

# Modeling the long-term population dynamics of benthic foraminiferal communities using field and experimental data

### **Abstract**

A mathematically simple model is used to simulate the long-term impact of variable food flux and oxygenation over decades. Input characteristics were offspring and generation length, the values of which are derived from laboratory experiments. Other input consisted of a parameter describing the sensitivity of taxa to variation in oxygenation; values for this constant were derived from field data. A fourth parameter describing sensitivity to competition was obtained by inverse modeling. We simulated a 30 years time series with initially high eutrophication and low oxygen values. The model showed that opportunistic taxa, characterized by a high reproductive success, could successfully compete in environments marked by periodically occurring severe oxygen stress. Under permanent low oxygen conditions they were replaced by deep infauna. Under improved environmental conditions, the assemblage was dominated by taxa that are adapted to food-limited conditions. Oxygen appeared to be a more important parameter than food in the recovery of the ecosystem after an initial eutrophic state. The simulated sequences were compared with the historic development of the Adriatic Sea over the past 160 years, which also documents a change between trophic extremes.

### **1. Introduction**

Oxygen is essential to sustain metabolic activity, having more impact with increasing body size (e.g., Vernberg and Vernberg, 1976). Characteristic faunal successions observed along bottom-water oxygen gradients (e.g., Rhoads and Morse, 1970; Wishner et al., 1990) show the sensitivity of benthic macrofauna to variation in oxygen concentrations. The oxygen-dependence of marine fauna is dramatically illustrated further by cases of mass mortality following severe oxygen depletion (e.g., Baden et al., 1990; Tyson and Pearson, 1991). In contrast to most macrofauna, certain benthic foraminifera appear to be tolerant to oxygen deficiency; these protozoa are found thriving under extremely low-oxygen conditions, which are

prohibitive to most metazoans (e.g., Josefson and Widbom, 1988; Bernhard and Reimers, 1991; Jannink et al., 1998). In permanently dysoxic environments characteristic foraminiferal communities are found, dominated by taxa tolerant to low-oxygen conditions (Sen Gupta and Machain-Castillo, 1993; Van der Zwaan et al., 1999). Studies of live benthic foraminiferal communities in seasonally oxygen-depleted environments (e.g., Matsushita and Kitazato, 1990; Barmawidjaja et al., 1992; Silva et al., 1996; Duijnste, 2001) suggest that maximum foraminiferal production occurs during periods of enhanced oxygenation, and is dominated by a few opportunistic species. Although the success of these taxa must partly be due to their tolerance to low-oxygen conditions, their potential for rapid population growth, which allows them to outnumber most other competing species, seems equally important. Under more constant and higher oxygen concentrations, competition between foraminiferal species may be expected to result in a higher degree of specialization, especially in the efficiency of using resources. In the well-oxygenated southern Adriatic Sea, foraminifera from shallow microhabitats in the sediment were found to have generally higher test production rates than deeper-dwelling foraminifera (De Stigter et al., 1999). The hypothesis put forward in that study is that life in the oxygen- and food-depleted subsurface habitat requires physiological adaptations of infaunal foraminifera, which go at the expense of their reproductive capacity. As a consequence, infaunal foraminifera would be unable to compete successfully with epifaunal foraminifera in well-oxygenated surface habitats. Inversely, epifaunal foraminifera would lack the low-oxygen resistance required to compete with infauna in subsurface habitats.

The above-mentioned notion of balance between competition, tolerance and reproduction, has never been verified although it has been mentioned repeatedly (e.g., Van der Zwaan et al., 1999). The main problem is the difficulty to measure the effect of each individual parameter on the population dynamics of a taxon. In general, population dynamics of individual species are poorly known, mainly due to difficulties in assessing time of reproduction and number of offspring. Next to birth, estimates of death rates are difficult as well, certainly in field studies. Over the past few years, a number of laboratory studies have been directed at assessing the effects of oxygen and food supply on the population dynamics of selected taxa. A laboratory study of Duijnste et al. (2001) suggests that food plays a role in the development of the population, but stress induced by disturbance and oxygen appeared to be even more important. Modeling studies are ideally suited to further explore the possible ways ecological parameters are affecting the population dynamics of taxa, and to assess the long-term effect of these dynamics on the foraminiferal communities. Yet, such studies are scarce in foraminiferal ecology. In a few attempts to model foraminiferal distribution patterns, the distribution was essentially considered to be a black box. It was assumed that along an environmental range species display a Gaussian distribution pattern with an optimum, and with limits beyond which reproduction does not occur any more. Calibration to real life was done by trial and error without any attempt to assess the effects of each parameter on birth and death. An example of this type is the study of Sjoerdsma and Van der Zwaan (1992), who modeled bathymetric distributions. Another, more recent example, is formed by the work of De Stigter et al. (1996), who attempted to model population dynamics and assess the effects of variation in these parameters on benthic foraminifera. Problem with this simulation was that the algorithms developed by them needed input parameters for birth, life span and death. Knowledge on these parameters was lacking, a problem solved by them by taking theoretical values for the simulation of a time series of about five years under seasonal

