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Experimental effects of immersion time and water temperature on body condition, burying depth and timing of spawning of the tellinid bivalve *Macoma balthica*

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Abstract The burying depth of many bivalve molluscs on intertidal mudflats varies throughout the year and differs between places. Many factors are known to influence burying depth on a seasonal or spatial scale, with temperature and tidal regime probably being very important. Burying depth, body condition and gonadal development of *Macoma balthica* were followed throughout winter and spring in an experiment in which water temperature and immersion time were manipulated. Unexpectedly, relative water temperature, in contrast to the prediction, did not generally affect body condition or burying depth. This was probably a consequence of the exceptionally overall low water temperatures during the experimental winter. Differences in temperature did, however, result in different timing of spawning: *M. balthica* spawned earlier at higher spring temperatures. Longer immersion times led to higher body condition only late in spring, but led to deeper burying throughout almost the whole period. There was no effect of immersion time on the timing of spawning. We conclude that a longer immersion time leads to deeper burying, independent of body condition. We also conclude that burying behaviour of *M. balthica* is not determined by the moment of spawning.

Keywords Feeding · Gametogenesis · Risk taking · Timing of reproduction · Wadden Sea

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Introduction

The tellinid bivalve *Macoma balthica* shows a seasonal pattern in burying depth. *M. balthica* live deepest in winter, bury shallower in spring, and deeper again in summer (Reading and McGroarty 1978; Zwarts and Wanink 1993). The actual burying depths vary considerably between years (Zwarts and Wanink 1993). Additionally Hulscher (1973) found that *M. balthica* low in the intertidal buried deeper than *M. balthica* high in the intertidal. There are many factors that can influence burying depth. Burying depth is correlated with body condition (Zwarts and Wanink 1991) and with siphon mass (Zwarts and Wanink 1989). The better the body condition, the deeper the bivalves are buried, and the longer the siphon, the deeper they are buried. Burying depth in *M. balthica* also seems to be influenced by feeding conditions. Lin and Hines (1994) showed that when the concentration of suspended algae in the water decreased, *M. balthica* switched from suspension feeding to deposit feeding and therefore moved closer to the surface. De Goeij and Honkoop (2002) showed experimentally that shorter immersion time led to shallower burying, presumably because time for suspension feeding was shorter and *M. balthica* had to compensate for this with deposit feeding.

Honkoop and Beukema (1997) experimentally demonstrated that when water temperatures in winter were lower and when body condition of *M. balthica* in the previous autumn was higher, body condition score of *M. balthica* in early spring was higher. The findings of Zwarts and Wanink (1991) and Honkoop and Beukema (1997) together suggest that colder winter water temperatures must lead to a higher body condition, and that this higher body condition could lead to deeper buried *M. balthica* in spring. Deeper burying in spring would mean a higher chance of survival, since burying deep provides safety against probing avian predators (Zwarts and Wanink 1993).

M. balthica spawns in the Wadden Sea in spring (Caddy 1967; Lammens 1967; Honkoop and van der

Meer 1997). Because this is also the period in which *M. balthica* is buried at its shallowest, spawning itself may force the animals to the surface.

For many predators on the intertidal flats the accessibility of their prey is of major importance. For example Zwarts and Wanink (1993) showed that fluctuations in burying depth of *M. balthica* was the main source of variation in biomass that could actually be harvested by red knots, *Calidris canutus*. In the present study we aim to throw some light on the factors that determine the accessible fraction of *M. balthica* in spring, a time of the year that red knots and other predatory shorebirds depend on them.

The first objective of this study is to experimentally test whether immersion time and water temperature influence burying depth of *M. balthica* from late winter to spring. The second objective is to test whether different burying depths are mediated by differences in body condition. The third objective is to find out whether burying behaviour in *M. balthica* is related to the timing of spawning.

