcavum	1							**1**	**0.2**	**0.3**
Agglutinates										
Ammodiscus anguillae			2	11	7			**20**	**4.9**	**2.0**
Ammoglobigerina shannoni	1							**1**	**0.2**	**0.3**
Ammolagena clavata	2							**2**	**0.5**	**0.3**
Ammoscalaria tenuimargo	4	1			1			**6**	**1.5**	**0.4**
Bigenerina nodosaria	6	6						**12**	**3.0**	**0.5**
Clavulina cylindrica			2	1	4			**7**	**1.7**	**2.0**
Cribrostomoides nitidum				1				**1**	**0.2**	**1.8**
Cribostomoides sublgobosum		1	5	1	1			**8**	**2.0**	**1.4**
Deuterammina grisea			1					**1**	**0.2**	**1.3**
Eggerelloides medius	2						1	**3**	**0.7**	**2.0**
Glomospira glomerata			1					**1**	**0.2**	**1.3**
Haplophragmoides sphaeriloculum					1			**1**	**0.2**	**2.5**
Hippocrepinella alba			2	2	2			**6**	**1.5**	**1.8**
Hippocrepinella candida	1							**1**	**0.2**	**0.3**
Hippocrepinella flexibilis		3						**3**	**0.7**	**0.8**
Hippocrepinella sp.1	1							**1**	**0.2**	**0.3**
Hormosinella guttifera				1				**1**	**0.2**	**1.8**
Hyperammina laevigata	1	1						**2**	**0.5**	**0.5**
Hyperammina spiculifera			1					**1**	**0.2**	**1.3**
Karreriella bradyi			3					**3**	**0.7**	**1.3**
Paratrochammina cf. *arenacea*	1							**1**	**0.2**	**0.3**
Psammosphaera fusca	9	5	5	3	1		2	**25**	**6.2**	**0.9**
Psammosphaera fusca testacea			1					**1**	**0.2**	**1.3**
Reophax agglutinans	4	4	1					**9**	**2.2**	**0.6**
Reophax bilocularis		2						**2**	**0.5**	**0.8**
Reophaxs curtus					1			**1**	**0.2**	**2.5**
Reophax excentricus			1					**1**	**0.2**	**1.3**
Reophax helenae						1		**1**	**0.2**	**3.5**

Reophax scorpiurus		1	1	2				1		**5**	**1.2**	**1.4**
Reophax cf. *scorpiurus*	12									**12**	**3.0**	**0.3**
Reophax spiculifer	15	4	8	1						**28**	**6.9**	**0.7**
Reophax subdentaliniformis				1						**1**	**0.2**	**1.8**
Reophax subfusiformis	9	1	3	2	2		1			**18**	**4.4**	**0.9**
Reophax testacea		1								**1**	**0.2**	**0.8**
Saccorhiza ramosa				1						**1**	**0.2**	**1.8**
Siphotextularia concava	2									**2**	**0.5**	**0.3**
Siphotextularia heterostoma		3	1							**4**	**1.0**	**0.9**
Technitella melo	1									**1**	**0.2**	**0.3**
Textularia sagittula		1	1	1						**3**	**0.7**	**1.3**
Tholosina cf. *protea*		2								**2**	**0.5**	**0.8**
Thurammina albicans			2	3			1			**6**	**1.5**	**1.6**
Thurammina papillata	2	1								**3**	**0.7**	**0.4**
Tritaxis challengeri	2				1					**3**	**0.7**	**1.0**
Totals	**158**	**85**	**60**	**46**	**34**	**9**	**8**	**5**	**0**	**405**		**1.1**

Station 57 (490 m). Counts of live (stained) benthic foraminifera 63-150 µm in 0-10 cm core (not normalised).

-	**0-0.5**	**0.5-1**	**1-1.5**	**1.5-2**	**2-3**	**3-4**	**Total**	**%**	**ALD_{10} (cm)**
Perforates							-	-	-
Abditodentrix asketocomptella	3						**3**	**0.2**	**0.3**
Alliatina primitiva	15	15	10	8	6		**54**	**3.9**	**1.0**
Amphycorina scalaris	4						**4**	**0.3**	**0.3**
Anomalinoides minimus	22	8	4	7	1		**42**	**3.1**	**0.7**
Bolivina albatrossi	3	2	2	1			**8**	**0.6**	**0.8**
Bolivina dilatata	2	3	1				**6**	**0.4**	**0.7**
Bolivina pacifica		1					**1**	**0.1**	**0.8**
Bolivina robusta	41	9	5				**55**	**4.0**	**0.4**
Bolivina subspinescens	8	2	1		1		**12**	**0.9**	**0.4**
Bolivina variabilis			1				**1**	**0.1**	**1.3**
Bulimina costata	8	4	1	1	1		**15**	**1.1**	**0.7**
Bulimina marginata	12	1					**13**	**0.9**	**0.3**
Cassidulina carinata	18	7			2		**27**	**2.0**	**0.4**
Cassidulina minuta	3	2					**5**	**0.4**	**0.5**
Cassidulinoides bradyi			4	13	5		**22**	**1.6**	**1.8**
Chilostomella oolina					1		**1**	**0.1**	**2.5**
Cibicides lobatulus	1	1					**2**	**0.1**	**0.5**

Dentalina communis				3		**3**	**0.2**	**1.8**
Epinoides tumidulus		1				**1**	**0.1**	**0.8**
Epistominella exigua			1			**1**	**0.1**	**1.3**
Epistominella vitrea	31	13		2		**46**	**3.4**	**0.4**
Fissurina apiculata	1					**1**	**0.1**	**0.3**
Fissurina bradii			1			**1**	**0.1**	**1.3**
Fissurina fimbriata				1		**1**	**0.1**	**1.8**
Fissurina kerguelensis	1					**1**	**0.1**	**0.3**
Fissurina aff. *radiata*	1			1		**2**	**0.1**	**1.0**
Glandulonodosaria calomorpha	1					**1**	**0.1**	**0.3**
Globocassidulina subglobosa	35	21	6		1	**63**	**4.6**	**0.5**
Gyroidinoides umbonatus	6	3	2	1		**12**	**0.9**	**0.7**
Hanzawaia boueana					1	**1**	**0.1**	**2.5**
Hyalina balthica		1			1	**2**	**0.1**	**1.6**
Lenticulina peregrina	5	1				**6**	**0.4**	**0.3**
Marginulina obesa	1					**1**	**0.1**	**0.3**
Melonis barleeanus	1	15	23	26	7	**72**	**5.2**	**1.4**
Nodosaria simplex	1	1				**2**	**0.1**	**0.5**
Nonionella iridea	1					**1**	**0.1**	**0.3**
Nouria harrisii			1			**1**	**0.1**	**1.3**
Paumotua terebra	24	27	3	1	1	**56**	**4.1**	**0.6**
Planulina ariminensis	1	3	1		1	**6**	**0.4**	**1.0**
Procerolagena gracillima	2					**2**	**0.1**	**0.3**
Pseudononion granuloumbilicatum	5	14	3	2		**24**	**1.7**	**0.8**
Robertina translucens		1	1			**2**	**0.1**	**1.0**
Rotamorphina involuta		2	2			**4**	**0.3**	**1.0**
Seabrookia earlandi	15	15	6	3	2	**41**	**3.0**	**0.8**
Trifarina angulosa	3	1			2	**6**	**0.4**	**1.1**
Trifarina bradyi	44	26	5	7	6	**88**	**6.4**	**0.7**
Trifarina fornasinii		1				**1**	**0.1**	**0.8**
Trifarina pauperata	14	1				**15**	**1.1**	**0.3**
Uvigerina elongatastriata			1			**1**	**0.1**	**1.3**
Uvigerina hispida	2					**2**	**0.1**	**0.3**
Uvigerina mediterranea	4	5				**9**	**0.7**	**0.5**
Uvigerina peregrina	15	8	1	1		**25**	**1.8**	**0.5**
						0		
Miliolids						**0**		
Biloculinella inflata	1					**1**	**0.1**	**0.3**
Biloculinella labiata var. *elongata*	1		2	1		**4**	**0.3**	**1.1**
Cornuspira foliacea	1					**1**	**0.1**	**0.3**
Cornuspira involvens	1					**1**	**0.1**	**0.3**
Quinqueloculina bosciana	1	2				**3**	**0.2**	**0.6**
Quinqueloculina pygmaea	1	2				**3**	**0.2**	**0.6**

Quinqueloculina stalkeri	1	1				**2**	**0.1**	**0.5**
Sigmoilinita tenuis	1	2	1			**4**	**0.3**	**0.8**
Sigmoilinita sp.1	1					**1**	**0.1**	**0.3**
Spiropthalmidium concavum	1	3				**4**	**0.3**	**0.6**
						0		
Agglutinates						**0**		
Adercotryma wrighti	9	10	3	5	2	**29**	**2.1**	**0.9**
Ammodiscus anguillae				1		**1**	**0.1**	**1.8**
Ammoglobigerina globigeriniformis	35	8	5	2	4	**54**	**3.9**	**0.6**
Bigenerina nodosaria	30	3	4	2		**39**	**2.8**	**0.5**
Buzasina ringens				1		**1**	**0.1**	**1.8**
Cribrostomoides bradyi		6	12	5	1	**24**	**1.7**	**1.3**
Cribrostomoides nitidum				1		**1**	**0.1**	**1.8**
Cribrostomoides subglobosus			1			**1**	**0.1**	**1.3**
Deuterammina grisea	1	1	1			**3**	**0.2**	**0.8**
Deuterammina montagui	1		3	1		**5**	**0.4**	**1.2**
Eggerelloides medius	45	7	2	1	1	**56**	**4.1**	**0.4**
Eratidus foliaceus	8	5		1	1	**15**	**1.1**	**0.7**
Eratidus foliaceus var. *recurvus*	5	1				**6**	**0.4**	**0.3**
Glomospira gordialis		1	3	4	3	**11**	**0.8**	**1.7**
Haplophragmoides sphaeriloculum	11				1	**12**	**0.9**	**0.3**
Hippocrepinella alba			1			**1**	**0.1**	**1.3**
Hippocrepinella candida	4	3	2			**9**	**0.7**	**0.6**
Hippocrepinella flexibilis	3	1	3			**7**	**0.5**	**0.8**
Hormosinella guttifera	7	4	2	1		**14**	**1.0**	**0.6**
Hormosinella sp.1	1					**1**	**0.1**	**0.3**
Hyperammina laevigata			1			**1**	**0.1**	**1.3**
Labrospira jeffreysii	1					**1**	**0.1**	**0.3**
Labrospira wiesneri		1		1		**2**	**0.1**	**1.3**
Morulaeplecta tenuissima	3		1			**4**	**0.3**	**0.5**
Nodellum membranaceum		2				**2**	**0.1**	**0.8**
Nouria harrisii		1		1		**2**	**0.1**	**1.3**
Paratrochammina cf. *arenacea*	1					**1**	**0.1**	**0.3**
Paratrochammina kelakasensis	1				10	**11**	**0.8**	**2.5**
Psammosphaera hadai				1		**1**	**0.1**	**1.8**
Pseudobolivina antarctica	2	3		1		**6**	**0.4**	**0.8**
Pseudobolivina fusiformis	10					**10**	**0.7**	**0.3**
Pseudonodosinella cf. *shorensis*	1					**1**	**0.1**	**0.3**
Reophax agglutinans	31	2	1	2		**36**	**2.6**	**0.4**
Reophax dentaliniformis				1	1	**2**	**0.1**	**2.1**
Reophax micaceus	5	3		1	2	**11**	**0.8**	**0.4**
Reophax scorpiurus				1		**1**	**0.1**	**1.8**
Reophax cf. *scorpiurus*	6	3		1		**10**	**0.7**	**0.4**

Reophax spiculifer	21	28	5	5			**59**	**4.3**	**0.7**
Reophax subdentaliniformis		2					**2**	**0.1**	**0.8**
Reophax subfusiformis	8	2	2	1			**13**	**0.9**	**0.6**
Reophax sp.2	45	10	1	1	2		**59**	**4.3**	**0.5**
Repmanina charoides		1	1	1			**3**	**0.2**	**1.3**
Siphotextularia heterostoma		1	1	3	1		**6**	**0.4**	**1.6**
Subreophax cf. *aduncus*	1						**1**	**0.1**	**0.3**
Textularia sagittula		2					**2**	**0.1**	**0.8**
Thurammina albicans	4	11	1	3			**19**	**1.4**	**0.8**
Tritaxis brittanica	1	1					**2**	**0.1**	**0.5**
Trochamminacean sp.1			1	2	15		**18**	**1.3**	**2.3**
							0		
Totals	**665**	**348**	**146**	**130**	**83**	**0**	**1372**		**0.8**

Station 56 (1002 m). Counts of live (stained) benthic foraminifera >150 μm in 0-10 cm core (not noramlised).

-	**0-0.5**	**0.5-1**	**1-1.5**	**1.5-2**	**2-3**	**3-4**	**4-5**	**5-6**	**6-7**	**Total**	**%**	**ALD_{10} (cm)**
Perforates												
Amphicoryna scalaris		1								**1**	**0.9**	**0.8**
Bulimina costata	5									**5**	**4.4**	**0.3**
Bulimina inflata	3									**3**	**2.6**	**0.3**
Globobulimina affinis			1		1	2		3		**7**	**6.1**	**3.9**
Globocassidulina subglobosa	2									**2**	**1.8**	**0.3**
Hanzawaia boueana	1									**1**	**0.9**	**0.3**
Lenticulina orbicularis	1									**1**	**0.9**	**0.3**
Lenticulina peregrina	1	1								**2**	**1.8**	**0.5**
Melonis barleeanus		1	2		2					**5**	**4.4**	**1.7**
Nuttallides convexus	6	2	1							**9**	**7.9**	**0.5**
Planulina ariminensis	2									**2**	**1.8**	**0.3**
Rotamorphina involuta		1								**1**	**0.9**	**0.8**
Siphogenerina columellaris					1					**1**	**0.9**	**2.5**
Siphonina reticulata	1	1								**2**	**1.8**	**0.5**
Trifarina fornasinii	1									**1**	**0.9**	**0.3**
Uvigerina mediterranea	14	11	3	1						**29**	**25.4**	**0.6**
Uvigerina peregrina	1	2	1	1						**5**	**4.4**	**1.0**
Miliolids												
Biloculinella cylindrica	1									**1**	**0.9**	**0.3**

Cornuspira involvens				1						**1**	**0.9**	**1.8**
Agglutinates												
Ammodiscus planorbis			1							**1**	**0.9**	**1.3**
Ammoscalaria tenuimargo	3									**3**	**2.6**	**0.3**
Clavulina cylindrica	1									**1**	**0.9**	**0.3**
Cyclammina trullissata	3	5	4	5	3	1				**21**	**18.4**	**1.4**
Cribrostomoides scitulum					1					**1**	**0.9**	**2.5**
Eggerella polita	1									**1**	**0.9**	**0.3**
Portatrochammina cf. *murrayi*	1									**1**	**0.9**	**0.3**
Reophax bradyi	1									**1**	**0.9**	**0.3**
Reophax spiculifer			1							**1**	**0.9**	**1.3**
Reophax sp.3	1									**1**	**0.9**	**0.3**
Repmanina charoides					1					**1**	**0.9**	**2.5**
Saccorhiza ramosa			2							**2**	**1.8**	**1.3**
												0.9
Totals	**50**	**25**	**16**	**8**	**9**	**3**	**0**	**3**	**0**	**114**		**1.0**

Station 56 (1002 m). Counts of live (stained) benthic foraminifera 63-150 μm in 0-10 cm core (not noramlised).

	0-0.5	**0.5-1**	**1-1.5**	**1.5-2**	**2-3**	**3-4**	**4-5**	**Total**	**%**	**ALD_{10} (cm)**
Perforates										
Alliatina primitiva	7		4					**11**	**3.3**	**0.6**
Anomalinoides minimus	1							**1**	**0.3**	**0.3**
Bolivina albatrossi	2		1					**3**	**0.9**	**0.6**
Bolivina robusta	2	1						**3**	**0.9**	**0.4**
Bulimina costata	6							**6**	**1.8**	**0.3**
Bulimina rostrata	3							**3**	**0.9**	**0.3**
Cassidulina carinata	4							**4**	**1.2**	**0.3**
Cassidulina minuta	2							**2**	**0.6**	**0.3**
Cassidulinoides bradyi					1			**1**	**0.3**	**2.5**
Cibicides phlegeri	2							**2**	**0.6**	**0.3**
Cibicidoides kullenbergi	1							**1**	**0.3**	**0.3**
Cibicidoides pachydermus		1						**1**	**0.3**	**0.8**
Dentalina communis		1						**1**	**0.3**	**0.8**
Epistominella exigua	4							**4**	**1.2**	**0.3**
Epistominella vitrea	10	4						**14**	**4.2**	**0.4**

Fissurina marginata						1	**1**	**0.3**	**3.5**
Globocassidulina subglobosa	7						**7**	**2.1**	**0.3**
Gyroidinoides umbonatus	5		1				**6**	**1.8**	**0.4**
Lenticulina peregrina	2						**2**	**0.6**	**0.3**
Melonis barleeanum		5	11	2	2		**20**	**6.0**	**1.3**
Nuttallides pusillus	3						**3**	**0.9**	**0.3**
Nuttalides umboniferus convexus	23	3		1	1		**28**	**8.4**	**0.3**
Paumotua terebra	9	1					**10**	**3.0**	**0.3**
Polymorphinidae sp.1					1		**1**	**0.3**	**2.5**
Seabrookia earlandi	1						**1**	**0.3**	**0.3**
Siphogenerina columellaris		1					**1**	**0.3**	**0.8**
Trifarina bradyi	34	9					**43**	**13.0**	**0.4**
Trifarina fornasinii	2	1					**3**	**0.9**	**0.4**
Trifarina pauperata	16						**16**	**4.8**	**0.3**
Uvigerina hispida	1						**1**	**0.3**	**0.3**
Uvigerina peregrina	9	3	4				**16**	**4.8**	**0.6**
Miliolids									
Cornuspira involvens	1						**1**	**0.3**	**0.3**
Miliolinella subrotunda	1						**1**	**0.3**	**0.3**
Quinqueloculina bosciana	1						**1**	**0.3**	**0.3**
Quinqueloculina pygmaea				1			**1**	**0.3**	**1.8**
Spiropthalmidium concavum	1						**1**	**0.3**	**0.3**
Agglutinates									
Adercotryma wrighti	4	4	2				**10**	**3.0**	**0.7**
Ammodiscus catinus		1					**1**	**0.3**	**0.8**
Cyclammina trullissata		1	2	1			**4**	**1.2**	**1.3**
Cribrostomoides bradyi				4			**4**	**1.2**	**1.8**
Eratidus foliaceus	1						**1**	**0.3**	**0.3**
Glomospira glomerata	1	2	4	3			**10**	**3.0**	**1.2**
Glomospira gordialis	2		2				**4**	**1.2**	**0.8**
Haplophragmoides aff. *kirki*		1					**1**	**0.3**	**0.8**
Hippocrepinella flexibilis		7					**7**	**2.1**	**0.8**
Hormosinella guttifera	3	4					**7**	**2.1**	**0.5**
Hyperammina sp.1		1					**1**	**0.3**	**0.8**
Lagenammina pacifica			2				**2**	**0.6**	**1.3**
Nodellum membranaceum	1	3	3				**7**	**2.1**	**0.9**
Portotrochammina sp.1	1						**1**	**0.3**	**0.3**
Psammosphaera fusca	1						**1**	**0.3**	**0.3**
Psammosphaera sp.1	6	2					**8**	**2.4**	**0.4**

Pseudobolivina antarctica		1						**1**	**0.3**	**0.8**
Pseudonodosinella cf. *nodulosa*	1	1	1					**3**	**0.9**	**0.8**
Recurvoides trochamminiforme	2							**2**	**0.6**	**0.3**
Reophax cf. *nana*	3		1					**4**	**1.2**	**0.5**
Reophax spiculifera	1							**1**	**0.3**	**0.3**
Reophax cf. *subfusiformis*		1						**1**	**0.3**	**0.8**
Repmanina charoides			1	2				**3**	**0.9**	**1.6**
Textularia sagittula	3		1					**4**	**1.2**	**0.5**
Thurammina albicans	1		6	2	3			**12**	**3.6**	**1.7**
Thurammina papillata		1	5	4				**10**	**3.0**	**1.4**
Tritaxis britannica	1							**1**	**0.3**	**0.3**
Totals	**192**	**60**	**51**	**20**	**8**	**1**	**0**	**332**		**0.6**

Station 55 (1374 m). Counts of live (stained) benthic foraminifera >150 μm in 0-10 cm core (not noramlised).

	0-0.5	**0.5-1**	**1-1.5**	**1.5-2**	**2-3**	**3-4**	**4-5**	**5-6**	**6-7**	**7-8**	**Total**	**%**	**ALD_{10} (cm)**
Perforates													
Bifarilaminella advena							1				**1**	**0.7**	**4.5**
Bulimina aculeata				1							**1**	**0.7**	**1.8**
Bulimina inflata	12	2	2		2					1	**19**	**12.6**	**0.4**
Cibicidoides pachydermus	1										**1**	**0.7**	**0.3**
Cibicidoides wuellerstorfi	1										**1**	**0.7**	**0.3**
Fissurina castanea			1								**1**	**0.7**	**1.3**
Galveninopsis translucens	4										**4**	**2.6**	**0.3**
Globobulimina affinis						18	3	5	3		**29**	**19.2**	**4.3**
Lenticulina cultrata	1										**1**	**0.7**	**0.3**
Lenticulina peregrina	1										**1**	**0.7**	**0.3**
Melonis barleeanus		3									**3**	**2.0**	**0.8**
Nuttallides convexus	1	1									**2**	**1.3**	**0.5**
Uvigerina hispida	1										**1**	**0.7**	**0.3**
Uvigerina mediterranea		1									**1**	**0.7**	**0.8**
Uvigerina peregrina	5	5									**10**	**6.6**	**0.5**
Miliolids													
Biloculina irregularis	1										**1**	**0.7**	**0.3**
Biloculinella cylindrica		1									**1**	**0.7**	**0.8**
Cornuspira involvens	1										**1**	**0.7**	**0.3**

Quinqueloculina auberiana		1									**1**	**0.7**	**0.8**
Quinqueloculina seminuda	1										**1**	**0.7**	**0.3**
Agglutinates													
Ammolagena clavata	1			1							**2**	**1.3**	**1.0**
Ammoscalaria tenuimargo					1						**1**	**0.7**	**2.5**
Ammoscalaria sp.1		1									**1**	**0.7**	**0.8**
Cribrostomoides scitulus			1								**1**	**0.7**	**1.3**
Cribrostomoides subglobosus		1	1								**2**	**1.3**	**1.0**
Cyclammina cancellata		1									**1**	**0.7**	**0.8**
Cyclammina trullissata	1									1	**2**	**1.3**	**0.3**
Cystammina pauciloculata			1	1	1						**3**	**2.0**	**1.8**
Evolutina rotulata				1							**1**	**0.7**	**1.8**
Glomospira gordialis			1								**1**	**0.7**	**1.3**
Hormosinella distans	1	1	1								**3**	**2.0**	**0.8**
Hormosinella guttifera			1								**1**	**0.7**	**1.3**
Paratrochammina sp.1	1										**1**	**0.7**	**0.3**
Reophax agglutinans	1										**1**	**0.7**	**0.3**
Reophax subfusiformis				1							**1**	**0.7**	**1.8**
Repmanina charoides		3									**3**	**2.0**	**0.8**
Psammosphaera testacea	1										**1**	**0.7**	**0.3**
Psammosphaera sp.1					1						**1**	**0.7**	**2.5**
Saccorhiza ramosa		1									**1**	**0.7**	**0.8**
Sorosphaera sp.1		1									**1**	**0.7**	**0.8**
Tholosina vesicularis var. *elongata*		2									**2**	**1.3**	**0.8**
Thurammina albicans	2	1	2	1							**6**	**4.0**	**0.9**
Thurammina papilata		16	12		3						**31**	**20.5**	**1.0**
Trochammina bellingshauseni		1	1								**2**	**1.3**	**1.0**
Totals	**38**	**43**	**24**	**6**	**8**	**18**	**4**	**5**	**3**	**2**	**151**		**1.6**

Station 55 (1374 m). Counts of live (stained) benthic foraminifera 63-150 μm in 0-10 cm core (not noramlised).

-	**0-0.5**	**0.5-1**	**1-1.5**	**1.5-2**	**2-3**	**3-4**	**4-5**	**5-6**	**6-7**	**Total**	**%**	**ALD_{10} (cm)**
Perforates												
Abditodentrix asketocomptella	2									**2**	**0.2**	**0.3**
Alliatina primitiva	3	3	2							**8**	**1.0**	**0.7**

Anomaloides minimus			3	2	2				**7**	**0.8**	**1.8**
Bolivina albatrossi	6	4	3		1				**14**	**1.7**	**0.8**
Bolivina dilatata	1								**1**	**0.1**	**0.3**
Bolivina pseudoplicata		1							**1**	**0.1**	**0.8**
Bolivina pseudopunctata	2								**2**	**0.2**	**0.3**
Bolivina subspinescens	1	1							**2**	**0.2**	**0.5**
Bulimina inflata	9	2	1						**12**	**1.4**	**0.4**
Bulimina rostrata	23	3		1					**27**	**3.2**	**0.3**
Cassidulina carinata	16								**16**	**1.9**	**0.3**
Cassidulina minuta	4	3							**7**	**0.8**	**0.5**
Cibicides phlegeri	9	1	1						**11**	**1.3**	**0.4**
Cibicides sp.1	19								**19**	**2.3**	**0.3**
Dentalina guttifera	1								**1**	**0.1**	**0.3**
Discorbinella araucana	6		1						**7**	**0.8**	**0.4**
Epistominella exigua	93	36	1		2	1	1	1	**135**	**16.2**	**0.4**
Epistominella vitrea	5								**5**	**0.6**	**0.3**
Fissurina sp.3	1								**1**	**0.1**	**0.3**
Fissurina semimarginata	1								**1**	**0.1**	**0.3**
Fissurina staphyllearia	1								**1**	**0.1**	**0.3**
Galveninopsis translucens	1	1							**2**	**0.2**	**0.5**
Globobulimina affinis						17	12	1	**30**	**3.6**	**4.0**
Globocassidulina subglobosa	16	2							**18**	**2.2**	**0.3**
Gyroidina orbicularis	3		2						**5**	**0.6**	**0.7**
Gyroidinoides umbonatus	4	6	4	1					**15**	**1.8**	**0.8**
Lenticulina cultrata	2								**2**	**0.2**	**0.3**
Melonis barleeanus	3	3	4	3	3	1			**17**	**2.0**	**1.4**
Nuttallides pusillus	12	9	3	1				1	**26**	**3.1**	**0.6**
Nuttallides convexus	15	1							**16**	**1.9**	**0.3**
Oolina sp.1	1								**1**	**0.1**	**0.3**
Procerolagena gracilis	1								**1**	**0.1**	**0.3**
Pullenia bulloides	1			2					**3**	**0.4**	**1.3**
Robertina translucens	2								**2**	**0.2**	**0.3**
Seabrookia earlandi	8	2							**10**	**1.2**	**0.4**
Stainforthia fusiformis							1		**1**	**0.1**	**4.5**
Trifarina bradyi	48	4		2			1		**55**	**6.6**	**0.3**
Trifarina pauperata	32	4	1		1			1	**39**	**4.7**	**0.3**
Uvigerina hispida	4								**4**	**0.5**	**0.3**
Uvigerina mediterranea	3								**3**	**0.4**	**0.3**
Uvigerina peregrina	15	5	1						**21**	**2.5**	**0.4**
									0		
Miliolids									**0**		
Cornuspira planorbis	3								**3**	**0.4**	**0.3**
Quinqueloculina pygmaea	2								**2**	**0.2**	**0.3**

Spiropthalmidium concavum	5									**5**	**0.6**	**0.3**
										0		
Agglutinates										**0**		
Adercotryma glomerata	8	2								**10**	**1.2**	**0.4**
Ammodiscus catinus	2	2		1						**5**	**0.6**	**0.8**
Ammoglobigerina globigeriniformis	14	1								**15**	**1.8**	**0.3**
Ammoglobigerina shannoni		1								**1**	**0.1**	**0.8**
Cribrostomoides bradyi	1			2	2					**5**	**0.6**	**1.8**
Cribostomoides scitulum			1							**1**	**0.1**	**1.3**
Cystammina argentea		4	1							**5**	**0.6**	**0.9**
Cystammina pauciloculata					1					**1**	**0.1**	**2.5**
Deuterammina montagui		1	1	1						**3**	**0.4**	**1.3**
Eratidus foliaceus	5									**5**	**0.6**	**0.3**
Glomospira glomerata		3			2					**5**	**0.6**	**1.5**
Glomospira gordialis	1									**1**	**0.1**	**0.3**
Hormosinella distans	6									**6**	**0.7**	**0.3**
Hormosinella guttifera	11	3								**14**	**1.7**	**0.4**
Hyperammina laevigata		1								**1**	**0.1**	**0.8**
Labrospira wiesneri					4					**4**	**0.5**	**2.5**
Lagenammina cf. *tubulata*			1		1					**2**	**0.2**	**1.9**
Nodellum membranaceum			3		11					**14**	**1.7**	**2.2**
Nodellum moniliforme		2	1							**3**	**0.4**	**0.9**
Paratrochammina kelakasensis						3	9	1		**13**	**1.6**	**4.3**
Psammosphaera sp.	39	3								**42**	**5.0**	**0.3**
Pseudobolivina antarctica		1								**1**	**0.1**	**0.8**
Reophax fusiformis		6	2	7	3					**18**	**2.2**	**1.5**
Reophax sp.2	47	3	1							**51**	**6.1**	**0.3**
Repmanina charoides	3	3	1		5		1			**13**	**1.6**	**1.4**
Saccammina consociata	1	1								**2**	**0.2**	**0.5**
Siphotextularia concava		1								**1**	**0.1**	**0.8**
Thurammina albicans	3		1							**4**	**0.5**	**0.5**
Thurammina papillata		3	4	3	3					**13**	**1.6**	**1.5**
Thurammina sp.2					1					**1**	**0.1**	**2.5**
Tritaxis britannica		3	5	1						**9**	**1.1**	**1.1**
Tritaxis sp 1	1									**1**	**0.1**	**0.3**
Trochammina sp. 1	2									**2**	**0.2**	**0.3**
Trochammina sp. 2	1									**1**	**0.1**	**0.3**
Totals	**529**	**135**	**49**	**27**	**42**	**22**	**25**	**5**	**0**	**834**		**0.8**

Station 53 (2475 m). Counts of live (stained) benthic foraminifera 150 μm in 0-10 cm core (not noramlised).

