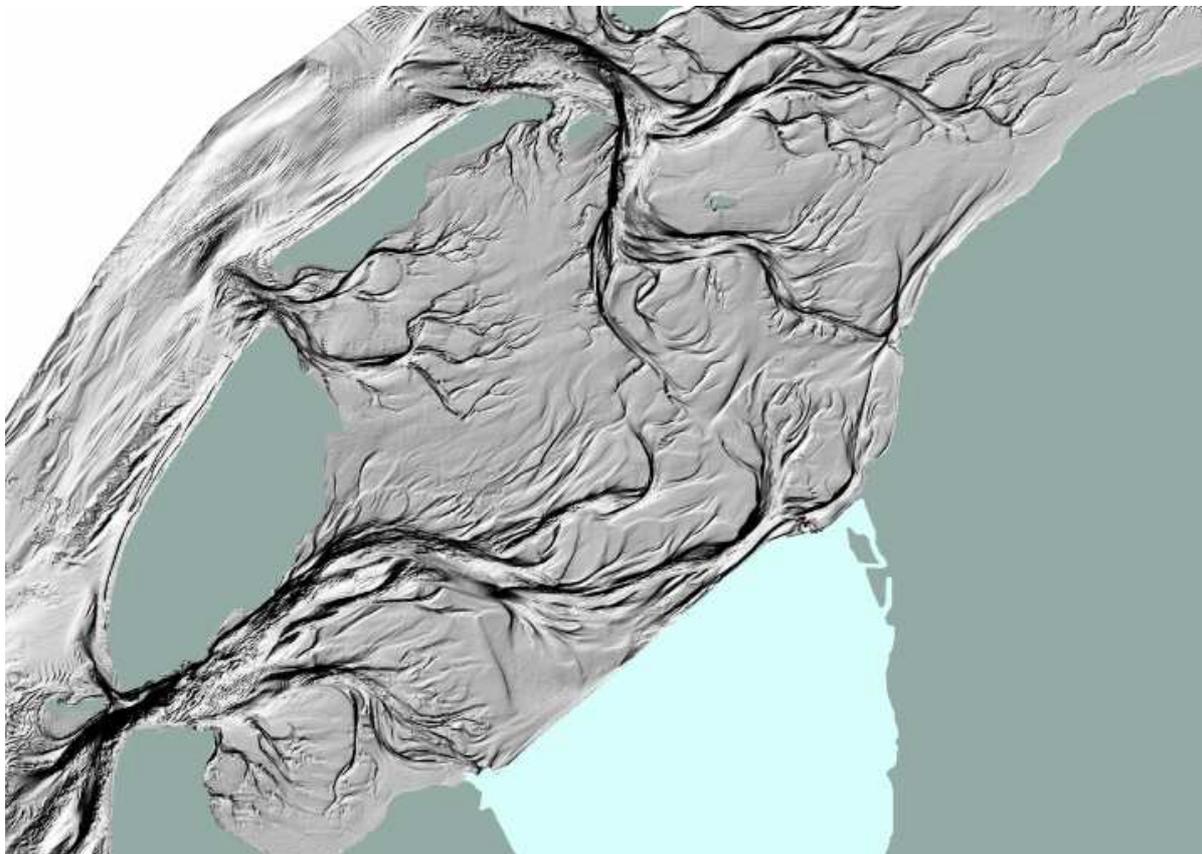


Tidal Basins and Mussel Beds

**An analysis of distributions and developments of littoral mussel beds in
the trilateral Wadden Sea**

Eelke Folmer



**PROGRAMMA NAAR EEN
RIJKE WADDENZEE**

Tidal Basins and Mussel Beds

An analysis of distributions and developments of littoral mussel beds in the trilateral Wadden Sea

Investigation commissioned by “Programma naar een Rijke Waddenzee” (PRW)

By Dr. Eelke Folmer

PRW contact: Dr. Folkert de Jong

2012

A Dutch version of this reports called “*Kombergingen en Mosselbanken - Hoe analyse van kombergingen gebruikt kan worden om ontwikkeling en voorkomen van mosselbanken te begrijpen*” has also been produced. The present report contains appendices which are mainly relevant for practitioners; they are not included in the Dutch version.

Contents

Summary	4
1. Introduction.....	6
1.1. Background	6
1.2. Littoral mussel beds and tidal basins.....	8
2. Distribution of littoral mussel beds in space and time	11
2.1. Mussel bed distributions in space	11
2.2. Mussel bed density through time.....	12
2.3. Occurrence frequency	14
2.4. Comparison of current occurrence frequency with past occurrence	15
2.5. Temporal trends	16
2.6. Population synchronization	17
3. Significance for policy and management	20
3.1. Habitat suitability and stability in occurrence.....	20
3.2. Population dynamics and food availability.....	21
3.3. The relevance of movement of larvae between tidal basins	21
References.....	23

Summary

Introduction

In 2010/2011 a prestudy was performed to investigate the relevance for research and policy of comparing the tidal basins of the trilateral Wadden Sea. Tidal basins are geomorphological units, connected to the open sea, between which there is relatively little exchange of water.

The comparative approach appeared promising. In continuation, the availability and utility of trilateral mussel bed data (i.e. the mussel case) has been examined. A comparison of intertidal mussel bed distributions was selected because of their importance for the functioning of the Wadden Sea ecosystem. It was also expected that an important knowledge gap could be filled by comparing large scale spatial and temporal patterns in the distribution of mussel beds. This report presents the most important outcomes.

We used data from the yearly mussel bed distribution surveys between 1999-2009 from Schleswig-Holstein, Lower Saxony and the Netherlands. Danish data were not used because they are collected in a different way. For a historical perspective use was made of the “Dijkema atlas” with information on the distribution of musselbeds in the 60s and 70s.

Results

Spatiotemporal analysis of the distribution of mussel beds revealed the existence of mussel bed “hot-spots”, i.e. locations at which mussel beds may not always be present but where they systematically tend to re-establish. A comparison of the recent and historical dataset shows that the locations where mussel beds currently tend to occur are virtually identical to the locations where they occurred in the 60s and 70s. Tidal basins that currently contain high densities of mussel beds were also rich in mussel beds in the 60s and 70s.

The distribution of mussel beds appears to be strongly related to the hydrodynamic climate in the tidal basins. Tidal basins that are relatively sheltered from tides and waves have a higher average density of mussel beds than tidal basins that are less sheltered. The same pattern emerges from a more detailed examination within tidal basins which shows that mussel beds tend to occur only in the sheltered parts of highly exposed tidal basins.

The observation that several sheltered tidal basins have low mussel bed densities implies that the hydrodynamic stress is not the only factor limiting mussel bed distributions. The observation might be explained by the fact that these areas are characterized by low primary production.

Analysis of temporal abundance patterns shows that there are large differences in timing of recruitment between tidal basins over large geographical scales. They analyses also show that there are clusters of nearby tidal basins in which recruitment tends to occur

simultaneously. Clusters of synchronizing tidal basins are found in the eastern Dutch Wadden Sea, Schleswig-Holstein and Lower Saxony. The total area of mussel beds and the temporal variation is relatively large in the eastern Dutch Wadden Sea. The reason is that this area has received large expanses of spatfall a couple of times. In Schleswig-Holstein and Lower Saxony the changes (i.e. declines) are more gradual due to the absence of large spatfall events.

The aforementioned clusters of synchronizing tidal basins are separated by physical barriers: tidal basins with important rivers and/or tidal basins which are highly exposed to hydrodynamic forces. This observation suggests that the dispersal of mussel larvae between tidal basins may be the cause of the observed synchronization in recruitment.

The analyses have made clear that the average density of mussel beds and population dynamics depend on the availability of suitable habitat, resource density and the connectivity of subpopulations. A research strategy in which ecological and hydrodynamic processes are integrated on large temporal and spatial scales is necessary to better understand the development of littoral mussel beds. It is likely that this is also the case for other ecosystem variables.

Relevance for policy and management

The findings are relevant for policy and management for the following reasons. Firstly, the analyses offer a (historical) perspective which may be used to generate realistic expectations and conservation targets for the development and distribution of mussel beds. For Natura 2000, judgment of the quality of silt and sand flats depends on the presence and density of mussel beds. The presented analyses illustrate that the absence of musselbeds should not necessarily lead to a negative judgment because the natural environmental conditions may limit the development and persistence of mussel beds. Secondly, this information may be used to evaluate water quality parameters which is a requirement for the Water Framework Directive (WFD) and the Marine Strategy Framework Directive (MSFD).

The regional differences in which recruitment occurs, leads to the question what is special about the conditions in the (Eastern) Dutch Wadden Sea where recruitment occurs regularly and the density of mussel beds is relatively high. The answer to that question could provide insight into possibilities to stimulate the development of mussel beds by human involvement.

Finally, this study has provided insight into the degree of synchronization of populations between tidal basins. The dispersal of larvae between tidal basins is of great interest for populations where the origin of birth is at great distance from where it reaches the adult stage. The hydrodynamic connectivity is important for policy and management because the protection of a particular region can turn out ineffective when recruitment strongly depends on the import of larvae.