oxygen deficiency. Their exercise was valuable since it gave some insight in long-term population dynamics, but worthless as far as a realistic outcome was concerned. Presently, however, a number of experiments give us a more accurate insight in parameters as birth and death. Therefore, we took the algorithms as presented by De Stigter et al. (1996) as starting point for a new attempt to construct a numerical population dynamic model. The present paper can be considered as a sequel to, and a revision of, the 1996 paper by De Stigter et al.

## 2. Conceptual background of the model

Over the past decade there has been a host of field studies trying to assess the role of oxygen and food, specifically in the context of the concept of microhabitats. The microhabitat model originally assumed a nice and rather constant distribution of taxa over the sediment column (Corliss, 1985), but in later studies a more dynamic and complex interplay of the redox regime and food was pointed out (Linke and Lutze, 1993; TROX models, see Jorissen et al., 1995 and Van der Zwaan et al., 1999; this thesis). In experimental studies it appeared very difficult to confirm the assumptions made in the various models, mainly because the time series studied were too short. Ideally, one would like to connect field and experimental studies with numerical modeling studies, the latter enabling close scrutiny of the various assumptions. This particularly pertains to the above-mentioned assumption that oxygen and competition decide on the microhabitat position, but also the generally accepted, but never validated, assumption that environmental variability is a very important characteristic in foraminiferal ecology.

Despite the selectivity for specific food types observed in many shallow-water species (e.g. Lee, 1980; Lipps, 1983), benthic foraminifera as a group display a variety of feeding mechanisms by which they are able to utilize a wide range of food resources present in the benthic environment (c.f. Lee and Anderson, 1993). Below the photic zone, benthic foraminiferal life is fueled mainly by the supply of organic detritus raining down from the productive surface water. The abundance and productivity of benthic foraminifera in the ocean are generally correlated with the organic carbon flux (e.g., Berger and Diester-Haass, 1989; Altenbach and Sarnthein, 1989; Van der Zwaan et al., 1990; De Stigter et al., 1996). In culture experiments, benthic foraminifera responded to an increase in food supply by increasing their population size (e.g. Bradshaw, 1955; Altenbach 1992; this thesis), as well as by increasing population growth rates (Lipps, 1983; Corliss and Silva, 1993). A rapid response to food supply may particularly be found in food-limited deep-sea environments. Observations by Gooday (1988; 1993) suggest that some deep-sea species may be able to rapidly colonize fresh phytodetritus aggregates on the seafloor. Increased reproduction in response to intermittent food pulses enables these foraminifera to compete effectively for the overall scarce food supply. Especially foraminifera in epifaunal habitats may be expected to have the potential to reproduce rapidly, since fresh organic detritus is mainly consumed at the sediment surface. The organic matter which is mixed down into the sediment by bioturbation is generally of a more degraded nature, being stripped of the more readily metabolizable components by the epifaunal community, although some high-quality organic matter may be conveyed from the sediment surface to the subsurface layer by macroinfaunal organisms.

Experiments by Duijnsteet al. (2001) and Ernst et al. (this thesis) basically support the notions as outlined above. Some foraminifera react rather sharply on food supply by reproduction, although on the short-term the response is less clear than the reaction on oxygen (this thesis). Disturbance, however, leads to very rapid reproduction, probably approaching maximal reproductive capacity. Duijnsteet al. (2001) expressed reproduction in so-called  $\lambda$ -values indicating the change in population size per unit time. Under a diminishing supply of food, foraminiferal populations must decrease in size. This is confirmed by experiments described in this thesis. As foraminifera may respond to adverse environmental conditions by postponing reproduction, thus increasing individual life span (Muller, 1975), the decrease in population size is more likely regulated by a decrease in productivity, rather than by mortality. Experiments by Muller (1975) on benthic foraminifera from salt marshes demonstrated that the generation length of these foraminifera increased from only a few days at optimum conditions of temperature, salinity and pH to more than 100 days under less favourable conditions. Measurements of metabolic activity in deep-sea foraminifera by Linke (1992) indicated that some species might remain active in times of starvation by metabolizing their protoplasm.