-	0-0.5	0.5-1	1-1.5	1.5-2	2-3	3-4	4-5	5-6	6-7	Total	%	ALD_{10} (cm)
Perforates												
Bulimina inflata	1									**1**	**0.6**	**0.3**
Bulimina rostrata					3					**3**	**1.7**	**2.5**
Cibicidoides kullenbergi	2	1								**3**	**1.7**	**0.4**
Cibicidoides robertsonianus	1									**1**	**0.6**	**0.3**
Epistominella exigua		1								**1**	**0.6**	**0.8**
Galveninopsis translucens						1				**1**	**0.6**	**3.5**
Gyroidina orbicularis	1	1								**2**	**1.1**	**0.5**
Hoeglundina elegans			1							**1**	**0.6**	**1.3**
Oridosalis umbonatus	1		1							**2**	**1.1**	**0.8**
Pullenia bulloides		1								**1**	**0.6**	**0.8**
Robertinoides bradyi			1							**1**	**0.6**	**1.3**
Uvigerina peregrina	12	2	1							**15**	**8.6**	**0.4**
Miliolids												
Miliolinella subrotunda	1									**1**	**0.6**	**0.3**
Pyrgo depressa	1									**1**	**0.6**	**0.3**
Pyrgo lucernula	1									**1**	**0.6**	**0.3**
Pyrgo sp.1		1								**1**	**0.6**	**0.8**
Sigmoilopsis schlumbergeri					1					**1**	**0.6**	**2.5**
Triloculina tricarinata	2									**2**	**1.1**	**0.3**
Agglutinates												
Adercotryma glomerata	1	1	1			2				**5**	**2.9**	**1.9**
Ammobaculites agglutinans			1			3	2			**6**	**3.4**	**3.9**
Ammobaculites filiformis	4									**4**	**2.3**	**0.3**
Ammodiscus planorbis							1			**1**	**0.6**	**4.5**
Ammolagena clavata		1								**1**	**0.6**	**0.8**
Cribrostomoides bradyi	1									**1**	**0.6**	**0.3**
Cribrostomoides latidorsatum	2	1	3	1						**7**	**4.0**	**1.0**
Crithionina pissum		1								**1**	**0.6**	**0.8**
Cyclammina cancellata	1									**1**	**0.6**	**0.3**
Cyclammina sp.1			1	1						**2**	**1.1**	**1.5**
Cystammina pauciloculata	1			2						**3**	**1.7**	**1.3**
Eggerella bradyi	1									**1**	**0.6**	**0.3**

Glomospira gordialis			1			1	1			**3**	**1.7**	**3.1**
Hormosina globulifera	4	4	3							**11**	**6.3**	**0.7**
Hormosinella distans			1							**1**	**0.6**	**1.3**
Hormosinella guttifera	1	1								**2**	**1.1**	**0.5**
Hormosinella sp.1		1								**1**	**0.6**	**0.8**
Hyperammina elongata		1	1				2			**4**	**2.3**	**2.8**
Karrerulina apicularis	3	3	3	3	4	4		1		**21**	**12.0**	**1.8**
Labrospira wiesneri							1			**1**	**0.6**	**4.5**
Nodosinella gaussica		2								**2**	**1.1**	**0.8**
Portatrochammina antarctica		5			1					**6**	**3.4**	**0.8**
Psammopshaera fusca						1				**1**	**0.6**	**3.5**
Recurvoides contortus		2								**2**	**1.1**	**0.8**
Reophax bacillaris		3								**3**	**1.7**	**0.8**
Reophax bilocularis					4					**4**	**2.3**	**2.5**
Reophax dentaliniformis						1	1			**2**	**1.1**	**4.0**
Reophax cf. *eximus*	1									**1**	**0.6**	**0.3**
Reophax fusiformis		3				1				**4**	**2.3**	**1.4**
Repmanina charoides		1	1		6	7	4			**19**	**10.9**	**3.4**
Saccorhiza ramosa		1								**1**	**0.6**	**0.8**
Thurammina albicans		2								**2**	**1.1**	**0.8**
Thurammina papillata			1	4		1				**6**	**3.4**	**1.7**
Trochammina sp.1	1	1				1				**3**	**1.7**	**1.5**
Trochammina sp.2			2							**2**	**1.1**	**1.3**
Indeterminate	1									**1**	**0.6**	**0.3**
Totals	**45**	**41**	**23**	**11**	**19**	**23**	**12**	**1**	**0**	**175**		**1.6**

Station 53 (2475 m). Counts of live (stained) benthic foraminifera 63-150 µm in 0-10 cm core (not noramlised).

	0-0.5	**0.5-1**	**1-1.5**	**1.5-2**	**2-3**	**3-4**	**4-5**	**5-6**	**6-7**	**Total**	**%**	**ALD_{10} (cm)**
Perforates												
Abditodentrix asketocomptella	4	2	1							**7**	**1.2**	**0.5**
Alliatina primitiva	3	2	1							**6**	**1.0**	**0.6**
Astrononion echolsi	3			1	2	3				**9**	**1.5**	**2.0**
Bolivina pseudoplicata								1		**1**	**0.2**	**5.5**
Bolivina subspinecans	1									**1**	**0.2**	**0.3**
Bulimina inflata	3									**3**	**0.5**	**0.3**
Bulimina rostrata	4	1			1		1			**7**	**1.2**	**0.4**

Buliminella translucens	5	4			1				**10**	**1.7**	**0.5**
Cibicides phlegeri	2	1	4		2	2			**11**	**1.9**	**1.7**
Epistominella exigua	7	8							**15**	**2.6**	**0.5**
Fissurina semimarginata								1	**1**	**0.2**	**5.5**
Globobulimina affinis							2		**2**	**0.3**	**4.5**
Globocassidulina subglobosa	20	8	1	1	1				**31**	**5.3**	**0.5**
Gyroidina orbicularis	3	1	1		1	2			**8**	**1.4**	**1.5**
Gyroidinoides umbonatus	4	4	6	1	1	5	2		**23**	**3.9**	**1.8**
Marginalina sp.1						1			**1**	**0.2**	**3.5**
Nonionella iridea	7		5						**12**	**2.0**	**0.7**
Nuttallides pusillus	3								**3**	**0.5**	**0.3**
Nuttallides umboniferus	1								**1**	**0.2**	**0.3**
Oolina cf. *globosa*						1			**1**	**0.2**	**3.5**
Planulina ariminensis	2								**2**	**0.3**	**0.3**
Pullenia salisburyi	2	23	6	6	10	6	1		**54**	**9.2**	**1.6**
Rosalina sp.1	3	5							**8**	**1.4**	**0.6**
Robertinoides bradyi					1				**1**	**0.2**	**2.5**
Seabrookia earlandi	2	2		1	1	5	1		**12**	**2.0**	**2.4**
Uvigerina peregrina	1	1							**2**	**0.3**	**0.5**
Miliolids											
Agathammina pusilla	2		1			4	1		**8**	**1.4**	**2.5**
Quinqueloculina bosciana			1		1	2			**4**	**0.7**	**2.7**
Sigmoilopsis schlumbergeri					1				**1**	**0.2**	**2.5**
Spirothalmidium pussilum			1		1				**2**	**0.3**	**1.9**
Agglutinates											
Adercotryma glomerata	4	1	2		1	11	1		**20**	**3.4**	**2.5**
Ammobaculites filiformis		3	2	1	2	2			**10**	**1.7**	**1.9**
Ammodiscus minimus	3	3	3	2	4		1		**16**	**2.7**	**1.5**
Ammoscalaria tenuitestata								1	**1**	**0.2**	**5.5**
Cribrostomoides bradyi		2	1		2				**5**	**0.9**	**1.6**
Cystammina argentea		2	8	6	5	2	4		**27**	**4.6**	**2.2**
Cystammina pauciloculata		1	1		1				**3**	**0.5**	**1.5**
Glomospira gordialis	1	1							**2**	**0.3**	**0.5**
Hippocrepinella flexibilis			1						**1**	**0.2**	**1.3**
Hormosinella distans	3				1		2		**6**	**1.0**	**2.0**
Hormosinella guttifera	3				2	1	2		**8**	**1.4**	**2.3**
Hyperammina laevigata	1								**1**	**0.2**	**0.3**
Karrerulina apicularis	2	4	3		1				**10**	**1.7**	**1.0**
Labrospira jeffreysii		1	1		1	2			**5**	**0.9**	**2.3**
Labrospira wiesneri	1	1	2	1	2	5	11		**23**	**3.9**	**3.4**
Lagenammina bulbosa	7	1	2				1		**11**	**1.9**	**0.5**

Lagenammina tubulata			2							**2**	**0.3**	**1.3**
Nodellum membranaceum	1	1	1	2	1					**6**	**1.0**	**1.4**
Paratrochammina sp.1				1	1	1				**3**	**0.5**	**2.6**
Portatrochammina antarctica	4		1							**5**	**0.9**	**0.5**
Pseudobolivina sp.1		1								**1**	**0.2**	**0.8**
Pseudonodosinella cf. *mortenseni*						1				**1**	**0.2**	**3.5**
Recurvoides contortos	1	2				1				**4**	**0.7**	**1.3**
Reophax dentaliniformis	1		1				1			**3**	**0.5**	**2.0**
Reophax fusiformis	1	12	5	1	4	3	6	0	0	**32**	**5.4**	**2.0**
Reophax sp.1				2	8	11		1		**22**	**3.7**	**3.0**
Reophax cf. *subfusiformis*			1							**1**	**0.2**	**1.3**
Repmanina charoides		1	1		6	6	42			**56**	**9.5**	**4.2**
Spiroplectammina biformis	5	9								**14**	**2.4**	**0.6**
Subreophax cf. *anduncus*					11	2	6			**19**	**3.2**	**3.2**
Textularia sp.1				1						**1**	**0.2**	**1.8**
Textularia sp.2					1					**1**	**0.2**	**2.5**
Thurammina albicans			1		2	2				**5**	**0.9**	**2.7**
Thurammina papillata	2		2			1				**5**	**0.9**	**1.3**
Trochammina sp.1	1					1				**2**	**0.3**	**1.9**
Trochammina sp 2	1									**1**	**0.2**	**0.3**
Trochammina sp.3		1	1				1			**3**	**0.5**	**2.2**
Trochammina sp.4	1				1					**2**	**0.3**	**1.4**
Trochammina sp.5	2									**2**	**0.3**	**0.3**
Trochammina sp.6	1									**1**	**0.2**	**0.3**
Totals	**128**	**109**	**70**	**27**	**81**	**83**	**86**	**4**	**0**	**588**		**2.0**

Station 52 (2908 m). Counts of live (stained) benthic foraminifera >150 μm in 0-10 cm core (not noramlised).

	0-0.5	**0.5-1**	**1-1.5**	**1.5-2**	**2-3**	**3-4**	**4-5**	**5-6**	**6-7**	**Total**	**%**	**ALD_{10} (cm)**
Perforates												
Cibicides wuellerstorfi	2									**2**	**1.5**	**0.3**
Cibicidoides kullenbergi	8			1	1					**10**	**7.5**	**0.3**
Cibicidoides robertsonianus			1							**1**	**0.8**	**1.3**
Epistominella exigua	4									**4**	**3.0**	**0.3**
Fursenkoina sp.2							1			**1**	**0.8**	**4.5**

Gyroidina sordanii	1								**1**	**0.8**	**0.3**
Hoeglundina elegans	2	3	1						**6**	**4.5**	**0.7**
Nuttallides umboniferous	4								**4**	**3.0**	**0.3**
Robertina translucens	1								**1**	**0.8**	**0.3**
Miliolids											
Biloculinella irregularis	1								**1**	**0.8**	**0.3**
Pyrgo murrhia						1			**1**	**0.8**	**3.5**
Pyrgoella sphaera						1			**1**	**0.8**	**3.5**
Quinqueloculina cf. *weaveri*	1								**1**	**0.8**	**0.3**
Quinqueloculina sp.1		1							**1**	**0.8**	**0.8**
Quinqueloculina sp.2				1					**1**	**0.8**	**1.8**
Sigmoilopsis schlumbergeri					1	1			**2**	**1.5**	**3.0**
Agglutinates											
Adercotryma glomerata					1				**1**	**0.8**	**2.5**
Ammobaculites agglutinans					1	1			**2**	**1.5**	**3.0**
Cribrostomoides bradyi						6	3	1	**10**	**7.5**	**4.0**
Cyclammina pussila			1						**1**	**0.8**	**1.3**
Cystammina pauciloculata	1			1	1	1	2		**6**	**4.5**	**3.4**
Deuterammina sp.1					2	1			**3**	**2.3**	**2.8**
Earlandammina inconspicua							1		**1**	**0.8**	**4.5**
Eggerella bradyi	1						1		**2**	**1.5**	**2.4**
Globotrochammina bellingshauseni					1	2			**3**	**2.3**	**3.2**
Globotrochamminopsis shannoni	1								**1**	**0.8**	**0.3**
Hippocrepinella flexibilis						1			**1**	**0.8**	**3.5**
Hippocrepinella sp.1	2								**2**	**1.5**	**0.3**
Hormosina globulifera	1				2		1		**4**	**3.0**	**2.4**
Hormosinella guttifera					2				**2**	**1.5**	**2.5**
Hormosinella sp.1	1								**1**	**0.8**	**0.3**
Hyperammina sp.1			1						**1**	**0.8**	**1.3**
Karrerulina apicularis	1				2		2	1	**6**	**4.5**	**3.3**
Psammosphaera fusca	2								**2**	**1.5**	**0.3**
Psammosphaera testacea	1		1	1					**3**	**2.3**	**1.1**
Recurvoides sp.1	3	2		1	4		1	1	**12**	**9.0**	**2.0**
Reophax agglutinans			1		1				**2**	**1.5**	**1.9**
Reophax cylindrica	2			1					**3**	**2.3**	**0.8**
Reophax eximus					1				**1**	**0.8**	**2.5**
Reophax fusiformis	4			1	5				**10**	**7.5**	**1.5**
Reophax pilulifera	1				1	1			**3**	**2.3**	**2.1**
Reophax sp.1	3								**3**	**2.3**	**0.3**
Reophax testacea	1	1							**2**	**1.5**	**0.5**
Subreophax sp.1	1								**1**	**0.8**	**0.3**

Textularia agglutinans	2									**2**	**1.5**	**0.3**
Thurammina papillata	3						1			**4**	**3.0**	**0.3**
												1.6
Totals	**55**	**7**	**6**	**7**	**26**	**16**	**13**	**3**	**0**	**133**		**1.8**

Station 52 (2908 m). Counts of live (stained) benthic foraminifera 63-150 μm in 0-10 cm core (not noramlised).

	0-0.5	**0.5-1**	**1-1.5**	**1.5-2**	**2-3**	**3-4**	**4-5**	**5-6**	**6-7**	**Total**	**%**	**ALD_{10} (cm)**
Perforates												
Abditodentrix asketocomptella	3		1	1						**5**	**0.6**	**0.8**
Alliatina primitiva	4	2	2	2						**10**	**1.1**	**0.9**
Astrononion echolsi	3		1		1					**5**	**0.6**	**0.9**
Bulimina inflata	1									**1**	**0.1**	**0.3**
Bulimina rostrata	7	4		1						**12**	**1.4**	**0.5**
Buliminella translucens	20	12	10	2	3					**47**	**5.4**	**0.8**
Cassidulina crassa		1								**1**	**0.1**	**0.8**
Cassidulinoides bradyi	1	2			2					**5**	**0.6**	**1.4**
Epistominella exigua	44	20	7	6	1					**78**	**8.9**	**0.6**
Fissurina annectens				1						**1**	**0.1**	**1.8**
Fursenkoina squammosa								1		**1**	**0.1**	**5.5**
Fursenkoina sp.1					4	1	3	1		**9**	**1.0**	**3.6**
Fursenkoina sp.2							1			**1**	**0.1**	**4.5**
Globobulimina pacifica								1		**1**	**0.1**	**5.5**
Globocassidulina subglobosa	11	20	11	10	10					**62**	**7.1**	**1.2**
Gyroidina umbonata	1		2	2	3	1	2	1		**12**	**1.4**	**2.6**
Gyroidina cf. *bradyi*	9	7	11	4	2	1				**34**	**3.9**	**1.1**
Gyroidina soldanii	2				1					**3**	**0.3**	**1.0**
Ioanella tumidula	3	4		1						**8**	**0.9**	**0.5**
Lagena felsinea		1				1				**2**	**0.2**	**2.1**
Lagena semilineata var. *spinigera*					1					**1**	**0.1**	**2.5**
Nonionella iridea		1								**1**	**0.1**	**0.8**
Nuttallides pusillus	42	37	13	11						**103**	**11.8**	**0.7**
Oridosalis umbonatus	1	1								**2**	**0.2**	**0.5**
Pullenia salisburyi	1	3	2		4	1	4			**15**	**1.7**	**2.4**
Rosalina sp.1	6	2	2	1						**11**	**1.3**	**0.7**
Seabrookia earlandi	3	2		2						**7**	**0.8**	**0.8**
										0		
Miliolids										**0**		

Agathammina pussila		1			1	2	1			**5**	**0.6**	**3.0**
Cornuspira involvens	1		1							**2**	**0.2**	**0.8**
Nummoloculina contraria		1								**1**	**0.1**	**0.8**
Pyrgoella sphaera			1							**1**	**0.1**	**1.3**
Quinqueloculina bosciana	1									**1**	**0.1**	**0.3**
Quinqueloculina pygmaea	1	2		1						**4**	**0.5**	**0.9**
Spirothalmidium pussilum			1							**1**	**0.1**	**1.3**
										0		
Agglutinates										**0**		
Adercotryma glomerata		7	4	6	4	10	5	1		**37**	**4.2**	**2.5**
Ammobaculites filiformis					1					**1**	**0.1**	**2.5**
Ammodiscus planus		1		1						**2**	**0.2**	**1.3**
Cribrostomoides bradyi					6	5	1	2		**14**	**1.6**	**3.4**
Crithionina sp.1					1					**1**	**0.1**	**2.5**
Cystammina argentea	1	5	5	7	9	5	1			**33**	**3.8**	**2.0**
Cystammina pauciloculata		1		1	3	4	1			**10**	**1.1**	**2.9**
Earlandammina inconspicua					2					**2**	**0.2**	**2.5**
Eggerrella advena	1		1	1						**3**	**0.3**	**1.1**
Globotrochamminopsis shannoni	2		1							**3**	**0.3**	**0.6**
Glomospira charoides	1						5			**6**	**0.7**	**4.5**
Haplophragmoides sphaeriloculum	1									**1**	**0.1**	**0.3**
Hippocrepinella alba	3		1		2					**6**	**0.7**	**1.2**
Hippocrepinella flexibilis	13	1	3		1					**18**	**2.1**	**0.6**
Hippocrepinella sp.1				2						**2**	**0.2**	**1.8**
Hormosinella cf. *carpenteri*	1		1	1	1	1				**5**	**0.6**	**1.9**
Hormosinella guttifera	18	11	6	5	0	2	3	0		**45**	**5.1**	**0.9**
Hormosinella sp.1	1		1	2		1				**5**	**0.6**	**1.7**
Hyperammina cylindrica			3							**3**	**0.3**	**1.3**
Karrerulina apicularis	1		1	1		1	5			**9**	**1.0**	**3.3**
Labrospira jeffreysii	2	1	6	2	2		1			**14**	**1.6**	**1.3**
Labrospira wiesneri							1			**1**	**0.1**	**4.5**
Nodellum membranaceum			1							**1**	**0.1**	**1.3**
Paratrochammina cf. *harti*	1	1	2							**4**	**0.5**	**0.9**
Paratrochammina pseudotricamerata			1							**1**	**0.1**	**1.3**
Paratrochammina scotiaensis	2									**2**	**0.2**	**0.3**
Pseudobolivina antarctica		1								**1**	**0.1**	**0.8**
Reophax cylindrica				1			1			**2**	**0.2**	**3.1**
Reophax eximus	3			2						**5**	**0.6**	**0.9**
Reophax fusiformis	10	16	17	23	45	14	7	0	0	**132**	**15.1**	**2.0**
Reophax micacea						1		2		**3**	**0.3**	**4.8**
Reophax nodulosus							3			**3**	**0.3**	**4.5**
Reophax scorpiurus		1								**1**	**0.1**	**0.8**
Reophax sp.1	5		1	4						**10**	**1.1**	**1.0**

Reophax sterkii			1	3						**4**	**0.5**	**1.6**
Reophax cf. *pulilifera*						1				**1**	**0.1**	**3.5**
Reophax sp.1					1					**1**	**0.1**	**2.5**
Resupinammina simplex						1		1		**2**	**0.2**	**4.5**
Spiroplectammina biformis	4	4	2	2	1					**13**	**1.5**	**1.0**
Subreophax anducus							1	1		**2**	**0.2**	**5.0**
Technitella cf. *spiculitesta*	2									**2**	**0.2**	**0.3**
Thurammina albicans			1	8	1	1				**11**	**1.3**	**1.9**
Thurammina papillata	1									**1**	**0.1**	**0.3**
Totals	**238**	**173**	**124**	**117**	**113**	**54**	**46**	**11**	**0**	**876**		**1.5**

Station 51 (3908 m). Counts of live (stained) benthic foraminifera >150 μm in 0-10 cm core (not noramlised).

	0-0.5	**0.5-1**	**1-1.5**	**1.5-2**	**Total**	**%**	**ALD_{10} (cm)**
Perforates							
Cibicidoides kullernbergi	1	1			**2**	**4.7**	**0.5**
Cibicidoides robertsonianus	1				**1**	**2.3**	**0.3**
Epistominella exigua		1	2		**3**	**7.0**	**1.1**
Oridosalis umbonatus			1		**1**	**2.3**	**1.3**
Uvigerina peregrina	1				**1**	**2.3**	**0.3**
Miliolids							
Cornuspira involvens	1	1			**2**	**4.7**	**0.5**
Pyrgo elongata			3		**3**	**7.0**	**1.3**
Agglutinates							
Ammobaculites agglutinans	1				**1**	**2.3**	**0.3**
Cribrostomoides latidorsatum	1				**1**	**2.3**	**0.3**
Eggerella bradyi		1			**1**	**2.3**	**0.8**
Globotrochamminopsis cf. *shannoni*		1			**1**	**2.3**	**0.8**
Hormosinella guttifera		1			**1**	**2.3**	**0.8**
Hyperammina friabilis	1				**1**	**2.3**	**0.3**
Karrerulina apicularis			1		**1**	**2.3**	**1.3**
Lagenammina spiculata		1			**1**	**2.3**	**0.8**
Paratrochammina cf. *earlandi*	1				**1**	**2.3**	**0.3**

Paratrochammina sp.1		1		**1**	**2.3**	**0.8**
Portatrochammina murrayi			1	**1**	**2.3**	**1.3**
Psammosphaera testacea	3		1	**4**	**9.3**	**0.5**
Psammosphaera sp.2	1			**1**	**2.3**	**0.3**
Recurvoides cf. *contortus*			2	**2**	**4.7**	**1.3**
Reophax cf. *rostrata*		1		**1**	**2.3**	**0.8**
Reophax cf. *eximus*	1			**1**	**2.3**	**0.3**
Reophax fusiformis		7		**7**	**16.3**	**0.8**
Saccammina consociata	1			**1**	**2.3**	**0.3**
Spiroplectammina sp.1		1		**1**	**2.3**	**0.8**
Thurammina papillata			1	**1**	**2.3**	**1.3**
Totals	**14**	**17**	**12**	**43**		**0.7**

Station 51 (3908 m). Counts of live (stained) benthic foraminifera 63-150 μm in 0-10 cm core (not noramlised).

	0-0.5	**0.5-1**	**1-1.5**	**1.5-2**	**2-3**	**3-4**	**Total**	**%**	**ALD_{10} (cm)**
Perforates									
Alliatina primitiva	2	1	1				**4**	**1.2**	**0.6**
Buliminella translucens	9	6	2				**17**	**5.2**	**0.5**
Cibicidoides kullenbergi	1						**1**	**0.3**	**0.3**
Cibicidoides robertsonianus		1					**1**	**0.3**	**0.8**
Epistominella exigua	14	12	3	1			**30**	**9.2**	**0.6**
Fursenkoina complanata	1						**1**	**0.3**	**0.3**
Globocassidulina subglobosa	2	1					**3**	**0.9**	**0.4**
Gyroidina cf. *bradyi*	6	2					**8**	**2.4**	**0.4**
Gyroidinoides umbonatus	1		4	1	1		**7**	**2.1**	**1.5**
Ioanella tumidula	2	1	1				**4**	**1.2**	**0.6**
Nuttallides umboniferus	1						**1**	**0.3**	**0.3**
Nuttallides pusillus	29	20	3	1			**53**	**16.2**	**0.5**
Oolina globosa	1						**1**	**0.3**	**0.3**
Oridosalis umbonatus	3						**3**	**0.9**	**0.3**
Parafissurina cf. *staphyllearia*	2						**2**	**0.6**	**0.3**
Pullenia salisburyi			1				**1**	**0.3**	**1.3**
Seabrookia earlandi	1						**1**	**0.3**	**0.3**
Miliolids									
Biloculinella irregularis	2	1					**3**	**0.9**	**0.4**

Cornuspira involvens	1						**1**	**0.3**	**0.3**
Pyrulina sp.1					1		**1**	**0.3**	**2.5**
Quinqueloculina bosciana	1	1					**2**	**0.6**	**0.5**
Quinquelocilina pygmaea	1	1			1		**3**	**0.9**	**1.2**
Agglutinates									
Adercotryma glomerata	5		6	1			**12**	**3.7**	**0.9**
Buzasina galeata	1	1					**2**	**0.6**	**0.5**
Deuterammina montagui	4	2	4	1			**11**	**3.4**	**0.8**
Earlandammina inconspicua					1		**1**	**0.3**	**2.5**
Eggerella advena	2						**2**	**0.6**	**0.3**
Eggerella bradyi	1	1					**2**	**0.6**	**0.5**
Glomospira gordialis	2						**2**	**0.6**	**0.3**
Hippocrepinella alba	3			1			**4**	**1.2**	**0.6**
Hippocrepinella flexibilis	10		2	1			**13**	**4.0**	**0.3**
Hormosinella guttifera	11		2				**13**	**4.0**	**0.4**
Karrerulina apicularis			1	1	1		**3**	**0.9**	**1.8**
Lagenammina tubulosa	1	3					**4**	**1.2**	**0.6**
Paratrochammina sp.1		1					**1**	**0.3**	**0.8**
Paratrochammina pseudotricamerata	4	2			1		**7**	**2.1**	**0.4**
Psammosphaera testacea	5	2	2				**9**	**2.8**	**0.6**
Recurvoides sp.1	3	4	1				**8**	**2.4**	**0.6**
Reophax cf. *rostrata*	1						**1**	**0.3**	**0.3**
Reophax fusiformis	43	8	1				**52**	**15.9**	**0.3**
Reophax sp.1	4	2					**6**	**1.8**	**0.4**
Repmanina charoides	1			1	1		**3**	**0.9**	**1.5**
Sammosphaera sp.1			1				**1**	**0.3**	**1.3**
Siphotextularia sp.1		1					**1**	**0.3**	**0.8**
Spirolocammina sp.1					2		**2**	**0.6**	**2.5**
Spiroplectammina sp.1	1						**1**	**0.3**	**0.3**
Thurammina albicans	4		1	1	1		**7**	**2.1**	**0.9**
Thurammina papillata	1			1	1		**3**	**0.9**	**1.5**
Thurammina cf. castanea	2						**2**	**0.6**	**0.3**
Trochammina bellingshauseni			1				**1**	**0.3**	**1.3**
Trochammina sp.1	1	1			1		**3**	**0.9**	**1.2**
Trochammina sp.2	1						**1**	**0.3**	**0.3**
Trochammina sp.3		1					**1**	**0.3**	**0.8**
Totals	**191**	**76**	**37**	**11**	**12**	**0**	**327**		**0.6**

Station 50 (4987 m). Counts of live (stained) benthic foraminifera >150 μm in 0-10 cm core (not noramlised).

	0-0.5	0.5-1	1-1.5	Total	%	ALD_{10} (cm)
Perforates						
Cibicidoides kullenbergi	2			**2**	**1.9**	**0.3**
Epistominella exigua	1			**1**	**1.0**	**0.3**
Nuttallides umboniferous	3			**3**	**2.9**	**0.3**
Miliolids						
Pyrgoella irregularis	1			**1**	**1.0**	**0.3**
Quinqueloculina pygmaea	1			**1**	**1.0**	**0.3**
Sigmoilopsis sp. 1	1			**1**	**1.0**	**0.3**
Agglutinates						
Ammobaculites agglutinans	5			**5**	**4.8**	**0.3**
Ammodiscus cf. *catinus*	2			**2**	**1.9**	**0.3**
Buzasina galeata	2			**2**	**1.9**	**0.3**
Eggerella bradyi	3	1		**4**	**3.8**	**0.4**
Globotrochamminopsis cf. *shannoni*	1			**1**	**1.0**	**0.3**
Haplophragmoides sphaeriloculum	2			**2**	**1.9**	**0.3**
Hormosina globulifera	14	2		**16**	**15.4**	**0.3**
Hormosinella distans	1			**1**	**1.0**	**0.3**
Hormosinella gutterifera	2			**2**	**1.9**	**0.3**
Lagenammina tubulosa	4			**4**	**3.8**	**0.3**
Psammosphaera sp.1	2			**2**	**1.9**	**0.3**
Psammosphaera sp.2	3			**3**	**2.9**	**0.3**
Recurvoides sp.1	6			**6**	**5.8**	**0.3**
Reophax dentaliniformis		1		**1**	**1.0**	**0.8**
Reophax fusiformis	21	5		**26**	**25.0**	**0.3**
Reophax gaussicus	1			**1**	**1.0**	**0.3**
Saccammina sp.1	1			**1**	**1.0**	**0.3**
Saccorhiza ramosa	1	3		**4**	**3.8**	**0.6**
Textularia cf. *agglutinans*	1			**1**	**1.0**	**0.3**
Thurammina cf. *faerleensis*	4			**4**	**3.8**	**0.3**
Thurammina papillata	6			**6**	**5.8**	**0.3**
*Trochammina*sp.1	1			**1**	**1.0**	**0.3**
Totals	**92**	**12**		**104**		**0.3**

Station 50 (4987 m). Counts of live (stained) benthic foraminifera 63-150 μm in 0-10 cm core (not noramlised).

	0-0.5	0.5-1	1-1.5	1.5-2	2-3	3-4	4-5	5-6	6-7	7-8	Total	%	ALD10 (cm)
Perforates													
Alliatina primitiva	5		2		1						**8**	**1.9**	**0.8**
Buliminella translucens	1										**1**	**0.2**	**0.3**
Cibicidoides kullenbergi	3	1									**4**	**1.0**	**0.4**
Epistominella exigua	9	2									**11**	**2.6**	**0.3**
Fissurina sp.1	1										**1**	**0.2**	**0.3**
Globocassidulina subglobosa	2										**2**	**0.5**	**0.3**
Gyroidina sp.1	6										**6**	**1.4**	**0.3**
Gyriodinoides umbonatus	1		2	3							**6**	**1.4**	**1.3**
Lagena sp.1	1										**1**	**0.2**	**0.3**
Nuttallides pusillus	15	2									**17**	**4.1**	**0.3**
Parafissurina felsinea						1				1	**2**	**0.5**	**5.5**
Paumotua terebra		3									**3**	**0.7**	**0.8**
Pullenia salisburyi			11	12	2	1			1		**27**	**6.5**	**1.7**
Miliolids													
Miliolid sp.1	1										**1**	**0.2**	**0.3**
Miliolid sp.2	1										**1**	**0.2**	**0.3**
Miliolina subrotunda			1								**1**	**0.2**	**1.3**
Pyrgoella irregularis	1										**1**	**0.2**	**0.3**
Quinqueloculina bosciana	4										**4**	**1.0**	**0.3**
Quinqueloculina pygmaea	1										**1**	**0.2**	**0.3**
Agglutinates													
Adercotryma glomerata	16	1									**17**	**4.1**	**0.3**
Ammobaculites filiformis	7										**7**	**1.7**	**0.3**
Ammobaculites sp.1	1										**1**	**0.2**	**0.3**
Ammobaculites sp.2	1		1	1							**3**	**0.7**	**1.1**
Ammobaculites sp.3	1	1									**2**	**0.5**	**0.5**
Ammoglobigerina globigeriniformis	3										**3**	**0.7**	**0.3**
Cribrostomoides crassimargo	1	1									**2**	**0.5**	**0.5**
Eggerella advena	2	1									**3**	**0.7**	**0.4**
Eggerella bradyi	10	2									**12**	**2.9**	**0.3**
Haplophragmoides sphaeriloculum	28										**28**	**6.7**	**0.3**

Hippocrepina pusilla	3										**3**	**0.7**	**0.3**
Hippocrepinella flexibilis	6										**6**	**1.4**	**0.3**
Hormosinella guttifera	10	2									**12**	**2.9**	**0.3**
Hormosinella sp.1	1										**1**	**0.2**	**0.3**
Karrerulina apicularis	4	2	3	1							**10**	**2.4**	**0.8**
Lagenammina difflugiformis	2	2	1	1							**6**	**1.4**	**0.8**
Lagenammina tubulata	35	1		1							**37**	**8.9**	**0.3**
Recurvoides sp.1	4	1									**5**	**1.2**	**0.4**
Reophax fusiformis	32	16	2	2	4	0	1	1	0		**58**	**13.9**	**0.6**
Reophax micaceous		2	2	1	1			3			**9**	**2.2**	**2.8**
Reophax cf. *rostrata*		1									**1**	**0.2**	**0.8**
Reophax sp.1	21	2	1	2					1		**27**	**6.5**	**0.4**
Repmanina charoides		1	2	1	1						**5**	**1.2**	**1.5**
Siphotextularia concava	5										**5**	**1.2**	**0.3**
Spirolocammina sp.1	4	6	3	2							**15**	**3.6**	**0.9**
Subreophax cf. *anduncus*	2			1							**3**	**0.7**	**0.8**
Textularia sp.1	1										**1**	**0.2**	**0.3**
Thurammina albicans	3										**3**	**0.7**	**0.3**
Thurammina cf. *albicans*	7	1	2								**10**	**2.4**	**0.5**
Thurammina cf. *faerleensis*	11	1									**12**	**2.9**	**0.3**
Thurammina murata	1										**1**	**0.2**	**0.3**
Thurammina papillata	4	1	1	1							**7**	**1.7**	**0.7**
Thurammina sp.1	1										**1**	**0.2**	**0.3**
Tritaxis britannica	3										**3**	**0.7**	**0.3**
Trochammina sp.2	1										**1**	**0.2**	**0.3**
-													
Totals	**283**	**53**	**34**	**29**	**9**	**2**	**1**	**4**	**2**	**1**	**418**		**0.7**

ANNEXE 2

APPENDIX 2

Nazaré Canyon terrace, Core 37 (968 m). Counts of live (stained) benthic foraminifera >150 µm in 0-10 cm core (not normalised).

