Vol. 151: 135-141, 1997 | MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser | Published May 22

Tolerance of the deposit-feeding Baltic amphipods *Monoporeia affinis* and *Pontoporeia femorata* to oxygen deficiency

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ABSTRACT: Tolerances of the 2 most common species of amphipods in the Baltic Sea to low oxygen concentrations were determined over a range of ambient salinities in the Baltic. For both species more than half of the tested individuals had died by the end of 24 h of exposure to nearly anoxic water (0.2 mg O_2 l^{-1}). Despite its higher respiration rate and level of activity, *Monoporeia affinis* was significantly more tolerant than *Pontoporeia femorata* both to short (1 to 5 d) and long (24 d) periods of exposure to low oxygen levels. As long as the amphipods survived the tested salinity, there were only minor effects of salinity on their tolerance to oxygen deficiency. Among the common macrobenthic soft-bottom species in the study area, *M. affinis* and *P. femorata* seem to be the most sensitive to oxygen deficiency.

KEY WORDS: Oxygen deficiency · Salinity · Amphipods · *Monoporeia affinis* · *Pontoporeia femorata* · Baltic Sea

INTRODUCTION

Today, benthic oxygen deficiency occurs as a short- or long-term phenomenon in many estuarine and shallow coastal areas. Density stratification of the water by a pycnocline, preventing oxygen exchange between surface and bottom water, is one important reason why oxygen deficiency occurs. Where present, eutrophication aggravates the phenomenon by enhancing oxygen consumption in the bottom water layer, often resulting in oxygen levels low enough to negatively affect the benthic community (Officer et al. 1984, Rosenberg et al. 1990, de Jong et al. 1994, Turner & Rabalais 1994, review in Diaz & Rosenberg 1995). In extreme cases, mass mortality (Steimle & Sinderman 1978, Jørgensen 1980) and emigration from affected areas have been reported (Baden et al. 1990). But long before such dramatic events occur, oxygen deficiency reduces benthic biomass (Gaston 1985, Friligos & Zenetos 1988), changes species composition (Llansó 1992), and depresses growth (Weber & Kramer 1983, Nilsson & Sköld 1996) and feeding rates (Widdows et al. 1989).

The present study is focused on the Baltic Sea proper, known for vast areas depleted of animals through oxygen deficiency (Andersin et al. 1978). The permanent halocline in the Baltic Sea prevents mixing of the water column, and as a result anoxia and hydrogen sulphide occur commonly in the deep water (Andersin et al. 1978). The area affected varies depending on intrusions of oxygenated water from the North Sea, which normally occur every 3 to 4 yr (Matthäus & Franck 1992). This oxygen deficiency is partly a natural phenomenon. However, during the present century the oxygen deficiency has worsened and the areas affected have increased due to eutrophication. The input of nitrogen to the Baltic Sea has increased about 4 times and that of phosphorus 8 times in this century (Larsson et al. 1985). These nutrients have stimulated pelagic primary production. Above the halocline the macrobenthic biomass has increased (Cederwall & Elmgren 1980) and below it the elevated sedimentation rate of organic material has increased oxygen consumption (review in Elmgren 1989). A decrease in number of species and macrofaunal biomass, or their total disappearance, has been reported as a result of oxygen deficiency (Cederwall & Elmgren

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1990). When the oxygen concentration increases, recolonization by macrofauna may follow (Leppäkoski 1969, Andersin et al. 1978, Gosselck & Georgi 1984, Andersin et al. 1990, Andersin & Sandler 1991).

The objective of this study was to measure the tolerance to oxygen deficiency of the 2 most abundant macrobenthic animals in the Baltic Sea, the amphipods *Monoporeia affinis* (Lindström) and *Pontoporeia femorata* Krøyer. Both live in soft sediments, *M. affinis* mainly from 20 m depth and downwards and *P. femorata* below 30 m depth (Segerstråle 1950, Järvekülg 1973). Most individuals are found in the upper 5 cm of the sediment, but they burrow down to 13 cm, with *P. femorata* on average found deeper than *M. affinis* (Hill & Elmgren 1987). Both species are deposit-feeders and primarily ingest the upper sediment layer (Lopez & Elmgren 1989). *P. femorata* has a lower respiration rate and is less active than *M. affinis* (Cederwall 1979). These amphipod species are important as prey for fish (Aneer 1975) and larger invertebrates (Abrams et al. 1990, Hill & Elmgren 1992), and probably also as effective bioturbators which influence the biogeochemical processes in the sediment as described for *Pontoporeia hoyi* (Robbins 1982). It is thus important to improve our knowledge of their tolerance to the oxygen deficiency that affects large areas of the Baltic Sea bottom.