Methods

Practical set up

We used the same experimental set-up as Honkoop and Beukema (1997). Briefly, the experimental set-up consisted of four double-walled and isolated basins ($1 \times w \times h = 265 \times 77 \times 61$ cm). A small part of each basin at the inlet side was used to adjust water temperature by either heating or cooling it. This part was separated from the rest of the basin by a wooden partition. Sea water pumped out of the Wadden Sea entered the inlet at a rate of 6 l min^{-1} . Cooled, heated, or untreated, it flowed over the wooden partition into the rest of the basin. Along its length the basin was divided into two compartments with different heights ('subtidal' and 'tidal'), each with an area of 0.65 m^2 (see Fig. 2 in Honkoop and Beukema 1997). We used sand without organic material with a median grain size of $291 \mu\text{m}$. The depth of the sediment layers was 17 cm in the subtidal and 30 cm in the intertidal area. To avoid temperature peaks due to solar radiation, and also to avoid growth of macroalgae, the basins were covered with a 4 cm layer of opaque isolating material.

Design and statistical analyses

Two replicate plots (basins) were used for each of two temperature levels. Each of these four plots was divided into the two previously mentioned compartments, one tidal and one subtidal. This "split plot" design (Cochran and Cox 1957) was statistically analysed with the appropriate ANOVA procedures in SYSTAT 7 (SPSS 1997). The effect of temperature (1 *df*) was tested using the plots within each temperature (2 *df*) as the error term. For the effects of tidal regime (1 *df*) and the interaction between temperature and tidal regime (1 *df*), the tidal regime by plots within each temperature (2 *df*) was used as the error term. Because of the low power of the experimental set-up (only one replicate per treatment), significance levels were set to $\alpha = 0.1$.

Temperature regime

The starting point of the temperature regime in the experimental basins was the water temperature of the nearby Marsdiep tidal inlet. Because the set-up was placed outdoors and was fed with

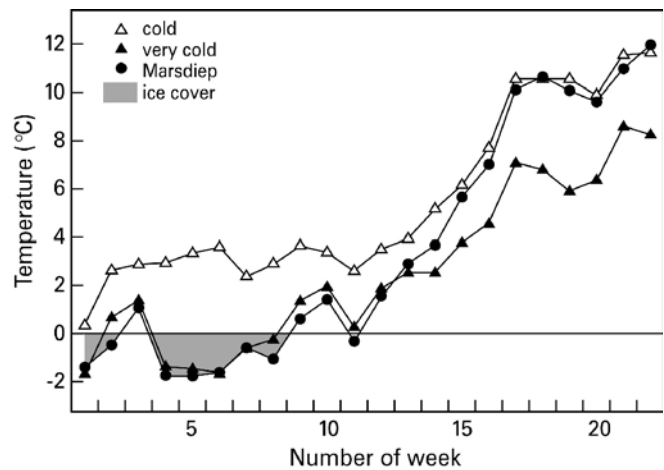


Fig. 1 Weekly mean water temperatures of the Marsdiep inlet, where the water from the experimental set-up was taken from, and weekly mean water temperatures for the two 'very cold' basins and the two 'cold' basins, during the period 1 January to 29 May 1996. Note that at water temperatures below about 0°C the basins were iced

Marsdiep water, the temperature of the inflowing water fluctuated with the water temperature of the Marsdiep inlet (Fig. 1). The aim was to simulate a 'mild' and a 'cold' winter, but since the winter of 1995/1996 was very cold we have simulated a 'cold' and 'very cold' winter. The water in two out of four basins was heated to simulate the 'cold' winter and the temperature of the water of the other two basins remained unchanged to simulate a 'very cold' winter. By 20 March the temperature of the seawater had become so warm that we stopped heating the 'cold' basins and started to cool the 'very cold' basins.

