Burrowing behaviour of the Baltic clam *Macoma balthica*: effects of sediment type, hypoxia and predator presence

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ABSTRACT: Burial in sediment-dwelling clams is affected by morphological features, such as shell shape and size, but also by biotic and abiotic factors, such as predator presence, oxygen deficiency and sediment characteristics. In the Baltic Sea, oxygen deficiency is a severe problem not only in the deep basins, but also in the shallow coastal areas, due to eutrophication. In the species-poor Baltic Sea, the bivalve *Macoma balthica* (L.) is a key species in both shallow and deep bottoms. This paper analyzes the impact of biotic and abiotic factors on the burrowing behaviour of *M. balthica*. Experiments were conducted to study the importance of sediment type, hypoxia, predator presence and algal mats on the burrowing behaviour (start of burial and burial velocity) of *M. balthica*. Results show that sediment type and the presence of the predatory isopod *Saduria entomon* did not affect the burrowing behaviour of *M. balthica*. In contrast, the burrowing behaviour was negatively influenced by hypoxia and drifting algae. Physical disturbance and oxygen deficiency are important forces that may displace *M. balthica* in the sediment and make it susceptible to predators at the sediment surface. Burial in the sediment is the only way in which infauna bivalves may escape predators, and this study shows that burrowing capability can be affected by poor environmental conditions.

KEY WORDS: *Macoma balthica* · Burial · Eutrophication · Hypoxia · Predation · Algal mats

INTRODUCTION

The Baltic clam *Macoma balthica* (L.) is 1 of 5 bivalve species found in the brackish northern Baltic Sea. It is the dominant bivalve in shallow and deep soft bottoms, and is considered a key species in these habitats (Segerstråle 1962). Eutrophication is an escalating problem in the area (Bonsdorff et al. 1997), inducing hypoxic conditions in shallow coastal areas (days to weeks). Severe hypoxia and anoxia have detrimental effects on benthic communities, especially for infaunal species with limited mobility (Vismann 1992, Diaz & Rosenberg 1995). Stress responses are often species-specific, and generally *M. balthica* is considered tolerant of hypoxia (Dries & Theede 1974). Drifting algal mats occur frequently in the northern Baltic Sea, varying seasonally in abundance and density (Bonsdorff 1992). Algal mats induce hypoxic conditions and have more severe effects on infauna than hypoxia alone (Norkko & Bonsdorff 1996a).

Infauna that inhabit soft sediments use these as foraging grounds and as refuges from predators. Species with limited mobility may change their vulnerability to predators by altering their burial depth in the sediment. In *Macoma balthica*, a facultative suspension and deposit feeder, decreased burial depth enhances the feeding area but increases the vulnerability to lethal and sublethal predation (Zwarts 1986, Zwarts et al. 1994). Burial depth can therefore be considered as a trade-off between feeding and predator avoidance. In areas affected by hypoxia and algal mats, infauna are often forced to the sediment surface and can thus be more vulnerable for epibenthic predators, such as flatfish or crustaceans (Jørgensen 1980, Baden et al. 1990, Norkko & Bonsdorff 1996a,b). Fishes have been shown
to use these areas as foraging grounds, moving in and out of hypoxic areas (Pihl et al. 1992, Rahel & Nutzman 1994).

Occasionally, infaunal bivalves may be forced to the sediment surface (by disturbance, hypoxia, algal mats); their capability to reburrow after such events was investigated in this study. The importance of bivalve size (shell length) and sediment type (sand vs mud) on the burrowing behaviour of *Macoma balthica* was studied in 2 experiments. Eutrophication-induced changes in burrowing behaviour was studied in 2 other experiments; 1 investigating the importance of hypoxia and predator presence, and 1 investigating the role of algal mats. The isopod *Saduria entomon* was used as a predator in this study. *S. entomon* is known to be a predator and siphon-cropper of *M. balthica* (Ejdung & Bonsdorff 1992, Bonsdorff et al. 1995), as well as of other infauna species (Sandberg & Bonsdorff 1990). *S. entomon* is tolerant of hypoxia, anoxia and hydrogen sulphide (Hagerman & Szaniawska 1990, 1992, Vismann 1991) and is abundant at mud sites together with *M. balthica*.