METHODS

General methods. Field collections and experiments were carried out during summer. Sediment and animals were collected with a benthic sled at 30 to 40 m in the Baltic Sea, close to the Askö Laboratory (80 km south of Stockholm), where natural sea water was obtained. The sediment was homogenised by sieving through a 0.5 mm screen. The amphipods were of the 1+ age class, hatched in early spring of the previous year. All experiments were run in a temperature-controlled room at 5°C. The light and dark periods were regulated with a timer, and a dim green light (simulating natural conditions) was on between 07:00 and 19:00 h in the first 2 experiments and between 05:00 and 21:00 h in the third tolerance experiment. Unless otherwise noted, the tank water had the same salinity as the water in which the amphipods had been collected (6.5‰).

The experiments were run in rectangular tanks, and the water was recirculated with a pump (440 l h^{-1}). The oxygen electrode was placed at the inlet end, and nitrogen gas was supplied at the outlet end, which was screened off from the animal containers. The oxygen concentration was monitored with an oxygen meter (AOWL2/KOB/421, Processtyrning AB, Sweden), and the readings were stored on a data logger (Analog Connection Jr and QuickLog PC, Strawberry Tree Inc., USA). The accuracies of the oxygen meters were regularly checked, and adjustments made if necessary, by comparing their readings with those obtained using the Winkler method. The oxygen concentration was decreased by increasing the flow of nitrogen gas, which was regulated by a magnetic valve controlled by the oxygen meter. The flow of nitrogen gas was automatically switched off once the desired oxygen concentration was reached. To obtain very low oxygen concentrations, the water surface was covered with Plexiglas or floating plastic. This resulted in a stable and homogeneous oxygen concentration. Air was continuously bubbled through the control tank.

Each replicate consisted of a round plastic beaker (380 ml volume) with a lid. Holes in the sides of the beakers, covered with fine netting (0.5 mm mesh size), allowed all replicates to receive the same oxygen concentration while keeping the amphipods apart. Each beaker contained sieved, 3 cm deep sediment. At the end of the experiments, the amphipods were transferred to well-oxygenated water and the number of survivors counted after 30 min.

Effect of artificial sea water. For *Monoporeia affinis* and *Pontoporeia femorata*, survival rates in natural and artificial sea water were determined at salinities of 6.5‰ and 9‰ for 34 d. The same tests were also carried out on *M. affinis* with an exposure time at salinity 6.5‰ of 62 d. The natural sea water was concentrated by evaporation to 9‰, and the artificial sea water was made up with special aquarium salt ('hw-Marinemix + Bio-elements', Wiegant GmbH, Germany). Intact plastic beakers (380 ml) were used, filled with 3 cm of sieved sediment. Five (34 d experiments) and 10 replicates of each treatment (62 d experiments), with 6 amphipods (~1800 m^{-2}) in each, were included.

Tolerance to oxygen deficiency. In the first experiment, the oxygen concentration was gradually decreased in consecutive steps in order to determine approximately how sensitive the amphipods were. The experimental tanks (215 × 42 × 15 cm) were filled with natural sea water. The oxygen concentration was rapidly decreased (within 6 h) to the target level. Exposure to each oxygen concentration lasted for 24 h, starting with 0.8 mg O_2 l^{-1} (6.5% oxygen saturation) followed by 0.7 (5.7%), 0.6 (4.9%), 0.4 (3.3%) and 0.3 mg O_2 l^{-1} (2.4%). For each species, 25 beakers with 4 amphipods each (~1200 m^{-2}), which is within their normal range of densities according to Ankar & Elmgren (1976), were placed in the experimental tank. Five beakers per species were taken out each day and the survival rates recorded. Five control beakers with 4 amphipods each were examined at the end of the experiment for each species.

