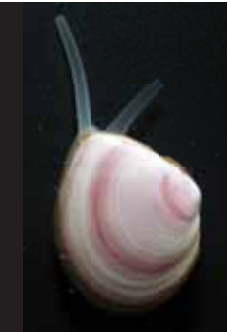


Long term monitoring of *Macoma balthica* populations

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Collecting and analysing long term data series is a fundamental way in which ecologists generate their hypotheses. These hypotheses always evolve around the central question of ecology: what biotic and abiotic factors underlie the patterns we see in species abundances in space and time? Bivalves offer the unique property of revealing their age: the seasonal cycles leave imprints ('rings') on their developing shell, of which the count is an age estimate. Most organisms lack this property and demand intensive tagging and tracking studies. Their rings make bivalves extraordinarily suited model organisms because recruitment and mortality which are the processes underlying abundance in these sessile organisms, can be readily estimated with repeated sampling of cohorts through time. We studied trends in abundance of *Macoma balthica* using three long term data series from different parts of the Dutch Wadden Sea to generate testable hypotheses on what are the most important factors underlying the development of this bivalve species in the Dutch Wadden Sea.

The study areas are the Balgzand tidal flats in the western Dutch Wadden Sea where NIOZ workers have maintained a macrozoobenthos sampling program for more than 40 years now and two other areas, Piet Scheveplaat and Groninger Wad, in the eastern part of the Dutch Wadden Sea. These last two monitoring series as well as three of the fifteen Balgzand stations are part of a national monitoring program of the Ministry of Transport, Public Works and Water Management. In recent years, numerical densities of *M. balthica* have dropped at Balgzand to unprecedented levels (fig. 1A), which was one of the incentives for starting the current comparison, and declines are now also seen at the more eastern study sites. The first two decades of the data series show some trends, too, but they are less concerted between the three areas.

Results of statistical analysis show that recruitment, i.e. initial juvenile density, is the main factor determining *M. balthica* abundance while the observed variability in adult survival only has a small effect. A pattern of an overall fine and occasionally excellent recruitment used to characterize all areas, but during the last five years recruitment has been very low everywhere (fig 1B). Survival of the juveniles is, throughout the entire study period and in all areas, strongly density dependent; at higher density, a smaller fraction of the recruits survives. Trends in adult survival are different for west and east (fig. 1C). At the Balgzand there was a recent dip in adult survival after two decades of stability. In the eastern Dutch Wadden Sea adult survival was more variable and has declined strongly during the last few years.

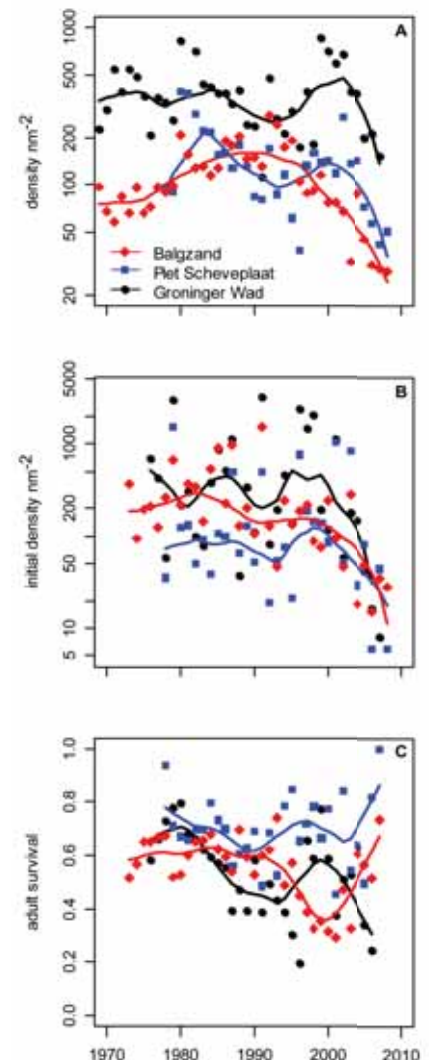


Fig. 1. Time series of *Macoma balthica* at three monitoring areas in the Dutch Wadden Sea. (A) Numerical densities in early spring. Symbols are averages of 15 stations for Balgzand, 3 stations at Piet Scheveplaat and 5 stations at Groninger Wad. (B) Initial densities estimates of *M. balthica* in summer. (C) Adult survival per cohort.

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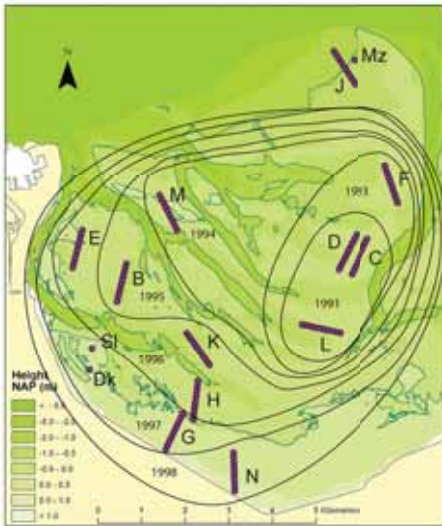


Fig. 2. Map of the Balgzand area with sampling stations and contour lines of the front of increased adult mortality of *M. balthica* calculated per cohort. The sudden increase of mortality happened first at stations C, D and L in the cohort of 1991 and then spread out finally affecting all stations. Stations J and Mz are omitted from the analysis because of the very low abundance of *M. balthica* at these sites.

A detailed spatial analysis of the drop in adult survival at the Balgzand shows that the central eastern study stations were first affected, followed by an eight year

spread over the remainder of the mud-flat (fig. 2). This pattern seems to suggest that a disease may be responsible for the *M. balthica* decline.

Other hypotheses generated by the analysis of these long term monitoring data series are related to increased winter temperature, altered nutrient input into the system and sediment coarsening. The increased winter temperatures may cause epibenthic predators like shrimp and crab to arrive earlier on the intertidal flats and consume a larger fraction of the settled young bivalves than before. Changed nutrient input may have deteriorated food conditions for the recruits.

Alternatively, worse food conditions for recruits may have resulted from the fact that the Wadden Sea sediment has overall grown coarser during the study period.

The combined analysis of three different long term monitoring data series has greatly facilitated the formulation of these hypotheses. Nevertheless, conclusive testing of and discriminating between the various hypotheses requires

experimental and modeling approaches. For example, testing the effects of predator exclusion on the initial density of *M. balthica* can be done in field experiments.

Gathering and analysing these long term monitoring data has proven invaluable for formulating basic, testable ecological hypotheses. Bivalves like *M. balthica* can be taken further in this respect than other species, because their growth rings give an estimate of which cohort they belong to. However, drawing conclusions depends entirely on supplementary modeling and, in particular, experimental approaches. Future work of this type will be able to disclose whether the decline of *M. balthica* in the Dutch Wadden Sea is caused by factors related to disease, climate change, changed nutrient input, and/or sediment composition.