In spite of the above-mentioned notion, we assumed in the model constant life spans; we further assumed that the number of offspring is dependent on both oxygen content and the carrying capacity of the environment as defined by the amount of available food.

Despite their remarkable tolerance to severe oxygen depletion, benthic foraminifera seem unable to survive prolonged periods of total anoxia. In the permanently dysoxic environment of the Californian Santa Barbara Basin (bottom-water  $[O_2]$  less than  $0.5 \text{ ml.l}^{-1}$ ), a thriving population of well-adapted, low-oxygen tolerant benthic foraminifera was found to have disappeared almost completely after the bottom water had remained anoxic for several months (Reimers et al., 1990; Bernhard and Reimers, 1991). The ultimate oxygen dependence of benthic foraminifera is also illustrated by their absence in some fossil anoxic sediments (Mullineaux and Lohmann, 1981; Van der Zwaan, 1982; Katz and Thunell, 1984; Nolet and Corliss, 1990; Verhallen, 1991; Rohling et al, 1993). However, it is not resolved to what extent the extinction of benthic foraminifera under total anoxia is caused by the absence of oxygen, or by the accumulation of noxious  $H_2S$  in the sediment and overlying water. The observation that foraminifera from low-oxygen environments, when subjected to complete anoxia, remain active or at least are able to survive for some time (Moodley and Hess, 1992; Bernhard, 1993; Bernhard and Alve, 1996), implies that selection through oxygen is not effectuated by an immediate effect on survival, but may rather be caused by differences in reproductive potential of species under different concentrations of oxygen. Very little is known about foraminiferal reproduction under oxygen-limited conditions. Large standing stocks in permanently dysoxic basins, much larger than in adjacent areas with higher oxygen concentration, suggest that enhanced production of foraminifera may occur under low-oxygen conditions. More likely, however, is that these high abundances are due to the almost complete exclusion of benthic macrofauna, resulting in a reduced loss of foraminifera by macrofaunal consumption (see for example Buzas, 1978), and increased food availability in the absence of macrobenthic competition (e.g. Van der Zwaan, 1982). Furthermore, the large standing stocks do not necessarily imply a high faunal turnover rate. As outlined in the introduction, we suspect that foraminifera in oxygen-depleted habitats have a low population growth capacity compared to foraminifera inhabiting well-oxygenated habitats. A justification for this assumption is that foraminiferal population growth rates apparently are controlled by food availability (e.g. Lipps, 1983), and thus basically by the availability of energy resources, and that anaerobic metabolizing

of organic carbon yields considerably less energy than aerobic metabolism (e.g. Zehnder and Stumm, 1988). In other words, with a similar amount of food, foraminifera in an anoxic environment can produce a lower amount of energy for maintenance of body mass and for reproduction than species in an oxic environment. Therefore, in the model we assume dependency of offspring on oxygen, while keeping the life span constant.

In many papers competition is mentioned (e.g. Gooday, 1986), especially in the context of microhabitat patterns. In an earlier paper (see Chapter 4) we could not demonstrate the quantitative effect of competition for space or resources in the context of crowding. A possibility is that in that particular experiment we never reached the carrying capacity upon which competition should become apparent. However, competition at carrying capacity is widely accepted and conclusively demonstrated for many organisms (e.g., Pianka, 1999). In combination with the previous statements on the impact of food, it can easily be assumed that food regulates foraminiferal population size especially at carrying capacity. As outlined above, for the sake of a simple model we opted for a constant life span and constant maximum numbers of potential offspring per species. But at the same time, we assume in the model that food supply is limiting, allowing each foraminifer the same per capita food supply. We introduced resource competition at carrying capacity, by assuming that under these circumstances some species could better reproduce offspring than others. The lesser competitors have to accept reduction of their maximum potential offspring when the total numbers arrives at carrying capacities.

### 3. Construction of a population dynamics model

We constructed a simple model, summarized in Fig. 1, on the basis of the assumption that the dynamics of the foraminiferal populations are primarily controlled by the availability of food and oxygen.