A second experiment was run in the same way, except that *Monoporeia affinis* alone was tested at a constant oxygen concentration of 0.3 mg O_2 l^{-1} (2.4%) in natural sea water for 3 d.

In a third experiment, survival after 24 d at low oxygen concentrations was measured for *Monoporeia affinis* and *Pontoporeia femorata*. The oxygen concentrations studied (mean ± SD) were 1.2 ± 0.3 (10%), 2.0 ± 0.1 (17%), 4.0 ± 0.1 (33%), 6.0 ± 0.1 (49%) and 11.7 ± 0.2 mg O_2 l^{-1} (95%, continuously air bubbled). Ten beakers for each treatment, with 4 amphipods in each (~1200 m^{-2}), were included. The experiment was conducted as described above, in tanks (250 × 40 × 20 cm) with artificial sea water.

Effect of salinity on tolerance to oxygen deficiency. Tolerance to a low oxygen concentration (0.2 mg O_2 l^{-1} = 1.6%) at slightly increased and decreased salinities was tested. Artificial sea water was used in tanks with dimensions of 54 × 34 × 32 cm. The amphipods were acclimatised for 2 wk, without sediment, to salinities of 4‰, 6.5‰ and 9‰. For each species and salinity, 18 beakers with 4 amphipods (~1200 m^{-2}) in each were included in each experimental treatment. The amphipods were exposed to the low oxygen concentration in the salinity of acclimation. The air-bubbled control consisted of 6 beakers for each species, and salinity and survival rate were determined at the end of the experiment.

In a second test of tolerance to oxygen deficiency at different salinities, the oxygen concentration was slightly higher, 0.6 mg O_2 l^{-1} (5%), and the salinities tested were 5‰, 6.5‰ and 9‰. The artificial sea water and tanks used were the same as those described above. The amphipods were acclimatised for 2 wk to the test salinities, without sediment. After the acclimation period, 20 beakers (for each species and salinity), with 6 amphipods (~1800 m^{-2}) each, were transferred to the test tanks. The control consisted of 6 beakers for each species and salinity and had a constant supply of air. The control survival rate was determined only once, at the end of the experiment.

Statistical methods. Results were statistically evaluated using analysis of variance (ANOVA). The multiple comparison test Student-Newman-Keuls (SNK) was used in cases where significant variation was found using the ANOVA, and the homogeneity of variance was tested with Cochran's *C*-test (Winer et al. 1991).

RESULTS

Test of artificial sea water

Survival rates over 34 d for the 2 species of amphipods did not differ significantly between water types (artificial vs natural) or salinities (6.5‰ vs 9‰). There was, however, a difference in survival between species, with *Monoporeia affinis* having a higher survival rate (88 to 100%) than *Pontoporeia femorata* (64 to 96%), (ANOVA, $F = 13.2$, $p < 0.001$). The 62 d survival rates for *M. affinis* likewise did not differ significantly between natural (92%) and artificial (90%) sea water.

Tolerance to oxygen deficiency

Pontoporeia femorata was significantly more sensitive to a stepwise reduction in oxygen concentration (from 0.8 to 0.3 mg O_2 l^{-1}) than *Monoporeia affinis* (2-factorial ANOVA, $F = 33.3$, $p < 0.001$). There was no significant difference in survival between days, and no interaction between day and oxygen concentration was found (Fig. 1). More than 70% of the initial number of *P. femorata* were dead after 5 d, by which time the oxygen concentration had been reduced to 0.3 mg O_2 l^{-1}, whereas all *M. affinis* were still alive. All amphipods in the control groups (11.5 mg O_2 l^{-1} = 94%) were still alive at the end of the experiment. Comparison between the experimental and control groups on Day 5 revealed a significant interaction between oxygen concentration and species (ANOVA, $F = 3.8$, $p < 0.01$): *P. femorata* in the low-oxygen treatment had a significantly lower survival rate compared with *M. affinis* in the low-oxygen treatment and both *M. affinis* and *P. femorata* in the control (SNK).