Burrowing behaviour was studied using 2 parameters; time for the start of reburial and burial velocity. The aim of this study was to increase knowledge of sublethal changes in infauna during and after hypoxic events, and to evaluate the importance of such changes to food-web interactions.

**MATERIALS AND METHODS**

*Macoma balthica*. Bivalves were sampled with sediment grabs (Ekman-Birge grab or a boxcorer) or with a shovel at shallow depths. They were extracted from the field sediment using a 1 mm mesh-size sieve, and then stored in tanks in the laboratory until use in experiments. The storage tanks were kept in temperature-controlled rooms at the same salinity (5 to 6‰) as that used in the experiments. The temperature was adjusted to ambient water temperature, and thus the temperature varied between experiments (Table 1). Sediment from the sampling sites was added to the storage tanks, and bivalves were kept in the same type of sediment from which they had been sampled. Acclimation time (time of storage in laboratory) varied between experiments (Table 1), but all bivalves within an experiment were sampled on the same day. After each experiment the length of the bivalves was measured with a calliper. All experiments were conducted under a 12:12 h light-dark photoperiod. Five replicate sediment samples were taken to determine the organic content in sediments. The sediment was dried for 24 h in 100°C to determine dry weight (DW), after which the samples were incinerated for 3 h at 500°C to determine ash-free dry weight. The experimental set-up varied between the experiments, depending on methods used and questions asked. The start of burial was registered when a bivalve lifted from its horizontal position to an upright position to start burrowing into the sediment, and burial time was determined as the time interval between start of burial and disappearance of the shell under the sediment surface.

**Importance of shell length and sediment type (Expts 1 and 2).** The importance of shell length on burial behaviour was studied in Expt 1 using 2 sediment types. Different-sized *Macoma balthica* were sampled at 2 sites, 1 with sandy sediment and 1 with mud. Sediment was sampled at each site and sieved through a 1 mm mesh-size sieve to exclude large predators. Bivalves sampled from the sandy habitat burrowed into sand, and bivalves sampled from the muddy habitat burrowed into mud treatments. Experiment aquaria were 11 plastic buckets with 5 cm of sediment covered with natural seawater (Table 1). Ten separate aquaria were used for each treatment and 1 bivalve at a time was allowed to burrow in each aquarium. Bivalves that did not burrow within 5 h were excluded from the analysis, resulting in 180 bivalves successfully burrowing in mud and 170 bivalves successfully burrowing in sand. The number of bivalves not burrowing within the time limit was <10 for both sediment types. Oxygen content was kept high by bubbling air into each aquaria.

About 1 kg of sediment of each sediment type was dried for 24 h at 100°C for grain-size analysis. The dried sediment was sieved onto a Franz separator with the mesh-sizes 1.000, 0.500, 0.250, 0.125, 0.074 and 0.062 mm.

In order to exclude size and site factors, the importance of sediment type was studied in Expt 2. *Macoma balthica* of an approximately similar size (11 mm), sampled at the sand site, were allowed to bury in both mud and sand sediment. The sediment that was used was sampled at the same time and at the same sites as for Expt 1. The experiment was done in similar aquaria as in Expt 1, with 1 bivalve per aquarium (Table 1). A total of 80 bivalves were allowed to burrow, 40 in each sediment type.

**Importance of predation and hypoxia (Expt 3).** Expts 3 and 4 were conducted in only 1 type of sediment to minimize the number of treatments. *Macoma balthica* and *Saduria entomon* were sampled from muddy sediment and the experiment was conducted in mud. The animals were kept in storage tanks with mud sediment and normoxic oxygen conditions until use in the experiment. Bivalves were treated with either hypoxia (<1 mg l⁻¹ O₂) or normoxia for 13 d. The hypoxic conditions were maintained by bubbling N₂ into seawater filled aquaria and oxygen saturation was automatically regulated.
Tallqvist: Burrowing behaviour of the Baltic clam

The effect of drifting algae on the burial behaviour of Macoma balthica was studied in Expt 4. Two different treatments were used: sand sediment (control), and sand sediment with algal mats. Bivalves and sediment were sampled at a shallow sandy site. The experiment was conducted in 11 l aquaria with a 6 cm sediment layer and 10 adult bivalves (11 to 12 mm in length) per aquarium (Table 1). The experiment time was 10 d and oxygen saturation and temperature was registered both under and above the algal mat and in the bottom water layer in the control treatment. The algae were collected 1 d before the start of the experiment at a sandy bottom site with loose-lying, drift algae. The algal mat consisted mainly of species of brown and green algae (Pilayella littoralis, Cladophora glomerata) and was added to the aquaria at a wet weight of 130 g per aquarium (2160 g WW m⁻²), corresponding to high densities of algal mats that can be found in the field (Bonsdorff 1992, Norkko & Bonsdorff 1996b). At the