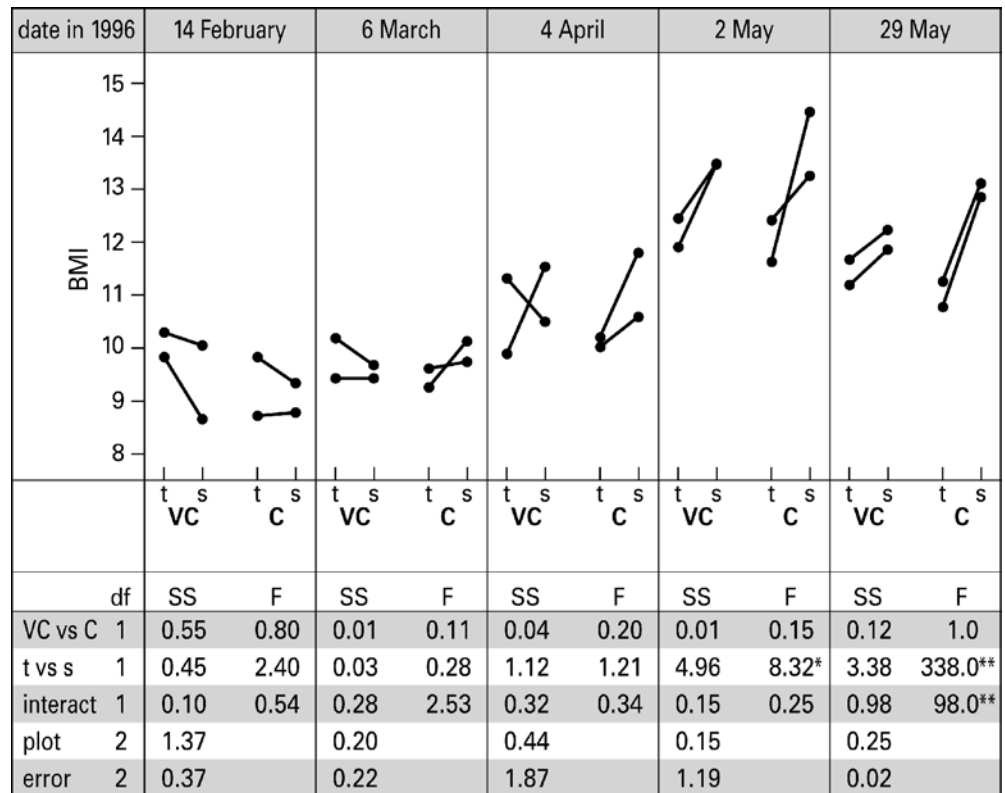
Tidal regime

The water level, and thus the time available for pelagic feeding, was manipulated manually by changing the height of the outlet overflow. During weekdays, the water was lowered to 11 cm above the subtidal area (low water level, LWL) from 0800 hours to 1700 hours, thus exposing the higher ('tidal') level. Once per week the water level was also kept low during the night. In this way the simulated low water level was maintained for 72 h a week, having a low tidal level for 43% of the time. The water level during the remaining part of the week (96 h) was kept 17 cm above LWL, resulting in submersion of both levels. The winter of 1995/1996 happened to be a very cold winter (see Fig. 1). Ice covered the 'cold winter' basins on two occasions. To prevent the animals from freezing during these two frost periods, the *M. balthica* were kept continuously submerged in all basins.

Burying depth, body mass, and gonadal development measures

From 13 to 15 December 1995, *M. balthica* with shell lengths between 14 and 17 mm were collected on an intertidal flat in the Wadden Sea at Balgzand. Shell length of each individual bivalve was measured with electronic calipers to the nearest 0.1 mm. A nylon thread of known length with a numbered tag was attached to each bivalve with adhesive and a small sticker (for a detailed description, see Zwarts 1986). On 19 December, 150 tagged bivalves were put on top of the sediment in each experimental plot where they could bury themselves. From 18 February to 29 May 1996 the burying depth of 60–100 individual bivalves was measured six times. The depth to which a bivalve buried could be calculated by measuring the length of the thread remaining above the sediment surface.

Fig. 2 Changes in body mass index (BMI) of *Macoma balthica* in the experimental set-up. Mean BMI values of 15 animals per plot per treatment were plotted. Each line connects the BMI value of the intertidal and subtidal group for each plot. For each sampling day the temperature (VC very cold, C cold) and the immersion treatment (t intertidal, s subtidal) are indicated. The Y-axis shows the BMI values expressed as M/L^3 (M ash free dry mass in milligrams, L shell length in centimetres). Below each part of the figure, ANOVA results are given. Significance levels are shown as ** if $P < 0.05$ and * if $P < 0.10$.



