THE ADAPTIVE VALUE OF MIGRATIONS FOR THE BIVALVE *MACOMA BALTHICA*

Hiddink Jan Geert

University of Groningen, Department of Marine Biology
PO Box 14, 9750 AA Haren, The Netherlands
Correspondentie-adres: School of Ocean Sciences,
Menai Bridge, Anglesey LL59 5AB, United Kingdom
E-mail: J.Hiddink@bangor.ac.uk

This thesis is about the movements of the coastal marine bivalve *Macoma balthica*. *M. balthica* migrates over several kilometres between nurseries at high tidal flats, where juveniles are found in high numbers, and the adult habitat on low-lying tidal flats.

Most benthic species in the Wadden Sea have been caught in the water column; also, *Macoma balthica* has been frequently caught. Although *M. balthica* normally lives buried in the sediment, it can migrate over large distances (kilometres) via a long byssus thread, which is secreted into the water column. This thin mucous thread increases drag force on the animal and allows it to be transported over large distances by the current.

In the Wadden Sea, juvenile *Macoma balthica* is normally mainly found in the high intertidal (the nursery). Juveniles settle in the low intertidal in May at a size of 300 μm. Subsequently, they migrate to the high intertidal in June, where they stay until winter. In winter, juvenile *M. balthica* (5 mm) migrate back to the low intertidal and to the North Sea. Adults are much more widespread in distribution, occurring both in the low and high intertidal, as well as the subtidal of the Wadden Sea and adjacent North Sea. Since the locations where adults and juveniles live are spatially separated, *M. balthica* has to undertake migrations between these locations.

Migration may be profitable if another habitat has a higher quality than the current one. However, migration takes time, uses energy and the journey may be dangerous. Mortality and fecundity (and thus fitness) are likely to be affected by migration: by its energy cost, by its effect on food supply and predation rates and by its other dangers. Therefore, migration costs must be balanced by the benefits of living in a more favourable environment. Thus, the decision of whether or not to migrate is a major component of a mobile organisms' life history strategy.

The quality of a location for an animal depends on the developmental stage of an animal. Due to ecological and physiological differences between juveniles and adults, they may prefer different habitats. Spatial variation in the environment may make costly migration worthwhile because of these different preferences of juveniles and adults.

The aim of this thesis is to determine why *Macoma balthica* migrates in the Wadden Sea; do these migrations increase the fitness of *M. balthica*? To answer this question the costs and benefits of migrations and nursery use were assessed using laboratory and field experiments. The costs were sought in increased mortality during migrations, benefits were sought in differences in predation pressure and growth between the low and high tidal flats. Eventually, the costs and benefits of migration and nursery use were weighed in a model that calculates fitness of *M. balthica* as a function of migration strategy. The next paragraphs present the results of the different studies.

First, I describe the results of a study in which I estimated the costs of migration for *Macoma balthica*. Migration may increase mortality rates among *M. balthica* populations, e.g. because migrating *M. balthica* run a greater risk to be eaten by predators than buried *M. balthica*, or may end up at unsuitable locations. I examined if mortality rates of the *M. balthica* population were higher during migration periods than outside these periods. Hence, population development of the 1998-year-class of the bivalve *M. balthica* was studied by repeated sampling of 57 stations at a 7 km^2 tidal flat (Groninger Wad) area in the Lauwers tidal basin in the eastern Dutch Wadden Sea from May 1998 to August 2000. Additional data was collected by sampling a tidal channel close to the study area, and by collecting *M. balthica*-densities for the Lauwers tidal basin and adjacent North Sea from the literature. During both spring and winter migration, many animals disappeared from the tidal flat population. Partly this could be explained by normal mortality and by emigration to the subtidal channels and the North Sea. The rest of the disappearance was probably due to the increased mortality, associated with the risk of migration.

One mechanism that may explain the high number of disappearing animals is that predation by fish and crabs is higher when *Macoma balthica* is migrating through the water column than when it remains buried in the sediment. I examined if this mechanism can explain the increased mortality rates during migration periods. Migration was induced in a circular aquarium by generating a current. Without current, *M. balthica* remained buried in the sediment. Under illuminated conditions, relatively more migrating than buried *M. balthica* were consumed by predators, whereas there was no difference between predation rates on migrating and buried *M. balthica* under dark conditions.

Because of this light-dark difference in predation rates, I expected that the number of migrating *Macoma balthica* in the Wadden Sea would be larger at night than in daytime, either because they are avoiding predation or because in daytime many migrating *M. balthica* are eaten by predators. 1-group *M. balthica* was indeed much more abundant in nocturnal than in diurnal samples collected from the field. Furthermore, no *M. balthica* were found in the stomach contents of fishes collected during daylight hours of the migration period.

In conclusion, enhanced predation on drifting as compared to buried *Macoma balthica* may be the mechanism that explains enhanced mortality during migration in light and may explain why *M. balthica* mainly migrates at night in the field. As we found no *M. balthica* in stomachs of pelagic fish, we do not know whether predation on byssus-drifting *M. balthica* exists in the field.

The benefits of nursery use are probably found in spatial differences in the environment. I examined if differences in predation pressure between the low and high tidal flats by size-selective predators may be a reason for migrations and nursery use.

Foraging time in the intertidal is limited by the tide. Shorebirds can only forage on exposed tidal flats. Therefore, predation pressure by birds on high tidal flats is probably higher than on low tidal flats. From earlier studies, it is known that shorebirds prefer large *Macoma balthica*. Marine predators, like shrimps, crabs and fish (the epibenthic predators) are only active at the tidal flats at high tide. In accordance with this, shrimps (*Crangon crangon*) were more abundant and larger on low than on high tidal flats. Crabs (*Carcinus maenas*) were more abundant on the high tidal flats, but were much larger on the low tidal flats. Size selection experiments and stomach content analysis showed that shrimps and crabs only consumed 0-group *M. balthica* smaller than 5 mm.