After 1, 2, 3, and 4 d of exposure to a constant concentration of 0.3 mg O_2 l^{-1} (2.4% oxygen saturation) mortality rates for *Monoporeia affinis* were 4, 20, 56

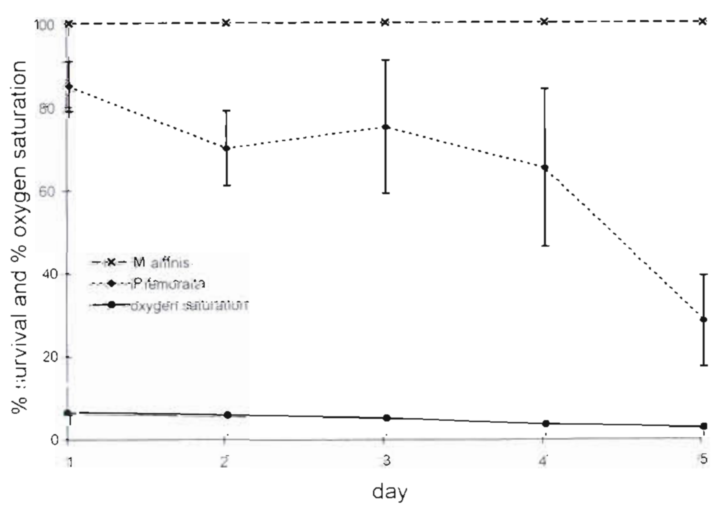

Fig. 1 *Pontoporeia femorata* and *Monoporeia affinis*. Survival rate [mean ± SEM (standard error of mean)] after a stepwise decrease during 5 d from 0.8 to 0.3 mg O_2 l^{-1}

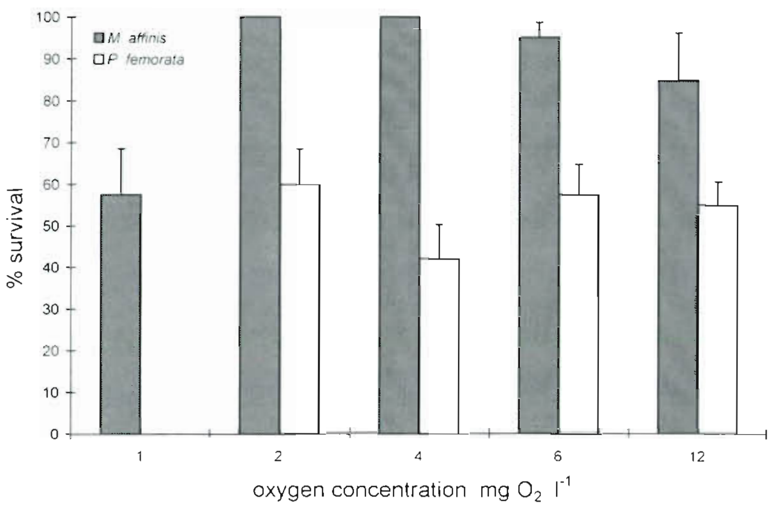

Fig. 2. *Pontoporeia femorata* and *Monoporeia affinis*. Survival rate (mean ± SEM) after 24 d of exposure to 1.2, 2.0, 4.0, 6.0 and 11.7 mg O_2 l^{-1}

and 70% respectively. By contrast, all control (11.3 mg O_2 l^{-1} = 92% oxygen saturation) *M. affinis* were still alive at the end of the experiment, and their survival rates were significantly higher compared with the group exposed to the low oxygen concentration at both Day 3 and 4 (ANOVA, $F = 10.8$, $p < 0.001$, SNK).

Tolerance to long-term oxygen deficiency

For both species, survival rates at 1.2 mg O_2 l^{-1} (10% oxygen saturation) were significantly lower compared with those at the other concentrations after 24 d (ANOVA, $F = 22$, $p < 0.001$, SNK, Fig. 2). *Monoporeia affinis* was more tolerant than *Pontoporeia femorata* (ANOVA, $F = 127$, $p < 0.001$). Lowest survival rate was found for *P. femorata* at 1.2 mg O_2 l^{-1}, intermediate for *M. affinis* at 1.2 mg O_2 l^{-1} and *P. femorata* at 2, 4, 6 and 11.7 mg O_2 l^{-1} and highest survival for *M. affinis* at 2, 4, 6, and 11.7 mg O_2 l^{-1} (SNK).