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Expt 1</th>
<th>Expt 2</th>
<th>Expt 3</th>
<th>Expt 4</th>
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</thead>
<tbody>
<tr>
<td>No. of replicates</td>
<td>170 (S), 180 (M)</td>
<td>40</td>
<td>9</td>
<td>6</td>
</tr>
<tr>
<td>Aquarium size (cm)</td>
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<td>10 x 10</td>
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<td>4</td>
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<td>Experiment time</td>
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<td>24 h</td>
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Shell length (mm)

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<tbody>
<tr>
<td>6.44 ± 0.23 (M)</td>
<td>2.59–14.43 (M)</td>
<td>0.2226 ± 0.01 (S)</td>
<td>0.0985–0.4121 (M)</td>
<td>–</td>
<td>–</td>
<td>0.0592–0.6226 (HP)</td>
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<tr>
<td>6.64 ± 0.23 (M)</td>
<td>2.59–14.43 (M)</td>
<td>0.2321 ± 0.01 (M)</td>
<td>0.0985–0.4121 (M)</td>
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<td>0.0592–0.6226 (HP)</td>
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<tr>
<th>Wet weight (g)</th>
<th>Sediment type</th>
<th>Sediment depth (cm)</th>
<th>Organic content (%)</th>
<th>Temperature (°C)</th>
<th>Salinity (ppt)</th>
<th>pH</th>
<th>Oxygen (mg l⁻¹)</th>
<th>Statistics</th>
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<tr>
<td>S, (M)</td>
<td>(S), (M)</td>
<td>5</td>
<td>0.38 ± 0.02 (S)</td>
<td>7</td>
<td>5.5</td>
<td>11.89</td>
<td>Linear regression</td>
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<tr>
<td>M</td>
<td>(M)</td>
<td>5</td>
<td>0.38 ± 0.02 (S)</td>
<td>8.41 ± 0.05 (M)</td>
<td>8.41 ± 0.05 (M)</td>
<td>8.4</td>
<td>11.89</td>
<td>Mann-Whitney U-test</td>
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<td>M</td>
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<td>Nested ANOVA</td>
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Importance of drifting algae (Expt 4). The effect of algal mats on the burial behaviour of Macoma balthica was studied in Expt 4. Two different treatments were used: sand sediment (control), and sand sediment with algal mats. Bivalves and sediment were sampled at a shallow sandy site. The experiment was conducted in 11 l aquaria with a 6 cm sediment layer and 10 adult bivalves (11 to 12 mm in length) per aquarium (Table 1). The experiment time was 10 d and oxygen saturation and temperature was registered both under and above the algal mat and in the bottom water layer in the control treatment. The algae were collected 1 d before the start of the experiment at a sandy bottom site with loose-lying, drift algae. The algal mat consisted mainly of species of brown and green algae (Pilayella littoralis, Cladophora glomerata) and was added to the aquaria at a wet weight of 130 g per aquarium (2160 g WW m⁻²), corresponding to high densities of algal mats that can be found in the field (Bonsdorff 1992, Norkko & Bonsdorff 1996b). At the
end of the experiment, the algae were removed from
the sediment surface and dried for 3 d at 60°C for dry
weight. The mean DW of algae in the aquaria was
19.30 ± 0.85 g, (mean ± SE), corresponding to 322 g
DW m–2. The temperature was 4.5 ± 0.1°C in the con-
trol treatment, and 4.5 ± 0.1°C above and 5.1 ± 0.1°C
under the algae in the algal treatment. Increased tem-
perature under algal mats under experimental condi-
tions has also been recorded by Norkko & Bonsdorff
(1996a). The oxygen conditions are presented in Fig. 1.

After 10 d, the number of bivalves at the sediment
surface was registered for both treatments. The bi-
valves were sieved out, the water was changed in both
treatments to fresh normoxic water, and the bivalves
were allowed to reburrow.

