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Tolerance of benthic foraminifera (Protista: Sarcodina) to hydrogen sulphide

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ABSTRACT: Benthic foraminifera are dominant members of the meiofauna, commonly occurring below the anoxic-oxic interface in marine sediments. The absence of oxygen in marine coastal sediments is often correlated with the formation of hydrogen sulphide. In this study the tolerance of benthic foraminifera (from the northwestern Adriatic Sea) to hydrogen sulphide was examined experimentally. Although the foraminiferal assemblage exhibited a high tolerance to short-term exposure (21 d), prolonged exposure to sulphidic conditions (66 d with a final concentration of 12 µM dissolved hydrogen sulphide) resulted in a significant reduction of total foraminiferal densities with time. Reproduction was evident under oxic conditions but none of the genera proliferated under sulphidic conditions. This implies that tolerance of sulphidic conditions was restricted to survival and that sulphide may be a prominent distributional factor for benthic foraminifera.

KEY WORDS: Hydrogen sulphide · Meiofauna · Foraminifera · Laboratory experiments

INTRODUCTION

Foraminifera are prevalent members of the benthic meiofauna (e.g. Yingst 1978, Ellison 1984, Rudnick et al. 1985, Josefson & Widbom 1988) and in soft sediments the majority occurs infaunally (Buzas et al. 1993). They have been encountered living to depths of 30 to 35 cm (e.g. Goldstein 1988, Moodley 1990, Goldstein et al. 1995), often below the anoxic-oxic interface (e.g. Bernhard 1989, 1992, 1996, Moodley 1990, Hunt & Corliss 1993, Moodley et al. 1998). Oxygen gradients are generally extremely steep in fine-grained coastal sediments (e.g. Rasmussen & Jørgensen 1992, Lohse et al. 1995) and therefore bioturbation and bio-irrigation are important factors governing the subsurface activity of benthic foraminifera (e.g. Buzas 1977, Collison 1980, Moodley 1990, Moodley et al. 1998). If the oxygen supply via bioturbation/irrigational fluxes ceases, a rapid oxygen depletion by bacterial consumption soon causes a change to hypoxic and anoxic conditions. Benthic foraminifera are very tolerant to oxygen depletion: among the meiofauna, foraminifera appear most resistant to hypoxic (Josefson & Widbom 1988) and prolonged anoxic conditions (Moodley et al. 1997). Some foraminiferal species are facultative anaerobes (Moodley & Hess 1992, Bernhard 1993, Bernhard & Alve 1996), capable of migrating through anoxic sediments (Moodley et al. in press b). However, in marine coastal sediments the absence of oxygen is often correlated with the formation of hydrogen sulphide (e.g. Fenchel & Riedl 1970, Sørensen et al. 1979, Jørgensen 1980, Revsbech & Jørgensen 1986), which may be a prominent distributional factor for benthic fauna (e.g. Theede 1973, Meyers et al. 1988, Vismann 1991, Giere 1992, Gamenick et al. 1996). Hydrogen sulphide can be toxic for animals already at nanomolar to micromolar concentrations (Giere 1993, Fenchel & Finlay 1995) and faunal tolerance to anoxia in combination with sulphide might be different (Diaz & Rosenberg 1995, Gamenick et al. 1996). Free hydrogen sulphide in sediment pore waters may be a decisive factor governing the infaunal activity of meiofauna and foraminifera (e.g. Ott 1972, Jensen 1987, Meyers et al. 1988, Ott &

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Novak 1989, Powell 1989, Moodley et al. 1998). So far, no quantitative experiments have been performed on the tolerance of benthic foraminifera to hydrogen sulphide exposure, but short-term sulphidic conditions (25 to 30 d) do not appear to qualitatively affect some common benthic foraminifera (Bernhard 1993, Moodley et al. 1997). A preceding study revealed that foraminifera from the northwestern Adriatic Sea have a high tolerance to prolonged anoxia (Moodley et al. 1997) and in the present study we examine the effect of prolonged anoxic and sulphidic conditions.

MATERIAL AND METHODS

Samples for the experiment were collected at a coastal station located off Cesenatico, Italy (44°18'25" N, 12°34'41" E) in the northwestern Adriatic Sea at a water depth of 19 m. The sediment was collected by SCUBA divers on 23 October 1996, by partially filling 500 ml plastic jars with the topmost 2 to 3 cm of the sediment. Directly upon arrival on board, the bulk sediment was sieved over a 0.5 mm sieve to remove macrofauna. The <0.5 mm fraction was stored in plastic jars (1 part sediment and 9 parts seawater) and transported to The Netherlands in a cooler maintained at 10°C.

Three days after collection, the sediment was first homogenized by gently shaking the plastic jars and then spread out evenly in rectangular dishes. The sediment was allowed to settle until the water on top cleared. Approximately 30 cm^3 of sediment was removed with a plastic syringe and transferred to culture vessels (10 cm inner diameter and 542 ml volume) which were then filled with unfiltered ambient seawater. A thin layer of approximately 1 mm (see Table 1) was used in order to ensure that sediments under oxic bottom waters were indeed oxic. The experimental setup has been described in detail by Moodley et al. (1997). In brief, the experimental set-up consisted of a circulating system that was made up of a series of culture vessels connected to a large volume (64 l) reservoir; one series for the oxic control and one series for the sulphidic treatment were maintained. The reservoir of the control series was constantly bubbled with air (oxic conditions, 234 ± 5 µM or 5.3 ± 0.1 ml O_2 l^{-1} as measured with a YSI 58 oxygen meter). The sulphidic treatment was achieved by first inducing anoxic conditions (the water in the reservoir tank was flushed with high quality nitrogen, type 6, i.e. 99.9999% N_2, until the reading on the oxygen meters in both the reservoir tank and the last culture vessel passed the zero value). To enhance the production of sulphide, an additional culture vessel, enriched with fresh organic matter (marine pennate diatoms: *Phaeodactylum tricornutum*) was connected to the system. The organic carbon content of the sediment was determined on freeze-dried sediment samples that were homogenized, acidified, and analyzed with a Carlo Erba NA 1500 CN Analyser. Samples for the sulphide determination were taken from the culture vessels with a 10 ml syringe and immediately transferred into 20 ml of a 2% ZnAc solution. Sulphide was measured with the methylene blue method according to Pachmayr (Trüper & Schlegel 1964). The pH of the water was measured using an electrode with a built-in reference electrode connected to a Radiometer pH/millivolt meter.