	0-0.5	0.5-1	1-1.5	1.5-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10	Totals	%	ALD_{10} (cm)
Perforates															
Bolivina alata		7	35	22	25	1	1	1					**92**	**4.1**	**1.8**
Bolivina dilatata		2											**2**	**0.1**	**0.8**
Bolivinita quadrilatera	1	6	4	4	1								**16**	**0.7**	**1.2**
Bulimina inflata	17	34	52	13	5	2	1			1			**125**	**5.6**	**1.1**
Cassidulinoides bradyi				1									**1**	**0.0**	**1.8**
Chilostomella oolina	3		4	13	36	38	37	18	30	26	6	4	**215**	**9.6**	**4.6**
Cibicidoides pachydermus	29	15	11	5	4	1	1		1	1			**68**	**3.0**	**1.2**
Fissurina bradyi				1									**1**	**0.0**	**1.8**
Gavelinopsis praegeri	6	1	1	1									**9**	**0.4**	**0.6**
Globobulimina turgida	1	2	2	3	16	8	25	20	23	21	6	5	**132**	**5.9**	**5.3**
Grigelis sp.1		1											**1**	**0.0**	**0.8**
Gyroidina neosoldanii	1	2	2	2									**7**	**0.3**	**1.1**
Hanzawaia boueana		1	4										**5**	**0.2**	**1.2**
Hyalina balthica	16	10	8	2	1				1				**38**	**1.7**	**0.7**
Lenticulina peregrina		1	1										**2**	**0.1**	**1.0**
Melonis barleeanus	192	221	281	241	175	36	35	35	12	7	5	5	**1245**	**55.5**	**1.7**
Siphogenerina columellaris	4	1	2	5									**12**	**0.5**	**1.1**
Sphaeroidina bulloides		1											**1**	**0.0**	**0.8**
Uvigerina mediterranea	1	3	2										**6**	**0.3**	**0.8**
Uvigerina peregrina			1										**1**	**0.0**	**1.3**
Vaginulinopsis tasmanica					1								**1**	**0.0**	**2.5**
Valvulineria bradyana	2	15	36	68	81	15	23	5	4			1	**250**	**11.2**	**2.4**
Miliolids															
Biloculinella globula		1											**1**	**0.0**	**0.8**
Cornuspira foliacea				1									**1**	**0.0**	**1.8**
Pyrgo elongata	1	1											**2**	**0.1**	**0.5**
Quinqueloculina bosciana			1										**1**	**0.0**	**1.3**
Triloculina tricarinata				1									**1**	**0.0**	**1.8**
Fossilising agglutinates															
Eggerella bradyi	1	1	1		1	1							**5**	**0.2**	**1.7**
Textularia sagittula								1					**1**	**0.0**	**5.5**
Totals	**275**	**326**	**448**	**383**	**346**	**102**	**123**	**80**	**71**	**56**	**17**	**15**	**2242**		**2.2**

Setúbal Canyon axis, Core 33 (969 m). Counts of live (stained) benthic foraminifera >150 µm in 0-10 cm core (not normalised).

	0-0.5	0.5-1	1-1.5	1.5-2	2-3	3-4	4-5	5-6	6-7	7-8	Total	%	ALD_{10} (cm)
Perforates													
Bolivina alata	1										**1**	**0.2**	**0.3**
Bolivina robusta				1				1			**2**	**0.3**	**3.6**
Bolivina tongi				1							**1**	**0.2**	**1.8**
Bulimina inflata	3						1				**4**	**0.6**	**0.3**
Cassidulina carinata			1								**1**	**0.2**	**1.3**
Chilostomella oolina			2	4	4	17	3	2	1		**33**	**5.2**	**3.3**
Cibicidoides pachydermus	21	6	3								**30**	**4.7**	**0.5**
Dentalina aphelis	1	1		1							**3**	**0.5**	**0.9**
Fissurina bradyiformata	3						1				**4**	**0.6**	**1.3**
Fissurina castanea			1		1		3	3	2		**10**	**1.6**	**4.7**
Fissurina sp.1	1						1				**2**	**0.3**	**2.4**
Gavelinopsis praegeri	9	6			1						**16**	**2.5**	**0.6**
Globobulimina affinis	1	1	7	15	30	6	2				**62**	**9.8**	**2.3**
Globobulimina turgida	1	1		5	7	4		4			**22**	**3.5**	**2.3**
Gyroidina neosoldanii	1	3	1								**5**	**0.8**	**0.8**
Hanzawaia boueana	20	7						1			**28**	**4.4**	**0.6**
Hyalina balthica	12	5		1							**18**	**2.8**	**0.5**
Lenticulina peregrina		1									**1**	**0.2**	**0.8**
Melonis barleeanus	20	37	28	23	2	1			1		**112**	**17.7**	**1.0**
Nonionella turgida				1							**1**	**0.2**	**1.8**
Nuttallides convexus	1				1		1				**3**	**0.5**	**2.4**
Planulina ariminensis	7	1			1						**9**	**1.4**	**0.6**
Pseudoglandulina comatula	1										**1**	**0.2**	**0.3**
Pullenia quinqueloba		4									**4**	**0.6**	**0.8**
Robertinoides translucens	1										**1**	**0.2**	**0.3**
Rosalina sp 1	2							1			**3**	**0.5**	**2.0**
Siphogenerina columellaris							1				**1**	**0.2**	**4.5**
Siphonina reticulata		1									**1**	**0.2**	**0.8**
Trifarina bradyi	1	1		1		1					**4**	**0.6**	**1.6**
Trifarina fornasinii	1										**1**	**0.2**	**0.3**
Uvigerina elongatastriata		1	4	1							**6**	**0.9**	**1.3**
Uvigerina mediterranea	63	20	7		4	3	2				**99**	**15.6**	**0.4**
Uvigerina peregrina	31	14	5	1	1	1					**53**	**8.4**	**0.6**
Miliolids													
Biloculinella globula	3										**3**	**0.5**	**0.3**
Cornuspira involvens	1										**1**	**0.2**	**0.3**
Pyrgo elongata	1										**1**	**0.2**	**0.3**
Quinqueloculina auberiana	2										**2**	**0.3**	**0.3**
Quinqueloculina pygmaea	1										**1**	**0.2**	**0.3**
Sigmoilopsis schlumbergeri	1		1								**2**	**0.3**	**0.8**

Fossilising agglutinates													
Bigenerina nodosaria	23	15	3	1							**42**	**6.6**	**0.5**
Eggerella bradyi		1									**1**	**0.2**	**0.8**
Karreriella bradyi	1	1									**2**	**0.3**	**0.5**
Martinotiella communis	2										**2**	**0.3**	**0.3**
Siphotextularia concava	1										**1**	**0.2**	**0.3**
Siphotextularia heterostoma	4	10	1	1							**16**	**2.5**	**0.7**
Textularia sagittula	6	4	1	1	2		1				**15**	**2.4**	**1.1**
Textularia truncata	2										**2**	**0.3**	**0.3**
Vulvulina pennatula	1										**1**	**0.2**	**0.3**
Totals	**251**	**141**	**65**	**58**	**54**	**33**	**16**	**12**	**4**	**0**	**634**		**1.2**

Cascais Canyon axis, Core 28 (1059 m). Counts of live (stained) benthic foraminifera >150 µm in 0-10 cm core (not noramlised).

	0-0.5	**0.5-1**	**1-1.5**	**1.5-2**	**2-3**	**3-4**	**4-5**	**5-6**	**6-7**	**7-8**	**Total**	**%**	**ALD_{10} (cm)**
Perforates													
Anomalinoides minimus	1										**1**	**0.1**	**0.3**
Bolivina alata	5	12	3	3							**23**	**2.5**	**0.8**
Bolivina dilatata	2	1									**3**	**0.3**	**0.4**
Bolivina robusta	9	5	4					1	2		**21**	**2.3**	**0.6**
Bolivina spathulata		1									**1**	**0.1**	**0.8**
Bolivina striatula	1	1									**2**	**0.2**	**0.5**
Bolivina subaeriensis	6							2	1		**9**	**1.0**	**2.1**
Bulimina costata					4	2	1	1	1		**9**	**1.0**	**3.7**
Bulimina inflata	7	1		2		1	1	5	2		**19**	**2.1**	**0.3**
Cassidulina carinata	3										**3**	**0.3**	**0.3**
Cassidulinoides bradyi	1										**1**	**0.1**	**0.3**
Chilostomella oolina	18	8	8	10	15	20	22	1	1		**103**	**11.3**	**2.5**
Cibicidoides pachydermus	100	14	3		*7*	17	12	12	5		**170**	**18.6**	**0.3**
Dentalina sp.1	1										**1**	**0.1**	**0.3**
Gavelinopsis praegeri	1			1							**2**	**0.2**	**1.0**
Glanduina ovula	7	2	1		1					1	**12**	**1.3**	**1.2**
Globobulimina affinis					1		1				**2**	**0.2**	**3.5**
Globobulimina turgida	3	5	1	3	2	2	15	13	3		**47**	**5.2**	**3.9**
Gyroidina neosoldanii	8	1	1	2		1					**13**	**1.4**	**0.8**
Hanzawaia boueana	4		1			1		1			**7**	**0.8**	**1.6**
Hyalina balthica	6										**6**	**0.7**	**0.3**
Hoeglundina elegans	1										**1**	**0.1**	**0.3**
Lenticulina sp.1								1			**1**	**0.1**	**5.5**
Melonis barleeanus	136	31	15	18	5	10	15	2	2	1	**235**	**25.8**	**1.1**
Nuttallides convexus	2	1	1	1	1	1					**7**	**0.8**	**1.5**
Planulina ariminensis	1					1		1			**3**	**0.3**	**3.1**
Pullenia quinqueloba	2	1	1	1							**5**	**0.5**	**0.9**
Rosalina globularis							1				**1**	**0.1**	**4.5**

Siphogenerina columellaris								1			**1**	**0.1**	**5.5**
Trifarina angulosa	2	1				1	1	1		1	**7**	**0.8**	**3.2**
Trifarina bradyi	6	1	1	2		3		2	1		**16**	**1.8**	**2.2**
Trifarina fornasinii	1	1					1				**3**	**0.3**	**1.8**
Uvigerina auberiana	1								1		**2**	**0.2**	**3.4**
Uvigerina elongatastriata	3		1								**4**	**0.4**	**0.5**
Uvigerina mediterranea	26	5	5		1		2	4	10		**53**	**5.8**	**0.5**
Uvigerina peregrina	18	3	1	1			1	3	5		**32**	**3.5**	**0.4**
Miliolids													
Biloculinella globula	1										**1**	**0.1**	**0.3**
Miliolinella subrotunda	1										**1**	**0.1**	**0.3**
Pyrgo comata			1	1							**2**	**0.2**	**1.5**
Pyrgo elongata			1								**1**	**0.1**	**1.3**
Pyrgoella sp.1		1									**1**	**0.1**	**0.8**
Quinqueloculina sp.1	4	1									**5**	**0.5**	**0.4**
Fossilising agglutinates													
Bigenerina nodosaria	1				1						**2**	**0.2**	**1.4**
Eggerella bradyi	2										**2**	**0.2**	**0.3**
Martinotiella communis	19		1		1						**21**	**2.3**	**0.4**
Siphotextularia concava	3	2	1	1		1		1			**9**	**1.0**	**1.6**
Siphotextularia heterostoma	2	3	1		1						**7**	**0.8**	**0.9**
Textularia sagittula	3	4	1	3	7	10			2		**30**	**3.3**	**2.5**
Vulvulina pennatula	3					1					**4**	**0.4**	**1.1**
Totals	**421**	**106**	**53**	**49**	**47**	**72**	**73**	**52**	**36**	**3**	**912**		**1.7**

Mondego slope, Core 36 (962 m). Counts of live (stained) benthic foraminifera >150 µm in 0-10 cm core (not normalised)

-	**0-0.5**	**0.5-1**	**1-1.5**	**1.5-2**	**2-3**	**3-4**	**4-5**	**5-6**	**Total**	**%**	**ALD_{10} (cm)**
-											
Perforates											
Bolivina seminuda			1		1				**2**	**1.4**	**1.9**
Bulimina inflata		1							**1**	**0.7**	**0.8**
Chilostomella oolina		1							**1**	**0.7**	**0.8**
Cibicides lobatulus		1							**1**	**0.7**	**0.8**
Cibicidoides pachydermus	2								**2**	**1.4**	**0.3**
Dentalina subemaciata					1				**1**	**0.7**	**2.5**
Fissurina sp.1	1								**1**	**0.7**	**0.3**
Gavelinopsis praegeri	3	1	1						**5**	**3.6**	**0.6**
Globocassidulina subglobosa	2	1	1	1					**5**	**3.6**	**0.9**
Gyroidina neosoldanii	1	1	1						**3**	**2.2**	**0.8**
Gyroidina soldanii	1								**1**	**0.7**	**0.3**

Hanzawaia boueana	4									**4**	**2.9**	**0.3**
Hoeglundina elegans	6									**6**	**4.3**	**0.3**
Hyalina balthica	3									**3**	**2.2**	**0.3**
Lenticulina calcar	1									**1**	**0.7**	**0.3**
Lenticulina gibba			1							**1**	**0.7**	**1.3**
Lenticulina orbicularis	2									**2**	**1.4**	**0.3**
Lingulina seminuda				1						**1**	**0.7**	**1.8**
Melonis barleeanus		4	4	3	1					**12**	**8.6**	**1.3**
Nuttallides convexus			1							**1**	**0.7**	**1.3**
Planulina ariminensis	3		2							**5**	**3.6**	**0.7**
Robertinoides translucens				1						**1**	**0.7**	**1.8**
Siphonina reticulata	1									**1**	**0.7**	**0.3**
Trifarina bradyi		1								**1**	**0.7**	**0.8**
Uvigerina auberiana		2								**2**	**1.4**	**0.8**
Uvigerina mediterranea	38	10						1		**49**	**35.3**	**0.4**
Miliolids												
Cribomiliolinella subvalvularis	1									**1**	**0.7**	**0.3**
Pyrgo depressa	3									**3**	**2.2**	**0.3**
Pyrgo inornata		1								**1**	**0.7**	**0.8**
Pyrgo luceruno	1									**1**	**0.7**	**0.3**
Pyrgo sp.1		1								**1**	**0.7**	**0.8**
Spiroloculina tenuisepta		1								**1**	**0.7**	**0.8**
Triloculina trigoluna		1								**1**	**0.7**	**0.8**
Fossilising agglutinates												
Bigenerina nodosaria	3	5	1							**9**	**6.5**	**0.6**
Clavulina humilis	1									**1**	**0.7**	**0.3**
Cylindroclavulina bradyi	1	1								**2**	**1.4**	**0.5**
Eggerella bradyi	1									**1**	**0.7**	**0.3**
Karrerulina bradyi		1								**1**	**0.7**	**0.8**
Siphotextularia heterostoma	1									**1**	**0.7**	**0.3**
Textularia sagittula			1							**1**	**0.7**	**1.3**
Vulvulina pennatula		1								**1**	**0.7**	**0.8**
Totals	**80**	**35**	**14**	**6**	**3**	**0**	**0**	**1**	**0**	**139**		**0.6**

Estremadura slope, Core 34 (1039 m). Counts of live (stained) benthic foraminifera >150 µm in 0-10 cm core (not normalised)

-	0-0.5	0.5-1	1-1.5	1.5-2	2-3	3-4	4-5	5-6	6-7	7-8	Total	%	ALD_{10} (cm)
Perforates													
Amphicorina scalaris	1	1									**2**	**1.0**	**0.5**
Bulimina costata	1										**1**	**0.5**	**0.3**
Bulimina inflata	2			1					1		**4**	**2.0**	**2.2**
Chilostomella oolina						1				1	**2**	**1.0**	**5.5**
Cibicides sp.1	1										**1**	**0.5**	**0.3**
Cibicidoides pachydermus	6	5			1						**12**	**6.1**	**0.6**
Dentalina aphelis	1										**1**	**0.5**	**0.3**
Dentalina bradyensis			1								**1**	**0.5**	**1.3**
Fissurina semimarginata	1										**1**	**0.5**	**0.3**
Gavelinopsis praegeri			1								**1**	**0.5**	**1.3**
Globobulimina affinis					3	4	5	4	5		**21**	**10.7**	**4.7**
Globocassidulina subglobosa	1										**1**	**0.5**	**0.3**
Gyroidina neosoldanii	2										**2**	**1.0**	**0.3**
Hanzawaia boueana	9				1						**10**	**5.1**	**0.5**
Hoeglundina elegans	2										**2**	**1.0**	**0.3**
Melonis barleeanus			4	4	1	1					**10**	**5.1**	**1.8**
Nuttallides convexus	1	1									**2**	**1.0**	**0.5**
Pullenia bulloides	1										**1**	**0.5**	**0.3**
Pullenia salisbury				1							**1**	**0.5**	**1.8**
Trifarina bradyi	2	3									**5**	**2.5**	**0.6**
Uvigerina auberiana	2										**2**	**1.0**	**0.3**
Uvigerina mediterranea	75	11	1		1						**88**	**44.7**	**0.3**
Uvigerina peregrina	4	1	1								**6**	**3.0**	**0.5**
Miliolids													
Cornuspira involvens	1										**1**	**0.5**	**0.3**
Cribromiliolinella sp.1	1										**1**	**0.5**	**0.3**
Pyrgo depressa	1										**1**	**0.5**	**0.3**
Pyrgoella sphaera		1									**1**	**0.5**	**0.8**
Spiropthalmidium concavum	1										**1**	**0.5**	**0.3**
Quinqueloculina seminula	1										**1**	**0.5**	**0.3**
Triloculina tricarinata	3	1									**4**	**2.0**	**0.4**
Fossilising agglutinates													
Bigenerina nodosaria		2									**2**	**1.0**	**0.8**
Clavulina humilis		4									**4**	**2.0**	**0.8**
Cylindroclavulina bradyi		2									**2**	**1.0**	**0.8**
Siphotextularia heterostoma	1										**1**	**0.5**	**0.3**
Vulvulina pennatula		1									**1**	**0.5**	**0.8**
Totals	**121**	**33**	**8**	**6**	**7**	**6**	**5**	**4**	**6**	**1**	**197**		**1.0**

Alentejo slope, Core 32 (974 m). Counts of live (stained) benthic foraminifera >150 µm in 0-10 cm core (not normalised)

	0-0.5	0.5-1	1-1.5	1.5-2	2-3	3-4	4-5	5-6	6-7	7-8	Total	%	ALD_{10} (cm)
Perforates													
Amphicorina scalaris	1										1	0.5	0.3
Bulimina inflata	49	1	1	1	2	1					55	28.2	0.4
Cibicides lobatulus	1										1	0.5	0.3
Cibicidoides pachydermus	2										2	1.0	0.3
Dentalina aphelis			1								1	0.5	1.3
Dentalina subemaciata	1										1	0.5	0.3
Fursenkoina bradyi				1	1						2	1.0	2.1
Globobulimina affinis				1	5	3	9		1		19	9.7	3.8
Globocassidulina subglobosa	1										1	0.5	0.3
Gyroidina neosoldanii	4	1									5	2.6	0.4
Hanzawaia boueana	3	2			1						6	3.1	0.8
Laminononion tumidum	1										1	0.5	0.3
Lenticulina convergens	1										1	0.5	0.3
Lenticulina orbicularis	2										2	1.0	0.3
Melonis barleeanus	2	2	3	3	4	1					15	7.7	1.6
Nuttallides convexus	1										1	0.5	0.3
Pullenia quinqueloba		1	2	1							4	2.1	1.3
Siphonina reticulata	2	1									3	1.5	0.4
Trifarina bradyi	1										1	0.5	0.3
Trifarina fornasinii		1	1								2	1.0	1.0
Uvigerina auberiana	1										1	0.5	0.3
Uvigerina mediterranea	30	1				3	2				36	18.5	0.3
Uvigerina peregrina	6	2				1	1				10	5.1	1.1
Miliolids													
Sigmoilopsis schlumbergeri	4										4	2.1	0.3
Pyrgo sp.1	1										1	0.5	0.3
Fossilising agglutinates													
Bigenerina nodosaria	8				2						10	5.1	0.7
Clavulina humilis	1										1	0.5	0.3
Siphotextularia heterostoma	8										8	4.1	0.3
Totals	**131**	**12**	**8**	**7**	**15**	**9**	**12**	**0**	**1**	**0**	**195**		**1.0**

Alentejo slope, Core 31 (282 m). Counts of live (stained) benthic foraminifera >150 µm in 0-10 cm core (not normalised)

-	0-0.5	0.5-1	1-1.5	1.5-2	2-3	3-4	4-5	5-6	6-7	7-8	Total	%	ALD_{10} (cm)
Perforates													
Bolivina spathulata							1				**1**	**0.3**	**4.5**
Bulimina inflata	34	16		1	2	1	2				**56**	**16.8**	**0.7**
Cibicides sp.1	1										**1**	**0.3**	**0.3**
Cibicidoides pachydermus	5	2									**7**	**2.1**	**0.4**
Fissurina annectans		2									**2**	**0.6**	**0.8**
Fursenkoina sp.1							1				**1**	**0.3**	**4.5**
Gavelinopsis praegeri	1	1									**2**	**0.6**	**0.5**
Grigelis sp.1		1									**1**	**0.3**	**0.8**
Globobulimina affinis						7	5				**12**	**3.6**	**3.9**
Gyroidina neosoldanii	2	4	4	1	1						**12**	**3.6**	**1.1**
Hanzawaia boueana	10	2									**12**	**3.6**	**0.3**
Hoeglundina elegans	1										**1**	**0.3**	**0.3**
Hyalina balthica	1										**1**	**0.3**	**0.3**
Lenticulina orbicularis		1	1								**2**	**0.6**	**1.0**
Melonis barleeanus	3	4	7	4	3						**21**	**6.3**	**1.3**
Nuttallides convexus	10		1								**11**	**3.3**	**0.3**
Planulina ariminensis	2										**2**	**0.6**	**0.3**
Robertinoides translucens				2							**2**	**0.6**	**1.8**
Siphogenerina columellaris	1										**1**	**0.3**	**0.3**
Siphonina reticulata			2								**2**	**0.6**	**1.3**
Trifarina angulosa					1						**1**	**0.3**	**2.5**
Trifarina bradyi		3									**3**	**0.9**	**0.8**
Trifarina fornasinii		1									**1**	**0.3**	**0.8**
Uvigerina auberiana	2	1									**3**	**0.9**	**0.4**
Uvigerina mediterranea	66	37	7	3	2	2	2				**119**	**35.7**	**0.7**
Uvigerina peregrina	11	7	2	1							**21**	**6.3**	**0.6**
Miliolids													
Cornuspira involvens	1										**1**	**0.3**	**0.3**
Pyrgo depressa	2										**2**	**0.6**	**0.3**
Pyrgoella sphaera	1										**1**	**0.3**	**0.3**
Pyrgoella sp.1	1										**1**	**0.3**	**0.3**
Quinqueloculina bosciana	1										**1**	**0.3**	**0.3**
Quinqueloculina sp.1		1									**1**	**0.3**	**0.8**
Sigmoilina distorta		1									**1**	**0.3**	**0.8**
Sigmoilopsis schlumbergeri	1	2									**3**	**0.9**	**0.6**
Fossilising agglutinates													
Bigenerina nodosaria	7	7		2							**16**	**4.8**	**0.7**
Eggerella bradyi	1										**1**	**0.3**	**0.3**
Siphotextularia heterostoma	2	1									**3**	**0.9**	**0.4**
Textularia conica		1									**1**	**0.3**	**0.8**

Textularia saggitula	1										**1**	**0.3**	**0.3**
Vulvulina pennatula	1					1					**2**	**0.6**	**1.9**
Totals	**169**	**95**	**24**	**14**	**9**	**11**	**11**	**0**	**0**	**0**	**333**		**0.8**

Estremadura slope, Core 27 (1039 m). Counts of live (stained) benthic foraminifera >150 µm in 0-10 cm core (not normalised)

-	**0-0.5**	**0.5-1**	**1-1.5**	**1.5-2**	**2-3**	**3-4**	**4-5**	**5-6**	**6-7**	**Total**	**%**	**ALD_{10} (cm)**
Perforates												
Bolivina albatrossi					1					**1**	**1.0**	**2.5**
Bulimina inflata	9	1								**10**	**9.8**	**0.3**
Cassidulina obtusa								1		**1**	**1.0**	**5.5**
Chilostomella oolina					1	1				**2**	**2.0**	**3.0**
Cibicidoides pachydermus	7	3								**10**	**9.8**	**0.4**
Globobulimina affinis						2	2	1		**5**	**4.9**	**4.3**
Gyroidina neosaldanii		1								**1**	**1.0**	**0.8**
Hanzawaia boueana	4									**4**	**3.9**	**0.3**
Hyalina balthica	1									**1**	**1.0**	**0.3**
Laminononion tumidum	2		2							**4**	**3.9**	**0.8**
Melonis barleeanus	1	1			2	1				**5**	**4.9**	**1.9**
Nuttallides convexus	3	1	1							**5**	**4.9**	**0.6**
Planulina ariminensis	1									**1**	**1.0**	**0.3**
Pullenia bulloides			1							**1**	**1.0**	**1.3**
Pullenia quinqueloba		1	1			1				**3**	**2.9**	**1.8**
Trifarina bradyi	1									**1**	**1.0**	**0.3**
Trifarina fornasinii	1	1								**2**	**2.0**	**0.5**
Uvigerina auberiana	4	2								**6**	**5.9**	**0.4**
Uvigerina mediterranea	13	11	3							**27**	**26.5**	**0.6**
Uvigerina peregrina		3								**3**	**2.9**	**0.8**
Miliolids												
Pyrgo lucerluna	1									**1**	**1.0**	**0.3**
Quinqueloculina seminula		1								**1**	**1.0**	**0.8**
Fossilising agglutinates												
Bigenerina nodosaria	2									**2**	**2.0**	**0.3**
Clavulina humilis	1									**1**	**1.0**	**0.3**
Martinotiella communis	1									**1**	**1.0**	**0.3**
Siphotextularia concava		1								**1**	**1.0**	**0.8**
Textularia sagittula	1									**1**	**1.0**	**0.3**
Vulvulina pennatula				1						**1**	**1.0**	**1.8**
Totals	**53**	**27**	**8**	**1**	**4**	**5**	**2**	**2**	**0**	**102**		**0.9**

ANNEXE 3

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LIVE BENTHIC FORAMINIFERAL FAUNAS ALONG A BATHYMETRICAL TRANSECT (282–4987 M) ON THE PORTUGUESE MARGIN (NE ATLANTIC)

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ABSTRACT

Live benthic foraminifera were studied in eight cores collected along a depth transect ranging 282–4987 m on the Portuguese margin. Total standing stocks (TSS) and species assemblages from both 63–150- and >150-μm fractions are compared between stations along the transect and with previous live foraminiferal studies from the Bay of Biscay and western Iberian margin. Based on the sedimentary organic matter contents and ecological traits of the retrieved foraminifera, three groups of stations are distinguished: (1) eutrophic upper-slope stations (282–1002 m) with faunas dominated by *Uvigerina mediterranea, U. elongatastriata, Melonis barleeanus, Bigenerina nodosaria, Trifarina bradyi, Epistominella vitrea, Cribrostomoides bradyi*, and *Bolivina robusta,* (2) mesotrophic middle- to lower-slope stations (1374–2475 m) with faunas dominated by *Uvigerina peregrina, Globobulimina affinis*, and *Repmanina charoides*, and (3) oligotrophic lower-slope and abyssal-plain stations (2908–4987 m) with faunas in the larger size fraction dominated by *Cibicides kullenbergi* and agglutinated species such as *Reophax fusiformis* and *Recurvoides* sp. 1. The smaller size fraction is dominated by opportunistic calcareous species such as *Bulimina translucens, Epistominella exigua*, and *Nuttallides pusillus,* along with *Reophax fusiformis*, but most of these species are diminished at 4987 m, where *Reophax fusiformis*, *Pullenia salisburyi*, and various monothalamous agglutinates are dominant. This succession of assemblages probably reflects the increasing scarcity of trophic resources with water depth. This hypothesis is corroborated by 1) the clear decrease of TSS with increasing water depth, and 2) the decreasing sediment phytopigment concentrations towards deeper sites. Moreover, the decreasing percentage of perforate calcareous foraminifera, and increasing percentage of agglutinated foraminifera with water depth, suggests that, in general, perforate calcareous species have higher trophic requirements than agglutinated ones.

INTRODUCTION

Benthic foraminifera are an important component of meiofaunal communities in many benthic environments, from intertidal to hadal depths. In the deep sea they may account for >50% of the total benthic biomass (Gooday and others, 1992). Because they often occur in high densities, small sediment volumes typically yield large numbers of specimens, making them particularly useful for ecological as well as paleoecological studies. There is a general consensus that the composition of benthic foraminiferal assemblages is strongly linked to the quantity and nutritive quality of the organic detritus reaching the ocean floor, and to the oxygenation of the interstitial waters (e.g., Jorissen and others, 1998, 2007; Gooday, 2003).

