Spatial ecology of intertidal macrobenthic fauna in a changing Wadden Sea

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Contents

Summary

The distribution and abundance of animals in space and time are central to ecology. Insight in species' distributions, however, not only poses methodological and analytical challenges, but also necessitates that we incorporate spatial autocorrelation as a functional element of a species' ecology. From an ecological point of view, spatial autocorrelation reflects life-history factors, competition, predation, feeding- and mobility-modes and species-environment relationships. The presence of positive spatial autocorrelation or spatial patterning implies that near abundances are more related than distant abundances (or inversely related in case of negative spatial autocorrelation), which affects statistical analysis, potentially leading to flawed conclusions. The work presented in this thesis focuses on landscape-scale communities of bivalves, worms and crustaceans, living hidden just beneath or at the surface of marine mudflats and sandflats in the Dutch Wadden Sea. As a case study we took a bird's eye view of benthos and linked changing benthic resources to carrying capacity and survival of a mollusc-eating shorebird, the red knot (*Calidris canutus*).

Due to multiple stressors such as increased eutrophication, increased human disturbance or intensified erosion, the Wadden Sea ranks among the more degraded coastal areas worldwide. To put the current distribution and abundance of macrobenthic fauna in perspective, we reconstructed a benthic baseline for two areas, Posthuiswad and Staart van Schieringhals. In 1930-1960 both areas had high densities of species that structured the intertidal mudflats such as mussels (*Mytilus edulis*) and cockles (*Cerastoderma edule*). By 1996 densities of bivalves had shown a 10-fold decrease with no recovery till at least 2005. Trends over time showed that crustaceans decreased as well, while worms remained stable. Benthic communities have become much poorer over the last half century, rendering a simplified and more homogenized seascape (**Chapter 2**).

In **Chapters 3-4** we describe the landscape-scale spatial patterns of a number of benthic species (*Macoma balthica, C. edule, Nereis diversicolor, Nephtys hombergii, Marenzelleria viridis, Scoloplos armiger, Corophium volutator* and *Urothoe poseidonis*), particularly focussing on methodological and analytical challenges. We evaluated three methods for analyzing spatial autocorrelation, (1) fractals, (2) variograms and (3) Moran's *I*, to find the best metric to capture spatial variation. On the basis of simulated spatial patterns we selected the latter method for the following reasons: (1) due to standardization results can be directly compared, (2) Moran's *I* is less difficult to evaluate, since it is related to the familiar Pearson's correlation coefficient, and (3) significance can be readily assessed. Consequently, Moran's *I* was used throughout this thesis to describe spatial patterns. For each species, spatial patterns were discernable at the landscape-scale. Due to our pretty much unrivalled landscape-scale sampling effort (225 km^2), combined with a large number of samples (about 2750 each year), comparisons with other studies were not possible (**Chapter 3**).

Thereafter, we extended these spatially explicit analyses and shifted from describing patterns to the analyses of the environmental processes that shape species distributions. At present the driving mechanisms of spatial variation in abundance are poorly understood and are one of the main frontiers in ecology. Fortunately, ongoing statis-

tical sophistication recently offered a way forward: generalised estimating equations (GEE). GEEs are best described as regression-models that explicitly account for spatial autocorrelation in the distribution of both response and explanatory variables. GEEs provide more precise and statistically sound estimates (larger confidence intervals) of environmental variables governing species' distributions. We tested these advanced methods on the landscape-scale distribution of the before mentioned species. Median grain-size and inundation-time were included as typical explanatory environmental variables. GEEs removed much of the residual spatial variation, indicating the importance of median grain-size and inundation time in shaping landscape-scale species distribution in the intertidal. Although, thus far, we only focussed on solving the methodological puzzles that accompany species-environment relationships, we concluded that this spatial approach extends current knowledge, and offers enhanced understanding of species distributions in a spatially patterned environment. GEEs present the necessary methodological advances to further step towards linking pattern to process. One problem to tackle would be the presumed shift in the distribution of adult *M. balthica* in the western Wadden Sea (**Chapter 4**).

Besides highlighting the natural history of benthic communities in the western Dutch Wadden Sea, which could provide standards for ecosystem restoration, we also scaled-up the geographical window towards northwest Europe to make a more contemporary comparison between benthic communities. Based on a sampling effort throughout the winter of 2003-2004, we collected benthic samples in intertidal areas in the Wadden Sea (The Netherlands), the Wash (England), Mont Saint-Michel Bay (France) and two bays on the central French Atlantic coast in the south of Brittany. On this large geographical scale species' abundances were predominantly site-specific, rather than similar throughout (**Chapter 5**).

Degrading impacts on marine intertidal ecosystems by man cascade up from the benthic invertebrate inhabitants to predators. We therefore highlighted the consequences of changing benthic resources at a landscape-scale for knots visiting the Dutch Wadden Sea in the non-breeding season. This ties together existing knowledge about knots' foraging ecology, physiological flexibility and spatial variation in prey abundances. We first described the extent to which mechanical cockle-dredging from 1998 to 2003 was selective with respect to non-target macrobenthic intertidal fauna. Cockle-dredging, which disturbs the top 5-cm of the sediment, ranks among the most destructive types of fisheries. Indeed, cockle-dredging took place in the most biodiverse areas of the western Dutch Wadden Sea, which also contained the greatest abundances of food for shorebirds. The short-term responses of benthic species to dredging appeared unpredictable, highlighting the need for an ecosystem approach to conservation that includes both target and non-target species (**Chapter 6**).

We consequently treated this overexploitation of benthic resources as an 'experimental' setting to link the suitable foraging area, spatial predictability of food and survival of the *islandica* subspecies of knot (*C. c. islandica*) between 1996 and 2005. The digestive rate model was applied to translate benthic stocks to resource landscapes for knots. This model predicts optimal diets that maximizes long-term intake rate for

knots, taking into account the possibility for digestive constraints. Over the 10 years, when accounting for a threshold value to meet energetic demands, knots lost 55% of their suitable foraging area. This ran parallel to a similar decrease of red knot-numbers by 42%. The decrease of spatial patterning, i.e. less information about the location of the suitable feeding sites, did not yet lead to an additional loss of birds. Furthermore, knot-survival, based on colour-ring resightings, declined in this same period from 89% to 82%. Densities of *islandica*-knots per unit suitable foraging area remained constant at 10 knots per hectare between 1996 and 2005, which suggested that they have been using the Dutch Wadden Sea to full capacity throughout (**Chapter 7**).

Similarly, the suitable foraging area for the *canutus* subspecies of knot (*C. c. canutus*), which passes through the area during southward migration to fatten-up before continuing to their West African wintering grounds, declined even stronger than for *islandica*: between 1996 and 2005, 86% of the area was lost. We could demonstrate on the basis of biometrics (body mass, primary moult and bill length) their proportional decline in mistnet catches. This hinted at *canutus*-knots skipping the Dutch Wadden Sea during southward migration. Given the large declines in suitable foraging area in the Wadden Sea, declining numbers in their main wintering areas in western Africa and increasing benthic prey stocks in these wintering quarters, this suggested that the Dutch Wadden Sea was the main bottleneck during the non-breeding season. This implied that the carrying capacity of knots in western Africa might be coupled to and limited by the carrying capacity of the Wadden Sea (**Chapter 8**).

To overcome the loss in suitable foraging area due to industrial fisheries, knots could increase the size of their muscular gizzard, thereby increasing the capacity to process lower quality prey. Indeed, knots adjusted their gizzard-size, however this did not compensate for the loss of extent and quality of suitable intertidal foraging areas. Consequently, local survival of knots declined. The decline of the necessary intertidal resources explains both a loss of knots from the Wadden Sea and the decline of the European wintering population (**Chapter 9**).

Finally, the main findings of the research described in this thesis are discussed in a broader context. I put forward one particularly exciting venue for future research by linking spatial ecology with ecosystem management to monitor the health of ecosystems. I propose using large-scale data from benthic monitoring programmes to describe species-environment relationships along gradients of disturbance with state-of-the-art spatially explicit models such as GEE. Such analyses can then be used as tools to infer habitat preferences of species and highlight losses of such habitats through the losses of species. This would increase forecasting capacity and possibly allow predictions of resilience, which is the long-term ability of an ecosystem to recover from disturbance, improving stewardship of ecosystems (**Chapter 10**).

Introduction

Casper Kraan

The distribution and abundance of organisms in space and time are central to ecology (Hutchinson 1953; Keitt *et al.* 2002; Begon *et al.* 2006). Understanding the mechanisms that govern species' distributions is the key to improved ecological theory and species management (Levin 1992; Keitt *et al.* 2002). The latter seems particularly pressing due to catastrophic shifts in ecosystems on a global scale (Scheffer *et al.* 2001; Hughes *et al.* 2005; Thrush *et al.* 2009; but see Worm *et al.* 2009). A mechanistic insight in species' distributions, however, requires an appreciation of scale. No single scale of research is the correct scale, since different processes operate at different scales (Wiens 1989; Kotliar & Wiens 1990; Levin 1992). A general assumption (see Fig. 1.1) is that environmental characteristics, such as winter ice or wind direction, are more important at large geographical scales (Wiens 1976; Thrush 1991; Legendre *et al.* 1997; Gray & Elliott 2009), whereas biological interactions, such as competition, facilitation and predation, dominate at small geographical scales (Thrush 1991; Legendre *et al.* 1997; Gray & Elliott 2009). Also, there are cross-scale interactions. Therefore, scaling issues are fundamental to ecological research and determine for a great deal their outcome (Wiens 1989; Kotliar & Wiens 1990; Levin 1992).
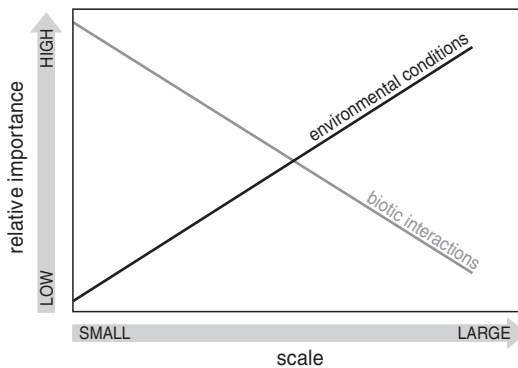
Figure 1.1. Conceptual relative importance of environmental characteristics and biotic interactions in structuring species abundances and distributions with increasing geographical scale. Modified from Zajac *et al.* (1998) and Gray & Elliott (2009).

Besides the geographical scale, the spatial structure of species' distribution and abundance should also be of prime interest to ecological research. Spatial structure or spatial autocorrelation, defined as nearby observations of species abundance being more similar than by random chance (Wagner & Fortin 2005), is a characteristic of a species' ecology. It reflects life-history factors, competition, predation, feeding- and mobility-modes, species-environment relationships (Thrush 1991; Legendre 1993) and, not unimportantly, autocorrelation is affecting statistical analysis (Lennon 2000; Liebhold & Gurevitch 2002; Wagner & Fortin 2005). However, since its introduction to ecology in the 1990s by the seminal papers of Levin (1992) and Legendre (1993), non-independence in the spatial distribution of organisms is treated as a mathematical
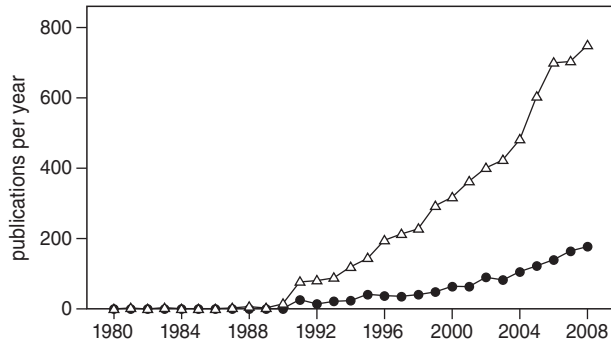
Figure 1.2. Increasing popularity of scale in ecological research between 1980 and 2008. The search, using Web of Science, included articles with *spatial scale* (triangles) or *autocorrelation* (filled dots) in the text and listed under the topic ecology.

puzzle that requires solving due to its influence on parameter estimates and model fit, rather than being pursued for its biological significance. Recently though, focus in this research field has shifted from treating autocorrelation as a statistical nuisance towards an appreciation of the role of environmental variables and biotic interactions shaping species distributions (e.g. Carl & Kühn 2007; Dormann *et al.* 2007). This shift is made possible by the development of statistical methods, and programmes such as *ArcView* and *R*, which are tailored for a broad audience. Currently, spatial problems in ecological research are 'hot' (Fig. 1.2; Ellis & Schneider 2008), and, what's more, spatially explicit methods become standard techniques in the ecologists' toolbox. Still, understanding animal-environment relationships within a spatial framework is one of the main frontiers in ecology (Gaston 2000; Thrush & Dayton 2002; Scheffer & Carpenter 2003; Rietkerk *et al.* 2004). At present, the driving mechanisms of spatial (and temporal) variation in abundance of species are poorly understood (Gaston 2000; Hughes *et al.* 2005). This limits our ability to aptly monitor the 'health' of an ecosystem and define baselines.

The approach taken in this study is to use tools from spatial ecology to 'understand, measure and model spatial patterns in biotic responses' (Liebhold & Gurevitch 2002). In this thesis I focus on landscape scale benthic communities in a changing western Dutch Wadden Sea (Piersma 2006, 2007b; Van Gils *et al.* 2009a) and highlight natural history, spatial patterns and anthropogenic disturbance of these communities. Interest in the abundance and distribution of organisms has a long tradition in benthic ecology and exists at least since the 1930s (Allee 1934; Wohlenberg 1937; Linke 1939), whereas interest in spatial patterns and historical abundance and distributions in this field are more recent (e.g. Reise 1982; Thrush *et al.* 1989; Reise *et al.* 2008). Up till now these lines of research existed in isolation from each other. As another layer, I will illustrate the consequences of these changes from a bird's eye view of benthos and describe the three-way relationship between suitable foraging area, the spatial predictability of food and red knot *Calidris canutus* survival. Red knots are Arctic-

breeding migrants that rely on shellfish-resources in intertidal areas during much of the year. They spend their non-breeding season in the Wadden Sea or use it as a (re)fuelling area (Piersma *et al.* 1993c; Nebel *et al.* 2000; Van de Kam *et al.* 2004); these birds serve as sentinels that indicate the 'health' of the Wadden Sea.

The dark side of the moon

My study system is the ecological community that lives hidden beneath or just at the surface of marine mudflats and sandflats, and is dominated both in abundance and biomass by bivalves, polychaetes and crustaceans (Beukema 1976, 1982). Even though such flats cover 70% of the planet (Snelgrove 1999), more is known about the dark side of the moon than these bottoms of the seas (Gray & Elliott 2009). However, of these 70%, intertidal flats are the easiest accessible and therefore relatively well known. The intertidal flats we study cover the western Dutch Wadden Sea (Fig. 1.3), a marine protected area of international importance (e.g. Van Gils *et al.* 2006b; Swart & Van Andel 2008). Since 1996 we annually sampled the abundance of macrozoobenthos and collected sediment samples in late summer by boat or on foot (see Fig. 1.4 for sampling tools) at this landscape scale (Piersma *et al.* 1993c, 2001; Van Gils *et al.* 2006b), roughly covering 170 km^2 of intertidal areas within the triangle Royal NIOZ at Texel, Harlingen and Terschelling (Fig. 1.3). These benthic samples, 2750 on average each year, and sediment samples, 150 on average per year, enabled us to map the distribution of benthic fauna and sedimentary characteristics in fine detail. Sampling positions were assigned in the first year and revisited in the years after (Van der Meer 1997). In addition, this benthic monitoring scheme also facilitated their interpretation as a resource landscape for red knots (e.g. Van Gils *et al.* 2005c, 2006c) and document the impact of mechanical cockle-dredging at the scale of the fishery (Piersma *et al.* 2001; Van Gils *et al.* 2006b).

Benthic baselines

The Wadden Sea ranks among the more degraded coastal areas worldwide (Lotze *et al.* 2006), mostly due to habitat destruction and overexploitation (Wolff 2000a; Lotze 2005). Thus, to be able to characterise the present abundance and distribution of macrobenthic fauna in the Wadden Sea, a reconstruction of historical richness that occurred in this area is necessary. Such reconstructions offer benthic baselines that serve as attainable goals for conservation and management (Jackson 2001; Dayton 2003; Jackson & Hobbs 2009) and may also provide the only 'controls' to assess human disturbance (Jackson 2001). However, these kinds of comparisons between historical and recent benthic diversity thus far only exist for German and Danish parts of the Wadden Sea (e.g. Reise *et al.* 1989; Jensen 1992b). Therefore, highlighting what was natural in the Dutch Wadden Sea is timely.
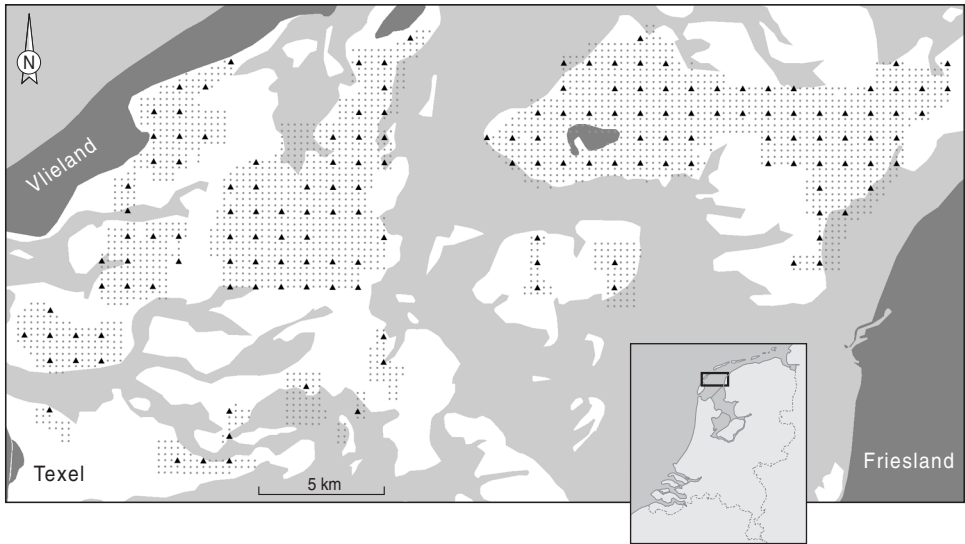
Figure 1.3. Map of our study area, the western Dutch Wadden Sea. All benthic (circles) and sediment (triangles) sampling stations, on a 250 m grid and 1000 m grid, are shown. White areas indicate mudflats exposed during low-water, intermediate grey areas indicate water, and land is represented by the darkest grey areas.
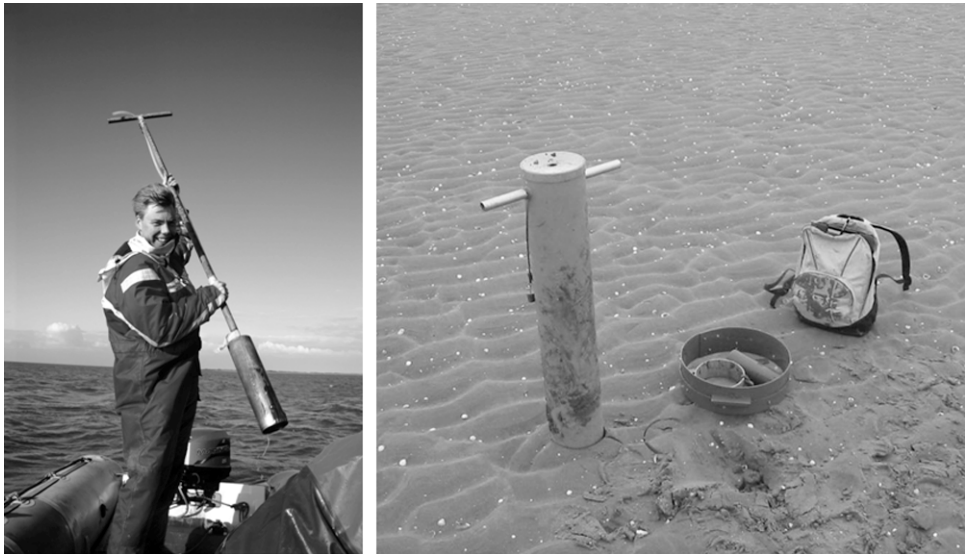
Figure 1.4. Key attributes to sampling benthic fauna: boat-corer (left) and corer and sieve for sampling stations sampled on foot (right). Photographs by Jan Drent and Pierrick Bocher.

