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Population dynamics of benthic shallow-water foraminifera: effects of a simulated marine snow event

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ABSTRACT: In this microcosm experiment, we determined the population dynamics of benthic foraminifera from the northern Adriatic Sea (from 32 m water depth) and how they were affected by an artificial marine snow event (AMS). The study focussed on the performance of individuals in 2 different size fractions: one commonly used in micropaleontological studies (with foraminifera >63 µm) and 1 with smaller individuals (38–63 µm). Microcosms were incubated for 2 or 4 wk, and under AMS or control conditions. For each, the numbers of live (Rose Bengal-stained) individuals of different species in both size fractions were counted. From this, demographic parameters (fecundity, survival, growth) of specimens in different size classes were assessed. With these data, population projection matrices were constructed for the 4 most abundant taxa (*Bolivina* spp., *Stainforthia fusiformis*, *Nonionella turgida* and *Hopkinsina pacifica*) and all foraminifera together. From the limit properties of these matrices, asymptotic population growth rates (λ) were derived. The results indicate that numbers of larger benthic foraminifera decline more strongly because of AMS than those of the smaller individuals, and that growth is seriously inhibited. AMS, however, enhanced fecundity. Under AMS conditions (i.e. temporary anoxia and, concomitantly, extra food), the foraminifera seem to shift to an alternative life-history pathway of rapid reproduction and limited growth. After the first 2 wk, values of demographic parameters increase under AMS conditions, resulting in quickly recovering populations. In our view, these demographic characteristics are beneficial for the observed species in periodically stressful and disturbed ecosystems, and could explain the increasing success of these species in the progressively eutrophicated northern Adriatic Sea.

KEY WORDS: Living benthic foraminifera · Population dynamics · Population projection matrices · Marine snow · Anoxia · Microcosm experiment

INTRODUCTION

The trophic state of the northern Adriatic Sea is mainly governed by the amount of macronutrients that is carried by the Po River from the Italian inland (Degobbis & Gilmartin 1990). The input of nutrients has been quite high for thousands of years, but augmented because of human activity in the last 200 yr. This eutrophication has had profound effects on Adriatic ecosystems and biotic communities (Justič 1987, 1991, Justič et al. 1987, Crema et al. 1991, Barmawidjaja et al. 1995, Duijnstee et al. 2004). When N, P, Si and energy (sunlight) are abundantly present in the northern Adriatic Sea, phytoplankton populations explode in extensive blooms (Justič et al. 1995). During such summer blooms, up to 80% of the photosynthetically fixed carbon may be released by the phytoplankton cells that produced it (Herndl 1992). These organic compounds coagulate and slowly rain down. At the strong pycnocline in the stratified water column, this organic matter further accumulates and forms aggregates of marine snow that can grow

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meters long and decimeters thick. A community of organisms develops embedded in the snow: the so-called false benthos that feasts on the gelatinous mucopolysaccharide matrix (Herndl 1992). When the stratification becomes unstable, the accumulated marine snow sinks down at once, suddenly covering the bottom of the sea. As decomposition of the marine snow proceeds, oxygen is withdrawn from the sediment, causing an anoxic environment lethal for many benthic organisms. Therefore, although this episodic organic input is a source of food that fuels the benthic ecosystem, it may also be considered a source of environmental stress. It is the interplay of these 2 factors, food and oxygen content, that is thought to be the main driving force in the ecology of the foraminifera, an important group of benthic meiofauna (Jorissen et al. 1995, Van der Zwaan et al. 1999).

Foraminiferida (a subphylum of the phylum Granuloreticulosa) are common marine protozoa inhabiting almost all benthic environments. Despite their ubiquity in the marine realm (see e.g. Murray 1991), their biological versatility (see e.g. Lipps 1983), and their importance in the carbon cycle (e.g. Gooday et al. 1992, Graf 1992, Moodley et al. 2000), modern benthic foraminifera have been seriously neglected by biologists. This lack of attention is compensated for by their popularity among paleontologists. The calcareous and agglutinated tests that foraminifera produce have such a high potential to fossilize that they are very abundant in old marine sediments. Some are found in deposits dating all the way back to Cambrian times (Culver 1991). Because of this, temporal and spatial distribution patterns of fossil foraminiferal species can be used as a tool for paleoenvironmental reconstructions (see Van der Zwaan et al. 1999, Gooday 2003). Reliability of such reconstructions largely depends on our knowledge of the ecology of the various foraminiferal taxa. In order to improve foraminifera-based paleoinvestigations, the study of spatial and temporal foraminiferal distribution patterns has recently been complemented by laboratory experiments with extant foraminiferal assemblages. Such experiments have yielded new insights into the response of foraminiferal species to environmental factors such as food availability (e.g. Moodley et al. 2000, Ernst 2002, Heinz et al. 2002), oxygen content (e.g. Alve & Bernhard 1995, Moodley et al. 1997, 1998, Duijnstee et al. 2003) and physical disturbance (e.g. Ernst et al. 2000, 2002, Langezaal et al. 2003).

In this microcosm experiment, we investigated the effect of a simulated marine snow event on the population dynamics of foraminiferal taxa from the northern Adriatic Sea. Three important factors play a prominent role here: (1) low oxygen content, (2) high food availability during presence of artificial marine snow and (3) physical disturbance caused by the act of conducting the experiment (i.e. sampling, transporting, sieving and mixing of the sediment). To test factors (1) and (2), we included a snow-free control situation in the experiment. A control situation was not possible for factor (3) as it is inherent in experiments such as these. A comparison with the field situation can, however, be made. The study was designed to separately monitor demographic dynamics of foraminifera in 2 different size classes: small foraminifera (38–63 µm) and larger ones (>63 µm). This division was necessary since in paleontology, only the larger foraminiferal size fractions are studied. In order to make a translation of the results from this experiment to paleontological applications possible, we need to understand the effect on both size classes separately. We calculated demographic parameters (fecundity, growth and survival) and asymptotic population growth rates (λ) using the limit properties of population projection matrices (Caswell 1989). The main question here is how growth, reproduction and survival are influenced by marine snow events, and how the (altered) demographic parameters affect the overall growth of the populations.

MATERIALS AND METHODS

Material collection and experimental set-up. In February 2000, sediment was collected from the bottom of the northern Adriatic Sea (using a Van Veen grab) at Station 108. This station is situated 25 km SE of the main Po River outlet (44° 45.4′ N, 12° 45.0′ E) at a depth of 32 m (see Duijnstee et al. 2004 for a more detailed description). The upper 2 cm of the sediment was collected and transported to the Netherlands in plastic jars (half filled with sediment and half with sea water). Two 10 cm cores (obtained by SCUBA divers) were immediately used on board to measure porewater oxygen concentrations at various depths in the sediment, using oxygen needle electrodes (Microscale Measurements, diameter 1 mm) with a Ag/AgCl reference electrode (Philips R11-D-SC) and a nanoAmpmeter (EDB-RUG MB05 NA).

The sediment to be used for the experiments was sieved over a 500 µm screen in order to remove the disturbing effect of macrofauna. Particles smaller than 500 µm were then sieved into 3 size fractions: >63 µm, 38–63 µm and <38 µm (Fig. 1). The smallest size fraction comprised the bulk of the sediment volume (>95%). All sediment of the 3 different size classes was mixed thoroughly and split dichotomously into 16 equal portions, using an Otto-microsplitter (first into 2 halves, then each half split into quarters, then eighths and then sixteenths).