The experiment was conducted in the dark and maintained slightly above ambient temperature (19 ± 0.6°C). No extra food was added to the experimental vessels beyond that already present in the sediment. For each sampling event, 2 culture vessels were disconnected from each system without altering the experimental conditions. In order to measure the volume of the compacted sediment, sediment from the culture vessels was first transferred to a measuring cylinder and allowed to settle for ~9 h. The sediment was finally preserved in alcohol with Rose Bengal for later enumeration and identification of the foraminifera. Rose Bengal stain was chosen because it is one of the most common and practical methods to distinguish live from dead foraminifera (Bernhard et al. 1997). It has been reported to be an accurate and reliable method to distinguish living tests (shells) from dead ones (e.g. Lutze & Altenbach 1991, Alve & Bernhard 1995). Foraminiferal protoplasm stains bright red whilst test walls and organic linings are either unstained or take on a light pink colour (Murray 1991). However, the stain is not vital, that is, it does not detect life. Degradation of dead protoplasm is by no means instantaneous (Bernhard 1988) but, in general, it is assumed that stained specimens reflect protoplasm-containing tests which were either alive at the time of collection or have been alive in the 'recent' past (Corliss & Emerson 1990, Murray 1991). Although this may suffice for field studies, it is a critical point in short-term experiments, especially when the resistance of foraminifera to extreme environmental conditions is examined. Therefore, prior to fixation of our samples in alcohol, we performed a 'life-check', i.e. the sediment was examined for living specimens using an inverted microscope. Cytoplasmic streaming and the formation of pseudopodial networks were used as the criterion to determine if an individual was alive (Goldstein 1988, Moodley, 1990, Goldstein et al. 1995, Moodley et al. 1997). This provides a qualitative check on whether Rose Bengal stained specimens were actually alive at the time of sampling.

Stained samples were sieved with tap water and the residue was examined (wet) for fauna. Although it is

more customary to use a 150 or 63 µm sieve in foraminiferal studies, the majority of the foraminiferal assemblages in some areas, such as the northwestern Adriatic Sea, is not retained on a 63 µm sieve (Moodley et al. 1997). Therefore a 38 µm sieve was employed in this study. Additionally, the number of juveniles was estimated from counts of stained specimens that passed through a 38 µm sieve but were retained on a 15 µm sieve. This fraction was subsampled by removing 10 ml from a stirred 80 ml sediment-water solution. Unfortunately, duplicate samples of the 15 µm fraction were lost during the life-check. To facilitate density comparisons, results were normalized to a standard volume of 10 cm^3 of sediment. Due to the lack of replicates and lack of high accuracy in sub-sampling the 15 µm fraction, data from this fraction were not included in the statistical analysis but remain a source of information.

This study was restricted to hard-shelled foraminifera (both calcareous and agglutinated), identified to genus level according to Barmawidjaja et al. (1992) and Boltovskoy et al. (1980). Faunal counts were done using a stereo-microscope (40× and 50× magnification for the 38 µm and 15 µm fraction respectively); the taxonomy of small specimens were verified using a scanning electron microscope. When in doubt, specimens were tallied as unidentified.

Statistical analysis of density data were done after $\ln(x+1)$ transformation and changes in the proportional abundance of the dominant genera (i.e. genera forming ≥5% of the assemblage in any one sample) were analyzed after arcsine transformation. Significance of changes with time was analysed by testing for difference in the slope of abundance with time for the oxic and sulphidic treatments. Analysis of regression slopes offers the advantage of giving estimates for the slope of abundance with time but has the disadvantage of assuming a linear form for the abundance-time relationship. However, results were similar to those obtained with a 2-way analysis of variance. The MGLH module of SYSTAT (Systat Inc.) was used for the analysis.

RESULTS

The organic carbon content of the sediment in the enriched vessel that was introduced to enhance the production of sulphide was much higher than in the experimental vessels (1.49% versus 0.90%). Furthermore, the higher reactivity of the organic material in the enriched vessel was indicated by its lower molar C/N ratio (7.9 versus 12.0 in the experimental vessels).

Table 1 Results of the life-checks; sediment thickness (values of duplicate vessels), pH, and oxygen and sulphide concentration in the overlying water in the different treatments. +: living foraminifera; –: no living foraminifera

Treatment	Day	Sediment thickness (mm)	pH	Dissolved sulphide (µM)	Dissolved O_2 (µM)	Life-check
Oxic	21	1.0/1.0	8.16	0.00	229	+
	42	1.2/1.3	8.09	0.00	234	+
	66	1.0/0.9	8.07	0.00	239	+
Sulphidic	21	1.0/1.0	8.03	6.66 ± 0.30	0.00	+
	42	0.9/0.9	7.86	11.90 ± 0.40	0.00	–
	66	1.0/1.0	7.81	11.70 ± 0.00	0.00	–

Upon initial flushing with nitrogen, sediments in the sulphidic series turned from yellowish brown to grey with a few black spots, indicating the production of iron sulphides as a result of sulphate reduction. The concentration of sulphide in the water increased with time (Table 1). Under prolonged sulphidic conditions there was no drastic change in pH (from 8.03 to 7.81). We estimate that sulphide toxicity remained comparable within this pH range as it does not result in important changes in sulphide dissociation (i.e. approximately 10 to 13% for undissociated sulphide). In contrast, under oxic conditions the sediment remained yellowish brown and free of sulphide.

