

An Experimental Mesocosm Study of Microhabitat Preferences and Mobility in Benthic Foraminifera: Preliminary Results

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ABSTRACT

Three small microcosm experiments were carried out to study the microhabitat preferences and mobility of benthic foraminifera from the northern Adriatic Sea. Following initial homogenization, the foraminiferal assemblages developed a clear microhabitat partitioning in the microcosms within 20 days. Most species occurred in the top cm of the sediment. Some species preferentially living deeper could be identified. The agglutinated foraminifer *Leptohalysis scottii* turned out to be the most prominent epifaunal/shallow faunal species. It appeared to be very intolerant to the environmental conditions in deeper sediment layers but demonstrated its ability to avoid and escape small-scale hostile environmental changes. Under more favourable circumstances (i.e., in the uppermost part of the sediment), *L. scottii* is in the position to exploit its competitive abilities, resulting in dominance of the assemblage in the top centimetre.

INTRODUCTION

Infaunal activity and habitat preferences of foraminifera are often the subject of field studies (e.g., Barmawidjaja *et al.*, 1992; Jorissen *et al.*, 1992; Corliss & Van Weering, 1993; Jorissen *et al.*, 1995; Loubere *et al.*, 1995; De Stigter, 1996; Jannink *et al.*, 1998) but less often of experiments (e.g., Moodley 1992; Alve & Bernhard, 1995; Moodley *et al.*, 1997). Presently, the accepted hypothesis based on field research is that the observed microhabitat structure is related to oxygen gradients in the water and sediment column. Recent field studies and laboratory experiments, however, show evidence that oxygen is possibly not a prime factor in regulating the distribution of benthic micro- and meiofauna (e.g., Sen Gupta & Machain-Castillo, 1993; Bernhard, 1996; Moodley *et al.*, 1997). To better assess effects of controlling parameters as oxygen, it is important to establish in what way and at what rate different species are able to respond to changes in their environment. This experimental study was carried out in order to get an indication of the microhabitat preferences and degree of mobility of benthic foraminifera from the northern Adriatic Sea. The experiments were conducted in an attempt to answer the following questions:

- 1) How fast is the microhabitat structure reorganised after disturbance?
- 2) Can any preferential direction of foraminiferal movement be detected?
- 3) Is there any evidence for the role of interspecific competition?

EXPERIMENTAL SET-UP AND METHODS

Sediment (containing living foraminifera) was collected from a coastal station off Cesenatico in the northwestern Adriatic Sea (19 m water depth, 44°18'25 N 12°34'41 E). The sediment was sieved over a 0.5 mm sieve in order to get rid of larger predators and bioturbators. The sediment (<0.5 mm) was gently mixed and equally distributed over 13 transparent perspex tubes (height 15 cm, diameter 5 cm). These microcosms were placed in an aquarium containing Adriatic Sea water. The microcosms were incubated at 14°C and the water continuously aerated. Therefore, the top part of the sediment column contained oxygen persistently.

Twenty days after the mixing (t=20) of the sediment (see Figure 1 for the experimental design), one microcosm was harvested (i.e., sliced in 1 cm intervals and stained with Rose Bengal in ethanol). Additionally, the first cm of sediment (0-1 cm) from 10 microcosms was sliced, put together, gently mixed and a part of it was put in a new microcosm. An identical procedure was used for the second (1-2 cm), third (2-3 cm) and fourth cm of sediment (3-4 cm). Here, the first and fourth cm's are discussed. Of the remaining microcosms, one was placed upside down, in such a way that the sediment remained intact, and the last microcosm was left unaffected.

After another 20 days (t=40), all remaining tubes were harvested. All samples were examined for living (Rose Bengal stained) benthic foraminifera (63-595 µm) from 1 cm depth intervals. Counted specimens involved only those that were intensely,

uniformly coloured red; all chambers except for the last one had to be stained, otherwise the specimen was regarded as dead.