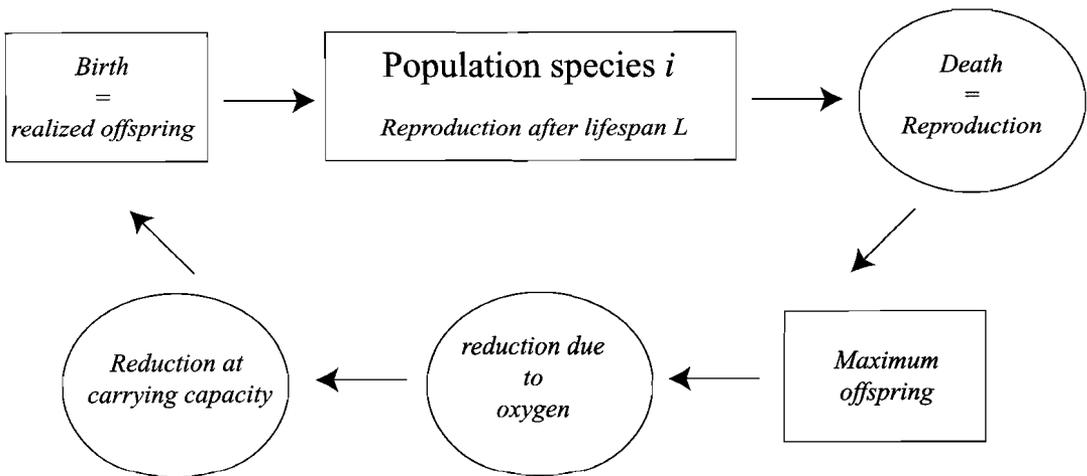


Figure 1 Flowchart of the model with all parameters involved.

Food supply is expressed as units per capita, assuming that all taxa need equal amounts of energy and food to maintain an individual specimen. The model assumes a homogeneous sediment layer; if needed, the model is able to calculate five sediment compartments from sediment-water interface down to deeper layers. Per sediment layer the amount of supplied food and oxygen need to be specified.

Population dynamics of species are modeled by iteration with time steps of one day according to the general equation:

$$N_{t+1}^{(i)} = N_t^{(i)} - D_t^{(i)} + B_t^{(i)} + 0.01 \quad (1)$$

where  $N_{t+1}^{(i)}$  and  $N_t^{(i)}$  are the total numbers of individuals of species  $i$  at day  $t+1$  and  $t$ , respectively, and  $D_t^{(i)}$  and  $B_t^{(i)}$  are, respectively, the number of deaths and births of species  $i$  on day  $t$ . The constant 0.01 is added to prevent extinction of any of the species, and can be seen as an import of juveniles from outside the model space.

Avoiding the complex subject of foraminiferal reproduction cycles (see for this subject e.g. Boltovskoy and Wright, 1976; Lee et al., 1991), we assume a simple relationship between birth and death of foraminifera, in which an individual reproduces only once, and dies in the event. Mortality other than related to reproduction, for example untimely death of juveniles or death caused by predators, is not taken into account in the model. We further assume that every living individual upon death produces an empty shell. The average life span of individuals is held constant, and assumed to be independent of environmental conditions. This implies that changes in population size in response to changes in the environment must be through changes in birth rate, and not through changes in mortality.

The total number of deaths in a species is given by the sum of deaths in each generation, as follows:

$$D_t^{(i)} = 1/L^{(i)} \quad (2)$$

where  $D_t^{(i)}$  is the number of deaths of species  $i$  at day  $t$ ,  $L^{(i)}$  is the maximum life span of species  $i$ , and  $B_t^{(i)}$  is the number of births of the species in the previous day.  $D_t^{(i)}$  represents also the shell flux to the fossil assemblage. As it is assumed that death of individuals is caused by reproduction, the number of births in species  $i$  is given by the number of deaths in species  $i$ , multiplied with the number of offspring per parent:

$$B_t^{(i)} = D_t^{(i)} \cdot B^{(i)}(F_t, O_t) \quad (3)$$

where  $B^{(i)}$ , and  $D^{(i)}$ , are, respectively, the number of births and deaths in species  $i$ ,  $B^{(i)}$  is the food (F) and oxygen (O) dependent number of offspring per parent of species  $i$ . The number of offspring per parent varies with food availability and oxygen concentration as follows:

$$B^{(i)}(F_t, O_t) = B_{max}^{(i)} \cdot ((F_t - (a \cdot N_t - D_t)) / F_t) \cdot (O_t / O_{max})^b \quad (4)$$

where  $B_{max}^{(i)}$  is the maximum attainable number of offspring per parent of species  $i$ ,  $F$  is the total food supply,  $N$  and  $D$ , are, respectively, the total number of living foraminifera and the total of deaths,  $O_t$  and  $O_{max}$  are, respectively, the actual oxygen concentration and the maximum oxygen concentration, and  $a$  and  $b$  are species-dependent constants.

#### 4. Values of parameters

Model parameters were estimated using data from experiments of previous field studies. Approximates of the life spans of five taxa were obtained using the data of Duijnsteet al (2001). They observed that at the onset of experiments benthic foraminifera started to reproduce extremely rapidly. Later on, much lower values of population increase were observed, apparently signaling equilibrium. They expressed this in so-called  $\lambda$ -values, indicating the population size increase or decrease per unit time, in their case 14 days. In this  $\lambda$ -value life span and number of offspring are thus combined and given the one, the other can be calculated. We assumed as life span 150 days, accepting reproduction roughly two times a year. This concurs with literature observations (see Murray, 1983) but is in essence arbitrarily chosen. Using that figure, we could calculate maximum offspring as observed in the experiment. In table 1 we show observed  $\lambda$ -values, and calculated offspring assuming a life span of 150 days. For *Ammonia* and *Elphidium*  $\lambda$ -values were not available. Life span and offspring were set at values using the average of values given by Murray (1983). The oxygen parameter  $b$  was taken from the fuzzy ranking presented by Duijnsteet (2001); in this fuzzy analysis he presents coefficients ranging from 0 to

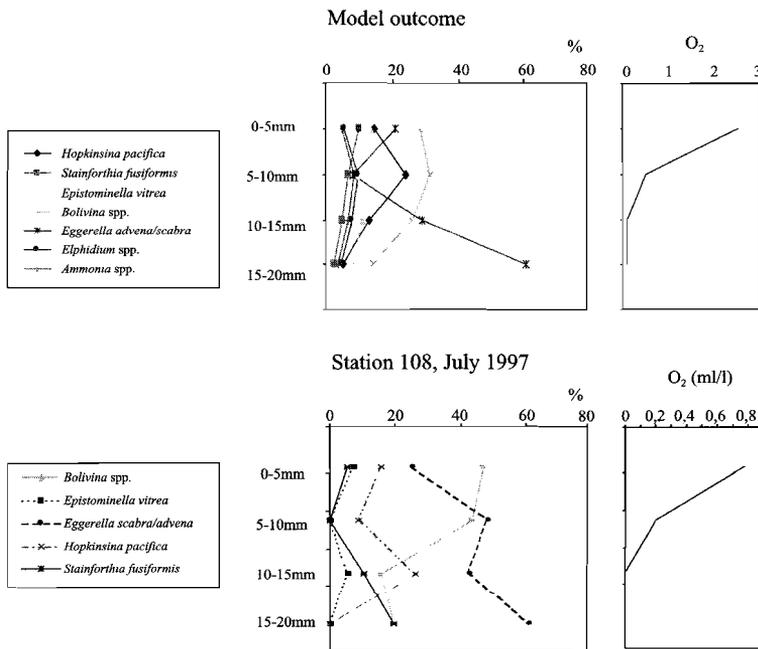


Figure 2 The resulting relative microhabitat distribution of the model, using the values in Table 1b for oxygen and food. This was done in order to fine-tune the model for the  $a$  and  $b$  coefficients by comparing these results with the relative field distribution in the field at station 108 in the Adriatic Sea, July 1998 (data of Duijnsteet, 2001).

+1, indicating extreme insensitivity for oxygen to extreme sensitivity. In Table 1a we summarized the used coefficients. Given these initial values and assumptions, we could let the model run except for a missing coefficient *a*, which denotes competition at carrying capacity. There are no data available for this constant; we solved this by using inverse modeling in the following way. We let the model run a great number of times, calculating four assemblages at given food and oxygen values (see Table 1b) to simulate a microhabitat distribution over 2 cm (see Fig. 2). The oxygen values were taken from a station in the Adriatic Sea (July 1996). In iterative calculation we arrived at *a* values (competition coefficients) that generated a microhabitat pattern that reasonably approached the observed patterns in the field (Fig. 2).