After each depth measurement, with the exception of 17 March, 15 *M. balthica* were taken randomly from the plots to determine their body mass index (BMI) and gonadal development. To determine BMI (the mass of the bivalve corrected for shell size), the soft parts were separated from the shell. Shell length of each individual bivalve was measured with electronic calipers to the nearest 0.1 mm. Ash-free dry mass (AFDM) was determined by drying the soft parts for 4 days at 60°C, weighing the samples to the nearest 0.01 mg, incinerating for 5 h at 580°C and then weighing them again after cooling to room temperature. The difference between dry mass and ash mass after incineration represents ash free dry matter (AFDM). The body mass index is expressed as total AFDM per cubic shell length (mg cm^{-3}).

Gonadal development was recorded by looking at the freshly opened bivalve. The gonadal stages were examined macroscopically and five scores were assigned, from completely full of eggs or sperm (=1) to empty (=0) with three stages in between. A gonad index was calculated for each treatment group by adding all individual scores within the same treatment and dividing this by the total number of *M. balthica* in the particular treatment.

Results

Water temperatures

With a mean water temperature of 0.1°C (Fig. 1) the Marsdiep waters were exceptionally cold during January–March 1996. The mean Marsdiep winter temperature for the period 1970–1995 was 4.1°C. The mean temperature of the four coldest years in that period was 1.5°C and of the four mildest years 6.1°C (Honkoop and Beukema 1997). As a result of the severe winter conditions in 1996, the simulated temperature regimes in the experiment were similar to a ‘very cold’ (0.3°C) and ‘cold’ (3.1°C)

winter. The ‘very cold’ basins had ice coverage for two periods. From the beginning of April onwards water temperatures in the ‘very cold’ basins were higher than 4°C, the temperature above which *M. balthica* are able to grow (Beukema et al. 1985). In the ‘cold’ basins, water temperatures were between 2°C and 4°C until mid-March. Then temperatures started to increase (Fig. 1).

The effect of water temperature on body mass index, burying depth and gonadal development

There were no significant differences in body mass indices of *M. balthica* subjected to the ‘very cold’ and ‘cold’ treatments (Fig. 2). A significant effect of water temperature on burying depth was only observed on the first and the last date of sampling. On 13 February, *M. balthica* subjected to the ‘cold’ treatment buried significantly deeper than the ones subjected to the ‘very cold’ treatment. On 29 May the direction of the effect of temperature was the opposite; in the ‘very cold’ treatment the bivalves were buried deeper than in ‘cold’ treatment (Fig. 3). On the three first sampling dates the gonads of all examined *M. balthica* were completely filled with gametes. The gonads extended all over the stomach and the intestines. On 2 May the first animals had released gametes (Fig. 4). In the ‘cold’ basins significantly more *M. balthica* had released gametes than in the ‘very cold’ basins. On 29 May more than 50% of the bivalves in the ‘cold’ basins had released their sperm or eggs. In the ‘very cold’ basins this percentage was significantly lower.

Fig. 3 Changes in burying depth (cm) of *Macoma balthica* in the experimental set-up. Mean burying depths of 60–100 animals per plot were plotted. Each line connects the burying depth of the intertidal and subtidal group for each plot. For each sampling day the temperature (VC very cold, C cold) and the immersion treatment (t intertidal, s subtidal) are indicated. The Y-axis shows the burying depth in centimetres. Below each part of the figure, ANOVA results are given. Significance levels are shown as ** if $P < 0.05$ and * if $P < 0.10$

