

## LARGE-SCALE DISTRIBUTION PATTERNS OF THE MUSSEL *MYTILUS EDULIS* IN THE WADDEN SEA OF SCHLESWIG-HOLSTEIN: DO STORMS STRUCTURE THE ECOSYSTEM?\*

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### ABSTRACT

The distribution of mussel beds in the Wadden Sea of Schleswig-Holstein was mapped by aerial surveys from 1989 to 1991. The number of mussel beds decreased from 94 in 1989 to 49 in 1990, as a result of severe storms in early 1990. Thereafter only small changes were observed. The mussel beds that remained in 1990 were found only in the shelter of islands; all beds in exposed areas had disappeared between the surveys of 1989 and 1990, leaving large areas without mussel beds. Storms are thus identified as a major factor limiting the distribution of mussel beds to the sheltered parts of the Wadden Sea. Beds in the exposed parts of the Wadden Sea are highly dynamic, whereas beds in sheltered areas may persist over long times. A comparison with distribution patterns of older surveys (from 1937, 1968 and 1978) revealed great similarities with the results of recent investigations, indicating a constant distribution pattern over a long period.

The results are discussed in relation to eutrophication and the structure of the benthic communities of the Wadden Sea. It is concluded that any eutrophication-induced increase of the mussel population would be restricted to the sheltered parts of the Wadden Sea. Storms will largely determine whether the communities of a given area have to compete with mussels, which are the most important filter feeders of the ecosystem. As competition for food is a major factor structuring the benthic communities of the Wadden Sea, it is assumed that storms indirectly affect all other communities, giving deeper-burying, storm-tolerant species a competitive advantage in exposed areas where epibenthic mussels are excluded. The impact of mussel fisheries will be different for persisting and dynamic beds: fishing on persisting beds in sheltered areas may remove the crucial reserve which mussel-feeding birds such as eiders or oystercatchers need in times of low mussel populations.

### 1. INTRODUCTION

The blue mussel *Mytilus edulis* is a major component of the Wadden Sea ecosystem with about a quarter of the average production and biomass of the macrobenthic communities (BEUKEMA, 1983). They occur in dense beds on the surface of the tidal flats where they generate their own substrate. The spat settles on existing beds, on hard substrates (such as oyster shells or stones in deep water) or it may be washed as clumps, to higher parts of the tidal flats (VERWEY, 1952).

The role of the mussels in the Wadden Sea ecosystem can be defined by their activities (oxygen, plankton and detritus uptake, release of nutrients and pseudofaeces) (BARKER-JØRGENSEN, 1990), as a food resource for crabs, birds, man etc. and as a habitat for other animals (ASMUS, 1987). As in other marine ecosystems (e.g. CLOERN, 1982; OFFICER *et al.*, 1982; RODHOUSE & RODEN, 1987) filter-feeding mussels play an important role in the carbon and energy flow. In

parts of the Wadden Sea mussels are so numerous that they may filter an amount of water equal to the whole water body in a few days (DANKERS *et al.*, 1989); phytoplankton biomass and primary productivity were found to be lowered in an area of high mussel densities (CADÉE & HEGEMAN, 1974). As food is supposed to be a main limiting factor for the secondary production of the system, competition can be assumed to be important in shaping the structure of the benthic communities (e.g. VAN DER VEER, 1989). This may especially be true of a bivalve-dominated system such as the Wadden Sea where only three species of filter feeders (*Mytilus edulis*, *Cerastoderma edule* and *Mya arenaria*), relying on the same food resources (KAMERMANS, 1992), contribute about 50% of the total macrobenthic production (BEUKEMA, 1983). Knowledge about the spatial and temporal dynamics of these species therefore seems to be of vital importance for the understanding of ecosystem processes.

A recent increase of the mussel population in parts of the Wadden Sea has been attributed to either