At this point it should be emphasized that at best we are still only loosely approximating reality. Values of  $\lambda$  enable us only to calculate maximum offspring if we assume a constant generation length of 150 days. This approximate is only acceptable as long as we lack accurate observations. The same holds for the oxygen coefficient, although the fuzzy ranking is probably the best method we presently have to estimate the relative impact of oxygen on the various taxa. Given all these assumptions, it is often used practice to use inverse modeling to find and fine-tune a last parameter, in our case the competition coefficient. Despite the fact that the model is still crude, we now have created an environment in which we can assess the impact of a number of variables separately.

### 5. The model outcome

We used the model to simulate the long-term development of an association of seven species, all frequent in the Adriatic Sea. We compared the simulated development with data from a shallow water

Taxon	$\lambda_{max}$	Max offspring	Generation length (days)	Competition factor <i>a</i>	Oxygen factor <i>b</i>
<i>Hopkinsina pacifica</i>	1.0	10	150	0.74	0.68
<i>Stainforthia fusiformis</i>	1.979	21.4	150	0.94	0.71
<i>Epistominella vitrea</i>	2.164	22.5	150	0.99	0.63
<i>Bolivina</i>	1.887	20.3	150	0.94	0.69
<i>Eggerella</i>	2.909	31	150	1.04	0.56
<i>Ammonia</i>	-	8.3*	150	0.76	0.51
<i>Elphidium</i>	-	7.9*	150	0.75	0.51

Table 1a)

Values of the parameters  $\lambda_{max}$ , maximum offspring, generation length, competition factor *a* and oxygen factor *b*, that were used in the model for the seven taxa.  $\lambda$ -values were extrapolated linearly from 14 to 150 days.

\*) Values are in the order of 6-10 (based on Murray, 1983); the used values give the most stable result in the model.

Depth in sediment (cm)	Oxygen	Food
0-1	2.5	200
1-2	0.5	75
2-3	0.1	75
3-4	0.1	50
4-5	0.02	50

Table 1b)

Values of oxygen and food used for fine-tuning the *a* and *b* coefficients by comparing the field and model results.

core covering the past 160 years, published earlier by Barmawidjaja et al. (1995). In this sense, we use the core as a way to validate the model, since we have convincing data on the cause of the faunal change in the Adriatic Sea over the past centuries. Barmawidjaja showed that increased eutrophication and decrease in bottom water ventilation caused the assemblage to change substantially. Therefore, we modelled a sequence over 30 years, starting with 1 specimen from each species and letting the assemblage develop first under eutrophic values and later under more oligotrophic conditions. The oxygen and food values were modulated by a sinus function with a yearly minimum and maximum. Maximum food values occur in spring followed by decreasing oxygen values with a lag of about 10–20 days. A second sinus function simulated the gradual change from eutrophic to oligotrophic conditions, followed by a gradual improvement of the bottom water oxygenation with a delay of 1000 days. All pertinent data used in the model are summarized in Table 1a.

The simulation experiment shows that after the initially equal proportions of the seven taxa, and under initially oligotrophic conditions, a few species rapidly gain in importance. Comparison with the