Effects of oxygen deficiency at different salinities

In the first experiment, *Monoporeia affinis* and *Pontoporeia femorata* were tested at salinities of 4‰, 6.5‰ and 9‰. At a salinity of 4‰, no results were obtained for *P. femorata* since it did not survive acclimation. The mean oxygen concentration was 0.2 mg O_2 l^{-1} 1.6% oxygen saturation) in the low-oxygen treatment and 10.6 mg O_2 l^{-1} (86% oxygen saturation) in the control. More than 50% of both species had died after 24 h of exposure to nearly anoxic water at 0.2 mg O_2 l^{-1} (Fig. 3). No significant differences were detected between species or salinities. When the control and oxygen-deprived groups were compared at salinities of 9‰ and 6.5‰, a 3-way interaction was found between oxygen concentration, species and salinity ($F = 10.2$, $p < 0.01$). All oxygen-deprived groups had a significantly lower survival rate than all control groups, and survival among the control groups was (for reasons unknown) lower for *P. femorata* at 9‰ (SNK).

In the next experiment, salinities of 5‰, 6.5‰ and 9‰ and an oxygen concentration of 0.6 mg O_2 l^{-1} (5% oxygen saturation) were used. The survival rate after acclimation was nearly the same for all salinities and both species (64 to 69% for *Monoporeia affinis*, 56 to 69% for *Pontoporeia femorata*). The mean (±SD) oxygen concentration in the experimental groups differed only marginally between treatments and was not significantly different; 5‰ = 0.64 mg O_2 l^{-1} (±0.04), 6.5‰ = 0.57 mg O_2 l^{-1} (±0.10), 9‰ = 0.58 mg O_2 l^{-1} (±0.01). The statistical analysis (3-factorial ANOVA) showed that *P. femorata* was significantly more sensitive to oxygen deficiency than *M. affinis* ($p < 0.001$). There was also a significant interaction between salinity and day ($p < 0.05$, Table 1, Fig. 4). *M. affinis* survived better than *P. femorata* at all 3 oxygen levels and *M. affinis* exposed to a salinity of 9‰ survived better than *M. affinis* at 6.5‰ and 5‰ in oxygen-deprived

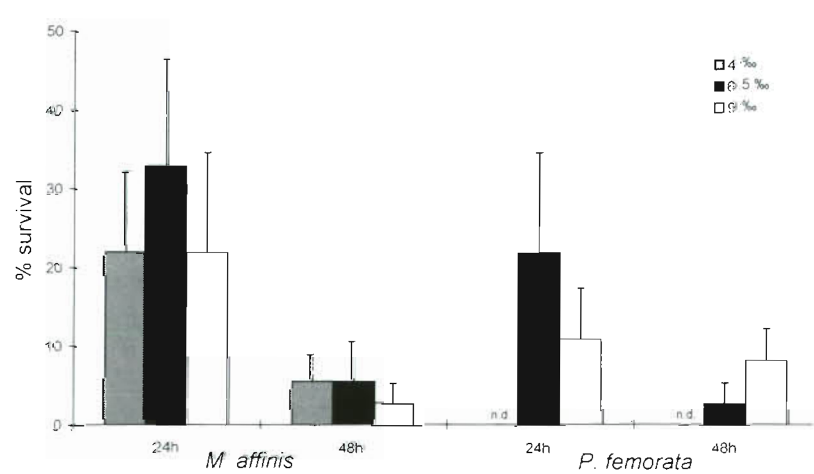

Fig. 3. *Monoporeia affinis* and *Pontoporeia femorata*. Survival rate (mean ± SEM) after 24 and 48 h at salinities of 4‰, 6.5‰ and 9‰ and oxygen concentrations of 0.2 mg O_2 l^{-1} Control at 10.6 mg O_2 l^{-1} not shown. n.d.: no data obtained

