Chapter 2

Deep-burying reduces growth in intertidal bivalves: field and mesocosm experiments with *Macoma balthica*

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On intertidal flats in north-west Europe, the bivalve *Macoma balthica* buries deep in the sediment in early winter, but ascends to the surface in late winter. Close to surface *Macoma* runs the risk of being eaten by epibenthic predators. We hypothesise that living shallow leads to more rapid growth in spring by allowing for higher food-intake rates. In three experiments, of which two took place in the field, we placed *Macoma* at fixed burying depths. We measured body condition and survival after 10-16 weeks. At the end of all three experiments, body condition of shallow-buried animals was significantly higher than that of the surviving deep-buried animals. Survival was lowest in the animals buried deepest; deceased animals may have died of starvation and/or perhaps suffocation. In the mesocosm experiment there was a negative relationship between burying depth and feeding (grazing) radius. Our experimental results are consistent with the idea that *Macoma* comes to the surface to feed efficiently in order to grow fast.
INTRODUCTION

The tellinid bivalve *Macoma balthica* living on intertidal flats in the Wadden Sea shows distinct seasonal changes in burying depth. The animals bury as deep as 8 cm in the sediment in autumn and winter, but ascend to depths of 2-4 cm in February, just before the growing season (Zwarts and Wanink 1993, Piersma et al. 1994, Zwarts et al. 1994). Differences in burying depth between winter and summer are likely to be caused by the absence of deposit feeding in winter (Hummel 1985, Zwarts and Wanink 1989). In addition to this hypothesis, siphon nipping by flatfish and other epibenthic predators can play a role by causing a reduction in siphon mass for *Macoma* of 35% in summer (De Vlas 1985, Zwarts and Wanink 1989). As the length of the siphon determines the maximum depth to which bivalves can bury, siphon nipping can lead to a decrease in burying depth. In early spring siphon nippers are not yet present on the intertidal flats (Kuipers 1977, Beukema 1991, Beukema 1992a).

Zwarts et al. (1994) postulate that by extending the siphon more, the feeding opportunity for deposit feeding bivalves will be maximised. According to many authors (Brafield and Newell 1961, Hughes 1969, Hummel 1985, Ólafsson 1986, Thompson and Nichols 1988), *Macoma* are so-called ‘facultative deposit feeders’ or ‘opportunistic feeders’. *Macoma* either stretch a large part of their siphons out of the sediment and ‘scrape’ diatoms and benthic algae from the surface of the sediment, or they extend their siphons just to the sediment surface to inhale algae from the water column. *Macoma* living close to the sediment-surface may incur two advantages: (1) suspension feeding is more efficient for physical reasons (Zaklan and Ydenberg 1997, Figure 2.1A,B), and (2), deposit feeding is more profitable as a longer part of the inhalant siphon can be stretched over the surface and the feeding radius can be increased (Figure 2.1C).

However, at shallow depths a bivalve runs larger risks to be preyed upon by birds, crabs and flatfish than deeper down (Virnstein 1977, Blundon and Kennedy 1982, Zwarts and Wanink 1989, Piersma et al. 1994). Indeed, survival was higher at greater burying depths in suspension feeding *Mya arenaria*, though food intake rates were reduced (Zaklan and Ydenberg 1997). In experiments to study trade-offs between food abundance and burying depth, Lin and Hines (1994) showed that *Macoma* buried deeper when the density of suspended food particles increased and when the number of conspecifics competing for the same resource decreased. This suggests that *Macoma* only takes the risk of living shallow when there is not enough food. The depth at which a bivalve is buried appears to be a compromise between the risks of starvation and predation (Zwarts 1986, Zaklan and Ydenberg 1997).

In the Wadden Sea, *Macoma* shows a single short period of growth in spring (March
through June), followed by a long period of nearly stagnant length and weight loss of soft parts (Beukema and De Bruin 1977, Beukema and Desprez 1986, Zwarts 1991, Zwarts and Wanink 1993). Only in the period March-June do water temperatures allow for growth (De Wilde 1975), and pelagic algae and benthic diatoms are abundant (Cadée and Hegeman 1977). We suggest that the best way for *Macoma* to capitalise on the short growing season is to come to the surface to achieve high intake rates. In this study we experimentally verified whether deep burying negatively affects growth. Our null hypothesis is that *Macoma* fixed at different burying depths do not show differences in growth.