1. Introduction

1.1. Background

A tidal basin is a subarea that is connected to the open sea by an inlet and is demarcated by the main land, islands and tidal divides. Tidal basins are useful for comparative research because they are natural units from morphological, hydrodynamic and ecological perspective. Within a tidal basin there is a high degree of uniformity in the water and sediment characteristics. Between tidal basins there are large differences (but also similarities) in physical and ecological conditions, fishery pressure, management and dredging activities. The idea is that much may be learned by comparing tidal basins with respect to natural values and management and the relationships between those aspects. For instance, comparative research may elucidate how differences in the presence and density of musselbeds is determined by natural conditions (currents, wave exposure, sediment conditions) and by human influences (fisheries, dredging, eutrophication).

A comparison is only useful when a large number of tidal basins is considered. This is acknowledged in the “building blocks report” (“bouwstenenrapport”) by the Dutch nature restoration programme “Towards a Rich Wadden Sea” (PRW). It proposes a project to compare all tidal basins (Figure 1) in the entire Wadden Sea on the basis of abiotic features, ecological development and the applied management and the interaction between the three elements, to obtain insight into the ways natural and anthropogenic factors influence the abiotic and ecological states of tidal basins. The comparison involves all tidal basins of the Dutch, German and Danish Wadden Sea. The kind of insight the comparison would provide is relevant for policy and management, in particular for the PRW goals and reporting under the Habitats Directive.

Between November 2010 and February 2011 a prestudy was carried out to investigate the relevance and possibilities to compare tidal basins on the basis of the availability and usability of necessary data. The prestudy provided an overview of:

1. the most urgent policy questions and related scientific questions;
2. the main parameter groups needed to describe the physical, chemical, and biological properties of tidal basins and human use;
3. the availability and quality of existing data.

The prestudy showed that comparative research may provide valuable information to support management and research in the Wadden Sea. Additionally, the prestudy made clear that, overall, there are substantial differences in the “density” at which data are collected between tidal basins and that the smaller tidal basins are underrepresented.

Furthermore, the prestudy made clear that information about human use on the level of tidal basins is scarce.

The prestudy also provided a first step towards an atlas of tidal basins by presenting maps with specific properties of the 39 tidal basins (Figure 1), like average depth and the relative proportion of intertidal mudflats (Figure 2).

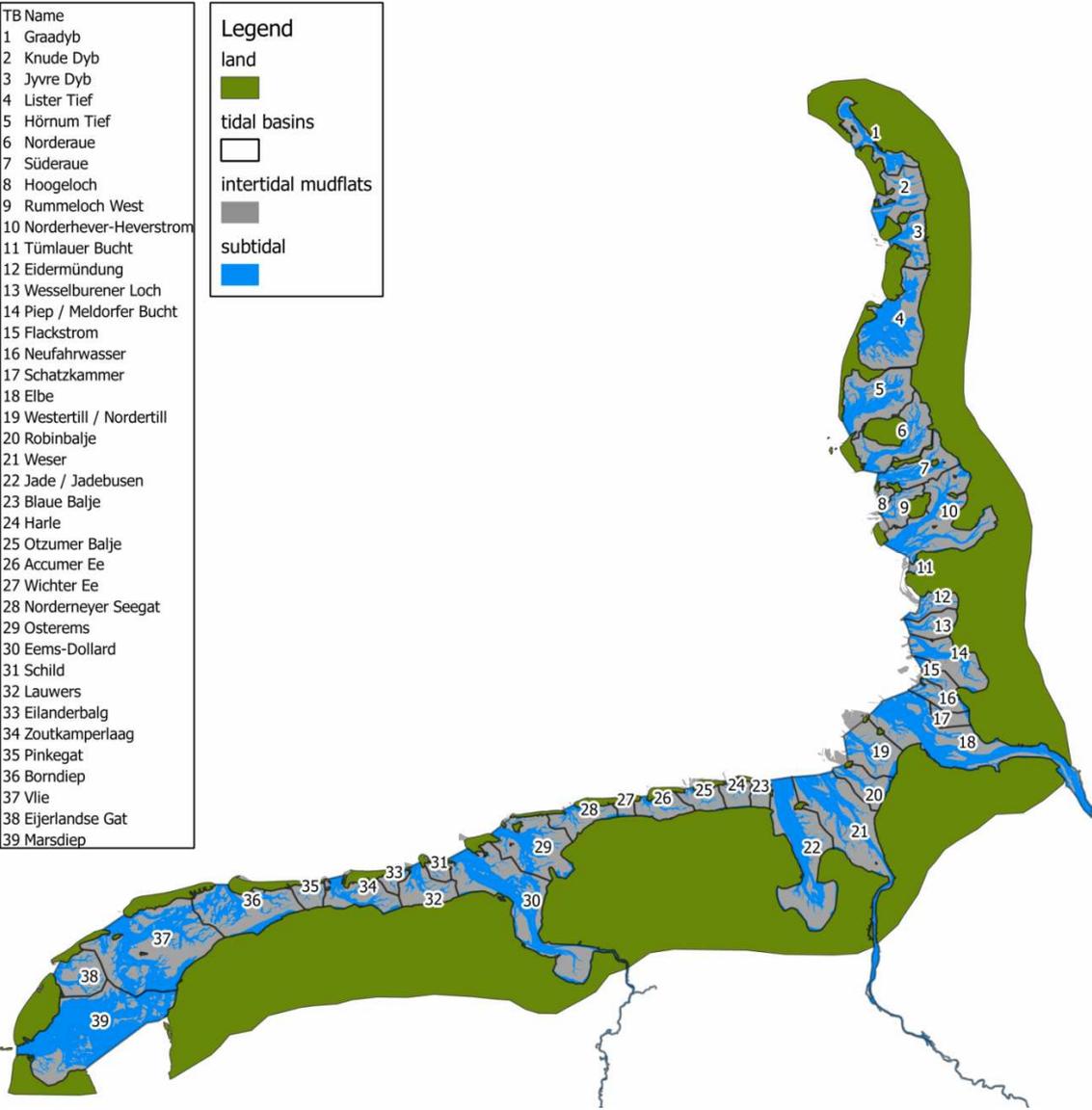


Figure 1. Tidal basins of the Wadden Sea according to Kraft et al.(2011).

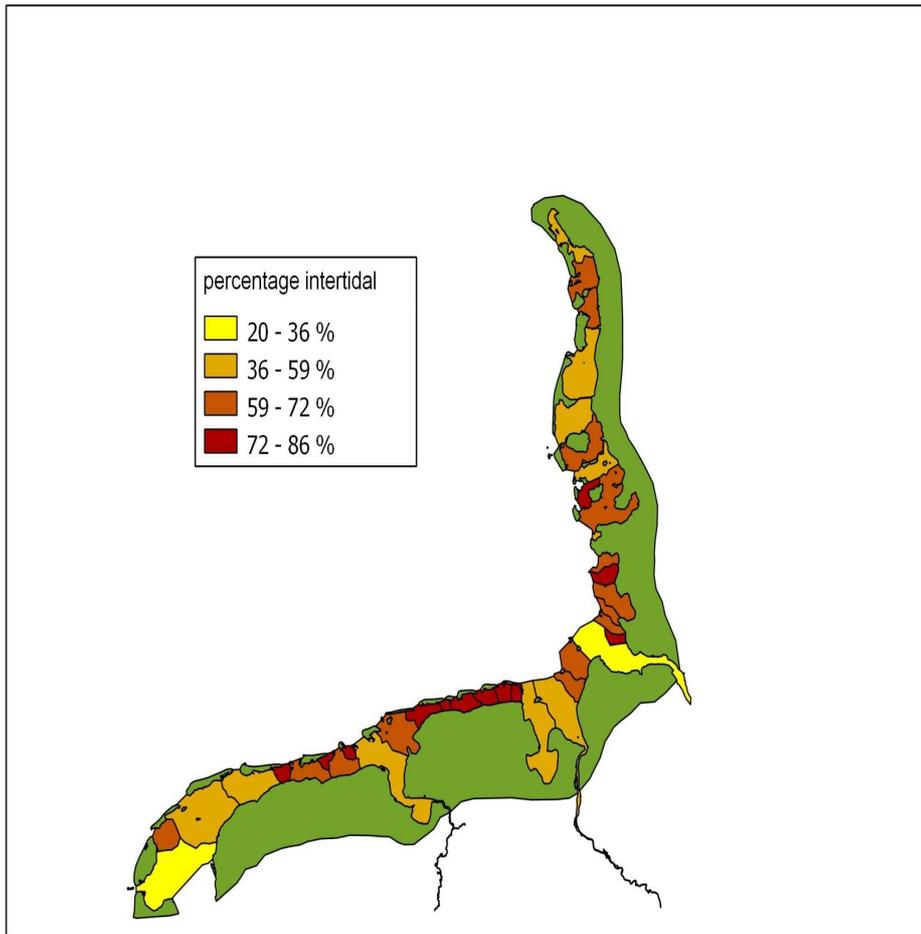


Figure 2. Proportion of intertidal mudflat by tidal basin in the Wadden Sea.