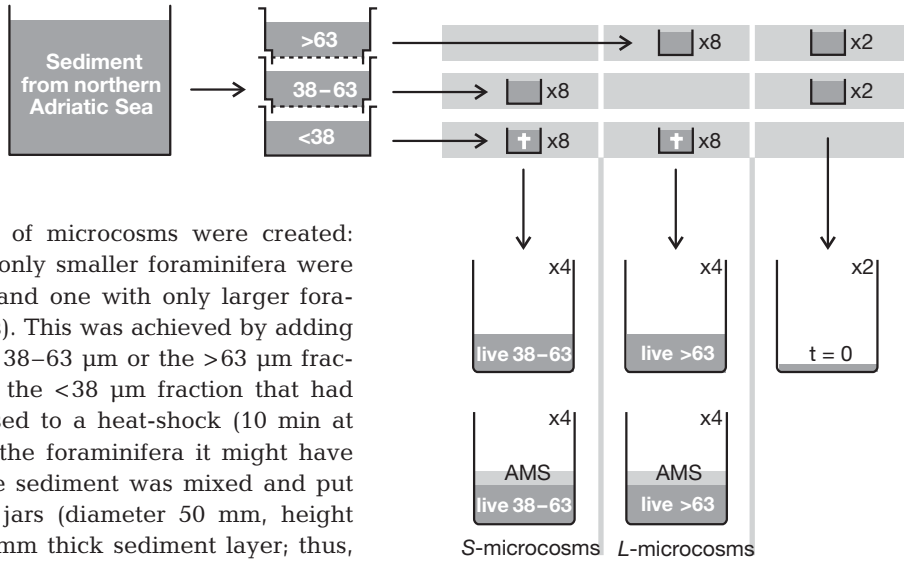

Fig. 1. Experimental set-up. In subsamples with a cross, all foraminifera were killed. Mesh sizes of the sieves were 38 and 63 µm

Two different kinds of microcosms were created: one in which initially only smaller foraminifera were living (*S*-microcosms) and one with only larger foraminifera (*L*-microcosms). This was achieved by adding 1 portion of either the 38–63 µm or the >63 µm fraction to one portion of the <38 µm fraction that had previously been exposed to a heat-shock (10 min at 90°C) in order to kill the foraminifera it might have contained (Fig. 1). The sediment was mixed and put in small open plastic jars (diameter 50 mm, height 55 mm) forming a 20 mm thick sediment layer; thus, 8 microcosms of each type were made. In half of each group, the sediment was covered with a 5 mm thick layer of artificial marine snow (AMS, see below), in accordance with field observations at the same Adriatic location. Incubation took place in an aquarium filled with seawater (salinity of 37‰) at a constant temperature of 17°C. The aquarium was permanently aerated and kept in the dark. For each type of microcosm, half of the jars with and without AMS were harvested after 2 wk of incubation. The other 8 microcosms were harvested after 4 wk. Harvesting was achieved by adding 40 ml of ethanol with 1 g l^{-1} Rose Bengal (RB). RB stains protoplasm remains brightly pink or red in living (or very recently deceased) foraminifera (Walton 1952). The foraminifera stayed in the RB solution for at least 3 wk to achieve maximum staining intensity (Lutze & Altenbach 1991).

After this, the sediment was sieved over 63 and 38 µm screens, and then dried. The 38–63 and >63 µm fractions of all samples were examined under the microscope. The RB-stained specimens (which were alive at, or shortly before, the time of harvesting) were picked out of the sample and mounted on a slide for the >63 µm fraction. In the case of the 38–63 µm size class, the numbers of stained individuals of different taxa were simply scored on a list instead of being picked out. In many cases, foraminifer-rich samples were split (using an Otto-microsplitter) until they contained at least 200 specimens. If there were less than 200 individuals, the total sample was analysed.

Before harvesting the foraminifera, oxygen profiles were made for the entire sediment column in the microcosms. This was done with oxygen needle electrodes (Microscale Measurements) with a Ag/AgCl reference electrode (Philips R11-D-SC) and a nano-Ampmeter (EDB-RUG MB05 NA).

At the beginning of the experiment, 2 portions of the 38–63 and the >63 µm fractions were put together and killed immediately by adding 20 ml of ethanol containing 1 g l^{-1} RB. These portions were used to determine the foraminiferal abundances at the beginning of the experiment ($t = 0$).

Artificial marine snow. The AMS was made to mimic conditions in the northern Adriatic Sea after a marine snow event. It consisted of 10 ml LB medium (i.e. 0.1 g 10% lactone-tryptane, 0.05 g 5% yeast-extract, 10 ml sea water), 0.125 g agar (70% agarose and 30% agaropectin), extract from the sediment with particles <10 µm (for the introduction of marine bacteria) and fresh cultured algae: *Dunaliella salina*, *Amphipora* sp. and *Phaeodactylum* sp. These taxa were chosen because they have been used for years as food in foraminiferal cultures (M. Holzmann pers. comm.). The LB medium and the agar were first heated in a hot bath to a temperature of 90°C, cooled down to 17°C, and then the sediment extract and algae were added. Just as true senescent marine snow, AMS is a gelatinous, polysaccharide matrix, rich in embedded bacteria and algae. The AMS is thought to be a high quality food source, but is also characterized by a high O_2 demand because of high rates of decay of organic matter. Furthermore, it inhibits O_2 diffusion from the water column into the sediment.

Demographic parameters and population projection matrices. Fig. 2 shows a simplified size-based life cycle of foraminifera in the 38–63 µm (α) and >63 µm (β) size classes (the latter is examined in most micropaleontological studies). The arrows indicate the demo-

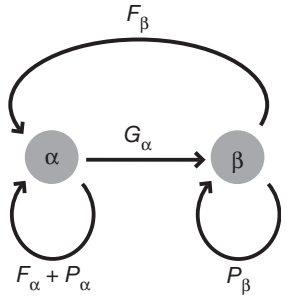

Fig. 2. Simplified size-based foraminiferal life cycle. A distinction is made between 2 size classes: α = 38–63 µm, β = foraminifera >63 µm. The arrows indicate contributions that a size class can make (during 1 time step of 2 wk) to that same size class or the other. These contributions are: reproduction (F = fecundity), the fraction of smaller individuals that grow into the larger size class (G = growth) or the fraction of individuals in a size class that is alive after 2 wk but still in the same size fraction (P = survival)

graphic parameters fecundity (F), survival (P) and growth (G) of these size fractions (a glossary of terms and symbols used in this paragraph can be found in Table 1). Note that Fig. 2 is not based on the (often complicated) reproductive cycle of the foraminifera. Instead, it is merely a size-based life cycle, in which the size intervals are chosen because of their relevance in paleontological studies and not because of their functionality in the life of the foraminiferal individual. Since it is not possible to accurately calculate F_α and P_α separately from the experiment data, only their sum ($F_\alpha + P_\alpha$) is shown in the life cycle.

If the values for F, P and G are known, they can be used to predict the number of individuals in size classes α and β in the future. The mathematical notation for this is a so-called population projection matrix (Eq. 1, after Caswell 1989). In order to project the abundances of foraminifera in both size classes after n timesteps ($t = T + n$), one must multiply the matrix, raised to the n^{th} power, a vector containing the initial abundances (at $t = T$):

$$\begin{pmatrix} \alpha_{t=T+n} \\ \beta_{t=T+n} \end{pmatrix} = \begin{vmatrix} F_\alpha + P_\alpha & F_\beta \\ G_\alpha & P_\beta \end{vmatrix}^n \cdot \begin{pmatrix} \alpha_{t=T} \\ \beta_{t=T} \end{pmatrix} \quad (1)$$

Due to the way the experiment is designed, calculating the demographic parameters for the first 2 wk is easy: e.g. larger foraminifera found in the *S*-microcosms after 2 wk must be the result of growth, smaller foraminifera showing up in *L*-microcosms are the result of reproduction. Unfortunately, this did not work for Weeks 3 to 4, since at the start of Week 3, the *S*-microcosms also contained larger individuals and the *L*-microcosms smaller ones. However, if we assume that $F_\alpha + P_\alpha$, F_β, G_α and P_β are the same in both types of microcosms, we can derive a general formula to calculate the demographic parameters.