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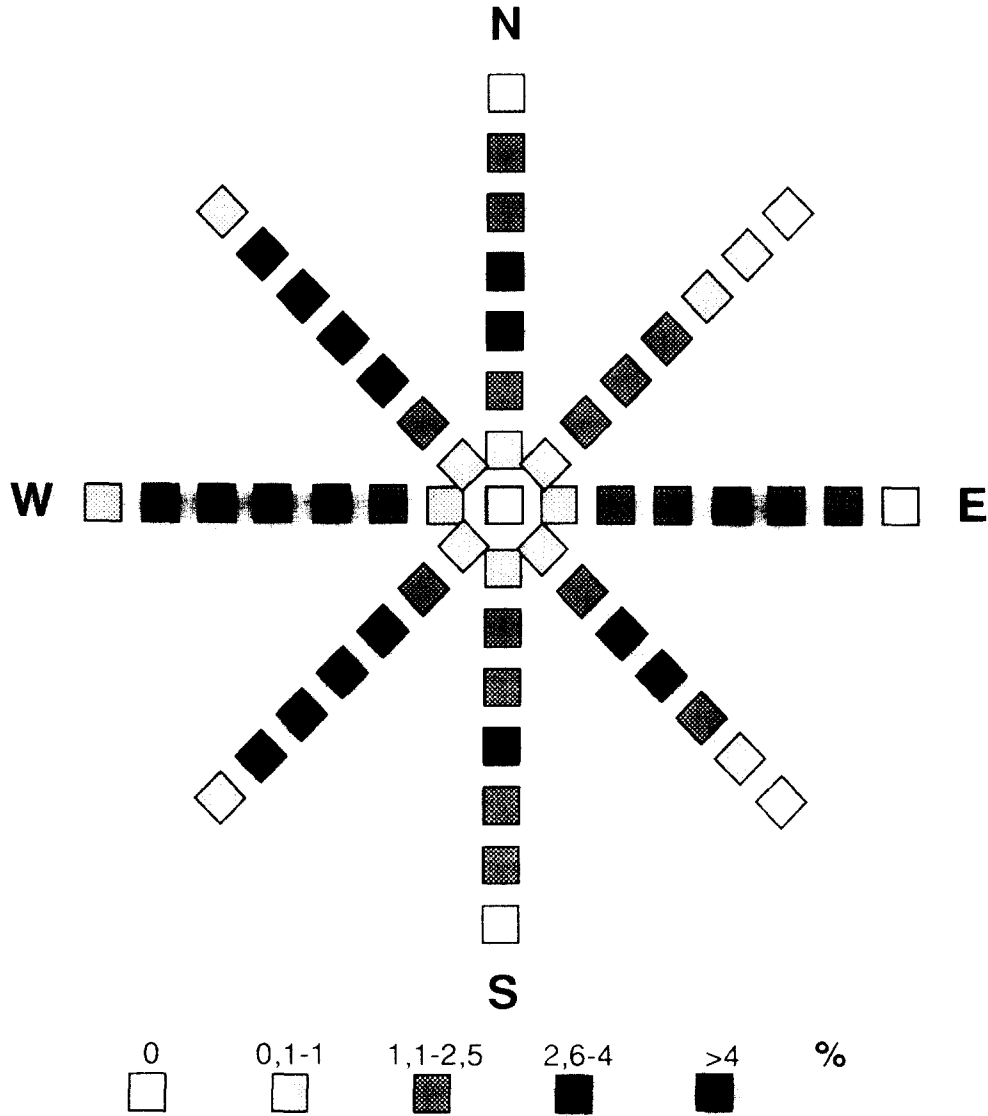


Fig. 1. Compass card of average windspeeds recorded at List, island of Sylt weather station. The graph gives the annual average of the frequency of wind direction and windspeed. Windspeed is given in 7 categories from 1 - 1.5 m·s<sup>-1</sup> in the center increasing to >17.2 m·s<sup>-1</sup> in the outer end of the compass card.

eutrophication or to mussel farming (MICHAELIS, 1987; REISE *et al.*, 1989; VAN DER VEER, 1989) but physical forces also act on the mussel beds. Cold winters and storms have been found to exert severe effects on the mussel beds of the Wadden Sea (*e.g.* VERWEY, 1952). However, little information has so far become available on major effects of abiotic factors, in either space or time.

In this paper we present maps showing the distribution of the intertidal mussel beds of the Wadden Sea of Schleswig-Holstein based on aerial surveys from 1989 to 1991 and compare our results with investigations from the years 1937, 1968 and 1978.

The aim of this study was to analyse the distribution pattern of the mussels in the Wadden Sea of Schleswig-Holstein during a period of mild winters in relation to storm events and to investigate whether any long-term changes in the distribution are detectable.