Living foraminifera were found in all oxic samples and in the 21 d sulphidic samples, but after 42 d of exposure to increasing sulphide concentrations, no living foraminifera (or metazoan meiofauna) were encountered during the life-check (Table 1). However, stained specimens were found in all samples. Two or three chambered specimens could not be identified to genus level. However, having viewed different size classes, it was possible to identify several tiny specimens to genus level (Fig. 1). There were 8 dominant genera, of which *Textularia* (predominantly *T. earlandi*) and *Reophax* (*R. scottii* and *R. nana*) were the dominant agglutinated genera. *Quinqueloculina* (predominantly *Q. seminula*), *Stainforthia* (predominantly *S. fusiformis*), *Bolivina* (predominantly *B. dilatata*), *Buliminella* (predominantly *B. elegantissima*), *Bulimina* (predominantly *B. marginata*) and *Hopkinsina* (predominantly *H. pacifica*) were the dominant calcareous genera.

A significant reduction in total foraminiferal densities (i.e. stained) with time was evident under prolonged sulphidic conditions (p_{slope} = 0.001, Fig. 2). Under sulphidic conditions a general trend of decreasing densities with time was seen for all genera (Fig. 3). In contrast, some genera exhibited an increase in density with time or remained relatively uniform under

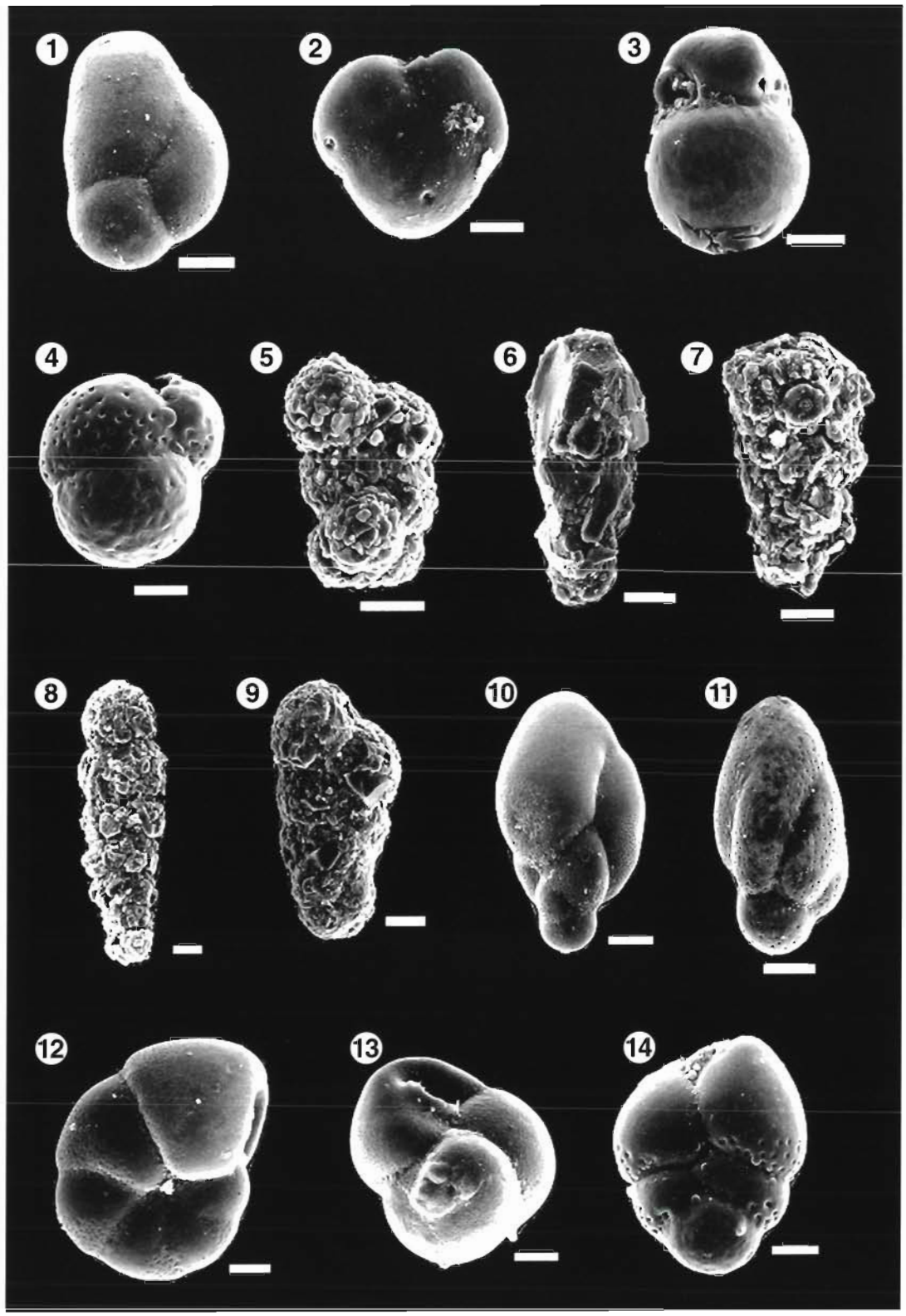

Fig. 1. Scanning electron micrographs of juvenile foraminifera. (1–7) Unidentifiable juveniles retained on a 15 µm sieve, except number 4, which was retained on a 38 µm sieve: (1–4) calcareous juveniles; (5–7) agglutinated juveniles. (8–11) Identifiable juveniles retained on a 15 µm sieve: (8) *Reophax*, (9) *Textularia*, (10) *Stainforthia*, (11) *Buliminella*. (12–14) Juveniles retained on a 38 µm sieve: (12) *Epistominella*, (13) *Bulimina*, (14) *Bolivina*. Scale bars = 10 µm