1.2. Littoral mussel beds and tidal basins

To obtain further insight into the viability of the “tidal basin approach”, PRW commissioned the author of this document to elaborate a specific and relevant case on the basis of the prestudy. A case was selected in consultation with PRW and various experts. A comparison of littoral blue mussel bed data (*Mytilus edulis*) was chosen because of its relevance for policy, management and research. Mussel beds are relevant for the following reasons:

- Mussel beds enhance biodiversity in that they provide habitat for a large number of species and because they are a food source for birds and other species (Gosling 1992, Nehls et al. 1997).
- Mussels may have positive impact on water quality by reducing phytoplankton concentrations and eutrophication (Beukema and Cadée 1996).

- Mussels have economic value and are commercially exploited.
- When mussels are abundant, they account for a significant part of secondary production and therefore they are of importance for ecosystem functioning. In addition, mussels may increase rates of nutrient cycling which affects primary production (Asmus and Asmus 1991).
- Mussel beds are ecosystem engineers in that they locally influence sediment properties of the mudflats and thereby affect other species.

The availability of long-term and large scale distribution data, in the trilateral Wadden Sea, enables investigation of the possibilities of a large-scale, tidal-basin approach to the mussel bed distribution problem.

Because of their importance for the Wadden Sea ecosystem, mussel bed habitats are under protection and trilateral targets have been agreed upon. Littoral mussel beds are important elements of habitat types 1140 under the Habitats Directive. Because mussel beds are a food source for various species of birds, they are also relevant for conservation objectives under the Birds Directive. There is a relationship between the density of mussel beds and water quality because mussels filter phytoplankton from the water column. Therefore, mussels are of importance for the Water Framework Directive. The Marine Strategy Framework Directive (MSFD) requires achieving good ecological status. In the case of the Wadden Sea, mussel beds may be of importance. In addition mussel beds are relevant for biodiversity, ecosystem processes and local geomorphological processes. These are some of the criteria under which the Wadden Sea has received World Heritage status. Therefore, the status and development of mussel beds are important to report to the World Heritage Committee (WHC). Lastly, blue mussel fisheries depend on the availability of sufficient seed mussels, as well as suitable conditions for mussel growth.

Firm knowledge and understanding of the development, distribution and functioning of mussel beds is a prerequisite for the development and implementation of policies for the protection of these habitats, as well as for developing sustainable mussel fisheries policies. Adequate assessment of the status of mussel bed habitats is required under the relevant EC Directives, the trilateral cooperation and the World Heritage status. Current knowledge about development and distribution of mussel beds is, however, still insufficient. Particularly, there is much debate and uncertainty concerning the natural spatial and temporal differences in distribution and development and its underlying causes. This is the main reason for PRW to investigate the relevance of comparing the development mussel beds on the scale of Wadden Sea tidal basins.

Comparative research of the spatial and temporal distribution of mussel beds, on the level of tidal basins, may provide insight into the ecology of mussel beds which in its turn may guide management of the Wadden Sea. This report presents the results of the analysis of the

spatio-temporal distribution of musselbeds in relation to properties of tidal basins and discusses the utility and comparability of the existing datasets.

Use is made of data from the period 1999 - 2009 from the Netherlands, Lower Saxony and Schleswig-Holstein. Danish data from this period were not used because they are collected bi-annually with different methods. In addition use is made of the so-called "Dijkema atlas" with mussel bed distributions from the 1960's and 70's.

The research has been achieved in combination with the WaLTER project which aims at developing an optimized monitoring program for the Wadden Sea. I am grateful to Folkert de Jong and PRW who made this research project possible. I thank IMARES, bureau MarinX, NLWKN and Bioconsult & LKN Tönning for making available their data and their kind assistance. Lastly I would like to thank Folkert de Jong, Hein Sas, Norbert Dankers, Katja Philippart and various others for interesting discussions and comments on this report.

2. Distribution of littoral mussel beds in space and time

Yearly maps of trilateral mussel distributions were constructed on basis of the provided data (for data details see Appendix A). This chapter presents the density of mussel beds by tidal basin through space and time.

2.1. Mussel bed distributions in space

Figure 3 presents the average densities of mussel beds for the period 1999 – 2009 in relation to the mudflat surface area per tidal basin. Density is defined as the yearly average percentage mudflat that is covered by mussel beds. The average densities vary considerably between the tidal basins. The highest densities occur in the tidal basins in the eastern Netherlands and in the tidal basins of western Lower Saxony. The densities are relatively low in Schleswig-Holstein, eastern Lower Saxony and in the western Dutch Wadden Sea. In a substantial proportion of these tidal basins mussel beds do not occur at all. In all of these tidal basins, the mudflats are relatively exposed to waves and currents due to long fetch, large tidal amplitude and/or lack of barrier islands. The mussel bed distribution patterns suggest that the rough hydrodynamic climate in southern Schleswig-Holstein, eastern Lower Saxony and the western Dutch Wadden Sea limit the possibilities for mussels to settle and survive in these areas. The influence of hydrodynamic impact on mussel beds in the Wadden Sea has previously – though on a smaller scale - been demonstrated by Nehls and Thiel (1993) and Brinkman et al. (2002).

In the northern Schleswig-Holstein the tidal basins seem to be suitable from a hydrodynamic perspective due to the shelter from barrier islands. However, the mussel bed densities in these tidal basins are lower than would be expected if hydrodynamic impact would be the only limiting factor. This observation suggests that other factors limit the density of mussels. Recently it has become clear that the last years there has been little or no recruitment of mussels and that the quality (mass of flesh per individual) of mussels has decreased (pers. comm. H. Büttger). A possible cause of these observations is that the availability of food resources is limiting. A limitation in phytoplankton may arise when nutrients for phytoplankton growth become limiting or may result from competition with other species. The last decades has indeed shown a decrease in the concentrations of nutrients and phytoplankton in this area while the density of pacific oysters simultaneously increased

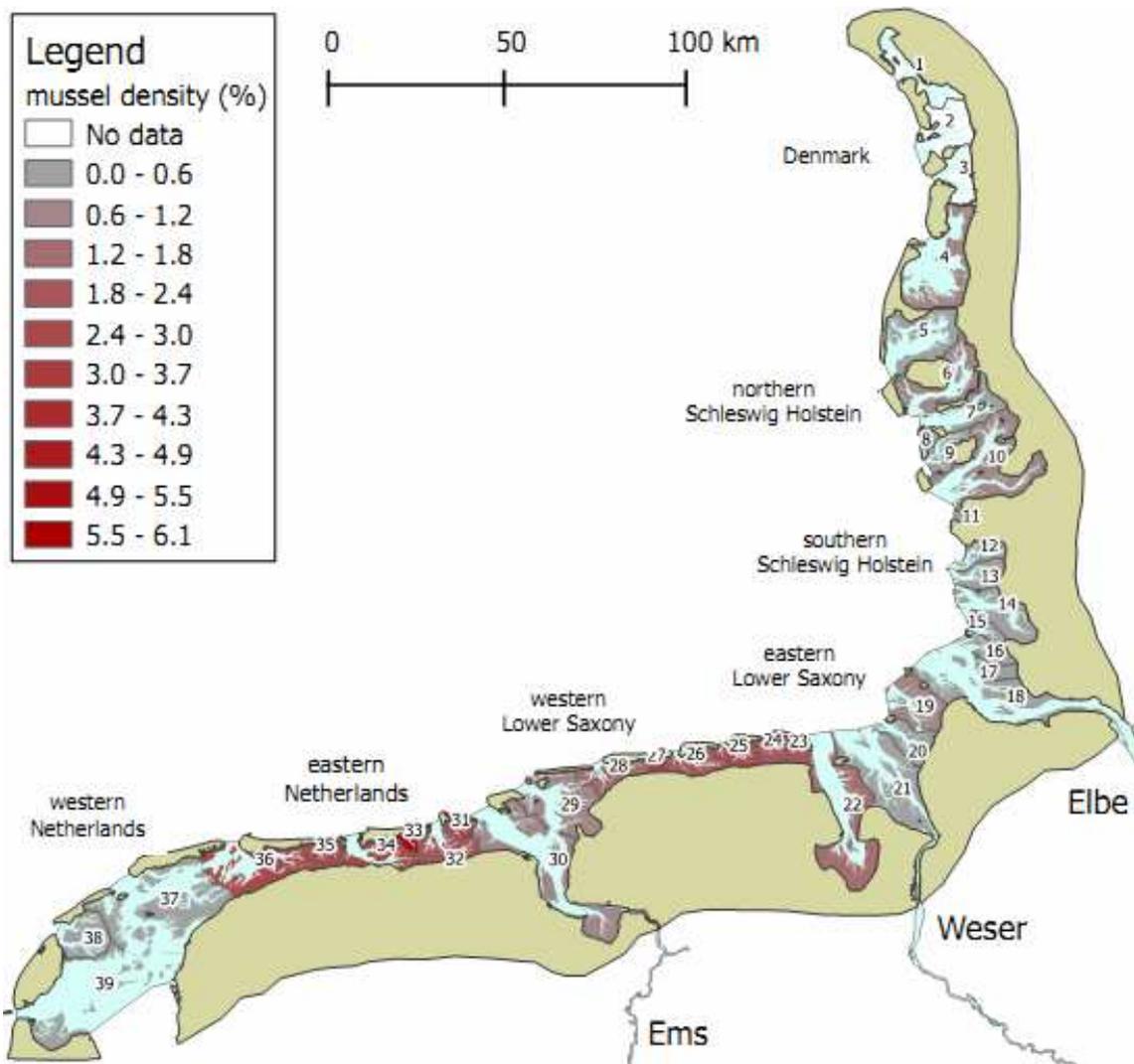


Figure 3. Tidal basins of the Wadden Sea with average densities of mussel beds between 1999 – 2009. Densities are defined as the percentage area mudflat that is covered by mussel beds.