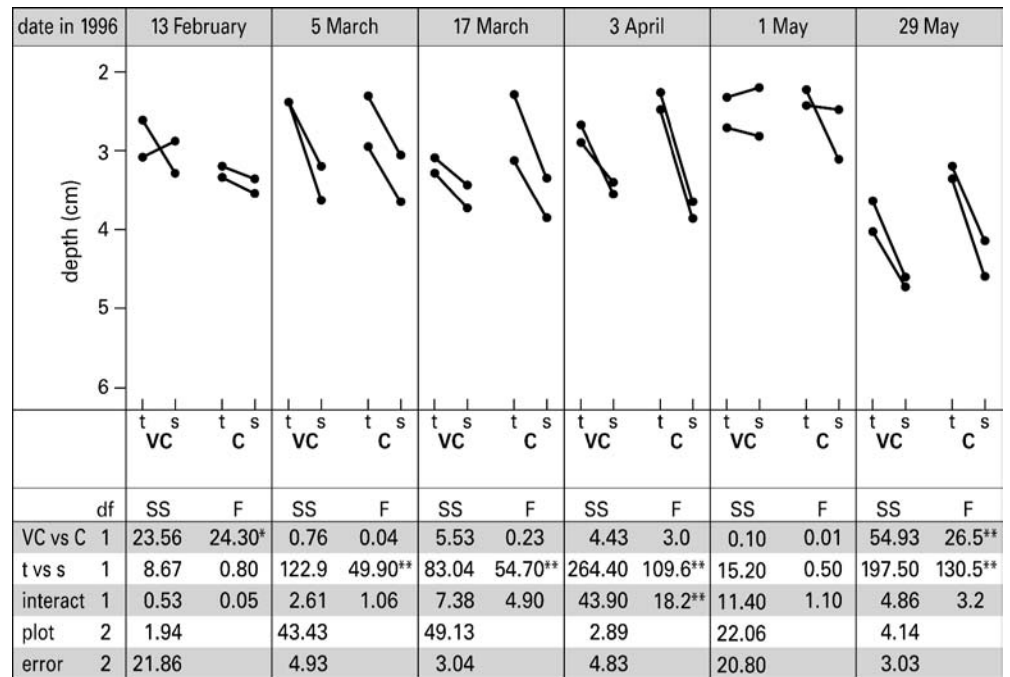
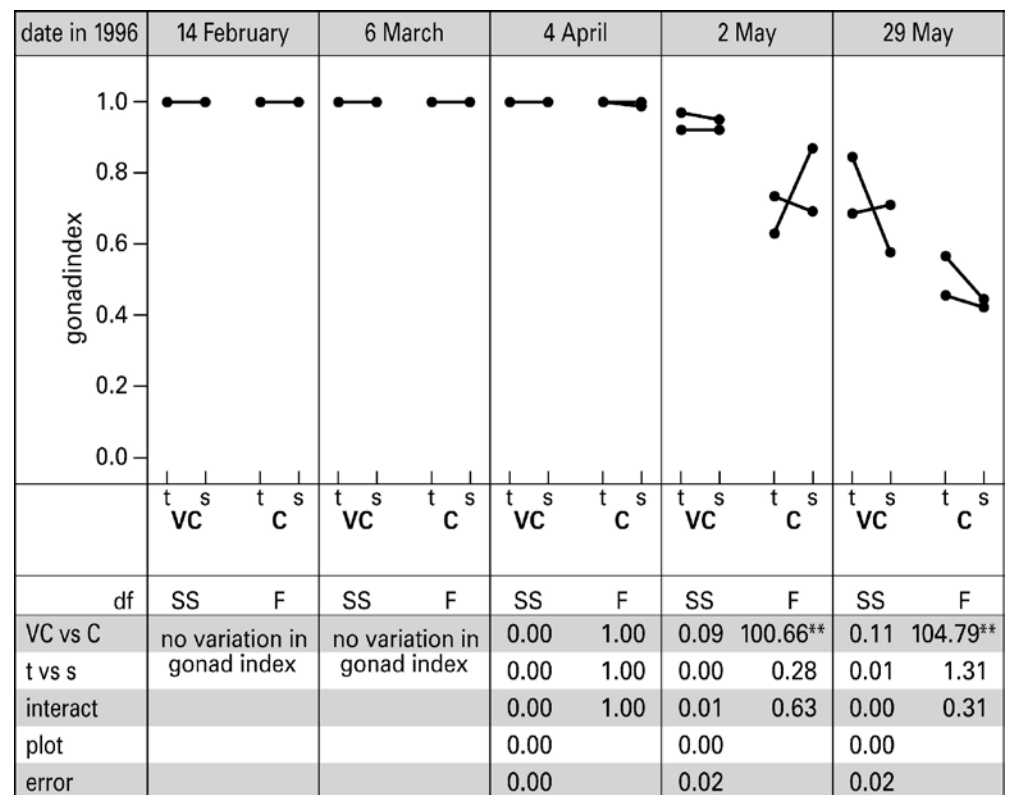