Spatial ecology

The necessity to include spatial autocorrelation in the analyses of spatial data stems from the notion that its presence violates the assumption of independent errors, thereby inflating type I errors and overestimating the degrees of freedom (Legendre 1993; Keitt *et al.* 2002; Fortin & Dale 2005). Or put differently 'everything is related to everything else, but near things are more related than distant things' (Tobler 1970). To accommodate this fact spatial statistics are required. These statistics originated in geography and mining in the 1950s and have developed in two directions since: (1) Geostatistics, that use the spatial structure to predict values at unsampled locations using interpolation techniques such as kriging (Cressie 1993; Diggle & Ribeiro Jr. 2007); (2) Spatial statistics, the framework applied throughout this thesis, which are used to estimate the degree of autocorrelation in the data (Fortin & Dale 2005) and account for this when modelling relationships between spatially structured variables (Wagner & Fortin 2005). A hierarchical framework, which is based on nested sampling designs (e.g. Kotliar & Wiens 1990), is less suitable for spatial analysis. Often sample-size at higher levels is very limited (Cole *et al.* 2001) and linking levels is difficult (but see Fauchald *et al.* 2000).

When dealing with spatial data, the first step, as in any other analyses, is data exploration to check for outliers or other potential errors (Fig. 1.5; Haining 2003; Zuur *et al.* 2007). Then, patterns in the variable of interest can be described by a whole array of methods that have been developed to highlight spatial autocorrelation (see review by Fortin & Dale 2005). Some of the more familiar are semi-variance (Rossi *et al.* 1992), Geary's *C*, and Moran's *I* (Moran 1950; Sokal & Oden 1978a; Cliff & Ord 1981). Although these methods are common practice in plant and landscape ecology (e.g. Sokal & Oden 1978a, 1978b; Cliff & Ord 1981), they seem underexplored in marine science (but see Thrush *et al.* 1989; Legendre *et al.* 1997).

Figure 1.5. Decision tree to choose between GLM, GLS or GEE, which depends on the presence or absence of autocorrelation in the model-residuals. Bold arrows highlight the pathway of this thesis.

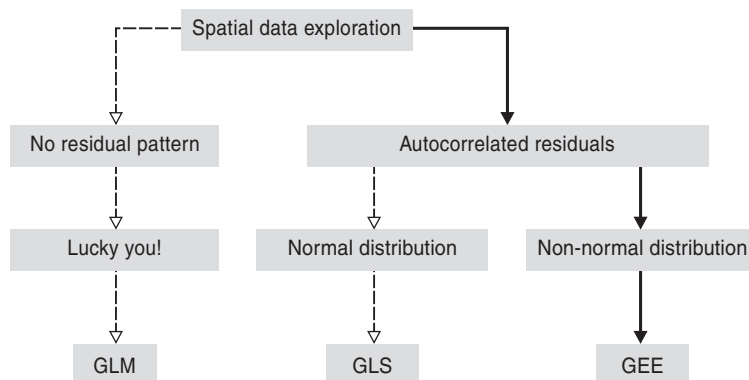Moran's *I*, illustrated here since it is the most commonly used method in ecology, describes the autocorrelation of a variable per distance class, e.g. in our sampling grid these classes are 250 m, 250–500 m, etc. It is closely related to the Pearson's product-moment correlation (Cliff & Ord 1981; Legendre & Fortin 1989) and values are standardized between −1 and +1; 0 indicates no autocorrelation, i.e. a random distribution, whereas a value of 1 indicates a strong positive autocorrelation and −1 indicates a strong negative autocorrelation. To apply Moran's *I* at least 20 sampling stations per distance class are required, as well as the occurrence of the variable of interest on a sufficient number of sampling stations (Legendre & Fortin 1989). When the values of Moran's *I* are plotted against distance-class a so-called 'correlogram' is created, which by its shape gives information about patch-size and spatial structuring in general (see Legendre & Fortin 1989; Fortin & Dale 2005).

$$I = \frac{n \sum_i \sum_j w_{ij}(x_i - \bar{x})(x_j - \bar{x})}{W \sum_i (x_i - \bar{x})^2}$$

n = number of localities (2750 on average in our sampling grid), w_{ij} =1 if the distance between two samples falls within the chosen distance class or 0 otherwise, *x* denotes the variate value, *W* is the sum of all w_{ij}.

When describing the spatial distribution of organisms in relation to, for example, environmental characteristics, regression-type of analysis are commonly used. Again methods such as Moran's *I* can be used to detect autocorrelation in the model-residuals. Preferably no residual autocorrelation is observed. However, depending on the presence of autocorrelated model-residuals, but also the distribution of response variables, different types of regression should be selected (Fig. 1.5). Current state-of-the-art models are generalised estimating equations (GEE; Liang & Zeger 1986; Zeger & Liang 1986; Hardin & Hilbe 2003), which are best described as cluster-models that explicitly account for autocorrelation in the distribution of both response and explanatory variables (Carl & Kühn 2007; Dormann *et al.* 2007). These methods are not just unnecessary complex. Selecting the correct analytical method to deal with autocorrelation may lead to surprising results, such as illustrated by Kühn (2007), who noticed an inversion of observed regression slopes between plant species richness and altitude after including autocorrelation!

Spatial case study: molluscivore shorebirds and industrial fisheries

Degrading impacts on marine intertidal ecosystems by man cascades up from the benthic invertebrate inhabitants to predators such as red knots (Atkinson *et al.* 2003; Baker *et al.* 2004; Van Gils *et al.* 2006b; Piersma 2007b), eider duck *Somateria mollissima* (Camphuysen *et al.* 2002) and oystercatchers *Haematopus ostralegus* (Atkinson *et al.* 2003; Verhulst *et al.* 2004). Yet, besides the amount of available prey on offer, also the spatial patterning of prey is important, since such predators optimize movement through their resource landscape by spending most time in rich areas (Van Gils

et al. 2006c; Klaassen *et al.* 2007; Van Gils 2009). Thus, human-induced degrading of intertidal areas poses a two-way challenge for staging molluscivore birds: declining prey stocks and changing predictability of that same prey. However, to be able to describe such relationships intricate knowledge is required about: (1) landscape-scale distributions of benthic stock that match the scale of disturbance, (2) the diet of the molluscivore predators, (3) a traceable disturbance, and (4) bird numbers and their survival.

As a case of such human-induced degradation and the effects on macrozoobenthos and their predators our research group could not avoid studying the effects of mechanical dredging for cockles *Cerastoderma edule* and harvesting of mussels *Mytilus edulis* in the Dutch Wadden Sea (Smit *et al.* 1998; Piersma *et al.* 2001; Hiddink 2003; Van Gils *et al.* 2006b). Cockle- and mussel-dredging rank among the most destructive types of fisheries (Collie *et al.* 2000; Kaiser *et al.* 2006) although this assessment is based on experimental studies with a rather small disturbed area compared to the scale of the fisheries. These types of fisheries, which take place in the most biodiverse intertidal areas (Piersma 2007b), already started in 1870 (Hoek 1911). However, during 1970s both fisheries increased their capacity and developed into an industry that harvested shellfish throughout the Dutch Wadden Sea (Dijkema 1997), including areas covered by our sampling grid (Fig. 1.3). On top of this, the wader populations in the East-Atlantic Flyway that depend most on the Wadden Sea show the steepest declines (Stroud *et al.* 2004; Van Roomen *et al.* 2005; Delany *et al.* 2009). Thus far, only for one of these waders, the red knot, sufficient detailed information on abundance (e.g. Van Roomen *et al.* 2005; Van Gils *et al.* 2006b), dietary demands and foraging routines (Piersma *et al.* 1993c; Van Gils *et al.* 2005a, 2005c, 2006c, 2007) are available to link changing benthic resources at a landscape scale (e.g. Van Gils *et al.* 2009a) to carrying capacity and survival of knots (Van Gils *et al.* 2006b), i.e. to show how red knots were dredged out of the Dutch Wadden Sea.

Outline of this thesis

In the first paper of this thesis, **Chapter 2**, we focus on natural history and document changes in the benthic community of Posthuiswad (Vlieland) and Staart van Schieringhals (south of Richel) in 1930-1960 and again between 1996 and 2005.

Chapter 3 describes landscape-scale spatial patterns in the distribution of four benthic species (*Macoma balthica, Cerastoderma edule, Nereis diversicolor* and *Nephtys hombergii*, respectively) for four consecutive years (2002-2005). Based on simulations we evaluate three different methods for analyzing autocorrelation, (1) fractals, (2) variograms, and (3) Moran's I, to find the best metric to capture spatial variation which thereafter is used to describe spatial variation in species distributions. Following this, we extend this spatially explicit analysis in **Chapter 4** and shift from describing patterns to analysis of the environmental processes that shape species distributions. To do so, we apply generalized estimating equations (GEE).

In addition to natural history (**Chapter 2**), we seek generality by scaling-up to a geographical scale that covers northwest Europe. In **Chapter 5** we compare benthic biodiversity of a number of intertidal areas scattered across the Dutch Wadden Sea, the Wash (England) and Mont Saint-Michel Bay and two bays on the Atlantic coast south of Brittany (France). This study encompasses 900 km of distance on a north-south axis.

The following chapters, **Chapter 6-9**, highlight the consequences of anthropogenic disturbance on the benthic community and molluscivore shorebirds visiting the Dutch Wadden Sea in the non-breeding season. They tie together all knowledge about red knots' foraging ecology, physiological flexibility and spatial variation of prey abundances. In **Chapter 6** we describe the effects of mechanical cockle-dredging on the benthic community. Specifically, we focus on short-term consequences of fisher patch-choice decisions for target and non-target benthic fauna. We address these short-term responses at the scale of the fisheries, which is the whole western Dutch Wadden Sea. In **Chapter 7** we treat the overexploitation of benthic resources as an 'experimental' setting to link the suitable foraging areas, spatial predictability of food and survival of red knots between 1996 and 2005. This enables us to describe bird-numbers per area unit, which in fact is carrying capacity. Whereas **Chapter 7** focused on the *islandica* subspecies of red knot (breeding Nearctic, wintering in the Wadden Sea), **Chapter 8** deals with the other subspecies of red knot, *Calidris canutus canutus*. This subspecies breeds in Siberia and winters in western Africa, but uses the Dutch Wadden Sea on their southward migration to fatten-up. We describe declining refuelling opportunities and staging intensity at a landscape scale between 1995 and 2005 in our study area. Furthermore, we discuss the possible direct causality between a decline in the quality of intertidal mudflats in the Dutch Wadden Sea and population declines in their West-African wintering quarters. **Chapter 9** illustrates, based on gizzard mass measurements and local survival of red knots, how overexploitation of benthic resources in the Wadden Sea between 1998 and 2002 can explain both a loss of red knots from this area and the decline of the European wintering population.

Acknowledgements

2

Now an empty mudflat: past and present benthic abundances in the western Dutch Wadden Sea

Casper Kraan, Anne Dekinga, and Theunis Piersma

Summary

The benthic fauna of two areas in the western Dutch Wadden Sea, Posthuiswad and Staart van Schieringhals, was described in 1930-1960 and again between 1996 and 2005. Here we document the changes. Whereas both areas formerly had high densities of species that structured the intertidal mudflats such as mussels Mytilus edulis and cockles *Cerastoderma edule*, by 1996 they had shown a 10 fold decrease in the densities of molluscs, with no recovery till 2005. Although the number of species of polychaetes and crustaceans may not have changed much, their relative abundance did. Nowadays more polychaete-species are common than before. We briefly discuss whether the changes in benthic community composition could be due to industrial fishery practices or eutrophication effects.

Introduction

Many mammals, turtles, and fish species of the world's oceans are in dire straits due to overexploitation (Jackson *et al.* 2001; Ellis 2003; Pauly & Maclean 2003). However worrying that is, inhabitants of the shallow parts of the oceans, areas exposed during low tide ('wadden'), suffered the same fate. In the last century, the European Wadden Sea lost structuring organisms like *Sabellaria*-reefs, inter- and subtidal *Zostera* meadows, and *Ostrea edulis* beds, due to overexploitation, diseases, and destruction (Reise 1982; Riesen & Reise 1982; Airoldi & Beck 2007; Van Katwijk *et al.* 2009). The major difference between the open oceans and the intertidal flats is that the former had a greater share of attention such that there is a general appreciation of their historical richness (e.g. Ellis 2003; Pauly & Maclean 2003), whereas for the Wadden Sea such synthesis, and the awareness that follows from it, is much more limited (but see Reise *et al.* 1989; Jensen 1992b; Piersma 2006).

In the German and Danish parts of the Wadden Sea there is a tradition of retrospective benthic analysis, that is comparing benthic biota from samples collected in the first half of the 20th century (e.g. Thamdrup 1935; Linke 1939) with data from the same areas collected more recently (Riesen & Reise 1982; Reise *et al.* 1989, 2008; Jensen 1992b). The aim of these studies is to show the pro- or regression an area has made over time, where the older benthic samples are treated as a baseline against which 'change' is measured (Reise *et al.* 1989). The idea is that these data from the first half of the 20th century represent a situation before the onset of, for example, increased eutrophication (Perus & Bonsdorff 2004), increased human disturbance (Riesen & Reise 1982), or intensified erosion (Reise *et al.* 1989).

For the Dutch part of the Wadden Sea, apart from assessments of extinctions and human exploitation of species (Wolff 2000a, 2005a), such kinds of historical reviews are not available, despite the fact that long-term benthic sampling programs have been carried out continuously since the 1970s (e.g. Beukema 1982; Zwarts & Wanink 1993; Essink *et al.* 1998). This is probably related to a mismatch between the geographical locations of these monitoring programmes at Balgzand (Beukema 1982) and coastal Groningen (Essink & Beukema 1986; Zwarts & Wanink 1993), and the locations of historical benthic studies in other parts of the western Wadden Sea (Kristensen 1957; Van der Baan *et al.* 1958; but see Kuenen 1942). However, a 'recent' (since 1996) benthic sampling programme, designed to monitor food for benthivorous shorebirds like red knots (*Calidris canutus*) and bar-tailed godwits (*Limosa lapponica*), covers most of the intertidal area in the western Dutch Wadden Sea (Piersma *et al.* 1993c; Van Gils *et al.* 2006c; Kraan *et al.* 2007, 2009b), thereby offering a possibility for comparisons that we exploit here.

The aim of this study is to compare macrobenthic communities of two intertidal areas just south of Vlieland, i.e. Posthuiswad and Staart van Schieringhals (Fig. 2.1), in the 1930-1950s and from 1996 to 2005. These areas were well-known for their richness of benthos, e.g. cockles *Cerastoderma edule* and mussels *Mytilus edulis* (Kreger 1940; Verwey 1952; Kristensen 1957), whereas nowadays Staart van Schieringhals in partic-

ular is nearly devoid of benthic life (personal observations). Since understanding the current state of an area may best be enhanced by reflection against a historical background (Riesen & Reise 1982; Reise 1995; Jackson *et al.* 2001), we not only focus on recent changes, but also try to paint the former richness of these areas, i.e. a benthic baseline.

Study areas and methods

In July-September 1996-2005 we collected benthic samples at Posthuiswad and Staart van Schieringhals (Fig. 2.1). This was done over a pre-determined 250 m grid (Fig. 2.1), on foot during low tide or by boat otherwise. To locate sampling sites we used hand-held GPS (Garmin 12 and 45; Garmin Corporation, Lenexa, Kansas, USA), where subsequently a core ($1/56$ m^2) to a depth of 20-25 cm was taken. After sieving over a 1-mm mesh, all fauna were counted and recorded. Crustaceans and molluscs were collected in plastic bags and stored at -20 °C for later analyses in the laboratory (see Piersma *et al.* 1993c; Kraan *et al.* 2007; Van Gils *et al.* 2006b, 2006c, 2009a).
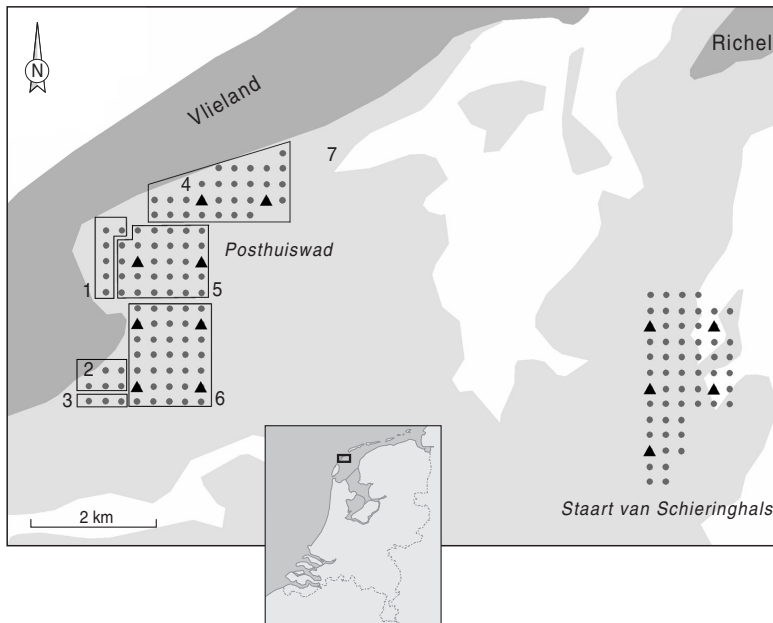
Figure 2.1. Study areas: Posthuiswad and Staart van Schieringhals. Both benthic (dot) and sediment (triangle) sampling locations are shown. Numbers 1-7 show the different zones (see 'Study areas and methods' and Table 2.1). Light grey areas indicate mudflats exposed during low-water at spring-tides, white areas indicate water, and land is represented by the darkest grey areas. Square inside the small map of the Netherlands shows the location within the Dutch Wadden Sea.

Additionally, within each km^2 a sediment sample was collected (Fig. 2.1) and analysed with a LS Coulter Counter (Zwarts *et al.* 2004; Bocher *et al.* 2007). Based on the descriptions and maps given by Kristensen (1957) and Van der Baan *et al.* (1958) we matched the geographical extent of both areas as close as possible to theirs (Fig. 2.1). For Staart van Schieringhals we validated our extent by comparing the positioning of the buoy closest to this area (IN1) in 1910 (Hoek 1911) with a recent map. This buoy still resided at its original location, which indicated that our placing of Staart van Schieringhals matched the historical one.

Although exact sampling locations are not given by Van der Baan *et al.* (1958), their detailed portrayal of the sampling sites at Posthuiswad (sampled during the summers of 1956 and 1957) made a similar division in zones possible by clustering sampling stations (Fig. 2.1). These zones were: (1) border between salt marsh and mudflat, i.e. 'Schor', (2) Vliehors high intertidal, (3) Vliehors low intertidal, (4) coast near the island, (5) Posthuiswad high intertidal and (6) Posthuiswad low intertidal. They also recorded densities of macrofauna just opposite the gully (7). Van der Baan *et al.* (1958), while sampling to a depth of 30–40 cm (C. Swennen, personal comment) with a standardized core and small-meshed sieve, focussed on common species only. Thus, species not dealt with were not necessarily absent, but were uncommon or rare. We could, however, compare average densities per zone for the species that they recorded and their present occurrence in those same zones.

The historical data presented by Kreger (1940) and Kristensen (1957) of the Staart van Schieringhals focussed on cockles and mussels only and gave information on sediment characteristics. Since we suspected that, unlike the early studies of Posthuiswad, only areas with high abundances were sampled, we gave mean densities and maximum observed abundances during summer 1996-2005. Kreger (1940) dug up all sediment within a square frame and Kristensen (1957) dug up 20 dm^2 to a depth of 3 cm. Both used a 1 mm sieve to collect and count cockles.

Based on Zwarts *et al.* (2004), who digitalized all sediment data from the 1950s to 2002 within the Dutch Wadden Sea and standardized methods to allow comparisons, mud fraction values (% of the sample with a grain-size <16 μm) at Posthuiswad were on average 3-8% from 1950–1955. Based on samples from the period 1996–2005, median grain-size was 190 μm and the mud fraction 5%.