Depending on the traditions and procedures of different laboratories, the study of foraminiferal faunas is mostly based on the >63, >125, and >150 μm size fractions. In many foraminiferal ecology studies, only the larger size fractions (e.g., >125, >150, or even >250 μm) are considered, as it is sometimes difficult to maintain consistent taxonomic concepts in smaller fractions where most juveniles are concentrated and where the risk of analyzing transported specimens is much higher. Additionally, many authors do not consider working the smaller size fractions (in most cases 63–125 or 63–150 μm) because they can be very tedious and time-consuming. Studies where multiple fractions are analyzed have an additional benefit of allowing direct comparisons with other studies, and can aid the picking process (e.g., the removal of large tubular taxa from smaller fractions). When dealing only with foraminiferal faunas from the large size fraction, many small species are overlooked (Duchemin and others, 2007). Some small-sized foraminifera have an opportunistic behavior characterized by rapid reproduction or growth in response to intermittent food supply at the sediment-water interface (e.g., Gooday, 1988, 1993; Cornelius and Gooday 2004). These small-sized foraminifera are therefore considered to be potential indicators of seasonal episodes of organic carbon flux in modern and ancient marine environments (Gooday, 1993, 2003; Smart and others, 1994; Duchemin and others, 2007). In fact, the foraminiferal response to phytodetritus deposits appears to be much stronger in the 63–150 μm fraction than in the corresponding >150μm fraction (e.g., Fontanier and others, 2003, 2006; Duchemin and others, 2007; Shepherd and others, 2007).

On the Portuguese margin (northeast Atlantic), the exported organic matter flux is a major factor controlling benthic foraminiferal dynamics in shelf and open-slope environments (Schönfeld 2001, Koho and others, 2008). However, no study on the smaller-sized (63–150 μm) fraction has been carried out in this rather well known area. Therefore we consider the live benthic foraminiferal faunas of the large (>150 μm) as well as small size (63–150 μm) fractions of eight stations along an upper-slope to abyssal plain depth transect (282–4987 m) from the Portuguese margin.

Our main objectives are 1) to analyze benthic foraminiferal assemblage and density variation with increasing water depth and varying sedimentary organic matter contents and biochemical composition, and 2) to compare the foraminiferal response to changing trophic conditions between the 63–150 and >150 μm fractions.

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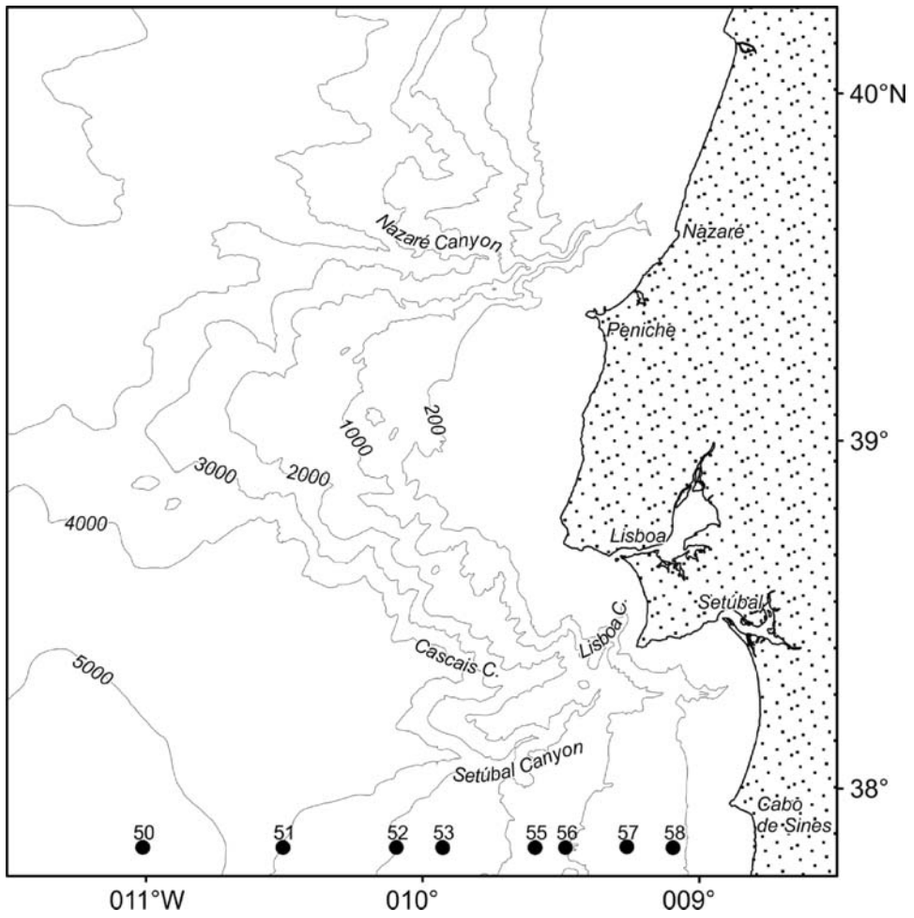

FIGURE 1. Map of the Cape Sines continental slope transect. All stations, sampled in September 2006, are marked in black circles.

MATERIAL AND METHODS

Study Area

We studied an east–west transect of stations located at depths ranging 282–4987 m on the open slope off Cape Sines, on the Portuguese Margin at 37°50′ N, 9°05′–11°W (Fig. 1). The shelf between the Setúbal Canyon and Cape Sines has a maximum width of 25 km. At 282 m depth, surface sediments consist of fine sands with a unimodal particle size distribution, with a peak at 169 μm. Towards deeper sites, these fine sands progressively become finer, until the modal grain size falls to ~5 μm at 1000 m depth. Still deeper, the modal grain-size distribution remains constant down to the Tagus Abyssal Plain at ~5000 m depth. Full details of materials and methods for grain size analysis are presented in de Stigter and others (2011) and the results of modal grain size distribution are summarized in Table 1. Steep slopes are only found at the intersection with the Setúbal Canyon, which incises the shelf in an E–W orientation. The slope is influenced by seasonally changing hydrodynamics as a result of the wind-driven upwelling system occurring along the western coasts of the Iberian Peninsula and Africa down to 15°N (Wooster and others, 1976). Conditions favorable for upwelling off Cape Sines occur between May and September as a result of strong and steady northerly winds and southward surface currents (Fiúza, 1984; Sousa and Bricaud, 1992; Huthnance and others, 2002).

The water column in this area comprises several water masses (García and others, 2003). Below the seasonally varying thermocline (30–600 m depth), the Eastern North Atlantic Central Water mass (ENACW) can be distinguished by its warm (12–16°C) and salty (≤36) properties (Fig. 2). Mediterranean Outflow Water (MOW) occurs between 600–1600 m and displays a strong salinity peak at 1100 m (>36). Two midwater maxima in temperature and salinity indicate the presence of two components of Mediterranean Water. The Northeast Atlantic Deep Water (NEADW), characterized by a lower temperature (2–10°C) and salinity (~35), forms the main water mass below the MOW. Finally, below ~4000 m is the Lower Deep Water (LDW) of Antarctic origin (Van Aken, 2000), recognizable by its cold (~2°C) and low-saline (<35) properties (Fig. 2).

Sample Preparation and Processing of Foraminifera

During Cruise 64PE252 of RV Pelagia, cores with a diameter of 6 cm and consisting of undisturbed sediment surfaces were collected using a MUC multicorer in September 2006. At each sampling site (Table 1, Fig. 1), a

TABLE 1. Water depth, geographical position, temperature (°C), salinity, water mass, and modal sediment size of the eight stations analyzed in this paper.

Station No.	Latitude (N)	Longitude (W)	Depth (m)	Temperature (°C)	Salinity (psu)	Water mass	Mode
58	37°50.00′	09°04.99′	282	12.8	35.8	ENACW	###
57	37°49.80′	09°14.95′	490	11.7	35.8	ENACW	66.4
56	37°49.99′	09°28.48′	1002	11.7	36.4	MOW	4.9
55	37°50.00′	09°35.00′	1374	10.7	36.3	MOW	4.9
53	37°49.98′	09°54.97′	2475	3.2	35.0	NEADW	4.9
52	37°50.00′	10°05.00′	2908	2.6	35.0	NEADW	5.4
51	37°50.01′	10°30.00′	3908	2.1	34.9	NEADW	4.9
50	37°50.01′	10°59.99′	4987	2.1	34.9	LDW	5.4

single corer was sliced at 0.5 cm intervals from 0–2 cm depth, and 1 cm intervals from 2–10 cm depth. All slices were subsequently stored in a solution of rose Bengal in 96% ethanol until further treatment in the laboratory. These samples were gently shaken for several minutes to disaggregate the sediment and ensure staining of all live foraminifera. In the laboratory, each sediment layer was carefully washed with tap water through sieves with 63 and 150 μm meshes, and residues were subsequently stored in 96% ethanol.

Stained foraminifera from both the 63–150 and >150 μm fractions were sorted from wet samples and placed onto Chapman slides. The decision whether or not a stained specimen was alive at the time of collection remains slightly subjective, particularly as the protoplasm of dead foraminifera may be relatively well-preserved under anoxic conditions deeper in the sediment (Corliss and Emerson, 1990). As a result, a strict staining criterion was applied, where only specimens that were stained brightly pink in all chambers except the last one were counted as alive; the staining of doubtful foraminifera from deeper in the sediment was compared with stained individuals of the same species from more superficial levels. When the interior of a specimen was not visible, opaque agglutinated and miliolid tests were broken in order to confirm if there was stained material inside. Another difficulty concerns the counting of fragmentary tests, particularly in the case of arborescent forms, such as the large tubular species of the genus *Rhizammina*. We decided to inventory only stained protochambers, which were considered to represent a single individual; all other fragments were counted separately and not included in the faunal description. Soft-walled monothalamous taxa were also excluded from this study. The total densities of the live foraminiferal fauna, expressed as the number of live foraminifera found in and below a 28 cm^2 surface area (and standardized to 50 cm^2), were determined by integrating the numbers of live individuals picked from all levels sampled in the upper 10 cm of the core. Descriptions of foraminiferal microhabitats are not included in this study due to the large size of the dataset. We calculated species richness (S), which is a count of living foraminiferal species for each station, and Fisher's α index (Fisher and others, 1943), a diversity index defined implicitly by the formula:

$$S = \alpha \times \ln(1 + n/a)$$

where, S is number of taxa, n is number of individuals and α is the index value.

Picking and identifying foraminiferal species in finer size fractions (<150 μm) is extremely time-consuming; hence; no replicate samples were studied at any of the eight stations.

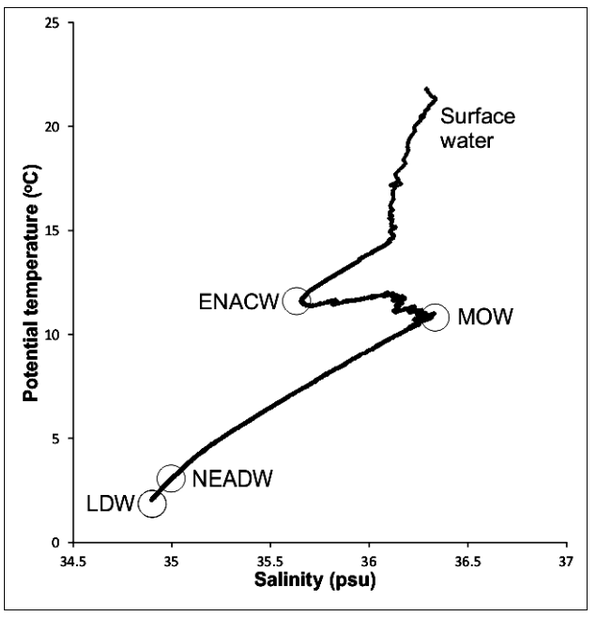

FIGURE 2. Potential temperature-salinity diagram constructed from CTD measurements along the Cape Sines transect. Temperature and salinity measurements for the Mediterranean Water (MW) at Gibraltar, and North East Atlantic Deep Water (NEADW) and Lower Deep Water (LDW) at the western Iberian margin according to Van Aken (2000).

PHYTOPIGMENT CONTENTS

Chlorophyll-a and phaeopigment analyses were carried out according to Lorenzen and Jeffrey (1980). Pigments were extracted (12 h at 4°C in the dark) from triplicate sediment core samples (about 1 g) at 0–1, 1–3, 3–5, and 5–10 cm intervals, obtained from independent deployments of the multicorer, using 3–5 ml of 90% acetone as the extractant. Extracts were analyzed fluorometrically to estimate chlorophyll-a, and, after acidification with 200 μl 0.1N HCl, to estimate phaeopigments. We avoided the use of fluorometric chlorophyll-a estimates as the unique tracer of organic C associated with algal material and instead summed the values of chlorophyll-a and phaeopigment concentrations (i.e., total phytopigments). Concentrations

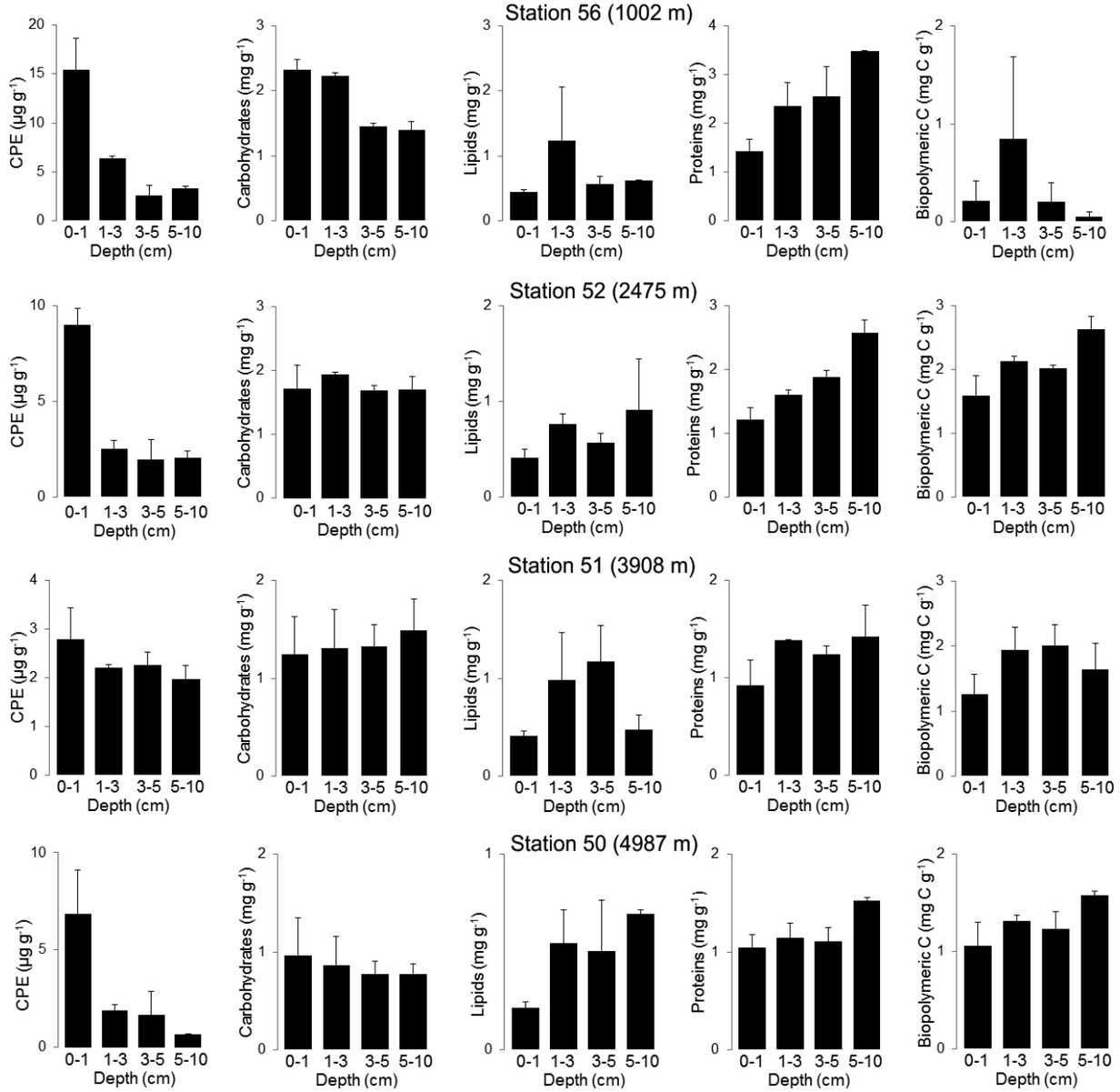

FIGURE 3. Components of organic carbon measured at 0–1, 1–3, 3–5, and 5–10 cm intervals downcore for four stations in this study.

of total phytopigments, once converted into C equivalents using 40 as a conversion factor (Pusceddu and others, 1999), are reported in µg g^{-1} DW.

Quantity and Biochemical Composition of Sediment Organic Matter

Protein, carbohydrate, and lipid sediment contents were analyzed spectrophotometrically in accordance with Pusceddu and others (2004) and their concentrations were expressed as bovine serum albumin, glucose, and tripalmitine equivalents, respectively. For each biochemical assay, blanks were obtained using pre-combusted sediments (450°C for 4 h). For all stations, the analyses were performed on triplicate sediment core samples (~0.5 g) at 0–1, 1–3, 3–5, and 5–10 cm intervals, obtained from independent deployments of a multiple or box corer. Carbohydrate, protein and lipid sediment contents were converted into carbon equivalents using the conversion factors of 0.40, 0.49, and 0.75 mg C mg^{-1}, respectively, and their sum defined as the biopolymeric organic carbon (Fabiano and others, 1995).

RESULTS

Organic Matter Components

All components have maximum values at the shallowest station for which we have data (1002 m) and generally decrease with increasing depth (Fig. 3). However, total

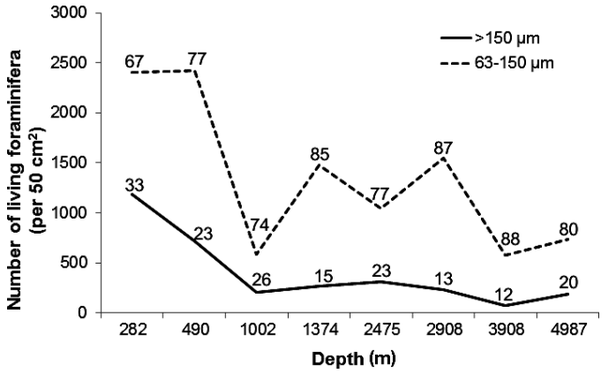

FIGURE 4. Density of foraminiferal faunas (total number of stained foraminifera per 50 cm^2) for >150 µm and 63–150 µm fractions along the bathymetrical transect. Percentage relative abundances of the total fauna (>63 µm) are provided for each data point.

phytopigment and protein contents have slightly raised values at the deepest station (6.9±2.2 µg g^{-1} and 1.0±0.1 mg g^{-1} at 4987 m respectively) in comparison to our 3908 m station (2.8±0.6 µg g^{-1} and 0.9±0.3 mg g^{-1} respectively). Conversely, carbohydrates, lipids, and biopolymeric carbon all have minimal values at our deepest station (1.0±0.4, 0.2±0.03, and 1.1±0.2 mg g^{-1} respectively. Total phytopigment contents show clear decreases towards deeper intervals in each of the four cores. However, all other measures of organic matter show rather stable values downcore, or even slight increases (Fig. 3).

Total Foraminiferal Densities

There was a general decrease in foraminiferal densities with increasing water depth for both the >150 µm and 63–150 µm fractions (Fig. 4). For the >150 µm fraction, our shallowest station at 282 m presented a maximum density ~1200 specimens/50 cm^2. Towards ~1000 m water depth, density drops to ~200 spec/50 cm^2. Standing stocks then increased slightly to ~300 specimens/50 cm^2 at 2475 m, then decreased until a minimum value of <80 individuals/50 cm^2 at 3908 m. For all stations, densities of the 63–150 µm fraction were more than two times higher than those of the >150 µm fraction. The depth pattern mimics that of the >150 µm fraction: the highest densities were recorded at 282 and 490 m with ~2400 live individuals per 50 cm^2, whereas our deepest stations at 4987 and 3908 m were much poorer with ~740 and ~580 live specimens per 50 cm^2, respectively. The relative importance of the 63–150 µm fraction (with respect to the >150 µm fraction) increased with water depth, from 67% at 282 m to as much as 88% at 3908 m. (Fig. 4).

Species Diversity

Species richness varies considerably between the stations, for both size fractions (Fig 5). In the >150 µm fraction the highest species numbers were found at the shallowest stations (79 at 282 m and 74 at 490 m). The deepest stations at 3908 and 4987 m have the lowest numbers of species (27 and 28 respectively). At 1002 m, species richness is also comparatively low (31 species). Generally, the species number shows

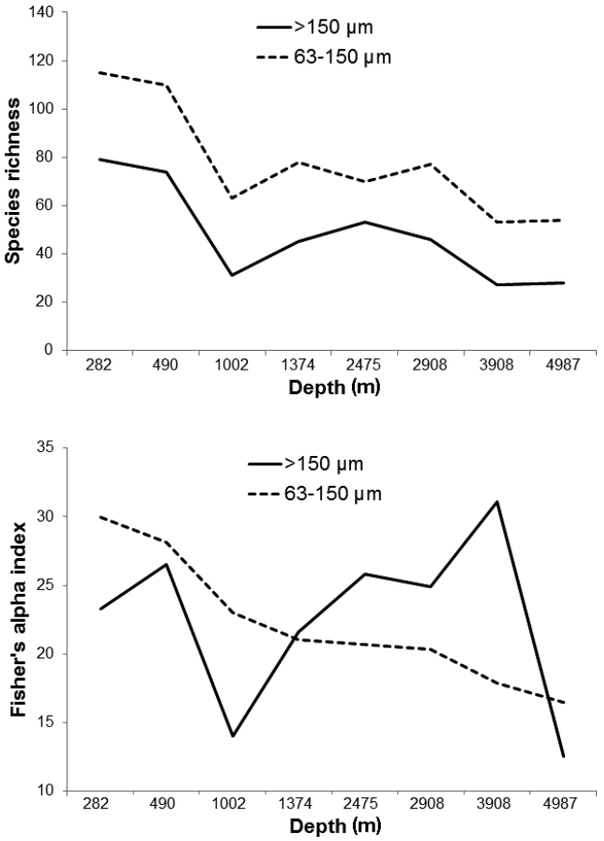

FIGURE 5. Species richness and Fisher's α index values of foraminiferal assemblages for >150 µm and 63–150 µm fractions along the bathymetrical transect.

the same trends as the foraminiferal density; apart from the minimum at 1002 m, there is a decrease in species richness with increasing depth. Surprisingly, Fisher's α values for the >150 µm fraction show a different pattern (Fig. 5): after a sudden fall from 27 at 490 m to 14 at 1002 m, there is a subsequent rise on the middle to lower slope with a maximum value of 31 at 3908 m. This is followed by a steep drop to a minimum value of 13 at 4987 m (Fig. 5).

In the 63–150 µm fraction. changes in species richness with depth basically mirror those of the >150 µm fraction by clearly decreasing with greater water depth. However, at all stations species richness is much higher in the 63–150 µm fraction than in the >150 µm fraction. Highest species richness is found at 282 m (115 species), whereas our deepest stations at 3908 and 4987 m have the lowest species richness with 53 and 54 species respectively. Unlike the >150 µm fraction, Fisher's α values for the 63–150 µm fraction show an overall decrease with water depth.

Bathymetrical Trends of Main Foraminiferal Groups

The foraminiferal assemblages comprise a mixture of perforate, porcellaneous and agglutinated forms, with the relative proportions changing with water depth (Fig. 6). In the >150 µm fraction, perforate and agglutinated foraminif-

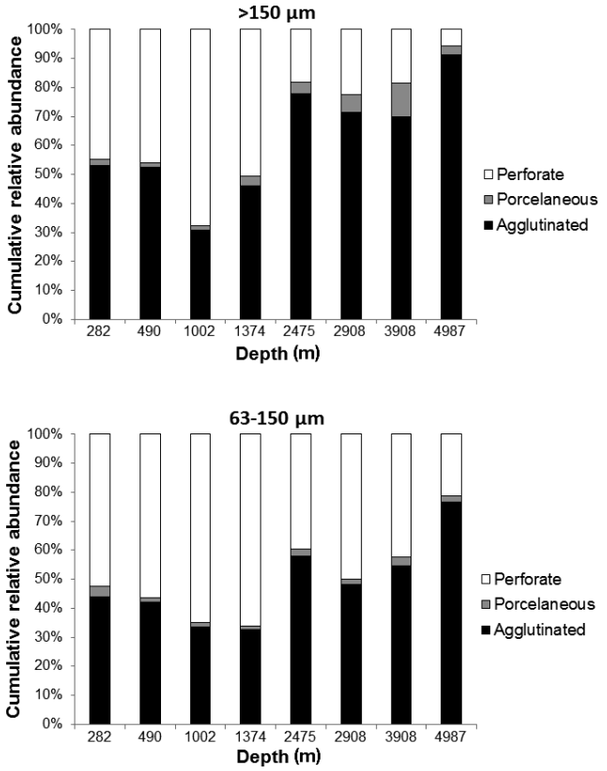

FIGURE 6. Relative percentage abundances of perforate, porcellaneous and agglutinated foraminiferal groups for both >150 µm and 63–150 µm fractions along the bathymetrical transect.

era form the main component of the assemblage, with a more-or-less equal contribution at 282 and 490 m. Slightly deeper, at 1002 m, perforate foraminifera dominate the assemblage (68%). At much deeper stations, there is a strong increase in the relative abundance of agglutinated foraminifera (91% at 4987 m), and a corresponding decrease in perforate foraminifera (6% at 4987 m). Porcelaneous foraminifera are rare at all stations (≤6%) with the exception at 3908 m, where they account for 12% of the assemblage. The 63–150 µm fraction shows a rather similar pattern. From 282–1374 m water depth, there is an increase in perforate species (~53% to ~66%) at the expense of the agglutinated taxa (~44% to 33%). Below 1374 m, perforate foraminifera decrease to ~21% of the total fauna at 4987 m, where agglutinates make up ~77% of the total assemblage. Similarly to the >150 µm fraction, porcelaneous foraminifera are rare, always accounting for <4%. Although the two size fractions show similar trends, it should be noted that at deeper stations, perforate foraminifera have a much higher relative abundance in the 63–150 µm than in the >150 µm fraction.

FAUNAL COMPOSITION

In both size fractions, the presence/absence as well as relative abundances of the dominant species show some remarkable patterns along the transect. Appendix 1 is the taxonomic list of species; Figures 7 and 8 show some common agglutinated and calcareous species, respectively.

>150 µm Fraction

Figure 9 presents the percentages of all species that are >5% of the >150 µm fraction from at least one station; it also suggests the presence of two main faunal boundaries, between stations 56 and 55 (between 1002–1374 m) and stations 53 and 52 (2475–2908 m depth). At 1002 m and shallower, *Uvigerina mediterranea* is a dominant species. Between 1374 and 2475 m, faunas are dominated by *Globobulimina affinis, Thurammina papillata*, and *Uvigerina peregrina*. At 2908 m and deeper, *Recurvoides* sp. 1, *Reophax fusiformis, Cibicides kullenbergi*, and *Epistominella exigua* are prominent.

At our shallowest station (282 m), the >150-µm faunas are dominated by *Reophax helenae* (~12%), which is accompanied by *Melonis barleeanus, Bigenerina nodosaria*, and *Uvigerina elongatastriata*, each accounting for ~8%, while *U. mediterranea, Textularia sagittula*, and *Buzasina ringens* each represent ~6% of the fauna. At 490 m, *U. mediterranea* increases to 27%, whereas *U. elongatastriata, M. barleeanus*, and the agglutinated species have much lower percentages (*B. nodosaria, T. sagittula*) or are even absent (*R. helenae, B. ringens*); other agglutinated species, such as *Reophax spiculifer, Psammosphaera fusca*, and *Ammodiscus anguillae*, show increased frequencies (5–7% each). At 1002 m, *U. mediterranea* (25%) remains strongly dominant and *Nuttallides convexus* (8%) appears. In the agglutinated assemblage, the previously dominant species (*R. spiculifer, P. fusca*, and *A. anguillae*) are much less abundant, and *Cyclammina trullissata* dominates (18%).

Between 1002 and 1374 m, there is a major faunal change. At 1374 m, *U. mediterranea* is virtually absent and *Globobulimina affinis* (19%), *Bulimina inflata* (13%), and *U. peregrina* (7%) dominate the calcareous assemblage. The previously dominant agglutinated species *C. trullissata* has strongly diminished, whereas *Thurammina papillata* accounts for 20% of the fauna. At 2475 m the perforate fauna is strongly diminished, and agglutinated species, such as *Karrerulina apicularis* (12%), *Repmanina charoides* (11%), and *Hormosina globulifera* (6%) dominate. *Uvigerina peregrina* (9%) is the most frequent perforate species.

At 2908 m, *Cibicides kullenbergi* (8%) is the dominant calcareous species. Among the agglutinants, *Recurvoides* sp. 1 (9%) *Cribrostomoides bradyi* (8%), and *Reophax fusiformis* (8%) dominate while *K. apicularis* has a lower percentage (5%), and *R. charoides* is absent. The standing stock at 3908 m is particularly poor and no species is represented by more than five individuals. The main species here include *R. fusiformis, Psammosphaera testacea, Epistominella exigua*, and *Pyrgo elongata*. The 4987 m station is dominated by agglutinated taxa. *Reophax fusiformis* (25%) is at its maximum relative abundance here. *Hormosina globulifera* (15%), after being absent at 3908 m, returns as a subdominant species. Other notable species include *Recurvoides* sp. 1 and *Thurammina papillata* (both 6%).