Fig. 4 Changes in gonad indices of *Macoma balthica* in the experimental set-up. Mean gonad indices of 15 animals per plot per treatment were plotted. Each line connects the gonad index of the intertidal and subtidal group for each plot. For each sampling day the temperature (VC very cold, C cold) and the immersion treatment (t intertidal, s subtidal) are indicated. The Y-axis shows the gonad index. Below each part of the figure, ANOVA results are given. Significance levels are shown as ** if $P < 0.05$ and * if $P < 0.10$



The effect of immersion time on body mass index, burying depth and gonadal development

Only in late spring, from 2 May onwards, were significant effects of immersion time on body mass observed. *M. balthica* subjected to subtidal conditions generally had larger body masses than *M. balthica* subjected to

tidal conditions (Fig. 2). Immersion time had an obvious and consistent effect on burying depth. Throughout the whole experimental period subtidally living *M. balthica* buried significantly deeper than intertidally living *M. balthica* (Fig. 3). The general pattern in burying depth is one of constant depth until the beginning of April. In April *M. balthica* come closer to the surface

until the beginning of May, when they bury deep again. Immersion time had no effect on the gonadal development or the moment of spawning (Fig. 4).

Discussion

The effect of temperature on BMI, burying depth and gonads

Body mass index

Under our experimental regimes *M. balthica* did not lose mass during the winter period and in winter BMI did not differ between temperature treatments. This is in contrast with a similar experiment, in which *M. balthica* subjected to high winter water temperatures (5.6°C and 3.1°C) lost body mass in February and March (Honkoop and Beukema 1997). *M. balthica* incur lower metabolic costs at lower temperatures (Honkoop and van der Meer 1997). It is possible that our experimental winter temperatures were so low that *M. balthica* in both treatments had the same energy expenditure in their dormant winter state. The prediction that with a colder winter temperature, a higher body mass in spring would be found (Beukema 1992; Zwarts 1991; Honkoop and Beukema 1997), also could not be confirmed.

When temperatures increased dramatically in April, BMI of *M. balthica* started to increase also. This pattern is congruent with the data of Beukema et al. (1985) who found that most of the yearly mass increase in *M. balthica* occurred at water temperatures between 4°C and 16°C. Also in late spring there were no differences in BMI between animals in the two temperature treatments, perhaps because food was already abundant enough to compensate for possible temperature-induced variance in energy expenditure.

Burying depth

On most experimental dates temperature differences were not correlated with differences in burying depth. We predicted that colder water would indirectly lead to deeper burying through higher body condition of *M. balthica*. Since we found no difference in BMI between temperature treatments either, this prediction can neither be confirmed nor rejected.

Gonads

It is known that during the coldest periods during winter, generally in January and February, gonadal development can cease (Bayne 1984) and resume, as temperatures become higher. At higher water temperatures, metabolic demands are higher and more eggs will be resorbed than at lower temperatures (Honkoop and van der Meer 1998). Since BMI values did not differ during the winter

it seems logical that gonad indices also did not differ. However, our gonad indices are qualitative and cannot be compared with counts of eggs as in Honkoop and van der Meer (1997).