At the Staart van Schieringhals, the median grain-size, based on samples collected between 1932 and 1955 (Postma 1957), was on average 100 μm. Kreger (1940), who sampled the area in 1937, mentioned the sediment as being 'very fine sand' with a median grain-size of 106 μm. Kristensen (1957), using samples from 1948 (but from the same data-set as Postma) reported median grain-sizes ranging between 87 μm and 104 μm. Zwarts *et al.* (2004) estimated a mud fraction for 1950-1955 between 1–3%. The average median grain-size in 1996–2005 was 144 μm with a mud fraction of 3%. From the limited amount of information it appeared that the median grain-size of Staart van Schieringhals was coarser in 1996–2005 than it was in 1932-1955 (see also Piersma *et al.* 2001); while for both areas the mud fraction has not changed.

Results

The intensive sampling south of Vlieland by Van der Baan *et al.* (1958) resulted in a detailed description of the zoned abundances of common species (Table 2.1). *Corophium volutator* and *Hydrobia ulvae* occurred in high densities throughout the area (Table 2.1). In 1996-2005, *H. ulvae* occurred in lower densities (Table 2.1), whereas *C. volutator* was only abundant in zone 1 and disappeared or was present in low numbers in other zones. Another species that thrived in zone 1 in 1996-2005 was *Abra tenuis*, which was rare before. Zone 2 transformed from a mollusc-rich area into an area with almost no shellfish. Instead, the polychaetes *Nereis diversicolor* and *Scoloplos armiger* were abundant in 1996-2005, as was *Bathyporeia* sp. In 1996–2005 zone 3 was characterised by high densities of S. armiger (Table 2.1), but historically *Heteromastus filiformis* was the dominant polychaete. Formerly *Zostera marina* was also present in this zone (Van der Baan *et al.* 1958). Closest to the coast, in zone 4, polychaetes were the most dominant species group in 1996–2005. However, in contrast to the 1950s, these occurred in reduced densities and consisted of different species. In the 1950s *Eteone longa, H. filiformis* and *S. armiger* were the main species; in 1996-2005 these were *H. filiformis, Lanice conchilega* and *N. diversicolor*, respectively. The high intertidal part of Posthuiswad (zone 5) used to show high densities of crustaceans (see Table 2.1), but in 1996-2005 densities were much lower. The polychaetes diversified (Table 2.1), with more species occurring in low abundances in 1996-2005. An area (Posthuiswad low intertidal) dominated by *C. volutator, H. ulvae* and *H. filiformis* in the past, in 1996-2005 showed high densities of *Bathyporeia* sp., but many other species also occurred in low densities. It was the most biodiverse zone (Table 2.1).

In 1939 Kreger (1940) visited a number of large cockle beds just south of Vlieland, 1 km off the coast. He encountered a maximum density of 1100 adult cockles per m^2, while spat was present with 2500 individuals per m^2. Cockles were so dense here that their shells dented during growth (Fig. 18 in Kreger 1940). Mussel spat was abundant over much of the area. When Van der Baan *et al.* (1958) visited presumably this area in 1956 they failed to find cockles, probably due to three severe winters prior to 1956 (Van der Baan *et al.* 1958). The next year (1957) cockles were present again (Table 2.1).

For the Staart van Schieringhals area, from the low water line onto higher parts of the mudflat, Kreger (1940) described the following for September 1937: '*The number of cockles was small up to 240 m from the low water line of the Inschot. At 300 m from this line it increased to 100 per m2, to become nearly 1000 at 360, and 2160 at 420 m, finally to fall to 1800 per m2 at 480 m from the water's edge*'. Kreger (1940) nicely visualised this by stating: '*Where cockles were lying densest, the bottom seemed paved*'. Also, there were beds of *M. edulis* (see Fig. 16 in Kreger 1940), as well as another large cockle bed a little bit further south. The highest cockle densities occurred higher on the mudflat, where also the finest sands were present. At his next visit in summer 1939 both cockle beds were all but completely turned into large mussel beds with an elevation of 75–100 cm (Kreger 1940). Historical records of mussel beds in this area date

	Schor (1)		Vliehors high (2)		Vliehors low (3)		Coast (4)		Posthuis high (5)		Posthuis low (6)		Cockle-beds eastside (7)
	1956	1996-2005	1956	1996-2005	1956	1996-2005	1956	1996-2005	1956	1996-2005	1956	1996-2005	1956
Polychaeta													
Are		77 (622)	30	34 (226)	15	15 (173)	50	29 (462)	35	40 (346)	40	32 (1129)	56
Ete		0 (0)	51	4 (56)		0 (0)	200	3 (173)	70	4 (230)	90	8 (288)	150
Het*		79 (847)	1357	74 (791)	560	17 (289)	1426	199 (3465)	1800	135 (1412)	1800	73 (4527)	4860
Lan		6 (195)		14 (283)		2 (57)		175 (6780)		78 (3955)		59 (1299)	2
Ner	77	33 (339)	230	255 (3465)		108 (520)		166 (974)		116 (1155)		131 (1039)	
Phy		0 (0)		0 (0)		0 (0)		1 (58)		1 (58)		3 (173)	50
Sco		92 (1245)	1000	442 (1921)	26	656 (2147)	1383	39 (982)	300	187 (4520)	26	631 (6215)	5800
Nemertea													
Nem		1 (58)		0 (0)		0 (0)		0 (0)		1 (58)	20	0 (0)	250
Crustacea													
Bat	10167	0 (0)	26	486 (6929)	410	387 (1698)	11900	2 (289)	70	37 (1444)	11140	847 (12429)	51
Cor		2662 (16949)		513 (7356)	100	91 (678)		100 (4545)	4400	411 (11318)		95 (8475)	1300
Cra		5 (65)		12 (113)		11 (113)		7 (325)	120	7 (231)		14 (452)	
Gam		17 (734)		35 (1412)		8 (113)		4 (289)	50	12 (1469)		9 (1469)	
Mollusca													
Abt		377 (2773)	230	21 (395)		0 (0)		3 (345)	900	25 (1977)	26	29 (3735)	
Cer s		8 (116)	102	8 (65)	50	0 (0)		9 (508)		21 (844)	38	6 (231)	77
Cer a		8 (173)		18 (169)		17 (168)		151 (2825)		109 (1864)		5 (170)	25
Hyd		357 (7488)	7990	242 (5405)	700	0 (0)	5122	3794 (245946)	700	3328 (282432)	8960	177 (15135)	
Mac s		277 (2655)	154	52 (678)	50	21 (169)		91 (3291)		269 (16554)	26	23 (1525)	104
Mac a		107 (791)		59 (226)		30 (115)	154	90 (1186)		123 (1412)		25 (1299)	100
Mya s		4 (130)	26	0 (0)		17 (404)		8 (455)		19 (909)	28	3 (130)	
Ret		0 (0)	461	0 (0)		0 (0)		0 (0)	70	1 (57)		1 (57)	

Table 2.1. (left) Mean (and maximum) abundance of benthic macrofauna (ind. per m²) at Posthuiswad in 1956–1957 and 1996–2005. Abbreviations: Are (*Arenicola marina*), Ete (*Eteone longa*), Het* (composite of *Pygospio elegans, Heteromastus filiformis* and *Capitella capitata*), Lan (*Lanice conchilega*), Ner (*Nereis diversicolor*), Phy (*Phyllodoce mucosa*), Sco (*Scoloplos armiger*), Nem (*Nemertine* sp.), Bat (*Bathyporeia* sp.), Cor (*Corophium* volutator), Cra (*Crangon crangon*), Gam (*Gammarus locusta*), Abt (*Abra tenuis*), Cer s (*Cerastoderma edule* spat), Cer a (*C. edule* adult), Hyd (*Hydrobia ulvae*), Mac s (*Macoma balthica* spat), Mac a (*M. balthica* adult), Mya s (*Mya arenaria* spat) and Ret (*Retusa obtusa*).

back at least to 1856 when Allan (cited in Hoek 1911) noted that substantial mussel beds were present at the Waardgronden (which includes Staart van Schieringhals), but that there was a lack of manpower to harvest them.

In 1947, eight years after Kreger (1940), a density of 170 cockles per m² was estimated for the northern part of Staart van Schieringhals and for the southern part 655 cockles per m² (Kristensen 1957). These abundances most likely refer to spat only, since after the severe winter of 1946-1947 cockles were almost exterminated from the intertidal mudflats (Kristensen 1957). Using two different sets of sampling stations (locations not given) Kristensen (1957) here also estimated densities of cockle spat, i.e. 101 and 738 individuals per m². In summer 1948, the cockle densities (adults and spat) varied from 30 (westward slope) to 395 per m² on the eastward slope of Staart van Schieringhals (Kristensen 1957). The same locations held 180 and 555 cockles per m² in July 1949 (Kristensen 1957).

During summer 1996-2005 we encountered a mean density of just 0.6 adult cockles per m² and 0.1 mussels per m². In this 10-year period the highest encountered density at any sampling location for both species was 58 individuals per m2.

Overall

The general pattern emerging from these comparisons was a decimation of molluscs, as well as a reduction of the crustaceans (Table 2.1). Polychaetes also changed; in 1996–2005 there was not one particular species that really dominated, but several species commonly occurred, although densities were in general lower than in 1956–1957 (Table 2.1). This can be illustrated by plotting the densities of species recorded in 1956–1957 at Posthuiswad against those same species in 1996–2005 (Fig. 2.2A–C). All but a few observations were below the line that marked equal densities (Fig. 2.2A–C). Above the line were *S. armiger* at Posthuiswad low intertidal (Fig. 2.2a), *Bathyporiea* sp. (Vliehors high intertidal) in one zone (Fig. 2.2B), and *Hydrobia ulvae* at Posthuiswad high intertidal (Fig. 2.2C).

Trends over time, from 1956–1957 to 2005 (Fig. 2.3), showed that molluscs and crustaceans decreased, while polychaetes remained 'stable' (Fig. 2.3). Note that *H. ulvae* was excluded as they would obscure the trends. For example, in 1997 their mean density was enormous (13484 ind. per m²), whereas in 2003 and 2004 they were absent.
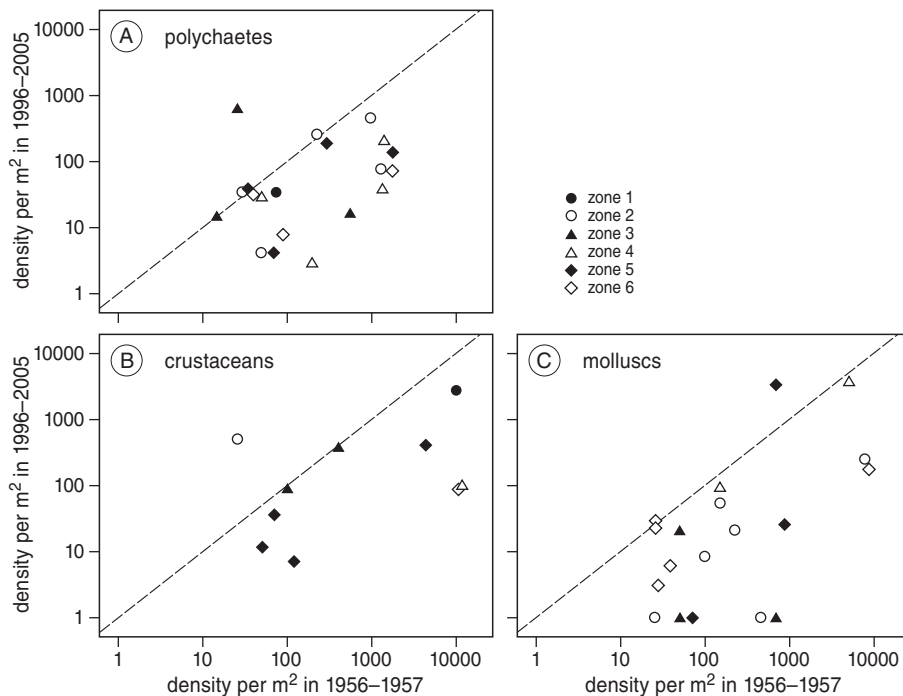
Figure 2.2. Benthic abundances in 1956–1957 and 1996–2005 of (A) polychaetes, (B) crustaceans, and (C) molluscs (both axes are log-scaled). The line marks equal abundances in 1956–1957 and 1996–2005. Zones (see Table 1) are: 1, 2, 3, 4, 5, 6.
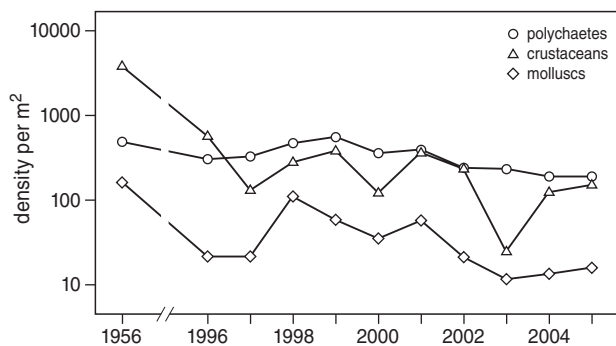
Figure 2.3. Long- (1950s vs. ca. 2000) and short-term (1996–2005) trends at Posthuiswad of polychaetes, crustaceans, and molluscs, respectively. H. ulvae was excluded from molluscs (see Table 2.1 for densities and Results section for explanation). The groups are determined according to Table 2.1. That is, for each zone the species occurring in 1956–1957 and those same species in 1996–2005 were used. Note the time-step on the x-axis, and the log-scaled y-axis.

Discussion

The first hurdle in retrospective analyses is finding ways in which different historical data-sets can be compared in unbiased ways. Usually the documentation of historical data are brief and do not contain many methodological details. This means that a conservative approach has to be taken towards using these data-sets (Reise *et al.* 1989). For example, Van der Baan *et al.* (1958) only gave densities of common species, which confined the comparisons to exact these same species. Kreger (1940) did not state sampling depth, but then he only focussed on *C. edule* and *M. edulis*, which both are living close to or on the surface (e.g. Smidt 1951; Verwey 1952). This, therefore, imposes no limitations.

Within the limits set by the historical data, it is clear that benthic communities of the two intertidal areas have become much poorer over the last half century. Staart van Schieringhals lost its large cockle and mussel beds, while at Posthuiswad both molluscs and crustaceans decreased, although polychaetes diversified (Table 2.1; Figs. 2.2-2.3). It appears that smaller bodied macrozoobenthic species have been flourishing recently, whereas many larger bodied, long-lived species all but disappeared. As documented for other parts of the Wadden Sea, polychaetes are taking over (*sensu* Reise 1982; Beukema 1991; Lotze *et al.* 2005). This impression, however, is created by the large decrease of molluscs and crustaceans and not so much by an increase of polychaetes (Fig. 2.3).

The observed changes are likely to reflect a whole array of factors that need to be assessed within a pluralistic framework (Reise 1995; Scheffer *et al.* 2005). Nonetheless, we believe that two factors, eutrophication and the mechanical harvesting of shellfish, warrant discussion (see also Beukema & Cadée 1997; Piersma *et al.* 2001; Van Raaphorst & De Jonge 2004; Van Gils *et al.* 2006b; Kraan *et al.* 2007). Nutrient levels rapidly increased since the 1950s (De Jonge *et al.* 1993; Van Raaphorst & De Jonge 2004) and in parallel the biomass and abundance of macrozoobenthos more than doubled (Beukema 1991; Beukema & Cadée 1997). The general consensus at the time was that intertidal benthos had been food limited up to that point (Beukema 1991; Beukema & Cadée 1997; Beukema *et al.* 2002). However, nutrient loadings decreased since the 1990s (Cadée & Hegeman 2002; Van Beusekom 2005), and unexpectedly total biomass still continued to increase (Dekker & Waasdorp 2007; Kuipers & Van Noort 2008). Moreover, large and persistent mussel beds, oyster reefs and cockle banks formerly existed in the western Dutch Wadden Sea, including our study areas, prior to increased nutrient levels (Hoek 1911; Kreger 1940; Verwey 1952; Kristensen 1957; Van der Baan *et al.* 1958). If, however, nutrients limited the development of new mussel and cockle beds in the western Dutch Wadden Sea, why did they not profit from eutrophication when food was no longer limiting? In the German, and possibly the Danish Wadden Sea, for example, mussel beds increased under mild eutrophication (Reise *et al.* 1989; Jensen 1992b).

Commercial harvesting of mussels and cockles in the western Dutch Wadden Sea date back to at least 1884, a year when 2068 kg of cockles were landed (Hoek 1911), and 1870 when the export of mussels to Belgium and England started, as well as a

fishery for mussel-spat (Hoek 1911; Dijkema 1997). In 1949 already 15 million kg of mussels were collected, which was an estimated one third of the total biomass present (Verwey 1952). After 1970 cockle-fisheries developed from a small scale fishery to an industry with 24 ships actively dredging for cockles with suction dredges (Dijkema 1997). Since that time, both the Staart van Schieringhals and Posthuiswad have been dredged on several occasions (Zwarts *et al.* 2004; Van Gils *et al.* 2006b; Kraan *et al.* 2007), until mechanical cockle-dredging was outlawed in 2003 (Kraan *et al.* 2007; Swart & Van Andel 2008). In 1990 nearly all intertidal mussels and cockles were harvested (Beukema & Cadée 1996; Beukema *et al.* 1998). Following this, in 1993 catches were regulated and some areas were closed from fisheries (Smit *et al.* 1998; Zwarts *et al.* 2004), but intertidal mussel beds and cockle banks never recovered in the areas open to fisheries (Smit *et al.* 1998; Herlyn & Millat 2000). Furthermore, in some closed areas like Posthuiswad, mussels have not re-established either (Piersma *et al.* 2001; Kraan *et al.* 2007; this paper). Note that hand-harvesting of cockles is still allowed in these areas. Our work has suggested that mechanical dredging has changed sediment characteristics (e.g. grain-size, but other characteristics as well) and nega-tively affected recruitment (Piersma *et al.* 1993c, 2001; Van Gils *et al.* 2006b).

Currently the Wadden Sea may rank among the more degraded coastal seas world-wide (Lotze *et al.* 2006), mostly due to habitat destruction and overexploitation (Wolff 2000a, 2005a; Lotze *et al.* 2005, 2006). So far, there are few signs of recovery, which may imply that the long-term multiple impacts have reduced the system's resilience (Piersma *et al.* 2001; Lotze *et al.* 2006). Attempts since 1991 to restore low intertidal *Zostera marina* beds in the western Dutch Wadden Sea have failed (Van Katwijk *et al.* 2009), *M. balthica* numbers continue a decline (Van Gils *et al.* 2009a) and intertidal mussel beds have not returned (Kraan *et al.* 2007; this study). This means that the area currently is in a state far from its historical baseline (Lotze *et al.* 2006). If the western Dutch Wadden Sea has been moved to another alternative stable state (*sensu* Scheffer *et al.* 2001; Scheffer & Carpenter 2003) over the last half century, what is necessary for its former richness to be restored?

Acknowledgements

Patchiness of macrobenthic invertebrates in homogenized intertidal habitats: hidden spatial structure at a landscape scale

Casper Kraan, Jaap van der Meer, Anne Dekinga, and Theunis Piersma

Summary

Many terrestrial habitats, and certainly man-made systems such as woodland and agricultural habitats, are characterised by a mosaic of different habitat-types. In contrast, most seafloors have a rather uniform visual appearance, which is enhanced by the cryptic nature of many of their inhabitants. This study aims to (1) describe landscape-scale spatial patterns of benthic infauna after (2) evaluating three methods for analyzing autocorrelations (Moran's *I*, semivariance and fractals), (3) compare the benthic patterns with patterns described for other organisms and (4) highlight shared characteristics. During four consecutive years (2002 to 2005) we assessed spatial structuring of 4 intertidal benthic invertebrates (*Cerastoderma edule, Macoma balthica, Nereis diversicolor* and *Nephtys hombergii*) in the Wadden Sea, The Netherlands. We annually sampled ~2750 stations, based on a 250 m grid, covering an area of ca. 225 km^2. On the basis of simulated spatial distributions, we selected Moran's *I* to analyze spatial patterns for the following reasons: (1) due to standardization, results can be directly compared, (2) Moran's *I* is less difficult to evaluate, since it is related to the familiar Pearson's correlation coefficient, and (3) significance can readily be assessed. The 4 benthic species were all spatially structured at the landscape scale, with spatial features being smaller than the physical structure of the intertidal environment, i.e. the intertidal extent. During the 4 yr, some species changed their distribution, but spatial characteristics, i.e. patch size and amplitude of autocorrelation, remained similar. Higher overall density resulted in stronger autocorrelation with no differences between species. A comparison between spatial structuring of benthic fauna with patterns encountered in other habitats, whether marine or terrestrial, was unsuccessful due to differences in extent and grain. We argue that future research should focus on spatial structure in species' distributions as an ecological relevant parameter.