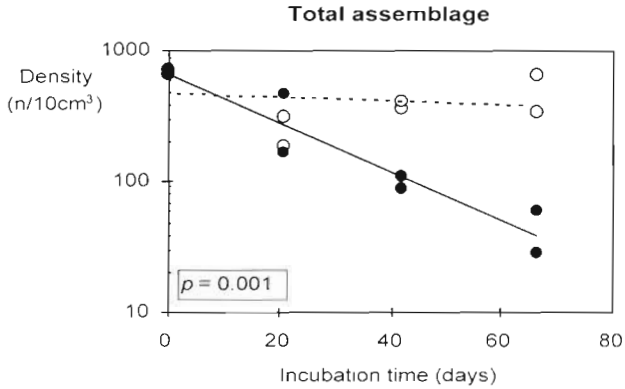

Fig. 2. Total densities of foraminifera retained on a 38 µm sieve from the oxic (○, dashed line) and the sulphidic (●, solid line) treatments. p is the significance of the difference in the slopes of abundance with time for the oxic and sulphidic treatments

oxic conditions (Fig. 3). Of the dominant genera, densities of *Textularia*, *Reophax*, *Quinqueloculina*, *Bolivina* and *Bulimina* were all negatively affected by the sulphidic conditions (Fig. 3). The density-time relationships of *Buliminella* and *Hopkinsina* were not significantly different between treatments, but neither genus exhibited an increase in density with time (Fig. 3). However, juveniles of *Buliminella* were encountered in the later samples under oxic conditions but not under sulphidic conditions (see Fig. 5), suggesting that this genus also was inhibited by sulphide. In contrast, the densities of *Stainforthia* decreased slower under sulphidic conditions than under oxic conditions (Fig. 3). However, the significant decrease in densities of *Stainforthia* under both treatments (Fig. 3) suggests that they did not reproduce but their survival was enhanced by conditions created by the sulphidic treatment.

The differential response of the dominant genera led to changes in the structure of the foraminiferal assemblages (Fig. 4). There was a significant difference between treatments in the change of the proportional abundance with time for *Textularia*, *Stainforthia* and *Hopkinsina* ($p_{slope} < 0.05$). The increase in dominance of *Textularia* under oxic conditions was primarily due to the strong increase in abundance of this genus with time (Fig. 3). However, the relative increase in dominance of *Stainforthia* and *Hopkinsina* under sulphidic conditions was not due to increase in their densities with time but a result of the relatively lower survival of the other genera under sulphidic conditions (Fig. 3).

The presence of juveniles on Day 0 in both the 38 µm and 15 µm fractions (Fig. 5) indicated that reproduction also took place just prior to field sampling. Therefore, assemblages of the 15 µm fraction in the experimental samples were the products of reproduction during the experiment and/or juveniles that were produced in the field but did not grow to size to be retained on a 38 µm sieve. Consequently, the presence of juveniles alone does not directly or necessarily reflect reproduction under experimental conditions. Total densities of the 15 µm fraction showed strong fluctuation with time in the oxic treatment but a decreasing trend was seen for the sulphidic treatment (Fig. 5) as also observed in the 38 µm fraction (Fig. 2). Therefore, juveniles found in the sulphidic samples were presumably not produced during the experiment. Changes in the composition of the 15 µm fraction were more pronounced under oxic conditions and after prolonged exposure to sulphidic conditions only 2 genera (*Stainforthia* and *Reophax*) were encountered (Fig. 5). The absence of *Textularia* under oxic conditions on Day 21 (*Textularia* may have been part of the unidentifiable agglutinates on Day 42) suggests that this genus did not reproduce until after Day 21 or that the juveniles found at Day 0 had probably grown and did not pass through the 38 µm sieve.

DISCUSSION

We estimate that the information gathered from our life-checks is representative of the foraminiferal assemblage. It was virtually impossible to examine every individual specimen for cytoplasmic activity, but for the oxic samples several living specimens were readily found in just a small fraction of the sample. For the sulphidic samples, a large portion of the sediment was inspected for foraminifera and other meiofauna after allowing a recovery period of ~15 to 20 h in oxygenated water. No living foraminifera or metazoan meiofauna were encountered in the life-check of Day 42 or Day 66 sulphidic samples and this raises serious doubt as to whether the stained specimens found in these samples were actually alive after prolonged exposure to sulphide. Although the life-check was not quantitative, the absence of living specimens after examining a large portion of the sediments alone suggests that densities were at least severely depressed under prolonged sulphidic conditions.

The analysis of the stained specimens showed that densities were significantly reduced under prolonged sulphidic conditions (Fig 2). If the analysis were restricted to samples where staining results were verified by the presence of living foraminifera, prolonged exposure to sulphidic conditions would be considered fatal to all foraminifera (no living foraminifera were found in the sulphidic samples from Days 42 and 66). There was, however, no significant difference in total densities (stained) between the sulphidic samples of Day 21 and samples from Day 0 (1-way ANOVA, $p = 0.215$) and relatively little change in the structure of