Assuming a data set with a to h representing the foraminiferal densities as we find them in our experimental results (a to d for the *S*-microcosm and e to h for the *L*-microcosm), then substitution of both a to d and e to h in Eq. (1), yields 4 equations with 4 variables:

$$\begin{pmatrix} b \\ d \end{pmatrix} = \begin{vmatrix} F_\alpha + P_\alpha & F_\beta \\ G_\alpha & P_\beta \end{vmatrix} \cdot \begin{pmatrix} a \\ c \end{pmatrix} \text{and} \begin{pmatrix} f \\ h \end{pmatrix} = \begin{vmatrix} F_\alpha + P_\alpha & F_\beta \\ G_\alpha & P_\beta \end{vmatrix} \cdot \begin{pmatrix} e \\ g \end{pmatrix} \quad (2)$$

Or:

$$b = a \cdot (F_\alpha + P_\alpha) + c \cdot F_\beta \text{ and } d = a \cdot G_\alpha + c \cdot P_\beta \quad (3)$$

and

$$f = e \cdot (F_\alpha + P_\alpha) + g \cdot F_\beta \text{ and } h = e \cdot G_\alpha + g \cdot P_\beta$$

The 4 variables can, thus, be expressed as combinations of a to h (i.e. the experimental results):

$$F_\alpha + P_\alpha = \frac{b \cdot g - c \cdot f}{a \cdot g - c \cdot e} \text{ and } F_\beta = \frac{a \cdot f - b \cdot e}{a \cdot g - c \cdot e} \quad (4)$$

and

$$G_\alpha = \frac{d \cdot g - c \cdot h}{a \cdot g - c \cdot e} \text{ and } P_\beta = \frac{a \cdot h - d \cdot e}{a \cdot g - c \cdot e}$$

As mentioned before, the experiment was carried out in duplicate. Since there are differences between the replicates, it would not be fair to only use the mean values in the analysis without any consideration for the measured differences; therefore, in order to utilize the observed differences, averages and standard deviations were calculated for the replicate counts of foraminifera in each type of microcosm and size fraction. Instead of using the mean values of a to h to calculate $F_\alpha + P_\alpha$, F_β, G_α and P_β, values were drawn stochastically from normal distributions defined by the mean and the standard deviation. Thus, derived values of $F_\alpha + P_\alpha$, F_β, G_α and P_β only represent one of the possible scenarios

Table 1. Glossary of symbols

Symbol	Definition
α	Foraminiferal size fraction 38–63 µm
β	Foraminiferal size fraction >63 µm
$F_\alpha + P_\alpha$	Fecundity and chance of survival of α during 1 time step (i.e. 14 d)
F_β	Fecundity of β during 1 time step
G_α	Fraction of α that grew to β within 1 time step
P_β	Chance of survival of individuals in β
λ_x	Dominant eigenvalue of the population projection matrix, i.e. the asymptotic growth rate of the entire population if the demographic parameters remained as they were during period x

that might have occurred during the experiment. In order to cover the full variation in the experimental data, this procedure was repeated 50 times, resulting in 50 possible demographic scenarios (that yielded values for $F_\alpha + P_\alpha$, F_β, G_α and P_β greater than 0) and an equal number of population projection matrices. Such analysis was undertaken for both treatments as well as for Weeks 1 to 2 and Weeks 3 to 4, for the total foraminiferal community and for the 4 most abundant species. This analysis yielded 1000 population projection matrices for which limit properties were assessed with the help of the program RAMAS/stage (©Applied Biomathematics).

Matrix limit properties. When n in Eq. (1) approximates to infinity, the matrix raised to the n^{th} power becomes a stable value: this is called the dominant eigenvalue (λ), which represents the asymptotic growth rate of the entire population if the life-history parameters in the experiment did not change (Caswell 1989). This is an excellent measure of the health of the population. For the 4 most abundant taxa and all summed species, λ (for 50 matrices each) was calculated, based on the demographic conditions of both Weeks 1 to 2 (λ_{0-14}) and Weeks 3 to 4 (λ_{14-28}) in the experiment.

RESULTS

The oxygen profiles are shown in Fig. 3. The observed patterns were identical at both sampling times (t = 14 and t = 28 d), and for both the *S*- and *L*-microcosms. There was a clear difference in oxygen profile of the jars with and without AMS (Fig. 3). The water column in the microcosms without AMS was almost saturated with O_2 (5.4 ml l^{-1}) down to the sediment-water interface. Within the sediment, the [O_2] declines sharply to 0 at about 6 mm depth. Due to the high O_2 demand in the AMS samples, the [O_2] decreases rapidly in the overlying water and approaches anoxia very quickly within the AMS layer near the sediment-AMS interface. The oxygen profile of the samples without AMS was similar to that measured in the field during sediment collection.

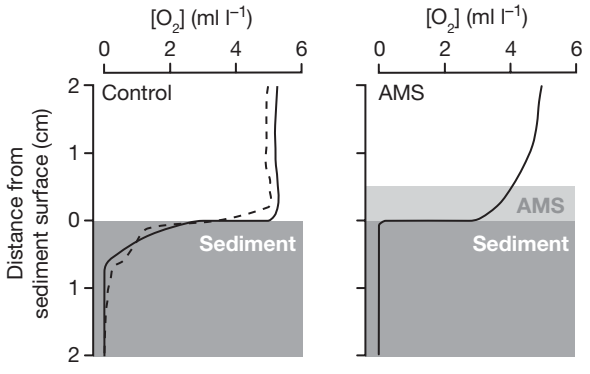

Fig. 3. Oxygen profiles around the sediment-water interface in the microcosms. The light grey layer in the graph on the right is the artificial marine snow (AMS) layer. The dashed line gives the oxygen profile measured in the field

The high speed at which oxygen is apparently consumed in the sediment of the AMS samples is confirmed by the rapid rate at which it turned black and started to smell of H_2S. This occurred within 7 d after the start of the incubation period.

The AMS in the 4 wk old microcosms showed clear signs of decay. The gelatinous texture of the AMS was less firm than earlier. Furthermore, the thickness of the AMS layer decreased locally.

Foraminiferal numbers

At the beginning of the experiment, the 4 most abundant taxa constituted two-thirds of the total foraminiferal standing stock. This group was comprised of *Bolivina* spp. (26%), *Stainforthia fusiformis* (18%), *Nonionella turgida* (14%) and *Hopkinsina pacifica* (9%). The first taxon is a combination of *B. seminuda*, *B. dilatata*, *B. spathulata* and their numerous intermediate morphotypes (see Barmawidjaja et al. 1992).

In all microcosms, the number of individuals in the initially introduced size fraction declined during Weeks 1 and 2 of the experiment (Figs. 4a,b & 5c,d). The decrease in the *L*-microcosm, however, was much stronger under the influence of AMS (Fig. 5c,d), although the number of larger foraminifera seemed to stabilize during Weeks 3 to 4. The decrease in numbers in the *S*-microcosm was similar for both treatments (Fig. 4a,b). All species declined at a similar rate, except for *Nonionella turgida*, whose numbers decreased less strongly at the beginning (and therefore its relative abundance increased), but its population shrank faster after 2 wk.