It was expected that spawning would start at water temperatures of 10°C and higher (Lammens 1967; de Wilde and Berghuis 1978). This temperature would be reached earlier in the 'cold' basins and therefore spawning should start earlier in the 'cold' treatment. Indeed, spawning started earlier in the 'cold' basins than in the 'very cold' basins, and lasted for at least 3 weeks. Thus spawning is not entirely synchronized, which is consistent with the field data of Caddy (1967), Lammens (1967) and J. Drent and P.C. Luttikhuisen (unpublished), who showed that multiple spawning events take place over a period of many weeks. As *M. balthica* stretch out much of their exhalent siphon into the water column during spawning, we expected burying depth to be influenced by the very event of spawning. That very shallow burying of *M. balthica* coincided with the start of spawning is congruent with this expectation, but the observation that *M. balthica* reburied to greater depths while there were still spawning events to come, contradicts the hypothesis. When we looked at individual *M. balthica*, those that were still full of gonads also buried deeper in May. Perhaps, an endogenous circannual clock (Gwinner 1986) primarily drives burying depth in spring.

The effect of immersion time on BMI, burying depth and gonads

Body mass index

We expected longer immersion times to lead to longer feeding times and higher BMI (Beukema et al. 1977; Cadée and Hegeman 1977; Hummel 1985; Honkoop and Beukema 1997; de Goeij and Honkoop 2002). Longer immersion periods did indeed lead to higher body masses of *M. balthica* from 4 April onwards, but the difference in body mass was only significant on 3 and 29 May. This may be an effect of different energetic demands during the experimental period. At the beginning of spring, metabolic costs were low because of low water temperatures (Honkoop and van der Meer 1997). As soon as temperatures started to increase, metabolic costs increased and so did the food requirement of *M. balthica*. This suggests that it be due to shortage of food that the bivalves in the tidal basins lagged behind in growth.

Burying depth

We also expected an effect of immersion time on burying depth (Lin and Hines 1994; Honkoop and Beukema 1997; de Goeij and Honkoop 2002); as the longer the immersion period would be, the longer the period for feeding would be and the deeper *M. balthica* could bury to increase safety. On most sampling dates, longer immer-

sion time indeed led to deeper burying. However, with the possible exception of 29 May, such an effect of immersion time on burying depth was not correlated with a higher body mass. The effect of immersion time on burying depth must therefore be a 'direct effect'; it leads to deeper burying independent of body condition.

M. balthica that were experimentally forced to remain deep in early spring starved (de Goeij and Luttikhuisen 1998). The advantage of shallower burying is that during suspension-feeding it leads to lower pumping costs through the siphon (Zaklan and Ydenberg 1997) and during deposit-feeding the feeding radius is greater (Zwarts et al. 1994). It seems that *M. balthica* can compensate for loss of feeding time by burying shallowly.

Gonads

We predicted that longer immersion time would lead to higher body masses in winter, and in turn this would lead to larger gonads in spring (Honkoop and van der Meer 1997). However, as body masses at the end of the winter did not differ, the lack of a difference in the development of the gonad index and the timing and extent of loss of gonadal tissue did not come as a surprise. Time course of spawning did not show any tidally related differences.

Conclusions

The aim of this research was to gain more insight into the factors that influence burying depth (accessibility) of the bivalve *M. balthica*, for predators such as the red knot. It was already known that body condition and siphon length (Zwarts and Wanink 1989, 1991) affect their accessibility. The present experiment shows that immersion time also affects burying depth. It was expected that the effect of immersion time would work indirectly through the body condition of *M. balthica* (Zwarts and Wanink 1991; de Goeij and Honkoop 2002). Longer immersion time would lead to more time for feeding and result in a higher body condition score. The better the body condition, the deeper *M. balthica* would bury. However, it is now clear that immersion time has a direct effect on burying depth independent of body condition.

It was also expected that winter water temperatures would affect burying depth indirectly through body condition (Honkoop and Beukema 1997). We could not find a difference in body condition or burying depth as a result of different winter water temperatures. However, this is most probably the result of extremely low temperatures during the winter in which we carried out the experiment. The third expectation was that the timing of spawning would affect burying depth of *M. balthica*. This was not the case.

To be able to predict the accessibility of *M. balthica* to different predators, it is still necessary to experimen-

tally test the relationship between body condition and burying depth, for example by starving the bivalves and by following their burying depth. That immersion time influences burying depth directly means that at different localities on the intertidal flats (with different immersion times), burying depth of *M. balthica* will be very different. This has to be taken into account when predictions are made about the accessibility of *M. balthica* for probing predators.

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