Size-dependent predation risk for young bivalves

Andresen, H.

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Summary

Bivalve shellfish play an important ecological role in intertidal areas. They make up about half of the biomass of animals living in and on the bottom of the Wadden Sea and, among other things, are an important food source for migratory birds. The population size of different bivalve species often fluctuates strongly from year to year. Analyses of long-term observations have shown that the number of young bivalves that survived until August in the Wadden Sea, also termed recruitment, is decisive for the strength of that year-class in the future. After that the death rate of the animals does not change the overall picture. It is especially remarkable, that the number of reproductive bivalves hardly has an influence on the number of surviving offspring. At some point after fertilization in spring, between the planktonic larval phase and the end of the first summer in the sea bottom, a high and variable mortality must take place. Years with extremely good recruitment have given a hint, what might cause this mortality. In summers after very cold winters, the predators of the millimeter sized bivalves – Brown shrimp (*Crangon crangon*) and Shore crabs (*Carcinus maenas*) – arrived late and in lower numbers at the tidal flats. The young shellfish had a head start and had soon grown too large to be eaten by the crustaceans.

In this thesis "Size-dependent predation risk for young bivalves" I studied more deeply the role of body size in this predator-prey relationship. Can size-dependent predation really be one of the main causes of mortality of bivalves in the early bottom-living phase? What is the influence of different winter temperature between regions? How fast do bivalves grow anyway when they are so small, and how big is the influence of bivalve size on the predation rate of brown shrimp exactly?

First I report in **chapter 2** the results of a simulation study. Wadden Sea ecologist Rob Dekker had been following the size development of young bivalves during summers in several years at the Dutch island Texel, and at the same time also observed the sizes of the present crustaceans. Using data of the Baltic tellin (*Macoma balthica*) and the Brown shrimp we tried to reproduce the observed change in the size distribution of the bivalves from one month to the next, under the assumption that the shrimp feed size-dependently on the young, growing bivalves. The model calculations were run with different size preferences by the shrimp and different growth rates of the bivalves. In half of the 14 investigated time periods, it was indeed possible to simulate size distributions that did not differ significantly from the bivalves collected in the field. In most of the cases also the best fitting size preferences and growth rates were realistic. That is remarka-

ble, considering that we assumed that the decrease in bivalve numbers is solely due to predation by shrimp. In contrast, when assuming that the loss of bivalves is random and size-independent, the size distribution simulated only with bivalve growth never fits the observed one.

In the simulation study, growth rates were estimated indirectly. It was plausible, that a considerable part of bivalve mortality was caused by shrimp. In **chapter 3** we report the results of an elaborate field experiment, in which we measured individual growth of bivalves and size selective loss directly. Young bivalves in the field were stained in the sediment with the fluorescent dye calcein. Ten days later samples were taken and under a special microscope with UV-lamp it was measured, how much shell material had been added since the uptake of the dye. This way individual growth of Baltic tellins and cockles (*Cerastoderma edule*) was measured for the first time in this fragile life stage, rather than being calculated from the change in average size. We found that there was much variation between individuals. To find out if the bivalves are preyed upon depending on their size, the staining was combined with a predator exclosure experiment. With small cages, which were covered with a 1 mm mesh screen, a part of the bivalves was protected from shrimp and other predators foraging on the sediment. With the fluorescent mark we could distinguish which bivalves had been present since the onset of the experiment and which had arrived later. We also could check if the protection with a cage possibly changed their growth. The study was conducted in two regions: at Texel in the westernmost part of the Wadden Sea in the Netherlands, and at the island of Sylt, in the North of the German Wadden Sea. In both regions in the first of two rounds of the experiment, fewer bivalves from the lower end of the size range survived in the unprotected sediment.