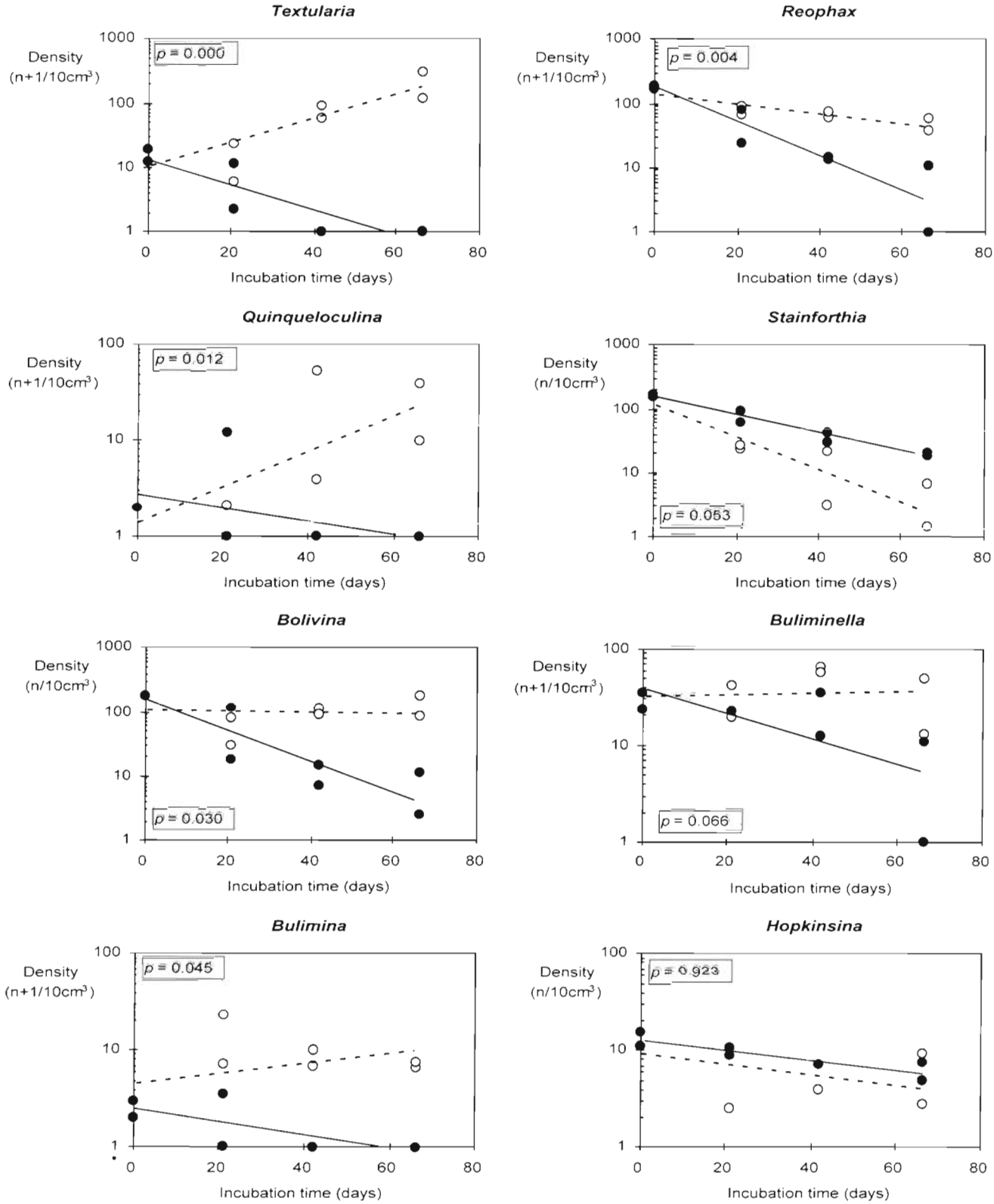

Fig. 3. Densities of dominant foraminiferal genera retained on a 38 µm sieve from the oxic (○, dashed line) and the sulphidic (●, solid line) treatments. p is the significance of the difference in the slopes of abundance with time for the oxic and sulphidic treatments. Note that $(n+1)/10$ cm^3 is plotted for the genera whose densities were 0 under sulphidic conditions

the assemblages (Fig. 4). This non-lethal effect of short-term exposure suggests that these foraminifera have a high tolerance to short-term sulphidic conditions, which is in accordance with earlier observations (Bernhard 1993, Moodley et al. 1997).

Assuming that degradation of protoplasm is similar for all genera, the relatively higher proportional abundance of stained *Hopkinsina* and *Stainforthia* under prolonged sulphidic conditions (Fig. 4) suggests that these genera may be more resistant to sulphide. On the other hand, changes in the proportional abundances may be a reflection of differential degradation of dead protoplasm (no live foraminifera were found in the life-checks of the Day 42 and Day 66 samples). This would then implicate that cytoplasmic degradation occurs at a relatively slower rate in the tests (shells) of *Stainforthia* (densities of *Hopkinsina* were very low, making it difficult to draw conclusions).

Our observations indicate that sulphide, even at these low environmental relevant concentrations, may be a prominent distributional factor for benthic foraminifera. Whether this is a direct physiological effect of sulphide itself or the effect of a variable covarying with sulphide (e.g. Fe oxides, bacterial populations, etc.) is impossible to ascertain. However, it can be expected that these variables covary with sulphide in the field too. Under sulphidic conditions, all genera exhibited a general decrease in density with time (Fig. 3) and the total abundance of the 15 µm fraction also showed a decreasing trend with time. This suggests that reproduction did not take place and that these foraminifera were inhibited by sulphide, even *Stainforthia*, the only genus that apparently benefitted from conditions created by the sulphidic treatment (Fig. 3). This indicates that tolerance to sulphide is restricted to survival. In contrast, reproduction did take place under oxic conditions (definitely for *Textularia*, *Quinqueloculina* and *Buliminella* and probably also *Bulimina*; Figs. 3 & 5). Decrease in the proportional abundance of *Stainforthia* under oxic conditions (Fig. 4) suggests that this

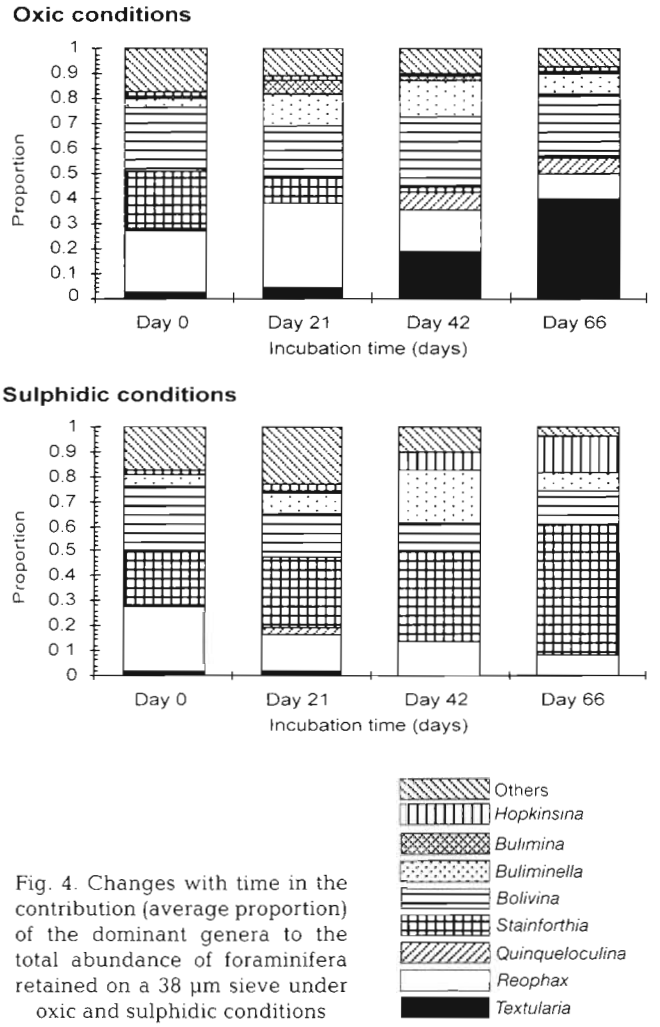

Fig. 4. Changes with time in the contribution (average proportion) of the dominant genera to the total abundance of foraminifera retained on a 38 µm sieve under oxic and sulphidic conditions