2.2. Mussel bed density through time

Figure 4 presents the densities of mussel beds per tidal basin for the period 1999 - 2009. The figure shows that the densities may fluctuate vigorously and that the fluctuations tend to be largest in those areas where the average densities are highest.

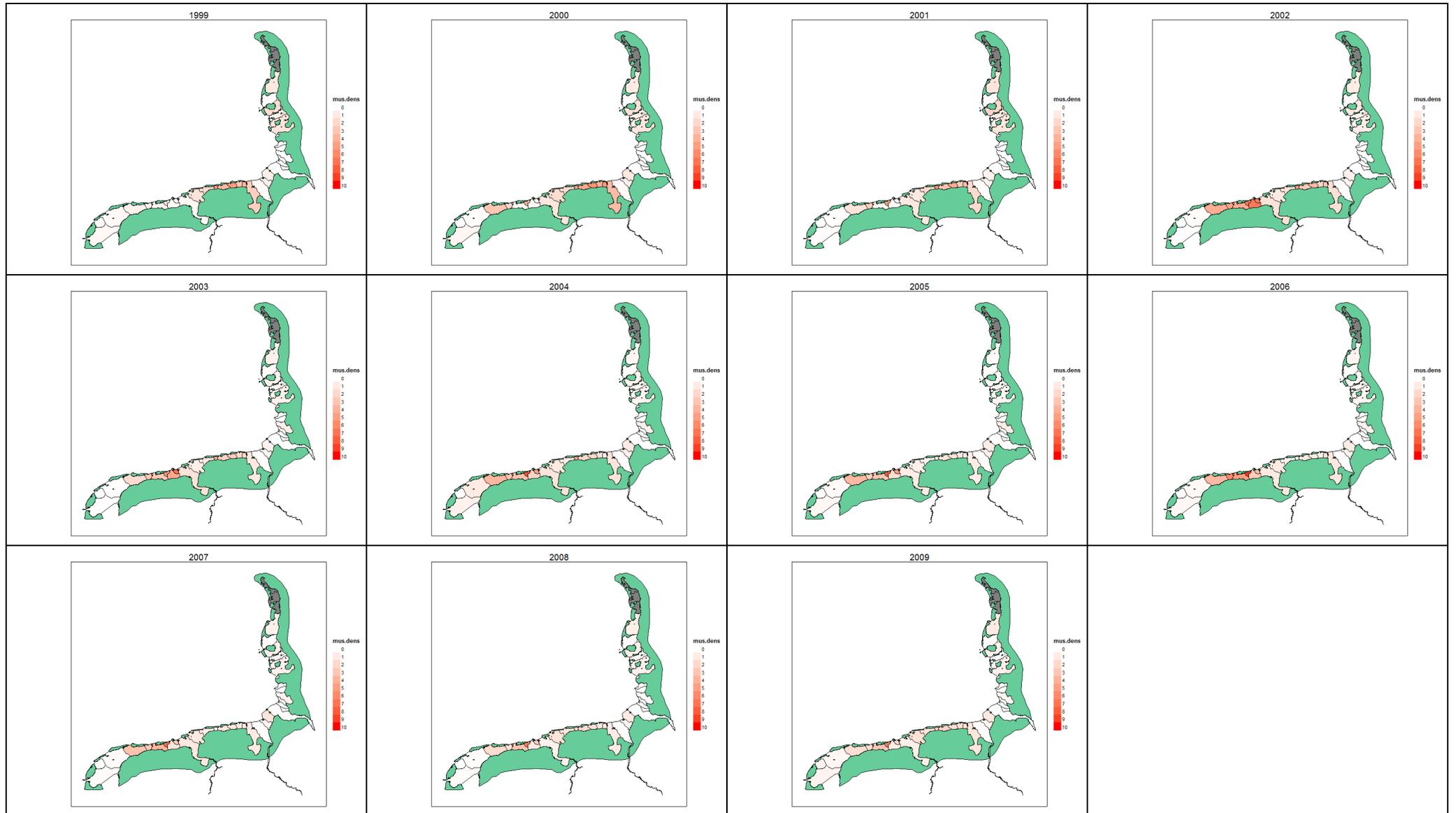


Figure 4. Density of mussel beds per tidal basin for the years 1999 – 2009.

2.3. Occurrence frequency

Occurrence frequency measures how often a location was occupied by a mussel bed in the period 1999 - 2009. The map with occurrence frequency (Figure 5) was constructed as follows: 1. a grid with cells of 250 × 250 m was created to cover the intertidal mudflats; 2. only the cells that intersect with the mudflats were retained. 3. the occurrence frequency is calculated by counting the number of years between 1999 and 2009 that each grid cell intersected with a mussel bed. The patchwork of cells gives a map that presents the occurrence frequency at each location (Figure 5).

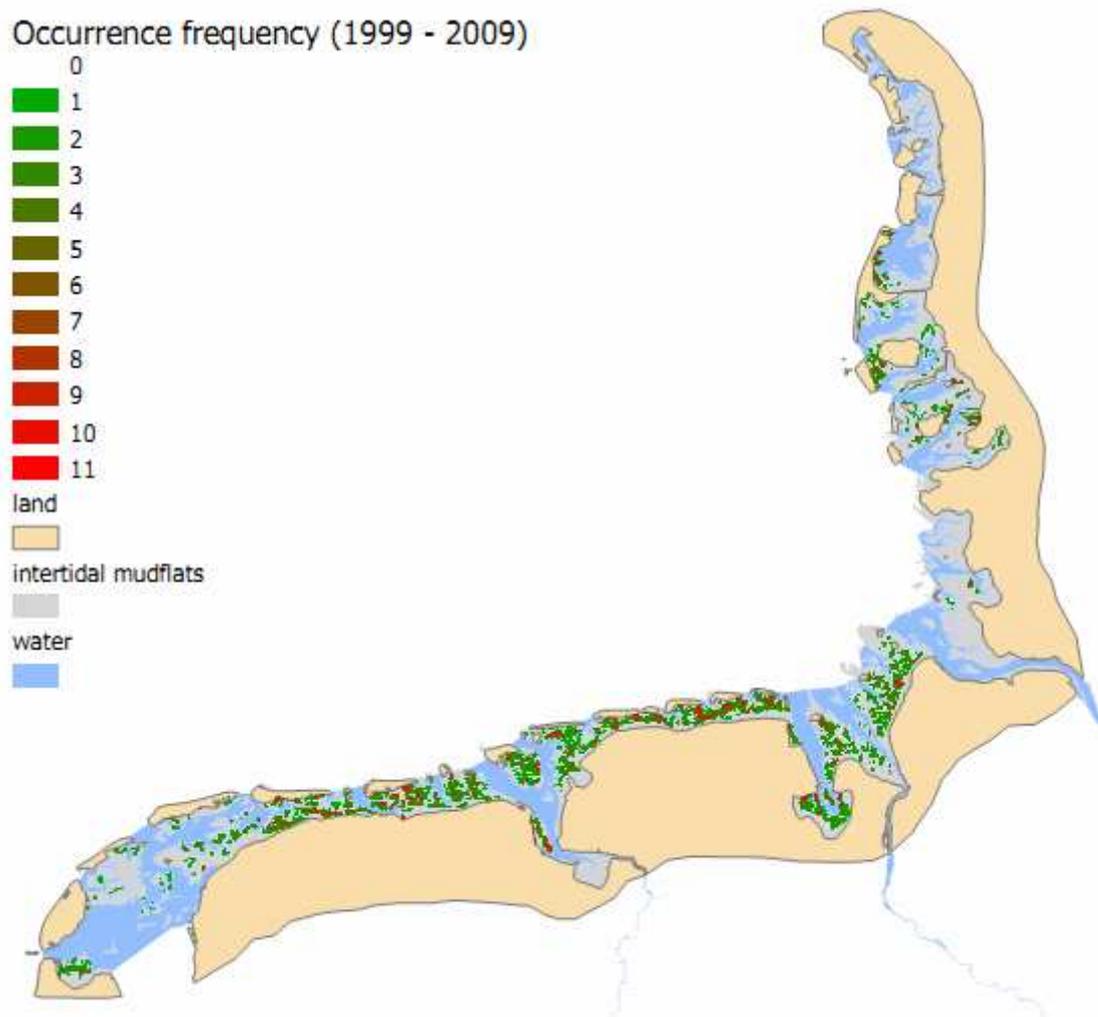


Figure 5. Occurrence frequency of mussel beds between 1999 and 2009. The more often a cell is occupied in the period 1999 – 2009 the more intensely red the cell is coloured.