## 2. MATERIAL AND METHODS

### 2.1. MUSSEL SURVEYS

From aerial surveys with either a single-engine Cessna 172 or a twin-engine Cessna 337 we mapped the distribution of mussel beds in the intertidal and

upper subtidal zones (up to 1 m below the low-water line) in the Wadden Sea of Schleswig-Holstein from the Elbe mouth to the Danish border. The surveys were carried out each autumn after spatfall had occurred and the green algal mats disappeared. We flew during low-tide periods at an altitude of 500 feet and covered all exposed flats (see NEHLS *et al.*, 1988 for flight route). The position of the mussel beds was determined in relation to the structure of the gullies and the extension of the mudflats and subsequently drawn on a map 1:100.000. The extension of the mussel beds was roughly taken into account, but, due to the different angles and distances from which the beds were seen, no quantification of the area covered by mussels could be made.

For examination of long-term trends we used a map given by PLATH (1943) for 1937, and data from two surveys carried out in 1968 and 1978 by Kühlmorgen (unpublished data of Bundesforschungsanstalt für Fischerei). Plath's investigations involved ground-based surveys and gave a rough overview of existing communities (for further information see PLATH, 1943). Kühlmorgen carried out ship-based surveys of the whole Wadden Sea of Schleswig-Holstein, concentrating on mussel beds of commercial interest. These surveys are probably incomplete but they do give a good indication of the situation for the two years covered. We did not use the maps given by DIJKEMA (1989), because his maps were based on aerial photographs taken in different years and thus cannot be used to study year-to-year fluctuations in mussel abundance.

## 2.2. METEOROLOGICAL BACKGROUND

Meteorological data were obtained from the weather station at List/Sylt. The winds in the German Bight predominantly come from the west (Fig. 1). Strong winds are almost always restricted to the western half of the compass card. Westerly winds may have a marked impact on the Wadden Sea of Schleswig-Holstein, which stretches in a north-south direction, because they enhance high tides and induce strong wave-action from the North Sea. On the other hand winds from easterly directions (coming from the land) cause lower tides and less wave-action. The study period included three especially severe storms in the early spring of 1990. Between 25 January and 1 March 1990 windspeeds of 12 Beaufort ( $>32.7 \text{ m}\cdot\text{s}^{-1}$ ) were recorded on 8 days including two with windspeeds  $>50 \text{ m}\cdot\text{s}^{-1}$  ( $=180 \text{ km}\cdot\text{h}^{-1}$ ). The average wind direction of the storms ranged between  $231^\circ$  and  $335^\circ$ , and the average for all hours when mean windspeed exceeded  $15 \text{ m}\cdot\text{s}^{-1}$  was  $262^\circ$ . Windspeeds of 12 Beaufort were recorded on 11 days in the period between the first and the second survey and on 3 days in the period between the second and the third survey.

## 3. RESULTS

In 1989 mussel beds were recorded at 94 localities (Fig. 2, Table 1). Most beds were found close to the low-tide line and some extended into the subtidal zone. With one exception, all mussel beds were found in the northern part of the Wadden Sea of Schleswig-Holstein ( $1700 \text{ km}^2$ ), whereas almost no mussels were found in the area south of the Eiderstedt peninsula ( $870 \text{ km}^2$ ). One year later, in 1990, only 49 mussel beds could be located (Fig. 2, Table 1) and most of the remaining beds were remarkably reduced in extent. The mussel beds situated along the east sides of the islands remained more or less unchanged, whereas those along exposed parts of the coast disappeared or were substantially reduced in size, thus indicating a strong effect of the preceding storms. A third survey in 1991 revealed only minor further decreases in the distribution pattern. Almost no new mussel beds were found between 1990 and 1991.

The comparison of our results with those of PLATH (1943) reveals a remarkable similarity for the main part of his study area (Fig. 2, Table 1). Plath mapped 19 mussel beds in his study area, which covered about 2/3 of the tidal flats north of Eiderstedt, and all were in locations where we still found mussels during our study. For the area south of the island of Föhr we found a distribution pattern very similar to that which existed 50 years ago, although the abundance of mussels now appears to be greater. Again nearly all mussel beds were situated in the shelter of the islands. In the areas east and north of Föhr, where Plath's (l.c.) map show no mussel beds, we mapped up to 9 natural mussel beds (1989). However, as Plath (l.c.) gives no information about the benthic communities of this area at all, it is not clear whether he actually visited it. If only the area south of Föhr is

TABLE 1

Numbers of mussel beds in the Wadden Sea of Schleswig-Holstein and in the study area of PLATH (1943) (see Fig. 2), excluding the area east of the island of Föhr (see text). A mussel bed present in one year and divided into two or more distinct patches in the other years was only counted once. The numbers given in the table therefore do not correspond exactly to the number of mussel beds shown in the maps (Fig. 2).

