Life history variation of a marine bivalve (Macoma balthica) in a changing world

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Summary

It is becoming increasingly clear that the world's temperature is increasing. In the Netherlands, too, temperature has been on the increase during the last decades and this trend is expected to continue. These changes may substantially impact communities of plants and animals. Climate has a strong influence on the distribution of species. What effects will a changing climate have on an ecologically important area like the Wadden Sea? The research presented here highlights a part of this broader question.

The Wadden Sea is an area of tidal flats intersected by deeper gullies. The sediment is inhabited by large numbers of bivalves and worms. Most live burrowed in the sediment, but some species, the mussel and at present also the Pacific oyster, are attached to the substrate and can in this way form large banks. The benthic fauna consumes mostly unicellular algae from the water and from the sediment surface. The bivalves and worms in their turn are eaten by large numbers of birds and fish, thus forming an important link in the Wadden Sea ecosystem. Without its benthic fauna the area would lack its role as a nursery for for instance plaice or as wintering and stopover area for waders.

What will happen to the community of the tidal flat sediment if the climate changes? To tackle this question, it was chosen to focus on one single species, the Baltic clam *Macoma balthica* (L.). The Baltic clam is a small bivalve mollusc that will grow to about 25 mm. The shells are white, pink, yellow or orange. The animal lives burrowed a few centimeters into the sediment, primarily in the tidal flats, but it can also be found in somewhat deeper waters, down to about 25 meters. The Baltic clam sucks up sand and food particles through its long and flexible siphon. In the shell cavity the animal sorts the collected material, ingests the edible particles for further digestion and excretes the rest as pseudofaeces. The Baltic clam is a widespread and common species that is found from the Gironde at the French coast near Bordeaux up to Nova Zembla in the high north. For the Baltic clam the Wadden Sea is therefore a fairly southerly location within its geographic distribution. On the basis of this it may be expected that this species is relatively sensitive to warming of the Wadden Sea, which was an important reason for choosing the Baltic clam as research object. Moreover, a long research tradition exists for *Macoma balthica*, as a result of which prior knowledge of its biology was extensive. Notably, a successful rearing technique had been developed, facilitating breeding experiments in the laboratory.

What happens to the Baltic clam when the temperature rises? There are really only two possibilities: adjust to the new circumstances or 'leave' for cooler places to the north, which implies local extinction. Adjustments to the surroundings operate at several levels, within an individual or between individuals. Within an individual the capacity to adjust to the environment is called phenotypic plasticity. The phenotype is the entire individual and comprises morphological, physiological and behavioural traits. Phenotypic plasticity can be divided into phenotypic flexibility and developmental plasticity. Phenotypic flexibility implies reversible changes in behaviour, physiology or even morphology: the changes tend to be rapid and enable responding to short term alterations of the environment. Developmental plasticity is the capacity of an individual to take on a particular phenotype, depending on the environment, during development. The latter is more pervasive and particularly suited for responding to environmental variation that is relatively small during an individual's lifetime. The different forms of plasticity will come into play depending on the spatial and temporal scales involved.

At some point the possibilities for an individual to respond to changes will be exhausted. It is then possible that at the population level there are some individuals that are still capable of coping, while others succumb. If these differences are genetically determined, the genetic constitution of the population will change. This process is called natural selection and takes place over several generations.

Phenotypic plasticity and genetic adaptations complement each other in a changing world. For the Baltic clam it was examined to what extent phenotypic plasticity and genetic adaptations are involved. In the most extreme cases, all adjustments could be either plastic or genetic. Molecular markers indicated that at the European scale genetic differences between populations are very pronounced. Baltic clams from the Baltic Sea are even so extremely different that they might be considered to be a separate species. But other populations, too, display clear differences that point to a strongly restricted exchange of individuals and thus genes between locations. As a consequence, Baltic clams may well be differentially adapted at locations with different circumstances. This result was unexpected because it was always assumed that Baltic clams effectively travel large distances when they drift freely in the water column as larvae. Unhampered larval dispersal would guarantee substantial mixing between populations, inhibiting genetic differences from arising and resulting in the inevitability that adjustments to differences in environment can happen only through phenotypic plasticity.

The results of the molecular marker study indicate that genetic adaptations to circumstances specific to local populations are indeed possible. By rearing Baltic clams of different origins under identical circumstances in the laboratory it is possible to determine to what extent particular traits are heritable (genetic). Adults were collected at various localities (Balsfjord, northern Norway; Wadden Sea and North Sea, the Netherlands; Gironde, France) and induced to spawn in the laboratory. The larvae were reared to the juvenile stage under controlled conditions. Any subsequent differences between offspring of parents from different origins are most likely genetically determined. Three aspects were studied: first, the foraging apparatus, second, sensitivity of Baltic clams to high temperatures and, finally, growth and development of larvae at different temperatures.

The water current with which particles from the sediment surface are sucked up through the siphon is generated by cilia on the gills in the shell cavity. Particles are filtered from the water current, also by the gills, and then transported to the so-called palps. On the palps, like the gills covered with cilia, the particles are sorted, after which the edible fraction is ingested by the mouth and the rest is excreted as pseudofaeces. Strong differences exist between populations in the ratio between the gills (collecting) and the palps (sorting). In the reared *Macoma balthica* the differences between populations turned out to be heritable and therefore genetic. An additional experiment demonstrated that the ratio between gills and palps changes with different sediment types. In course sand the gills are large and the palps small, and this is reversed in silt. This is probably related to the amount of particles that enters at a particular pumping capacity. A volume of sand contains far fewer particles than the same volume of silt and therefore sorting out a volume is much less work if it consists of sand than if it contains a lot of silt. In contrast to the differences between populations, different gill/palp ratios within populations are to a large extent flexible and will respond to the local circumstances.