63–150 µm Fraction

For the 63–150 µm fraction, all species that account for >5% in any of the stations are presented in Figure 10. It is important to note that many of the species that dominate this fraction are not also present in the >150 µm fraction,

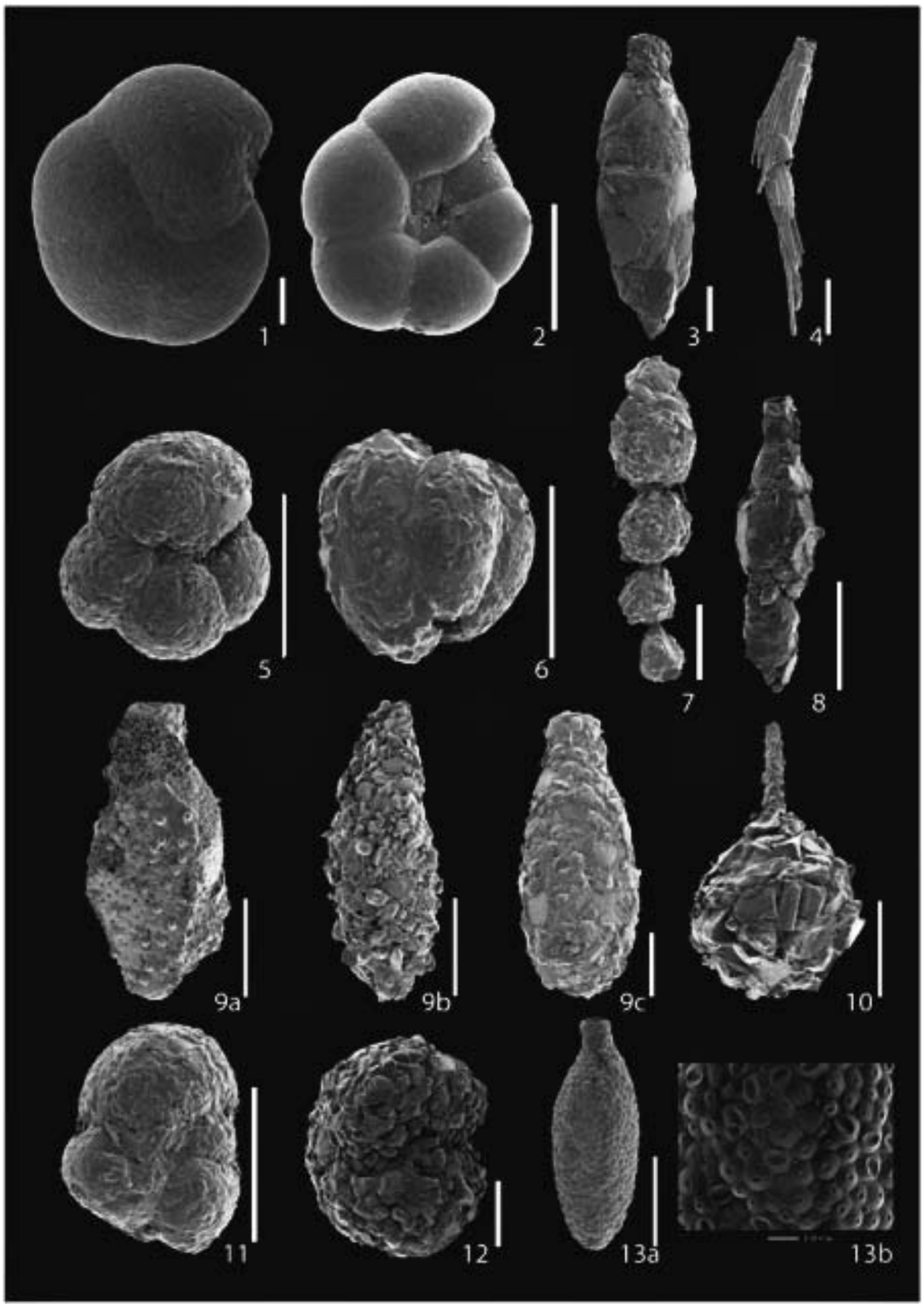

FIGURE 7. Some agglutinated foraminifera observed from both size fractions in this study. Scale bar = 100 μm unless stated otherwise. **1** *Buzasina ringens*, station 58, 282 m (0.5–1 cm). **2** *Cribrostomoides bradyi*, station 58, 282 m (0–0.5 cm). **3** *Reophax helenae*, station 58, 282 m (0.5–1 cm). **4** *Reophax spiculifer*, station 57, 490 m (0–0.5 cm). **5** *Ammoglobigerina globigeriniformis*, station 57, 490 m (0–0.5 cm). **6** *Adercotryma glomerata*, station 55, 1374 m (0–0.5 cm). **7** *Hormosinella guttifera*, station 55, 1374 m (0–0.5 cm). **8** *Reophax* sp. 1, station 51, 3908 m (0–0.5 cm). **9** *Reophax fusiformis*: a, calcareous morphotype, station 51, 3908 m (0–0.5 cm); b, rough-quartz morphotype, station 50, 4987 m (0–0.5 cm); c, smooth-quartz morphotype), station 50, 4987 m (0–0.5 cm). **10** *Lagenammina tubulata*, station 50, 4987 m (0–0.5 cm). **11** *Haplophragmoides sphaeriloculum*, station 50, 4987 m (0–0.5 cm). **12** *Recurvoides* sp. 1, station 50, 4987 m (0–0.5 cm). **13** *Spirolocammina* sp. 1, station 50, 4987 m (0–0.5 cm); b, close-up of coccolith wall texture made up of *Calcidiscus quadripeforatus*.

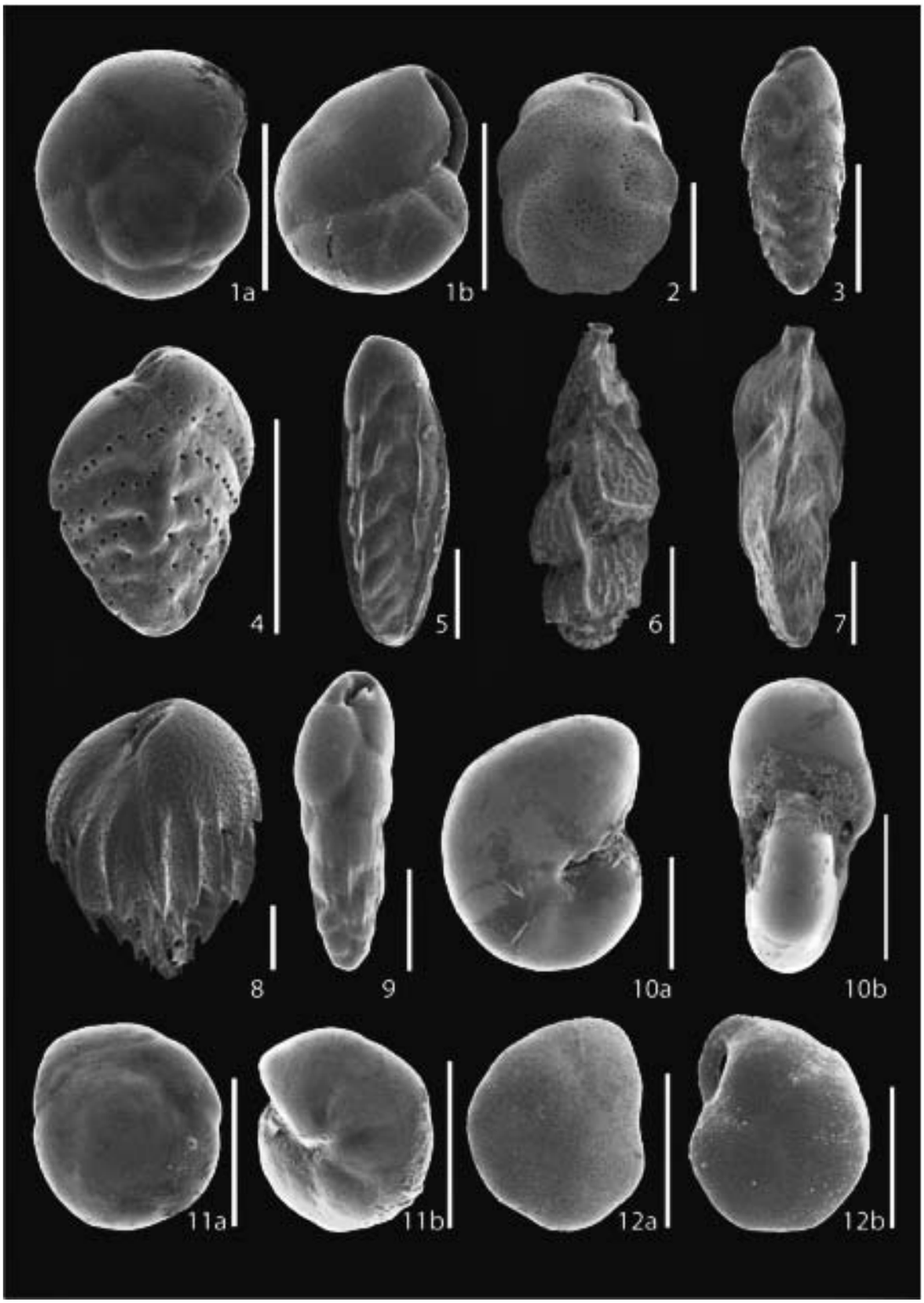

FIGURE 8. Common calcareous foraminifera found in this study. Scale bar = 100 μm. **1** *Epistominella vitrea*, station 58, 282 m (0–0.5 cm). **2** *Cassidulina carinata*, station 58, 282 m (0.5–1 cm). **3** *Bolivina dilatata*, station 58, 282 m (0.5–1 cm). **4** *Bolivina robusta*, station 58, 282 m (0–0.5 cm). **5** *Bolivina tongi*, station 58, 282 m (0–0.5 cm). **6** *Trifauna pauperata*, station 56, 1006 m (0–0.5 cm). **7** *Trifauna bradyi*, station 56, 1006 m (0–0.5 cm). **8** *Bulimina inflata,* station 55, 1374 m (0–0.5 cm). **9** *Buliminia translucens,* station 52, 2908 m (0–0.5 cm). **10** *Pullenia salisburyi*, station 50, 4987 m (1.5–2 cm). **11** *Nuttallides pusillus,* station 50, 4987 m (0–0.5 cm). **12** *Epistominella exigua*, station 50, 4987 m (0–0.5 cm).

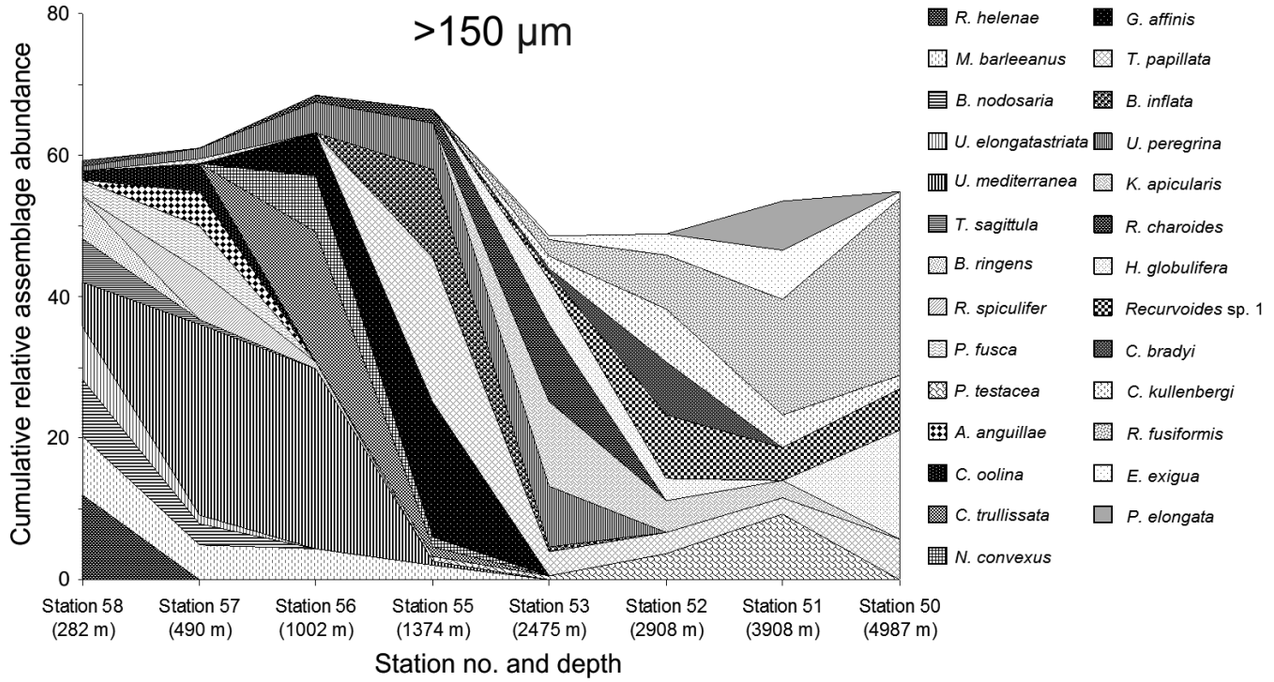

FIGURE 9. Composition of the live benthic live foraminiferal faunas (in % of the total faunas) of the >150 µm fraction. All species with a relative abundance >5% at any one station are presented.

particularly most representatives of *Bolivina* and *Epistominella*. Faunal changes appear to be more gradual in the 63–150 µm fraction, although large faunal differences occur between stations 55 and 53 (1374–2475 m) and stations 53 and 52 (2475–2908 m). At 1374 m and shallower, *Trifarina bradyi* and *Melonis barleeanus* are conspicuous elements. The 2475 m station is dominated by *Repmanina charoides* and *Pullenia salisburyi*, whereas at 2908 m and deeper, *Reophax fusiformis* and *Nuttallides pusillus* are dominant elements.

The shallowest station at 282 m is dominated by *Cribrostomoides bradyi* (10%), followed by *Epistominella vitrea* (8%), *Bolivina robusta* (5%), and *B. tongi* (5%). At 490 m, the most abundant species are *Trifarina bradyi* (6%), *Melonis barleeanus* (5%), *Globocassidulina subglobosa* (5%), and *B. robusta* (4%). Several *Reophax* species together account for 14% of the assemblage. At 1002 m, there is a higher percentage of *T. bradyi* (13%), *Nuttallides convexus* (8%) appears, and the relative abundance of *M. barleeanus* (6%) also increases, whereas bolivinids are no longer present. At 1374 m, *Epistominella exigua* (16%) replaces *E. vitrea* as the dominant *Epistominella* species. In addition, two agglutinated species that construct their tests with calcareous particles, *Psammosphaera* sp. 1 and *Reophax* sp. 2, each account for 6% and 5% respectively. *T. bradyi* (7%) remains a key component of the assemblage.

At 2475 m, *Trifarina* species are no longer present, and *E. exigua* (3%) has decreased significantly. Instead, there is an increase in *G. subglobosa* (5%) and juveniles of *Repmanina charoides* (10%) and *Pullenia salisburyi* (9%) are dominant elements.

The 2908 m station is dominated by *Reophax fusiformis* (15%). Also *Nuttallides pusillus* (12%), *Epistominella exigua* (9%), *Globocassidulina subglobosa* (7%), and *Bulimina translucens* (5%) show increased percentages. The fauna at 3908 m continues to be dominated by *N. pusillus* (16%), *R. fusiformis* (16%), *E. exigua* (9%), and *B. translucens* (5%). Conversely, *Pullenia salisburyi* and *G. subglobosa* are almost absent at this station. At our deepest station (4987 m), *E. exigua, N. pusillus*, and *Bulimina translucens* all fall below 5%. Instead, agglutinated taxa such as *R. fusiformis* (14%), *Lagenammina tubulata* (9%), *Haplophragmoides sphaeriloculum* (7%), and *Reophax* sp. 1 (7%) dominate. *Pullenia salisburyi* (7%) is the only calcareous species >5% at this station.

DISCUSSION

Density and Diversity

It is generally accepted that foraminiferal standing stocks vary as a function of the amount of labile organic carbon arriving at the sea floor (e.g., Thiel, 1983; Berger and Diester Haas, 1988; Altenbach and Sarnthein, 1989; Koho and others, 2008; Mojtahid and others, 2010). Some species specialize on particular foods, such as diatoms, bacteria, or specific components of phytodetritus (e.g., Bertram and Cowen, 1999; Moodley and others, 2000; Suhr and others, 2003; Suhr and Pond 2006; Nomaki and others, 2006). Our samples from the shallowest stations at 282 and 490 m contain around five times more stained foraminifera than those of the deeper stations at 3908 and 4987 m. This general decrease of faunal density with increasing water depth corresponds to the expected decreasing flux of labile organic matter, as underlined by total phytopigment contents (Fig. 3). When we compare the faunal densities

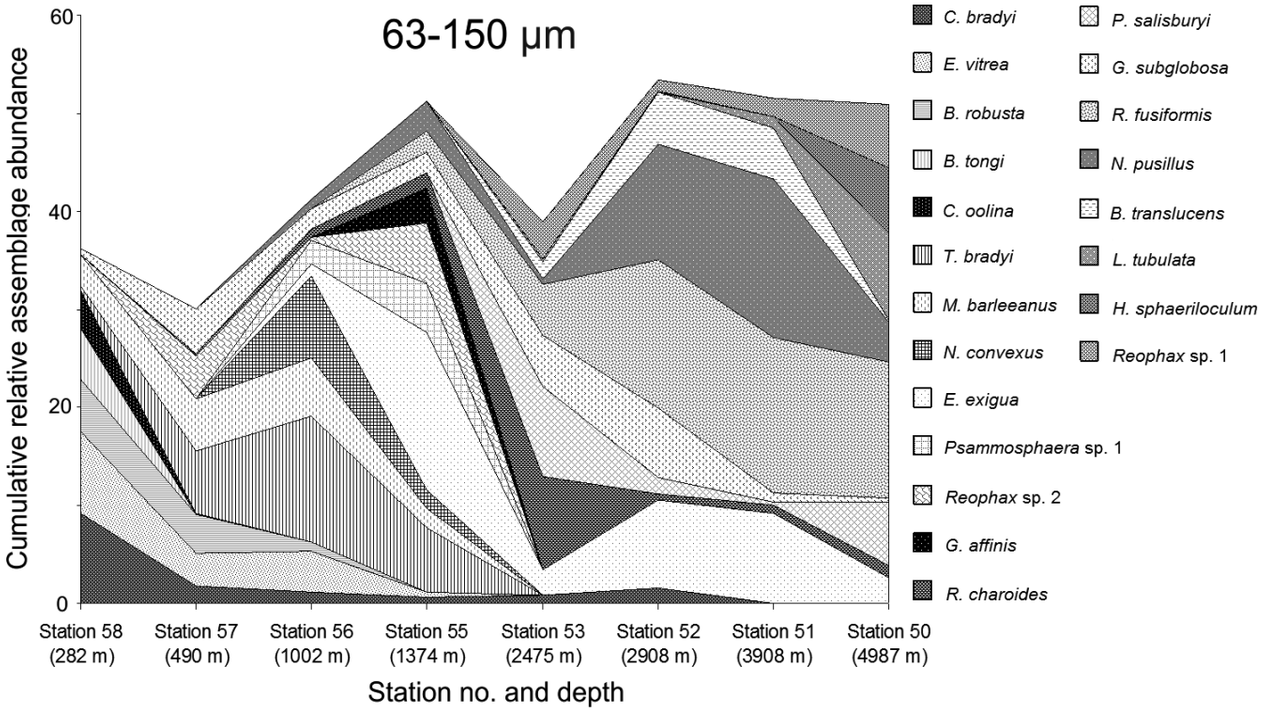

FIGURE 10. Composition of the live benthic live foraminiferal faunas (in % of the total faunas) of the 63–150 µm fraction. All species with a relative abundance >5% at any one station are presented.

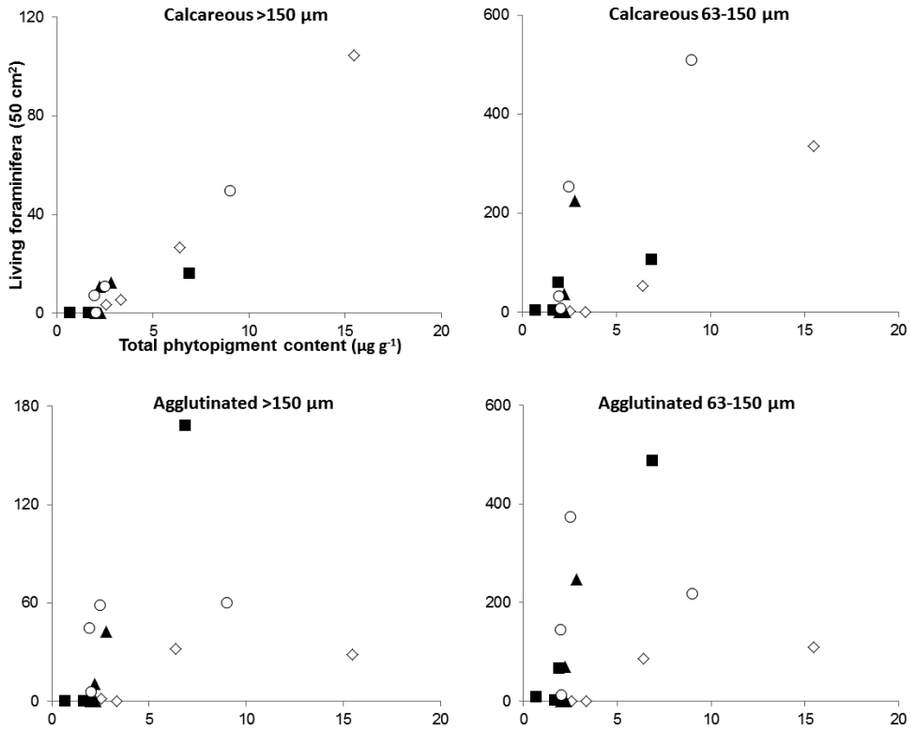

FIGURE 11. Density of living (Rose Bengal stained) calcareous and agglutinated foraminifera of both >150 µm and 63–150 µm fractions from four stations relative to total phytopigment contents from their relative sediment levels. Filled squares and triangles, and unfilled circles and diamonds represent samples from 4987, 3908, 2908, and 1002 m respectively. Calcareous foraminifera >150 µm: $r = 0.96$, $p = 0.00001$; calcareous foraminifera 63–150 µm: $r = 0.69$, $p = 0.002$; agglutinated foraminifera >150 µm: $r = 0.38$, $p = 0.070$; agglutinated foraminifera 63–150 µm: $r = 0.31$, $p = 0.120$.

with total phytopigment contents of surface and deeper sediment levels (Fig. 11), it appears that the calcareous fauna of the >150 μm fraction strongly correlates with total phytopigment content ($r = 0.96$, $p < 0.001$), while this correlation is much weaker for the calcareous fauna of the 63–150 μm fraction ($r = 0.069$, $p = 0.0023$). Agglutinated taxa from both size fractions show no significant correlation with total phytopigment content ($r < 0.4$, $p > 0.05$). In other continental shelf to abyssal plain transects, agglutinated foraminifera replace calcareous ones as the dominant foraminiferal group at deep-sea sites (e.g., Cornelius and Gooday, 2004; Koho and others, 2008). This is usually attributed to increasingly oligotrophic conditions. Consequently, it has been suggested that agglutinated foraminifera are generally less dependent upon labile organic matter availability, in particular the total phytopigment content of the sediment, than calcareous forms (Koho and others, 2008); an observation that is repeated in our study. Our study found no relation between foraminiferal standing stock and the contents of other organic compounds. Species richness shows a pattern similar to standing stock: by far the highest numbers of taxa found in both fractions are 138 at 282 m on the outer shelf and 139 at 490 m on the upper slope, while stations at 3908 and 4987 m have only half as many species (66 and 70 respectively). It appears therefore that both foraminiferal standing stocks and species richness are directly related to the phytopigment component of the labile organic matter analyzed in this study. The comparatively poor total fauna at 1002 m is surprising in view of the high total phytopigment content at this site. Two other studies of Portuguese margin open-slope sites from similar water depths (Griveaud and others, 2010; Nardelli and others, 2010) show comparably low densities. However, Griveaud (2010) showed very high spatial patchiness at a site 980 m deep at 37°31′ N, 9°45′ W. It is evident that single time samplings without replicates may yield unrepresentative densities in a context of important spatial and temporal faunal variability.

Changes in Test Size with Water Depth

The increase of the relative proportion of the 63–150 μm fraction with increasing water depth (Fig. 4) suggests that foraminiferal species with a small test size may be favored at greater water depth, where there less organic matter available. A recent study by Geslin and others (2011) confirmed a strong positive relationship between estimated biovolume (test size) and respiration rates in benthic foraminifera. The results of this study also suggest that compared to other benthic meiofaunal groups, foraminifera have lower metabolic rates. Nevertheless, smaller life forms such as prokaryotes and protists (including foraminifera) contribute to 70% of the total benthic carbon respiration in lower-slope and abyssal environments, whereas their contribution is much less (~23%) on the upper slope and shelf (Heip and others, 2001). We suggest that this pattern can be explained by the fact that foraminifera with greater biovolumes necessarily have more elevated trophic requirements (even if their metabolic rates would be lower, as is suggested by Giere, 2009), and consequently cannot survive below critical threshold values of C_{org} availability. Therefore, we think the observed trend towards smaller benthic foraminifera at greater water depth may be an adaptation to food-limited environments in the deep sea. Additionally when we consider calcareous and agglutinated foraminifera groups separately (Fig. 12), with increasing water depth calcareous foraminifera become more strongly concentrated in the 63–150 μm fraction ($r = 0.83$, $p = 0.006$) than agglutinated ones ($r = 0.60$, $p = 0.05$). This suggests that calcareous species are more impacted by increasingly oligotrophic conditions and show a stronger response by having smaller test sizes overall when compared to agglutinated species. The greater importance of smaller organisms relative-to larger ones with increasing water depth is documented as a general phenomenon of the deep sea and commonly attributed to declining food resources (e.g., Thiel, 1975; Rex and others, 2006); our study suggests this also applies to foraminifera when studied as an individual group. However, trophic resources may not influence all meiofaunal groups in the same way, such as in the case of nematode faunas that have overall reduced body size in organically enriched deep-sea sites (Danovaro and others, 2002).

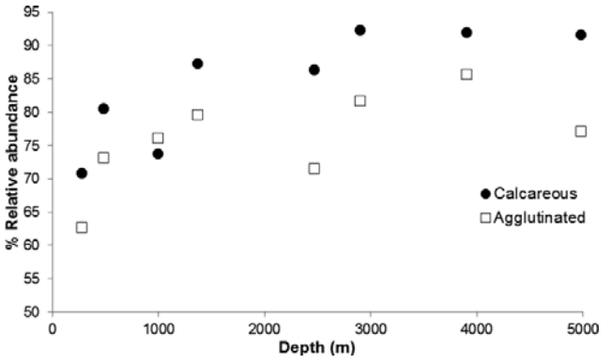

FIGURE 12. Percentage relative proportion of the 63–150 μm fraction (versus total faunas, 63–150 plus >150 fractions) for calcareous and agglutinated foraminifera. Calcareous fauna: $r = 0.83$, $p = 0.0006$; agglutinated fauna: $r = 0.60$, $p = 0.05$.

Faunal Trends with Depth

During the 1970s, bathymetric distributions of benthic foraminifera were thought to mainly reflect the water mass characteristics (e.g., Pujos-Lamy, 1973; Streeter, 1973; Schnitker, 1974; Streeter and Shackleton, 1979). More recent studies tend to discredit this concept (e.g., Mackensen and others, 1990; Schmiedl and others, 1997; Jorissen and others, 2007; Koho and others, 2008; Mojtahid and others, 2010), mainly because important water mass boundaries do not systematically coincide with the boundaries of the main faunal components. Also in our data, species occurrences do not seem to be related to water masses. In fact, none of the dominant species appear to be restricted to a single water mass, and also our main faunal changes (between 1000–1300 m and between 2500–2900 m, respectively) do not coincide with water mass boundaries. Several authors have suggested that many foraminiferal species have critical thresholds of organic flux, which delimit the range in which

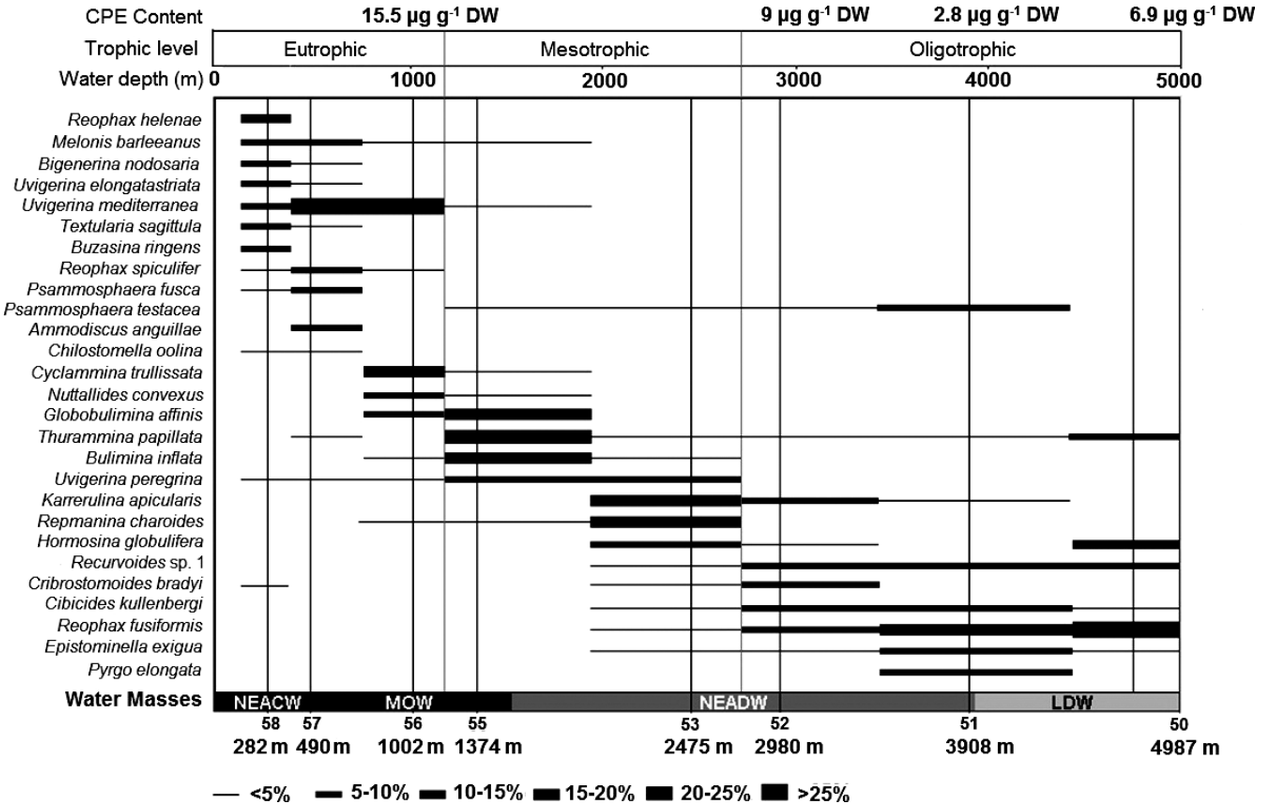

FIGURE 13. Relative densities (>150 ìm) of the important live foraminifera species (present with percentage higher than 5% in at least one station) along the eight-station bathymetric transect.

they are most competitive. Therefore, at present, organic flux is generally supposed to be the main factor responsible for bathymetrical species successions (e.g., Altenbach and others, 1999, 2003; De Rijk and others, 2000; Fontanier and others, 2002; Morigi and others, 2001; Eberwein and Mackensen 2006; Koho and others, 2008; Mojtahid and others, 2010). On the continental slope, with increasing water depth, the majority of "eutrophic" species disappear and the assemblages become progressively dominated by other species more adapted to mesotrophic or oligotrophic conditions. In Figures 13 and 14, we plotted the depth distribution of the main (≥5%) species encountered along our bathymetrical transect in the >150 and 63–150 µm fractions respectively, together with total phytopigment sediment contents measured at four of our stations. The changes in species composition of the foraminiferal are consistent with a general decrease in organic fluxes from the outer continental shelf to the abyssal plain on the Portuguese margin. We observe high densities of species that have previously been considered typical of eutrophic conditions at our shallower stations, which gradually disappear with increasing depth and decreasing trophic level. In turn, species better adapted to lower trophic levels appear. On the basis of the information summarized in these figures, we can separate our stations, as well as the dominant species at these stations, into three categories: eutrophic, mesotrophic, and oligotrophic (Figs. 13, 14).

COMPARISON WITH PREVIOUS STUDIES

Similar studies have been performed in nearby areas of the Portuguese margin around Nazaré and Setúbal canyons (Koho and others, 2007, 2008) and in the Bay of Biscay (Fontanier and others, 2002, 2003, 2006; Duchemin and others, 2007; Mojtahid and others, 2010). With the exception of Duchemin and others (2007), all were concerned with the fraction >150 µm.

