POPULATION REGULATION OF THE INTERTIDAL BIVALVE MACOMA BALTHICA IN THE WESTERN WADDEN SEA

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Density-dependent survival of baby bivalves

The intertidal soft-sediment bivalve Macoma balthica shows a large year-to-year variation in numbers and biomass in the western Wadden Sea. Analysis of long-term monitoring data (>30 years) from the Balgzand tidal flat area, revealed that the variation in adult numbers of this bivalve is a reflection of the variation in recruits. In other words, recruitment determines the adult population size. Hence, understanding adult variation required recruitment studies.

Reproductive output (total number of eggs m^{-2}) of *Macoma* is proportional to adult biomass density. Therefore the number of *Macoma* eggs produced per m^{-2} can be estimated. Recruitment density of the Balgzand, however, shows no relationship with average egg density (or adult biomass density) (Fig. 1). A stock-recruitment relationship is lacking. This implies that the probability of a fertilised egg to survive to a recruit is much lower at high adult densities than at low adult densities. Thus, survival of young *Macoma* is strongly density-dependent in the first months of their life.

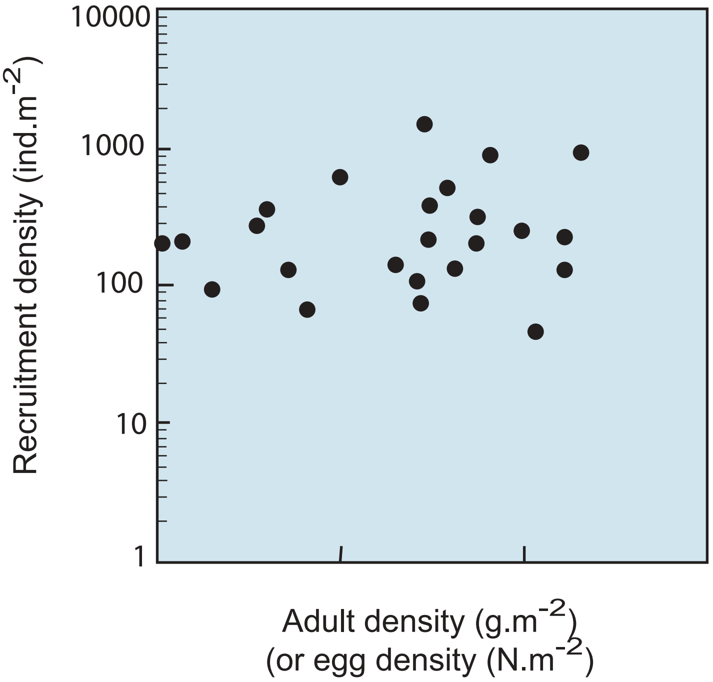

Fig 1. Stock-recruitment relationship of *Macoma balthica* (Van der Meer, 1997)

What causes density-dependent survival?

In this study we searched for mechanisms that could explain the density-dependent survival of larvae and/or juvenile *Macoma*. We put forward several hypothetical mechanisms. High larval densities in the water column may reduce food levels for the larvae, with death as a consequence. Alternatively, high larval densities may result in frequent collisions between individuals, reducing food uptake rates. Furthermore, high densities may enhance the spread of diseases, or attract predators like fishes. By means of multi-factorial laboratory experiments we have tried to identify some of the mechanisms.

To conduct the experiments we needed *Macoma* larvae. Hence, adults full of gametes were collected in the field in spring. In the laboratory males and females were artificially induced to spawn, after which we fertilised the eggs with the sperm according to techniques developed in 1997 at the NIOZ (Fig. 2).

To test the effect of larval density, algal density and their combination on the growth rate of larvae and the survival rate of larvae, we set up experiments in a 15ºC climatised laboratory. In one of these experiments we combined 4 densities of larvae (0.5 to 32 larvae ml^{-1}) with 4 densities of algae (0 to 80,000 cells ml^{-1}) to obtain 16 different treatments. The experiment showed that (1) higher larval densities led to lower larval survival, independent of food levels and (2) higher food levels led to higher larval growth rates. This indicated that larvae died from something associated with the higher larval density, e.g. viral diseases, but not from food shortage.

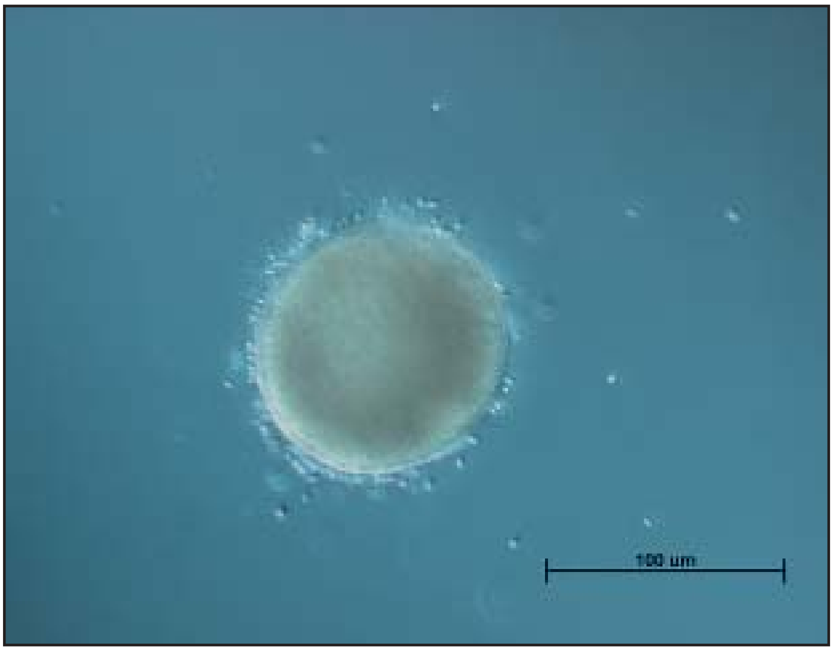

Fig 2. *Macoma balthica* sperm in a battle to fertilise an egg (Photo: Jolanda van Iperen, Axiovert 200, 10 ´ 40)

The role of larval food limitation

The hypothesis arose that increased food levels could still play a role in an enhanced survival of larvae or juveniles, but indirectly, by lowering predation risks. It would therefore be a great advantage for larvae to be able to grow and metamorphose quickly in the pelagic phase to continue life in the benthos. To see how growth rates were affected under more realistic circumstances, we concentrated on the relation between natural food levels and larval growth and development rates.

