Benthic foraminifera: ecological indicators of past and present oceanic environments

- A glance at the modern assemblages from the Portuguese submarine canyons

Foraminifera are single celled protists, and among the most abundant unicellular organisms in the modern ocean. Many build a mineral shell, often referred to as 'test'. The test is typically made of calcium carbonate or an agglutinated bundle of grains (see figure 1 for examples). Some foraminifera, known as allogromids, have a completely organic test. The agglutinated foraminifera can be extremely selective while building their tests. Some species prefer to pick only sponge spicules or coccoliths (figure 1, specimens 11–12), while others are less specific and can use anything from a quartz grain to shell fragments of other foraminifera (figure 1, specimen 14).

The shape, or morphology, of the test is extremely important in the taxonomy of foraminifera. To date, more than 2140 benthic (ocean floor-dwelling) species have been recognised (Murray 2007), while some 40–50 modern species of planktonic (water column dwelling) foraminifera have been described (Sen Gupta, 1999). Benthic foraminifera are commonly found in all ocean sediments, inhabiting vast ranges of environments from the coastal zone to the deep ocean trenches. In addition, a few benthic species have been described from fresh water (Holzmann and Pawlowski 2002) and even in damp terrestrial environments (Meisterfeld et al. 2001).

Benthic foraminifera have been extensively studied by geologists due to their good fossilisation potential. Traditionally, changes in foraminiferal morphology have been used to define stratigraphic marker horizons without investigating the ecological reasons for faunal changes. However, during the second half of the 20th century Fred B. Phleger (e.g. Phleger 1951, 1954) pioneered research into foraminiferal ecology, and accordingly it was understood that the modern foraminiferal distribution can be used as an analogue for the past distributions recorded in sediments. From this point, foraminifera, or forams, took centre stage in the science of palaeoclimatology the interpretation of Earth's climate history.

Nowadays, it is commonly believed that deep sea foraminiferal assemblages are mainly controlled by two often inversely co-varying parameters: oxygen and food (or in fact, labile organic carbon) availability. This relationship was well demonstrated by Jorissen et al. (1995) in terms of the TROX (TRophic OXygen) model (figure 2). According to this model, in food-limited and well-oxygenated environments, foraminiferal communities are restricted to the surficial sediments due to low food supply, and consist of epifaunal, or surface dwelling, taxa specialised to live in oligotrophic regions. In eutrophic environments, where food is plentiful and the pore water oxygen content is often reduced, the foraminiferal assemblage is dominated by infaunal taxa.

Submarine canyons are interesting environments to further our ecological understanding of benthic foraminifera. Canyons act as under water river systems transporting sediment and other detritus from the shallow seas to the abyss (van Weering et al. 2002). Further, they can operate as sediment traps, obstructing across-slope sediment transport, thus leading to elevated sedimentation rates (van Weering et al. 2002, de Stigter et al. 2007) and enhanced carbon deposition (Epping et al. 2002) in the canyons in contrast to the open slope environment. Due to the active sedimentary regime of these environments, organisms living in the canyons must adapt to the prevailing conditions, and thus the presence of highly specialised faunal assemblages may be anticipated. The canyon activity, however, may vary in time and space, thus during a dormant period more stable ecosystems may develop.

A detailed study of living benthic foraminiferal assemblages from the Nazaré and Lisbon-Setúbal canyons (southern Portugal) was carried out as part of my PhD thesis. The sediment samples were collected using a multiple corer (figure 3), in order to retrieve undisturbed deep sea sediments. The collected cores were sliced horizontally into segments to investigate changes in species distribution with depth. Foraminiferal assemblages were investigated down to 5 cm depth in sediment, assuming that the majority of living fauna is found within this sediment zone. The samples were then