Under eutrophic conditions (>15 µg g^{-1} DW), found at our shallow stations (<1200 m), a high annual organic carbon flux promotes rich and ecologically diverse calcareous and agglutinated faunas, including surface-dwelling, infaunal, and opportunistic species. The dominant species of the >150 µm fraction, the opportunistic surface-dweller *Uvigerina mediterranea*, and the infaunal *Melonis barleeanus* and *Uvigerina elongatastriata* are also key elements of the relatively eutrophic and shallower assemblages (<1000 m) in the Bay of Biscay (Fontanier and others, 2002, 2003; Mojtahid and others, 2010) and on the Portuguese margin, where they thrive in sediments with total phytopigment contents ≥10µg cm^{-3} (Koho and others, 2008). However, the dominant eutrophic agglutinated species observed in our study area do not occur consistently in the other two areas, except for *Bigenerina nodosaria*. For instance, *Reophax helenae* is not recorded in the Bay of Biscay, but has been documented (as *Reophax*

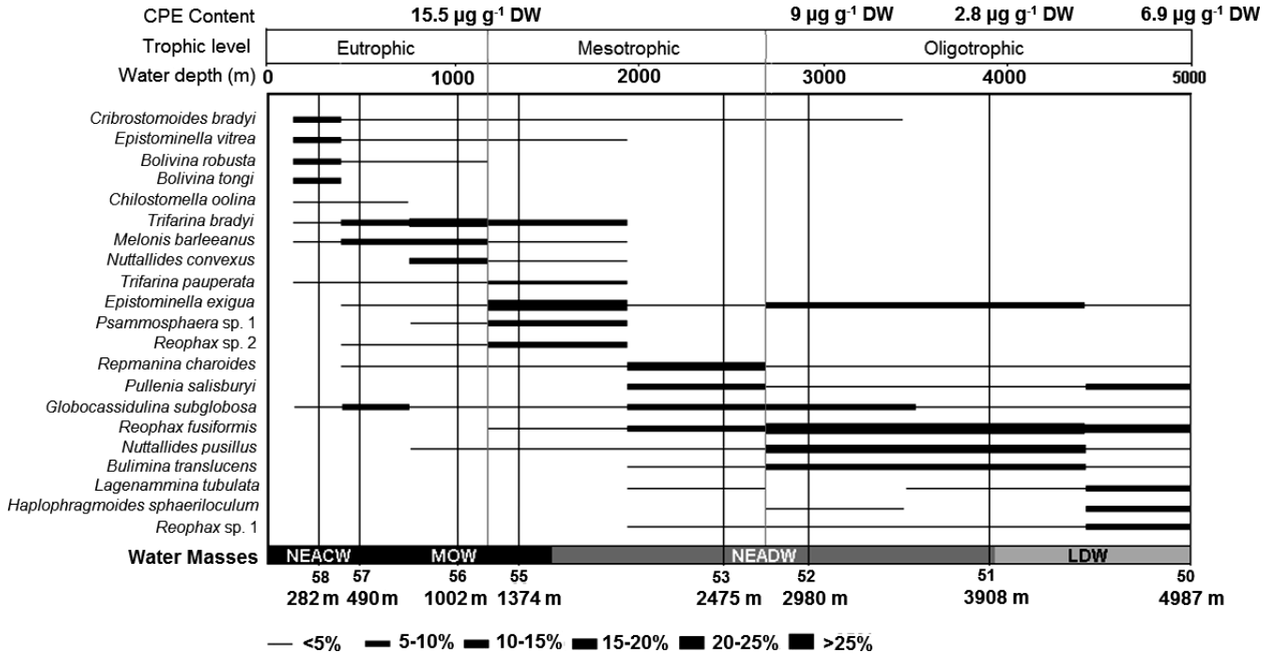

FIGURE 14. Relative densities (63–150 µm) of the important live foraminifera species (present at >5% in at least one station) along the eight-station bathymetric transect.

sp. 1) at eutrophic shallow stations (≤500 m) at both canyon and open-slope locations on the Portuguese margin (Koho and others, 2007, 2008). Also, *Cyclammina trullissata*, a major infaunal taxon at our 1002 m site, is not recorded in either of the other two areas. In the 63–150 µm fraction, *Trifarina bradyi* is strongly dominant between 490–1374 m depth, with a maximum relative abundance at 1002 m. *Trifarina pauperata* occurs in association with *T. bradyi* and shows an identical distribution but with somewhat smaller populations. In the Bay of Biscay, *T. bradyi* occurs only as a minor component at 550 m (Fontanier and others, 2003), whereas *Trifarina pauperata* is supposed to be related to seasonally eutrophic environments in the Bay of Biscay at 1000 m (Duchemin and others, 2007). Our 282 m station also shows elevated numbers of *Cribrostomoides bradyi* (*Haplophragmoides bradyi* in Duchemin and others, 2007), *Epistominella vitrea*, and *Bolivina robusta* (*B. spathulata* in Duchemin and others, 2007), all of which diminish in abundance with increasing depth. In the Bay of Biscay, these three species occur at the most eutrophic environments, between 90–140 m.

The onset of relatively mesotrophic conditions (total phytopigment contents ranging 10–15 µg g^{-1} DW) at mid-depths (1374–2475 m) is marked by a reduced number of calcareous species, particularly in the >150 µm fraction (Fig. 6). However, the shallow infaunal species *Uvigerina peregrina* and *Bulimina inflata* are still dominant at 2475 m. On the open Setúbal slope, *U. peregrina* occupies a relatively broad range of trophic conditions, from sediments containing total phytopigment contents ranging >18 g cm^{-3}, where *U. peregrina* var. *celtica* morphotypes dominate, to ~5 µg cm^{-3}, which favors the true *U. peregrina* morphotype (Koho and others, 2008). Because there is a continuous morphological transition between the two morphogroups, we decided not to split them in our study. Nonetheless, *U. peregrina* var. *celtica* morphotypes tend to dominate at 1374 m, whereas at the morphotypes at 2475 m are predominantly *U. peregrina*. In the Bay of Biscay, Fontanier and others (2003, 2006) suggested that, among species in the >150 µm fraction, *U. peregrina* has the strongest response to surface water phytoplankton blooms and associated phytodetritus deposits at 550 and 1000 m. In the smaller size fraction, small calcareous opportunistic species known to exploit phytodetritus (e.g., *Epistominella exigua*) start to increase. Among the calcareous deep and intermediate infauna, only *Globobulimina affinis* occurs in significant numbers (at 1374 m), while infaunal agglutinants remain relatively rich. At 1000 m in the Bay of Biscay, *G. affinis* dominates a deep infaunal assemblage (Fontanier and others, 2002), while *Globobulimina* spp. occur from 300–1760 m on the Setúbal open slope, in sediments ranging from relatively rich to poor in phytopigments (Koho and others, 2008). Along our transect, *G. affinis* is absent deeper than 1374 m depth, and agglutinated species such as *Karrerulina apicularis* and *Repmanina charoides* dominate the infauna at 2475 m. This transition may reflect a further decrease in trophic level.

Under oligotrophic conditions (total phytopigment content <10 µg g^{-1} DW) on the lower slope and abyssal plain (2908–4987 m depth), small, opportunistic, calcareous species attain their maximum relative abundance, whereas infaunal agglutinated species become less common. *Bulimina translucens*, *Epistominella exigua*, and *Nuttallides pusillus* have elevated relative abundances at 2908 and 3908 m depth. These three small species are mostly

restricted to the 63–150 μm fraction, have thin-walled tests, and occupy shallow-infaunal niches. A similar *E. exigua-N. pusillus* association was recorded in the Bay of Biscay at 1000 m by Duchemin and others (2007), who interpreted their high abundances as a response to spring phytodetritus deposits. *Reophax fusiformis* is a dominant element of the agglutinant assemblages in both size fractions. In the Setúbal open-slope and canyon environments on the Portuguese margin, Koho and others, (2008) recorded *Reophax fusiformis* (as *Lagenammina* sp.) under strongly oligotrophic conditions, with total sediment phytopigment contents ≤ 2 μg cm^{-3}. Gooday and others (2010) suggested that similar morphotypes (assigned to *Lagenammina*) in the Porcupine Abyssal Plain may be connected with phytodetritus deposits. Below the critical organic flux threshold between 4000–5000 m, seasonal phytodetritus may become too rare to sustain a significant number of opportunistic calcareous species. Nonetheless, small opportunistic agglutinants, as well as agglutinants with less-opportunistic life strategies, thrive at this depth and exploit eutrophic microenvironments created by phytodetritus falls in otherwise oligotrophic settings.

CONCLUSIONS

We have investigated the distributional patterns of live (rose Bengal-stained), small- (63–150 μm) and large-sized (>150 μm) benthic foraminifera along a bathymetric transect from outer shelf (282 m) to abyssal plain (4987 m) environments on the Portuguese margin. The results of our study show that with increasing depth and declining availability of food particles in the sediments (i.e., trophic conditions), there is a succession of different groups of foraminifera characterized by different test sizes, wall types, and life-histories. Calcareous foraminifera are more strongly impacted by increasingly oligotrophic conditions than agglutinated ones, as indicated by the decreased proportion of perforate calcareous foraminifera, and the increased proportion of agglutinated foraminifera, between 1374–4987 m, overall suggesting that calcareous foraminifera have more elevated trophic requirements. These findings could have important implications for our understanding of different foraminiferal groups and their relative contributions to carbon cycling in deep sea.

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APPENDIX 1

Taxonomic reference list. For all species (>5%) determined to species level, a modern reference is given, in which the species is correctly figured.

Ammodiscus anguillae Høgland, 1947—Jones, 1994, pl. 38, figs. 1–3

Bigenerina nodosaria (d'Orbigny, 1826) —Jones, 1994, pl. 44, figs. 19–24

Bolivina robusta Brady, 1881—Jones,1994, pl. 53, figs. 7–9

Bolivina tongi Cushman, 1929—Schiebel, 1992, pl 1. figs 10a, 10b

Bulimina inflata (Seguenza, 1862) —Van Leeuwen, 1989, pl. 8, fig. 4.

Bulimina translucens Parker, 1953—Van Leeuwen, 1989, pl. 8, fig. 7.

Buzasina ringens (Brady, 1879)—Jones, 1994, pl. 40, figs. 17, 18.

Chilostomella oolina (Schwager, 1878) —Jones, 1994, pl. 55, figs. 12–14.

Cibicidoides kullenbergi (Parker, 1953)—Koho and others, 2008, pl. 1, fig. 1.

Cribrostomoides bradyi (Robertson, 1891)—Timm, 1992, pl. 3, fig. 13.

Cyclammina trullissata (Brady, 1879)—Jones, 1994, pl. 40, figs. 13.

Epistominella exigua (Brady, 1884)—Duchemin and others, 2007, pl. 2, figs. 1, 2.

Globobulimina affinis (d'Orbigny, 1839)—Hess, 1998, pl. 10, fig. 13.

Globocassidulina subglobosa (Brady, 1881)—Van Leeuwen, 1989, pl. 8, fig. 11.

Haplophragmoides sphaeriloculum Cushman, 1910—Hess, 1998, pl. 6, fig. 10.

Hormosina globulifera Brady, 1879—Jones, 1994, pl. 39, figs. 1–4, 6.

Karrerulina apicularis (Cushman, 1911)—Murray and Alve, 1994, fig. 19.13.

Lagenammina tubulata (Rhumbler, 1931)—Hess, 1998, pl. 2, fig. 10.

Melonis barleeanus (Williamson, 1858) —Van Leeuwen, 1989, pl. 13, figs. 1, 2.

Nuttallides convexus (Parker, 1958) —Van Leeuwen, 1989, pl. 15, figs. 5–10.

Nuttallides pusillus (Parr, 1950)—Van Leeuwen, 1989, pl. 14, figs. 4–12.

Psammosphaera fusca Schulze, 1875—Jones, 1994, pl. 18, figs. 1–8.

Psammophaera testacea Flint, 1899—Hofker, 1972, pl. 7 figs. 6, 7

Pullenia salisburyi Stewart and Stewart, 1930—Stewart and Stewart, 1930, pl. 8, fig. 2.

Reophax fusiformis (Williamson, 1858) —Wollenburg and Mackensen, 1998, pl. 1, fig. 12.

Reophax helenae (Rhumbler, 1913)—Hess, 1998, pl. 3, fig. 9.

Reophax spiculifer Montfort, 1879—Jones, 1994, pl. 31, figs. 16, 17.

Repmanina charoides (Jones & Parker, 1860)—Cimerman and Langer, 1991, pl. 3, figs. 6–9.

Textularia sagittula Defrance, 1824—Jorissen, 1988, pl. 3 fig. 12.

Thurammina papillata Brady, 1879—Jones, 1994, pl. 36, figs. 7–18.

Trifarina bradyi (Cushman, 1923)—Jones, 1994, pl. 67, figs. 1–3.

Trifarina pauperata (Heron-Allen and Earland, 1932)—Duchemin and others, 2007, pl. 3, figs. 14, 15.

Uvigerina elongatastriata (Colom, 1952)—Koho and others, 2008, pl. 1, fig. 5.

Uvigerina mediterranea (Hofker, 1932)—Koho and others, 2008, pl. 1, fig. 6.

Uvigerina peregrina (Cushman, 1923)—Hess, 1998, pl. 11, figs. 2, 3.

ANNEXE 4

Calcareous benthic foraminiferal biofacies along a depth transect on the southwestern Marmara shelf (Turkey)

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ABSTRACT: A total of 200 calcareous benthic foraminiferal species were identified in 30 surface samples collected across a depth transect in the southwestern Marmara Sea. Q-mode cluster and canonical correspondence analyses performed on the foraminiferal species abundance data revealed three clusters. Environmental parameters collected at each sampling station allowed the correlation between foraminiferal clusters and watermass characteristics, such as water depth, temperature, salinity and dissolved oxygen concentrations. Cluster A (55–130 m) is characterized by species typical of muddy substrates in the circa-littoral zone and related to declining dissolved oxygen values. Cluster B (140–350m) is characterized by deep-infaunal dysoxic and suboxic species indicative of circa-littoral and upper epibathyal environments and strongly related to low dissolved oxygen values and increased water depth. Cluster C (15–50m) is characterized by neritic species typical of the infra-littoral environment. This cluster is further subdivided into three subclusters that reflect brackish surface flow (influenced by low salinity, higher temperature), pycnocline (rising salinity, falling temperature) and infra-littoral to circa-littoral transitional environments (higher oxygen from the Mediterranean countercurrent and the subsurface chlorophyll maximum), respectively.

INTRODUCTION

Species diversity and spatial distribution of benthic foraminiferal assemblages are strongly controlled by environmental parameters, particularly the salinity, temperature and dissolved oxygen concentration of the bottom water masses, and the availability of food (e.g., Parker 1958; Schnitker 1994). However, there is still much debate as to which environmental factors have the most significant effect on calcareous assemblages. Dissolved oxygen (Kaiho 1991, 1994, 1999), organic carbon flux (Jorissen 1988), sediment substrate (Basso and Spezzaferri 2000) and, increasingly, the detrimental effects of various types of pollution (Yanko et al. 1998), have all been proposed as principal factors that control the abundance and distribution of benthic foraminifera and their morphotypes. The present study describes the calcareous benthic foraminiferal thanatocoenosis in order to document depth-related faunal patterns and investigate the influence of environmental parameters on modern foraminifera from the Marmara Sea. The southwestern Marmara Sea was selected for study because strong environmental gradients are present in this area, and there is less impact from shipping and other human activities compared to the eastern part of the Sea (Ikis et al. 2008). An additional purpose of this study was to provide depth calibration for modern foraminiferal biofacies in order to better constrain the Holocene foraminiferal record analysed in piston cores from the southwestern Marmara Sea by Aksu et al. (2002) and Kaminski et al. (2002).

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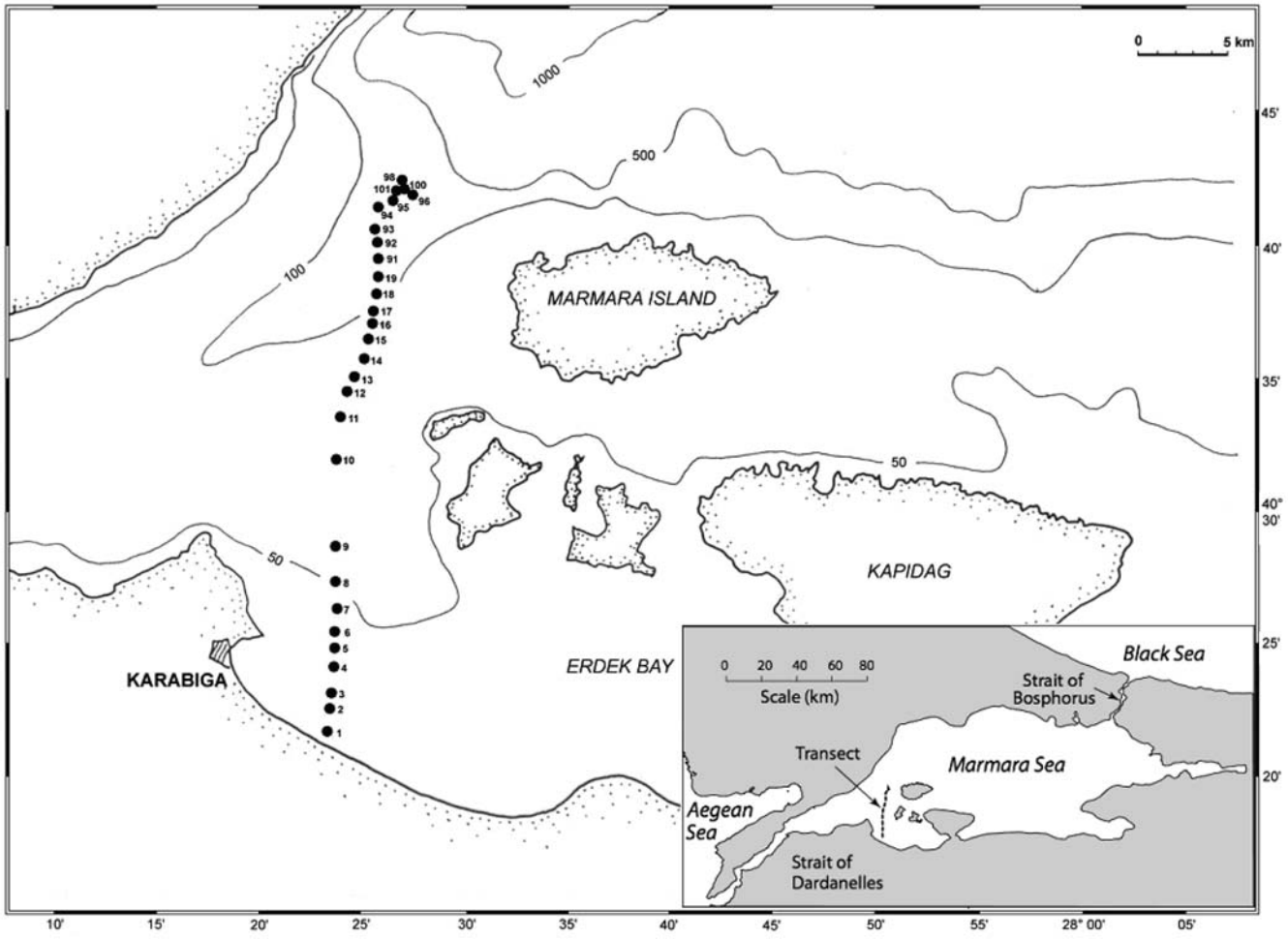
The Marmara Sea forms a gateway between the world's largest permanently anoxic basin, the Black Sea, and the Aegean Sea (text-fig. 1). It is connected to the Black Sea through the Bosphorus Strait (sill at ~40m depth) and to the Aegean Sea through the Dardanelles Strait (sill at -70m). The water exchange between the Black Sea and the eastern Mediterranean Sea occurs through the Bosphorus and Dardanelles and the intervening Marmara Sea as a two-layer flow (e.g., Besiktepe et al. 1994; Mudie et al. 2004). A cooler (5-15°C) and lower-salinity (17-20) surface layer originates from the Black Sea, and flows south and southwest across the straits, and upon entry forms a surface layer up to 30m thick in the Marmara Sea. The warmer (15-20°C) and high-salinity (38-39) Mediterranean water flows north and northeast across the Strait of Dardanelles and occupies the Marmara basin below the low salinity surface layer. The brackish Black Sea outflow creates a strong halocline throughout the Marmara Sea, generating low-oxygen and stratified conditions below the thin surface layer (Aksu et al. 2002; Kaminski et al. 2002).

In a preliminary study of the influence of water-mass properties on calcareous benthic foraminiferal thanatocoenosis, Chendeş et al. (2004) identified two distinct assemblages across a N-S transect in southwestern Marmara Sea: a shallow-water assemblage consisting of genera such as *Ammonia* and *Elphidium* corresponded to the brackish surface water mass, and a deeper assemblage characterized by genera such as *Brizalina, Bulimina* and *Globobulimina,* associated with the more saline and stratified water mass. The present study builds upon the preliminary findings of Chendeş et al. (2004), and aims to (i) provide more detailed taxonomic census of the calcareous benthic foram-



TEXT-FIGURE 1
Positions of the sites where grab samples were collected along a depth transect on the southwestern Marmara shelf and slope during the MAR-02 Cruise.

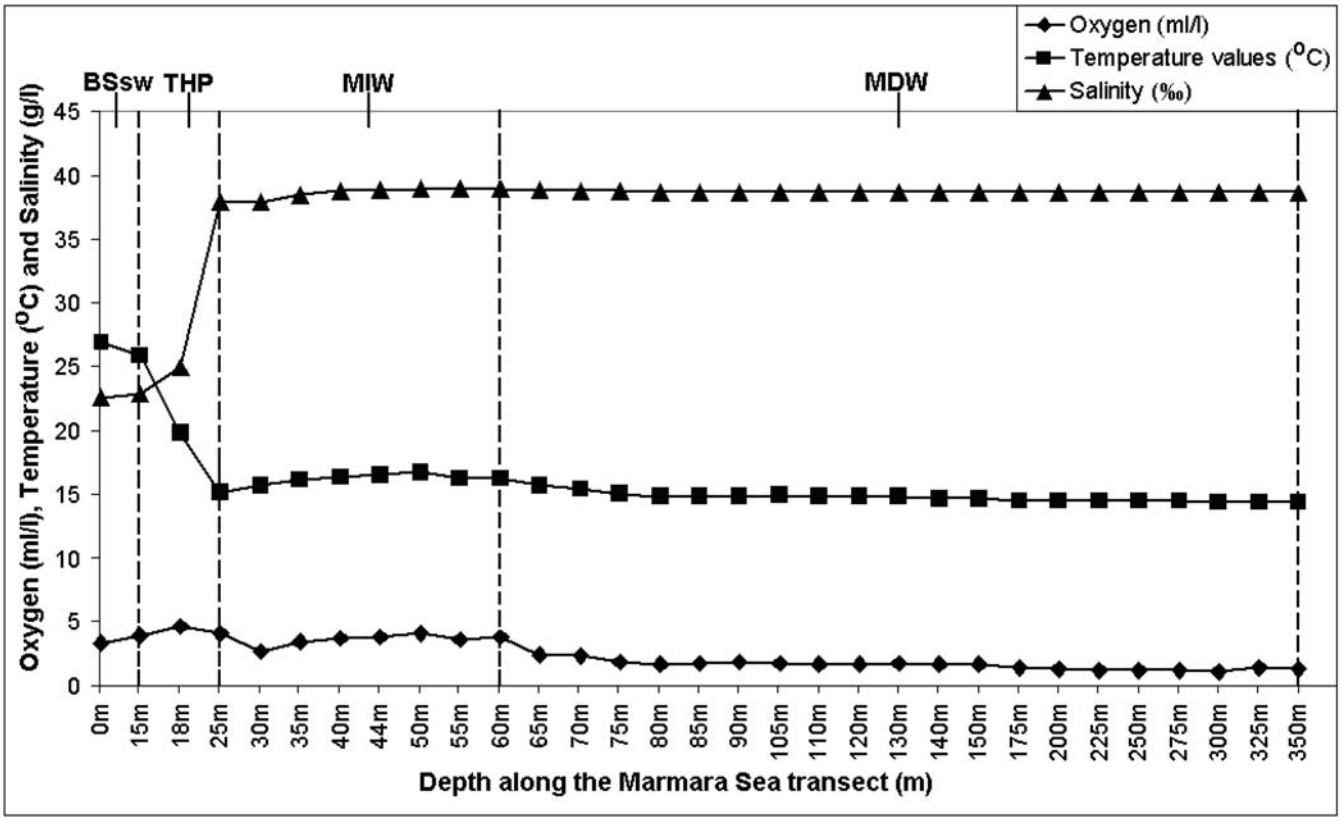
inifera across an inner neritic to upper bathyal transect on the southwestern Marmara Sea shelf, and (ii) assess the degree to which calcareous benthic foraminiferal death assemblages reflect various hydrographic parameters measured at the same stations.

Previous studies

Benthic foraminifera from the Eastern Mediterranean have been studied by Parker (1958) and Cimerman and Langer (1991), who produced a workable taxonomic framework for the region. This framework has been expanded by faunal studies in the Gulf of Naples (Italy) by Sgarrella and Moncharmont Zei (1993) and more recently the Kallithea Bay Section from Rhodes (Greece) by Rasmussen (2005). Shallow-water benthic foraminifera have been studied from Iskundrun Bay on the Mediterranean coast of Turkey (Basso and Spezzaferri 2000). These studies provide calibration of the depth ranges of neritic benthic foraminifera in these sectors of the eastern Mediterranean and Aegean Seas. Many of the same species are found in our samples from the southwestern Marmara Shelf. However, the eastern Mediterranean and Aegean Seas have a much higher salinity than the Marmara Sea. Black Sea foraminifera have been documented by Yanko and Troitskaja (1987), and their ecology summarized by Yanko (1990). These studies are relevant to ours because Black Sea surface water flows out into the Marmara Sea. The only published studies of benthic foraminifera from the Marmara Sea include: (1) the early work of Alavi (1988), who examined two sediment cores collected from a depth of 1200m in the deep basin south of Istanbul, (2) descriptions of upper Pliocene to Holocene foraminifera from geotechnical boreholes in the Gulf of Izmit (Meriç et al. 1995), (3) initial studies of Kaminski et al. (2002) on benthic foraminifera from three gravity cores, one of which was from the southern Marmara Shelf, (4) a preliminary study by Chendeş et al. (2004) of modern benthic foraminiferal assemblages and water mass properties along a transect of the southern shelf of the Marmara Sea and (5) an assessment of benthic foraminiferal assemblages, comprising 74 species, from 15 bottom samples (29-57m water depth) collected in Erdek Bay to the southeast of our study area (Avşar et al. 2006).

MATERIALS AND METHODS

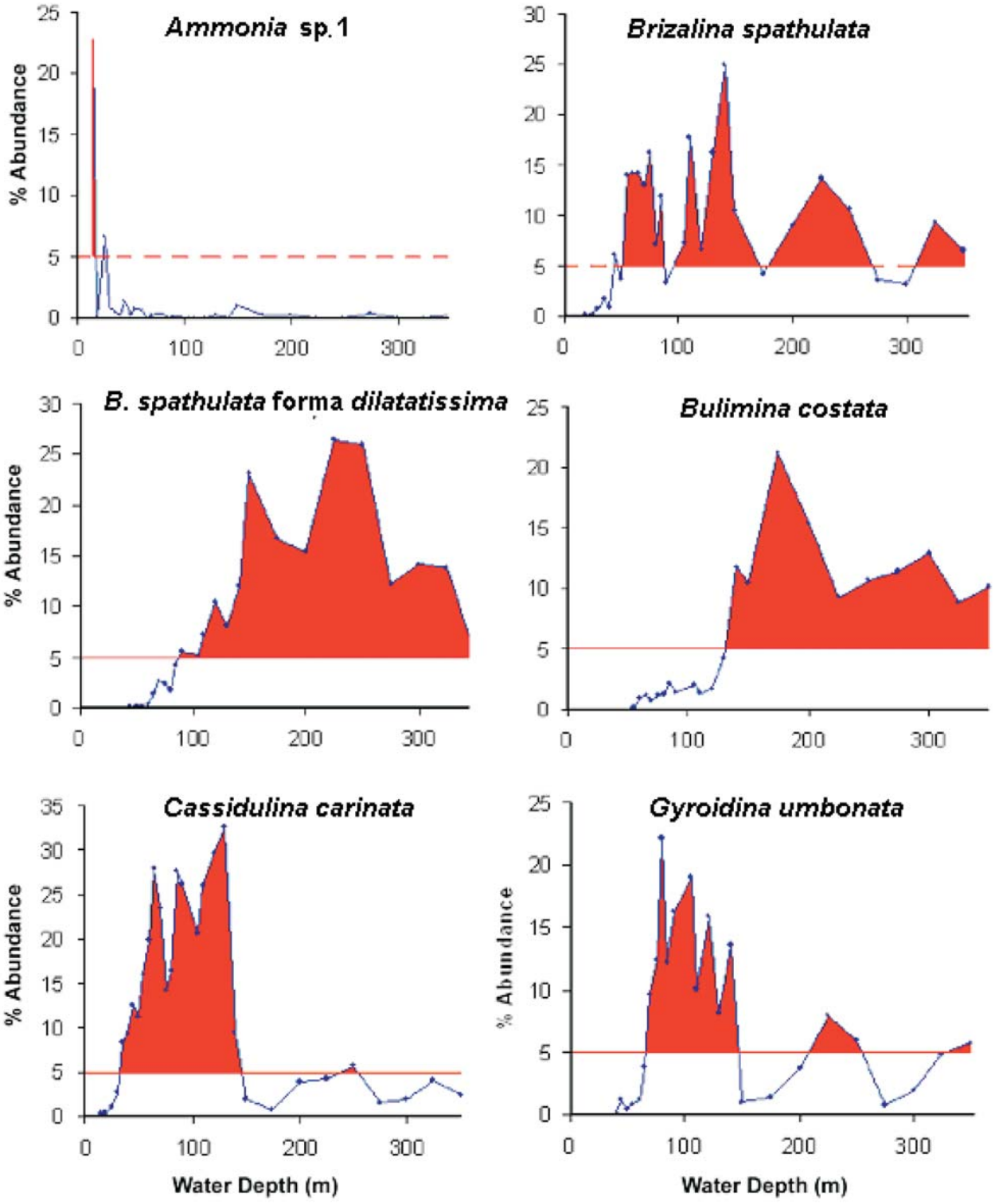
Surface sediment samples were collected using a Shipeck grab from the R/V *Koca Piri Reis* of the Institute of Marine Sciences and Technology, Dokuz Eylül University (Izmir, Turkey) during the MAR-02 cruise (text-fig. 1). Samples were obtained at 30 stations along a 350m depth transect across the infralittoral



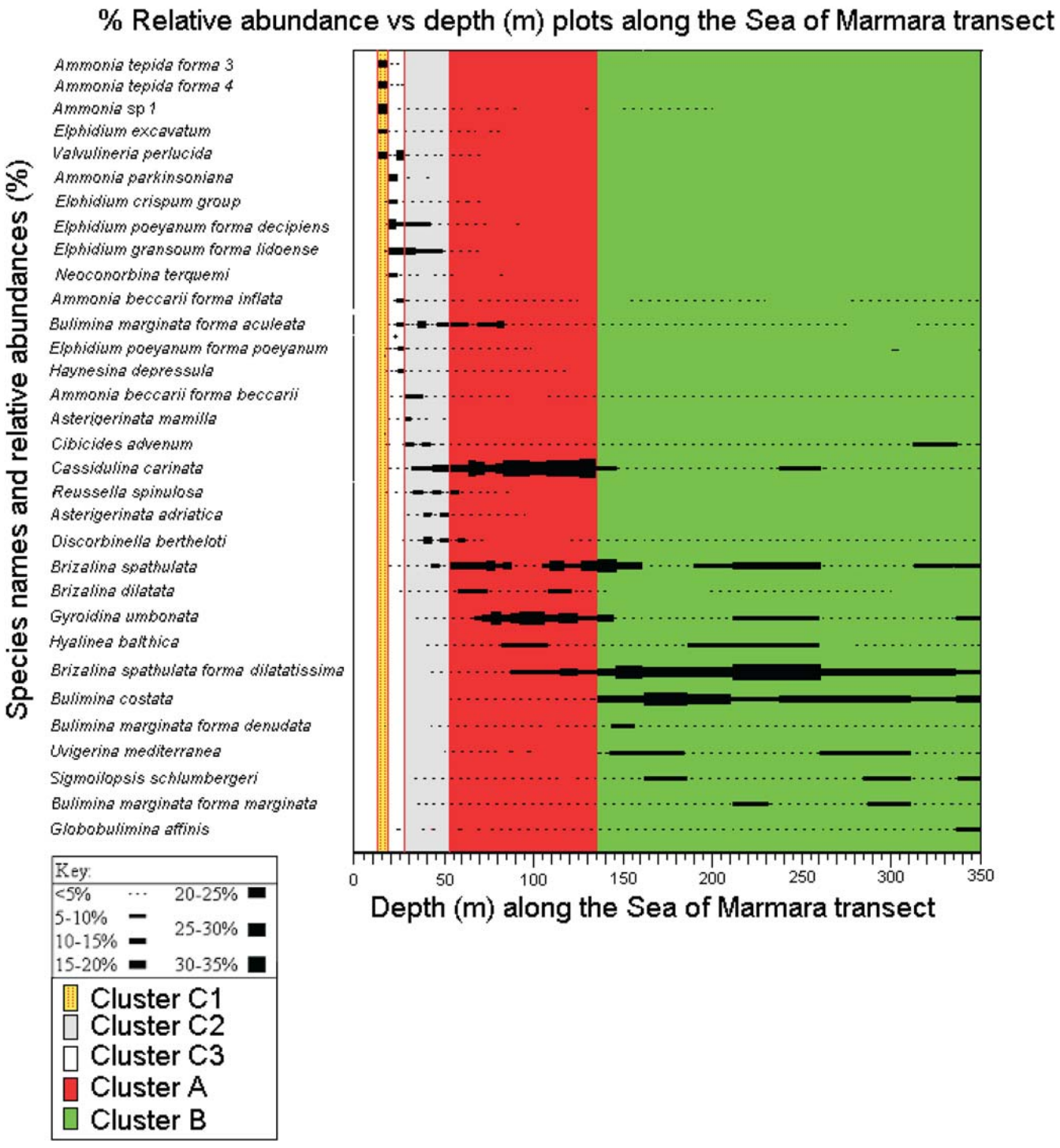
TEXT-FIGURE 2
Dissolved Oxygen content (ml/l), Temperature (°C), and Salinity (measured at 1 meter above the sea floor plotted against water depth along the southwestern Marmara Sea transect. The four dashed intervals represent the following water masses: BSsw = Black Sea surface water (0-15m); THP = Thermocline, Halocline and Pycnocline (15m-25m); MIW = Marmara Intermediate Water (25m-60m); MDW = Marmara Deep Water (60m-350m).