Numerical and statistical analysis. Burial-time data
was used to calculate burial velocity (Sakurai et al.
1996) as shell length (mm)/burial time (s).

The data was tested for normality and homogenity of
variances. Parametric tests were used if these condi-
tions were met, in other cases a nonparametric test was
chosen. In all cases, a significance level of p < 0.05 was
used. In Expt 1 the relationship between shell length
and burrowing behaviour was tested by linear regres-
sion. The slopes of regression lines were compared to
reveal possible significant differences in burial behav-
avour between sand and mud sediment (Fowler & Cohen
1990).

In Expt 2, the 10 aquaria were tested against each
other (Kruskal-Wallis test), and when there was no dif-
fERENCE between the aquaria, each bivalve was used
as a replicate when testing differences between treat-
ments by the nonparametric Mann-Whitney U-test.

A nested ANOVA with fixed factors was used to test
the differences between treatments in Expts 3 and 4,
where there were several bivalves per aquarium, and
the aquaria were thus nested within the treatments.

RESULTS

Importance of shell length (Expt 1)

Linear regression analysis revealed a significant pos-
tive relationship between the shell length of Macoma
balthica and the start of burial in both sediment types
(Fig. 2a). Burial time was also significantly related to
shell length in both sand and mud sediment (Fig. 2b).
However, the R² values for these equations were very
low, indicating poor predictive power. There was no
significant difference in start of burial or time of burial
between sand and mud sediment when comparing
slopes of the regression lines.

The grain size results (given as the relative fraction
of the total sample) were 12.8% on 0.250 mm, 82.3%
on 0.125 mm and 4.9% on the 0.074 mm mesh-size
sieve for the sand sediment and 3.1% on 0.250 mm,
Importance of sediment type (Expt 2)

There was no significant difference in burial behaviour of *Macoma balthica* between different aquaria (Kruskal-Wallis test), and therefore, each bivalve was used as a replicate when comparing means between the 2 sediment types. The start of burial was 292 ± 33 s (mean ± SE) in sand and 321 ± 62 s in mud (Fig. 3a). Mean burial velocity was 0.089 ± 0.005 mm s⁻¹ in sand and 0.068 ± 0.005 mm s⁻¹ in mud (Fig. 3b). There was no significant difference in the burrowing behaviour parameters between the sediment treatments (Mann-Whitney U-test).

Importance of predation and hypoxia (Expt 3)

The nested ANOVA analysis revealed a significant difference between treatments for the start of burial (p = 0.0338, F-value = 3.268) and for burial velocity (p = 0.0001, F-value = 21.212). The analysis revealed no significant effect of the aquaria for these parameters. There was a significant difference in the time of the start of burial of *Macoma balthica* (Fig. 4a) between the predator (256 ± 34 s) and hypoxia (507 ± 62 s) (Student-Newman-Keuls comparison) treatments. The time for start of burial was 370 ± 42 s in the control treatment and 379 ± 44 s in the hypoxia + predator treatment. Mean burial velocity differed between the control treatment (0.115 ± 0.01 mm s⁻¹) and the hypoxia (0.059 ± 0.004 mm s⁻¹) and hypoxia + predator (0.072 ± 0.005 mm s⁻¹) treatments (Fig. 4b). The predator treatment (0.113 ± 0.01 mm s⁻¹) also differed significantly from hypoxia and hypoxia + predator treatments. There was no significant difference in any of the burial parameters when comparing control to predator treatment or hypoxia to hypoxia + predator treatment. For the start of burial, both predator treatments had lower mean values than the treatments without predators, but the difference was not significant. The mean length of *Saduria entomon* was 47.0 ± 1.4 mm in normoxia and 47.5 ± 1.5 mm in the hypoxia treatment.

Importance of drifting algae (Expt 4)

All bivalves survived in both the control and algal treatment. At the beginning of the experiment all bivalves buried into the sediment. At the end of the experiment all bivalves remained burrowed in the control treatment, but in the algal treatment the mean number of bivalves on the sediment surface was 6.5 ± 0.92 (i.e.
about 65%). There was a significant difference between the control and the algae treatment in the number of *Macoma balthica* on the sediment surface (Student’s *t*-test). There was also a significant difference in the mean number of bivalves that reburrowed: 9.7 ± 0.22 (97%) in the control treatment compared to 7.8 ± 0.60 (78%) in the algal treatment after 24 h.

