Figure 1
Ice formation in the intertidal Wadden Sea during the winter of 1995/96

Recolonization Patterns of Benthic Fauna in the Intertidal Wadden Sea after the Severe Winter of 1995/96

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The recolonization pattern of two cold-sensitive species was studied in the intertidal Wadden Sea near Sylt after their populations had been almost completely eliminated by the severe winter of 1995/96. Because of low predation pressure juvenile cockles *Cerastoderma edule* quickly recolonized the area in high numbers during the first summer. In contrast, the polychaete *Lanice conchilega* needed three years until the population reached similar densities as before the severe winter. In the first two years, the coastal *Lanice* population was too small to release sufficient amounts of larvae to recolonize the intertidal fringe of its distributional range. These results stress that populations in the Wadden Sea, in some cases, crucially depend on exchange processes with the North Sea.

Introduction

The strength of the winters in the Wadden Sea may turn out very differently. During mild winters, there is hardly any ice formation, whereas severe winters are characterized by long lasting freezing periods with extensive ice coverage on the intertidal flats (Fig. 1). While most winters of the last decade turned out rather mild, the winter of 1995/96 went its own way. With an average ice coverage of 49 days on the German North Sea coast, it belongs to the ten strongest winters of the last century (Strübing 1996). Here, I report some results of a winter project that was conducted near the island of Sylt in the North Frisian Wadden Sea. A thorough account of the effects of the winter of 1995/96 in the East Frisian Wadden Sea is given in Dittmann (1999).

Such severe winters have a high impact on the Wadden Sea ecosystem, since they cause dramatic population changes for many species. Cold sensitive species such as the bivalve *Cerastoderma edule* or the polychaete *Lanice conchilega* are not adapted to the low temperatures and are usually almost completely eliminated from the intertidal flats and sometimes even from the adjacent shallow subtidal areas. Mussel beds *Mytilus edulis* and their associated flora and fauna are often destroyed by ice-floes that scour the sediment surface. However, severe winters have not only catastrophic effects. Some species such as the peculiar worm *Echiurus echiurus* may be regarded as winners be-

cause they reach unusually high densities after severe winters. These species seem to benefit from reduced predation or competition pressure.

The general effects of previous severe winters have been well described by several authors. In this study the severe winter of 1995/96 is viewed as a natural large scale experiment from which much can be learned about the factors that rule the high numerical variability of many species, which is generally poorly understood. Our study focused on the recolonization pattern of intertidal flats near the island of Sylt by the cockle *Cerastoderma edule* and the polychaete *Lanice conchilega*. Like many other benthic marine species, the life cycle of *Cerastoderma* and *Lanice* includes a planktonic phase of the larvae. The larvae may cover long distances while being transported in the water column for a few weeks until they settle onto the sediment and develop into benthic juveniles. In order to assess the importance of the larval supply for the recolonization process, we sampled the planktonic larvae and the benthic juveniles in the three consecutive years after the severe winter.

Case Study One: the Cockle *Cerastoderma edule*

More than 80% of the adult cockles died on the intertidal flats near Sylt during the winter of 1995/96. However, juvenile cockles immediately recolonized these flats in high numbers in summer 1996. By September 1996, the flats were crowded with up to 3000 cockles per m^2 of about 1cm size (Fig. 2). This rapid recolonization was not unexpected since high numbers of juvenile bivalves were a frequently reported observation after similar severe winters in the past (see references in Beukema et al. 1998). According to one theory, the high reproductive success of bivalves after severe winters is caused by reduced predation pressure by juvenile shore crabs *Carcinus maenas* and shrimp *Crangon crangon*. These important predators of young bivalves are known to appear later on the intertidal flats after severe winters than after mild ones. And, indeed this theory was confirmed by predator exclusion experiments that we conducted after the severe winter and after the following two milder ones. The predation pressure on juvenile cockles was much lower after the severe winter than after the milder winters.

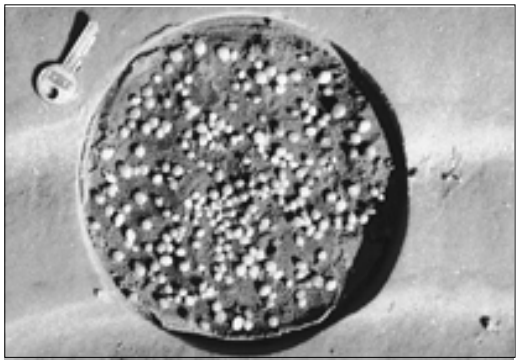

Figure 2
Juvenile cockles *Cerastoderma edule* in September 1996

Another factor could have contributed to the high numbers of juvenile cockles after the severe winter. During cold winters, cockles and other bivalves spend less energy for their metabolism than during warmer winters. The resulting surplus of energy is invested in higher egg production (Honkoop & Van der Meer, 1998) and could have resulted in enhanced larval supply after the severe winter. However, near Sylt the amount of cockle larvae was actually lower after the severe winter than after the following two milder winters, so that this factor was of little importance. Nevertheless, the amount of larvae was obviously high enough to warrant the recolonization.

Case Study Two: the Polychaete *Lanice conchilega*

The sand mason Lanice lives in sand tubes that protrude a few centimeters out of the sediment. The tubes carry very characteristic ragged fringes at the top, which help to catch food out of the water column. After mild winters, Lanice may form dense clusters in the lower intertidal zone (Fig. 3). However, the intertidal Lanice population near Sylt was entirely eliminated by the severe winter of 1995/96. In contrast to the cockle, the recolonization process was slower. In the first two years after the severe winter only a few Lanice were found in the study area. It was not until the third year that Lanice reached a similar density and distribution pattern as before the severe winter. The retarded recolonization corresponded well with the amount of Lanice larvae in the plankton near Sylt. That is, the number of larvae was much lower in the first two years than in the third year. It should be noted that after the severe winter of 1995/96 Lanice was not only eliminated from the intertidal zone, but densities had also sharply decreased in the coastal subtidal areas near Sylt. Apparently, in the first two years the population in the coastal subtidal was too small to release sufficient numbers of larvae to bring about a successful recolonization of the intertidal zone.

Figure 3
Dense clusters of *Lanice conchilega* in the lower intertidal zone

Conclusions

The study of the recolonization pattern of two species that were eliminated from intertidal flats by the severe winter of 1995/96 broadens our knowledge about factors which may govern the population dynamics of benthic animals with planktonic larvae. In case of the cockle, the amount of larvae in the water column was of minor importance. Instead, the rapid recolonization of the intertidal flats was caused by reduced epibenthic predation. This is a factor which acts after settlement. In contrast, for the recolonization of the intertidal flats by the polychaete *Lanice* the factor larval supply – which acts before settlement - was the decisive one.

Although the quick recolonization of cockles was mainly caused by a factor that acted on the benthic life stage, the larval phase was also involved. Without a certain quantity of larvae a successful recolonization would be impossible. Where do these larvae come from? After the elimination of most adult individuals in the intertidal, the recolonization process depends on the production of offspring by the surviving subtidal adults. While cockles are mainly restricted to the coastal zone of the North Sea, the polychaete *Lanice* is also found abundantly further offshore. The retarded recolonization of the intertidal zone by *Lanice* indicates that the near-shore population was not big enough to compensate for the losses caused by the severe winter. Apparently the near-shore population cannot sustain itself entirely but depends to a certain extent on the input from metapopulations in the open North Sea. Therefore, there is no justification for a near-shore boundary of the Wadden Sea.

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