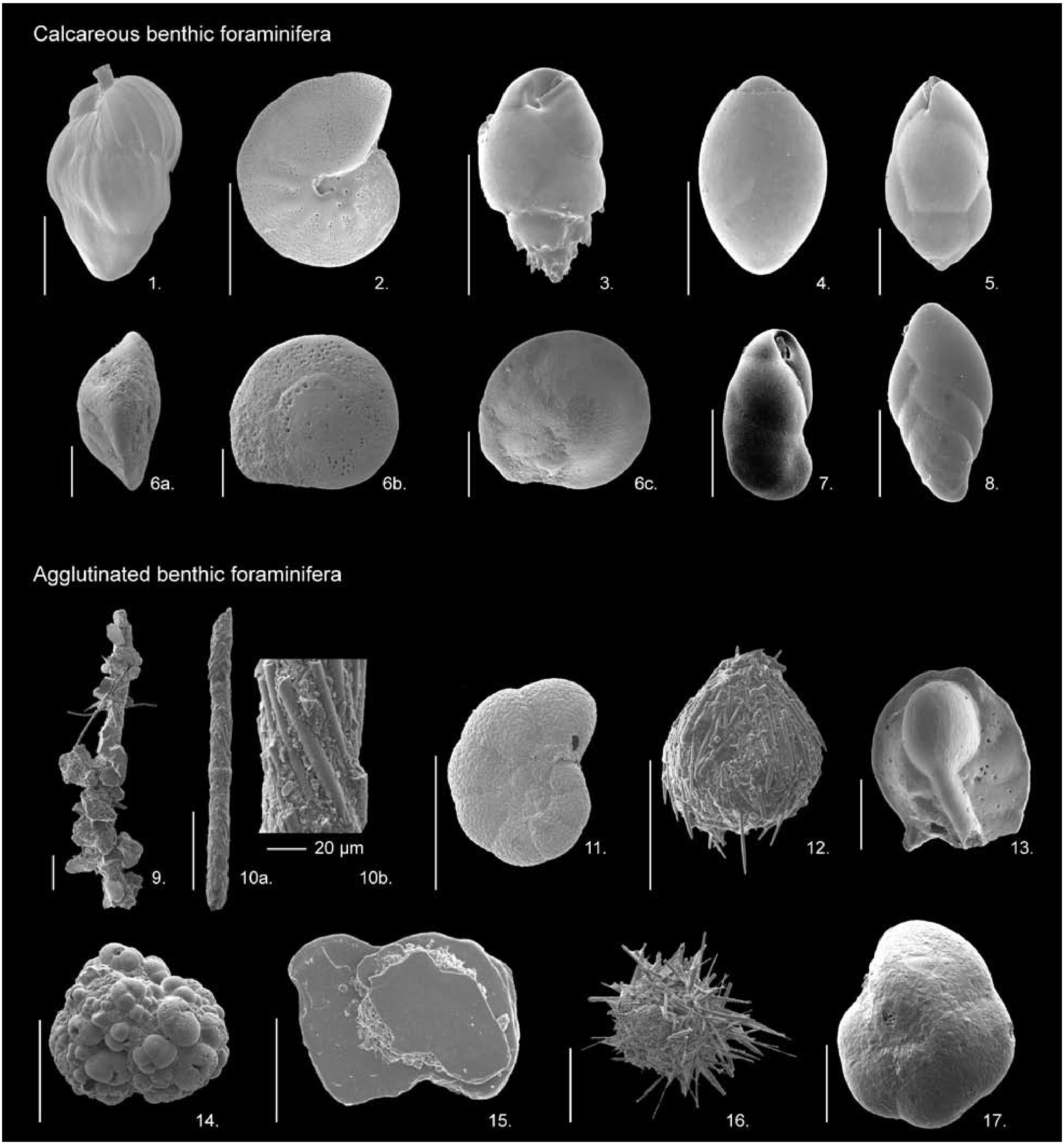

Figure 1. Benthic foraminifera come in many wonderful shapes and sizes. Some large agglutinated foraminifera can be several centimetres in length while others are only tens of microns across. All specimens shown here originate from the Portuguese canyons (the Nazaré and Lisbon-Setúbal Canyons) or the adjacent continental slope. Scale bar 200 µm, unless specified otherwise.
1. Uvigerina mediterranea; 2. Melonis barleeanus; 3. Bulimina marginata; 4. Chilostomella oolina; 5. Globobulimina affinis; 6. Cibicides kullenbergi (a. side-, b. spiral- and c. umbilical view); 7. Cassidulinoides brady; 8. Fursenkoina sp.; 9. Hyperammina sp.; 10. Bathysiphon strictus (a. fragment b. close up view of the wall structure); 11. Trochammina sp. (the wall is completely made of Helicosphaera coccoliths); 12. Technitella melo (using sponge spicules); 13. Ammolagena clavata (encrusting on top of Cibicides test).; 14. Trochammina sp. (using small planktonic foraminifera to make the test); 15. Crithionina sp. ('mica sandwich'; test is made of two mica flakes glued together with white sediment detritus); 15. Crithionina hispida; 16. Buzasina cf. ringens.

placed in 96% ethanol and rose Bengal (1g/l) solution to preserve and allow the distinction of the living foraminifera from the dead ones.