year	Wadden Sea of Schleswig-Holstein	study area of Plath	source
1937	n.o.	19	PLATH (1943)
1968	30	19	Kühlmorgen, unpubl.
1978	10	0	Kühlmorgen, unpubl.
1989	94	45	this paper
1990	49	23	this paper
1991	53	15	this paper

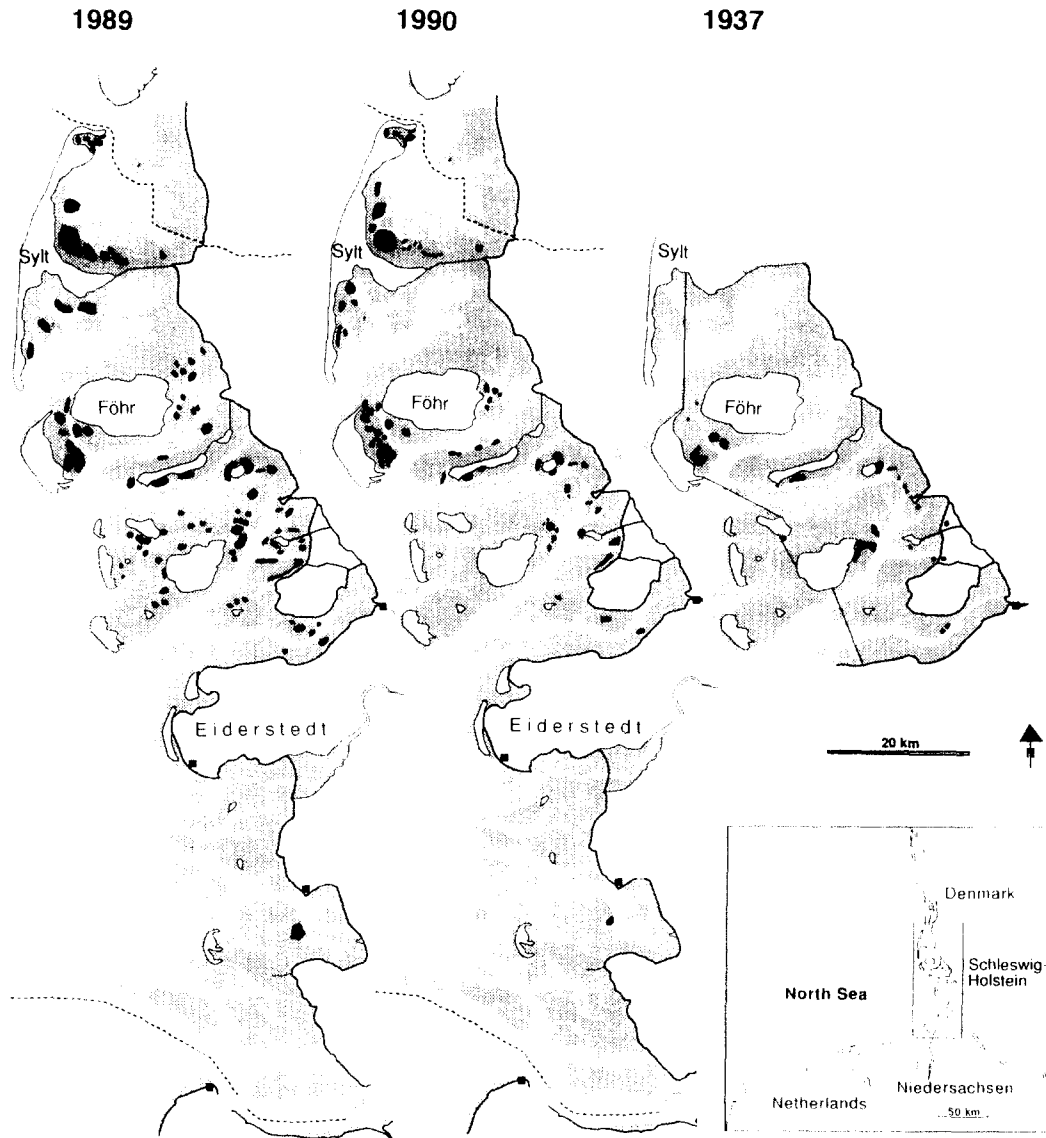


Fig. 2. Location of mussel beds in the Wadden Sea of Schleswig-Holstein as derived by aerial surveys in 1989 and 1990 and as mapped by PLATH (1943) in 1937. The solid line in the map of 1937 indicates the western border of Plath's study area.

regarded, the number of mussel beds found during the surveys of 1989 to 1991 were 45, 23 and 15 respectively, compared to 19 in 1937.