(0m-40m), circalittoral (40m–100m) and epibathyal (100m–350m) environments. They were collected at 10m intervals, except in the bathyal zone where the depth increments were increased to 25m. Sediment samples were washed on board ship through a 63µm sieve, and preserved in ethanol with Rose Bengal. Samples were subsequently washed again, dried, and split into aliquots using a modified Otto microsplitter. Dead benthic foraminifera were picked from the >125µm fraction and mounted on cardboard reference slides. Calcareous benthic foraminiferal specimens were identified according to Parker (1958), Cimerman and Langer (1991), Sgarrella and Moncharmont Zei (1993) and Rasmussen (2005). Species such as *Ammonia beccarii, Ammonia parkinsoniana, Bulimina marginata*, *Elphidium granosum* and *Elphidium poeyanum* were further split into forms and morphotypes following criteria outlined by Jorissen (1988). This was done in order to observe any differences in the distributions of morphotypes of individual species along the transect. Only complete tests devoid of Rose Bengal stained protoplasm were included in the thanatocoenosis count and reported in this study. Stained calcareous foraminiferal tests, as well as all agglutinated foraminiferal species were omitted from the study as it is planned to use the data matrix for testing the BFOI method of Kaiho (1991, 1994, 1999) in the Marmara Sea (Kaminski et al. in prep.). Throughout this paper all references to oxic, suboxic and dysoxic environments follow the definitions outlined by Kaiho (1994). The thanatocoenosis count was analysed by multivariate statistical methods (Q-mode hierarchical cluster analysis and canonical correspondence analysis) using the PAST statistical software. Only taxa with abundances >5% in at least one sample were used to create a matrix of data for statistical analysis. Rare and accessory taxa (<5% relative abundance) were omitted and assumed to have an insignificant effect on the formation of the major groups. *Elphidium crispum* and *Elphidium macellum* and *Nonionella opima* and *Nonionella turgida* were grouped together for statistical treatment into the *Elphidum crispum* group and *Nonionella turgida* group following the taxonomic proposals of Jorissen (1988) and Rasmussen (2005), respectively. Diversity (Fisher α index) values and percent dominance values were also calculated to further characterize the assemblage structure.

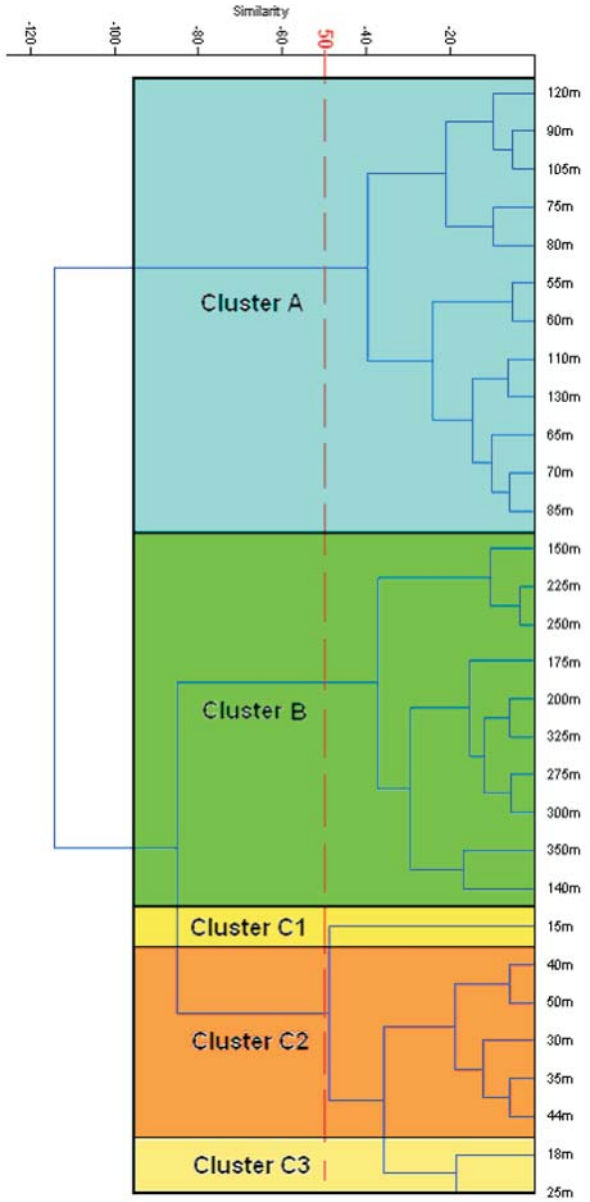
Environmental parameters, including water depth (m), temperature (°C), salinity (‰) and dissolved oxygen (ml/l), were measured at each sampling station at 1-meter intervals using a SBE-9 CTD, equipped with pressure, temperature, conductivity and dissolved oxygen sensors.



TEXT-FIGURE 3
Percent abundances vs. water depth (m) of the dominant taxa (>20% abundance in at least one sample) in the southwestern Marmara Sea transect.



TEXT-FIGURE 4
Distribution of common benthic foraminifera plotted against water depth on the southwest Marmara Sea. Thickness of line is proportional to abundance classes, with thickest lines representing proportions >30%.



TEXT-FIGURE 5
Q-Mode cluster analysis dendogram of the sample stations, based on the total abundances of species >5%. The arbitrary value of 50% dissimilarity that represents a statistically significant cluster is marked with a dashed red line.

RESULTS

Water mass properties

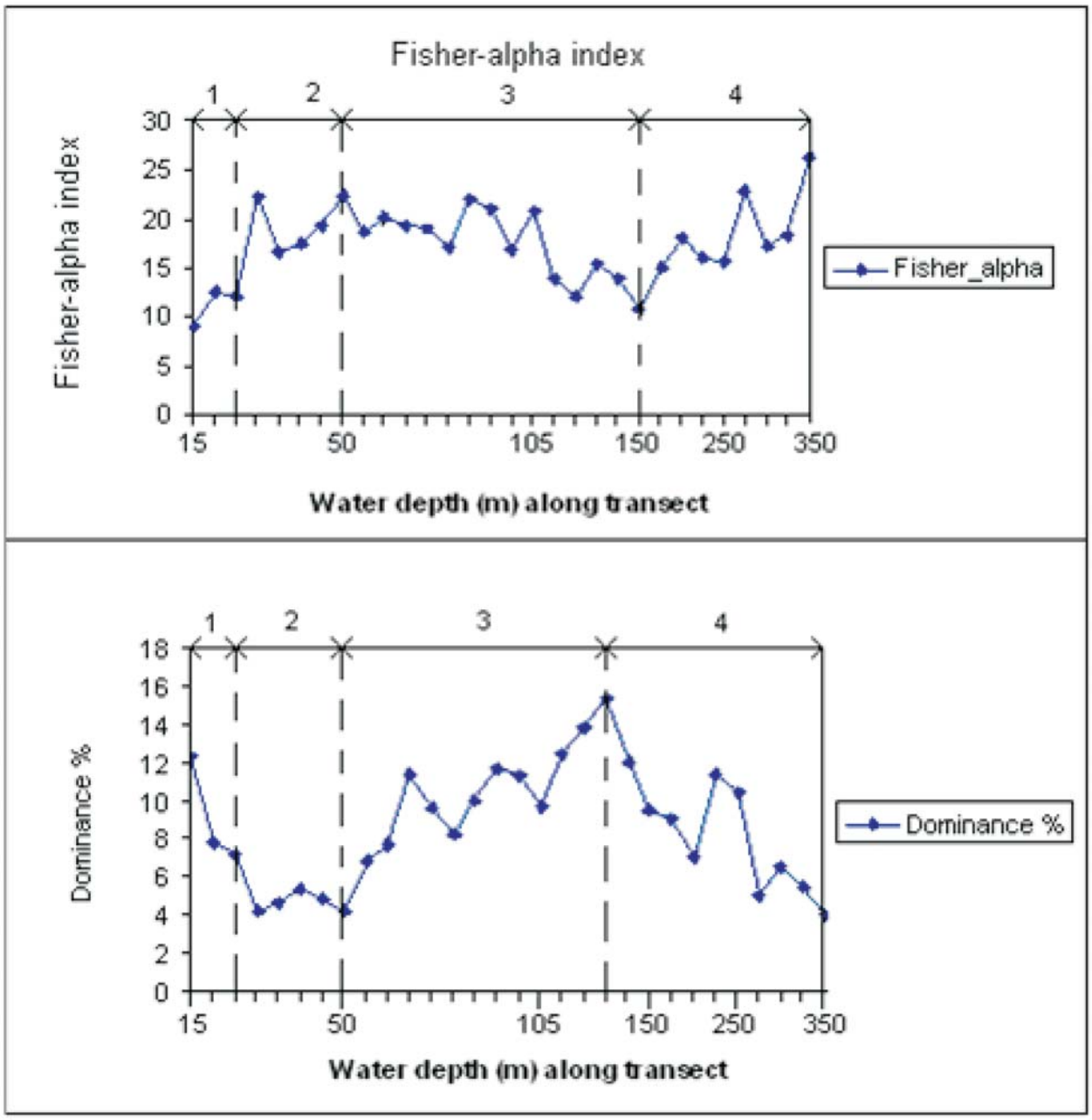
The physical oceanographic data collected during the MAR-02 cruise reveal the presence of three distinct water masses in the southwestern Marmara Sea (text-fig. 2). The surface water mass originates from the Black Sea. It extends from the sea surface to a depth of ~15m, and is brackish (salinity 22.6–22.8) with seasonally variable temperatures and oxygen values reaching 4.3ml/l. The thermocline, halocline, and pycnocline occur between 15m and 25m water depth, and are seasonally variable (Doğan Yaşar, personal communication). This zone is characterized by a rapid decline in temperature from 25.8 to 19.8°C, and an increase in salinity from 22.8 to 37.9. The relatively high dissolved oxygen values across this zone are attributed to seasonal photosynthetic activity within the subsurface chlorophyll maximum. The Marmara intermediate water mass extends from the base of pycnocline to about 60m depth. It is characterized by a rise in dissolved oxygen, temperature and salinity values. This zone represents the inflow of the warm, saline Mediterranean water mass from the Straits of Dardanelles. The Marmara Sea deep water mass extends from 60m to 350m depth, and is characterized by gradually declining temperature (16.2–14.4°C), salinity (38.6–38.8), and dissolved oxygen (3.79–1.09ml/l) values.

Benthic foraminiferal distribution

The samples yielded few 'living' (Rose Bengal stained) calcareous benthic foraminifera; they are present in elevated percentages only at 70m where they represent 7.8% of the total (live plus dead) assemblage. In this sample, living calcareous foraminifera show a strong relationship with the dead assemblage. For example, the majority of stained tests belong to *Cassidulina carinata*, the most abundant taxon in the dead assemblage. This study therefore concentrates on the thanatocoenoses formed by the dead specimens.

A total of 200 calcareous benthic foraminiferal species belonging to 67 genera were identified in the 30 surface samples from the southwestern Marmara Sea (Appendix 1). Among these, 26 species (32 including associated morphotypes) show relative abundances higher than 5% in at least one sample from the Marmara transect. *Ammonia* sp. 1 (*sensu* Cimerman and Langer 1991), *Brizalina spathulata*, *Brizalina spathulata* forma *dilatatissima, Bulimina costata, Cassidulina carinata* and *Gyroidina umbonata* are the dominant species in the samples from the southwestern Marmara Sea, exhibiting abundances exceeding 20% (text-fig. 3). *Ammonia parkinsoniana*, *A. tepida* morphotypes 3 and 4, *Bulimina aculeata, Elphidium granosum* forma *lidoense*, *E. poeyanum* forma *decipiens* and *Valvulineria perlucida* are common with abundances ranging between 10 and 20%.

When species are plotted against water depth, five depth-related intervals are apparent (text-fig. 4). These intervals are represented by faunal breaks, notably the sharp fall in the relative (%) abundance of *Cassidulina carinata* and the appearance of *Bulimina costata* between 130m and 140m, which separate clusters A and B. These intervals are confirmed by cluster analysis. The resulting dendrogram of Q-mode cluster analysis (text-fig. 5) represents the grouping of samples according to the relative abundance of calcareous species. At < 50% dissimilarity, the dendogram reveals three distinct clusters, A, B, and C, with Cluster C further subdivided into three subclusters. Subcluster C1 (one sample from 15m) is dominated by morphotypes of *Ammonia tepida* (note that morphotypes 3 and 4 were combined for Q-mode analysis), *Ammonia* sp. 1, *Elphidium excavatum* and *Valvulineria perlucida*. Subcluster C2 (samples from 30–50m) is represented by *Bulimina marginata* forma *aculeata, Cassidulina carinata, Discorbinella bertheloti* and *Elphidium granosum* forma *lidoense*. Subcluster C3 (two samples from 18–25m) is dominated by *Ammonia parkinsoniana, Elphidium granosum* forma *lidoense, Elphidium poeyanum* forma *decipiens, Neoconorbina terquemi* and *Valvulineria perlucida*. Cluster A (12 samples from 55–130m) is dominated by *Brizalina spathulata, Cassidulina carinata* and



TEXT-FIGURE 6
Variation of Fisher α index diversity values and percent dominance against water depth along the southwestern Marmara Sea transect.

Gyroidina umbonata. Cluster B (10 samples from 140 to 350m) is characterized by *Brizalina spathulata, Brizalina spathulata* forma *dilatatissima* and *Bulimina costata*. These clusters represent six distinct foraminiferal assemblages that may be viewed as foraminiferal biofacies and are interpreted as reflecting different ecological conditions, such as oxygen, temperature and salinity, which are associated with bathymetry, shelf morphology and substrate.

Diversity and Dominance

Fisher α index values along the southwest Marmara Shelf transect range from 8.9 in the shallowest sample (15m depth) to 26.7 in the deepest sample (350m depth), while dominance generally shows an inverse pattern to Fisher α index values (text-fig. 6). A high Fisher α index value indicates high diversity while high dominance is associated with low diversity. Along the transect, four distinct depth-related intervals were identified, reflecting changes in diversity and dominance.

1. The depth interval from 15–25m displays the lowest diversity and declining dominance, likely related to strong environmental gradients across the pycnocline.

2. The interval from 25 to 50m depth shows a rise in the Fisher α index and minimal dominance values. It correlates well with elevated temperature and oxygen concentrations associated with the Marmara Intermediate Water (text-fig. 2). This part of the Marmara Shelf is influenced by the summer influx of warmer, more oxygenated water of Mediterranean origin (Kaminski et al. in preparation).

3. The interval between 50 and 150m depth shows variable but generally declining Fisher α index values and (between 50 and 130m) rising dominance. It correlates well with a gradual but steady decline in temperature and oxygen concentrations. This depth interval represents the upper part of the Marmara Sea deep water (text-fig. 2), which is characterized by comparatively constant temperature and salinity below the main body of summer Mediterranean water flowing into the Marmara Sea. The slight mismatch between the dominance peak at 130m and the Fisher α minimum at 150m reflects the maximum percentage abundance of *Cassidulina carinata* at 130m.

4. The depth interval from 150 to 350m depth shows a steady rise in the Fisher α index and declining dominance values. This does not correlate with any observed trend identified in the hydrographical data in text-figure 2. However, a small rise in oxygen values at 325m depth (text-fig. 2) has been interpreted as possible evidence for a stronger winter Mediterranean inflow current that introduces better oxygenated water at this depth.

DISCUSSION

Benthic Foraminiferal Assemblages

The Q-mode cluster analysis identifies three depth-related associations of dead calcareous foraminifera across the Marmara transect:

Cluster A (55m – 130m)

Calcareous benthic foraminiferal assemblages are characterized by *Brizalina spathulata, Cassidulina carinata* and *Gyroidina umbonata.* These taxa are characteristically found in suboxic and dysoxic environments (definitions following Kaiho 1994). *Brizalina dilatata, Brizalina spathulata, Bulimina aculeata, Discorbinella bertheloti, Hyalinea balthica* and *Reussella spinulosa* are other important taxa. Elsewhere in the eastern Mediterranean, *Brizalina spathulata* (often confused with *Brizalina catanensis*) is reported from the infralittoral, and more commonly from the circalittoral zones and in epibathyal muds. It is found along with *Brizalina spathulata* forma *dilatatissima* in areas with low dissolved oxygen content on muddy substrates (Parker 1958). *Cassidulina carinata* is typical of circalittoral and bathyal muds from 70 to 700m (Parker 1958; Sgarrella and Moncharmont Zei 1993). *Gyroidina umbonata* is also typical of bathyal muds from 50–70m and deeper (Sgarrella and Moncharmont Zei 1993). *Brizalina dilatata* is reported as a mud dwelling species distributed from shallow to very deep water (Parker, 1958). *Brizalina spathulata* forma *dilatatissima* is a mud dweller found at all depths from near-shore environments to the deep ocean. In the Mediterranean, it is most common on the continental shelf and upper slope (Sgarrella and Moncharmont Zei 1993) in the depth range 100-200m. *Bulimina marginata* forma *aculeata* is widespread in the infralittoral area between 15 and 35m and is abundant at circalittoral and epibathyal depths down to about 300m (Sgarrella and Moncharmont Zei 1993). *Discorbinella bertheloti* is reported as frequent in the infralittoral and circalittoral zone, particularly on sandy substrates in the depth range 60–100m (Jorissen 1988). *Hyalinea balthica* is typical of the circalittoral zone and is more frequent in epibathyal muds between 90 and 500m (Parker 1958).

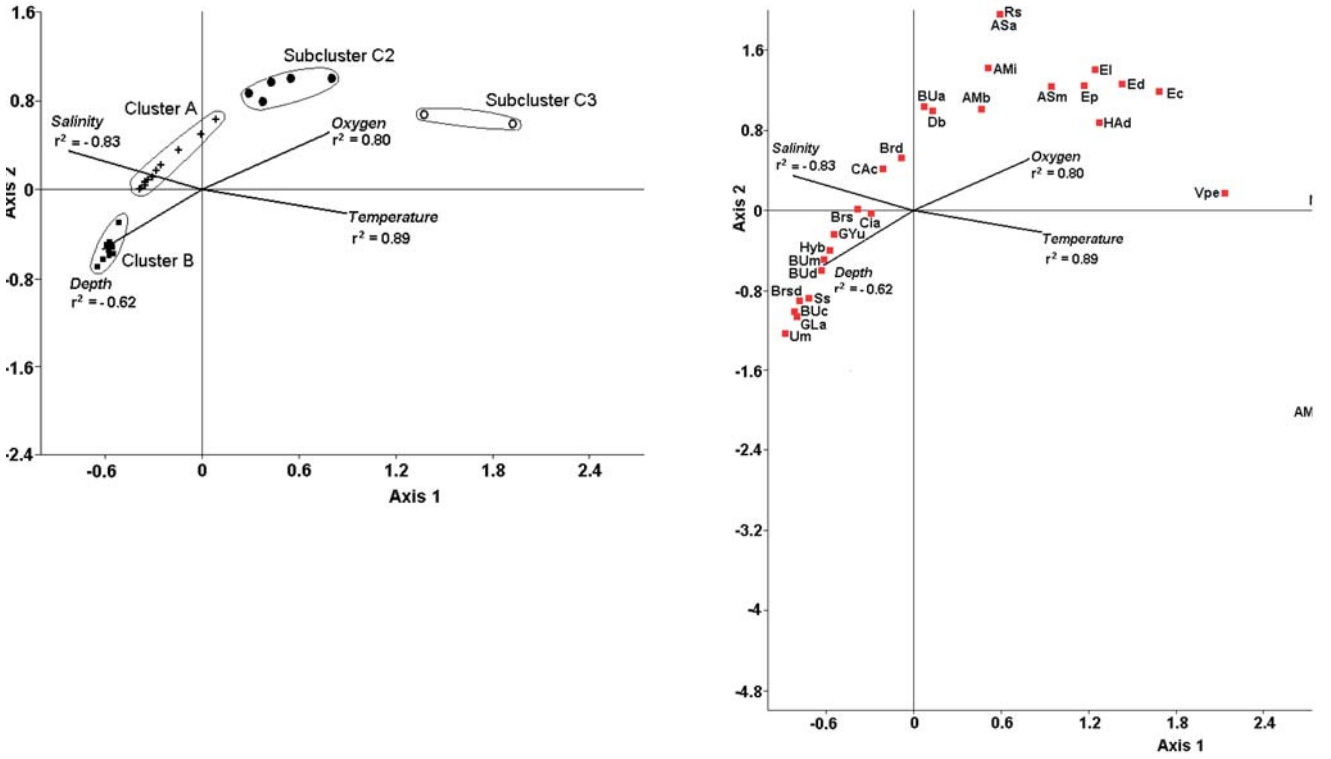
The Fisher α index values of samples comprising Cluster A range from 21.9 to 12.1 with a mean value of 18.0. This cluster coincides with interval 3 in text-fig. 6 and is characterized by decreasing diversity values with depth along the transect. Temperature and salinity are stable and oxygen values gradually decline, reflecting a water mass below the body of Mediterranean water flowing into the Marmara Sea. It is likely that the declining values of dissolved oxygen in this poorly mixed water mass promote lower diversity (Martins et al. 2007). This interpretation is supported by an observed rise in dominance, with peak of 15.3% at 130m (text-fig. 6).

Cluster A contains taxa that typically occur in circalittoral, mud-rich, suboxic to dysoxic settings. It can be characterized as the *Cassidulina carinata - Brizalina spathulata - Gyroidina umbonata* assemblage. This assemblage is comparable to the *Cassidulina carinata* and *Brizalina spathulata* assemblages from the eastern Mediterranean, which typically occur in the circalittoral zone and are associated with high productivity and low oxygen conditions (Rasmussen 2005).

Cluster B (140m – 350m)

Cluster B is dominated by *Brizalina spathulata, Brizalina spathulata* forma *dilatatissima* and *Bulimina costata*. Other abundant taxa include *Bulimina marginata* forma *denudata, Bulimina marginata* forma *marginata, Cibicides advenum, Globobulimina affinis, Gyroidinaumbonata, Hyalinea balthica, Sigmoilopsis schlumbergeri* and *Uvigerina mediterranea.*

Bulimina costata is recorded from the circalittoral zone and becomes abundant at deeper localities below 90-100m in bathyal muds (Sgarrella and Moncharmont Zei 1993). *Bulimina marginata* forma *denudata* is recorded from the infralittoral zone, is frequent in circalittoral and bathyal muds and able to live in seasonally stressed environments (Jorissen 1988). *Bulimina marginata* forma *marginata* is recorded in deep-water assemblages down to 1,016m (Parker 1958) and is found frequently in circalittoral and bathyal muds (Sgarrella and Moncharmont Zei 1993). *Cibicides advenum* occurs in close association with *Cibicides lobatulus* in the Marmara Sea samples. They share similar morphologies (distinguished mainly by the lobateness of the test) and therefore may have similar ecological characteristics. *Cibicides lobatulus* lives attached to firm substrates in turbulent or current-influenced environments (Sgarrella and Moncharmont Zei 1993). *Globobulimina affinis* is recorded from circalittoral and bathyal depths (Sgarrella and Moncharmont Zei 1993) and tolerates dysoxic conditions. *Sigmoilopsis schlumbergeri* is reported from muddy circalittoral and bathyal substrates at depths to 1,000m (Sgarrella and Moncharmont Zei 1993). *Uvigerina mediterranea* is recorded from the circalittoral zone downwards, but is more abundant in bathyal muds, with maximum abundances recorded between 400 and 1000m. It has been suggested that the bathymetric range of this species in the Eastern



Species markers:

AM1 =	*Ammonia* sp.1	BUa =	*Bulimina aculeata*	El =	*E. lidoense*
AMt =	*A. tepida*	BUc =	*Bu. costata*	Ep =	*E. poeyanum*
AMb =	*A. beccarii beccarii*	BUd =	*Bu. denudata*	GLa =	*Globobulimina affinis*
AMi =	*A. beccarii inflata*	BUm =	*Bu. marginata*	GYu =	*Gyroidina umbonata*
AMp =	*A. parkinsoniana*	CAc =	*Cassidulina carinata*	Hd =	*Haynesina depressula*
ASa =	*Asterigerinata adriatica*	Cia =	*Cibicides advenum*	Hb =	*Hyalinea balthica*
ASm =	*As. mamilla*	Db =	*Discorbinella bertheloti*	Nt =	*Neoconorbina terquemi*
Brd =	*Brizalina dilatata*	Ec =	*Elphidium crispum*	Rs =	*Reussella spinulosa*
Brs =	*Brizalina spathulata*	Ed =	*E. decipiens*	Ss =	*Sigmoilopsis schlumbergeri*
Brsd =	*Br. spathulata dilatatissima*	Ee =	*E. excavatum*	Um =	*Uvigerina mediterrenea*
				Vp =	*Valvulineria perlucida*

TEXT-FIGURE 7
Canonical correspondence analysis biplots of (a) sample-environment and (b) foraminiferal species-environment for the Marmara Sea transect. In a) the lone triangle represents the 15 m station; open circles represent stations 18m–25m; closed circles represent stations 30m–50m; crosses represent stations 55m–130m; squares represent stations 140m–350m. Only species with relative abundances higher than 5%.were included.

Mediterranean is reduced by poorer ventilation (Sgarrella and Moncharmont Zei 1993).

The Fisher α index values of samples included in Cluster B range from 14.0 to 26.3 with a mean value of 17.4. This cluster coincides with interval 4 in text-fig. 6 and is characterized by an increasing trend in Fisher α index values with depth along the transect. Temperature and salinity are stable and there is a rise in dissolved oxygen at 325m (text-figure 2). This could reflect the inflow of a more oxic water mass below the less well-ventilated body of Mediterranean water that characterizes Cluster A. The rise in oxygen promotes a higher diversity and consequently higher Fisher α index values (Martins et al. 2007). This interpretation is supported by a fall in percent dominance, with a minimal value of 4% at 350m (text-fig. 6).

This assemblage contains both circalittoral and upper epibathyal environmental indicators. It can be characterized as the *Brizalina spathulata* forma *dilatatissima – Bulimina costata* assemblage and is comparable to deep-water faunas reported from the Adriatic Sea (Jorissen 1988).

Cluster C (15m – 50m)

Cluster C comprises typical infralittoral and upper circa-littoral species. It is subdivided into three subclusters.

Subcluster C1 is the shallowest (at 15m) and is characterized by *Ammonia* sp 1 (*sensu* Cimerman and Langer 1991), *Ammonia tepida* (morphotypes 3 and 4), and *Valvulineria perlucida*. *Elphidium excavatum* is also found here in significant numbers. These species are known to tolerate hyposaline conditions and to be resistant to pollution (Rasmussen 2005). This subcluster, which is present at a single station, coincides with the interval of the lowest Fisher α index values (8.96) observed on the transect (text-fig. 6). It is associated with the brackish conditions observed at 15m, to which relatively few species are adapted. Species such as *Ammonia tepida* and *Valvulineria perlucida* are tolerant to hyposaline conditions and therefore dominate the assemblage. This is reflected in the high (12.43%) dominance value found at this station.

Subcluster C2 (the deepest of the three subclusters at 30–50m) is characterized by *Bulimina marginata* forma *aculeata, Cassidulina carinata, Discorbinella bertheloti* and *Elphidium granosum* forma *lidoense*. Other significant taxa include *Ammonia beccarii* forma *beccarii, Asterigerinata adriatica, Asterigerinata mamilla, Cibicides advenum, Elphidium poeyanum* forma *decipiens* and *Reussella spinulosa*. The assemblage contains taxa typical of infralittoral and circalittoral environments and both sandy and muddy substrates (Sgarrella and Moncharmont Zei 1993; Rasmussen 2005). This biofacies corresponds to the infralittoral–upper circalittoral zone. The Fisher α index ranges from 16.7 to 22.4 with an average of 19.6; there is a rising trend in diversity in this subcluster corresponding to interval 2 in text-figure 6. This rise in diversity is attributed to the inflow of the Mediterranean countercurrent that brings better-oxygenated, highly saline and warmer waters into the Marmara Sea at these depths during the summer. A corresponding decline in percent dominance is also observed in this cluster, with a low value of 4.9% at 50m.

Subcluster C3 (18m–25m) is characterized by *Ammonia parkinsoniana, Elphidium granosum* forma *lidoense, Elphidium poeyanum* forma *decipiens, Neoconorbina terquemi* and *Valvulineria perlucida.* Other significant taxa include *Ammonia beccarii* forma *inflata, Bulimina marginata* forma *aculeata, Elphidium crispum, Elphidium poeyanum* forma *poeyanum* and *Haynesina depressula*. These species are reported from muddy sands of the infralittoral zone (Sgarrella and Moncharmont Zei 1993; Rasmussen 2005). Fisher α index values range from 12.6–12.1 and indicate a rise in diversity deeper into the pycnocline. This is associated with an increase in salinity at 18 – 25m that provides favourable conditions, allowing more species to survive at these depths. The dominance values fall to 7.2% as a result.

The cluster C assemblage consists of predominantly infralittoral species that inhabit muddy and sandy substrates. The assemblage can be characterized as the *Ammonia* spp - *Elphidium* spp assemblage and is comparable to many Mediterranean neritic assemblages (Jorissen 1988; Rasmussen 2005).