Figure 5 shows pronounced differences in the occurrence frequency between the tidal basins of the Wadden Sea. Particularly, littoral blue mussel beds most regularly occur in the relatively sheltered tidal basins of the eastern Dutch and western Lower Saxony Wadden Sea while mussel beds are virtually absent in the tidal basins of southern Schleswig-Holstein that

lack barrier islands. The occurrence frequency may be explained by the predominating south-western winds in the Wadden Sea area.

If exposure or hydrodynamic impact were the only limiting factor, a higher mussel bed density would be expected in northern Schleswig-Holstein. Particularly, there seem to be various sheltered locations in northern Schleswig-Holstein at which mussel beds do not occur.

2.4. Comparison of current occurrence frequency with past occurrence

While the current methodology of demarcating mussel beds differs from the methodology applied in the Dijkema atlas (Dijkema et al. 1989), it is possible to compare the spatial distributions globally. The mussel beds from the Dijkema atlas are presented in Figure 6.

The similarities in the distribution patterns of figure 5 and 6 are striking. The locations that were regularly occupied in the period 1999 – 2009 are also the locations where mussel beds occurred in the 60's and 70's. For instance, in the 60's and 70's the density is high in the eastern Dutch and western Lower-Saxon Wadden Sea while mussels did not occur in the exposed areas of southern Schleswig-Holstein. Additionally, the density in northern Schleswig-Holstein was low at that time period too. Lastly it is noted that the density of mussel beds in western Dutch Wadden Sea is low in both the period 1999 – 2009 and in the 60's and 70's.

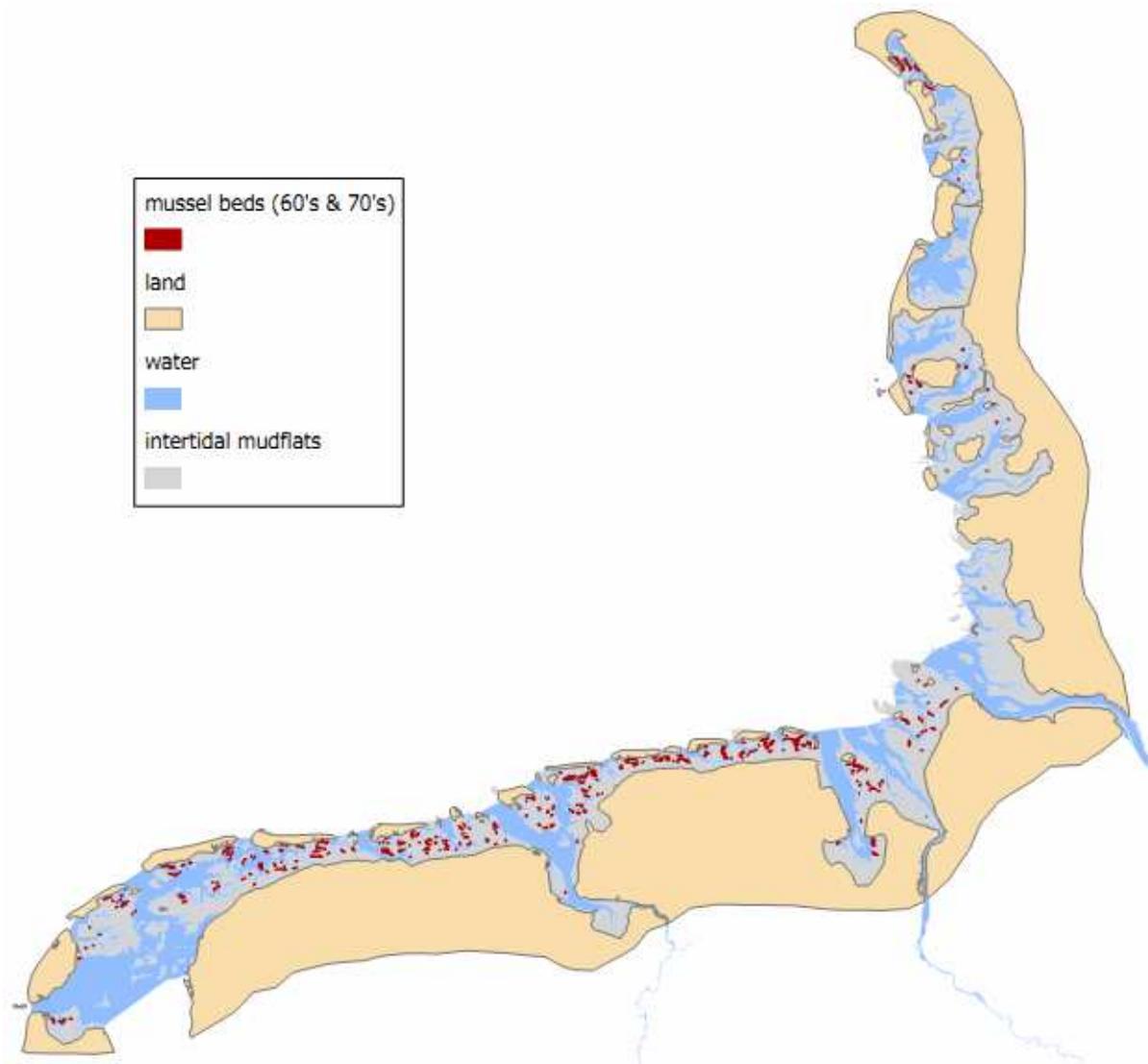


Figure 6. Spatial distribution of littoral blue mussels in the Wadden Sea in the 60's and 70's on the basis of the Dijkema atlas. To illustrate the occurrence more clearly, the size of the mussel beds are plotted somewhat larger than in reality.

2.5. Temporal trends

Trends in area of intertidal mussel beds were determined for the Netherlands, Lower Saxony and Schleswig-Holstein (Figure 7). The combination of the datasets show distinct patterns for each of the three regions. In Lower Saxony and Schleswig-Holstein after an initial increase in 2000 there is gradual decline between 2000 and 2005 after which gradual but slight increase is observed until 2009. In the Netherlands, the population is relatively small in 1999. But the recruitment in 2000 (due to spatfall event in 1999) more than doubles the area of mussel beds. The recruitment event of 2002 (due to spatfall of 2001) brings the area of musselbeds from less than 1000 ha to approximately 3000 ha. After 2002 frequent spatfall

events in the Netherlands result in variable population size. In contrast, the populations in Lower Saxony and Schleswig-Holstein are much less “jumpy”.

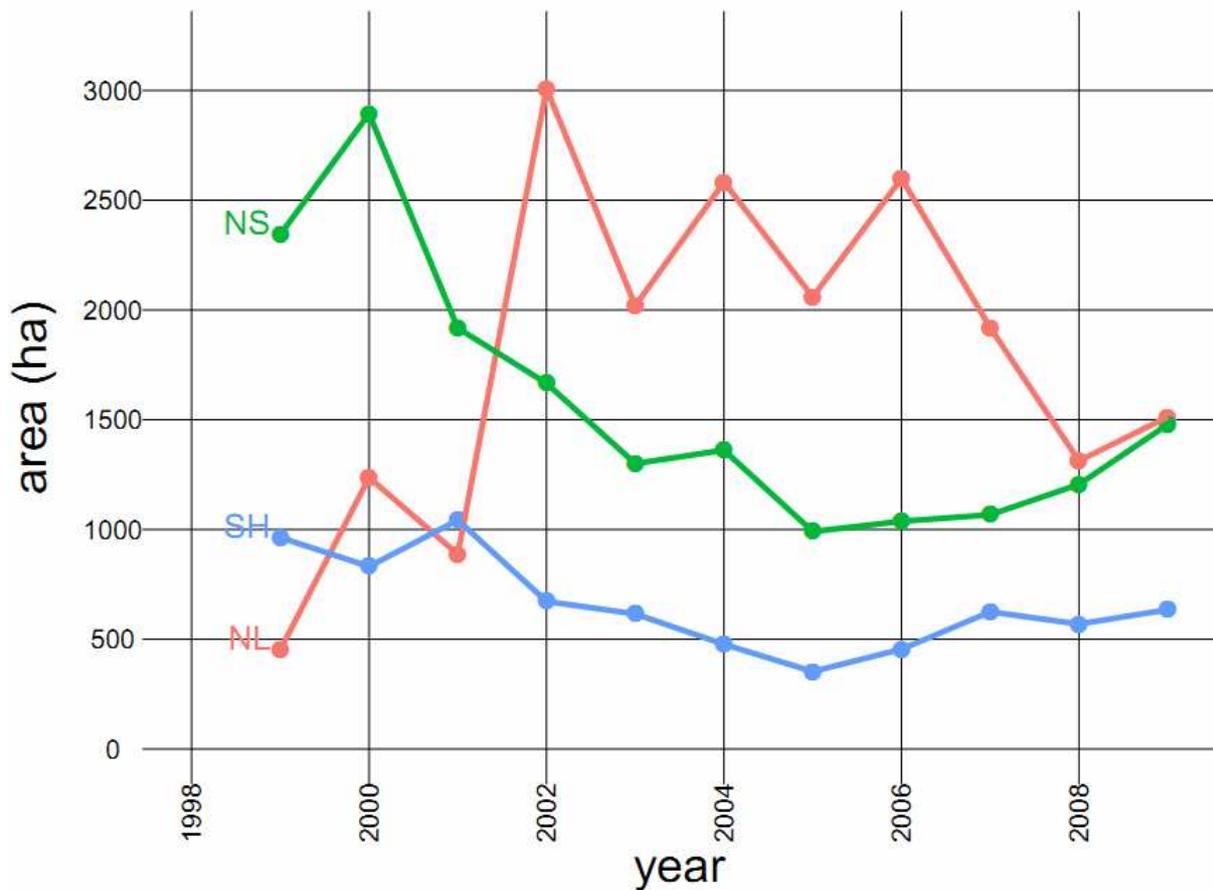


Figure 7. Trends in total area of intertidal mussel beds in the Netherlands (NL), Lower Saxony (NS) and Schleswig-Holstein (SH) for the period 1999 - 2009.