The rate of reproduction of foraminifera from the larger size fraction in the first 2 wk can be inferred from Fig. 5, by comparing the first bar in Fig. 5c,d (number of adults at t = 0) with the second bar in Fig. 5a,b (number of offspring after 2 wk). Adult reproduction was comparable in microcosms of both treatments. During Weeks 3 and 4 of AMS conditions, however, the number of small individuals increased, while it did not under oxygenated conditions.

In contrast to the situation in snow-free microcosms, growth of smaller individuals to the larger size fraction was virtually absent during the first 2 wk in the AMS samples (Fig. 4c,d). During Weeks 3 and 4 of the experiment, the number of large individuals in the *S*-microcosm seemed to have increased somewhat, but their total number was still very low.

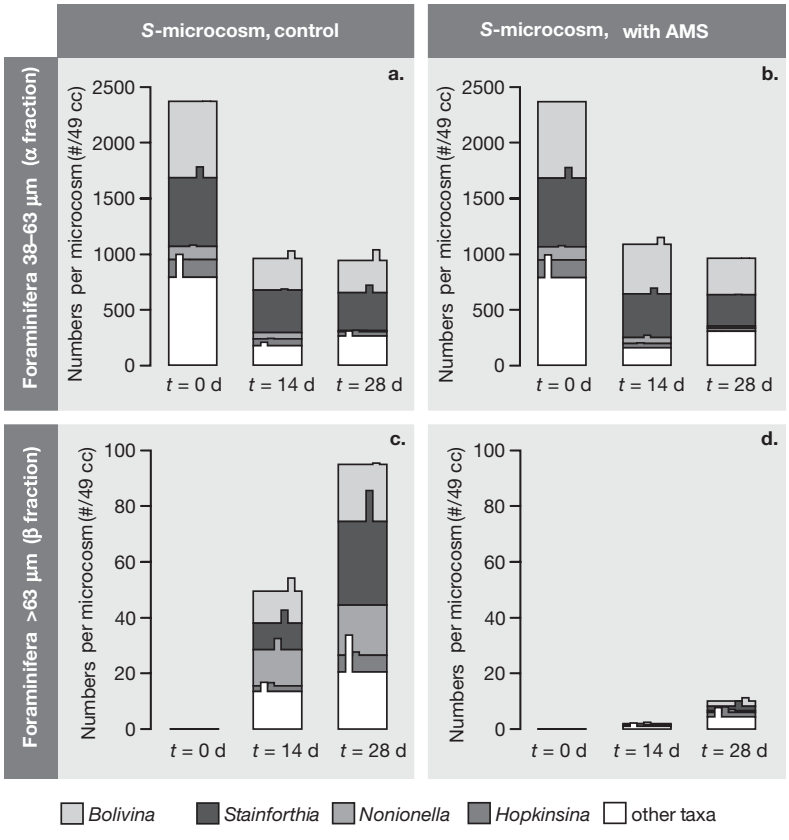

Fig. 4. Average foraminiferal densities in *S*-microcosms (containing only smaller foraminifera initially); (a) 38–63 µm fraction in control microcosms; (b) 38–63 µm fraction in AMS microcosms; (c) >63 µm fraction in control microcosms; (d) >63 µm fraction in AMS microcosms. Standard deviations are shown as narrow bars

Demographic parameters

The average values for the demographic parameters for all foraminiferal taxa (each based on 50 matrix scenarios) are represented graphically in Fig. 6. The relative changes of the demographic parameters in time or because of the AMS treatment are summarized in Table 2, and the significance of the observed differences can be found in Table 3. During the experiment, the relatively low values for survival and reproduction ($F_\alpha + P_\alpha$), and growth (G_α) of the smaller foraminifera increased significantly as time went by. In addition, survival and fecundity of larger individuals (P_β and F_β) were higher in Weeks 3 to 4, but not in the control microcosms. When only snow-free conditions are considered, there was a significant negative time effect on the demographic parameters of the β-fraction. In all cases, the presence of AMS had a significant positive effect on the reproduction of larger foraminifera (F_β) and a strong negative effect on the growth of smaller ones (G_α). The survival of larger individuals (P_β) was significantly lower during the first 2 wk because of AMS, whereas in Weeks 3 to 4, AMS appeared to be beneficial.

Fig. 7 shows the demographic parameters for the 4 most abundant taxa. In general, the patterns described above are also true for the taxa separately, except for *Nonionella turgida*. This species lacked the demographic improvements during Weeks 3 to 4, except for growth of small individuals. Furthermore, it had the lowest reproductive values of the 4 taxa, whereas growth of small individuals in the control microcosms was relatively high. *Stainforthia fusiformis* stood out because of its high fecundity of larger specimens in the first 2 wk of the experiment and/or in the AMS microcosms.

Population growth rates

The outcome of the 50 population matrices with respect to the asymptotic growth rates of the simulated populations (λ) of all foraminifera is shown in Fig. 8. Simulations for the first 2 wk of AMS conditions only yielded values of $\lambda < 1$, indicating ultimately shrinking populations under the governing demographic conditions. The other situations are characterized by dominant eigenvalues, both larger and smaller than 1. In the first 2 wk of the control situation, the scenarios with shrinking populations dominate; in the second 2 wk, λ exceeded 1 about 50% of the time. During the second 2 wk in AMS microcosms, we observed mainly growing populations. The same pattern was observed in the dominant eigenvalues of *Bolivina* spp., *Stainforthia fusiformis* and *Hopkinsina pacifica* (Fig. 9a,b,d). The latter 2, however, performed somewhat better in the first 2 wk under snow-free conditions than with AMS. During Weeks 3 to 4, the opposite was true. Again, *Nonionella turgida* (Fig. 9c) is different, with shrinking populations in almost all scenarios.

The averaged values of λ for the varying experimental conditions are listed in Table 4. In Table 5, the differences between the averaged values of λ are summarized (the significance of these differences are indicated in Table 6). If we disregard *Nonionella turgida*, the general trend was that dominant eigenvalues increased during the experiment in AMS microcosms, whereas in the control situation, this was only true for *Bolivina* spp. and all foraminifera combined. AMS had a negative effect on the population growth rates in Weeks 1 to 2, but a positive effect in Weeks 3 to 4.

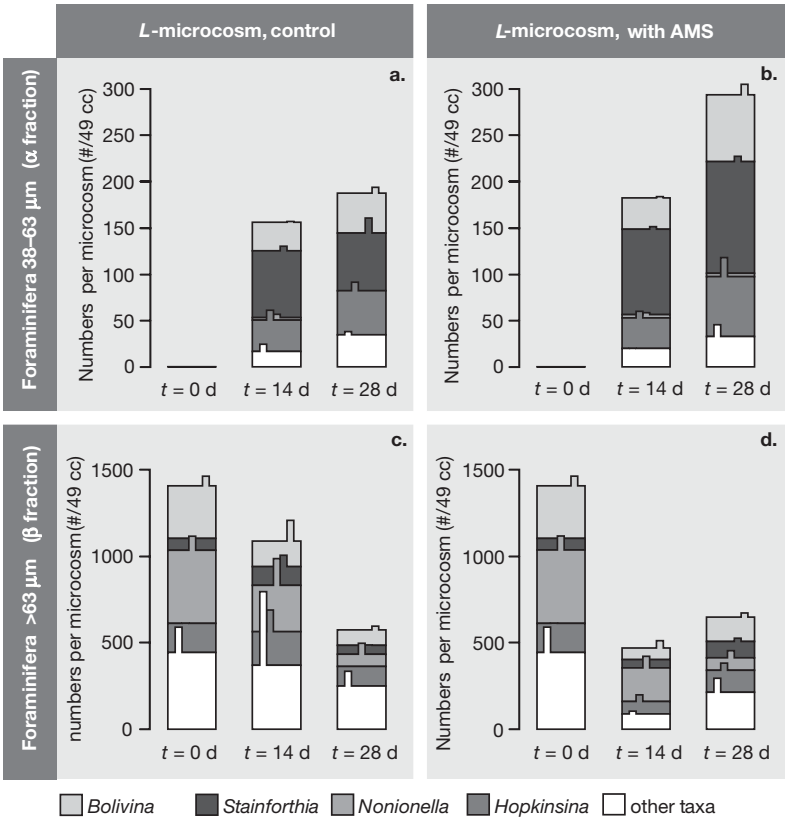

Fig. 5. Average foraminiferal densities in *L*-microcosms (containing only larger foraminifera initially); (a) 38–63 µm fraction in control microcosms; (b) 38–63 µm fraction in AMS microcosms; (c) >63 µm fraction in control microcosms; (d) >63 µm fraction in AMS microcosms. Standard deviations are shown as narrow bars

