RECRUITMENT OF *MACOMA BALTHICA* (L.): IS THERE A ROLE FOR LARVAL FOOD LIMITATION?

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The Baltic tellin *Macoma balthica*

The Baltic tellin (*Macoma balthica*) occurs from the Gironde Estuary in Southwest France to the icy waters in the polar region in Greenland and Siberia. In our study area, the Western Wadden Sea, *M. balthica* is a common macrobenthic inhabitant: densities range from tens to hundreds of individuals per square meter. They live buried in the sediment at depths of 2-11cm. In spring, *M. balthica* reproduces, i.e. it releases its eggs and sperm in the water column where the fertilisation takes place. The embryo develops within two days to a larva that develops a velum with which it can swim and feed. This stage is called the veliger stage and lasts about two weeks. Then a foot is developed, which serves to bury in the sediment, while the velum gradually disappears. Finally, after three weeks, the larva settles on the sediment at a size of about 280μm, where it further develops to a juvenile with siphons.

Population dynamics of *Macoma balthica*

The population of the Baltic tellin on the Balgzand, a large tidal flat area (45km^2) in the Western Wadden Sea, has been studied ever since 1969. In this sampling programme, recruitment of *M. balthica* is defined as the number of juveniles m-2 in August, retained on a 1mm-mesh sieve.

From the analysis of the recruitment time series two features have become clear. First, the variation in stock density is merely a reflection between the recruit density, particularly in the first winter after recruitment. Second, there is no relation between the recruit densities and stock densities, i.e. the slope of the regression line through the recruit densities is not significantly different from 0. This means that in the Western Wadden Sea there appears to be a limiting factor (carrying capacity) in the pelagic larval or juvenile stages of *M. balthica* that determines recruitment density. Hence, in years with high adult stock, the probability for an egg to survive to a recruit is lower than in years with low adult stock. Strong density-dependent mortality due to e.g. food limitation, predation or diseases must therefore occur in the larval phase or in the period after settlement but before recruitment. However, density-independent processes such as the timing of the phytoplankton bloom or offshore transport of larvae may also play an important role in determining recruit densities. Hence, to understand the population dynamics of *M. balthica*, both density-dependent factors and density-independent ('variable') factors affecting the egg-to-recruit mortality should be studied. In this PhD-thesis the role of food limitation, both as a density-dependent (Chapter 2)

and density-independent factor (Chapters 3, 4 and 5) in the larval phase of *M. balthica* is addressed.

The role of density-dependent food limitation in the larval phase

Food limitation can be density-dependent as a result of interference competition, i.e. larvae can reduce each other's intake rate due to hindering interactions between individuals. The mechanism would be that larvae, when disturbed by tactile stimulus, stop swimming and draw in their velum, which decreases their feeding time and hence their food intake rates. To test this an experiment was run where *M. balthica* larvae were reared in different combinations of larval densities (0.5 to 32 larvae ml^{-1}) and food densities (0-80 x 103 cells.ml^{-1}). The results show that larval growth rate (mean: 3.8μm d^{-1}) increased with increasing food densities, but did not show a consistent pattern with increasing larval densities. Larval mortality (mean: 0.18d^{-1}) was neither affected by food density, nor by larval density. Hence, it appears that food limitation in the larval phase is not caused by density-dependent interference competition. From model calculations, it was furthermore shown that resource competition between larvae was also not very likely. Food limitation in the larval phase may, however, be density-dependent if there is competition between larvae and the adult stock.

The role of density-independent food limitation in the larval phase

Food limitation can be density-independent as a result of environmental influences, such as a mismatch between larvae and their food due to the weather. In contrast to the effects of density-dependent food limitation, the effects of density-independent food limitation during the larval phase were very clear. Density-independent effects of larval food limitation were tested in the laboratory. The hypothesis was that low food availability would lead to high larval mortality rates and high food availability to low larval mortality rates.

Food limitation of bivalve larvae appears to be very common in nature, as was demonstrated by estimates of larval energetic needs, contrasted to estimates of the energetic value of available food in the field (Chapter 3). Furthermore, the food availability in the field is usually very variable.

To test the effects of a variable food limitation on larval growth, development and mortality rates, I performed an experiment (Chapter 4) in which larvae were reared for three weeks with a starvation period of one week in the first, second or third week. Furthermore, two food densities (high and low) were applied. The results suggest that larvae do not die immediately from food limitation and that they can adapt themselves to varying food conditions by a flexible development. In more detail: at low food densities (4,000 *Isochrysis galbana* cells.ml^{-1}), larvae metamorphosed later (19.3d) at smaller size (244 μm), than at high food densities (80,000 cells.ml^{-1}, 16.5d, 263μm). In addition, an early starvation resulted in a slower growth and development than a later starvation. In contrast to our expectations, larvae that were subjected to the lower food levels had a slightly but significantly lower mortality rate (0.027.d^{-1}) than those subjected to the higher food levels (0.036.d^{-1}).

Previous analyses of long-term data series had shown a strong correlation between the strength of recruitment of M. balthica in autumn and the match/mismatch of the timing of spawning of M. balthica and the timing of the phytoplankton bloom in spring. The idea is that larvae are not always in the seawater when the food is there. A mismatch between larvae and their food would lead to an increased mortality. Such a match/mismatch situation may occur since M. balthica spawning is triggered when a threshold seawater temperature (8.4°C) is passed, while the phytoplankton bloom starts when enough sunlight is available.

To test the match/mismatch hypothesis, an experiment was run in which different batches of larvae were reared in natural seawater at different times during the spring phytoplankton bloom. I found for M. balthica in this match/mismatch experiment (Chapter 5) that growth and development rates of larvae that were offered natural seawater were significantly affected by the timing of spawning, while those of the control larvae, which were fed ad libitum with live I. galbana algae, were not. Despite the absence of a correlation between growth and development rates and the phytoplankton abundance, it is very plausible that some factor, e.d. food quality, has caused the observed differences in growth and development in early April and late May.

In conclusion, it appears that food limitation in the larval phase is not caused by density-dependent interference competition. Also resource competition between larvae was not very likely. I can, however, not yet conclude that food limitation in the larval phase is never density-dependent, since the link with the adult stock remains to be explored. In contrast, effects of density-independent food limitation during the larval phase were clear. Estimates of larval energetic needs, contrasted to estimates of the energetic value of available food in the field, suggested that larvae are usually food limited. Experiments showed that food limitation leads to differential growth and development rates, resulting in a relatively early metamorphosis at large size during a match between larvae and the phytoplankton bloom, and in a relatively late metamorphosis at smaller size during a mismatch. However, food limitation did not or did even negatively correlate with larval mortality.

Implications of larval food limitation for recruitment of *Macoma balthica*

It's now thought that in years with a mismatch between the larvae and their food, larvae stay in the dangerous water column for a longer time due to slower development and settle at sediment at a smaller size than in years with less food limitation. The mortality may occur after settlement, when small larvae are an easier prey for e.g. size-selective shrimp. Such predation by shrimps could, in combination with effects off resource competition between M. balthica adults and larvae, contribute to density-dependent mortality of the larvae. The spatial distribution of M. balthica spat and shrimps may also contribute to strength of juvenile mortality, since the intertidal area supposedly is shorter exposed to shrimp predation. This could mean that in years with a match, both juveniles in the intertidal and in the subtidal could have a good survival (too large to be eaten by shrimps), while in years with a mismatch, only those juveniles in the intertidal, out of reach of the predators would survive. The effects of global warming on the seawater temperature of the Wadden Sea will probably only increase the mismatch between larvae and their food and therefore possibly negatively affect M. balthica recruitment.