2.6. Population synchronization

From the perspective of the entire population of mussels, the tidal basins in the Wadden Sea are connected via water movement. The reason is that the dispersal of planktonic mussel larvae is mostly a passive¹ process in that larvae can only swim small distances in relation to the currents. Connectivity between populations in various tidal basins are determined by the movement of water between basins in the larval phase. Because the larval phase has a duration of a few weeks, it is likely that a substantial proportion of larvae originates from nearby basins. To obtain further insight into the level of synchronization, the change of mussel bed densities between tidal basins was considered. Synchronization can occur because distribution of larvae takes place between tidal basins but also when similar external factors affect reproduction and survival.

¹ Mussel larvae can influence dispersion by attaching to substrate. When a larvae resides in the water column it is not able to influence its dispersion.

Figure 8 illustrates that tidal basins that are in each other's vicinity more strongly synchronize that when the distances between tidal basins are large. The figure also reveals clusters of tidal basins in which the populations vary synchronously. The first block is made up of TB 4 – 10, the second of TB 22 – 30 and the last block of TB 30 – 36. These results suggest that the causes of population change (and thus of recruitment) within blocks are similar or that the connections between tidal basins within clusters are stronger than the connections between clusters.

The three clusters are separated by large tidal basins with large currents and by tidal basins that are exposed to strong hydrodynamic forces. It is possible that these structures obstruct transport of larvae. Hydrodynamic modelling of water movement between tidal basins can lead to further insight into the potential distribution of larvae between tidal basins.

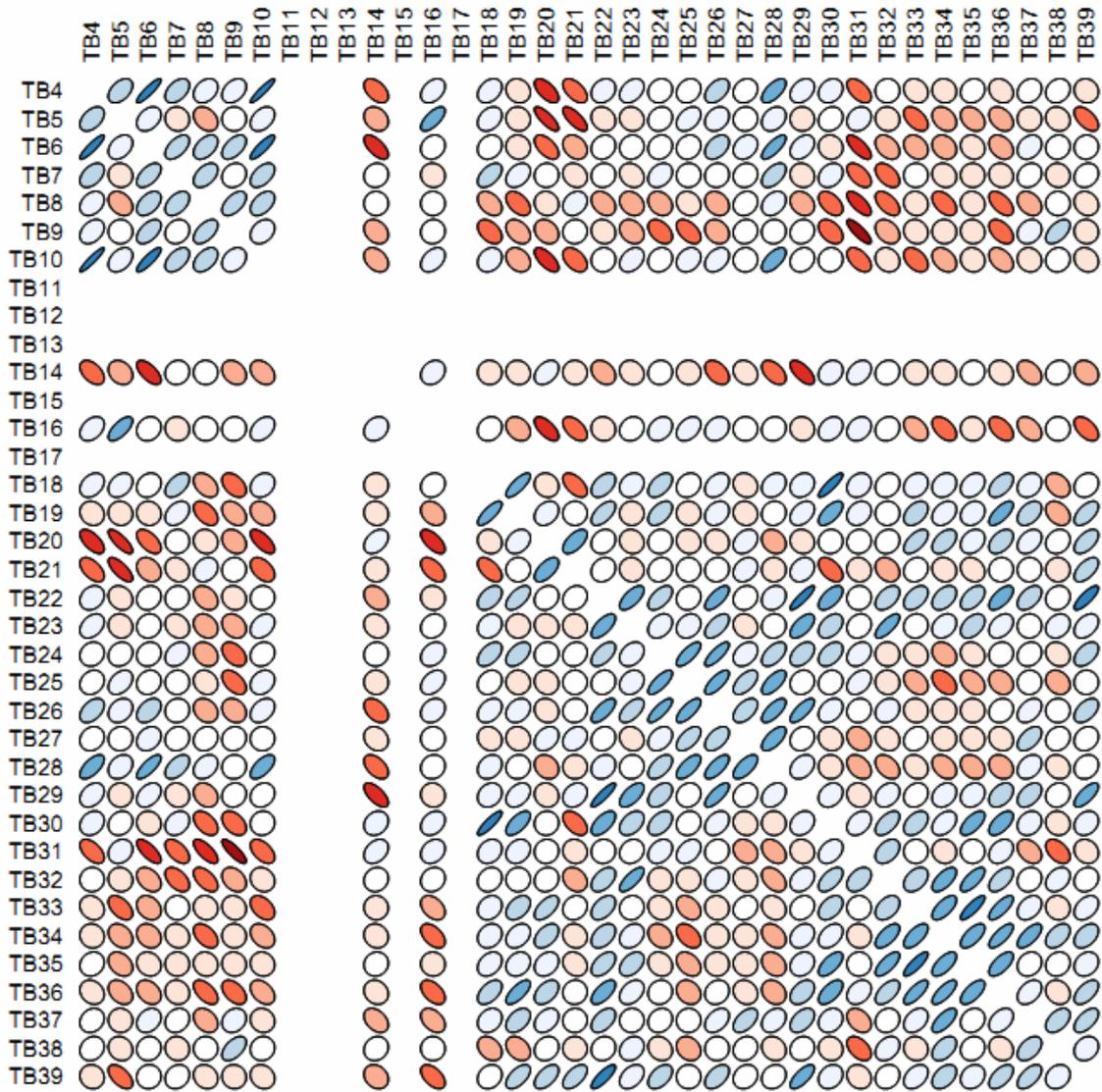


Figure 8. Population synchronization matrix. Ellipse matrix representing the correlations of the population growth rate (i.e. change in area of mussel beds) between tidal basins. In the case of positive correlation, the colour of the ellipse is blue. In the case of negative correlation, the colour is red. The intensity of the colour relates to the (absolute) size of the correlation coefficient. Mussels were not observed in TB11 – 13, 15 and 17. Correlations of the elements along the diagonal are always 1 and not informative (and thus not presented).

3. Significance for policy and management

The dataset, maps and analyses provide information that may guide management decisions concerning conservation of mussel beds and their habitat. This chapter discusses the basic results in terms of their potential use for policy and management.

3.1. Habitat suitability and stability in occurrence

There are large differences in densities of mussel beds between the different types of tidal basins. Particularly, the more sheltered tidal basins in the eastern Dutch Wadden Sea and western Lower Saxony have relatively high densities while in the more exposed tidal basins in southern Schleswig Holstein - which lack barrier islands – mussel beds are virtually absent. The historical (60s & 70s) and current (1999 - 2009) mussel bed distributions show striking similarity in that mussel beds tend to occur at the same locations during the two periods. The similarity of the distribution patterns suggests that the conditions at the locations at which mussel beds occur are consistently suitable. These findings - in combination with results from previous research at smaller spatial and temporal scales by Nehls and Thiel (1993) and Brinkman et al. (2002) – imply that hydrodynamic impact is the main limiting factor for the occurrence of mussel beds. These conclusions are in line with the more detailed distribution patterns within tidal basins presented in this report.

The results further suggest that hydrodynamic stress is not the only factor limiting mussel bed distributions. Particularly, the observation that sheltered locations in the Northern Wadden Sea – characterized by low chlorophyll a concentrations - often do not contain mussel beds suggests that food resources may be limiting.

The fact that hydrodynamic stress and possibly also food resources are important limiting factors for the potential maximum densities of mussel beds, is extremely relevant for policy and management. Particularly, Natura 2000 aims at increasing the quality of mud- and sand flats (H1140) to increase biodiversity and preserve them for roosting and foraging shorebirds and as resting areas for seals. Hydrodynamic stress, which is a natural structuring factor, limits the extent of suitable habitat and therefore the density of mussel beds. The quality assessments of habitat type 1140 (sand and mudflats) is done for the whole national part of the Wadden Sea. The quality status of these habitat types depends on the presence and density of mussel beds. If specific areas or tidal basins are not suitable for mussel bed development – for instance, because of the hydrodynamic regime - this should not lead to a negative scoring. Moreover, according to the N2000 objectives, all blue mussel bed stages must be present. On the basis of this study, it seems like an unrealistic objective that might require reconsideration. Sheltered tidal basins are more suitable for mussel beds than the

more exposed tidal basins and policy and management should take into account the natural suitability of the different regions.