DISCUSSION

Experimental limitations and assumptions

A shortcoming of this experiment was that we only sampled 2 replicates for each treatment and each sample moment. Of course, differences observed between replicates do not give a clear picture of the true spread in foraminiferal numbers that would exist if we had had an infinite number of microcosms. Therefore, the normal distributions around the mean values of both replicates, used in the population projection models, only give an indication of what the true range of values might have been.

For the calculation of the demographic parameters, we assumed that *F*, *G* and *P* of both size fractions were identical in corresponding *S*- and *L*-microcosms. Theoretically, the initial absence of larger foraminifera in *S*-microcosms (and absence of smaller ones in *L*-microcosms) might affect the population dynamics (the same applies for the initial absence of specimens <38 µm in both types of microcosms). This is true when density-related effects such as competition play an important role. However, in a comparable microcosm experiment with sediment from the same Adriatic locality, Ernst et al. (2002) demonstrated that density-dependent processes in this relatively foraminifer-poor and food-rich sediment do not play an appreciable role.

A number of assumptions have been made in the simplified foraminiferal life cycle (Fig. 2) and associated matrices. Firstly, it is assumed that foraminifera can only be a member of the <38 µm size class for a period shorter than 1 time step (i.e. 2 wk). If not, this size fraction should have been included explicitly in the life cycle. Given the small number of chambers foraminifera can possess when <38 µm, it is likely that this is a reasonable assumption. Secondly, it is assumed that within 1 time step, an individual cannot contribute to a size class via 2 demographic transitions: i.e. reproduce and the offspring grow to a larger size class within 2 wk (α-α-β, β-α-β), or first grow and then reproduce (α-β-α), or reproduce and offspring reproduce (α-α-α, β-α-α). In the case of β-α-β, for instance, F_α would be

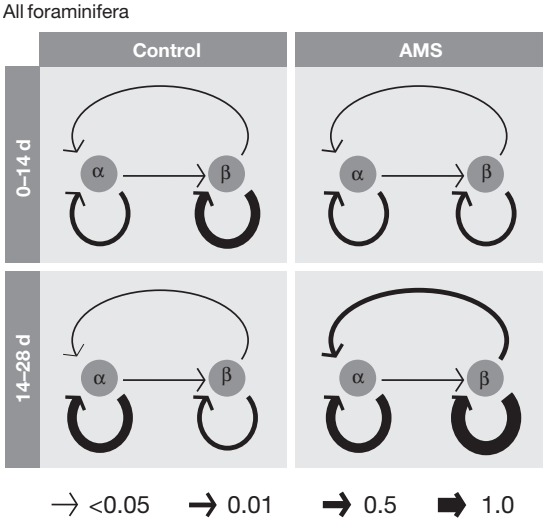

Fig. 6. Demographic parameters in the foraminiferal life cycle shown and explained in Fig. 2, for all foraminiferal species combined. The thickness of the arrows corresponds to the mean values for $F_\alpha + P_\alpha$ (arrow from α to α), F_β (arrow β-α), G_α (arrow α-β) and P_β (arrow β-β) per 14 d (see legend)

Table 2. Relative changes in demographic parameters with regard to time and treatment. For this, mean demographic values for the second 2 wk were divided by those of the first 2 wk (time effect), and values for AMS microcosms were divided by those of control microcosms (AMS effect). The value of these ratios is indicated with pluses or minuses: +++: >4; ++: 2–4; +: 1–2; –: 0.5–1; – –: 0.25–0.5; – – –: <0.25. Ratios between the means of 2 groups of values that were not significantly different, are shown in brackets (see statistics in Table 3)

	Time effect			AMS effect		
	Control	AMS	Overall	0–14 d	14–28 d	Overall
$F_\alpha + P_\alpha$	++	+	++	+	(+)	(+)
G_α	++	+++	+++	– – –	– – –	– – –
F_β	–	++	+	+	+++	++
P_β	–	++	+	–	+	(+)

overestimated at the cost of G_α and F_β. We have no indication, however, that this happened during the experiment. α-α-β and β-α-β would lead to higher values of G_α and P_β, respectively (possibly even exceeding 1), while F_α would be underestimated. In some of the simulation matrices that were derived from the experiment, P_β was indeed >1, suggesting that a 2 wk time step in our experiment was too long rather than too short. Unfortunately, detailed information on the demography of benthic foraminifera is rare. In an experiment by Groß (1998), the first months in the life of *Bulimina marginata* (also a member of the foraminiferal assemblage in this experiment) were monitored. Groß (1998) considered this species to be fast growing. In his discussion, he mentioned observed growth rates of 100 µm mo^{-1} for juveniles. This would be too fast for the time step of 2 wk in our study. The data he presented, however, revealed average growth rates of 1.8 µm d^{-1} or 25 µm in 14 d.

Unfortunately, the presence of other meiofauna (such as nematodes) was not investigated. Since these organisms might be competing with foraminifera for food, or preying on them, they might have affected the foraminiferal populations. As several weeks of exposure to anoxia is lethal for most other meiofauna (Moodley et al. 1997), their presence in the control situation and absence in AMS microcosms might have influenced the results.

A possible limitation in this experiment is that the use of RB does not provide a very accurate viability test. Beside living foraminifera, RB also stains recently deceased foraminifera that retain undecayed protoplasm. In some cases, tests are known to stain red weeks after the foraminifer died (see e.g. Bernhard 1988, 2000, Corliss & Emerson 1990, Murray & Bowser 2000). Since we chose time intervals of 2 wk, this could have been a serious problem. The decaying time for protoplasm, however, is extremely variable, depending on environmental conditions and biovolume. Fortunately, in this experiment, all foraminifera were relatively small (<150 µm). In general, relatively high temperatures (17°C was used) facilitate a higher decay rate of organic matter. The decay is further accelerated by the high bacterial activity in the sediment of this eutrophicated part of the Adriatic Sea (Tahey et al. 1996). These factors explain why we do not see an obvious effect of the non-vital staining of RB in our data, despite the short time intervals. The results that had the highest risk of being biased by wrong staining were the ones from the AMS microcosms, since the anoxia and high sulphide content may slow down protoplasm decay. Yet, we saw no sign of overestimation of the number of living foraminifera (such as stable or growing numbers where you would expect declining densities). Our findings are corroborated by the work of Lutze & Altenbach (1991), who concluded that the RB method applied to foraminifera, when used with great care, was wrong in only 4 % of the 400 cases they tested.