The importance of stable sediment substrate

An active sedimentary regime, i.e. frequent gravity flows and diurnal sediment resuspension was recorded by de Stigter et al. (2007) in the upper Nazaré Canyon. This type of sedimentary disturbance appears to have an adverse affect on the foraminiferal communities, hindering a stable ecosystem development. Significantly lower foraminiferal abundances were found along the active canyon axis than on the stable terrace stations, which were inhabited by abundant and more diverse foraminiferal communities (Koho et al. 2007). Nevertheless, a very special species of foraminifera, Technitella spp. (figure 1, specimen 12), was found to flourish along the canyon axis at 1118 m water depth; a site experiencing very high maximum sediment fluxes (788.3 g/m2·d; de Stigter et al. 2007). This indicates that Technitella spp. may be a highly opportunistic recoloniser of newly exposed habitats, or alternatively it may be able to tolerate the high sedimentation rates, frequent resuspension of surface sediments and severe turbulence. Previously, Technitella melo was described as a recoloniser following a turbidite event in the Cap Breton Canyon (Anschutz et al. 2002), supporting the first interpretation. Nevertheless, resuspension of the surficial sediments takes place diurnally along the upper Nazaré axis (de Stigter et al. 2007). Thus it may be likely that this species is able to live permanently under the 'hostile' conditions. The dynamic nature of the station in the upper Nazaré axis was also recorded in the metazoan meiofaunal community (Garcia et al. 2007), which was dominated by two opportunistic nematode genera, Sabatieria sp. and Metalinhomoeus sp., commonly found in dredged sediments (e.g. Boyd et al. 2000).

Food supply and redox chemistry – key players in the foraminiferal distribution in sediment

Not only the quantity but more importantly the quality of organic matter seems to play an important role in abundance of foraminifera and their reproduction (Koho 2008, Koho et al. 2008, Koho et al. in revision). The canyon sediments can be relatively rich in organic carbon even at abyssal depths (1.8 wt%; the Nazare Canyon at 4969 m water depth). Nevertheless, a lot of material arriving in the deep canyon may be laterally and/or down- canyon transported, thus leading to an enrichment of 'old' non-reactive carbon (Epping et al. 2002), thus non-edible for meiofauna. In this study the quantity of biologically available carbon was determined as the quantity of chloroplastic pigment equivalents (CPE), the sum of the cholorophyll a and phaeopigments. A good, linear relationship was found especially for the abundance of calcareous foraminifera and the sedimentary CPE content, indicating that the benthic foraminifera benefit directly from the fresh marine organic matter (Koho et al. in revision).

A laboratory study investigating the influence of a simulated diatom bloom on benthic foraminifera further highlighted the importance of fresh (labile) organic matter (Koho et al. 2008). Measurable reproduction, represented by addition of juvenile foraminifera, was only observed in the experiments where fresh algae were added. In contrast, in the control situation, where no diatoms were added, the number of juvenile foraminifera declined significantly.

Not only foraminiferal abundances, but also assemblages reflect the trophic conditions on the sea floor (Koho et al. in revision; see also figure 2). Some species, such as Uvigerina mediterranea (figure 1, specimen 1) and Melonis barleeanus (figure 1, specimen 2) are found in sediments relatively rich in fresh phytopigments only. Once the pigment (or food) concentrations start to decline foramiferal assemblage changes from a 'mesotrophic' Cibicides kullenbergi (figure 1, specimen 6a-c) assemblage to an 'oligotrophic' assemblage, including calcareous Nuttalides umbonifera and generally more agglutinated foraminifera.

The availability of labile organic matter is tightly coupled to the sediment and pore water chemistry, with higher organic carbon concentrations leading to enhanced oxygen consumption rates and thus shallower oxygen penetration in sediment (Canfield 1993). In the laboratory, it was possible to separate the two parameters by adding algae while aerating the aquarium vigorously; hence providing enough oxygen for aerobic remineralisation and preventing major changes in the pore water chemistry (Koho et al. 2008). The results suggest that the vertical distribution of some infaunal taxa (e.g. Melonis barleeanus and Chilostomella oolina) in the sediment is mainly relat-