3.2. Population dynamics and food availability

The temporal trends in mussel bed density show clear differences between the Dutch and German regions. Particularly, the densities in the Netherlands vary (both increase and decrease) strongly which is due to the fact that spatfall events occur regularly. Large increases in mussel beds have on the other hand not occurred in Schleswig-Holstein and Lower Saxony. This observation raises the question what is special about the situation in the Dutch Wadden Sea. The answer to that question could provide crucial understanding which may possibly be used to stimulate recruitment in the parts of the Wadden Sea where recruitment is an important limiting factor.

There are various possible explanations for the observed differences. Firstly, there are important differences in the suitability of the habitat. Secondly, there are large differences in the food availability (phytoplankton) of the areas. Particularly, the southern Wadden Sea (NL and Lower Saxony) is relatively nutrient rich which makes the area relatively eutrophic (Van Beusekom et al. 2009) which implies that there is high density of food for mussels. Due to these differences, the potential growth of mussels and the potential production of spatfall are higher in the more eutrophic basins.

In addition to primary production, competition for food with other bivalve species may play an important role for the availability of food. Important competitors are the Pacific oyster² (*Crassostrea gigas*) and American razor clam (*Ensis Americanus*).

3.3. The relevance of movement of larvae between tidal basins

Bivalve populations in the Wadden Sea are open in that larvae disperse over large distances. As a consequence, the densities of mussel beds per tidal basin strongly depend on the import of larvae. This is important for policy and management because it might imply that protection of a particular place may turn out ineffective if the source populations are not protected. On the other hand, it is possible that larvae that are born at a particular location, due to water movement always end up in unsuitable habitat. The potential contribution of a particular mussel bed to the production of larvae that reach the adult stadium – and thus contribute to the total mussel bed population – is therefore location-specific. There is, however, little known about the source and sink populations in the Wadden Sea. This is similar for other bivalve species. To obtain insight into the possible sources and sinks of the meta-population it is important to know local water movement during the larval stadium in

² This concerns an opposite effect of the positive effect that the Pacific oyster may have by forming attachment substrate for juvenile mussels .

combination with the suitability of the habitat and food availability and the presence of predators.

The observed synchronization of the different tidal basins can be considered as an indicator of the level of connectedness between tidal basins. Conceivably, the connectivity within the identified blocks of tidal basins is high such that within the blocks much dispersal takes place. This hypothesis is supported by the observation that the barriers of the blocks are located at locations where physical barriers that prevent movement of water between tidal basins.

References

- Asmus, R. M., and H. Asmus. 1991. Mussel beds: limiting or promoting phytoplankton? *Journal of Experimental Marine Biology and Ecology* 148:215–232. doi: 10.1016/0022-0981(91)90083-9.
- Beukema, J. J., and G. C. Cadée. 1996. Consequences of the Sudden Removal of Nearly All Mussels and Cockles from the Dutch Wadden Sea. *Marine Ecology* 17:279–289. doi: 10.1111/j.1439-0485.1996.tb00508.x.
- Van Beusekom, J. E. E., P. V. M. Bot, J. Carstensen, J. H. M. Goebel, H. Lenhart, T. Pätsch, T. Petenati, T. Raabe, K. Reise, and B. Wetsteijn. 2009. Eutrophication. Thematic Report No. 6. In: Marencic, H. & Vlas, J. de (Eds.). Thematic Report, Common Wadden Sea Secretariat, Trilateral Monitoring and Assessment Group, Wilhelmshaven, Germany.
- Brinkman, A., N. Dankers, and M. Van Stralen. 2002. An analysis of mussel bed habitats in the Dutch Wadden Sea. *Helgoland Marine Research* 56:59–75.
- Dijkema, K. S., G. Van Thienen, and J. G. Van Beek. 1989. Habitats of the Netherlands, German and Danish Wadden Sea. Research Institute for Nature Management, Veth Foundation, Leiden, Texel.
- Gosling, E. G. 1992. *The Mussel Mytilus*: Ecology, Physiology, Genetics, and Culture. Elsevier, Amsterdam.
- Kraft, D., E. O. Folmer, J. Meyerdirks, and T. Stiehl. 2011. Data Inventory of the Tidal Basins in the Trilateral Wadden Sea. Page 43. *Programma naar een Rijke Waddenzee*, Leeuwarden. Retrieved April 12, 2012, .
- Nehls, G., I. Hertzler, and G. Scheiffarth. 1997. Stable mussel *Mytilus edulis* beds in the Wadden Sea - They're just for the birds. *Helgolander Meeresuntersuchungen* 51:361–372. Retrieved July 6, 2011, .
- Nehls, G., and M. Thiel. 1993. Large-scale distribution patterns of the mussel *Mytilus edulis* in the Wadden Sea of Schleswig-Holstein: Do storms structure the ecosystem? *Netherlands Journal of Sea Research* 31:181–187. doi: 16/0077-7579(93)90008-G.

Annex: Institutes and data collection

This section describes the protocol that is agreed upon by the Dutch, German (Lower Saxony and Schleswig-Holstein) and Danish institutes that are responsible for the collection of mussel bed distribution data in the Wadden Sea. It furthermore describes how the collaborating institutes collect mussel bed data in practice. It presents an overview of the data that have been made available for the current investigation. Finally, this section presents the “Dijkema atlas” (1989), constructed on the basis of aerial photographs of the entire Wadden Sea in 1969 and 1976.

Current protocol of demarcating littoral mussel beds

In 2002, a common definition of mussel beds was developed to facilitate trilateral comparisons (*Blue Mussel Monitoring. Report of the Second TMAP Blue Mussel Workshop on Ameland, 8-10 April 2002. 2002, Herlyn 2005*) (

Fig). The definition of mussel beds is based on structure:

‘A mussel bed is a benthic community structured by blue mussels. It may consist of a spatially well-defined irregular collection of more or less protruding smaller beds, which may be called patches, separated by open spaces. This description also includes young beds with a high abundance of small mussels. The described structure may not be so distinct in young beds or just settled beds (spatfall).’ (from Wadden Sea Quality Status Report 2004 2005)

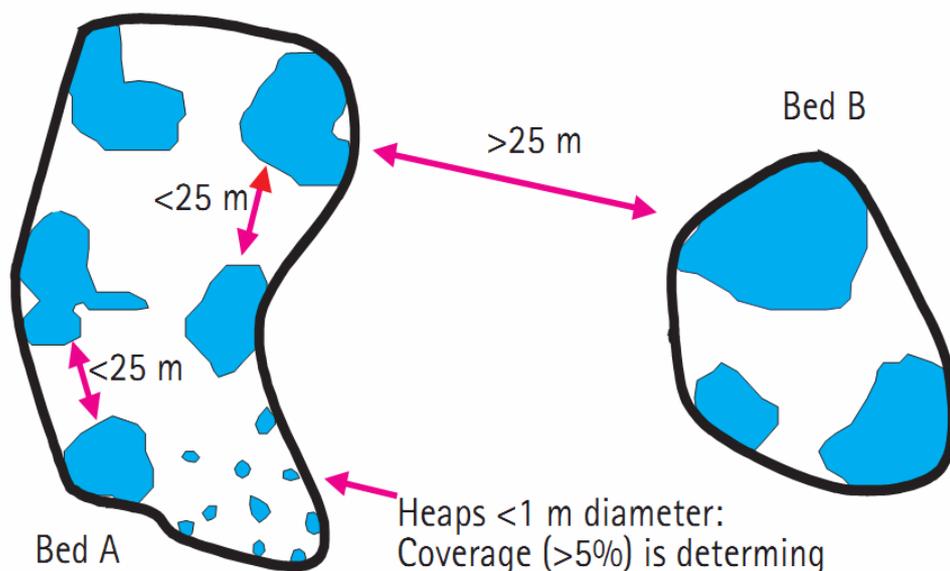


Figure A1. Visual representation of the demarcation of mussel beds (from Quality Status Report 2002).

In most parts of the Wadden Sea, the pacific oyster (*Crassostrea gigas*) has been increasing in density since the late 1990s and is occupying original mussel beds (Reise 1998, Diederich 2005, Nehls et al. 2006, Van Stralen et al. 2012). The consequence is that the observed beds often contain a mix of mussels and oysters. The relative contribution of the pacific oyster and mussels to the shellfish beds are measured in terms of dominance. Details of how the mix of oysters and mussels are determined by the various institutes is described below.

Data availability and methodology per institute

This section describes the littoral mussel bed data sets that are made available by the collaborating institutes. Despite the protocol agreed upon in 2002, the different institutes maintain slight differences in their methodology which are described under the following sub-sections.

The Netherlands: IMARES

Since 1995, IMARES (Institute for Marine Resources & Ecosystem Studies, Texel, NL; previously RIVO) and MarinX have on a yearly basis, in spring, mapped all the littoral mussel and oyster beds in the Dutch Wadden Sea. During low tide, researchers equipped with a GPS walk around the beds to demarcate the contours after which they are imported into GIS. Characteristics of the beds, such as percentage cover of mussels and oysters, are also recorded. Within the available time, as many as possible locations are visited which implies that not all mussel bed locations will always be visited. To choose the locations to be visited by foot, an educated guess of which locations are likely to contain mussel beds is made on the basis of earlier surveys and inspection of the area from an airplane flying at an altitude of 500 m. For unvisited locations, use may be made of the dataset from the year after. For example, if in year 2008 a 2-year old mussel bed is found at a particular location which was not recorded in 2007, the 2007 dataset is updated to include that mussel bed.