Foraminiferal response to AMS

Enhanced reproduction

Foraminifera, in this experiment, react to the AMS event by enhanced reproduction. Population sizes of benthic foraminifera are known to react rapidly to environmental changes such as increased flux of

Table 3. Significance of differences in demographic parameters with regard to time and treatment. Variance ratios (F) obtained from ANOVAs and their probabilities (p) are shown

	Time effect						AMS effect					
	Control		AMS		Overall		0–14 d		14–28 d		Overall	
	$F_{1,99}$	p	$F_{1,99}$	p	$F_{1,199}$	p	$F_{1,99}$	p	$F_{1,99}$	p	$F_{1,199}$	p
$F_\alpha + P_\alpha$	148.5	<0.001	775.1	<0.001	473.3	<0.001	15.3	<0.001	0.3	0.588	3.4	0.066
G_α	73.4	<0.001	105.9	<0.001	103.0	<0.001	146.0	<0.001	97.4	<0.001	154.5	<0.001
F_β	26.1	<0.001	42.7	<0.001	13.3	<0.001	14.6	<0.001	85.8	<0.001	98.0	<0.001
P_β	8.0	0.006	100.2	<0.001	16.0	<0.001	26.9	<0.001	45.3	<0.001	1.5	0.219

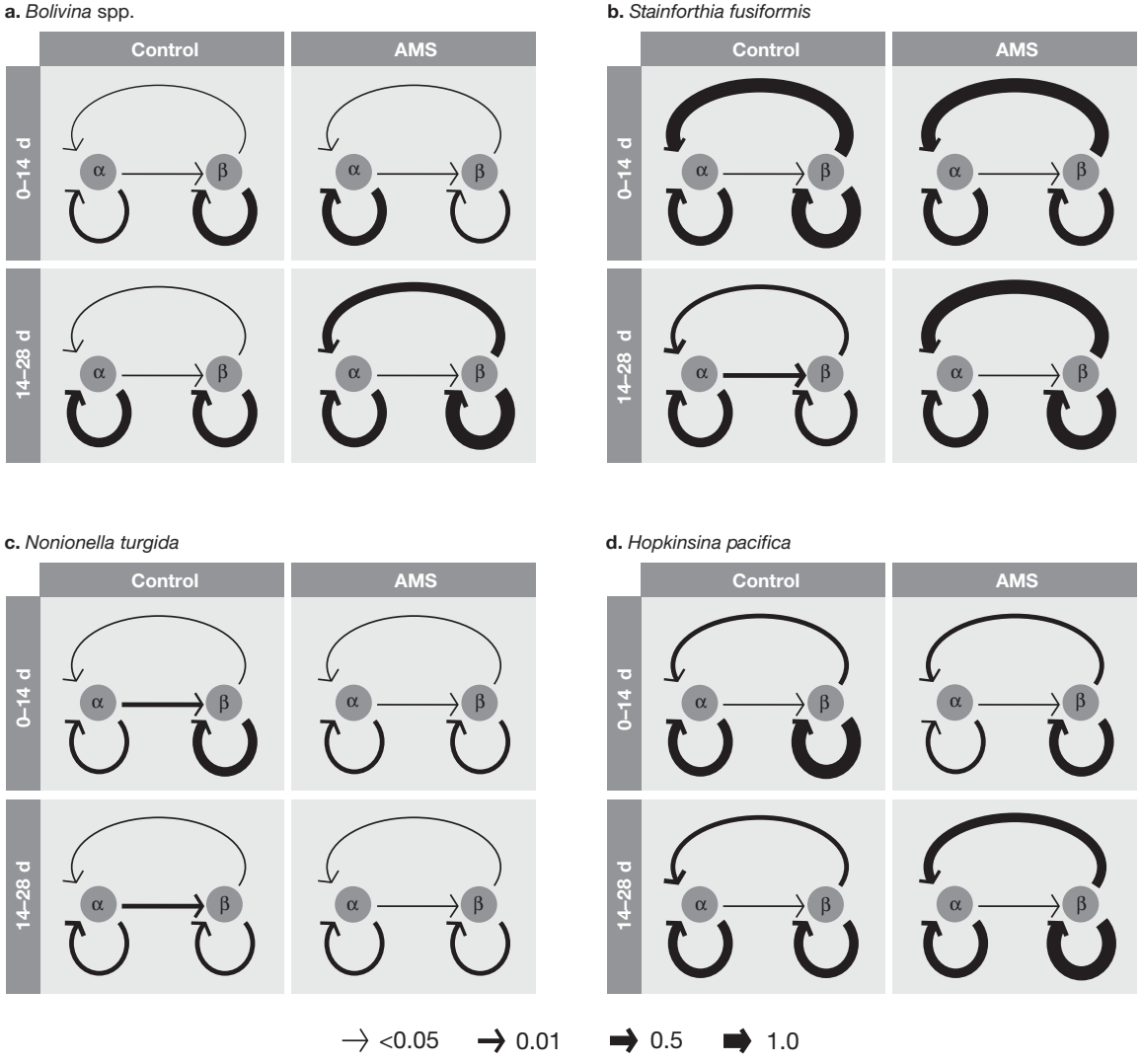

Fig. 7. Demographic parameters in the foraminiferal life cycle shown and explained in Fig. 2, for the 4 most abundant taxa. The thickness of the arrows corresponds to the mean values for $F_\alpha + P_\alpha$ (arrow from α to α), F_β (arrow β to α), G_α (arrow α to β) and P_β (arrow β to β) per 14 d (see legend)

organic material after phytoplankton blooms (e.g. Gooday & Turley 1990). Sometimes, responses of benthic communities can be traced within days (Graf 1989). Foraminiferal population growth during such events is generally ascribed to changes in food availability. This is not surprising since foraminifera prove to be rapid consumers of organic carbon arriving at the seafloor (Moodley et al. 2002). However, in the first 2 wk of this experiment, we saw that foraminifera decreased in number more rapidly under AMS conditions than in the control situation. Moreover, smaller individuals no longer grew into the larger size class when exposed to AMS. Therefore, the organic flux in the form of AMS, which is accompanied by anoxia of the sediment and sulphide production, is initially mainly a source of stress. It is possible that the observed enhanced reproduction was stress-induced instead of being triggered by an extra input of food.

Moodley et al. (1997) conducted a microcosm experiment with sediment from the northern Adriatic Sea that was exposed to prolonged anoxia. Although the authors reported that they had no evidence that reproduction took place during the experiment, results show that in the anoxic series, the mean density in the 38–63 µm fraction of all 5 dominant genera was higher after 11 d than initially. In fact, the abundances of representatives from the genera *Bolivina* and *Stainforthia* grew approximately 55%. In the oxygenated series of the experiment, however, foraminiferal densities in this size fraction were stable or even decreased during the first 11 d. In our view, the rise in numbers amongst small foraminifera during oxygen stress can be interpreted as a

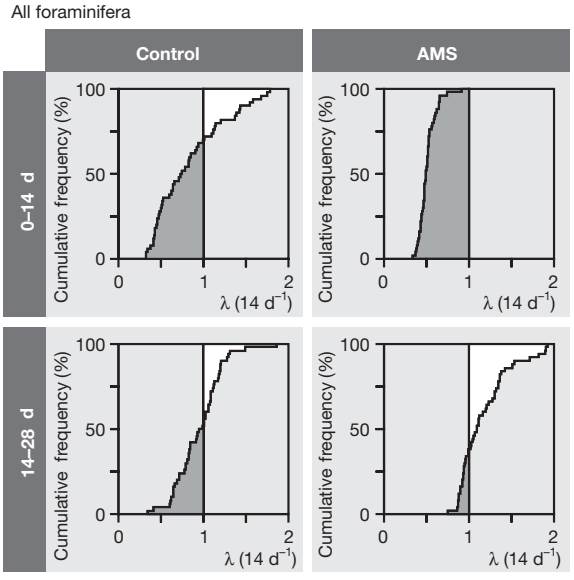

Fig. 8. Distribution of values of λ for all foraminiferal species combined. Each sub-graph was based on the outcome of 50 population projection matrices. Population growth rates <1 and >1 are emphasized in dark grey and white, respectively

result of reproduction. As in our experiment, this enhanced reproduction could be induced either by an oxygen-stress related factor, or by a changed food availability. In the experiment of Moodley et al. (1997), however, no extra food was added. This seems to suggest that the enhanced reproduction could be a direct result of the stress caused by anoxia. Some changes in food availability might have occurred though, because several meiofaunal organisms died, thus providing extra food and/or reducing the competition for food. It is also possibile that the enhanced reproduction is not a result of an increased number of 'births', but of a higher chance of survival of foraminifera <38 µm. This might be the case if meiofaunal predators that specifically prey on very small foraminifera died because of the anoxia. Unfortunately, in our study other meiofauna, such as nematodes, were not enumerated.