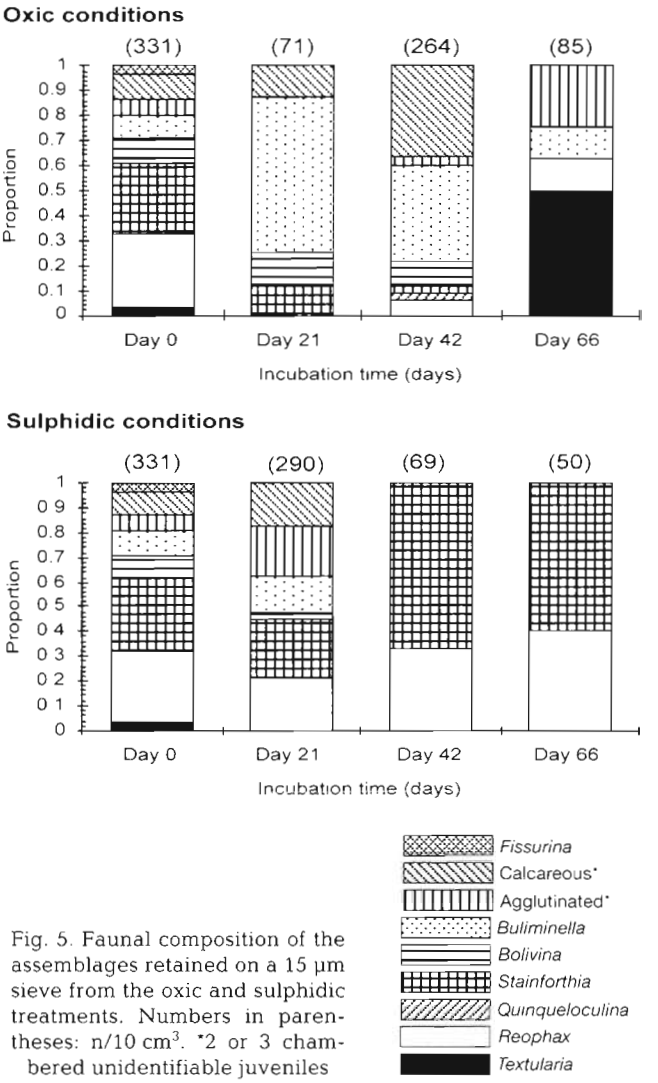

Fig. 5. Faunal composition of the assemblages retained on a 15 µm sieve from the oxic and sulphidic treatments. Numbers in parentheses: n/10 cm^3. *2 or 3 chambered unidentifiable juveniles

genus was outcompeted by other genera. This is supported by the relatively higher survival rates under conditions where the development of dominant genera or other taxa are inhibited (in this case, sulphidic conditions; Fig 3). A similar trend was observed under prolonged anoxia (Moodley et al. 1997), suggesting that biological interactions (e.g. disturbance, competition) may be an important factor governing this genus. Alternatively, *Stainforthia* could have been directly inhibited by the high oxygen concentration in the oxic treatment. However, no conclusions can be drawn with respect to differential success under high oxygen concentrations. Reproduction would also depend on the timing of the experiment in relation to the seasonal patterns of reproduction in the different species. It can also be argued that thin sediment layers do not represent natural environmental conditions. However, although foraminifera were observed not to reproduce in the absence of sediment, they did so in the presence of a thin film of sediment and phytoplankton food (<1 mm thick; Chandler et al. 1996, this study).

Changes found in the foraminiferal assemblage under oxic conditions were evidently inhibited by sulphide in the sulphidic treatment and prolonged exposure to sulphidic conditions was most probably fatal to all foraminifera. This may be due to their small body sizes (cf. Jahn et al. 1996, 1997). These foraminfera have, however, been recently observed to be highly resistant to prolonged anoxia (Moodley et al. 1997); this confirms the general rule that anoxia in combination with sulphide is more toxic than anoxia alone (Diaz & Rosenberg 1995, Gamenick et al. 1996). However, it is possible that foraminifera inhabiting environments where sulphidic conditions commonly occur may have a higher resistance, as observed for some bivalves; populations of the benthic clam *Macoma balthica* showed different degrees of sulphide tolerance in relation to sulphide contamination of the natural habitats (Jahn & Theede 1997). Free hydrogen sulphide is not commonly encountered in coastal northwestern Adriatic sediments under natural conditions (Barbanti et al. 1995, Moodley et al. in press), which has been related to the high reactive Fe content of the sediment (Barbanti et al. 1995).