In **chapter 4** we compared the arrival times of bivalves and crustaceans between the two regions mentioned above. In the year of the field experiment, the bivalves settled at about the same time at Sylt and Texel, while the young shrimp arrived later at Sylt. As the bivalves grew slower at Sylt and at the same time the shrimp had a lower average size than at Texel, the size ratios of predator and prey were very similar at the two islands. In both regions about the same proportion of predator-prey encounters could be fatal for the bivalves. A comparison of Rob Dekkers data from Texel with data that had been collected in coinciding years by Matthias Strasser at Sylt shows, that the bivalves usually settle at the same time in the two distant regions. Only the coldest winter led to a delay at Sylt. At Texel, the arrival of crustaceans differed stronger between years than that of the bivalves. This resulted in very different size relationships. Sometimes the bivalves could outgrow the danger quickly, sometimes they remained in the risky size range. A growth advance for the bivalves did not always lead to advantageous relative sizes. Advantageous size ratios appeared to be a prerequisite, but no guarantee for good recruitment.

In **chapter 5** we investigated feeding rates of Brown shrimp on Baltic tellins in aquarium experiments. We wanted to know what influence the size of the clams has on the time required to find and to handle them. Additional to the shell size, we also varied the densities offered, because at low density searching time has the biggest influence on the feeding rate. At high prey density the handling time limits the number of prey individuals consumed within a certain time. Even at the lowest densities, shrimp were motivated and effective finding their prey. Bigger shells were more difficult to find, because they can burrow deeper. Also handling of the bivalves took longer the larger they were. By these two advantages, the risk to be eaten was about a third lower for the largest than for the smallest shells. That is remarkable, as the "big" bivalves were with 0.85 mm length not even a fourth of a millimeter longer than the smallest animals in this experiment. The consumption by shrimp was disturbingly high. If they could reach this in nature, they could easily erase the whole new year class.

In **chapter 6** we investigated density dependence of the mortality of young bivalves. As described earlier, the number of reproductive adults has little influence on recruitment success. Still, more adults produce more larvae. That means that the relative mortality is higher at high than at low densities of offspring. Through what and when exactly mortality is density-dependent is thus far unknown. Data by Matthias Strasser on Sylt were suitable to analyze them with respect to density dependence. We applied a special statistical analysis that accounts for measurement variation and process variation. We found density-dependent mortality of young Baltic tellins in three of eight cases, but in no case out of six for young cockles. This corresponds to the observation that the cockle population fluctuates stronger from year to year. We had anticipated to detect a pattern when density dependence occurs, and to infer from that on the causes. Yet, the three periods during which the decrease in bivalve numbers was density-dependent had nothing obvious in common. Thus we could not draw conclusions if density dependence is for example related to competition for food among bivalves or to foraging behavior by the predators. Predation rather seemed to add variation. Stochastic variation for example in food availability or environmental factors certainly played an important role, too, in the studied period and region.

Each of the different approaches – pure field observations and their mathematical analysis, field experiments and lab experiments – has its own strengths and weaknesses. Together, they form the picture that size-dependent losses of young bivalves are the rule and that mortality by predation can be substantial. Usually mainly the smallest individuals are affected. It is especially striking, how small changes already can have a strong effect. The timing of the annual reproduction of Baltic tellins is very similar along the European coast; it is adjusted to the environmental conditions. The bivalves hardly have a chance to adapt to an earlier appearance of the crustaceans, because the growth conditions are insufficient.

In this project I focused on the size dependence of the predator-prey relationship. To further improve our understanding of the influence of crustaceans on young bivalves, the feeding rates that can be realized in nature should be investigated further. Prey choice in the presence of alternative prey species will probably play an important role. Further, there is still need for research on density dependence of mortality in the early life of bivalves. In our analysis of field observations there was no sufficient circumstantial evidence for an underlying cause. Possible processes could be investigated experimentally. High mortality at high densities does not necessarily imply that a population can recover at low densities. The population of Baltic tellins in the western Dutch Wadden Sea has decreased so strongly in recent years that their reproductive success is even in danger.