From an energy-budgetary point of view, reproducing under stressful conditions seems to be of no selective benefit. A higher number of individuals, however, means an increase of copies of the individual's genome, thus increasing the chance that at least 1 copy will survive the stressful episode.

Changing life-history strategy?

A result of the presence of AMS is the stagnation of growth of smaller individuals. This is something that is predicted by Grime's conceptual model (1977, 1979), in which he postulates that there is a trade-off between 3 types of life-history strategies: competitive strategy (*C*), stress-tolerant strategy (*S*) and the ruderal strategy (*R*). This model was first developed for herbaceous plants, but proved broadly applicable. Ruderal and stress-tolerant strategies are preferred under the selection processes of disturbance and stress, respectively. Here, disturbance is defined as the destruction of biomass and stress as external constraints on biomass production (Grime 1984). When stress and disturbance intensities are low, rapid population growth leads to competition for food and space. Silvertown et al. (1992) made an effort to bridge the gap between Grime's life-history theory and demographically-based theories. They argued that there are *a priori* grounds for an analogy between them both: competitors invest more energy in growth, stress tolerators in survival and disturbance tolerators (ruderals) in high fecundity, or: *C* ~ growth, *S* ~ survival and *R* ~ fecundity. The combination of these models predicts that in our experiment (with its high levels of initial disturbance and AMS-related stress), a shift in strategy from *C* to *R* and *S* would be beneficial. In other words, the foraminifera exhibit an investment of energy in fecundity and survival at the cost of growth, or an inhibition of growth during stress and disturbance. The experimental results are consistent with this prediction and suggest that some foraminiferal species are capable of switching to alternative life-history pathways. If this is true, this means that the size distribution of foraminifera in fossil assemblages could contain information about the intensity of periodic stress or disturbance.

Recovery

After 4 wk, the sediment of the AMS microcosms was still anoxic. Despite this, foraminiferal abundances recovered to control levels. It is unclear, however, if this was possible because of gradual acclimation of the surviving individuals, less competition due to a lack of other meiofauna or if foraminifera were able migrate into the top part of the partially decayed AMS where some oxygen is present and organic matter abundant.

Comparison with the field situation

Population growth rates

The lowest values observed for λ in the control microcosms (Table 4) are comparable to the minimum growth factors in the field (Table 7, based on data

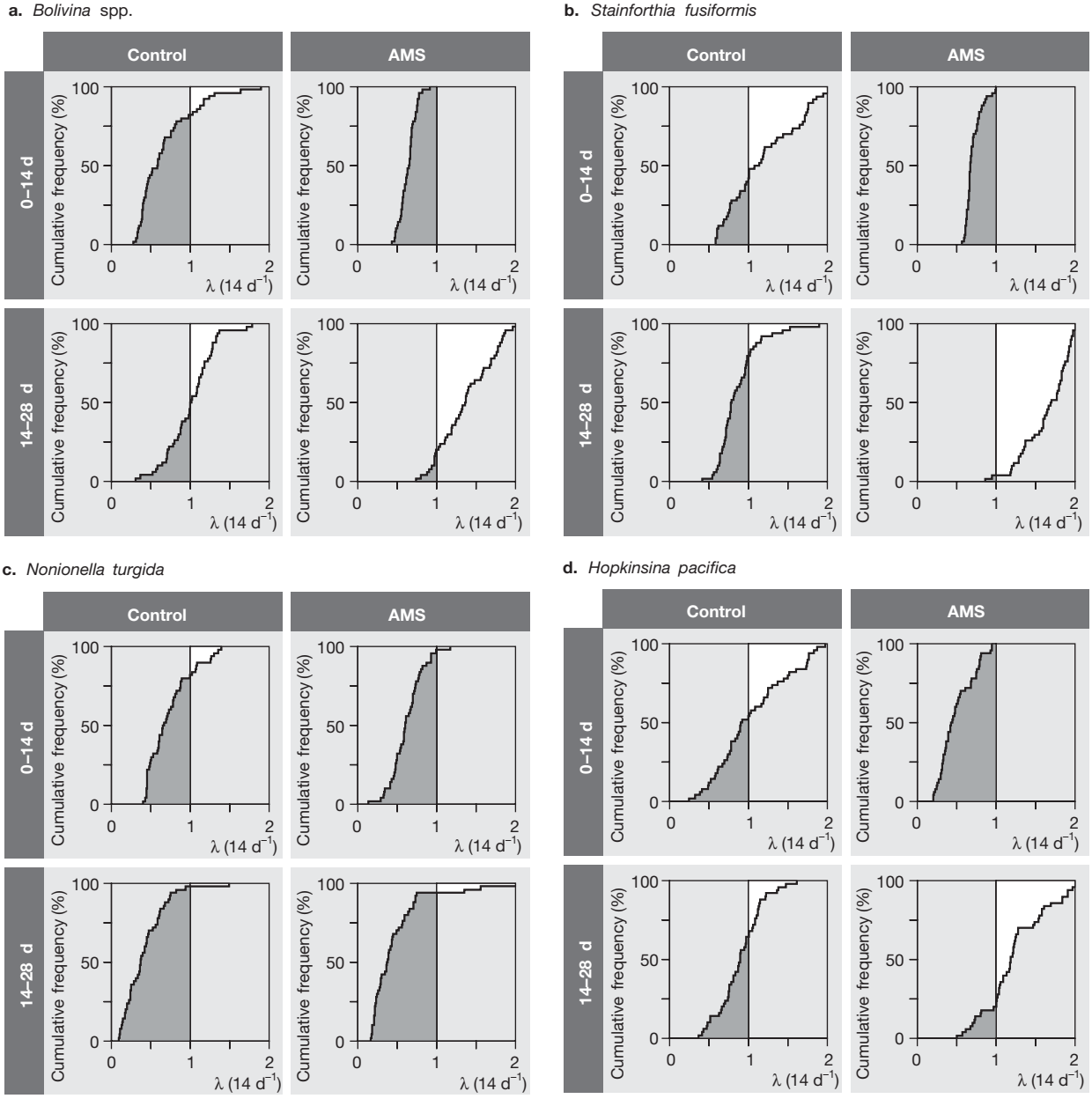

Fig. 9. Distribution of values of λ for the 4 most abundant taxa. Each sub-graph was based on the outcome of 50 population projection matrices. Population growth rates <1 and >1 are emphasized in dark grey and white, respectively

Table 4. Mean values for the asymptotic population growth rates (λ). Each value is based on 50 matrix scenarios. The standard deviation is in brackets