The nested ANOVA analysis revealed a significant difference between treatments for the start of burial (*p* = 0.0260, *F*-value = 6.815) and for burial velocity (*p* = 0.0021, *F*-value = 16.839). The analysis revealed no significant effect of the aquaria for these parameters. The start of burial (Fig. 5a) was significantly faster in the control treatment (1844 ± 314 s) than in the algal treatment (3210 ± 493 s). The mean burial velocity was 0.032 ± 0.002 mm s⁻¹ in the control treatment and 0.021 ± 0.001 mm s⁻¹ in the algal treatment (Fig. 5b). The mean burial velocity was significantly lower in the algal than in the control treatment.

**DISCUSSION**

**Burrowing behaviour and shell morphology**

Generally, small specimens burrow more rapidly than larger ones, which was shown to be true for *Macoma balthica* in this study. The correlation was not very strong, since the individual variation within size classes was high. In a study by Stanley (1970), burrowing time in the bivalve *Donax denticulatus* was found to be almost linearly correlated to shell length. Shell shape, length, thickness and ornamentations have been shown to influence the burial rate of bivalves (Stanley 1970). In the present study, the start of burial was found to be significantly related to shell length for *M. balthica*, with increasing time for the start of burial with increasing shell length. As for burial time, the relationship was weak due to large variation between individuals of the same size. The overall time for the start of burial ranged from 50 to 3257 s (54 min) in this experiment, indicating that large individual variability could be of importance when rapid reburial after disturbance is required. Since the variability was not completely explained by shell length, other factors such as condition and nutrition might explain the variance. This is also supported by the fact that start of burial and burial velocity varied in the control treatments between the different experiments. The start of burial was for example much faster in the sand treatment in Expt 2 compared to the sand treatment without algae in Expt 4. This could have been due to a slightly larger mean length in bivalves in Expt 4 than in Expt 2, but could more probably be due to the fact that Expt 4 was run in late autumn and Expt 2 in early summer and that temperature and acclimation time was different between the 2 experiments. Expt 3 again was run at another biological station than the other experiments, and in sediment that was characterized as mud, but probably differed from the mud sediment in the other experiments due to different sampling sites. Shell length, water temperature, nutritional and reproductive stage of the bivalves, sediment characteristics and possible differences in laboratory conditions could be the reason for differences between the experiments. Within an experiment, however, all bivalves were sampled and handled in the same way.

Shell length has also been related to burial depth which, however, was not measured in this study. Zwarts & Wanink (1989) showed that burial depth increased with size in *Macoma balthica* smaller than 10 mm. For larger clams the size did not affect burial depth.

**Burrowing behaviour in relation to substrate**

*Macoma balthica* is found in a variety of soft substrate types in the northern Baltic Sea and can be considered abundant both in sand and mud (Bonsdorff et al. 1996). As shown in Expt 2, reburrowing behaviour did not differ significantly between the 2 sediment
influenced burial velocity of sediment. The results from Expt 3 show that hypoxia surviving specimens may be able to reburrow into the mortality, but if the hypoxic conditions are periodic, Bonsdorff 1996a). Prolonged hypoxia causes faunal 1980, Baden et al. 1990, Vismann 1992, Norkko & Strayer 1998). ing was recorded at moderate oxygen levels (Sparks & as siphon extension, gaping, foot extension and surfac-

Abiotic factors affecting burrowing behaviour—the role of hypoxia and algal mats

Infaunal bivalves are generally thought to be quite tolerant of hypoxic conditions (Theede et al. 1969), and LT_{50} value for Macoma balthica was measured to be over 500 h at 0.15 mg l^{-1} O_2 at 10°C and 17% salinity (Dries & Theede 1974). Behavioural changes in benthic organisms might occur at sublethal oxygen levels (Sandberg 1994, Sandberg et al. 1996, Tallqvist et al. 1999). In a unionid bivalve, behavioural changes such as siphon extension, gaping, foot extension and surfacing was recorded at moderate oxygen levels (Sparks & Strayer 1998).