If Baltic clams in the north and in the south are both adapted to their local circumstances, the southern bivalves should be better able to cope with high temperatures. This was studied by utilizing the fact that proteins denature when exposed to higher than optimal temperatures. If this happens inside a cell a special type of proteins, the heat shock proteins (HSPs), is synthesized to either repair the damage or render the damaged proteins harmless and deport them. The concentration of HSPs is therefore a measure of temperature stress. A comparison between four groups of laboratory reared Baltic clams, from Norway, the North Sea, the Wadden Sea and France, showed that populations do differ in temperature tolerance but also that these differences were not easy to couple to the original environment. Interestingly, individuals smaller than 5 mm had much higher levels of HSPs than larger ones. This difference may be ascribed to temperature differences between the places where Baltic clams of different sizes tend to be located. Smaller individuals are burrowed close to the sediment surface, while larger ones are burrowed more deeply. Close to the surface temperatures fluctuate more and will also reach higher levels, especially when a mudflat is exposed around noon. Moreover, small Baltic clams are on average located higher up in the tidal zone than larger ones, which serves mainly to escape predators like crabs and shrimp. These places are submerged less long and can therefore heat up more during low tide than the lower tidal zone. It would therefore appear that as a Baltic clam grows, the temperature of its surroundings fluctuates less and also reaches lower maxima. It will then need HSPs less often to react to protein damage caused by high temperatures and therefore have less of these proteins in stock.

After fertilization of the eggs, larvae develop. The larvae remain in the water column for a few weeks. This is a time that is characterized by high mortality rates and could be a limiting factor for the occurrence of Baltic clams. The effect of temperature on the development of larvae of Baltic clams from the Balsfjord in Norway and from the Gironde in France was studied in a rearing experiment in the laboratory. Larvae of both populations grew and developed faster at high temperatures but also displayed a higher mortality rate. French larvae developed faster than Norwegian larvae. Remarkably, the Norwegian larvae still developed successfully at a water temperature of 20°C. This is approximately 15°C higher than normal in the Balsfjord! Larvae clearly tolerate a wide range of temperatures.

All three experiments with reared Baltic clams uncovered genetically determined differences between populations, but the most notable observation was that in all cases the individuals were capable of responding effectively to variable circumstances. The Baltic clam is genetically adapted to local circumstances, but, foremost, reacts phenotypically plastic to variations in its surroundings.

The effects of temperature on the Baltic clam were studied further among individuals from the Wadden Sea using field observations and laboratory experiments. Temperature has a strong influence on biological processes. In cold-blooded animals like *Macoma balthica* energy demand increases steeply as it becomes warmer. Earlier research had already pointed out that a higher energy demand in mild winters reduces the number of produced eggs compared to cold winters. In a starvation experiment, subjecting *Macoma balthica* to different temperatures, the Baltic clams were found to be capable of allocating their energy effectively towards synthesis of eggs even at winter temperatures above average.

Besides having an influence on process rates, temperature may also regulate the breeding season. Baltic clams spawn after the water temperature exceeds a certain threshold, and it is assumed that this represents a direct reaction. Baltic clams that live in tidal flats would then possibly spawn earlier than their conspecifics in deeper water, because at low tide the sun warms the flats and much less so the bottom of the gullies. While tracking the reproductive status of Baltic clams no difference in timing was observed between the tidal flats and the gullies. It was however noted that the time during which spawning takes place is long, at least two months. Individuals spawn several times during this period. We suppose that in this way they enlarge their chances to produce offspring at a favourable time, a kind of bet-hedging.

To get an idea of the actual temperature differences between populations, a comparison was made between field sites along the European coast. Baltic clams were collected at a large number of sites and the growth rate estimated from the growth rings on the shells. The expectation was that Baltic clams of more northerly populations grow more slowly due to the lower temperatures. The observed pattern, however, is not unequivocal. This points to the importance of other factors such as food availability. Of the three populations Balsfjord, Wadden Sea and

Gironde the seasonal cycle of body mass and gonad development was estimated. From this, an energy budget could be reconstructed and it appeared that Baltic clams from the Balsfjord devote more energy to reproduction than the more southerly clams from the Wadden Sea and the Gironde. This can mainly be ascribed to the lower temperature, which leaves more energy for body maintenance. Furthermore, it could be deduced that food availability differs between the populations.

The results of the separate parts of this study all point to a high level of tolerance to differences in environmental variables. At the same time genetic adaptations to local circumstances exist. It seems that genetic adaptations exist for certain consistent differences between populations, while superimposed on this, flexible traits enable the individuals to respond to their variable environment.

Do these results imply that the Baltic clam is safeguarded against changes in its environment due to its phenotypic plasticity? The answer is no. Long-term research of the Royal Netherlands Institute for Sea Research at the Balgzand and other areas in the western Wadden Sea shows that since the end of the nineteen eighties the population of *Macoma balthica* is declining. While average density used to be around 100 adults per square meter, now it is merely 10 per square meter. The causes of this decline are still uncertain. On the basis of the results in this thesis it is not probable that direct effects of climate on the physiology of the Baltic clam are responsible. Indirect effects through interactions with other species that respond differently to climate or other environmental factors are more likely. For example, the spatfall of Baltic clams may have severely decreased due to predation by shrimp. Shrimp are particularly numerous on the tidal flats at the time of spatfall after mild winters. However, when conducting research into effects of human-induced changes in ecosystems, in this case climate, it must be realised that human influences are varied. Pollution, eutrofication and not forgetting fisheries all have undoubtedly influenced the current development of Baltic clams and other benthic fauna of the Wadden Sea.