NL: When the cover of mussels is greater than 5% and the cover of pacific oysters is less than 5% the bed is called a pure mussel bed. When the cover of oysters is greater than 5% and the cover of mussels is less than 5% the bed is called a pure oyster bed. When the cover of both oysters and mussels are each greater than 5%, the bed is denoted a mixed bed.

IMARES³ and MarinX⁴ have made available mussel bed distribution data for the period 1999 – 2009. These data may be used under the condition that there will be open communication about the way in which the data are used.

³ In the name of Jeroen Jansen and Karin Troost.

⁴ Marnix van Straalen

Lower Saxony: NLWKN

Niedersächsischer Landesbetrieb für Wasserwirtschaft Küsten- und Naturschutz (NLWKN⁵) are responsible for data collection in Lower Saxony. NLWKN willingly cooperates and have shared mussel bed distribution data.

The NLWKN has since 1999 mapped mussel beds based on aerial photographs in combination with ground truthing. Aerial photographs and ground-surveys are used to determine the location, size and shape of mussel beds. Photographic surveys are carried out in spring. The reason that photographic surveys are carried out in spring is because the surface covered by mussel beds can increase through recruitment during the summer months. Additionally, mussel cover will often decrease during autumn and winter due to storms and/or ice-scour. The mapping period is between March and July which is a relatively stable period. A stereoscope is used to recognize intertidal mussel beds on aerial photographs. Mussel bed distribution data collected between 1999 and 2009 have been made available for trilateral comparison.

Based on the structure and ground truth, the cover of mussels inside the beds is always greater than 5% in all the identified mussel beds.

Schleswig-Holstein: Bioconsult & LKN Tönning

The Schleswig-Holstein Wadden Sea National Park is managed by the Regional Office of the National Park Service (LKN Tönning). Mussel bed inventories are carried out by Bioconsult⁶. Bioconsult willingly cooperates in the current project and their data have been shared by permission of LKN Tönning⁷.

Bioconsult has made available data in the form of shapefiles from 1998 – 2010 and shapefiles based on 1958 and 1989 aerial photographs. In Schleswig-Holstein the data collection is a combination of aerial photographs and on-location sampling. Aerial photographs are recorded in autumn and therefore potentially include new spatfall of the year.

All the observed beds contain mussels but the percentage-cover of mussels is unknown.

Denmark

DTU Aqua National Institute for Aquatic Resources is part of the Technical University of Denmark. DTU Aqua is responsible for monitoring of mussel beds in the Danish Wadden Sea.

⁵ In the name of Gerald Milat.

⁶ Contact person is Heike Büttger.

⁷ In name of Kai Eskildsen.

The method of data collection that DTU applies, differs from the method applied by the German and Dutch institutes. Particularly, mussel beds are identified on aerial photographs (with resolution 0.3×0.3 m) by means supervised classification resulting in a map of classified pixels. The resulting map is basically different from the polygons map as constructed by the method presented in section 0 (combination of aerial photographs and walking around the beds). Figure presents the resulting maps from the two methods. It is concluded that the Danish data are not comparable with the Dutch and German datasets in their current form. There might be possibilities to harmonize the Danish dataset. This, however, requires discussion and close cooperation with the Danish partners.

Blue mussel data from 2000, 2002, 2004, 2006 and 2007 have, however, been made available for the current project.

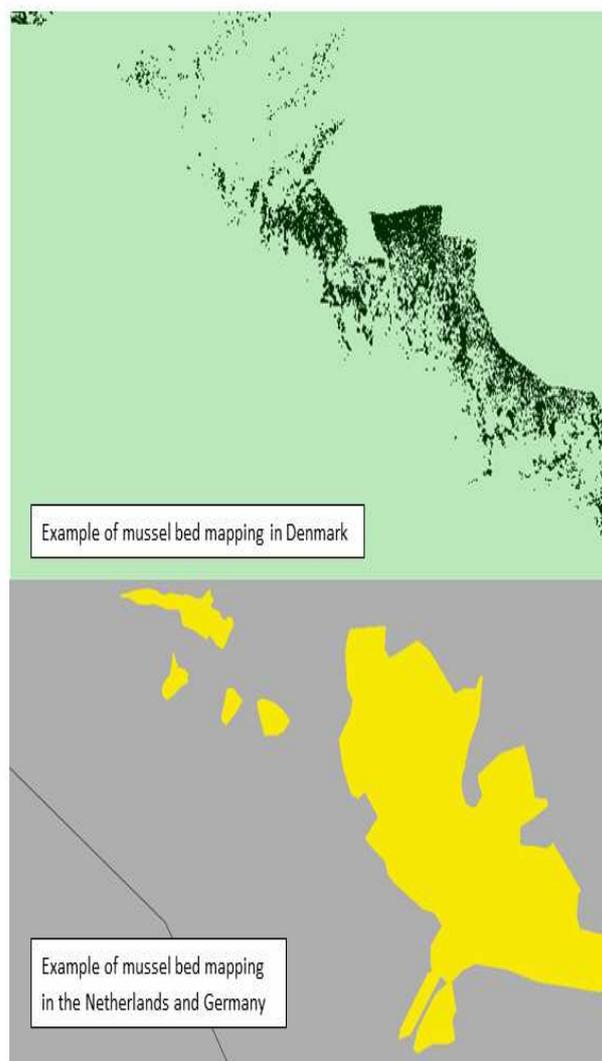


Figure A2. Maps of mussel beds in Denmark and in the Netherlands and Germany. Different methodologies lead to different types of demarcations in the countries.

Dijkema atlas

Dijkema *et al.* (1989) performed an intertidal mussel bed inventory of the entire Wadden Sea based on aerial photographs recorded in 1968, 1973, 1974, 1975 and 1976. The inventory was combined with ground observations in 1978.

The methodology used by Dijkema *et al.* (1989) differs from the current Dutch and German methodology. Firstly, aerial photographs were examined with a mirror stereoscope to identify musselbeds. The contours around the musselbeds were drawn more loosely than is currently done (see 0). Secondly, musselbeds smaller than 10 ha were not recorded in the Dijkema atlas. Hence, currently more precision is obtained in that mussel beds are more accurately demarcated (personal communication Norbert Dankers).

Based on the Dijkema atlas the estimation was that there was circa 4100 ha of mussel beds present in the Netherlands in the period 1969/1976. At the end of the 1980s the last of these habitats were removed.

In addition to the mussel beds, Dijkema also classified land, saltmarshes and mudflats. The mudflats were further classified into muddy, sandy and mixed sand and mud type of sediment. Additionally, two elevations of the habitats were distinguished. The atlas thus forms an important historical reference.



FigureA3. Overview of the 'Dijkema' atlas.

Overview

Based on the data and methodology described in the previous sections, it is concluded that the Dutch and German (both Schleswig-Holstein and Lower Saxony) data (i.e. mussel bed cover) are comparable in their present forms for the years 1999 – 2009. The Danish data, however, are not comparable to the Dutch and German data. The Danish part of the Wadden Sea is relatively small in that it contains “only” 3 of the 39 tidal basins in total and thus represents a small fraction. There might be possibilities to harmonize the Danish dataset. This, however, requires discussion and close cooperation with the Danish partners.

Table A1. *Overview of mussel bed distribution data availability and comparability.*

Period	Netherlands	Lower Saxony	Schleswig-Holstein	Denmark
1958			Aerial	
1959				
1960				
1961				
1962				
1963				
1964				
1965				
1966				
1967				
1968				
1969	Dijkema	Dijkema	Dijkema	Dijkema
1970	Dijkema	Dijkema	Dijkema	Dijkema
1971	Dijkema	Dijkema	Dijkema	Dijkema
1972	Dijkema	Dijkema	Dijkema	Dijkema
1973	Dijkema	Dijkema	Dijkema	Dijkema
1974	Dijkema	Dijkema	Dijkema	Dijkema
1975	Dijkema	Dijkema	Dijkema	Dijkema
1976	Dijkema	Dijkema	Dijkema	Dijkema
1977				
1978				
1979				
1980				
1981				
1982				
1983				
1984				
1985				
1986				
1987				
1988				
1989			Aerial	
1990				
1991				
1992				
1993				
1994				
1995				
1996				
1997				
1998			Bioconsult	
1999	IMARES	NLWKN	Bioconsult	
2000	IMARES	NLWKN	Bioconsult	DTU aqua
2001	IMARES	NLWKN	Bioconsult	
2002	IMARES	NLWKN	Bioconsult	DTU aqua
2003	IMARES	NLWKN	Bioconsult	
2004	IMARES	NLWKN	Bioconsult	DTU aqua
2005	IMARES	NLWKN	Bioconsult	
2006	IMARES	NLWKN	Bioconsult	DTU aqua
2007	IMARES	NLWKN	Bioconsult	DTU aqua
2008	IMARES	NLWKN	Bioconsult	
2009	IMARES	NLWKN	Bioconsult	
2010			Bioconsult	

Green cells represent data that were made available for the current project. Cells are purple when data probably exists but have not been made available. The data of cells with similar colour are mutually comparable.