Although these foraminifera exhibit a high tolerance to prolonged anoxia and short-term exposure to sulphidic conditions, tolerance is evidently limited to survival. As under prolonged sulphidic conditions, there was no evidence of reproduction under prolonged anoxic conditions (Moodley et al. 1997), indicating that reproduction and probably also growth are dependent on oxic conditions but not necessarily high oxygen concentrations (i.e. upper end of the oxic range; Moodley et al. 1997). In a recent long-term laboratory experiment examining the migratory activity of benthic foraminifera to changing bottom water oxygen content Alve & Bernhard (1995) observed that the majority of the individuals of one dominant epifaunal species (*Bulimina marginata*) were juveniles and suggested that this indicated reproduction throughout the experiment, i.e. under oxygen concentrations varying from 2 to <0.2 ml l^{-1} O_2 (or 88 to < 8.8 µM O_2). Given this bottom-water oxygen content of <8.8 µM O_2 and organic-rich sediments, it was suggested that suboxic/anoxic conditions are expected to prevail in most, if not in all, of the 4 cm thick sediment layer examined for foraminifera and therefore reproduction under these conditions would demonstrate that foraminifera flourish under short-term anoxia (Moodley et al. 1996). This is not supported by recent observations (Moodley et al. 1997, this study). As already discussed, the presence of juveniles alone is no direct proof of reproduction at that specific time, and the juveniles found in Alve & Bernhard's experiments under waters having a oxygen content of <8.8 µM O_2 (and therefore most probably suboxic/anoxic sediments) were most probably produced before the oxygen content of the bottom water was decreased to trace amounts. Because of their high resistance to severe oxygen depletion (Moodley & Hess 1992, Bernhard 1993, Bernhard & Alve 1996, Moodley et al. 1997), living (stained) foraminifera were still present. However, because juveniles were present throughout Alve & Bernhard's long-term experiment (246 d), it is valid to assume that *B. marginata* did reproduce during the experiment, i.e. under dysoxic conditions (Bernhard et al. 1996).

Given that infaunal foraminifera cannot maintain contact with the overlying oxygenated waters like some macrofauna do and that they are relatively slow moving (Kitazato 1988, Wetmore 1988), a certain amount of tolerance to anoxia and sulphidic conditions would seem a prerequisite to survival in soft sediments. The non-lethal effect of short-term exposure suggests that foraminifera may be capable of migrating through sulphidic-enriched sediment layers. However, these foraminifera are also inhibited by sulphidic conditions, which suggests that sulphidic conditions can be one stimulus for migration in the sediment column and the avoidance of sulphide may provide a direction of migration upon burial in deeper sediment layers, as found for some metazoan meiofauna (Meyers et al. 1988).

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LITERATURE CITED

Alve E, Bernhard JM (1995) Vertical migratory response of benthic foraminifera to controlled oxygen concentrations in an experimental mesocosm. Mar Ecol Prog Ser 116: 137–151

Barbanti A, Bergamini MC, Frascari F, Miserocchi S, Ratta M, Rosso G (1995) Diagenetic processes and nutrient fluxes at the sediment-water interface, northern Adriatic Sea, Italy. Mar Freshwat Res 46:55–67

Barmawidjaja DM, Jorissen FJ, Puskaric C, Van der Zwaan GJ (1992) Microhabitat selection by benthic foraminifera in the northern Adriatic Sea. J Foraminiferal Res 22: 297–317

Bernhard JM (1988) Postmortem vital staining in benthic foraminifera: duration and importance in population and distributional studies. J Foraminiferal Res 18:143–146

Bernhard JM (1989) Distribution of benthic foraminifera with respect to oxygen concentration and organic carbon levels in shallow-water Antarctic sediments. Limnol Oceanogr 34:1131–1141

Bernhard JM (1992) Benthic foraminiferal distribution and biomass related to pore-water oxygen content: central California continental slope and rise. Deep Sea Res 39: 585–605

Bernhard JM (1993) Experimental and field evidence of Antarctic foraminiferal response to anoxia and hydrogen sulfide. Mar Micropaleontol 20:203–213

Bernhard JM (1996) Microaerophilic and facultative anaerobic benthic foraminifera: a review of experimental and ultrastructural evidence. Rev Paleobiol 15:261–275

Bernhard JM, Alve E (1996) Survival, ATP pool, and ultrastructural characterization of benthic foraminifera from Drammensfjord (Norway): response to anoxia. Mar Micropaleontol 28:5–17

Bernhard JM, Alve E, Reilly AA (1996) Response to the comment by Moodley et al. Mar Ecol Prog Ser 145:305–307

Bernhard JM, Sen Gupta BK, Borne PF (1997) Benthic foraminiferal proxy to estimate dysoxic bottom-water oxygen concentrations: Santa Barbara Basin, U.S. Pacific continental margin. J Foraminiferal Res 27:301–310

Boltovskoy E, Giussani G, Watanabe S, Wright R (1980) Atlas of benthic shelf foraminifera of the southwest Atlantic. Dr W Junk Publishers, The Hague

Buzas MA (1977) Vertical distribution of foraminifera in the Indian River, Florida. J Foraminiferal Res 7:234–237

Buzas MA, Culver SJ, Jorissen FJ (1993) A statistical evaluation of the microhabitats of living (stained) infaunal benthic foraminifera. Mar Micropaleontol 20:311–320

Chandler GT, Williams DF, Spero HJ, Xiaodong G (1996) Sediment microhabitat effect on carbon stable isotopic signatures of microcosm-cultures benthic foraminifera. Limnol Oceanogr 4:680–688

Collison P (1980) Vertical distribution of foraminifera off the coast of Northumberland, England. J Foraminiferal Res 10:75–78

Corliss BH, Emerson S (1990) Distribution of Rose Bengal stained deep-sea foraminifera from the Nova Scotian continental margin and Gulf of Maine. Deep Sea Res 37:381–400

Diaz RJ, Rosenberg R (1995) Marine benthic hypoxia: a review of its ecological effects and the behavioural responses of benthic macrofauna. Oceanogr Mar Biol Annu Rev 33:245–303

Ellison RL (1984) Foraminifera and meiofauna on an intertidal mudflat, Cornwall, England: population; respiration and secondary production; and energy budget. Hydrobiologica 109:131–148

Fenchel T, Finlay BJ (1995) Ecology and evolution in anoxic worlds. Oxford University Press Inc. New York

Fenchel T, Riedl RJ (1970) The sulfide system: a new biotic community underneath the oxidized layer of marine sand bottoms. Mar Biol 7:255–268

Gamenick I, Jahn A, Vopel K, Giere O (1996) Hypoxia and sulphide as structuring factors in a macrozoobenthic community on the Baltic Sea shore: colonization studies and tolerance experiments. Mar Ecol Prog Ser 144:73–85

Giere O (1992) Benthic life in sulphidic zones of the sea — ecological and structural adaptations to a toxic environment. Verh Dtsch Zool Ges 85:77–93

Giere O (1993) Meiobenthology. The microscopic fauna in aquatic sediments. Springer-Verlag, Berlin