Introduction

The ecological world is patterned and patchy (Sparrow 1999; Wiens 2000); however, there are large differences in the physical appearance of this environmental heterogeneity. For example, arable farmland, with intensively managed fields separated by semi-natural field margins, comprises a heterogeneous mosaic of habitat types (Stewart *et al.* 2000). Woodland, as depicted in detail by Elton (1966), also is characterized by many different habitat types. Arguably, at the other end of the range are soft-sediment seafloors. They are fairly homogeneous and featureless, without sharp boundaries between habitat types, only limited in extent by the low-water mark (e.g. Verwey 1952; Peterson 1991). The animal assemblages of such flats are dominated by invertebrates that live hidden beneath the muddy or sandy surface (Peterson 1991; Thrush 1991). Other features also separate coastal marine habitats from terrestrial habitats, amongst others the spatial scale of gene flow and the openess of communities (Carr et al. 2003).

An element that most habitats have in common is anthropogenic interference (associated with resource extraction, land use and development) as the dominant form of landscape disturbance. When these activities occur on a large-scale they often tend to homogenize landscape patterns (Watling & Norse 1998; Wiens 2000). For example, mussel beds (*Mytilus edulis*) provide some structural heterogeneity on intertidal mudflats in the Dutch Wadden Sea (Verwey 1952; Dankers & Zuidema 1995). However, these beds were mechanically harvested between 1989 and 1991 (Piersma *et al.* 1993c) and have not yet returned, which can be credited partially to another bottom-touching fishery, i.e. cockle-dredging (Kraan *et al.* 2007).

The intertidal flats of the Wadden Sea are well studied with respect to species, numbers and biomass of macrobenthic fauna (Beukema *et al.* 1993; Piersma *et al.* 1993c; Zwarts & Wanink 1993; Flach 1996b; Dekker & Beukema 1999) and to a lesser extent with respect to the impacts of industrial harvesting of shellfish (but see Piersma *et al.* 2001; Van Gils *et al.* 2006b; Kraan *et al.* 2007). However, a spatially explicit description of macrobenthic species' distributions, using tools from landscape ecology in an integrative and interdisciplinary approach (Wu & Hobbs 2002), has not been conducted.

Based on a large-scale benthic research effort in the Dutch Wadden Sea (see Piersma *et al.* 2001; Kraan *et al.* 2007), we here describe spatial patterns of macrozoobenthic species in homogenized intertidal sandflats at an ecologically relevant landscape scale and describe shape and size of patches, as well as consistency of patches in time. Four abundant macrozoobenthic species, 2 bivalves (*Macoma balthica* and *Cerastoderma edule*) and 2 polychaete worms (*Nereis diversicolor* and *Nephtys hombergii*), were chosen to illustrate hidden spatial patterning within intertidal sands.

A literature survey, based on ecological studies that (1) sample a grid, (2) apply one of 3 methods for spatial analysis tested below and (3) do not use remote sensing or satellite data, indicates that our study effort belongs to the selected few that combine a large sampling area (> 1 km^2) with a large number of samples (> 1000
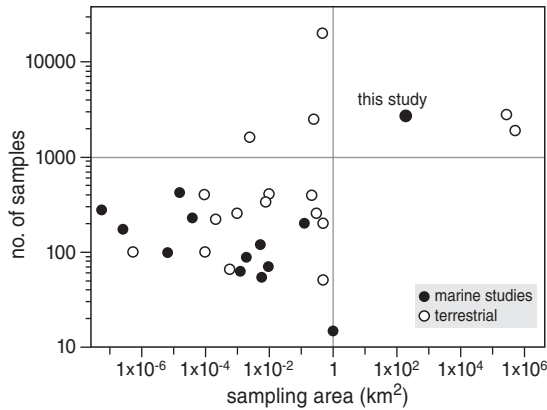
Figure 3.1. Numbers of samples taken and the total area covered (km^2) in published spatial papers. The vertical line denotes a sampling area of 1 km^2, whereas the horizontal line divides studies with more than 1000 samples from studies with fewer samples.

samples) (Fig. 3.1; Table 3.1). Usually, spatial research is performed at either a large scale with few sampling stations (e.g. Morrisey *et al.* 1992; Thrush *et al.* 1994; Fauchald *et al.* 2002) or at a small-scale with close-range coring (e.g. Reise 1979; Hewitt *et al.* 1997b; Legendre *et al.* 1997).

To decide which of 3 different methods best describes spatial structures of benthic infauna, we simulated a range of distributions to create a spectrum of spatial patterns. The simulated patterns were used to examine the behaviour of Moran's *I* (Moran 1950; Sokal & Oden 1978a; Cliff & Ord 1981), semivariance (e.g. Rossi *et al.* 1992) and fractals (Burrough 1981; Palmer 1988), not only to develop a better understanding of the translation from process to pattern, but also to note possible differences between the methods applied. So far, Moran's *I* has been scarcely used in marine ecological research (e.g. Volckaert 1987; Hewitt *et al.* 1997a, b; Legendre *et al.* 1997); the remaining two are popular in plant and landscape ecology (Rossi *et al.* 1992; He *et al.* 1994; Fortin & Dale 2005).

Materials and methods

Study area
The surveyed intertidal areas in the western part of the Dutch Wadden Sea (53 °N, 4-5 °E) (Fig. 3.2) covered a surface of approximately 225 km^2. The area mainly consists of gullies, intertidal and subtidal mudflats, and is bordered from west to east by the barrier islands of Texel, Vlieland and Terschelling. The western Wadden Sea has a semi-diurnal tide and tidal amplitude varying between 1.5 m at neap tides to 2.5 m at spring tides. About three-quarters of this area consists of soft-sediment flats, exposed

Table 3.1. Literature-overview, showing studies that based their spatial analysis on Moran's *I*, semivariance or fractals, sampled an evenly spaced grid and did not use remote-sensing or satellite-data.

| Topic	Environment	Country	Site size (km^2)	Samples (n)	Source
Macrozoobenthos	Marine	The Netherlands	1.75×10^2	2750	Present Study
Zoobenthos	Marine	Sweden	1.50×10^{-5}	432	Bergström *et al.* (2002)
Meiofauna & microalgea	Marine	USA	5.42×10^{-8}	288	Pickney & Sandulli (1990)
Meiofauna & microalgea	Marine	USA	5.42×10^{-8}	288	Sandulli & Pickney (1999)
Bivalves	Marine	New Zealand	3.60×10^{-5}	230	Hewitt *et al.* (1996)
Bivalves	Marine	New Zealand	1.25×10^{-1}	200	Legendre *et al.* (1997)
Polychaetes	Marine	Canada	2.50×10^{-7}	175	Volckaert (1987)
Ecklonia radiata	Marine	New Zealand	5.00×10^{-3}	121	Cole & Syms (1999)
Macrozoobenthos	Marine	USA	6.45×10^{-6}	100	Jumars *et al.* (1977)
Chione stutchburyi	Marine	New Zealand	1.80×10^{-3}	90	McArdle & Blackwell (1989)
Macrozoobenthos	Marine	New Zealand	9.00×10^{-3}	72	Thrush *et al.* (1994)
Bivalves	Marine	Scotland	1.23×10^{-3}	64	Hu×am & Richards (2003)
Macrozoobenthos	Marine	New Zealand	5.50×10^{-3}	55	Hewitt *et al.* (1997)
Mactra ordinaria	Marine	New Zealand	1.00×10^0	15	Cole *et al.* (2001)
Tree diversity	Other	Malaysia	5.00×10^{-1}	20000	He *et al.* (1994)
Freshwater turtles	Other	Spain & Portugal	2.77×10^5	2772	Segurado *et al.* (2006)
Plants	Other	China	2.50×10^{-1}	2500	He *et al.* (2007)
Bird diversity	Other	South Africa	1.26×10^6	1858	Van Rensburg *et al.* (2002)
Perennial vegetation	Other	Spain	2.50×10^{-3}	1600	Maestre *et al.* (2005)
Ambrosia dumosa	Other	USA	1.00×10^{-2}	400	Perry *et al.* (2002)
Soil seedbank	Other	Spain	1.00×10^{-4}	400	Reiné *et al.* (2006)
Plant abundance	Other	Spain	1.00×10^{-4}	400	Reiné *et al.* (2006)
Cattle	Other	Switzerland	2.32×10^{-1}	393	Kohler *et al.* (2006)
Plant abundance	Other	USA	8.40×10^{-3}	336	Fortin (1999)
Erythronium grandiflorum	Other	USA	1.02×10^{-3}	256	Thomson *et al.* (1996)
Dyschirius globosus	Other	The Netherlands	3.20×10^{-1}	252	Rossi *et al.* (1992)
Silene latifolia	Other	USA	2.20×10^{-4}	220	Real & McElhany (1996)
Acer saccharum	Other	Canada	5.00×10^{-1}	200	Fortin *et al.* (1989)
Tsuga Canadensis	Other	Canada	5.00×10^{-1}	200	Legendre & Fortin (1989)
Potamogeton pectinatus	Other	The Netherlands	1.00×10^{-4}	100	Klaassen *et al.* (2006)
Balanus balanoidus	Other	The Netherlands	5.63×10^{-7}	100	Rossi *et al.* (1992)
Liatris cylindracea	Other	USA	5.94×10^{-4}	66	Sokal & Oden (1978)
Macaranga lowii	Other	Malaysia	5.00×10^{-1}	50	Bellehumeur & Legendre (1998)
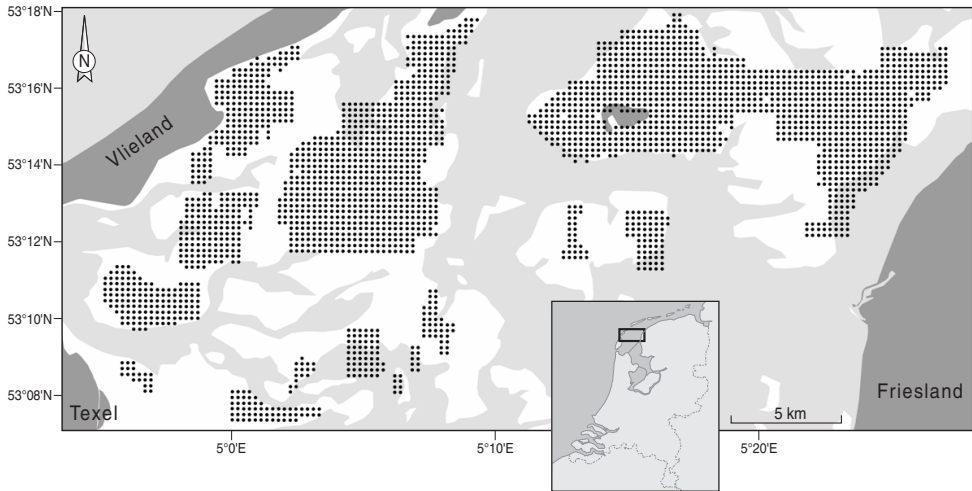
Figure 3.2. Map of all benthic sampling stations (•) on a 250 m grid in the western Dutch Wadden Sea. White areas indicate mudflats exposed during low low-water at spring-tides, light grey areas indicate water and the dark grey area indicates land.

at low tides. The sediment composition of the intertidal flats can be characterized as sands and muddy sands, with median grain sizes ranging from 140 to 200 μm (Piersma *et al.* 1993c; Zwarts *et al.* 2004).

Sampling

Benthic samples were collected in August and September 2002 to 2005 and were part of long-term benthic research efforts that began in 1988 (Piersma *et al.* 1993c, 2001; Van Gils *et al.* 2006b, 2006c). Measured densities of benthic fauna do not demonstrably change over this 2 mo sampling period (Piersma *et al.* 1993c). We collected samples over a predetermined 250 m grid that covered the intertidal mudflats (Fig. 3.2), using hand-held GPS (Garmin 12 and 45) to locate sampling sites. These sampling positions were assigned in the first year and revisited in the years after (Van der Meer 1997). On average we sampled 2750 stations annually with maximum of 2784 stations in 2005 and a minimum of 2732 stations in 2002.

Some of the sampling stations were visited on foot during low tide, others by boat during incoming, high or outgoing tides. On foot, 1 sediment core of 0.018 m^2 down to a depth of 20 cm was taken. By boat a total surface of 0.017 m^2 divided over 2 cores, also to a depth of 20 cm, was sampled at each station. Maximum water coverage to allow boat sampling was approximately 2 m. A comparison between both sampling methods, based on neighbouring sampling stations, showed no differences (Kraan *et al.* 2007). After sieving over a 1 mm mesh, all fauna were counted and recorded. All crustaceans and molluscs were collected in plastic bags and stored at –20 °C for later analyses in the laboratory (for details see Piersma *et al.* 1993c; Van Gils *et al.* 2006b, 2006c).

Simulations

Spatial structures were simulated using a 20 × 20 lattice with cell values ranging between 1 and 10 (see Fig. 3.3). Note that simulation entailed manually rearranging cell values to create the desired spatial structure. Structures varied from complete randomness, via a gradient, to different sized random patches, effectively covering the most extreme and instructive results of spatial partitioning (Fig. 3.3). Geographical coordinates were assigned by using column and row-number, respectively. All simulations were done in *Excel*, and spatial patterns were analyzed with GS+ (Robertson 2000).

Spatial analysis

To rule out the possibility that the patterns we describe are identical to the physical structure of intertidal mudflats, a grid with an equal extent (i.e. the total area covered) and grain (i.e. the sampling interval, e.g. Hewitt *et al.* 1998) as the research programme was created in a GIS environment. Stations that overlapped with sampled positions were given a 1 and stations outside the sampled positions were set at 0, followed by an analysis of spatial patterns. This allowed a direct comparison between all-directional autocorrelation patterns of the benthic species – based on abundances at sampled stations only, and the physical environment – using the imposed grid. This background autocorrelation is presented as dashed lines in Figs. 3.4-3.7.

Moran's *I* estimates the autocorrelation coefficient of a variable for all pairs of sampling stations at a given spatial interval (Cliff & Ord 1981; Fortin & Dale 2005). Like its close relative, the Pearson's product-moment correlation, Moran's *I* is sensitive to deviations from the mean and asymmetry in the distribution (Legendre & Fortin 1989; Legendre & Legendre 1998). These deviations may result in violation of stationarity, implying that the mean and variance are not stable across the extent studied. To stabilize the mean and variance as much as possible, prior to analysis all abundance data were log-transformed x' = log (x + 1) (Zar 1996). The null-hypothesis of no autocorrelation was tested with a Monte Carlo procedure using 999 runs (see Manly 1997; Rangel *et al.* 2006). Patch sizes are normally set at the point where Moran's *I* is no longer different from random (Sokal & Oden 1978a). In our case, however, due to the very large number of pairs in each lag, almost all values were statistically significantly different from random. To be able to assign meaningful patch sizes, we chose to set the threshold value of what we consider biologically meaningful at $I = 0.1$, since all but the most extreme values occurred between –0.1 and 0.1. To evaluate the robustness of this admittedly arbitrary choice, we also determined patch sizes using $I = 0.08, 0.12, 0.14$ and 0.16 as threshold values. Exactly the same patterns were derived, since patch sizes just shifted some distance classes up or down. Generally, the shape of a correlogram is regarded as the key characteristic, since this is associated with a certain spatial structuring of the data (Legendre & Fortin 1989).

Another way to capture spatial structure is to use semivariance, which is also calculated per distance class (Rossi *et al.* 1992). A plot of semivariance values against the spatial lags is called a (semi-)variogram. Spatial interpolation, e.g. kriging, uses the

information captured by a variogram to interpolate a surface (e.g. Van der Meer & Leopold 1995). The derived parameters 'nugget', 'sill', and 'range' give information on variation captured by the model, unexplained variation, and the range of autocorrelation, respectively (Bellehumeur & Legendre 1998). Unlike Moran's *I*, semivariance is not standardized and is in the same units as the original data.

When plotting semivariances for the different distance intervals on a log-log scale, the slope can be used to calculate the fractal dimension (Burrough 1981). This is a mathematical coefficient that measures the fractal geometry (non-integer dimension) of objects in space. The double-log semi-variogram need not be linear and may display so-called spatial breaks with differing fractal dimensions (Johnson *et al.* 1995; Fortin & Dale 2005). Self-similarity thus occurs within a certain scale range, indicating that the fractal dimension is not necessarily a constant function of scale (Palmer 1988), and points at different levels of organization in space and a change in structuring ecological processes. Double-log variograms and fractals are illustrated by Burrough (1981), Palmer (1988), and Fortin & Dale (2005). Analyses were done with *GS*+ (Robertson 2000) or *SAM* (Rangel *et al.* 2006).

Results

Simulations

For a randomly distributed mosaic of differing values without clear patches (Fig. 3.3A), none of the 3 methods showed significant autocorrelation, indicating the absence of spatial structure. The double-log variogram (Fig. 3.3A) indicated that the distribution was a constant function of scale; it was completely self-similar. When values were structured along a gradient (Fig. 3.3B), short-distance positive autocorrelations typically were coupled with very negative autocorrelations at the largest distances in the correlogram. The strength of structuring processes gradually decreased with increasing distance, shown by points farther apart having very different abundances. The semivariogram, as well as the double-log variogram, showed increased semi-variance values with increased distance classes, the same as given by the correlogram.

Arrangements of values in a way that generated one large patch (Fig. 3.3C) gave significant positive autocorrelations at the shortest and longest intervals and negative values at intermediate distances in the correlogram. The patch size was approximately 7 units; this is the point where the correlogram crosses the 0-line. The variogram is a mirror image of the correlogram, with highest values at intermediate distances, showing the same spatial range. The double-log variogram contained no linear part; there were no spatial breaks or spatial ranges with a constant fractal dimension D.

Evenly spaced multiple small patches of equal size (Fig. 3.3D) were represented by a repetition of patterns in the correlogram, variogram and double-log variogram. The distance between the first peak and the first through in the correlogram indicates the patch size (~2.0 units), and the continuing oscillation with decreasing amplitude revealed a repetitive pattern of patches. The 2 other methods also gave the same repeti-
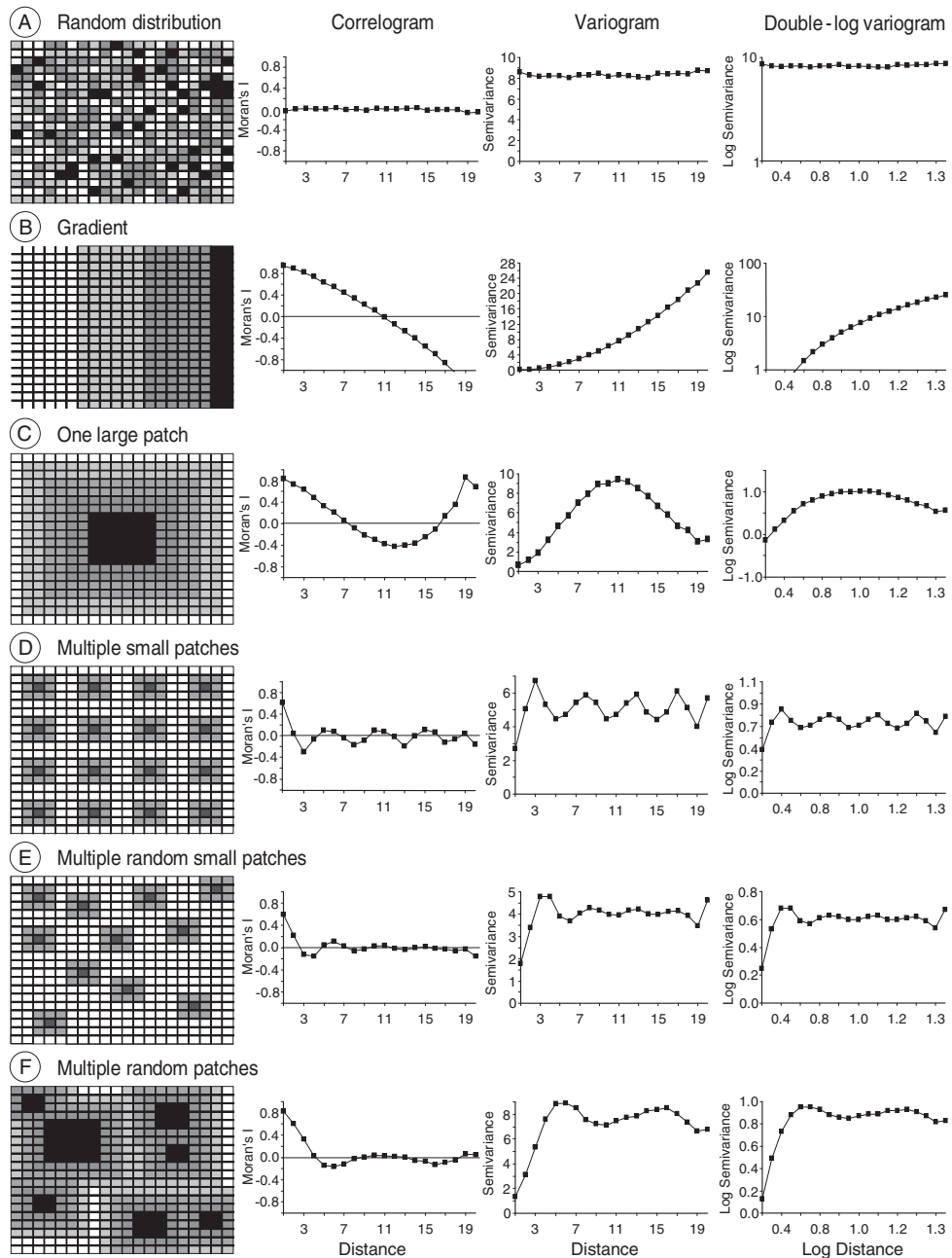
Figure 3.3. Simulated spatial patterns where the value increases from 1 (white) to 10 (black), analyzed with Moran's *I* (correlogram), semivariance (variogram) and fractal dimension (double-log variogram). The complexity of simulated pattern increases from top to bottom.

tive pattern. The fractal dimension therefore was only constant until a distance of 2 units; the rest can be considered noise.