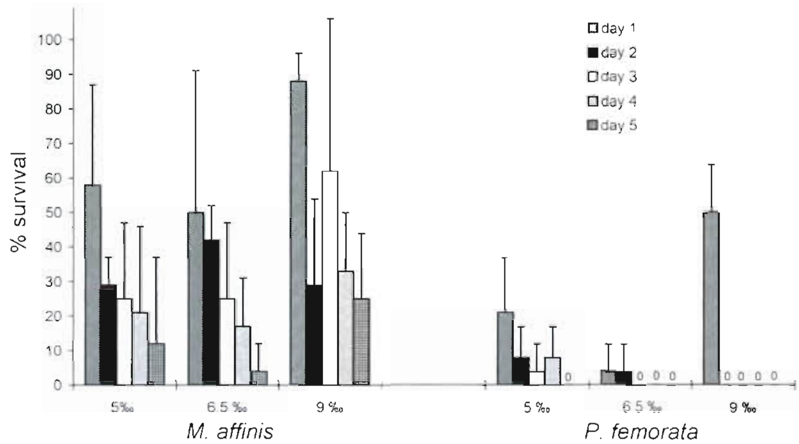

Fig. 4. *Monoporeia affinis* and *Pontoporeia femorata*. Survival rates on Days 1 to 5 at salinities of 5‰, 6.5‰ and 9‰ and an oxygen concentration of 0.6 mg O_2 l^{-1} Controls at 11.2 mg O_2 l^{-1} not shown. 0 = no survival

Table 1. Effects of the factors Species, Salinity and Day, and their interactions on the survival of *Pontoporeia femorata* and *Monoporeia affinis* at 0.6 mg O_2 l^{-1}. ns: not significant

Effect	*F*-value	p-value
Species	66.7	<0.001
Salinity	6.5	<0.01
Day	14.6	<0.001
Species × Salinity	1.9	ns
Species × Day	1.9	ns
Salinity × Day	2.2	<0.05
Species × Salinity × Day	0.6	ns

treatments. Furthermore, the survival rate on Day 1 was higher at a salinity of 9‰ compared with survival rates for each of the other 4 days and salinities. Survival rates in the high-oxygen treatment (56 to 69% survival, 11.2 mg O_2 l^{-1} = 91% oxygen saturation) did not differ significantly between species or salinities. Furthermore, on Day 5, the control amphipods showed significantly higher survival than the amphipods exposed to the low-oxygen treatment (ANOVA, F = 125, $p < 0.001$).

DISCUSSION

In this study, *Monoporeia affinis* and *Pontoporeia femorata* tolerated low oxygen values in the same range as those tolerated by other amphipods (Sprague 1963, Gamble 1970, Bulnheim 1979, Ritz 1980, Agnew & Taylor 1985, Agnew & Jones 1986, Nebeker et at 1992, Winn & Knott 1992, Maltby 1995). Mortality was below 50% for both *M. affinis* and *P. femorata* after 24 h exposure to nearly anoxic water (0.2 mg O_2 l^{-1}). In 3 experiments *M. affinis* tolerated oxygen deficiency better than *P. femorata* did.

Since more active animals have a higher metabolic rate and greater energy requirements, they are normally more sensitive to decreases in oxygen concentration (review in Davis 1975). For example, a comparison of the 2 brittlestars *Amphiura filiformis* and *Amphiura chiajei* showed that *A. chiajei*, the species with the lower oxygen uptake, was more tolerant to oxygen deficiency (Rosenberg et al. 1991). *Pontoporeia femorata* has a lower respiration rate and is less active than *Monoporeia affinis* (Cederwall 1979) and was therefore expected to be the more tolerant of the 2 species of amphipods. Another fact suggesting that *P. femorata* should be more tolerant of oxygen deficiency is that, compared to *M. affinis*, it is found deeper in the sediment, where oxygen concentrations tend to be lower (Hill & Elmgren 1987). However, it turned out that *M. affinis* was the more tolerant of the 2 species. *M. affinis* is a brackish-water species whereas *P. femorata* is a marine species (Segerstråle 1950, 1959), and brackish-water amphipods have been reported to be more tolerant to oxygen deficiency than marine amphipods (Bulnheim 1979, Ritz 1980). The salinity in the Askö area, where the amphipods were collected, is about 6.5‰, close to the lower limit of survival for *P. femorata*. It was therefore of interest to determine whether salinity-related stress could explain the lower tolerance to oxygen deficiency of *P. femorata*, compared with *M. affinis*. However, for as long as the amphipods survived the experimental salinity, there were only minor effects of salinity on their tolerance to oxygen deficiency. Other authors have reported the tolerance of marine invertebrates to oxygen deficiency to be affected at decreased salinity, with lower survival rates and earlier onset of impaired physiological responses (Theede et al. 1969, Stickle et al. 1989, Kristoffersson & Kuosa 1990). Theede et al. (1969) suggested that euryhaline species are not affected by lowered salinity as long as the critical salinity limit is not reached. No significant effect of low salinity was detected in this study, even when *P. femorata* was tested close to its lower tolerance limit of 5‰.