Hypoxia and algal mats have been shown to cause infauna to emerge to the sediment surface (Jørgensen 1980, Baden et al. 1990, Vismann 1992, Norkko & Bonsdorff 1996a). Prolonged hypoxia causes faunal mortality, but if the hypoxic conditions are periodic, surviving specimens may be able to reburrow into the sediment. The results from Expt 3 show that hypoxia influenced burial velocity of Macoma balthica in mud, with slower burial in bivalves treated with hypoxia compared to normoxia (Fig. 4). Expt 4 showed that reburial capacity varied between bivalves in sand exposed to normoxic conditions compared to bivalves experiencing hypoxia induced by algal mats (Fig. 5). The start of burial was faster in the control bivalves than those exposed to algal mats, indicating a change in reburial capacity due to the hypoxia induced by the algae. Burial velocity was also slower in M. balthica in the algal treatment. Later and slower burial might enhance the exposure time to predators. Since about 20% of the bivalves from the algal treatment remained unburied (but alive) even when oxygen conditions improved to normoxic levels, the effect might be of importance in predator-prey dynamics. It has been suggested that M. balthica can be more susceptible to lethal predation by the crustaceans Saduria entomon and Crangon crangon and the flounder Platichthys fles- sus after stress by algal mats (Norkko & Bonsdorff 1996a). In the same study, about 70% of adult M. balthica emerged from the sediment with algal treat- ment (17 d), corresponding to 65% found in the pre-

Burrowing responses to predator presence

Many studies investigate the lethal effects of preda-
tors on their prey species, but sublethal effects are less well studied. Sublethal effects on prey species include siphon-cropping of bivalves by juvenile flatfish or crustaceans (de Vlas 1979, Bonsdorff et al. 1995, Sandberg et al. 1996, Tallqvist et al. 1999) and feeding on poly-
chaete tentacles (Woodin 1982), or changes in prey morphology, physiology, chemistry, life history or behaviour (Sih 1987).

For infauna that are not very mobile (e.g. bivalves), the only effective way to avoid predation by epibenthic predators is to burrow deep into the sediment out of reach of the predators. In nature, however, several factors influence the burial behaviour of bivalves, and predator avoidance can conflict with feeding needs (Zwarts 1986). Lin & Hines (1994) showed that food concentration affected the feeding mode of Maconoma balthica (a facultative deposit and suspension feeder), increasing deposit-feeding and reducing burial depth with lower concentration of suspended food particles. Feeding mode is also affected by the presence of siphon-cropping predators, reducing the deposit feeding activity (Skilleter & Peterson 1994). Maximal burial depth is directly related to siphon size (Zwarts & Wanink 1989), but feeding strategies and predator avoidance influence the actual burial depth (Zwarts 1986, Lin & Hines 1994, Zaklan & Ydenberg 1997). It has been shown that M. balthica burrow deeper in the winter than in the summer because of decreased deposit feeding in winter (Zwarts & Wanink 1989). Because of decreased predation pressure, bivalves that burrow deeper into the sediment have a higher survival than shallower-burrowing specimens of the same species (Zaklan & Ydenberg 1997). On the other hand, de Goeij & Luttikhuizen (1998) showed that an increased burial depth reduced growth and increased mortality in M. balthica, probably through lack of sufficient food.

It is advantageous for infauna to reburrow into the sediment as soon as abiotic conditions are better (e.g. when algal mats are washed away, or storms recirculate hypoxic bottom waters) to decrease the risk of lethal predation. There was no significant effect of the presence of the isopod Saduria entomon on reburrowing behaviour of the bivalve Maconoma balthica in this study. The mean start of reburial was slower in the treatments without predators than in the presence of predators in both normoxic and hypoxic conditions (Fig. 4a), but due to large individual variations the difference was not significant. Bivalves that are extracted from the sediment by a siphon-cropping predator reburrow within a few minutes (Ansell 1995); however, no control treatments monitoring reburial without predators was used in that study.

Conclusions

Conflicting demands might influence the behavioural patterns that animals show in response to hypoxia. As a response to algal mats and oxygen deficiency, an altered reburrowing behaviour was detected in the infaunal bivalve Maconoma balthica. As M. balthica is an important prey species in the Baltic Sea, these effects can alter predator-prey relationships and have effects on higher trophic levels. Future studies should focus on behavioural patterns in animals under the stress of oxygen deficiency. Only by learning more about the sublethal effects of biotic and abiotic stress can we evaluate the importance of possible functional changes that often occur before structural changes can be recorded in the field.

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