**MATERIALS AND METHODS**

**Experiments**

The first experiment (I) took place in the field in 1994. We fixed single-sized *Macoma* at
two depths and measured differences in growth over time. Due to the high mortality in this experiment, we decided to repeat the experiment using a different method to fix *Macoma* at a certain depth in the sediment. During this second field experiment (II), in 1995, *Macoma* of one size were actually fixed at a range of depths. Simultaneously, the same experimental design was used in a mesocosm (experiment III). In contrast to the field experiments, the mesocosm experiment allowed us to measure feeding radius of *Macoma* fixed at a range of depths (cf. Zwarts et al. 1994).

For each experiment the bivalves were collected by hand on the intertidal flats of Balgzand in the western part of the Dutch Wadden Sea (52°55' N, 4°48' E). For experiment I, *Macoma* of 14.0-14.9 mm were used, for experiment II *Macoma* between 15.5 and 16.4 mm, and for experiment III *Macoma* between 14.0 and 15.4 mm. These represent reproducing animals, size classes that are relatively common on the intertidal flats, and *Macoma* of a size ingestible by one of their main predators, the knot *Calidris canutus* (Zwarts and Blomert 1992, Piersma et al. 1995). For experiment I the bivalves were stored 35 days in the sediment of an outdoor basin before entering the experiment. Before experiment III *Macoma* were stored for 25 days. In the outdoor basin food was available and siphon nippers were absent. The animals used in experiment II were not stored. At the start of all experiments subsamples were collected. The density of *Macoma* in the experiments was lower than the lowest densities in the field (79 *Macoma*/m²).

**Experiment I**

*Macoma* were collected on 8 and 9 March 1994. Each bivalve was glued to an individual plastic strip (Luxaflex) 40 cm long and 15 cm wide. Each strip was marked with a unique plastic label. On 5 and 6 April, 500 plastic strips with bivalves were buried and randomly assigned to depths of 2 cm and 8 cm (250 each) on the collection site at Balgzand (silt content: 2.9% and a density of 167 *Macoma*/m²). Every two weeks we checked the sediment surface for signs of erosion. On the four corners of the plot sticks were dug in the mud and a dash was carved on each stick 10 cm above the surface of the sediment. Every two weeks we connected the sticks with a string and measured the distance between the string and the surface of the sediment at intervals of 2 metres. We did not notice much changes in the height of the sediment surface over the plot during the experimental period. On 7 and 8 June the plastic strips with *Macoma* were taken out and the experimental animals processed as outlined in 'Measurements'.

**Experiment II**

In 1995 we used a different method to fix *Macoma* at a certain depth. We manufactured mini-cages, which consisted of two PVC rings which fitted over each other (50 and 52
mm diameter respectively, inner height when put together 17 mm). The upper ring was covered with plastic mesh with a diameter of 5 mm. The diameter of the mesh on the bottom ring was 2 mm. Water, air and other elements could flow through the box. In each mini-cage one bivalve was kept and the cages were marked with an inscription. Tests had demonstrated that siphons were easily stretched through the mesh. In the mini-cages the animals were able to move horizontally. The bivalves were collected on 10 April. On 12 April 201 cages were buried, randomly assigned to depths of 3 or 7 cm. Every two weeks we checked the sediment surface for signs of erosion as described in 'Experiment I'. On 13 June, at the end of the experiment, the cages appeared not to be buried exactly at the intended depths, but in a range between 1 and 7 cm.

Experiment III
This mesocosm experiment was conducted in an outdoor basin from 24 May to 1 September 1995. The basin (2.5 x 2.5 m) was filled with 20 cm sediment with a silt content of 0.03% and median grain size of 291 µm. Seawater was pumped directly from the Wadden Sea. A tidal regime was simulated with six hours high (40 cm) and six hours low tide (0 cm). The experimental animals were collected on 18, 19 and 20 April. They were buried in 210 mini cages, and were randomly assigned to 7 different depths (30 each). It was our intention to bury the cages with the upper side at exactly 2, 3, 4, 5, 6, 7, and 8 cm, but in practice this was unrealistic. During a check after 10 days, most cages were nevertheless buried at depths that approximated the intended values.