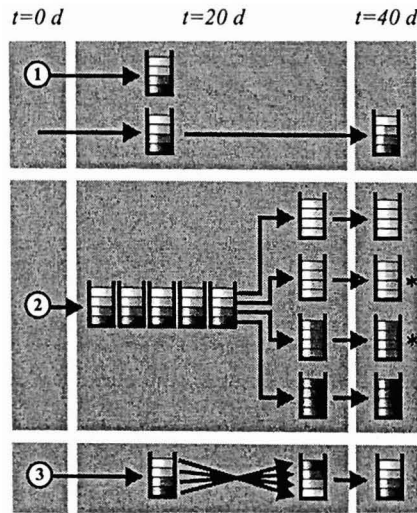


Figure 1. Experimental design: (1) re-establishment of the microhabitat structure after mixing; (2) recombination of the 'first cm' up to 'fourth cm' assemblages; (3) reversing of the sediment column (*data not shown).

RESULTS

The first sampling of the microcosms took place after 20 days ($t=20$): the colouring of the sediment showed differentiation (darker sediment below the dysoxic front), implying that a geochemical gradient had developed. This is supported by needle microprobe measurements in similar experimental setups (unpublished results) suggesting that oxygen gradients are installed within days after onset of the experiment. A clear microhabitat partitioning had developed within 20 days (Figure 2a): *Leptohalysis scottii* (Figure 5) and *Nonionella turgida* are clearly the most prominent shallow infaunal species. Other species as *Hopkinsina pacifica* and *Stainforthia fusiformis* seem to prefer the top layer, but occupy deeper layers as well. *Bolivina* spp., *Eggerella scabra/advena* and *Reophax nana* display a more uniform distribution in the sediment column. After another 20 days ($t=40$, Figure 2b), the species distribution appeared essentially similar, although in the top cm *L. scottii* is present in larger numbers and other species like *H. pacifica* and *Bolivina* spp. are less abundant.

The associations that were recombined to form new assemblages taken from the first and fourth cm, developed a new microhabitat partitioning within the 20 days after recombination (Figure 3a and 3b). The recombined 'first cm' assemblage shows that through this procedure typically shallow living species, as *Leptohalysis scottii*, indeed become very dominant in the top cm. *Hopkinsina pacifica*, *Stainforthia fusiformis* and *Bolivina* spp. are again found throughout the sediment column.

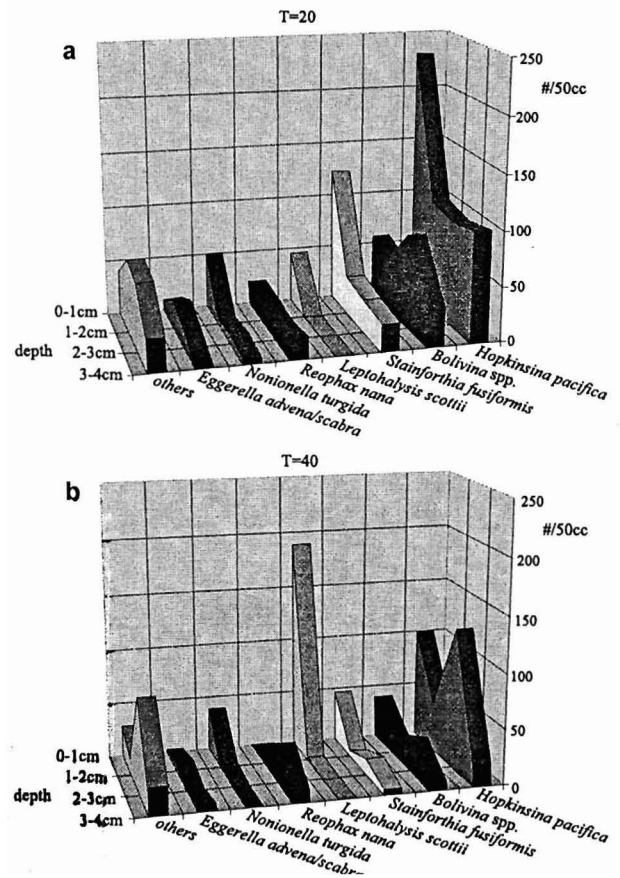


Figure 2. Foraminiferal distribution (in numbers per 50 cc): a) 20 days after mixing ($t=20$), b) 40 days after mixing ($t=40$). The 'others' category consists of *Ammonia* spp., *Bulimina marginata*, *Buliminella* sp., *Elphidium* spp., *Epistominella exigua*, *Textularia* spp., *Haplophragmoides* spp. and spec. indet.

In the recombined 'fourth cm' assemblage, *Leptohalysis scottii* and *Nonionella turgida* are strongly underrepresented.