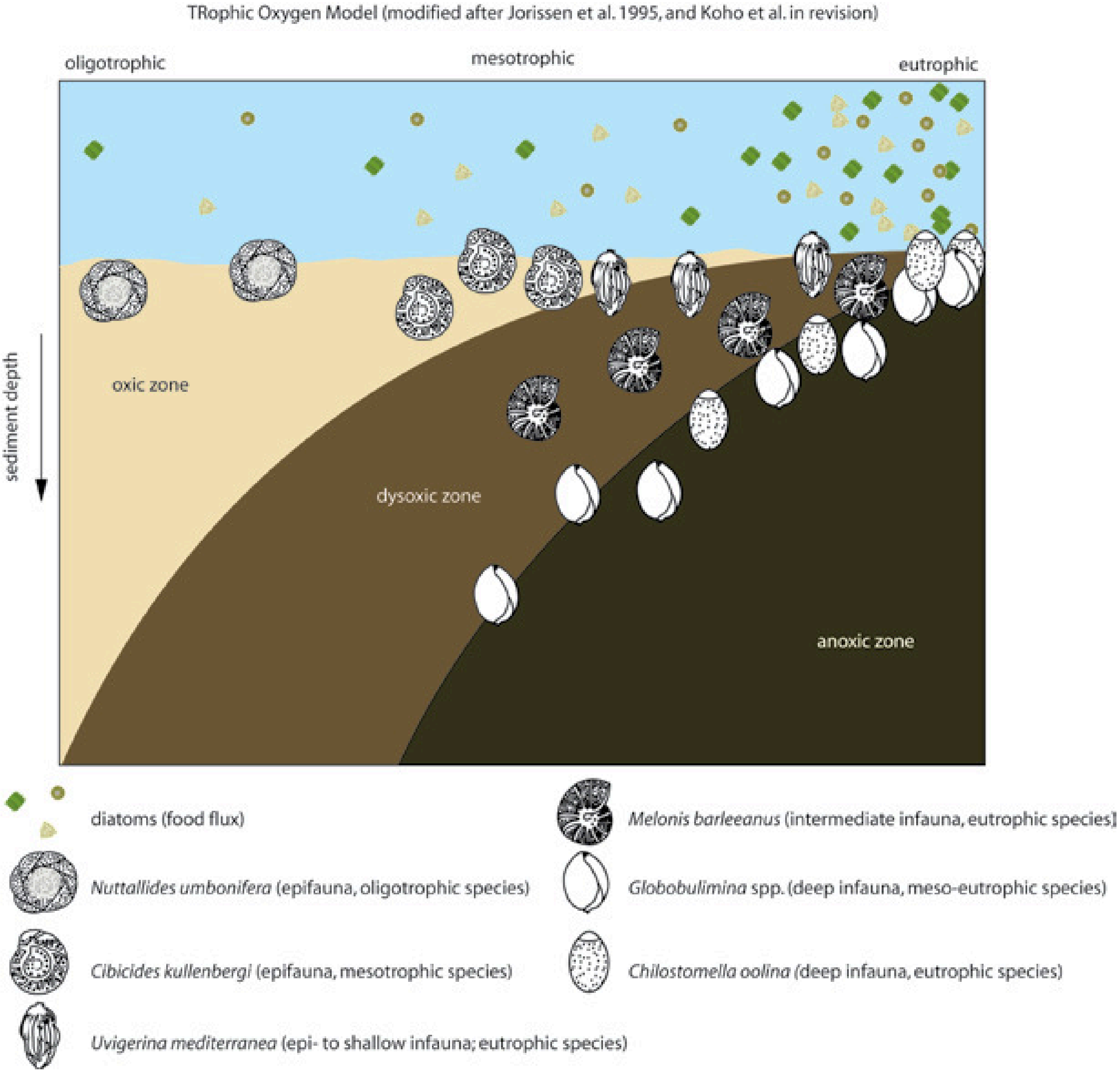

Figure 2. Schematic representation of the Trophic Oxygen model (TROX model; Jorissen et al. 1995). The model outlines both lateral and in-sediment changes in foraminiferal distribution. Foraminiferal numbers are highest in the most eutrophic sediment and lowest in the oligotrophic setting. However, the in-sediment distribution is also related to pore water oxygen content as well as the food abundance. In the eutrophic sites, only infaunal species are found which can tolerate low oxygen conditions. In contrast in the oligotrophic sites, only epifaunal species are present, restricted to the surface sediments due to low food supply. In the mesotrophic situation, relatively diverse foraminiferal communities can be found, comprising of both epi- and infaunal taxa. An example of oligotrophic, mesotrophic and eutrophic species are given; based on Koho et al. (in revision).

Figure 3. The research vessel Pelagia from the Royal Netherlands Institute for Sea Reseach (NIOZ) was used to collect all the study material. Foraminifera were sampled using a multiple corer in order to collect undisturbed deep sea sediment. Pictures taken by Rosa Garcia.

ed to sediment and pore water chemistry (or redox conditions) as no measurable changes were observed in the microhabitat of these species following the addition of food. Recently, it was also discovered that under anoxic conditions the infaunal foraminifera Globobulimina pseudospinescens can respire through denitrification of an intracellular nitrate pool (Risgaard-Petersen et al. 2006). In our field study (Koho et al. in revision) the distribution of Globobulimina spp. was also closely related to denitrification zone in sediment.

In summary, foraminifera are interesting organisms to study both from a geological and a biological perspective. Historically, they have been used in geology, more specifically in stratigraphy by detailed observation of their morphological changes on geologically relevant time scales. More recently, their potential as tools in paleo-ecological and paleoclimatic reconstructions has been recognised. For these applications knowledge about their biological and ecological functioning is imperative.

For more information on foraminifera, please feel free to download a copy of my thesis from http://igitur-archive.library.uu.nl/dissertations/2008-0312-200510/koho.pdf

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