When deposit-feeding, *Macoma* leave traces on the sediment surface where they have grazed away detritus and benthic algae with their inhalant siphon (see Hulscher 1982: Figure 2). After 10 days, the radii of these feeding traces on the sediment were measured with a ruler (along with the depths of the mini-cages). In the weeks that followed, an invasion of *Nereis diversicolor* larvae made it impossible to reliably measure the feeding radii, as the small ragworms disturbed the sediment-surface. On 11 September the depth of the mini-cages was measured again and the cages taken out. In the laboratory the caged *Macoma* were processed as described in 'Measurements'.

Measurements
At the beginning and end of each experiment, 50-80 free-living animals of the source population were sampled to determine body mass. Of each experimental animal, the individuals from subsamples taken at the start of the experiments, and field-samples of the source population, shell length along the longest axis was measured to the nearest 0.01 mm with callipers. Soft parts were removed from the shell and placed individually in porcelain cups. Ash-free dry mass (AFDM) of the soft parts was determined after drying for
3 days at 60°C, weighing, incinerating for 4 hours at 580°C and weighing again. The mass loss at 580°C was considered to represent the ash-free dry mass. As a measure of body condition we use the body mass index (BMI). BMI is defined as the AFDM of total soft body (mg) / shell length to the third power (cm³). By using BMI it is possible to compare the body masses of animals with different shell lengths. Individuals infected with the parasite Parvotrema affinis (Swennen & Ching 1974) were omitted from the analyses.

RESULTS

Mortality

During experiment I, 285 out of 500 bivalves died. Survival was much higher at 2 cm depth (76%) than at 8 cm depth (38%), equalling daily instantaneous mortality rates of 0.0040 d⁻¹ and 0.0140 d⁻¹, respectively. At the end of experiment II, 118 out of 201 bivalves had died. Again survival decreased with burying depth (rs= -0.76, p< 0.001). Mortality was especially high for animals buried deeper than 4 cm. In experiment III, 153 out of the 210 animals had died (Table 2.1). Survival decreased significantly with burying depth (rs= -0.99, p< 0.001); few animals deeper than 3-4 cm survived. For Macoma experimentally buried at shallow depths (1-3 cm), daily instantaneous mortality rates were very similar among experiments (ca. 0.004 d⁻¹).
Growth

There were consistent negative relationships between burying depth and body condition at the end of all three experiments. In each case, final values of BMI were higher in shallow buried animals than in deeper buried animals (Figure 2.2). The effect of burying depth on body condition was statistically significant in experiment I (two-way ANOVA, \( F_{1,242} = 77.24, p < 0.001 \)). Animals buried at 2 cm had a higher average BMI than the animals at 8 cm. In experiments II and III, Spearman rank correlation coefficients for burying depth on BMI were -0.58 (\( p < 0.005 \)) and -0.50 (\( p < 0.001 \)), respectively. Compared to the growth in the field, growth was normal for *Macoma* in experiment I, but much lower for the animals in experiments II and III (Table 2.2).

Feeding radius

In the mesocosm experiment (III), the feeding radii of *Macoma* 10 days into the experiment, were negatively correlated with depth (\( r_s = -0.43, p < 0.001 \); Figure 2.3).

**DISCUSSION**

**Mortality**

The instantaneous daily mortality rates of *Macoma* in our experiments are high compared to these of free-living *Macoma* (Van der Meer and Beukema 1997; \( Z (d^{-1}) = 0.0023 \) in summer).

<table>
<thead>
<tr>
<th>Depth (cm)</th>
<th>Plastic strip field (I)</th>
<th>Mini-cage field (II)</th>
<th>Mini-cage mesocosm (III)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>n start</td>
<td>n final</td>
<td>%S</td>
</tr>
<tr>
<td>1</td>
<td>8</td>
<td>3</td>
<td>37</td>
</tr>
<tr>
<td>2</td>
<td>250</td>
<td>189</td>
<td>76</td>
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<tr>
<td>3</td>
<td>53</td>
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<tr>
<td>7</td>
<td>6</td>
<td>2</td>
<td>33</td>
</tr>
<tr>
<td>8</td>
<td>250</td>
<td>95</td>
<td>38</td>
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Table 2.1 Percentage survival (% S) of *Macoma balthica* for the experimental periods and instantaneous daily mortality rates (\( Z (d^{-1}) \)) in relation to burying depth, measured at the end of the three fixed burial experiments.
This is especially true for the deep-buried animals and may have been due to “stress”, suffocation, emaciation and/or anoxic sediments. Our fixation method may have caused stress. Especially the deep buried animals which could not feed enough, may have tried to bury shallow, in which case their ineffectual burying movements would have led to high energy expenditure. Another reason for the high mortality may have been our
method of reburial. Blundon and Kennedy (1982) reburied *Mya arenaria* gradually: the bivalves were given 6 h to push their siphons up through each additional layer of sediment before more sand was added. In this study, the immediate rather than the gradual burial of *Macoma* may have led to suffocation. We believe, however, that emaciation due to low intake rates (in combination with high expenditures, *i.e.* a negative energy balance) explains the differential mortality best in view of the fact that survival was lowest in the experiment where competition for benthic algae was obviously highest (experiment III, with *Nereis* as food competitors). At the end of this experiment (and also in experiment II), during which *Macoma* showed little growth compared to animals in the field (Table 2.2), the distribution of BMI values (Figure 2.2) was truncated below the minima of 5 reported for *Macoma* in the field (J.J. Beukema pers. 