Twenty days after the microcosm was turned upside down ($t=40$, Figure 4), most species had established skewed distribution curves again, so that most specimens were located at the top. The most outspoken shallow infaunal species, however, *Leptohalysis scottii* and *Nonionella turgida*, were almost absent throughout the column.

DISCUSSION

The microhabitat partitioning in the deeper sediment layers 40 days after mixing of the sediment, did not differ very much from the distribution of species after 20 days in the deeper sediment layers. In the top cm however, *Leptohalysis scottii* was more abundant after 40 days. Other species, *Bolivina* spp., *Hopkinsina pacifica* and *Stainforthia fusiformis*, dominate the top cm after 20 days, while after 40 days their importance decreases in the top cm.

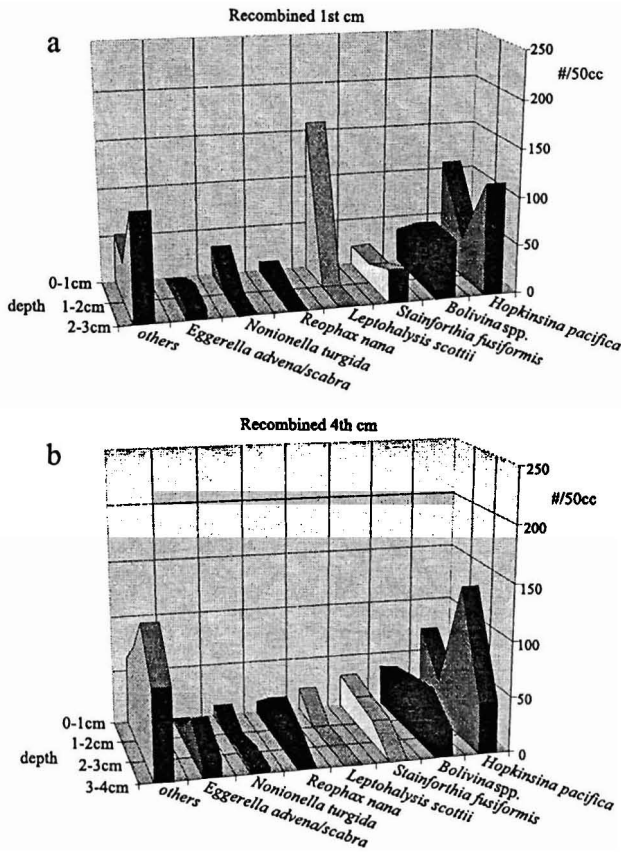


Figure 3. Foraminiferal distribution (in numbers per 50 cc): a) 20 days after the recombination of the 'first cm' assemblage (t=40), b) 20 days after the recombination the 'fourth cm' assemblage (t=40).

The recombined microcosms for the "first cm" and the "fourth cm" assemblages indicate that, if allowed, most species prefer the top layer. In the "first cm" assemblage shallow (infaunal) living species like *Leptohalysis scottii* and *Nonionella turgida*, are very dominant in this top cm. In the absence of these two species in the 'fourth cm' assemblage other species (*Hopkinsina pacifica*, *Bolivina* spp. and *Stainforthia fusiformis*) start to dominate the assemblage in the top layer.

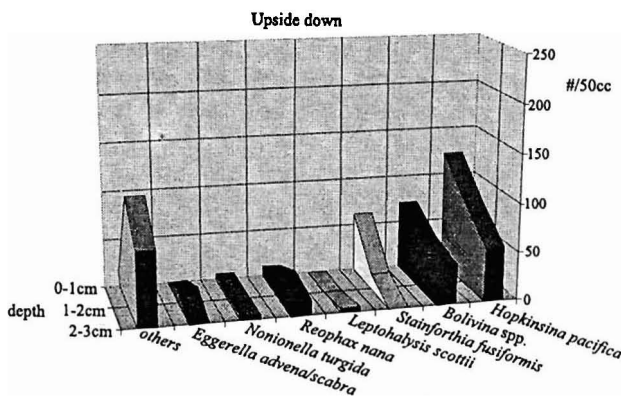


Figure 4. Foraminiferal structure (in numbers per 50 cc), 20 days after reversing the microcosm (t=40).