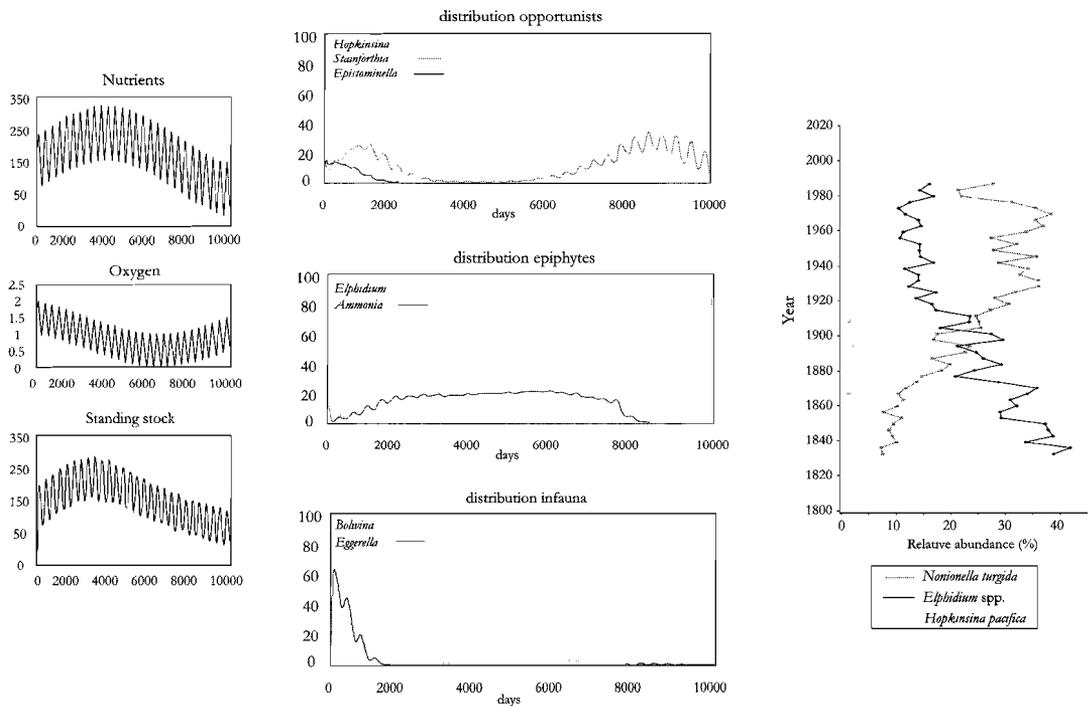


Figure 3

a) Outcome of the model (a period of 10.000 days simulated); the used values for the oxygen and food levels are shown in the smaller graphs on the left.  
 b) Relative abundance in the field of the opportunistic species Hopkinsina pacifica and Nonionella turgida, and the epifaunal Elphidium spp. during the past 160 years at station 108 in the Adriatic Sea (based on Barmawidjaja et al., 1995).

data from the Adriatic Sea (fig. 3) shows that quite realistically a few taxa dominate under eutrophic conditions and that the epiphytic taxa, indicating the presence of submarine vegetation as sea grass, are virtually absent.

The decrease of nutrients, and subsequent improved oxygenation of the bottom waters due to decreased oxygen demand of decaying organic matter, is reflected by a gradual restoration of the epiphytic assemblages at the expense of opportunists and infauna. Although we cannot validate the model properly, the outcome is encouraging in the sense that the model reflects the historical patterns rather nicely.

In an attempt to sort out the respective effects of oxygen and nutrients, we let the model run a second time (fig. 4), but now with only changing nutrient conditions. The oxygen was set at a low level to observe what the impact is of continuous poor ventilation under increasingly more oligotrophic conditions. The simulation now shows initial recovery of the association, and decreasing frequencies of opportunistic taxa. But at a certain stage the assemblage collapses and the recovery is ended by increasing dominance of opportunistic taxa and infauna. This suggests that oxygen is the dominant parameter steering the faunal patterns. It further implies that improvement of the nutrient input in the modern Adriatic Sea by reducing river effluents is only working well if the ventilation is improving as well. Although bottom water oxygenation is closely coupled to nutrient input through bioproduction, stratification is important as well. The model simulation shows that if nutrients are reduced, resulting in decreasing bioproduction, and the supply of oxygen is not improving as well, for instance due to increasing stratification related to warmer climates, recovery of the benthic assemblages is not very likely.

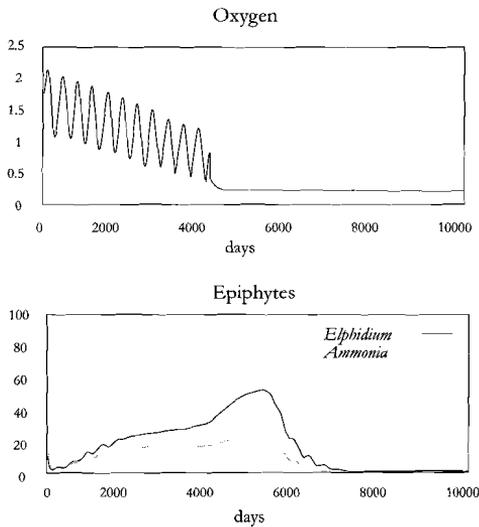


Figure 4 Outcome of the model, run under eutrophic conditions and with oxygen levels gradually decreasing in the first 4 days, and kept from then on at a constant low level.

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