

Perishing blue mussels and invading aliens – What are the reasons for ecological turnover in the Wadden Sea ?

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Introduction

Failing spatfall and decreasing blue mussel *Mytilus edulis* beds are a source of continuous concern to Wadden Sea ecologists. Following periods of very low blue mussel stocks in the Netherlands and Niedersachsen, blue mussel beds have been strongly decreasing for more than a decade in the northern parts of the Wadden Sea. At the same time, two introduced species, the American slipper limpet *Crepidula fornicata* and the Pacific oyster *Crassostrea gigas* are prospering. The spread of the Pacific oyster especially has attracted the attention of both scientists and the public and – as with the slipper limpet at the time of its introduction – the newcomer is considered as a plague to the Wadden Sea ecosystem and often taken as a reason for decreasing blue mussel beds. Both introduced species preferably settle on blue mussel beds and an increasing portion has turned into dense limpet layers or oyster reefs. Experimental investigations demonstrated negative impacts of oysters and slipper limpets settling on blue mussels and as both introduced species are filter feeders, competition not only for space but also for food can be assumed. However, whether invading oysters and slipper limpets can be considered as a reason for declining blue mussel beds is questionable and it should be considered that the observed reciprocal trends may be coincidental and not a result of competitive displacement.

Decreasing blue mussel beds

The development of blue mussels and invading bivalves in the Wadden Sea of Schleswig-Holstein in fact shows a marked reciprocal trend. At the end of the eighties, blue mussel beds covered the so far highest recorded area of about 1500 ha, which is about 1.15 % of the intertidal mudflats between the Eiderstedt peninsula and the Danish border. Blue mussel stocks decreased after this and were not fully restored after the severe winter 1995/96. In 1999, blue mussel bed area reached 1000 ha and has more than halved since then (Figure 1). Total biomass of blue mussels was estimated at 12,000 t which is only a fifth of the 60,000 t estimated in 1989 (Nehls & Ruth, 2004). Mussel beds vanished in all parts of the Wadden Sea of Schleswig-Holstein and it is especially notable that even in the sheltered areas behind the islands of Sylt and Amrum blue mussel stocks are today very low. These areas traditionally hold extensive and stable blue mussel beds as the islands offer protection against storms with westerly winds which are – apart from very cold winters – generally the main cause of blue mussel beds being lost. Most blue mussel beds in these areas are visited regularly in the course of the blue mussel monitoring program within the Wadden Sea National Park of Schleswig-Holstein and it became obvious that the decrease of blue mussel beds is not caused by single storm events but a continuous process. It appears that even small losses in

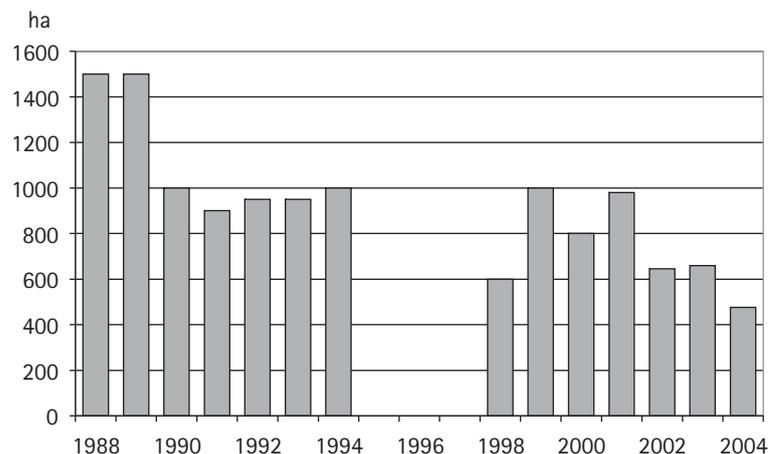


Figure 1:
Development of blue mussel bed area in the Wadden Sea of Schleswig-Holstein.

Figure 2:
Dense assemblages of
slipper limpets cover a blue
mussel bed in the Lister
Deep



blue mussel bed area are not compensated by spatfall, so annual losses accumulate and lead to a permanent decrease.

In this respect, it is particularly interesting that the establishment of new blue mussel beds was a rare event for almost a decade. After the cold winter 1995/96 many blue mussel beds were replenished by a strong spatfall in summer 1996 and from the data of the monitoring program it can be estimated that about 60 blue mussel beds were re-established. In the following years, very limited spatfall occurred and few blue mussel beds were re-established or increased in size. Since 2000 no newly established blue mussel bed have been recorded in the area between Eiderstedt and the Danish border. Spatfall into existing beds was noticed but it was, however, insufficient to allow a stable population.