Not all species, however, demonstrate a clear preference for the uppermost part of the sediment. Some species (e.g., *Eggerella scabra/advena*) show clearly a persistent subsurface maximum in all the different treatments. Two mechanisms could be responsible for this observed phenomenon. The first one is based on the (weak) competitive ability (Gooday, 1986) of these species. This results in their absence in the crowded top cm of the sediment, and in a maximum at depths with less interspecific interactions and where the geochemical conditions are not too hostile yet. The second one involves a possible trophic specificity of these species. In that case species could be grazing on specific bacterial clusters, that participate in the re-mineralisation of organic matter. These bacteria are constrained to specific redox states at more or less fixed sediment depths. That would result in a maximum of the foraminifera at these depths.

Leptohalysis scottii

Inverted microscope observations of living specimens of *Leptohalysis scottii* revealed a quickly responding and active species. Pseudopodial activity, and active gathering of sediment and other particles, is initiated almost immediately after isolation and removal of the specimen from the sediment into a petri-dish. These observations are in accordance with the relatively high respiration rates of similar *Reophax* species (= *Leptohalysis* sp.) by Hannah et al. (1994).

The potential of high activity and mobility indicates that this species is possibly well-equipped to compete with other species for the epifaunal microhabitat. It seems certainly able to avoid or escape small-scale environmental disturbances or adverse conditions. The experiments indicate that *Leptohalysis scottii* (as well as *Nonionella turgida*) is almost always able to occupy the top sediment layers. This is a preferable position for a species with a limited tolerance to oxygen deficiency. Moreover, the top sediment layers are the site of accumulation of fresh organic matter, which, from a nutritional point of view, is an advantage. If we compare the patterns of *L. scottii* with those of species with a subsurface maximum, we are inclined to conclude that *L. scottii* (and others as *N. turgida*) is a strong competitor which forces other species to live deeper in the sediment column. Support for such a hypothesis can be found in the faunal patterns in the absence of *L. scottii* where normally deep living species are more equally distributed over the sediment column.

In his "spatial distribution model", Tilman (1994) assumes there are trade-offs between competitive ability, colonization capacity and longevity of species. To a certain extent, this idea is applicable to the vertical distribution of benthic foraminifera. If *Leptohalysis scottii* is a good competitor indeed, Tilman's model predicts that it is very stress-sensi-

tive. This is supported by the results of the reversed sediment column. The most striking feature in these results is the virtual absence of the most prominent surface dweller. It seems that *L. scottii* is unable to penetrate the intact adverse chemical barriers, redox fronts, it encounters on the way back upward, in spite of its ability to move quickly to the top of the sediment as demonstrated in the other two experiments. Compaction degree of the sediment next to the adverse chemical conditions might have played a role here as well. This could be the case if *L. scottii* is able only to penetrate loose, flocculated (surface) sediment, and unable to migrate through deeper and more compacted sediment.

In this experiment, assemblages are reorganised within 20 days after disturbance. Most specimens start to migrate upward toward the top cm and interspecific competition appears to have played a role in the subsurface distribution. Future studies and experiments (with replicates) are necessary to understand these results better.

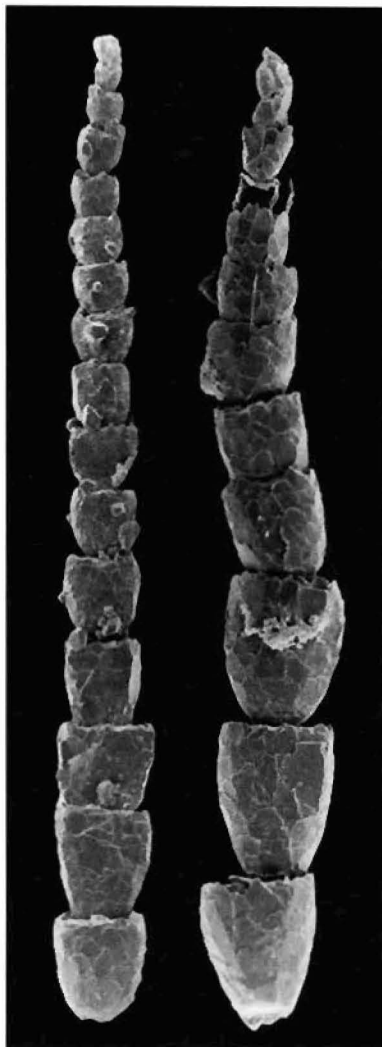


Figure 5. *Leptohalysis scottii* = *Reophax scottii* Chaster, total length: a) = 600 μ m, b) = 540 μ m.

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