When repeating the same simulated patches as above, but now randomly distributed across the area (Fig. 3.3E), the only obvious pattern was that of positive autocorrelations over small distances in the correlogram, the maximum semivariance value already at a small spatial range in the variogram and the absence of a linear part in the double-log variogram. The repetition of patches, though of the same size as in the previous simulation, was not clearly captured by any of the methods.

Differently sized random patches (Fig. 3.3F) created a pattern that was characterized by strong short distance positive autocorrelations, followed by non-significant random variation with increasing distance. This variation is due to the differing patch sizes and differing inter-patch distances. Again there was no linear element in the double-log variogram.

The correlogram and the variogram showed similar spatial structuring on the basis of simulated distributions (Figs. 3.3A–F), but the correlogram was easier to understand, being so similar to the Pearson's product-moment correlation. The double-log variogram, used to determine the fractal dimension D, added the least information to the outcome of the analyses. Due to the absence of a linear relation between log distance-interval and log semivariance, D often did not capture the spatial characteristics. Based on these results, we carried out the spatial analysis of census-data with Moran's I only.

Intertidal macrozoobenthos

The intertidal mudflat habitat itself has a certain physical structure in space, and this spatial structure was shown with Moran's I values and presented in Figs. 3.4-3.7 for comparison with the spatial characteristics of the distribution of benthic species (see 'Materials and Methods'). On average, the patch size of these intertidal habitats was 4000 m.

The edible cockle *Cerastoderma edule* was distributed patchily across the intertidal areas (Fig. 3.4). Indeed, densities showed positive autocorrelations at the smallest distance-classes, followed by random oscillations around zero. In 2005, a year with higher than average densities due to spatfall, not only were the autocorrelations stronger than in other years (as shown by the higher value of Moran's I in the first distance-class), but there was also a second peak at a distance of 9 km that indicated repetition of patches. Cockles more or less displayed the same distribution across the intertidal areas for all years, as shown by the distribution maps, with a gravitational centre of occurrence in the eastern part of the western Dutch Wadden Sea (Fig. 3.4). The maps show that the areas with the highest occurrence of cockles remained in place; only the density changed. In general, the spatial range or patch size was approximately 2000 m.

Macoma balthica was undergoing a decline in the western Dutch Wadden Sea during the 4 study years (left panels, Fig. 3.5), something that is also reflected in the spatial structuring. With decreasing abundance and an increasingly homogeneous distribution, the amplitude of Moran's I in the first distance-class decreased between

Figure 3.4. *Cerastoderma edule*. Distribution from 2002 to 2005 (left panels) and the correlogram (solid line) of their spatial patterns; on the x-axis the distance (in m) and on the y-axis Moran's *I*. The dotted, horizontal lines in the correlogram indicate the 95% CI. The background autocorrelation, determined by the extent of intertidal flats, is represented by the dashed line.

2002 ($I = 0.4$) and 2005 ($I = 0.3$) (Fig. 3.5), with patch sizes of *M. balthica* decreasing from 8000 m in 2002 to 3500 m in 2005, a value only marginally lower than the overall physical patchsize (dashed line).

Ragworms *Nereis diversicolor*, as shown by the maps, showed high densities and variation in their distribution across the western Dutch Wadden Sea between years (Fig. 3.6). In 2002 they were most common in the western part of our research area; in 2005 the highest densities were found in the middle and east of our sampling grid. The

Figure 3.5. *Macoma balthica*. Distribution from 2002 to 2005 (left panels) and the correlogram (solid line) of their spatial pattern; on the x-axis the distance (in m) and on the y-axis Moran's *I*. See Fig. 3.4 for further explanation.

correlograms were quite similar throughout, with a spatial structure that ranged between 3000 and 4000 m, although there was a second peak at ~20 km in 2002 and not afterwards.

The predatory polychaete *Nephtys hombergii* generally occurred in low densities throughout our sampling area (Fig. 3.7), with highest abundances in more sandy areas (pers. obs.). *N. hombergii*, besides short-distance autocorrelation, showed no other spatial structure. Especially in 2004, the distribution approached randomness.
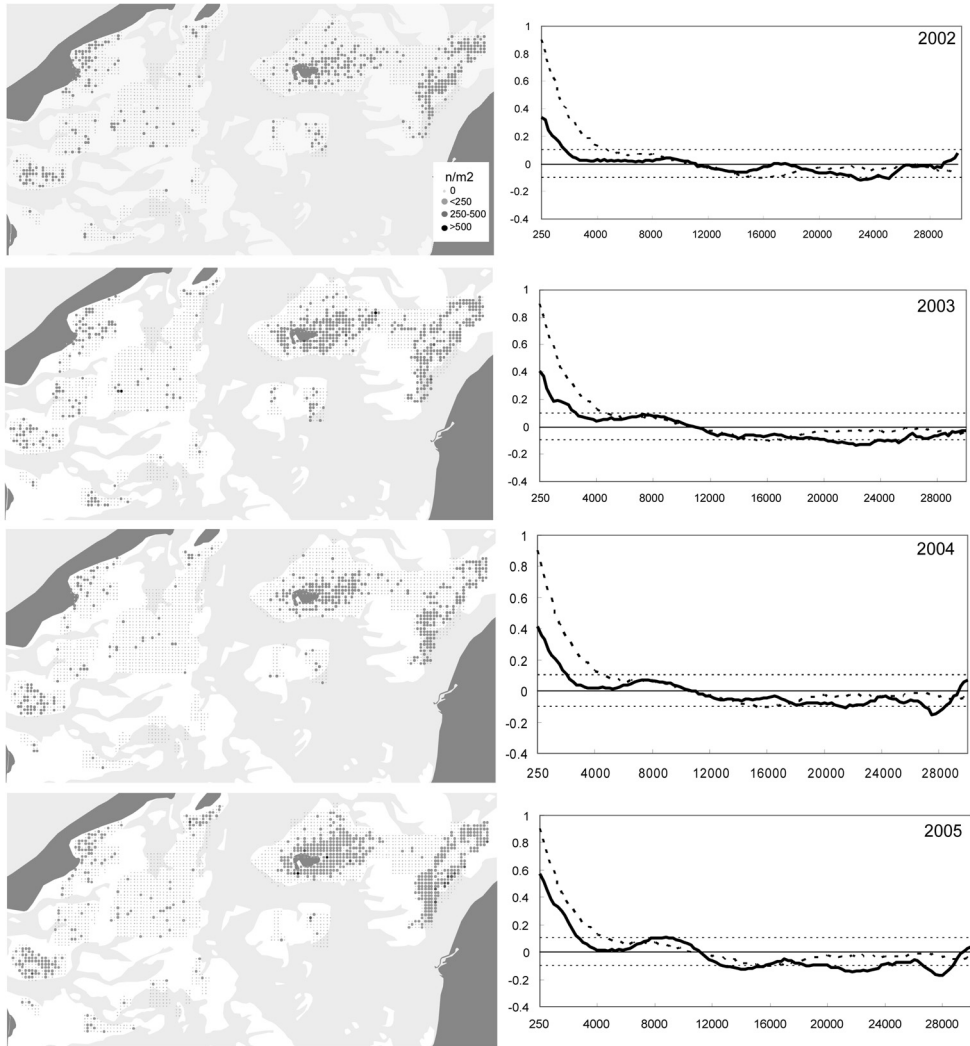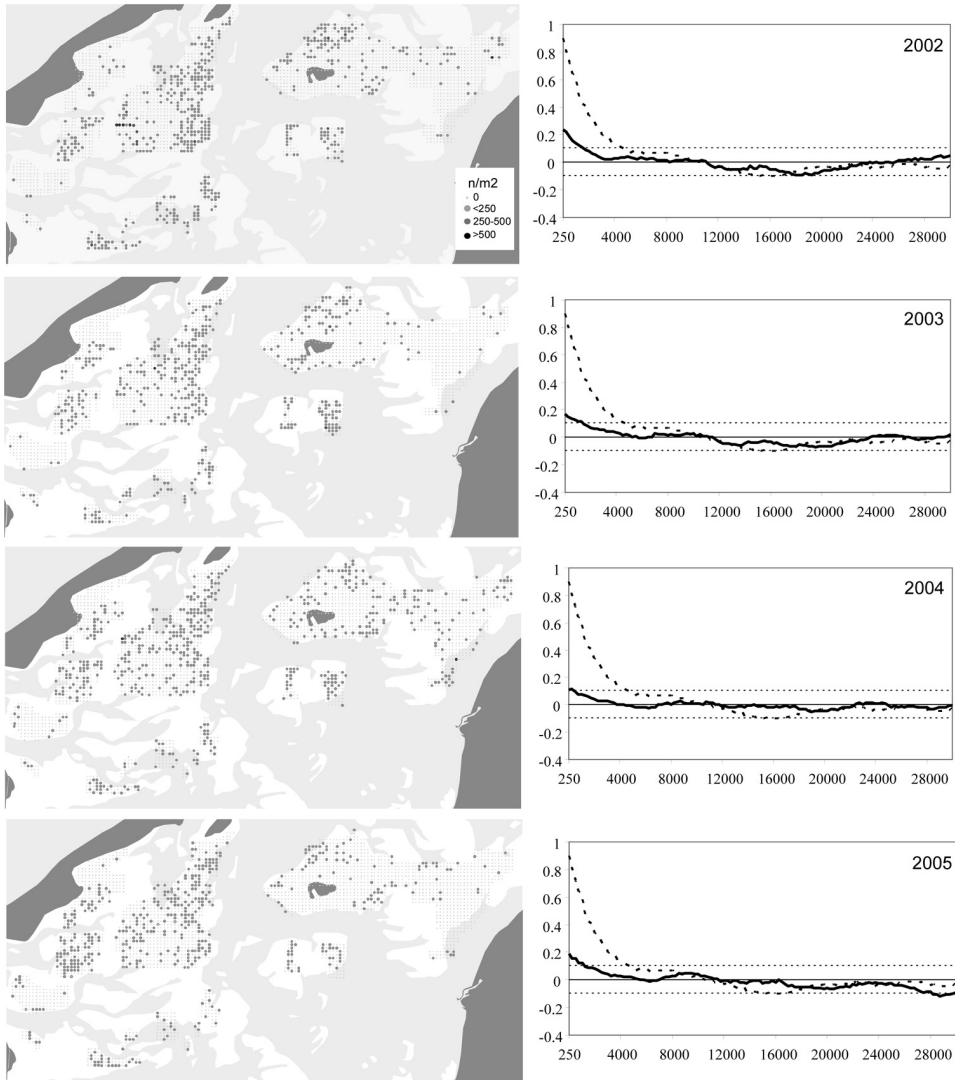
Figure 3.6. *Nereis diversicolor*. Distribution from 2002 to 2005 (left panels) and the correlogram (solid line) of their spatial pattern; on the x-axis the distance (in m) and on the y-axis Moran's *I*. See Fig. 3.4 for further explanation.

Overall comparison

In general, the more striking spatial structures are shown by the most abundant species. Not only is patch size larger in these species (Fig. 3.8), they also reveal higher amplitudes in the correlograms (Figs. 3.4-3.7). An ANCOVA (Systat Software) confirmed that slope and intercept were not statistically different between species (slope $F_{3,11} = 2.052$, $p = 0.17$; intercept $F_{1,11} = 1.95$, $p = 0.19$). Regression analysis
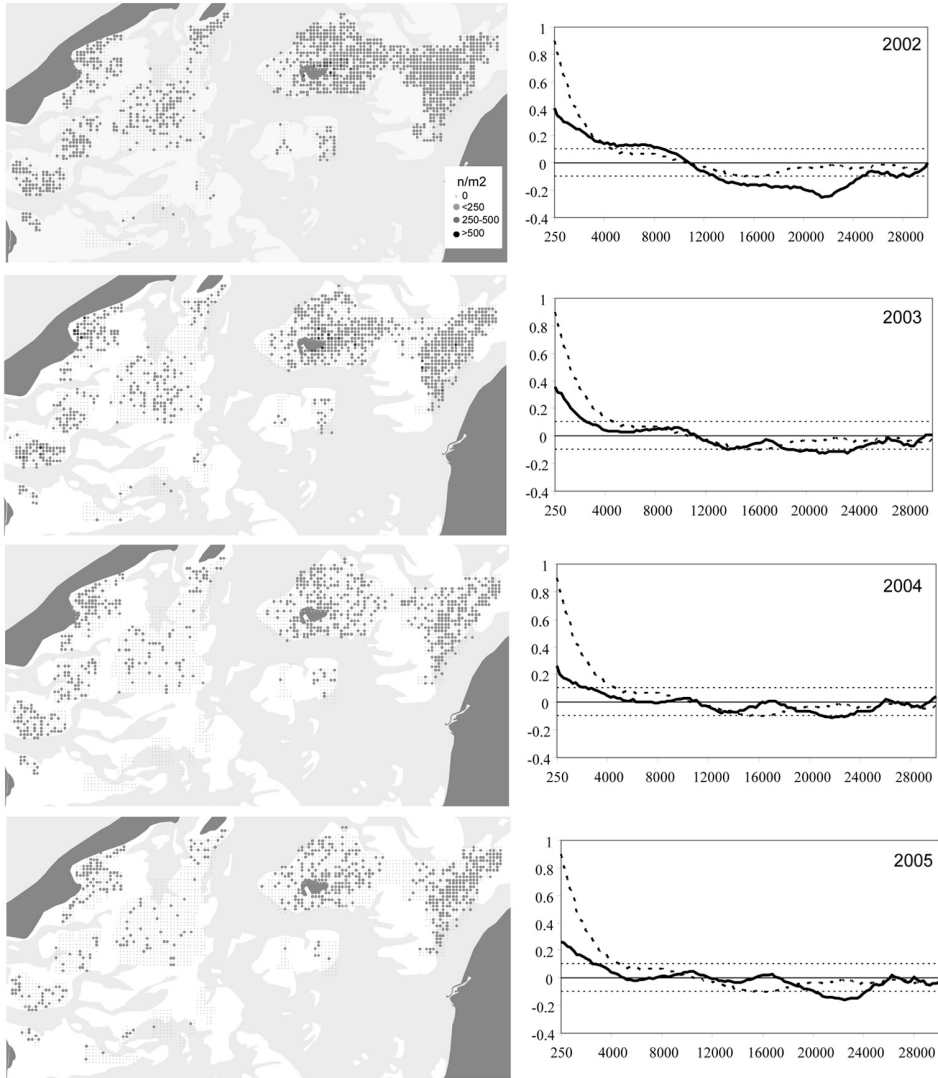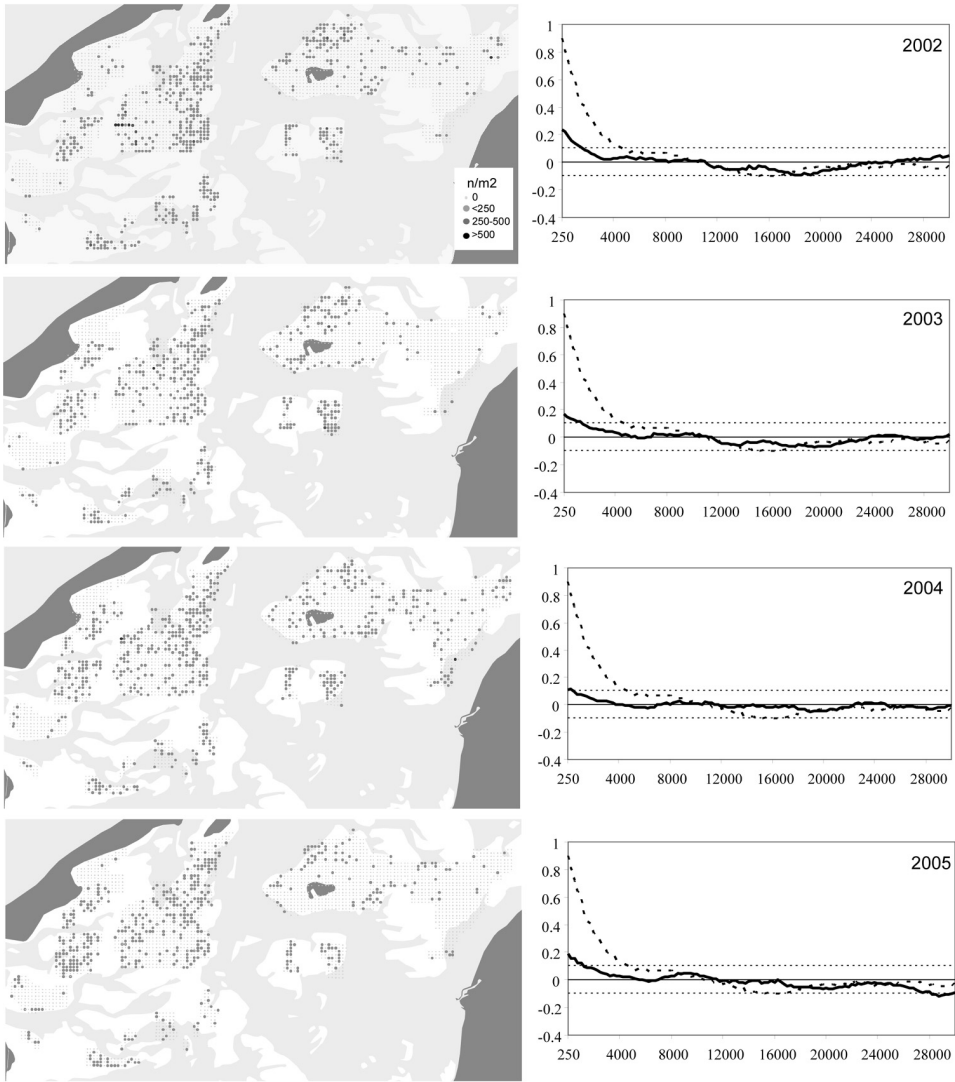
Figure 3.7. *Nephtys hombergii*. Distribution from 2002 to 2005 (left panels) and the correlogram (solid line) of their spatial pattern; on the x-axis the distance (in m) and on the y-axis Moran's *I*. See Fig. 3.4 for further explanation.

showed a significant relation between density and patch size ($F_{1,14} = 9.531$, $p < 0.01$, $R^2 = 0.44$). This pattern was maintained when the threshold-value for significance was varied (see 'Materials and Methods'). Overall, the correlograms visually best resembled the simulated patterns of randomly distributed and differently sized patches (Fig. 3.3F) and multiple random small patches (Fig. 3.3E), both characterized by short-distance positive autocorrelation and noise at larger distances.
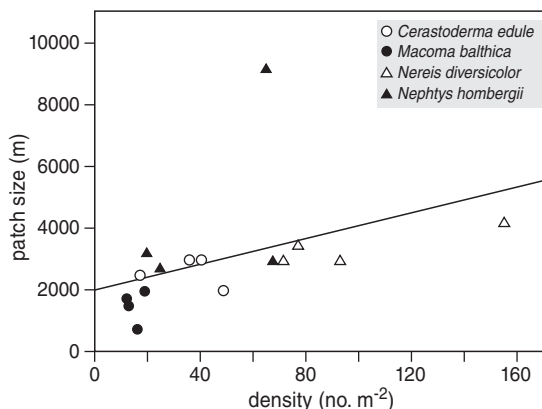
Figure 3.8. Patch size in relation to the density of the 4 benthic species studied (*Cerastoderma edule, Macoma balthica, Nereis diversicolor* and *Nephtys hombergii*) from 2002 to 2005 (see Figs. 3.4-3.7).