Taxon	Control				AMS			
	0–14 d		14–28 d		0–14 d		14–28 d	
All foraminifera	0.834	(0.416)	0.952	(0.276)	0.510	(0.102)	1.172	(0.298)
Bolivina spp.	0.672	(0.354)	1.004	(0.299)	0.635	(0.101)	1.373	(0.339)
Stainforthia fusiformis	1.184	(0.446)	0.863	(0.267)	0.709	(0.099)	1.636	(0.290)
Nonionella turgida	0.733	(0.272)	0.415	(0.263)	0.619	(0.169)	0.497	(0.545)
Hopkinsina pacifica	1.040	(0.462)	0.899	(0.277)	0.497	(0.213)	1.232	(0.397)

Table 5. Relative changes in the values of λ listed in Table 4, with regard to time and treatment. For this, mean dominant eigenvalues for the second 2 wk were divided by those of the first 2 wk (time effect), and values for AMS microcosms divided by those of control microcosms (AMS effect). Symbols as in Table 2. See Table 6 for statistics

Taxon	Time effect			AMS effect		
	Control	AMS	Overall	0–14 d	14–28 d	Overall
All foraminifera	(+)	++	+	–	+	(–)
Bolivina spp.	+	++	+	(–)	+	+
Stainforthia fusiformis	–	++	+	–	+	+
Nonionella turgida	–	(–)	–	–	(+)	(–)
Hopkinsina pacifica	(–)	++	+	– –	+	–

from Duijnstee et al. 2004 on foraminifera >63 µm from the top 2 cm of sediment cores, taken in 1996 to 1998). This means that the disturbance inherent in conducting the experiment did affect the foraminiferal populations, but not to an extent that surpassed demographic phenomena in the field situation in 1996 to 1998. Given that the actual time between cruises was 51 to 177 d, the extreme values of λ in the field on a true 14 d scale must have been greater than those recorded in Table 7. The only exception was *Nonionella turgida* in the control microcosms, which had an average value for λ_{14-28} of approximately 0.5 $(14\ d)^{-1}$, whereas in the field, the lowest value was around 0.8 $(14\ d)^{-1}$.

Generic differences

Among the 4 most abundant taxa, the decline in population size of *Nonionella turgida* was the strongest. The species with the highest population growth rates was *Stainforthia fusiformis*. This is in accordance with the results of a disturbance experiment by Ernst et al. (2002) with material from the same Adriatic location (Station 108). In their microcosms, densities of *S. fusiformis* increased, while those of *Bolivina*, *Hopkinsina* and *Nonionella* declined. In the 2 yr field study of foraminiferal densities at Station 108 (Table 8, Duijnstee et al. 2004), a dramatic drop in foraminiferal numbers was observed between 24 August and 7 November 1996. *Bolivina* spp., *N. turgida* and *Hopkinsina pacifica* lost 65, 64 and 49% of their standing stock, respectively. This event was interpreted as being the result of a marine snow event (as witnessed by a low bottom-water $[O_2]$ of 1.1 ml l^{-1}, Duijnstee et al. 2004). Only *S. fusiformis* managed to increase in number by 11%. This all fits the profile of *S. fusiformis* as a good recolonizer of formerly anoxic sediments (Alve 1994, 1995) and an opportunist of organically-enriched conditions (Gooday & Alve 2001). By 28 January 1997, the densities of *Bolivina* spp., *S. fusiformis* and *H. pacifica* in the field were several times higher than those observed in August 1996. The abundance of *N. turgida*, however, was much lower than before the crisis. It seems that this species, although very resistant to short-term anoxia, tends to become less abundant in the foraminiferal community after prolonged AMS conditions.

Table 7. Net population growth rates (14 d^{-1}) of foraminifera >63 µm, encountered in the field (at the site where our sediment was collected) in 1996 to 1998, based on 8 periods of 51 to 177 d from data published in Duijnstee et al. 2004. Rates were calculated as follows: $(n_{t+x}/n_t)^{14/x}$, where n_t is the initial foraminiferal abundance and n_{t+x} is the abundance after x d

Taxon	Population growth rates (14 d^{-1})		
	Minimum	Maximum	Mean
All foraminifera	0.864	1.285	1.042
Bolivina spp.	0.771	1.382	1.041
Stainforthia fusiformis	0.819	1.297	1.067
Nonionella turgida	0.793	1.401	1.085
Hopkinsina pacifica	0.787	1.501	1.071

Table 6. Significance of differences in λ with regard to time and treatment. Variance ratios (F) obtained from ANOVAs and their probabilities (p) are shown

Taxon	Time effect						AMS effect					
	Control		AMS		Overall		0–14 d		14–28 d		Overall	
	$F_{1,99}$	p	$F_{1,99}$	p	$F_{1,199}$	p	$F_{1,99}$	p	$F_{1,99}$	p	$F_{1,199}$	p
All foraminifera	2.8	0.096	221.7	<0.001	87.5	<0.001	28.6	<0.001	14.6	<0.001	1.6	0.212
Bolivina spp.	25.6	<0.001	217.6	<0.001	168.2	<0.001	0.5	0.476	33.4	<0.001	16.2	<0.001
Stainforthia fusiformis	19.1	<0.001	456.6	<0.001	50.5	<0.001	54.2	<0.001	191.9	<0.001	12.1	0.001
Nonionella turgida	35.2	<0.001	2.2	0.139	20.2	<0.001	5.7	0.019	0.9	0.340	0.1	0.750
Hopkinsina pacifica	3.4	0.067	133.4	<0.001	35.8	<0.001	57.0	<0.001	23.6	<0.001	4.5	0.035

Table 8. Population size of foraminifera >63 µm and growth rates encountered in the field around a marine snow event (between August and November 1996). Population size is expressed relative to the densities on 24 August 1996 (Duijnstee et al. 2004). Population growth rates were calculated as in Table 7

Taxon	Population size relative to Aug 96 (%)			Population growth rates (14 d^{-1})	
	Aug 96	Nov 96	Jan 98	Aug 96–Nov 96	Nov 96–Jan 96
Bolivina spp.	100	35	235	0.824	1.382
Stainforthia fusiformis	100	111	294	1.020	1.182
Nonionella turgida	100	36	58	0.825	1.087
Hopkinsina pacifica	100	51	554	0.884	1.501

CONCLUSIONS

Initially, most foraminifera responded to the simulated marine snow effect by (1) enhanced reproduction, (2) inhibited growth of smaller individuals and (3) a higher mortality than in the control situation. Enhanced reproduction was caused either by the enhanced nutritional situation or by the oxygen stress, directly or indirectly (i.e. less competition or predation due to possible anoxia-related mortality of other meiofauna). Inhibited growth and elevated mortality were most likely the result of oxygen stress or adverse conditions associated with anoxic conditions (e.g. high [H_2S]). Since the population sizes under AMS conditions were rapidly declining, the stress factor initially outweighed positive effects of the higher food availability. Although reproduction usually leads to empty tests ('mortality'), it is not very likely that the observed enhanced reproduction can account for the high mortality in the AMS microcosms.

After 4 wk, the negative effects of AMS on the population dynamics largely disappeared, resulting in recovering, growing populations, in marked contrast to the still-shrinking control populations.

The foraminifera in this study seemed to be able to change their life-history pathway to one that is more beneficial during stress and disturbance in the beginning of the experiment. The observed demographic characteristics of most taxa in this experiment are beneficial in periodically stressful and disturbed ecosystems, and could explain the increasing success of these species in the last 100 yr (Barmawidjaja et al. 1995, Duijnstee et al. 2004) in the progressively eutrophicated northern Adriatic Sea.

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