Relationship between foraminiferal assemblages and environmental parameters

The canonical correspondence analysis confirms the presence of the three clusters and subclusters identified in the Q-Mode cluster analysis when plotted in ordinance space (text-fig. 8a). The method involves a correspondence analysis of a site/species matrix where each site has known values for one or more environmental variable; in the present study these variables are temperature, salinity, oxygen and depth. The ordination axes are linear combinations of the environmental variables that allow a direct gradient analysis. Any changes in species abundances are considered to be a response to these gradients. The lengths of the environmental arrows indicate their relative importance in explaining the variance in the foraminiferal data. The orientation of the arrows represent their correlation to the ordination axes. Within the present data set, correlations of environmental variables with axes 1 and 2 show that temperature and salinity are correlated to axis 1 and depth and oxygen are jointly correlated to axis 1 and 2. The ordination can be divided into two sections. Clusters A and B plot on the left side and are related to greater water depth, lower oxygen and temperature and higher salinity. The more neritic assemblages represented by the three subclusters of cluster C plot on the right side and are related to shallower water depths, higher oxygen and temperature, and low salinity. In addition, subcluster C1, represented by a single station at 15m, is the most positively associated with axis 1 and the most negatively associated with axis 2; it represents the high temperature, low salinity, shallow depth, and high oxygen conditions characteristic of Black Sea surface water. Conversely, subclusters C3 and C2, which reflect the pycnocline and the Mediterranean countercurrent, respectively, weigh progressively more negatively along axis 1 and are shifted to positive positions along axis 2, where high oxygen concentration becomes the dominant environmental factor, while temperature falls and salinity increases. Cluster A, which represents stations of intermediate depths, plots negatively along axis 1 and positively against axis 2 and is associated with increasing salinity and a shift from high to progressively lower oxygen conditions as depth increases. Cluster B corresponds to the deepest stations and plots negatively on axes 1 and 2, which represent the influence of depth and dissolved oxygen as important controls on foraminiferal distributions.

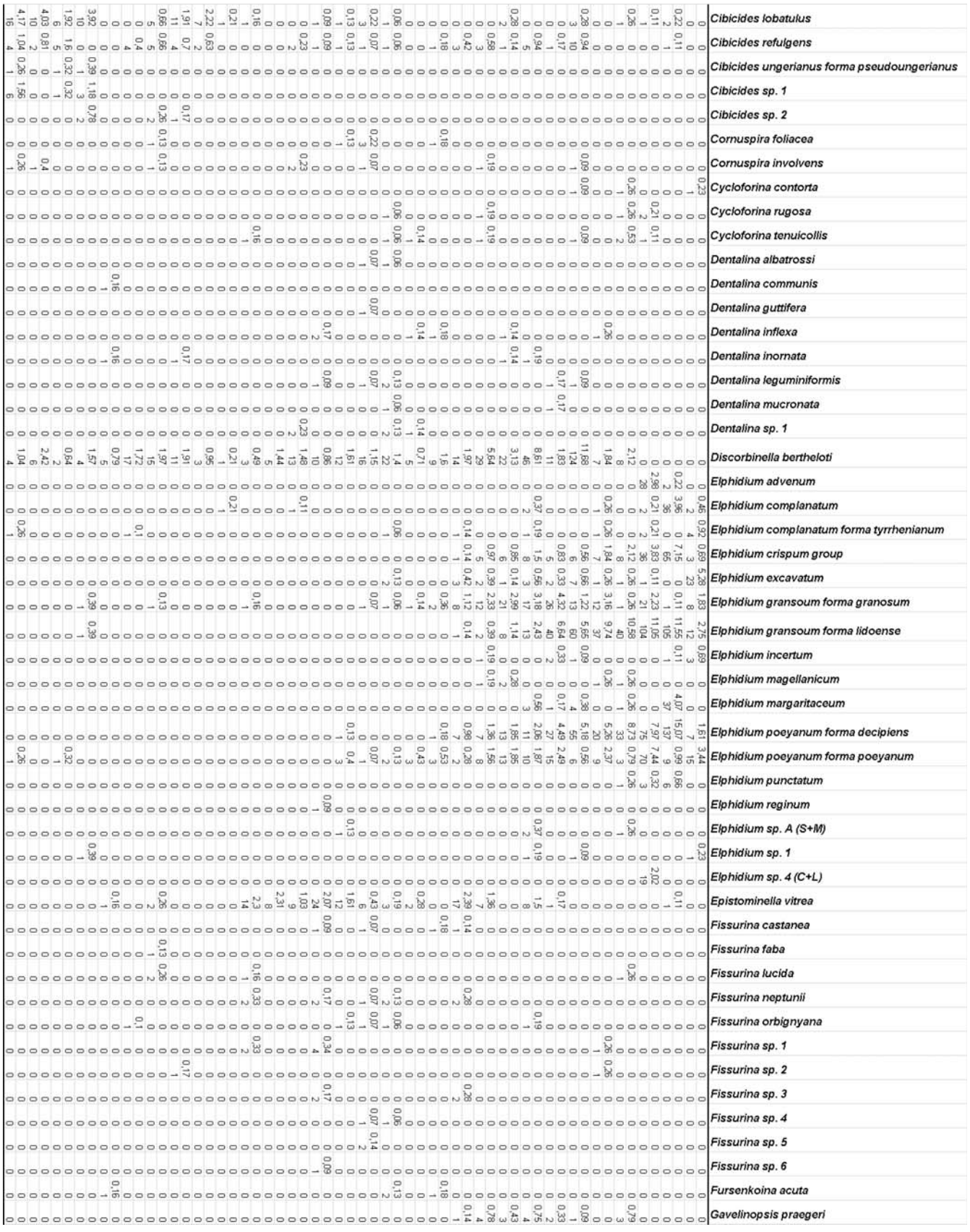
On the species-environment biplot, the position of species (projected perpendicularly onto the environmental arrows) approximates their weighted average optimum along each environmental variable (text-fig. 8b), making it possible to identify species characteristic of a particular environment. For example, neritic genera such as *Ammonia*, *Elphidium* and *Asterigerinata* plot on the right side of the biplot (associated with high temperature, low salinity, shallower water and high oxygen concentrations). In contrast, genera such as *Brizalina* and *Bulimina* are found on the left side of the biplot (related to lower temperature, higher salinity, deeper water depth and lower oxygen concentrations). In addition, most species share ordinance spaces that are comparable to the six clusters observed in the station-environment plot (text-fig. 8a), a pattern that is consistent with our interpretations of the different foraminiferal assemblage clusters discussed above. From the deepest to the shallowest cluster, the patterns observed are as follows:

Cluster B: Of all the environmental parameters, increased depth and reduced bottom-water oxygen concentrations seem to exert the dominant controls on species such as *Bulimina costata Bulimina marginata* formas *marginata* and *denudata*, *Brizalina spathulata* forma *dilatatissima* that plot negatively on both axes. These species are characteristic of Cluster B (stations between 140 and 350m) and plot within their ordination range (see figure 8a)**.**

APPENDIX 1
Numbers of foraminiferal specimens counted in each sample.

Sample Number
Adelosina carinata-striata
Adelosina italica
Adelosina pulchella
Adelosina longirostra
Ammonia beccarii forma beccarii
Ammonia beccarii forma inflata
Ammonia parkinsona
Ammonia tepida type 1
Ammonia tepida type 2
Ammonia tepida type 3
Ammonia tepida type 4
Ammonia sp. 1 (C+L)
Ammonia sp. (2 C+L)
Amphicoryna hispida
Amphicoryna intercellularis
Amphicoryna proxima
Amphicoryna scalaris
Astacolus crepidulus
Asterigerinata adriatica
Asterigerinata mamilla
Biloculinella depressa
Biloculinella globula
Biloculinella labiata
Biloculinella wiesneri
Bolivina aenariensis
Bolivina pseudopuncata
Bolivina striata
Bolivina variabilis
Bolivina sp. 1
Brizalina alata
Brizalina catanensis
Brizalina dilatata
Brizalina spathulata
Buccella granulata
Bulimina aculeata
Bulimina costata
Bulimina denudata
Bulimina elongata
Bulimina marginata
Bulimina pagoda
Cassidulina carinata
Cassidulina obtusa
Challengerella bradyi
Chilostomella mediterranensis
Cibicidella variabilis
Cibicides advenum
Cibicides dutemplei

APPENDIX 1, *continued.*
Numbers of foraminiferal specimens counted in each sample.

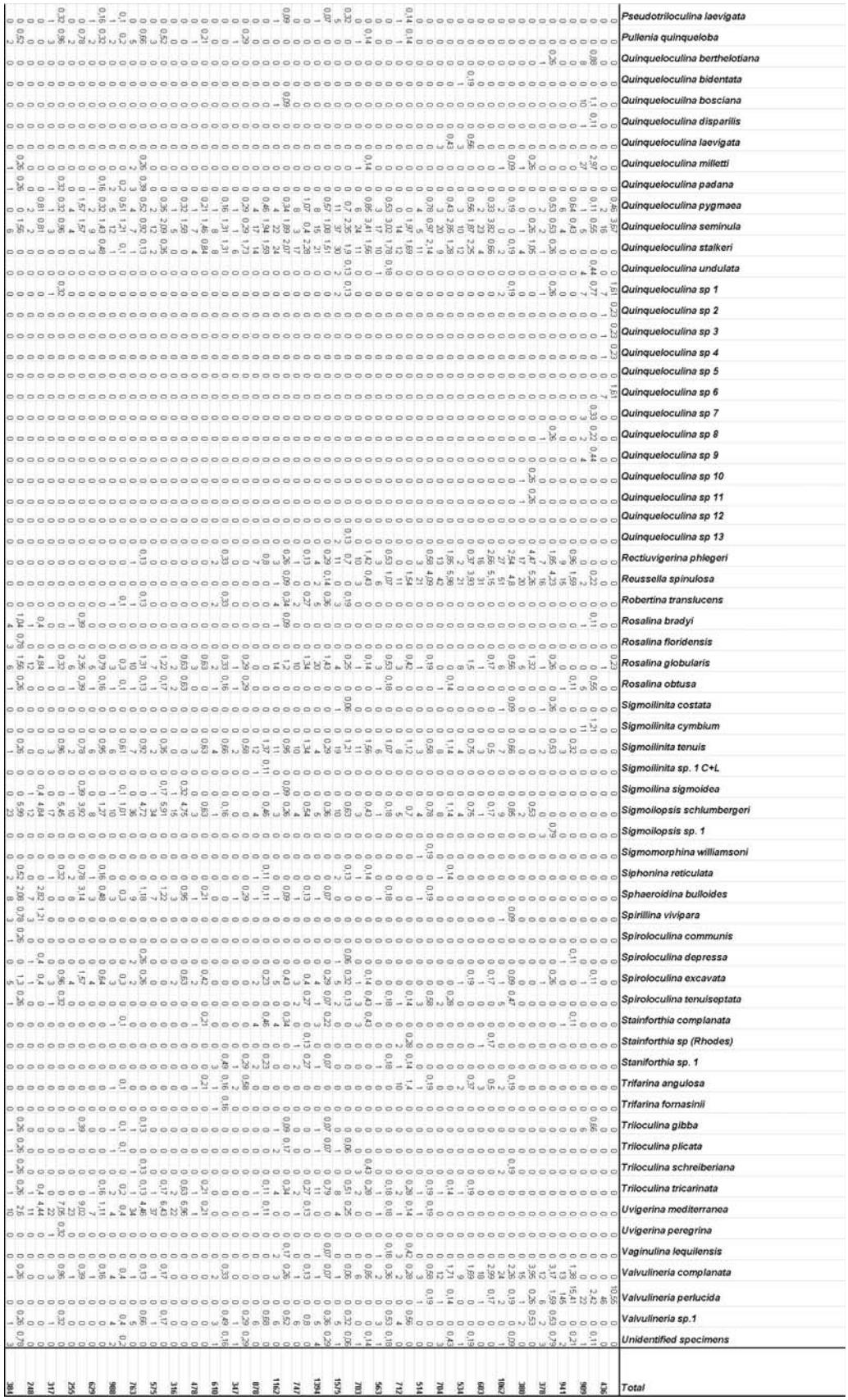


Cibicides lobatulus
Cibicides refulgens
Cibicides ungerianus forma pseudoungerianus
Cibicides sp. 1
Cibicides sp. 2
Cornuspira foliacea
Cornuspira involvens
Cycloforina contorta
Cycloforina rugosa
Cycloforina tenuicollis
Dentalina albatrossi
Dentalina communis
Dentalina guttifera
Dentalina inflexa
Dentalina inornata
Dentalina leguminiformis
Dentalina mucronata
Dentalina sp. 1
Discorbinella bertheloti
Elphidium advenum
Elphidium complanatum
Elphidium complanatum forma tyrrhenianum
Elphidium crispum group
Elphidium excavatum
Elphidium gransoum forma granosum
Elphidium gransoum forma lidoense
Elphidium incertum
Elphidium magellanicum
Elphidium margaritaceum
Elphidium poeyanum forma decipiens
Elphidium poeyanum forma poeyanum
Elphidium punctatum
Elphidium reginum
Elphidium sp. A (S+M)
Elphidium sp. 1
Elphidium sp. 4 (C+L)
Epistominella vitrea
Fissurina castanea
Fissurina faba
Fissurina lucida
Fissurina neptunii
Fissurina orbignyana
Fissurina sp. 1
Fissurina sp. 2
Fissurina sp. 3
Fissurina sp. 4
Fissurina sp. 5
Fissurina sp. 6
Fursenkoina acuta
Gavelinopsis praegeri

APPENDIX 1, *continued.*
Numbers of foraminiferal specimens counted in each sample.

0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0,09	0	0	1	0,07	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*Glandulina laevigata*
21	5,47	8	3,23	11	3,53	8	3,14	7	1,11	16	1,62	7	0,92	12	2,09	4	1,27	10	2,09	3	0,49	0	0	4	0,46	8	0,69	4	0,54	6	0,43	23	1,46	0	0	5	0,89	0	0	0	0	2	0,28	0	0	2	0,33	2	0,19	0	0	0	0	1	0,11	0	0	0	0	*Globobulimina affinis*
4	1,04	0	0	2	0,64	0	0	1	0,16	2	0,2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0,07	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*Globobulimina turgida*
1	0,26	2	0,81	10	3,21	4	1,57	7	1,11	11	1,11	15	1,97	8	1,39	4	1,27	1	0,21	0	0	0	0	1	0,11	5	0,43	2	0,27	7	0,5	4	0,25	1	0,14	4	0,71	1	0,14	11	2,14	13	1,85	20	3,75	17	2,82	51	4,8	13	3,42	8	2,12	0	0	0	0	0	0	*Globocassidulina oblonga*
0	0	0	0	1	0,32	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0,07	1	0,06	0	0	0	0	2	0,28	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*Globocassidulina subglobosa*
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0,06	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0,23	*Guttulina lactea*
22	5,73	12	4,84	6	1,92	2	0,78	37	5,88	78	7,89	28	3,67	8	1,39	3	0,95	65	13,6	50	8,2	55	15,85	88	10,02	219	18,93	122	16,33	170	12,2	348	22,1	87	12,38	54	9,59	27	3,79	6	1,17	6	0,85	2	0,37	7	1,16	2	0,19	0	0	0	0	0	0	0	0	0	0	*Gyroidina umbonata*
0	0	0	0	0	0	0	0	4	0,64	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0,13	1	0,07	1	0,06	0	0	1	0,18	8	1,12	0	0	2	0,28	0	0	5	0,83	10	0,94	6	1,58	8	2,12	49	5,21	14	1,54	11	2,52	*Haynesina depressula*
0	0	0	0	0	0	0	0	1	0,16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0,29	0	0	0	0	2	0,36	3	0,42	1	0,19	1	0,14	1	0,19	3	0,5	7	0,66	5	1,32	4	1,06	1	0,11	2	0,22	3	0,69	*Haynesina sp. 1 (C+L)*
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0,16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0,11	7	0,77	1	0,23	*Haynesina sp. 2 (C+L)*
1	0,26	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0,17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0,09	0	0	2	0,53	1	0,11	1	0,11	1	0,23	*Haynesina sp. 3 (C+L)*
8	2,08	3	1,21	8	2,56	0	0	37	5,88	51	5,16	40	5,25	17	2,96	9	2,85	16	3,35	18	2,95	12	3,46	30	3,42	86	7,4	63	8,43	99	7,1	53	3,37	30	4,27	17	3,02	4	0,56	5	0,97	5	0,71	1	0,19	6	1	0	0	0	0	0	0	0	0	0	0	1	0,23	*Hyalinea baltica*
0	0	0	0	0	0	0	0	0	0	1	0,1	0	0	1	0,17	0	0	0	0	0	0	1	0,29	0	0	2	0,17	0	0	2	0,14	2	0,13	0	0	1	0,18	0	0	0	0	0	0	1	0,19	1	0,17	0	0	2	0,53	0	0	0	0	1	0,11	0	0	*Lagena doveyensis*
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*Lagena gracillima*
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0,16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*Lagena laevis*
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0,13	2	0,14	3	0,19	0	0	0	0	0	0	0	0	1	0,14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*Lagena striata*
0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0,17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0,13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*Lagena semistriata*
0	0	0	0	0	0	0	0	0	0	0	0	1	0,13	0	0	0	0	1	0,21	0	0	0	0	0	0	4	0,34	0	0	0	0	1	0,06	1	0,14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0,26	0	0	1	0,11	0	0	0	0	*Lagena substriata*
0	0	0	0	0	0	0	0	0	0	0	0	1	0,13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*Lagena sp 1*
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0,06	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*Lagena sp 2 C+L*
2	0,52	2	0,81	1	0,32	4	1,57	4	0,64	0	0	3	0,39	2	0,35	0	0	0	0	1	0,16	1	0,29	1	0,11	3	0,26	3	0,4	3	0,22	3	0,19	0	0	0	0	1	0,14	0	0	1	0,14	0	0	1	0,17	0	0	0	0	0	0	0	0	0	0	0	0	*Lenticulina cultrata*
1	0,26	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0,09	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*Lenticulina gibba*
0	0	0	0	0	0	0	0	1	0,16	1	0,1	0	0	1	0,17	0	0	0	0	0	0	0	0	0	0	1	0,09	0	0	1	0,07	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*Lenticulina peregrina*
5	1,3	2	0,81	3	0,96	2	0,78	2	0,32	2	0,2	5	0,66	4	0,7	4	1,27	3	0,63	1	0,16	4	1,15	2	0,23	2	0,17	7	0,94	5	0,36	6	0,38	3	0,43	5	0,89	2	0,28	0	0	4	0,57	2	0,37	0	0	1	0,09	0	0	0	0	0	0	0	0	0	0	*Melonis barleanum*
0	0	1	0,4	0	0	0	0	2	0,32	2	0,2	2	0,26	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0,43	11	0,7	4	0,57	0	0	0	0	1	0,19	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*Miliolinella elongata*
0	0	1	0,4	0	0	0	0	1	0,16	1	0,1	1	0,13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0,14	0	0	2	0,28	0	0	0	0	0	0	0	0	0	0	0	0	1	0,26	0	0	0	0	0	0	*Miliolinella dilatata*
1	0,26	0	0	0	0	1	0,39	0	0	2	0,2	0	0	2	0,35	1	0,32	1	0,21	0	0	0	0	1	0,11	3	0,26	0	0	2	0,14	1	0,06	0	0	0	0	0	0	0	0	0	0	2	0,37	0	0	0	0	0	0	1	0,26	0	0	0	0	0	0	*Miliolinella labiosa*
6	1,56	1	0,4	0	0	0	0	6	0,95	10	1,01	6	0,79	6	1,04	1	0,32	3	0,63	12	1,97	1	0,29	4	0,46	19	1,64	11	1,47	27	1,94	31	1,97	17	2,42	5	0,89	5	0,7	2	0,39	4	0,57	1	0,19	4	0,66	3	0,28	3	0,79	13	3,44	2	0,21	4	0,44	0	0	*Miliolinella subrotunda*
0	0	0	0	0	0	1	0,39	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*Neoconorbina posidonicola*
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0,06	0	0	0	0	0	0	0	0	0	0	1	0,19	1	0,17	0	0	0	0	4	1,06	1	0,11	81	9,05	0	0	*Neoconorbina terquemi*
0	0	0	0	0	0	0	0	0	0	0	0	1	0,13	5	0,87	0	0	0	0	2	0,33	1	0,29	0	0	1	0,09	3	0,4	1	0,07	5	0,32	3	0,43	3	0,53	8	1,12	1	0,19	5	0,71	8	1,5	2	0,33	3	0,28	1	0,26	8	2,12	3	0,32	0	0	4	0,92	*Neoconorbina sp 1*
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*Neolenticulina peregrina*
1	0,26	0	0	0	0	0	0	1	0,16	1	0,1	0	0	0	0	0	0	1	0,21	1	0,16	0	0	2	0,23	5	0,43	3	0,4	4	0,29	10	0,63	2	0,28	1	0,18	1	0,14	2	0,39	0	0	1	0,19	1	0,17	1	0,09	4	1,05	0	0	0	0	0	0	0	0	*Nonionella stella*
3	0,78	0	0	1	0,32	0	0	1	0,16	3	0,3	0	0	1	0,17	0	0	2	0,42	1	0,16	1	0,29	3	0,34	7	0,6	4	0,54	3	0,22	10	0,63	2	0,28	1	0,18	1	0,14	5	0,97	5	0,71	2	0,37	8	1,33	13	1,22	9	2,37	11	2,91	45	4,78	0	0	0	0	*Nonionella turgida group*
1	0,26	1	0,4	0	0	1	0,39	0	0	0	0	0	0	0	0	0	0	0	0	1	0,16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*Nonionella sp A*
0	0	0	0	0	0	0	0	2	0,32	2	0,2	0	0	0	0	0	0	1	0,21	3	0,49	0	0	1	0,11	5	0,43	2	0,27	2	0,14	3	0,19	3	0,43	0	0	2	0,28	1	0,19	0	0	1	0,19	1	0,17	0	0	2	0,53	0	0	0	0	0	0	0	0	*Nonionella sp B*
0	0	1	0,4	0	0	0	0	0	0	1	0,1	0	0	0	0	0	0	5	1,05	1	0,16	0	0	1	0,11	2	0,17	1	0,13	6	0,43	10	0,63	6	0,85	3	0,53	4	0,56	2	0,39	5	0,71	0	0	0	0	1	0,09	1	0,26	0	0	1	0,11	0	0	0	0	*Nonionella sp C*
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0,66	1	0,29	4	0,46	10	0,86	0	0	2	0,14	6	0,38	1	0,14	0	0	4	0,56	4	0,78	1	0,14	2	0,37	1	0,17	0	0	3	0,79	0	0	0	0	0	0	0	0	*Nonionella sp D*
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*Oolina acuticostata*
2	0,52	0	0	0	0	0	0	0	0	0	0	0	0	1	0,17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0,07	0	0	1	0,14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*Oolina hexagona*
1	0,26	0	0	0	0	0	0	0	0	1	0,1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*Oolina melo*
0	0	0	0	0	0	0	0	0	0	1	0,1	0	0	0	0	0	0	0	0	2	0,33	0	0	0	0	1	0,09	0	0	4	0,29	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*Ophthalmidium acutimargo*
1	0,26	0	0	0	0	0	0	2	0,32	0	0	2	0,26	0	0	0	0	0	0	0	0	0	0	0	0	3	0,26	1	0,13	3	0,22	1	0,06	0	0	2	0,36	4	0,56	2	0,39	0	0	0	0	1	0,17	0	0	0	0	0	0	0	0	0	0	0	0	*Parafissurina staphyllearia*
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0,09	0	0	0	0	0	0	0	0	0	0	*Parafissurina sp 1*
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0,09	0	0	0	0	1	0,06	0	0	0	0	0	0	1	0,19	0	0	1	0,19	3	0,5	6	0,56	0	0	2	0,53	0	0	16	1,76	0	0	*Parrellina verriculata*
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0,11	0	0	*Patellina corrugata*
3	0,78	2	0,81	0	0	2	0,78	0	0	0	0	0	0	1	0,17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0,19	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*Pygro anomala*
3	0,78	1	0,4	0	0	1	0,39	0	0	2	0,2	1	0,13	6	1,04	0	0	1	0,21	0	0	0	0	0	0	2	0,17	1	0,13	0	0	3	0,19	2	0,28	0	0	0	0	1	0,19	3	0,43	0	0	0	0	2	0,19	0	0	0	0	0	0	0	0	0	0	*Pygro elongata*
0	0	1	0,4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*Pygro inornata*
2	0,52	0	0	1	0,32	1	0,39	4	0,64	2	0,2	7	0,92	3	0,52	0	0	1	0,21	0	0	1	0,29	1	0,11	3	0,26	6	0,8	16	1,15	8	0,51	7	1	7	1,24	6	0,84	12	2,33	23	3,28	15	2,81	9	1,5	37	3,48	7	1,84	2	0,53	0	0	0	0	1	0,23	*Planorbulina mediterranensis*
0	0	0	0	1	0,32	1	0,39	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0,26	1	0,11	0	0	0	0	*Pseudoeponides falsobeccarii*

APPENDIX 1, *continued.*
Numbers of foraminiferal specimens counted in each sample.



Cluster A: Species that plot negatively with axis 1 but positively with axis 2 include *Brizalina dilatata, Brizalina spathulata* and *Cassidulina carinata*. These species are characteristic of Cluster A (stations between 55 and 130m) and plot within their ordination range. However, it remains unclear whether salinity plays a significant role in foraminifera distributions here as taxa plot on a linear trend similar to that of taxa plotting within Cluster B. Species appear to be significantly influenced by low oxygen concentrations and increased depth, suggesting that these are key factors in determining species distribution between 55 and 130m with a third factor (salinity or perhaps another factor not taken into account in this study such as substrate) offsetting the trend.

Cluster C2: Species that plot positively on both axes include *Bulimina marginata* forma *aculeata*, *Discorbinella bertheloti* and *Elphidium granosum* forma *lidoense*; these species are characteristic of Cluster C2 (stations between 30 and 50m) and plot broadly within their ordination range, although there is more scatter in their distribution than in other clusters. In this case, high dissolved oxygen values (elevated by the introduction of the Mediterranean countercurrent) seems to be the dominant environmental factor influencing foraminiferal distributions. However, the amount of scatter suggests that other factors not considered in this study, in addition to oxygen and depth, may significantly influence some species.

Cluster C3: This cluster, which corresponds to the pycnocline (between 18 and 25m), seems to comprise two groups of species that are influenced by different environmental variables. Species that plot positively on axis 2 but are close to 0 on axis 1, such as *Ammonia parkinsoniana*, *Valvulineria perlucida* and *Neoconorbina terquemi,* are characteristic of the pycnocline and are influenced significantly by temperature and salinity rather than dissolved oxygen and depth. On the other hand, species such as *Elphidium crispum*, *Elphidium poeyanum* forma *decipiens* and *Haynesina depressula* correlate with dissolved oxygen.

Cluster C1: Species that plot positively with axis 1 and negatively with axis 2 include *Ammonia tepida, Ammonia* sp. 1 and *Elphidium excavatum*; these species are characteristic of Cluser C1 and reflect the Black Sea surface water. Elevated temperature and reduced salinity appear to be the dominant influences on the distribution of these species.

CONCLUSIONS

The continental shelf and upper slope of the southwestern Marmara Sea is characterized by a diverse assemblage of dead calcareous benthic foraminifera, with 200 species recognized and Fisher α index values ranging from 8.9 to 26.7. A total of 26 species and their respective morphotypes show a relative abundance >5% in at least one sample. Q-Mode Cluster Analysis based on these common species allows the recognition of three distinct foraminiferal assemblages:

Cluster A occurs at depths between 55 and 130m and comprises characteristic dysoxic and suboxic, circalittoral taxa, notably *Brizalina spathulata, Cassidulina carinata* and *Gyroidina umbonata*. Diversity (Fisher α index) decreases with depth while dominance increases. This assemblage is related to a fine-grained, muddy substrate and a poorly ventilated watermass leading to decreasing bottom-water oxygen concentrations.

Cluster B occurs at depths between 140 and 350m and is characterized by suboxic and dysoxic species typical of circalittoral and upper epibathyal environments. A small rise in oxygen concentration at 325m coincides with higher diversity and a fall in dominance.

Cluster C is found in the shallower samples ranging from 15 to 50m depth and comprises characteristic infralittoral species. The cluster can further be subdivided into subclusters C1, C3 and C2, representing assemblages associated, respectively, with the brackish Black Sea surface flow (0-15m), the pycnocline (15-25m), and the inflow of warm, saline Mediterranean water within the Marmara intermediate water mass (30–50m). Subcluster C1 exhibits low diversity and high dominance values at the shallowest brackish sites, with higher diversity values and lower dominance associated with more saline Mediterranean waters (C2).

Canonical correspondence analyses suggest that depth, dissolved oxygen, temperature and salinity all have significant influences on the distribution of foraminiferal assemblages along the transect. Above 25m, temperature and salinity are the dominant factors influencing species present in Cluster C1 (15m) and C3 (18–25m), representing the Black Sea surface water and pycnocline respectively. Below 25m, clusters C2 (30–50m), A (55–130m), and B (140–350m) are influenced predominantly by dissolved oxygen and depth. The C2 assemblage is influenced by higher oxygen concentrations, whereas Clusters A and B are related to a trend of decreasing oxygen, with increasing depth.

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RÉSUMÉ

Les faunes de foraminifères vivants (colorés au Rose Bengale) ont été analyses à 8 stations le long d'un transect bathymétrique (282-4987 m) sur la marge portugaise. Du plateau externe vers la plaine abyssale, une succession d'assemblages est trouvée en relation avec la diminuation du niveau trophique. La densité des faunes, la richesse spécifique et la diversité diminuent plus rapidement avec la profondeur pour les foraminifères carbonatés que pour les foraminifères agglutinés. Aux sites mésotrophes et oligotrophes les espèces carbonatées sont généralement limitées au centimètre supérieur. Les espèces agglutinées sont peu diversifies à la station la moins profonde, à cause d'une competition avec les espèces carbonatées et la pénétration d'oxygène très faible. Aux stations plus profondes, leurs diversité et ALD_{10} augmentent en réponse à la penetration d'oxygène et la bioturbation plus importantes. Aux stations les plus profondes, les foraminifères agglutinés montrent une faible diversité, et sont de nouveau limités à la surface du sediment. Un transect latitudinal regroupe 7 autres stations, de pente ouverte et de canyon ouvert, à une profondeur d'environ 1000 m. Dans les canyons sousmarins, les densités des faunes, dominées par des espèces endopéliques intermédiares et profondes, sont largement supérieures, en accord avec des teneurs en CPE plus élévées. Dans le canyon de Nazaré, des faibles teneurs en oxygène causent une diversité minimale. La variabilité temporelle apparait ètre beaucoup plus importante dans les canyons sous-marins, où des perturbations sédimentaires et les apports organiques sont maximaux.

ABSTRACT

Live (Rose Bengal stained) foraminifera were analysed at 8 stations along a latitudinal bathymetric transect (282-4987 m) across the Portuguese margin open slope. A succession of foraminiferal assemblaghes occurs with increasing depth, related to the decrease of trophic level. Standing stocks, species richness and diversity decrease more rapidly with depth for calcareous than for agglutinated taxa. Calcareous taxa are generally restricted to the uppermost cm in mesotrophic and oligotrophic sites. Agglutinated taxa have low diversity at the most shallow, eutrophic station due to competition with calcareous foraminifera and very shallow oxygen penetration. At greater depths, their diversity and ALD_{10} increase in response to deeper oxygen penetration and macrofaunal bioturbation. At the deepest, oligotrophic environments, where their diversity is low, agglutinated taxa are again restricted to shallow microhabitats. Another 7 stations from ~1000 m water depth were sampled along a longitudinal transect consisting of open slope and canyon environments. Total foraminiferal standing stocks, dominated by intermediate and deep infaunal species, are much higher in canyon stations than on the open slope, related to the elevated CPE concentrations within the canyons. Low oxygen conditions decrease foraminiferal diversity on the Nazaré canyon terrace by inhibiting many shallow infaunal taxa and increasing the dominance of intermediate and deep infaunal species. Temporal variability appears to be much greater in canyon environments, where both sedimentary disturbance and organic supplies are maximal, compared to the relatively stable open slope environment.