From these findings, I expected a higher predation pressure on small *Macoma balthica* in the low intertidal, due to selective consumption of small *M. balthica* by epibenthic predators, and a higher predation pressure on large *M. balthica* in the high intertidal, due to selective consumption of large *M. balthica* by birds. This would make nursery use and migrations of *M. balthica* beneficial. The hypothesis was tested in an exclosure experiment, where birds and epibenthic predators were selectively exclosed from experimental plots, at the low and high tidal flats. *M. balthica* density in plots without predation was compared with density in control areas with normal predation rates after several months. Bird predation had no significant effect on densities of large and small *M. balthica*. Densities of small *M. balthica* were higher in cages where epibenthic predators were excluded, compared to plots where these predators had normal access. This effect was, as expected, stronger in the low than in the high intertidal. Therefore, juvenile *M. balthica* can reduce epibenthic predation by living in the high intertidal.

Apart from birds and epibenthic predators, predation by polychaete worms may be important for the nursery use of *Macoma balthica* and was studied. Infaunal polychaetes reach much higher densities on tidal flats than epibenthic predators and birds. Therefore, a comparatively small *M. balthica*-consumption per polychaete may still negatively affect densities. Small *M. balthica* (<1.5 mm) were found in the stomach contents of the lugworm *Arenicola marina* and the ragworm *Nereis diversicolor*, showing that polychaetes really ingest small bivalves. Laboratory experiments showed that these polychaetes could reduce densities of small *M. balthica*. The impact of polychaete predation on *M. balthica* densities was examined in the field in an experiment where densities of polychaetes were manipulated. *Nereis* densities were experimentally increased in small cages (0.03 m^2), *Arenicola* densities were manipulated in 0.25 to 1 m^2 plots. The effect on densities of small and large *M. balthica* was examined after several weeks. These experiments showed that both polychaete species significantly negatively affected densities of very small 0-group *M. balthica*.

Consumption rates, calculated from stomach contents and field experiments, were 45 to 102 *Macoma balthica* m^{-2} d^{-1} for *Arenicola* and 5 to 116 *M. balthica* m^{-2} d^{-1} for *Nereis*. These values are higher than consumption rates of shrimps and crabs in the same area. Nevertheless, between-year differences in year-class-strength could not be explained from the abundance of these polychaetes. Since both polychaete species were distributed rather homogeneously over the low and high tidal flats, the strongly size-selective predation by these species does not seem to provide an incentive for migration for *M. balthica*.

Besides predation, differences in growth rate between low and high tidal flats may be an incentive for migrations of *Macoma balthica*. For *M. balthica* on the tidal flats of the Groninger Wad, there are only small differences in shell-length and biomass between the low and high tidal flats. Growth rates in exclosures, without predators that crop siphons and inhibit feeding, did also hardly differ between high and low tidal flats. Therefore, differences in growth rate between low and high tidal flats are probably no major reason for the nursery use.

To determine to what extent the studied factors can explain the observed mortality, empirical predation rates from the Groninger Wad and literature values were combined in a model that calculated monthly mortality rates of the *M. balthica* population. The model showed that a large fraction of the mortality as observed on the Groninger Wad could be explained from predation by shrimps, small and larger crabs, polychaetes and oystercatchers.

All costs and benefits of migrations and nursery use for *Macoma balthica* were weighed against each other, in a model, to determine the effect of these migrations on the fitness of *M. balthica*. In the model, survival and reproduction was calculated for *M. balthica* living on the low and high tidal flats. Survival and reproduction were a function of mortality due to predation by shrimps, small and larger crabs, polychaetes and oystercatchers. Additional to these predators, the effect of the parasitic trematode *Parvatrema affinis* was added to the model. *Parvatrema* only infects *M. balthica* larger than 9 mm at high tidal flats. An infection by this parasite results in parasitic castration and therefore reduces the fitness of a *M. balthica* to zero.

I examined under what conditions the costs of migration are traded-off by an increased reproductive output and which settlement and migration strategy (location of settlement and timing of migrations) yielded the highest fitness. I examined all strategies that started with settlement at the low or high tidal flats, followed by an optional migration to the high tidal flats (if applicable) and subsequently an optional migration back to the low tidal flats. Therefore, the minimal number of migrations was zero (always high or low) and the maximal number of migrations to two (low-high-low). The factors responsible for the observed patterns were identified by varying the relative impact of each factor and examining the effect on the migration strategy that yielded the highest reproductive output.

Fitness was maximised for *Macoma balthica* that settle directly in the high intertidal and migrate to low tidal flats at an age of approximately nine months. High shrimp predation rates make living on the low tidal flats unfavourable for small *M. balthica*. Parasitation by the trematode *Parvatrema affinis* makes it beneficial for *M. balthica* to leave the high intertidal around the age of nine months. Of the other examined predators (crabs, birds and polychaetes), some did affect fitness, but none of them had an effect on the migration strategy that maximises fitness, because spatial differences in predation pressure of these species were not large enough to trade off migration costs.

In conclusion, migrations of *Macoma balthica* to and from nurseries on high tidal flats of the Wadden Sea may be seen as an adaptation to avoid shrimp predation on the juveniles and parasite infection of the adults. The migration increases fitness because the shrimp *Crangon crangon* and the parasite *Parvatrema affinis* are size selective and show a large difference in abundance on the low and high tidal flats. During its first year, *M. balthica* changes from a prey for shrimps, which can be avoided at the high tidal flats, into a host for *Parvatrema*, which can be avoided on the low tidal flats. Although the costs of migration are large, fitness is increased due to the migration because it is traded off by an increased reproductive output.