Goldstein ST (1988) Foraminifera of relict salt marsh deposits, St. Catherines Island, Georgia: taphonomic implications. Palaios 3:327–334

Goldstein ST, Watkins GT, Kuhn RM (1995) Microhabitats of salt marsh foraminifera: St. Catherines Island, Georgia, USA. Mar Micropaleontol 26:17–29

Hunt AS, Corliss BH (1993) Distribution and microhabitats of living (stained) benthic foraminifera from the Canadian Arctic Archipelago. Mar Micropaleontol 20:321–345

Jahn A, Gamenick I, Theede H (1996) Physiological adaptations of *Cyprideis torosa* (Crustacea, Ostracoda) to hydrogen sulphide. Mar Ecol Prog Ser 142:215–223

Jahn A, Janas U, Theede H, Szaniawska A (1997) Significance of body size in sulphide detoxification in the Baltic clam *Macoma balthica* (Bivalvia, Tellinidae) in the Gulf of Gdansk. Mar Ecol Prog Ser 154:175–183

Jahn A, Theede H (1997) Different degrees of tolerance to hydrogen sulphide in populations of *Macoma balthica* (Bivalvia, Tellinidae). Mar Ecol Prog Ser 154:185–196

Jensen P (1987) Differences in microhabitat, abundance, biomass and body size between oxybiotic and thiobiotic free-living nematodes. Oecologia (Berl) 71:564–567

Jørgensen BB (1980) Seasonal oxygen depletion in the bottom waters of a Danish fjord and its effect on the benthic community. Oikos 34:68–76

Josefson AB, Widbom B (1988) Differential response of benthic macrofauna and meiofauna to hypoxia in the Gullmar fjord basin. Mar Biol 100:31–40

Kitazato H (1988) Locomotion of some benthic foraminifera in and on sediment. J Foraminiferal Res 18:344–349

Lohse L, Malschaert HFP, Slomp CP, Helder W, Van Raaphorst W (1995) Sediment-water fluxes of inorganic nitrogen compounds along the transport of organic matter in the North Sea. Ophelia 41:173–197

Lutze GF, Altenbach A (1991) Technik und Signifikanz der Lebendfärbung benthischer Foraminiferen mit Bengalrot. Geol Jb A128:251–265

Meyers MB, Powell EN, Fossing H (1988) Movement of oxybiotic and thiobiotic meiofauna in response to changes in pore-water oxygen and sulfide gradients around macroinfaunal tubes. Mar Biol 98:395–414

Moodley L (1990) Southern North Sea seafloor and subsurface distribution of living benthic foraminifera. Neth J Sea Res 27:57–71

Moodley L, Heip C, Middelburg JJ (in press) Benthic activity in sediments of the northwestern Adriatic Sea: sediment oxygen consumption, macro-and meiofauna dynamics. J Sea Res

Moodley L, Herman PMJ, Middelburg JJ, Heip CHR (1996) Subsurface activity of benthic foraminifera. Mar Ecol Prog Ser 145:303–304

Moodley L, Hess C (1992) Tolerance of infaunal benthic foraminifera for low and high oxygen concentrations. Biol Bull (Woods Hole) 183:94–98

Moodley L, Van der Zwaan GJ, Herman PMJ, Kempers L, Van Breugel P (1997) Differential response of benthic meiofauna to anoxia with special reference to Foraminifera (Protista: Sarcodina). Mar Ecol Prog Ser 158:151–163

Moodley L, Van der Zwaan GJ, Rutten GMW, Boom RCE, Kemper L (1998) Subsurface activity of benthic foraminifera in relation to porewater oxygen content: laboratory experiments. Mar Micropaleontol 34:91–106

Murray JW (1991) Ecology and palaeoecology of benthic foraminifera. Longman Scientific & Technical, Harlow

Ott JA (1972) Determination of fauna boundaries of nematodes in an intertidal sand flat. Int Rev Ges Hydrobiol 57: 645–663

Ott JA, Novak R (1989) Living at the interface: meiofauna at the oxygen/sulphide boundary of marine sediments. In: Ryland JS, Tyler PA (eds) Reproduction, genetics and distribution of marine organisms. Proc 23rd Eur Mar Biol Symp, Swansea, 5–9 September 1988. Olsen & Olsen, Fredensborg, p 415–422

Editorial responsibility: Otto Kinne (Editor), Oldendorf/Luhe, Germany

Powell EN (1989) Oxygen, sulfide and diffusion: why thiobiotic meiofauna must be sulfide-insensitive first-order respirers. J Mar Res 47:887–932

Rasmussen H, Jørgensen BB (1992) Microelectrode studies of seasonal oxygen uptake in a coastal sediment: role of molecular diffusion. Mar Ecol Prog Ser 81:289–303

Revsbech NP, Jørgensen BB (1986) Microelectrodes: their use in in microbial ecology. Adv Microb Ecol 9:293–352

Rudnick DT, Elmgren R, Frithsen JB (1985) Meiofaunal prominence and benthic seasonality in a coastal marine ecosystem. Oecologia 67:157–168

Sørensen J, Jørgensen BB, Revsbech NP (1979) A comparison of oxygen, nitrate and sulphate respiration in coastal marine sediments. Microb Ecol 5:105–115

Theede H (1973) Comparative studies of the influence of oxygen deficiency and hydrogen sulphide on marine bottom invertebrates. Neth J Sea Res 7:244–252

Trüper HG, Schlegel HG (1964) Sulphur metabolism in Thiorhodaceae. I. Quantitative measurements on growing cells of *Chromatium okenii*. Antonie van Leeuwenhoek. J Microbiol Serol 30:225–238

Vismann B (1991) Sulfide tolerance: physiological mechanisms and ecological implications. Ophelia 34:1–27

Wetmore KL (1988) Burrowing and sediment movement of benthic foraminifera as shown by time-lapse cinematography. Rev Paléobiol 2:921–927

Yingst JY (1978) Patterns of micro- and meiofaunal abundance in marine sediments, measured with the adenosine triphosphate assay. Mar Biol 47:41–54

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