The surveys carried out by Kühlmorgen (unpubl.) closely resemble the described pattern. In 1968, when he encountered a relatively high mussel population (Table 1), mussel beds were found in exposed areas such as west of the islands of Pellworm and Nordstrand and even in some locations where no mussels were present in 1989. However, in 1978, when the mussel population appeared to be at a low level, he mapped mussel beds only in the sheltered areas east of the islands of Sylt and Amrum.

#### 4. DISCUSSION

The results of our surveys and the comparison with earlier investigations reveal high fluctuations in the population of mussels in the Wadden Sea of Schleswig-Holstein (Table 1). The maps of the mussel beds in the Wadden Sea of Schleswig-Holstein (Fig. 2) show a remarkably heterogeneous distribution pattern with most mussel beds concentrated in a few tidal inlets behind the islands, thus leaving large areas without any mussel beds. The mussel population appeared to be at a high level at the time of the first survey in 1989. Most of the mussels originated

from a spatfall in 1987; the older year-classes were missing due to three preceding cold winters with extensive ice-cover on the tidal flats. As the following winters 87/88 and 88/89 were very mild, survival was high and extensive mussel beds could be established on the flats (Ruth, pers. comm. and own observation).

The comparison of 3 successive years, with a decrease in the number of mussel beds between 1989 and 1990 suggests that storms may be the main factor responsible for the observed spatial and temporal variation during this period. Within the Wadden Sea, mussels are the only sessile epibenthic animals with a high biomass that occur on the bare flats. Their attachment to each other with byssal threads, which is strongest in periods of high wave action (PRICE, 1982), offers some protection against the driving force of the sea. However, settling on bare sediments sets limits to this protection. Wave action induced by storms is known to affect mussel populations severely, even on rocky shores which offer far better possibilities for attachment (WITMAN, 1986, 1987; PRICE, 1982). The growth of epiphytes on older beds may increase their risk of being washed away (WITMAN, 1987). In the nearby Baltic Sea storm effects on mussel beds were recorded to depths below 12 m (BREY, 1989; MEISSNER, 1992).

Predation might be considered as an alternative explanation for declining mussel populations (e.g. OBERT & MICHAELIS, 1991), but so far no evidence exists for this hypothesis. Eiders, which are the most important predators of adult mussels on intertidal beds, appear to have only moderate effects (NEHLS & KETZENBERG, in press), so predation cannot be responsible for the loss of complete beds.

Shelter behind the islands seems to be the only effective protection for Wadden Sea mussel beds to persist over the years. Consequently, the storm risk is taken as an important criterion for the quality of mussel cultures in the Wadden Sea (DANKERS *et al.*, 1989). Fishing activities have certainly contributed to the loss of mussel beds. On many beds traces of the dredges were visible in 1989, but this cannot account for the observed distribution pattern in 1990 and 1991, as unfished mussel beds also disappeared. However, it is possible that fishing activities enhance the vulnerability of the beds, since the dredges break up the structure of a mussel bed, even if it is not fully harvested. The fact that the mussel beds found by PLATH (1943), before extensive mussel fishing started, and in 1978 by Kühlmorgen (unpubl.) were also situated in the shelter of the islands supports these findings. Even over the long period from 1937 to 1991 the distribution of the mussel beds appears to be rather similar, although temporal variation is high. Most mussel beds found in the surveys of Plath and Kühlmorgen were still present in our study. New mussel beds that persisted throughout our study period were found almost exclusively near the already existing beds. We thus conclude that apart from erratic spat-

fall and other causes of natural mortality (especially cold winters), storms are a major factor in causing the high fluctuations of the mussel population in the Wadden Sea of Schleswig-Holstein. Unlike spatfall and cold winters, storms act differently from region to region and are, due to the general climate, more predictable than the other factors (see Fig. 1). The consistent distribution pattern over the last 50 years gives a good impression of the continuous effects of strong winds and how they limit the spatial distribution of mussel beds.