<table>
<thead>
<tr>
<th>Experiment</th>
<th>Exp. Start</th>
<th>Exp. end</th>
<th>Field start</th>
<th>Field end</th>
</tr>
</thead>
<tbody>
<tr>
<td>I. Plastic Strip Field</td>
<td>7.8 (2.0, 35)</td>
<td>12.3 (2.9, 279)</td>
<td>8.7 (1.8, 83)</td>
<td>11.4 (3.2, 62)</td>
</tr>
<tr>
<td>II. Mini-cage Field</td>
<td>7.0 (0.7, 30)</td>
<td>7.0 (2.0, 80)</td>
<td>7.8 (1.5, 50)</td>
<td>10.8 (2.9, 62)</td>
</tr>
<tr>
<td>III. Mini-cage Basin</td>
<td>9.7 (1.1, 43)</td>
<td>7.2 (2.3, 53)</td>
<td>9.2 (1.4, 79)</td>
<td>12.5 (2.2, 74)</td>
</tr>
</tbody>
</table>

Figure 2.3 Feeding radii (cm) of all active *Macoma balthica* as a function of burying depth (cm), measured after 10 days from the beginning of the outdoor basin experiment. To lead the eye, a running mean is given (LOWESS routine, tension= 0.75).
With increasing burying depths, increasing proportions of Macoma died when reaching this BMI value. Interestingly, Macoma with BMI values lower than 5.6, just above the apparent starvation threshold, do not produce eggs (Honkoop and Van der Meer 1997).

The effect of anoxic sediments on the growth and survival of Macoma at different depths, is most probably negligible. First of all, we performed the field experiments in a sandy substrate with a low silt content and the mesocosm experiment in a very sandy sediment with a low silt content. In sandy sediments with low silt contents on intertidal flats, anoxic conditions are not common (G.J. Brummer, pers. comm.). We never noticed any anoxic conditions (black, smelly layer) during our experiments. Also, Macoma with their long siphons are able to take the oxygen from the water covering the tidal flats (and the experimental basin) half of the time.

Impact of burying depth on growth

Our experiments clearly demonstrate that with increasing burying depth, body condition of Macoma decreases. In experiment III, the observed feeding radius decreased with increasing depth, suggesting that the animals tried to use a certain proportion of their siphon to graze the surface. The grazed surface increases with siphon length in a quadratic way. This implies that stretching the siphon a little more over the surface translates into a disproportional increase in grazing area, food intake and by implication growth (Zwarts 1986). Zaklan and Ydenberg (1997) provided an alternative or supplemental explanation for the fact that food intake rate decreases with increasing burying depth for the suspension feeding Mya. Their explanation is based on a physical principle known as the ‘Hagen-Poiseuille equation’ for flow through a tube: flow will be reduced through a longer tube at similar pumping effort (Vogel 1988). Our experiments do not allow us to evaluate the relative importance of Zwarts’ “intake” and Zaklan and Ydenberg’s “expenditure” hypotheses, but they demonstrate convincingly that animals buried at shallow depths attain relatively favourable energy balances (and enhanced growth or reduced mass loss).

CONCLUSION

We reject the null hypothesis that burying depth does not influence growth of the bivalve Macoma balthica. Even in a situation where siphon nippers are present it is worthwhile for Macoma to come to the surface in spring and summer. To grow and reproduce in spring, Macoma on intertidal flats are apparently prepared to take a survival risk by burying shallow to obtain higher food intake rates, thus exposing themselves to predation by epibent-
ACKNOWLEDGEMENTS

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