Generally, *Pontoporeia femorata* showed a lower survival rate than *Monoporeia affinis* in long-term experiments (natural vs artificial water and tolerance), even at higher oxygen concentrations, which is in agreement with previous laboratory observations (Johansson unpubl.). However, in short-term experiments, no difference in survival of control *P. femorata* and *M. affinis* was found, except for *P. femorata* at 9‰, in the first salinity experiment.

In addition to *Monoporeia affinis* and *Pontoporeia femorata*, the below-thermocline macrobenthic community in the study area (near the Askö laboratory) includes the bivalve *Macoma balthica*, the isopod *Saduria entomon*, the priapulid *Halicryptus spinulosus* and the polychaete *Harmothoe sarsi*. Of these species, *H. spinulosus* is the most tolerant to oxygen deficiency, being able to withstand anoxia for as long as 60 d (Oeschger 1990). *M. balthica* is also very tolerant to anoxia, as indicated by a 50% mortality rate after 52 d (Dries & Theede 1974), whereas *S. entomon* can only withstand anoxia for about 10 d (Hagerman & Szaniawska 1988, Kristoffersson & Kuosa 1990). Few data are available on the tolerance of *H. sarsi* to low oxygen levels. In a pilot study, small individuals (0.5 to 1 cm) survived oxygen concentrations below 0.2 mg O_2 l^{-1} for 2 d, but all were dead after 4 d (Johansson unpubl. data). *H. sarsi* is, however, an early recolonizer in areas affected by low oxygen concentrations and, based on field data, considered to tolerate such conditions fairly well (Andersin et al. 1978). Thus the result here for the 2 amphipod species indicated that they are the least tolerant to oxygen deficiency of the macrobenthic species in the region of interest.

In the Gulf of Finland, no amphipods were found after an extended period with low oxygen concentrations, whereas after an increase in oxygen concentration, they recolonized the area (Andersin & Sandler 1991). Gaston (1985) reported similar results, with amphipod numbers markedly reduced at oxygen concentrations below 2 mg O_2 l^{-1}. Such reductions may have further ecological consequences since amphipods in the sediment are probably responsible for much of the bioturbation of the sediment. The deposit-feeding amphipod *Pontoporeia hoyi* was capable of creating a homogenised upper sediment layer (Robbins 1982). This means that processes taking place at or near the sediment-water interface will be disturbed if the amphipods die or become immobilised. In a review by Krantzberg (1985), bioturbation affected the nitrogen dynamics in the sediment by increasing nitrification and denitrification rates. Thus the inhibition of denitrification could reinforce the effects of nutrient enrichment by allowing increased rates of NH_4^+ recycling, as suggested by Kemp et al (1990).

Due to their normally high abundance and importance as prey for fish and invertebrates, as well as their important contribution to biogeochemical cycling through their bioturbating activity, the 2 studied deposit-feeding species of amphipods are central components of the Baltic benthic assemblage (Elmgren et al. 1990). The present study shows them to be particularly sensitive to oxygen deficiency, with *Pontoporeia femorata* being most susceptible.

Acknowledgements. I thank Lars Byrén, Britt Stämfors and Barbro Söderlund for field and laboratory assistance, and Ragnar Elmgren for comments on the manuscript. The Stockholm Centre for Marine Research provided access to boat and field station facilities. This study was supported by the Swedish Natural Science Research Council and the Swedish Environmental Protection Agency.

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This article was submitted to the editor

Manuscript first received: November 7, 1996
Revised version accepted: March 18, 1997