The differences observed between the various surveys are thus probably of a short-term, rather than a long-term, nature. In spite of the high mussel population found in 1989, our results do not indicate an increase of mussels in the intertidal zone over the last decades as the surveys of 1990 and 1991 gave comparable results to the survey of 1937. However, our results clearly indicate that any increase in the mussel population will be restricted to the sheltered parts of the Wadden Sea. In the exposed areas such as the southern half of Schleswig-Holstein, mussels cannot settle for long although spatfall may occur regularly (e.g. KÜHLMORGEN-HILLE, 1978). Therefore they cannot take longlasting benefit from the increased food supply. As mussel culturing is restricted to sheltered areas, a possible effect of this activity will not alter the observed distribution pattern. The two areas of the Wadden Sea of Schleswig-Holstein, for which an increase in the mussel population has been postulated, viz. the areas east of Föhr (REISE & SCHUBERT, 1987) and east of Sylt (REISE, 1982; RIESEN & REISE, 1982; but see REISE *et al.*, 1989), are the main centres of mussel culturing in Schleswig-Holstein. The latter investigations were restricted to the subtidal and no earlier information exists about intertidal mussel beds. As mussel culturing plots may persist for decades if placed on suitable sites (MCGRORTY *et al.*, 1990), this may indeed be the source for the observed increase.

The fate of the mussels washed away from the intertidal areas is not clear. At least some of them may survive in the subtidal parts of the Wadden Sea, which would then act as a dumping ground for mussels from the higher flats. Mussels have been found to be abundant in the subtidal parts of the western and northern end of the Wadden Sea and in some parts of the subtidal face even better conditions than in the intertidal (RIESEN & REISE, 1982; REISE & SCHUBERT, 1987; DEKKER, 1989; REISE *et al.*, 1989), but so far no information is available for the central parts where gullies are narrow and tidal ranges and currents high (DIJKEMA *et al.*, 1983). Our study and other studies on smaller areas (DANKERS & KOELEMALJ, 1989; REISE *et al.*, 1989; OBERT & MICHAELIS, 1991) have shown that intertidal beds may persist over long periods, but no information is available on the dynamics of subtidal mussel beds. However, as storms will certainly affect almost all subtidal parts of the Wadden Sea (few gul-

lies exceed 10 m in depth), this does not offer a safe refuge. Storms thus create a heterogeneous distribution pattern of intertidal and subtidal mussel beds, with persistent beds in the shelter of the islands, a highly dynamic pattern in moderately sheltered areas and large areas without any mussel beds in the exposed parts of the Wadden Sea. The last category is found in the central part (Jade to Eider) of the Wadden Sea which is exposed to the west and contains few islands, whereas the first case is more typical of the western (Jade to Den Helder) part, which stretches west to east behind a chain of islands. In the northern part (Eiderstedt to Esbjerg) the living conditions of the mussels will greatly depend on their position in relation to the islands.

Consequently, the impact of mussel fisheries will differ regionally. Mussel fisheries in exposed areas may just take the mussels before they are washed away, whereas fishing in sheltered areas may remove the crucial reserve which mussel-feeding birds such as eiders or oystercatchers need in times of low mussel populations. This should be taken into account for further conservation strategies of the Wadden Sea.

Clearly, the observed distribution pattern of the mussels must have a significant impact on the whole system, most obviously on those species that live in close association with mussels (e.g. ASMUS, 1987). Their distribution will be as steady or unsteady as the distribution of mussels, though the spread of mussel clumps by wave action may extend their distribution locally (THIEL & REISE, 1993). Less obvious, but probably of great significance, could be the effect that the presence or absence of mussels has on those species which compete with them for food. Filter-feeding bivalves are able to deplete their food resources substantially. In tidal areas, where the food is supplied by horizontal transport rather than *in situ* production, the living conditions of filter feeders will vary along gradients in relation to the position to food resources, e.g. tidal inlets (see PETERSON & BLACK, 1987; KAMERMANS, 1992, for experimental evidence). Extensive beds of mussels situated on the border of tidal inlets and tidal flats and depleting the incoming water column (e.g. ASMUS & ASMUS, 1991) may therefore affect populations of other filter feeders even if they live at considerable distances. Endobenthic molluscs living on the tidal flats of the Wadden Sea that are less likely to be affected by storms might thus benefit from exposed areas where mussels are absent. By controlling the distribution of mussel beds in the Wadden Sea, storms would indirectly influence the other benthic communities as well. Responses of the benthic communities to eutrophication (e.g. BEUKEMA, 1991) should therefore vary regionally in relation to the vulnerability to storms.

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