Discussion

Although spatially explicit analytical methods are common practice in plant and landscape ecology (e.g. Sokal & Oden 1978a; Cliff & Ord 1981), with notable exceptions (Thrush *et al.* 1989; Hewitt *et al.* 1997a, 1997b; Legendre *et al.* 1997), they seem underexplored in marine science. The multitude of different techniques available (e.g. Fortin & Dale 2005), ranging from Moran's *I* to the Mantel statistic, can be daunting. We tested and compared 3 methods to determine spatial structuring on artificial data, i.e. Moran's *I*, semivariance and fractals.

Calculating the fractal dimension is informative when the variogram is linear (Fortin & Dale 2005), which only occurs when species are distributed randomly or as gradients across the area under study. Analysis of the simulated spatial patterns showed that the presence of structure dismissed fractals as a relevant statistic. *A posteriori* our decision was validated by patterns encountered in the benthic data; gradients and random distributions were never encountered (Figs. 3.4-3.7). The 2 other methods were able to capture all computer-generated patterns. However, Moran's *I*, unlike semivariance, is standardized and all correlograms are therefore expressed on the same scale and allow direct comparison. Consequently, we choose Moran's *I* as the most appropriate method to analyze spatial patterns of intertidal benthos.

The 4 macrobenthic species displayed spatial structuring at the scale of our benthic monitoring programme, i.e. the western Dutch Wadden Sea. This landscape-scale description of spatial patterns, as shown by the literature survey (Fig. 3.1; Table 3.1), is only rivalled by a limited number of studies, none of which were marine. The most obvious structures were small-scale patches, with a range of a few distance classes (Figs. 3.4–3.7), reaching a diameter of up to 9000 m. These patterns, comparable to the simulated multiple random patches (Fig. 3.3F), persisted across the years, although

some species (e.g. *Nereis diversicolor*) changed their distribution from west to east. The only noticeable change was the amplitude that increased with the occurrence of successful recruitment or decreased due to mortality and/or a more even distribution (Figs. 3.4–3.7). Apart from McArdle & Blackwell (1989), also a marine study, the present study is the only one extending the analysis beyond a single snap-shot in time, which allowed us to show the temporal constancy of spatial patterns.

Patterns also differed from the intrinsic autocorrelation imposed by the monitored points (reflecting the physical structure of the mudflats), showing that species distributions are shaped by processes other than the extent of mudflats. To the best of our knowledge this is the first attempt to disentangle species' spatial patterns from that of the physical extent of their environment. It is likely that a combination of factors such as sediment composition, inundation time, spatial variation in recruitment or interspecific interactions determines spatial patterning of benthic infauna (Thrush 1991; Legendre *et al.* 1997). This, however, still awaits verification within a framework that also explicitly takes the spatial variation of environmental parameters into account. Generalised estimation equations (GEE) seem to offer an elegant solution (Dormann *et al.* 2007).

Currently, in every study a sampling design is chosen, with a certain extent and grain that matches its questions or funding. However, patterns change with scale and what appears a gradient on a large scale can be described as patchy on smaller scales (Levin 1992). Therefore, every study is reduced to a description of spatial pattern for a specific area with a specific sampling scheme. However, what unifies all studies is the occurrence of spatial heterogeneity in the distribution of their study organism ranging from a few meters to landscape-scale patterns (Table 3.1).

It is obvious that the ecological world is spatially structured (Sparrow 1999; Wiens 2000). Currently 2 approaches exist to deal with this spatial variability. One focuses on the mathmathical aspects of spatial structure (e.g. He *et al.* 2007), whereas another views autocorrelation as an ecological parameter (e.g. Kohler *et al.* 2006). It is this last approach which is the most rewarding, since it potentially could enhance an ecological understanding of, for example, benthos-sediment relationships in intertidal areas within a spatially explicit framework.

4

The role of environmental variables in structuring landscape-scale species distributions in seafloor habitats

Casper Kraan, Geert Aarts, Jaap van der Meer, and Theunis Piersma

Summary

Ongoing statistical sophistication allows a shift from describing species' spatial distributions towards statistically disentangling the possible roles of environmental variables in shaping species distributions. Based on a landscape-scale benthic survey in the Dutch Wadden Sea, we show the merits of spatially explicit generalized estimating equations (GEE). The intertidal macrozoobenthic species, *Macoma balthica, Cerastoderma edule, Marenzelleria viridis, Scoloplos armiger, Corophium volutator* and *Urothoe poseidonis* served as test cases, with median grain-size and inundation time as typical environmental explanatory variables. GEEs outperformed spatially naïve generalized linear models (GLMs), and removed much residual spatial structure, indicating the importance of median grain-size and inundation time in shaping landscape-scale species distributions in the intertidal. GEE regression coefficients were smaller than those attained with GLM, and GEE standard errors were larger. The best fitting GEE for each species was used to predict species' density in relation to median grain-size and inundation time. Although no drastic changes were noted compared to previous work that described habitat suitability for benthic fauna in the Wadden Sea, our predictions provided more detailed and unbiased estimates of the determinants of species-environment relationships. We conclude that spatial GEEs offer the necessary methodological advances to further steps towards linking pattern to process.

Introduction

'Spatial autocorrelation: trouble or new paradigm?' (Legendre 1993) was an eye-opener in the early 1990s. It marked the beginning of a new framework that underlined the key role of spatial heterogeneity in both statistical analyses and ecological theory (e.g. Wagner & Fortin 2005). Many researchers now routinely include spatial patterning of their focal species as an important ecological variable (e.g. Aarts *et al.* 2008; Kraan *et al.* 2009a, 2009b). Now that spatial autocorrelation is accepted as a general phenomenon (Sparrow 1999; Wagner & Fortin 2005), interest recently shifted from pattern to process, i.e. the role of environmental variables in shaping species distributions (Keitt *et al.* 2002; Dormann *et al.* 2007).

In marine ecosystems a range of methods such as canonical correlation (Van der Meer 1999) and logistic-regression (Ysebaert *et al.* 2002; Compton *et al.* 2009) have been used to describe macrozoobenthos-environment relationships. However, none of these methods encompass spatial structure in the distribution of either explanatory or response variables. Autocorrelation violates the assumption of independent errors, leading to underestimation of parameter standard errors and biased parameter estimates and model fits (Tognelli & Kelt 2004; Dormann 2007; but see Diniz-Filho *et al.* 2007). It may lead to flawed conclusions (Lennon 2000; Keitt *et al.* 2002); Kühn (2007) even observed an inversion of regression slopes between plant species richness and altitude. Therefore, in the likely occurrence of autocorrelation when dealing with spatial datasets, spatially explicit methods are a necessity.

Based on a large-scale benthic research programme in the western Dutch Wadden Sea (Kraan *et al.* 2009a, 2009b; Van Gils *et al.* 2009a) we highlight the landscape-scale distributions of *Macoma balthica, Cerastoderma edule, Marenzelleria viridis, Scoloplos armiger, Corophium volutator* and *Urothoe poseidonis* (Appendix A) and the environmental variables that structure their spatial patterns. It is generally assumed that large-scale spatial patterns are a response to environmental variables, whereas small-scale spatial patterns are related to biological interactions (Thrush 1991; Legendre 1993). Since we study animal-environment relationships at a landscape-scale, we expect to find a strong decrease of spatial structuring in the distribution of our benthic species after accounting for environmental variability.

To handle autocorrelation in response and explanatory variables, as well as non-Gaussian distributions, we apply 'generalized estimating equations' (GEE; Liang & Zeger 1986). These are best described as models extending generalized linear models (GLM) with a spatial variance-covariance matrix. We illustrate the impact of autocorrelation on the results for spatially naive GLMs and GEEs with varying assumptions about the correlation structure. In addition to these methodological puzzles, we demonstrate how spatially explicit methods can be used to advance our understanding of species distributions.

Methods

Study area

The western Dutch Wadden Sea (53°N, 4-5°E) mainly consists of intertidal- and subtidal mudflats, and gullies, and is bordered to the west and north by the barrier islands of Texel, Vlieland and Terschelling and to the south by the mainland coast of Friesland. About three-quarters of this area consist of soft sediment flats exposed at low tides. Our study area of about 225 km^2 is covered with a grid of fixed sampling stations at 250 m intervals (Fig. 4.1).

Benthic sampling

Intertidal macrozoobenthos was sampled in July–September 2005 by rubberboat during high tide or on foot during low tide. Sampling locations, 2784 in total, were found with handheld GPS (Garmin 45 and 12, using WGS84 as map datum) and at each station 1/56 m^2 was sampled to a depth of 20–25 cm. The sampling cores were sieved over a 1 mm mesh and all individuals were counted and identified (Van Gils *et al.* 2006a, 2006b, Kraan *et al.* 2009a, 2009b).

Environmental variables

Sediment samples in a fixed 1000 m grid were also taken (Fig. 4.1), consisting of sediment from the top 5 cm of the seabed. These samples, 157 in total, were used to determine sediment characteristics, such as median grain-size (MGS; see Bocher *et al.* 2007). To assign a sediment-value to each benthic sampling station, MGS-values were interpolated across the whole study area by means of inverse distance weighting (Compton *et al.* 2009).

Elevation (cm) relative to Dutch Ordinance Level (see Van Gils *et al.* 2006b) was appointed to the nearest sampling station. Furthermore, by comparing elevation with values obtained from an average tide with a sinusoidal curve, inundation time (IT) per tidal-cycle of 12.25 hrs was calculated. We based calculations on an ideal tide from Harlingen situated on the mainland coast of Friesland (Fig. 4.1). The number of explanatory variables was limited to MGS, IT, their quadratic terms, as well as their interaction. Other environmental variables, such as distance to gully, were highly collinear with the before mentioned variables and therefore excluded to obtain the most parsimonious model.

Response variables

Response variables were species-counts (*n* per sample). From three groups of benthic fauna we have chosen the two most abundant species (Appendix A). (1) Bivalves consisted of *M. balthica* and *C. edule*. *M. balthica* was divided in adults (≥ 1 growth ring) and juveniles (no growth rings), since different habitat preferences are expected because of juvenile migration (e.g. Beukema 1993). (2) Polychaetes entailed *M. viridis* and *S. armiger*. (3) Crustaceans comprised *C. volutator* and *U. poseidonis*.
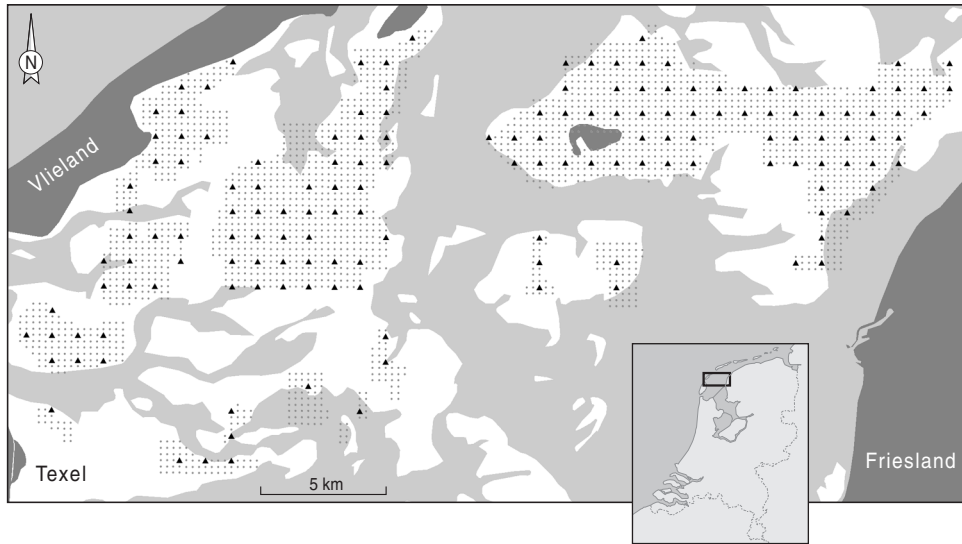
Figure 4.1. Map of all benthic (circles) and sediment (triangles) sampling stations, on a 250 m grid and 1000 m grid, respectively, in the western Dutch Wadden Sea. White areas indicate mudflats exposed during low-water, intermediate grey areas indicate water, and land is represented by the darkest grey areas.

Spatial modeling

Because of the presence of spatial autocorrelation, as shown previously for intertidal benthic fauna in the Dutch Wadden Sea (Kraan *et al.* 2009a, 2009b), we opted for GEEs to account for autocorrelation in both the spatial distribution of benthic species and the explanatory environmental variables. Fitting GEEs involves a series of steps. (1) First a GLM assuming a Poisson error distribution was fitted under the assumption that species-counts were independent from each other. (2) This GLM was used to estimate the spatial correlation matrix of the residuals. (3) The regression model is then extended by incorporating the spatial correlation matrix. Prior to these iterative steps (2 and 3) the data were clustered into smaller blocks of 2×2, 3×3, or 4×4 sampling stations to reduce computation time. Correlations within each cluster were included in the model, while correlations between clusters were assumed to be absent (Carl & Kühn 2007; Koper & Manseau 2009).

The correlation within a cluster can be specified by two different structures. (1) *Quadratic*, where the correlation varies with distance class (Carl & Kühn 2007). For example, a block of 2×2 sampling stations contains 2 distance classes, therefore 2 correlation parameters need to be estimated. (2) *Exchangeable*. All correlations within a cluster are equal. A third structure, *fixed*, where the correlation decreases with distance and can be estimated by Moran's *I* of GLM residuals (therefore clustering is not needed [Dormann *et al.* 2007]), was omitted. This structure may lead to contradicting results, such as a large reduction of residual autocorrelation combined with, on

occasion, smaller estimated standard errors than the non-spatial models. Another downside is the long computation time and large matrices, often failing convergence (Dormann *et al.* 2007). More details of GEEs and comparison with other methods see Hardin & Hilbe (2003) and Dormann *et al.* (2007).

To choose the most appropriate correlation structure and cluster-size, we visually compared the correlograms (e.g. Kraan *et al.* 2009a) of the residuals of the full GLM and Pearson residuals of the GEEs standardized by the working correlation (e.g. Carl & Kühn 2007) (Fig. 2). We selected the correlation structure and cluster-size leading to the lowest small-scale (i.e. 250 m) residual autocorrelation (e.g. Carl & Kühn 2007, Dormann *et al.* 2007). Next task was to obtain the minimal adequate model. GEE uses a quasi-likelihood framework for model estimation (Liang & Zeger 1986); therefore, a maximum-likelihood based method for model selection such as Akaike's Information Criterion is not valid. Instead, we used backward model selection based on the *quasi-likelihood-under-the-independence-model information criterion* or QIC (Pan 2001).

$$\text{QIC} = -2Q + 2\text{trace}(\hat{\Omega}_I^{-1}\,\hat{V}_R)\ ,$$

Q is the quasi-likelihood calculated as $Q = y\log\mu - \mu$, where μ represents the mean (McCullagh & Nelder 1989, Appendix C). The p-dimensional matrices $\hat{\Omega}_I$ and $\hat{V}_R$ are variance estimators of the regression coefficients under the correlation structures I (independence) and R (GEE-based), respectively (Cui & Feng 2009).

In the presence of spatial autocorrelation we expect, under the model (incorrectly) assuming independent data, an underestimation of the parameter variances. Accounting for spatial autocorrelation will most likely lead to higher parameter variances and hence a larger trace($\hat{\Omega}_I^{-1}\,\hat{V}_R$). Like Akaike's Information Criterion the model with the lowest QIC is the best model (Pan 2001). Note that QIC is not suitable for selecting the most appropriate correlation structure (Koper & Manseau 2009; but see Hin *et al.* 2007). QIC, by definition, seems to favor those models with the lowest trace($\hat{\Omega}_I^{-1}\,\hat{V}_R$). However, it does allow determining the best subset of covariates (Cui 2007). In general, model-selection under spatial autocorrelation has still to be developed and no general guidelines exist yet (Dormann *et al.* 2007; Koper & Manseau 2009). All analyses were done using *R* (R Development Core Team 2008; version 2.6.2; Appendix C for code) following Carl & Kühn (2007).

Results

A clear dichotomy existed between residual-patterns of spatial and non-spatial models describing species-environment relationships in intertidal areas of the western Dutch Wadden Sea. Intercept-models (species-counts only) and *independent* correlation structures, which approximate spatially naïve GLMs, contained residual patterning (Fig. 4.2; Table 4.1). Spatial models reduced spatial autocorrelation (Fig. 4.2; Table 4.1).
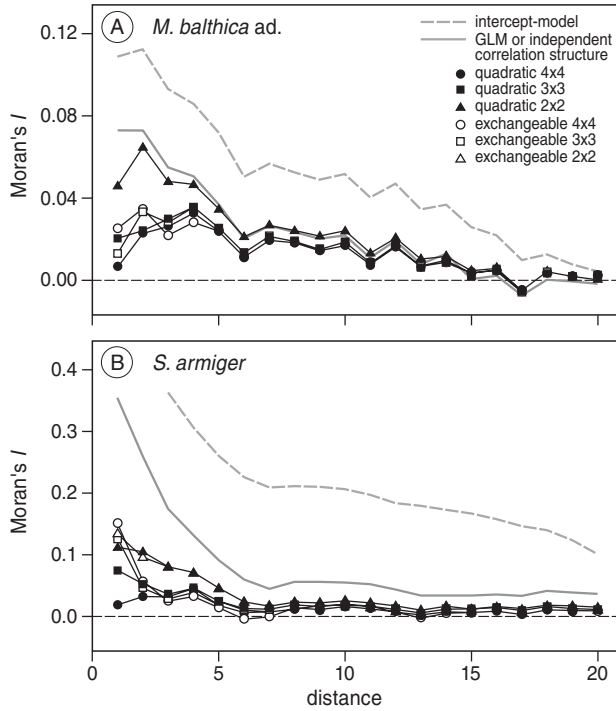
Figure 4.2. Residual autocorrelation (Moran's *I*) of differently structured GEEs of the full model illustrated for: (A) *M. balthica* adult and (B) *S. armiger*. Distance intervals on the X-axis are per 250 m interval (1 = 250 m, 2= 500 m, etc.).

Overall, an *independent* correlation structure was under no circumstances selected as the best correlation structure to model the spatial interaction between species and explanatory environmental variables (Table 4.1). Also, a 2×2 cluster-size never appeared to be the best cluster-size (Table 4.1). The 4×4 *quadratic* correlation structure was selected for all species, except for *C. volutator* (3×3 *exchangeable*) and *U. poseidonis* (3×3 *quadratic*). For *C. edule* we illustrated the effects of accounting for spatial auto-correlation (Appendix D), by comparing a spatially naïve GLM and a spatially explicit GEE, assuming a *quadratic* correlation structure and a 4×4 cluster-size. Indeed, as expected, the standard errors became much larger (Appendix D). Consequently, the absolute values of all GEE parameters, except the intercept, became smaller. This showed that ignoring spatial autocorrelation not only leads to a different assessment of the significance of an environmental variable, it also illustrated that slopes became flatter.

Given the best correlation structure and cluster-size (Table 4.1), we used backward model-selection to determine the importance of the environmental variables IT and MGS, their quadratic terms and interactions (Table 4.2). If deleting a variable lowered

Table 4.1. Selection of the best correlation structure (bold), i.e. *independence, quadratic* or *exchangeable*, and best cluster-size illustrated for (A) *M. balthica* adult and (B) *S. armiger*, based on the residual autocorrelation (Moran's *I*) at distance-class 1 (250 m).