Prospering invaders

In contrast to blue mussels, Pacific oysters and slipper limpets successfully spread out in the Wadden Sea of Schleswig-Holstein and strongly increased. The Pacific oyster, introduced to North Sea waters in the sixties, is found settling on blue mussel beds since 1991 and since then spread out. Four strong spatfall events since 2001 – facilitated by warm summer water temperatures – have strongly increased the size of the oyster population and this species is now taking over the dominance on many blue mussel beds (Diederich et al., 2005). The species is found on almost all blue mussel beds and all other hard substrates in the Wadden Sea of Schleswig-Holstein but the two main centers of its distribution still have the highest numbers: the Lister Deep behind the

island of Sylt, where oysters started to spread in the vicinity of the local oyster farm, and the tidal flats behind Amrum. These two areas are so far the only places where high densities of oysters on the blue mussel beds occur, whereas in the other parts their density is still below 1 oyster/m². On the blue mussel beds near Amrum oyster density on the blue mussel beds reached 50 oyster/m² in 2005, whereas in the Lister Deep, a mean density of about 500 oysters/m² was recorded with highest values reaching 1000 oysters/m². Some parts of the blue mussel beds have now turned into dense layers of oysters attached to each other forming a very solid structure. The development of the oysters in Schleswig-Holstein indicates at least two different origins: the initial development in the Lister Deep is associated with the local oyster culture, whereas the spread in the southern parts since 2000 reflects the general spread of oysters in the Wadden Sea moving from west to east along the Dutch and Niedersachsen Wadden Sea.

The American slipper limpet, which was unintentionally brought to Europe in the 1870s was introduced to the Wadden Sea of Schleswig-Holstein seventy years ago probably with Dutch oysters to the Lister Deep. Today it is found in all parts of the Wadden Sea wherever a suitable substrate in the lower intertidal and subtidal is available. As blue mussels form a very suitable substrate for settlement, highest densities are found on blue mussel beds which are partly covered and formed into limpet layers (Figure 2). Although the slipper limpet has been regarded as a threat to native species since its introduction to Europe, its spread in the Wadden Sea has led only locally to dominance in the benthic communities



Figure 3:
The race is still open: blue mussels settling on top of Pacific oysters.

which is mainly a cause of cold winters leading to severe mortality and thereby forcing major drawbacks in population development (Thieltges et al., 2004). In the last decade slipper limpets were not much constrained by cold winters and thus strongly increased and maximum values of 300 to 400 specimen/m² were recorded on blue mussel beds in the Lister Deep and locally it forms dense single-species layers.

Competitive displacement ?

At present it looks as if blue mussel beds in the northern part of the Wadden Sea are being replaced by introduced species and forming into oyster reefs and limpet layers. The classical view on this development is to blame the invader. However, no evidence has yet been presented that this is the case (Nehls *et al.*, submitted). There are two facts which strongly oppose the hypothesis of competitive displacement through the invaders. First, the decline of the blue mussel beds occurred in all areas of the Wadden Sea of Schleswig-Holstein, irrespective of the presence of oysters and slipper limpets. Even in sheltered areas such as east of the island of Amrum, blue mussel beds declined and vanished before oysters spread on the remaining fragments of the blue mussel beds. Second, the invaders until now cover only a rather small fraction of the former blue mussel beds. For the Lister Deep we estimate that dense oyster reefs only cover 10 to 20 % of the blue mussel bed area of 1999 and the portion covered by slipper limpets is even smaller. Despite a high density of oysters and slipper limpets, even in the Lister Deep blue mussel biomass still exceeds the biomass of the invaders.

Climate change as driving force

So what are the reasons for declining blue mussel beds? As outlined above, the results from mussel monitoring indicate repeated failures of blue mussel recruitment and over the last six years, no new blue mussel beds were established in the area between Eiderstedt and the Danish border. Decreasing or failing recruitment success has been reported for blue mussels from other parts of the Wadden Sea as well as for other bivalve species. As a rule of thumb, the recruitment success of blue mussels and other bivalves of the Wadden Sea is good after cold winters. This is because the main predators of bivalve postlarvae and spat, shrimps and crabs, move later into the Wadden Sea if water is cold, giving settling bivalves a relief from predation (Strasser, 2002; Beukema & Dekker, 2005). In a warming Wadden Sea, cold winters occur less frequently and so will good recruitment of blue mussels and other native species. In contrast to this, recruitment success of Pacific oysters and slipper limpets appear to be much less affected by predation, allowing these species to successfully reproduce in the presence of potential predators and take full advantage of the warming climate. A warming Wadden Sea will allow the oyster, originating from warmer climates, to reproduce successfully more frequently and winter mortality of slipper limpets will be reduced. Taking this into account, invading oysters and limpets may well take over the remaining blue mussel beds but whether they have the potential to fully replace them is still an open question. However, every single cold winter may change the observed developments and eventually oysters may find

themselves to be a suitable habitat for settling blue mussels (Figure 3).

We conclude that there is yet no evidence that the invaders are the cause of perishing blue mussel beds. The driving factor behind this marked turnover in a highly important benthic community of the Wadden Sea appears to be the changing climate, which facilitates the spread of the invaders but restrains blue mussel reproduction. In this respect, the expected climate change may provoke more than just a change in the dominance within native communities, but allow further invaders to prosper in the Wadden Sea.

The work of Georg Nehls is supported by the Regional Office of the Wadden Sea National Park of Schleswig-Holstein.

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