In the Wadden Sea phytoplankton levels vary a lot, even within a period of days during the time that larvae are present in the water. As a first approach tot mimic nature, we introduced one week of food absence within the three weeks of the larvae’s planktonic life. The experiment was performed at two food levels and at one larval density. The results demonstrate that (1) larvae were very sensitive to food absence immediately after hatching, resulting in a retarded larval growth and development, compared to food absence in the second or third week, and (2) metamorphosis of larvae was a very flexible process. Larval survival did not show a clear pattern across treatments.

From statistical analyses of the *Macoma* recruitment densities of the last 30 years, we learnt that survival was indeed partly related to food levels. In those years in which the peak of the phytoplankton bloom did not coincide with the occurrence of larvae in the water column, the recruitment success was lower than in those years in which food and larvae were present at the same time. We hypothesised that a mismatch would result in low growth and development rates of larvae, which then would be an easier prey for size-selective shrimps (Fig. 3). To see whether this match/mismatch of larvae and the phytoplankton bloom could be mechanistically understood, we went into the laboratory again.

We conducted a laboratory experiment in which we reared batches of larvae during the anticipated wax and wane of the phytoplankton spring bloom (April-May 2002). One group of larvae was reared in seawater with the natural phytoplankton assemblage, while the other group served as a control, and was reared in 1µm-filtered seawater enriched with cultured algae (*Isochrysis*). The results strongly suggest that larvae are indeed food limited under natural food circumstances, since there was a clear increase in larval growth and development rates from April till May in the experimental group and not in the control group. However, the phytoplankton densities in the seawater did not show the expected large increase.

Larvae and energy budgets

In the final stage of the project we are focussed on the integration of our laboratory results in a Dynamic Energy Budget (DEB) model. The model will allow us to estimate under which conditions bivalve larvae are food limited considering their size and temperature.

Finally we will use the model outcomes to predict whether bivalve larvae could be food limited under natural circumstances. To do so, we will compare bivalve densities, which were monitored throughout the year 2000 at locations in the Wadden Sea, Schelde estuary, Sylt (Germany) and Limfjorden (Denmark), to the phytoplankton densities at the same locations.

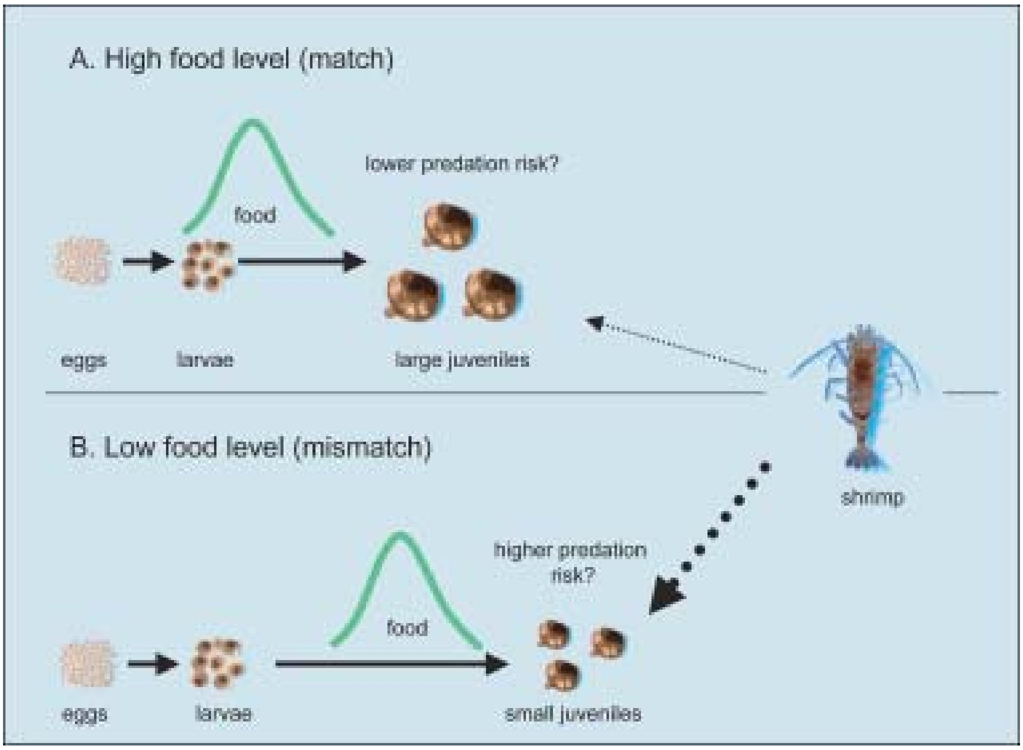

Fig. 3. Possible mechanisms behind the statistically observed dependence of recruitment success on the match/mismatch of the spring phytoplankton peak and the larval peak. A match of the phytoplankton peak and the larval peak results in a better recruitment success than a mismatch, since well-fed juveniles are better able to escape predators.