Model-type	QIC	Quasi-Likelihood	Trace	Moran's *I* at class 1	Moran's *I* at class 5
(A) *M. balthica* ad.					
GEE *ind.*	2558.94	-1275.01	4.46	0.09	0.06
GEE *quad.* 4×4	**2567.97**	**-1276.25**	**7.74**	**0.01**	**0.02**
GEE *quad.* 3×3	2565.41	-1275.86	6.84	0.02	0.03
GEE *quad.* 2×2	2560.53	-1275.06	5.20	0.05	0.05
GEE *exch.* 4×4	2568.72	-1276.37	7.99	0.03	0.03
GEE *exch.* 3×3	2565.33	-1275.84	6.83	0.01	0.03
GEE *exch.* 2×2	2560.52	-1275.06	5.20	0.05	0.05
(B) *S. armiger*					
GEE *ind.*	-766.10	386.73	3.68	0.31	0.17
GEE *quad.* 4×4	**-660.73**	**339.95**	**9.58**	**0.02**	**0.03**
GEE *quad.* 3×3	-686.11	350.42	7.36	0.07	0.05
GEE *quad.* 2×2	-742.41	376.95	5.74	0.11	0.08
GEE *exch.* 4×4	-722.99	371.42	9.93	0.15	0.06
GEE *exch.* 3×3	-688.41	351.67	7.47	0.13	0.05
GEE *exch.* 2×2	-741.19	376.35	5.75	0.13	0.09

Table 4.2. Model selection, to obtain the minimal adequate model (bold), based on QIC values. Shown is model improvement after backward selection of an explanatory variable or an interaction between variables. Variables increase in importance from top to bottom. For each species the best correlation structure and cluster-size was applied.

(A) *M. balthica* ad. Model	QIC	(B) *M. balthica* juv. Model	QIC	(C) *C. edule* Model	QIC	(D) *M. viridis* Model	QIC
Full	**2567.97**	**Full**	**1539.82**	**Full**	**3066.09**	**Full**	**-15420.0**
- IT	2572.91	- IT	1540.78	- MGS^2	3068.26	- MGS x IT	-15385.9
- MGS^2	2587.68	- MGS^2	1543.26	- MGS	3110.07	- IT	-14206.6
- MGS	2615.96	- MGS x IT	1549.65	- IT	3137.24	- IT^2	-14011.9
- MGS x IT	2617.13	- IT^2	1840.45	- IT^2	3165.55	- MGS	-10883.1
- IT^2	2677.24	- MGS	2189.62	- MGS x IT	4216.42	- MGS^2	598.2

(E) *S. armiger* Model	QIC	(F) *C. volutator* Model	QIC	(G) *U. poseidonis* Model	QIC
Full	**-660.73**	**Full**	**-44938.5**	Full	-17719.7
- MGS x IT	-649.65	- MGS x IT	-44800.4	**- MGS x IT**	**-17776.3**
- IT	-428.52	- IT	-44286.5	- IT	-15731.9
- IT^2	-132.43	- MGS	-43200.7	- IT^2	-14088.5
- MGS^2	587.49	- IT^2	-35830.1	- MGS^2	-11617.6
- MGS	2092.86	- MGS^2	-7495.29	- MGS	-6926.49
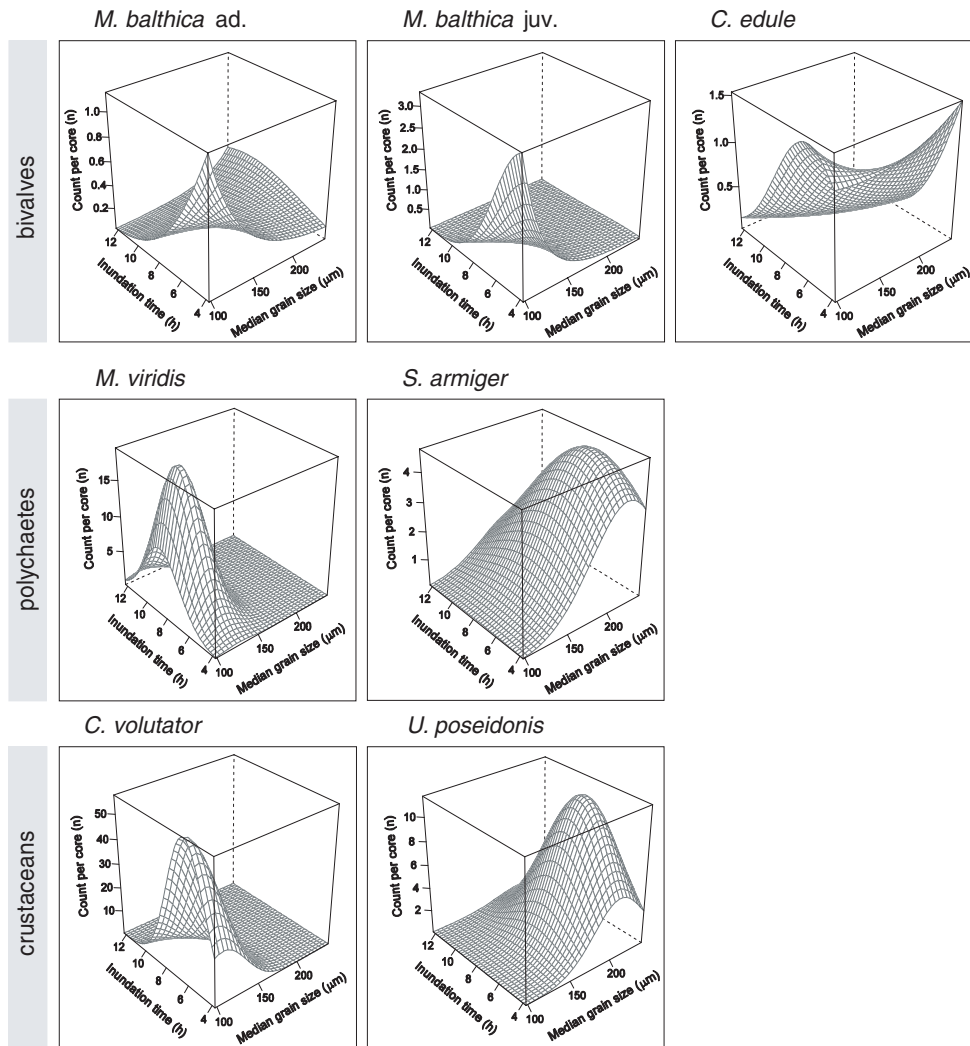
Figure 4.3. Fitted preference of macrobenthic species in relation to MGS and IT in the western Dutch Wadden Sea. For each species the minimal adequate GEE was applied (Table 4.3).

the QIC, it so suggested a better model than the full model with which we started. In practice, however, only the interaction MGS x IT for the *U. poseidonis*-model was excluded (Table 4.2G).

The best model for each species was used to predict species' density or 'perceived preference' (preference subsequently) for the environmental variables MGS and IT. Predictions were only made for IT- and MGS-values larger than the 0.01 quantile and smaller than the 0.99 quantile (Appendix B). These restrictions downsized potential

over-emphasis of scarce and unlikely MGS and IT combinations. The analysis showed highest densities for both adult and juvenile *M. balthica* in muddy sandflats with a short to medium IT (Figs. 4.3A-B). In addition, adults also preferred coarse sediments with a long IT (Fig. 4.3A). *C. edule* preferred a wide range of MGS with an IT of 6–8 h (Fig. 4.3C). The spionid *M. viridis* preferred a particularly narrow range of environmental characteristics, i.e. a MGS range of 100–150 µm and an IT of 8–10 h (Fig. 4.3D). *S. armiger* mainly preferred coarse sediments over the complete range of available IT (Fig. 4.3E). *C. volutator* (Fig. 4.3F) preferred muddy sediments with an IT of 6–8 h. *U. poseidonis* combined a preference for coarse sediments with intermediate IT (Fig. 4.3G).

Discussion

In marine ecosystems, thus far species-environment relationships have been analyzed with methods that do not take spatial autocorrelation into account. Although this does not necessarily imply that these analyses are flawed (Diniz-Filho *et al.* 2003; but see Lennon 2000), some bias in model-coefficients (Dormann 2007; Bini *et al.* 2009) and decrease in model parsimony probably did occur. Our results support that species-environment relationships should be done with spatially explicit methods, such as GEE or alternatives such as generalized linear mixed models (GLMM, Pinheiro & Bates 2000) or Bayesian model-based geostatistics (Diggle & Ribeiro Jr. 2007). The kind of correction appears to be of minor importance, as long as a correction is made (see Results; Keitt *et al.* 2002). However, efficiency gains can still be made by using the best correlation structure and best cluster-size, followed by model 'fine-tuning' based on QIC (Fig. 4.2).

Thus far, the number of studies applying spatial GEEs is very limited (Carl & Kühn 2007); our study constitutes only the second application on a landscape-scale with survey data and a large number of samples, and is the first in a marine setting. GLMMs or model-based geostatistics would be equally suitable for these kinds of spatial analyses (Dormann *et al.* 2007); however, the size of the data set is a limiting step, which is circumvented by GEEs that slice the data into clusters. Note that these latter methods are better suited for spatial prediction and interpolation than GEEs because spatially correlated errors can be predicted for non-sampled stations (Diggle & Ribeiro Jr. 2007; Dormann *et al.* 2007).

As hypothesized, residual structure was greatly reduced after accounting for environmental variability. Indeed, the landscape-scale distribution of hidden marine intertidal species in the western Dutch Wadden Sea could, for a larger part, be attributed to IT and MGS (Tables 4.1-4.2). The remaining residual spatial variation, which represents variation not accounted for by the selected physical parameters, can be credited to either an environmental variable not included in the analyses or biotic interactions between or within species (Keitt *et al.* 2002; Wagner & Fortin 2005). Disentangling these is an important goal (Wagner & Fortin 2005; Dormann *et al.* 2007). In this

respect, dynamic regressions that estimate competition coefficients could be rewarding (Pfister 1995), especially if this approach would be extended with a variance-covariance matrix to include autocorrelation. In addition, there remains a possibility that the included environmental variables are driven by other, unknown, spatially patterned factors (Keitt *et al.* 2002; Diniz-Filho *et al.* 2003). However, this feature is shared by all regression-type analyses and can not be solved without experiments. Nevertheless, acknowledging and accounting for spatial autocorrelation, as presented here, is a marked improvement from spatially naïve analyses. Better models can be derived and pinpoints that ecology should encompass spatial autocorrelation (e.g. Sparrow 1999; Wagner & Fortin 2005).

The spatially explicit framework applied for Wadden Sea benthic fauna likely offers precise and statistically sound estimates of environmental variables governing species abundances, compared to spatially naïve approaches (Appendix D). The question remains how robust previous spatially naïve analyses of species-environment associations in this area actually are? Unfortunately, no such analyses at a landscape-scale overlap the extent of our study area. Therefore, we can not evaluate former results and determine if drastic differences occur, as previously shown by Tognelli & Kelt (2004) and Kühn (2007). However, habitat associations of macrobenthic fauna in marine intertidal areas have been particularly centered on the use of sediment grain-size distributions to approximate habitat suitability (e.g. Ysebaert *et al.* 2002; Compton *et al.* 2009). Indeed, the present study also indicates this is the most important habitat characteristic (Table 4.2). Yet, IT also contributed significantly to habitat suitability for benthic fauna, as did the interaction between IT and MGS (Fig. 4.3; Table 4.2). Without applying spatially explicit analyses, such ecological patterns would leave room for discussion about the correct relationships between variables.

Ignoring the different scales of research, a few studies offer insight in species-environment relationships in the Wadden Sea, and allow qualitative comparisons of habitat preferences. Some examples: (1) similar to our results (Fig. 4.3B), others (e.g. Beukema 1993) show that juvenile *M. balthica* prefer short IT, areas high in the intertidal zone. (2) Because of their peculiar downslope winter migration (Beukema 1993), adult *M. balthica* should occur in the middle and lower zones in the intertidal (e.g. Beukema 1993); this is only partially apparent in our results (Fig. 4.3A). Our more recent analyses seem to suggest that a large part of the adults do not migrate from the shallow and muddy areas towards the deeper and sandier regions of the Wadden Sea. Given the rapid decline of the population in the western Dutch Wadden Sea (Van Gils *et al.* 2009), their habitat preferences might have shifted in recent times.

To sum up, our results do not show drastic changes, but indicate that we achieved a more detailed and unbiased insight in determinants of species-environment relationships in intertidal ecosystems in the Dutch Wadden Sea. This spatial approach extents current knowledge, and offers enhanced understanding of species distributions, which still is underexplored in marine science (Compton *et al.* 2009; Thrush *et al.* 2009). GEEs offered the necessary methodological advances to describe species distributions in a spatially patterned environment.

Acknowledgements

Appendix A. Minimum and maximum (mean) counts per sampling station of the benthic species.

Species	Ecological characteristics	Counts
Macoma balthica	Tellinid bivalve. Mainly a deposit-feeder, but has the ability to switch to suspension-feeding	0 - 3 (0.18) ad. 0 - 8 (0.13) juv.
Cerastoderma edule	Suspension-feeding bivalve. A widely distributed species, living in sandy mud, sand, and fine gravel sediments	0 - 14 (0.40)
Marenzelleria viridis	Deposit-feeding, spionid, polychaete. Exotic species permanently established in our study area since 1990-1991	0 - 186 (2.61)
Scoloplos armiger	Widely distributed polychaete species. Mobile, sub-surface, deposit-feeder that occupies most suitable habitat	0 - 36 (2.32)
Corophium volutator	Small, deposit-feeding, amphipod. Lives in semi-permanent burrows in the upper 5 cm of the sediment	0 - 206 (3.91)
Urothoe poseidonis	Commensal deposit feeding amphipods with lugworms *Arenicola marina*; it lives inside the feeding pocket of *A. marina*	0 - 105 (3.80)

Appendix B. Scatterplot of MGS and IT. The response-landscapes (Fig. 4.3) were based on the area within the box, representing a data-range between the 0.01 and 0.99 quantiles for both MGS and IT.
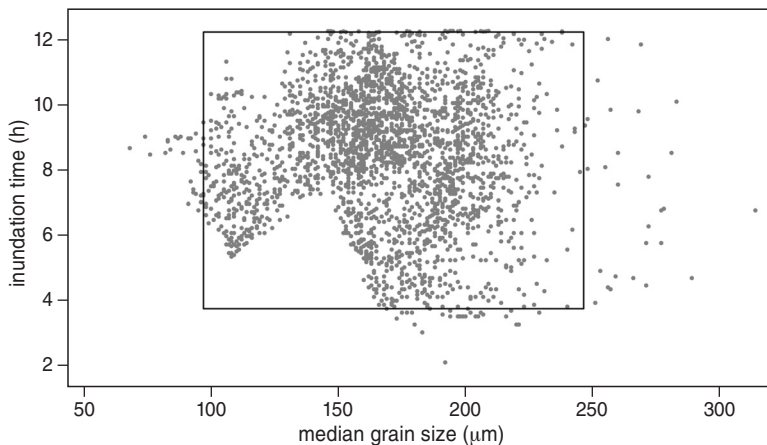
Appendix C. Script to run GEEs in R and use QIC-values to select the best model. GEEs are based on Carl & Kühn (2007, *Ecological Modelling* **207**, 159-170) and QIC-values are based on Pan (2001, *Biometrics* **57**, 120-125. R-script specific for GEE are available as appendix from Carl & Kühn (2007) and Dormann *et al.* (2007).

```
###################################################################
# Path to data
  setwd("/media/i/projecten/rekendesktop/gee/")
# Load libraries
  library(geepack);library(gee);library(ncf)
# Get functions
  source("GEE_function.r") #See Carl & Kühn (2007); Dormann et al (2007)
  source("QIC4.r") #Appended at the end of this script
# Read data
  grid2005<- read.table("2005.txt", header=T, sep="\t")
# Select species
  spec.names<-names(grid2005)[6:12]
########################### START LOOP###########################
# loop
  for (sp in 1:7)
  {
# select species
  spec.n<-spec.names[sp]
# Create data-set for GEE by selecting & ordering columns
  data <- data.frame(grid2005[,c(spec.n,names(grid2005[c(3:5,1:2)]))])
  data$spec.nrs<-data[,spec.n]
# Attach data to R
  attach(data)
# Total number of rows in data-set
  nn<- nrow(data)
# Group X- and Y-coordinates together
  coord<- cbind(data$x,data$y)
# Fit models
  mac.ind<-
  GEE(spec.nrs~median +ITTide + I(median^2) + I(ITTide^2) + median*ITTide,
  family="poisson",data=data, cbind(data$x,data$y),"independence",4,plot=F,graph=F)
  mac.gee4.quad<-
  GEE(spec.nrs~median +ITTide + I(median^2) + I(ITTide^2) + median*ITTide,
  family="poisson",data=data, cbind(data$x,data$y),"quadratic",4,plot=F,graph=F)
  mac.gee3.quad<-
  GEE(spec.nrs~median + ITTide + I(median^2) + I(ITTide^2) + median*ITTide,
  family="poisson",data=data, cbind(x,y),"quadratic",3,plot=F,graph=F)
  mac.gee2.quad<-
  GEE(spec.nrs~median + ITTide + I(median^2) + I(ITTide^2) + median*ITTide,
  family="poisson",data=data, cbind(x,y),"quadratic",2,plot=F,graph=F)
  mac.gee4<-
  GEE(spec.nrs~median + ITTide + I(median^2) + I(ITTide^2) + median*ITTide,
  family="poisson",data=data, cbind(x,y),"exchangeable",4,plot=F,graph=F)
  mac.gee3<-
  GEE(spec.nrs~median + ITTide + I(median^2) + I(ITTide^2) + median*ITTide,
  family="poisson",data=data, cbind(x,y),"exchangeable",3,plot=F,graph=F)
  mac.gee2<-
  GEE(spec.nrs~median + ITTide + I(median^2) + I(ITTide^2) + median*ITTide,
  family="poisson",data=data,cbind(x,y),"exchangeable",2,plot=F,graph=F)
# STORE MODEL RESULTS IN TABLE
  cor.results<-data.frame(Covariance=c("Independent", "quadratic 4x4","quadratic 3x3","quadratic 2x2","exchange-
  able 4x4","exchangeable 3x3","exchangeable 2x2"),
  Quasi.L=rep(NA,7),Trace=rep(NA,7),Trace_naiv=rep(NA,7),r1=rep(NA,7),r1_5=rep(NA,7))
  cor.results[1,2:5]<-c(QIC(nonind.var      = mac.ind$gee$geese$vbeta,
                  nonind.var.naive = mac.ind$gee$geese$vbeta.naiv,
                  nonind.beta      = mac.ind$gee$geese$beta))
  cor.results[2,2:5]<-c(QIC(nonind.var      = mac.gee4.quad$gee$vbeta,
                  nonind.var.naive = mac.gee4.quad$gee$vbeta.naiv,
```

```
                       nonind.beta     = mac.gee4.quad$gee$beta))
 cor.results[3,2:5]<-c(QIC(nonind.var      = mac.gee3.quad$gee$vbeta,
                       nonind.var.naive = mac.gee3.quad$gee$vbeta.naiv,
                       nonind.beta     = mac.gee3.quad$gee$beta))
 cor.results[4,2:5]<-c(QIC(nonind.var      = mac.gee2.quad$gee$vbeta,
                       nonind.var.naive = mac.gee2.quad$gee$vbeta.naiv,
                       nonind.beta     = mac.gee2.quad$gee$beta))
 cor.results[5,2:5]<-c(QIC(nonind.var      = mac.gee4$gee$robust.variance,
                       nonind.var.naive = mac.gee4$gee$naive.variance,
                       nonind.beta     = mac.gee4$gee$coefficients))
 cor.results[6,2:5]<-c(QIC(nonind.var      = mac.gee3$gee$robust.variance,
                       nonind.var.naive = mac.gee3$gee$naive.variance,
                       nonind.beta     = mac.gee3$gee$coefficients))
 cor.results[7,2:5]<-c(QIC(nonind.var      = mac.gee2$gee$robust.variance,
                       nonind.var.naive = mac.gee2$gee$naive.variance,
                       nonind.beta     = mac.gee2$gee$coefficients))
# Calculating Moran's I of the GLM-residuals
# fit GLM
  model1<- glm(spec.nrs~median + ITTide + I(median^2) + I(ITTide^2) +
  median*ITTide,family="poisson",data=data)
  require(ncf)
# Calculate correlations and put in list
  correlogs<-list()
  correlogs[[1]] <- correlog(x,y, residuals(model1),na.rm=T, increment=1, resamp=1)
  correlogs[[2]] <- correlog(x,y, mac.ind$resid, na.rm=T, increment=1, resamp=1)
  correlogs[[3]] <- correlog(x,y, mac.gee4.quad$resid, na.rm=T, increment=1, resamp=1)
  correlogs[[4]] <- correlog(x,y, mac.gee3.quad$resid, na.rm=T, increment=1, resamp=1)
  correlogs[[5]] <- correlog(x,y, mac.gee2.quad$resid, na.rm=T, increment=1, resamp=1)
  correlogs[[6]] <- correlog(x,y, mac.gee4$resid, na.rm=T, increment=1, resamp=1)
  correlogs[[7]] <- correlog(x,y, mac.gee3$resid, na.rm=T, increment=1, resamp=1)
  correlogs[[8]] <- correlog(x,y, mac.gee2$resid, na.rm=T, increment=1, resamp=1)
 # store correlations in cor.results
  for (i in 2:8)
  {
  cor.results[i-1,6]<-correlogs[[i]]$correlation[1]
  cor.results[i-1,7]<-mean(correlogs[[i]]$correlation[1:5])
  }
# Write table with correlation structure results
  write.csv(cor.results,paste("cor_results_",spec.n,".csv",sep=""),row.names=F)
# Save final model
  min_r1_row<-(1:nrow(cor.results))[cor.results$r1==min(cor.results$r1)]
  if (min_r1_row == 2) gee.final<-mac.gee4.quad
  if (min_r1_row == 3) gee.final<-mac.gee3.quad
  if (min_r1_row == 4) gee.final<-mac.gee2.quad
  if (min_r1_row == 5) gee.final<-mac.gee4
  if (min_r1_row == 6) gee.final<-mac.gee3
  if (min_r1_row == 7) gee.final<-mac.gee2
# Detach and close loop
  detach(data)
# Save workspace
  save.image(paste(spec.n,"corstr_nodist.rdata",sep="_"))
   }
######## MODEL SELECTION OF ENVIRONMENTAL COVARIATES ########
# Path to data
  setwd("/media/i/projecten/rekendesktop/gee/")
# Load libraries
  library(geepack);library(gee);library(ncf)
# specify species
  spec.names<-c("cer","cor","macad","macjuv","mar","sco","uro")
  for (spec.n in spec.names)
  {
# Load workspace
  load(paste(spec.n,"corstr_nodist.rdata",sep="_"))
  data<-data[,1:7]
```

```
  attach(data)
# Get final model
  min_r1_row<-(1:nrow(cor.results))[cor.results$r1==min(cor.results$r1)]
  if (min_r1_row == 2) gee.final<-mac.gee4.quad
  if (min_r1_row == 3) gee.final<-mac.gee3.quad
  if (min_r1_row == 4) gee.final<-mac.gee2.quad
  if (min_r1_row == 5) gee.final<-mac.gee4
  if (min_r1_row == 6) gee.final<-mac.gee3
  if (min_r1_row == 7) gee.final<-mac.gee2

# Define correlation structure and number of bins
  corstr_nchar <- nchar(as.character(cor.results[min_r1_row,1]))
  corstr      <- substr(cor.results[min_r1_row,1],1,corstr_nchar-4)
  bin_size    <- as.numeric(substr(cor.results[min_r1_row,1],corstr_nchar,corstr_nchar))

# Define model components
  model.comp<-c("median","ITTide","I(median^2)","I(ITTide^2)","median:ITTide")

# construct table with model selection
var.selection<data.frame(var_removed=as.character(c("full",rep("NA",4),"Intercept")),QIC=rep(Inf,6),quasi_L=rep(N
  A,6),AIC=rep(NA,6),L=rep(NA,6))
  var.selection$var_removed<-as.character(var.selection$var_removed)

# save full model
  var.selection[1,2:3]<-cor.results[2,2:3]
  var.selection[1,5]<-sum(dpois(data$spec.nrs,gee.final$fitted,log=F))
  var.selection[1,4]<-2*(length(model.comp)+1)-2*var.selection[1,5]

# Start loop
  var.incl<-model.comp
  var.removed<-c()

  for (fits in 2:6)
  {
  for (v in var.incl)
  {
# Specify model to fit
   model.vars<-var.incl[is.element(var.incl,v)==F]
   if (fits<=5){
   form<-parse(text=paste("spec.nrs~",paste(model.vars,collapse="+"),sep=""))

 # Fit model
mac.gee4.quad<-GEE(eval(form),family="poisson",data=data, cbind(x,y),corstr,bin_size,plot=F,graph=F)

mac.ind<-GEE(eval(form),family="poisson",data=data, cbind(x,y),"independence",4,plot=F,graph=F)}

       else{
mac.gee4.quad<-GEE(spec.nrs~1,family="poisson",data=data, cbind(x,y),corstr,bin_size,plot=F,graph=F)
mac.ind<-GEE(spec.nrs~1,family="poisson",data=data, cbind(x,y),"independence",4,plot=F,graph=F)}

# Calculate QIC and Quasi likelihood
  if (corstr=="quadratic") {
  QIC_Quasi<-c(QIC(nonind.var      = mac.gee4.quad$gee$vbeta,
              nonind.var.naive = mac.gee4.quad$gee$vbeta.naiv,
              nonind.beta      = mac.gee4.quad$gee$beta))}
  if (corstr=="exchangeable") {
  QIC_Quasi<-c(QIC(nonind.var      = mac.gee4.quad$gee$robust.variance,
              nonind.var.naive = mac.gee4.quad$gee$naive.variance,
              nonind.beta      = mac.gee4.quad$gee$coefficients))}

  QICv<-QIC_Quasi[[1]]
  quasi<-QIC_Quasi[[2]]

# Calculate AIC and likelihood
```

```
lik<-sum(dpois(data$spec.nrs,mac.gee4.quad$fitted,log=F))
AIC<-2*(length(var.incl)+1)-2*lik
# If QIC bigger than QIC stored in var.selection, save the results in var.selection table
if (QICv<var.selection$QIC[fits])
{
var.selection$var_removed[fits]<-v
var.selection$QIC[fits]<-QICv
var.selection$quasi_L[fits]<-quasi
var.selection$AIC[fits]<-AIC
var.selection$L[fits]<-lik
var.to.remove=v
}
print(var.selection)
}
# remove variable to remove from var.incl
var.incl<-var.incl[-match(var.to.remove,var.incl)]
}
# write table
write.csv(var.selection,paste("var_selection_",spec.n,".csv",sep=""),row.names=F)
# save workspace
save.image(paste("var_selection_",spec.n,".rdata",sep=""))
# detach data
detach(data)
}
######################### SAVE FINAL MODEL#####################
# Path to data
setwd("/media/i/projecten/rekendesktop/gee/")

# specify species
spec.names<-c("cer","cor","macad","macjuv","mar","sco","uro")
for (spec.n in spec.names){

# load workspace
load(paste("var_selection_",spec.n,".rdata",sep=""))

# Fit final model
# "cer"
if (spec.n=="cer"){
final_GEE<- GEE(spec.nrs~median +ITTide + I(median^2) + I(ITTide^2) +  median*ITTide,
  family="poisson",data=data, cbind(data$x,data$y),"quadratic",4,plot=F,graph=F)
final_IND<- GEE(spec.nrs~median +ITTide + I(median^2) + I(ITTide^2) +
  median*ITTide,family="poisson",data=data, cbind(data$x,data$y),"independence",4,plot=F,graph=F)}

    # "cor"
if (spec.n=="cor"){
final_GEE<- GEE(spec.nrs~median +ITTide + I(median^2) + I(ITTide^2) +
  median*ITTide,family="poisson",data=data, cbind(data$x,data$y),"exchangeable",3,plot=F,graph=F)
final_IND<- GEE(spec.nrs~median +ITTide + I(median^2) + I(ITTide^2) + median*ITTide,
  family="poisson",data=data, cbind(data$x,data$y),"independence",3,plot=F,graph=F)}

    # "macad"
if (spec.n=="macad"){
final_GEE<- GEE(spec.nrs~median +ITTide + I(median^2) + I(ITTide^2) +
  median*ITTide,family="poisson",data=data, cbind(data$x,data$y),"quadratic",4,plot=F,graph=F)
final_IND<- GEE(spec.nrs~median +ITTide + I(median^2) + I(ITTide^2) + median*ITTide,
  family="poisson",data=data, cbind(data$x,data$y),"independence",4,plot=F,graph=F)}
    # "macjuv"
if (spec.n=="macjuv"){
final_GEE<- GEE(spec.nrs~median +ITTide + I(median^2) + I(ITTide^2) +
  median*ITTide,family="poisson",data=data, cbind(data$x,data$y),"quadratic",4,plot=F,graph=F)
final_IND<- GEE(spec.nrs~median +ITTide + I(median^2) + I(ITTide^2) + median*ITTide,
  family="poisson",data=data, cbind(data$x,data$y),"independence",4,plot=F,graph=F)}

    # "mar"
```

```
if (spec.n=="mar"){
final_GEE<- GEE(spec.nrs~median +ITTide + I(median^2) + I(ITTide^2) +
   median*ITTide,family="poisson",data=data, cbind(data$x,data$y),"quadratic",4,plot=F,graph=F)
final_IND<- GEE(spec.nrs~median +ITTide + I(median^2) + I(ITTide^2) +
   median*ITTide,family="poisson",data=data, cbind(data$x,data$y),"independence",4,plot=F,graph=F)}

     # "sco"
if (spec.n=="sco"){
final_GEE<- GEE(spec.nrs~median +ITTide + I(median^2) + I(ITTide^2) +
   median*ITTide,family="poisson",data=data, cbind(data$x,data$y),"quadratic",4,plot=F,graph=F)
final_IND<- GEE(spec.nrs~median +ITTide + I(median^2) + I(ITTide^2) +
   median*ITTide,family="poisson",data=data, cbind(data$x,data$y),"independence",4,plot=F,graph=F)}

     # "uro"
if (spec.n=="uro"){
final_GEE<- GEE(spec.nrs~median +ITTide + I(median^2) + I(ITTide^2), family="poisson",data=data,
   cbind(data$x,data$y),"quadratic",3,plot=F,graph=F)
final_IND<- GEE(spec.nrs~median +ITTide + I(median^2) + I(ITTide^2), family="poisson",data=data,
   cbind(data$x,data$y),"independence",3,plot=F,graph=F)}

#    save workspace
save.image(paste("final_model_",spec.n,".rdata",sep=""))
}

###QIC FUNCTION FOR MODEL-SELECTION OF SPATIAL MODELS #########
# gee.ind        GEE with an independence structure
# gee.nonind     GEE fitted (FIXED or EXCHANGEABLE structure)

QIC<-function(response      = mac.ind$gee$y,
        Xmat          = mac.ind$gee$geese$X,
        nonind.var    = gee.nonind$gee$robust.variance,
        nonind.var.naive = gee.nonind$gee$naive.variance,
        ind.var       = mac.ind$gee$geese$vbeta.naiv,
        nonind.beta   = gee.nonind$geese$beta,
        ind.beta      = mac.ind$gee$geese$beta
        )
{

# Get library
 require(MASS)

# Calculate the QIC: Make difference between gee & geepack
 trace.user<-sum(diag(ginv(ind.var)%*% nonind.var))
 trace.user.naive<-sum(diag(ginv(ind.var)%*% nonind.var.naive))

# Get the fitted values
 mu.ind<-exp(Xmat%*%ind.beta)
 mu.user<-exp(Xmat%*%nonind.beta)

# quasi-likelihood (Poisson)
 #quasi.ind<-sum((response*log(mu.user))-mu.user-(response*(log(response+0.00001)-1)))
 quasi.ind<-sum((response*log(mu.user))-mu.user)

# Calculate QIC
 qic.user<-2*(trace.user-quasi.ind)

# return output in a list
 return(list(QIC=qic.user, quasi.lik=quasi.ind, trace=trace.user,trace.naive=trace.user.naive))

}

##########THREE-DIMENSIONAL PREDICTION LANDSCAPES##############
library(lattice)
Env.3d.plot<-function(model.coef=gee.final$gee$beta)
```

```
{
model.coef=final_GEE$gee$beta

median.v<-seq(min(data$median), max(data$median), length=50)
ITTide.v<-seq(min(data$ITTide), max(data$ITTide), length=50)
pred.table<-data.frame(intercept=rep(1,length(median.v)*length(ITTide.v)))
pred.table<-cbind(pred.table,expand.grid(median=median.v,ITTide=ITTide.v))
pred.table$median2<-pred.table$median^2
pred.table$ITTide2<-pred.table$ITTide^2
pred.table$median.ITTide<-pred.table$median*pred.table$ITTide
names(pred.table)<-c("(Intercept)","median","ITTide","I(median^2)",
          "I(ITTide^2)","median:ITTide")
pred.M<-as.matrix(pred.table[,names(model.coef)])
pred.table$prediction<-exp(pred.M%*%model.coef)
#pred.table<-pred.table[(pred.table$median<150 & pred.table$ITTide<5)==F,]
pred.table<-pred.table[(pred.table$median>quantile(data$median,0.01) &
            pred.table$median<quantile(data$median,0.99) &
            pred.table$ITTide>quantile(data$ITTide,0.01) &
            pred.table$ITTide<quantile(data$ITTide,0.99)),]

#M<-matrix(pred.table$prediction,length(median.v),length(ITTide.v))
wireframe(prediction~median + ITTide, data=pred.table,col=grey(0.4),theta=20,
    xlab=list(label=expression(paste("Median grain size (",mu,"m)",sep="")),cex=1.3,rot=30),
    ylab=list(label="Inundation time (h)",cex=1.3,rot=-40),
    zlab=list(label=expression(paste("Count per core (n)")),cex=1.3,rot=95),
    phi=30,
    ticktype="detailed",
    scales= list(arrows = FALSE,cex=1.2))
}

Env.3d.plot(model.coef=final_GEE$gee$beta)
Env.3d.plot(model.coef=final_GEE$gee$coefficients)
```

Appendix D. Comparison between regression coefficients and robust standard errors (S.E.) of a quasi-Poisson GLM and a GEE with a quadratic 4x4 correlation-structure for the minimal adequate model for *C. edule* (see Table 4.2c).

	GLM		Quadratic 4×4	
Coefficients	Estimate	S.E	Estimate	S.E
Intercept	-4.49300	2.21000	-2.66099	3.74390
MGS	0.01738	0.01477	0.00949	0.02390
IT	1.45800	0.33940	1.07602	0.55480
MGS2	0.00003	0.00003	0.00002	0.00004
IT2	-0.07276	0.01504	-0.05726	0.02211
MGS x IT	-0.00543	0.00105	-0.00427	0.00190

Site- and species- specific distribution patterns of molluscs at five intertidal soft-sediment areas in northwest Europe during a single winter

Pierrick Bocher, Theunis Piersma, Anne Dekinga, Casper Kraan, Michael G. Yates, Thierry Guyot, Eelke O. Folmer, and Gilles Radenac

Summary

In this study we aim to provide a basic description and comparison of the spatial distribution and population structure of the common intertidal mollusc species, sampled within a single winter along a latitudinal gradient of different soft-sediment areas spanning 8° of latitude (46°-54°N) and 900 km of distance in northwest Europe. Sediment samples were collected from December 2003 to early March 2004 in the Wadden Sea (The Netherlands), the Wash (United Kingdom), Mont Saint-Michel Bay (France) and two bays on the central French Atlantic coast in south of Brittany. Core-sampling over 250 m grids allowed us to cover 3–30 km^2 at nine separate intertidal subsites, with a grand total of 2,103 points visited. Among the 15 bivalve and 8 gastropod species collected, we focused on the four most common and abundant bivalve species (*Cerastoderma edule, Macoma balthica, Scrobicularia plana* and *Abra tenuis*) that together represented 96% of all collected bivalves, and on the mudsnail *Hydrobia ulvae* that comprised 99% of all collected gastropods. *C. edule* and *M. balthica* were the most widespread bivalves, with higher densities occurring at higher latitudes. *S. plana* and *A. tenuis* were more abundant at southern sites, both with a clear preference for muddy sediments. The mudsnail *H. ulvae* occurred commonly and in comparable densities at all study sites, except in Mont Saint-Michel Bay where it was very rare. Mean sizes of the common molluscs were highly variable between sites, without clear north-south gradients. The mollusc distribution patterns at the five intertidal areas and nine subsites were predominantly site-specific. Mollusc community composition showed greater similarity within than between the regions north and south of the Brittany peninsula.

Introduction

Invertebrate grazers, and among them suspension- and deposit-feeding bivalves, play a central role in the food-webs of intertidal soft-sediment habitats due to their top-down controls on sediment characteristics and primary producers, and their bottom-up effects on a range of invertebrate, fish and shorebird predators (Reise 1985, 2001; Piersma 1987; Piersma & Beukema 1993; Raffaelli 1996; Bertness 1999). The western seaboard of Europe, and especially the shores along the southern North Sea and the Channel Sea area, offer intertidal flat systems of a wide variety with respect to extent, climate, tidal range, sediment characteristics and estuarine inputs. Although the ecology of many of these intertidal areas has received detailed scientific attention at local levels, only with respect to the genetics and ecophysiology of key species have the tidal flats of northwest Europe been considered as a single system (e.g. Hummel *et al.* 1995; Luttikhuizen *et al.* 2003b; Drent *et al.* 2004). In this study, we examined European intertidal flats as an assemblage of comparable communities due to shared habitat characteristics, but deeply interconnected by historical patterns of gene flow between local populations of macrozoobenthic animals (Luttikhuizen *et al.* 2003a) and also, from day to day, by single populations of migratory shorebird predators (e.g. Smit & Piersma 1989; Piersma *et al.* 2005).

In looking at the similarities and differences among and between European inter-tidal soft-sediment communities, we focused on a taxonomically and ecologically distinct assemblage of benthic invertebrates, the molluscs (bivalves and gastropods). This choice was inspired by their ease of study. Although usually invisible at the surface, densities, size distributions and biomass values of bivalves and gastropods dominating the intertidal study sites can be straightforwardly obtained from repetitive core-sampling. In addition, these molluscs form the entire potential diet of a single population of the most numerous mollusc predator occurring at intertidal flats across north-western Europe, the red knot *Calidris canutus islandica*, a shorebird specialised in finding, eating and digesting hard-shelled molluscs buried in soft-sediments (e.g. Piersma *et al.* 1994, 1998; Battley & Piersma 2005; Van Gils *et al.* 2005a). In fact, we have used the distribution of this specialized molluscivore as a starting point to select our study sites. Thus, red knots as top-predators of the mollusc populations examined have provided the filter, the imposed perceptual bias (Levin 1992), through which a set of five European intertidal systems have been observed (Piersma *et al.* 1993a).

Based on a core-sampling effort over 250 m grids, we aimed to describe the gross attributes of distribution and abundance of the intertidal molluscs: densities, degree of patchiness, zonation and mean shell sizes (Andrew & Mapstone 1987). Respectable descriptive studies in marine biology require the definition of the scale parameters of the study (Underwood *et al.* 2000). In this case each of the study sites covered 3–30 km^2 of intertidal flat and the sites spanned 8° of latitude (46°-54°N) and 900 km distance. To avoid the problem of inter-annual differences, due to strong spatial and temporal synchrony of the highly variable bivalve recruitment rates (Beukema *et al.* 2001), the

study was carried out within the 4 months of a single winter when the growth is stopped or very slow (Jensen 1992a; Guillou & Tartu 1994).

Having documented the differences in densities between sites, we were particularly interested in the conformity across sites in distributional characteristics of the common mollusc species. Using the distribution maps as the basis, we asked ourselves whether differences in distributional attributes (i.e. living close or far away from the low water line, extent to which different sediment types are used, occurrence of areas with high densities separated by empty space, etc) between species are repeatable across the different sites (cf. Armonies & Reise 2003)? In short, are the mollusc distribution patterns predominantly site-specific or predominantly species-specific?

Study sites

The five study areas (four of which contained two subsites) were selected on the basis of published and personal knowledge to represent the greatest variety of large intertidal soft-sediment systems in northwest Europe, whilst harbouring significant wintering populations of red knots (Smit & Piersma 1989; Stroud *et al.* 2004). Two areas in the southern North Sea basin were selected, the Wadden Sea in The Netherlands (Abrahamse *et al.* 1976) and the Wash in eastern England (Davidson *et al.* 1991). Furthermore, we selected an area on the north Brittany coast of France, Mont Saint-Michel Bay, and two areas south of Brittany, on the Atlantic coast of France between the estuaries of Gironde and Loire Rivers (Verger 2005). Sediment characteristics were summarised using data collected during this study (see Materials and Methods). Within the intertidal areas sampled in this study, changes in the height of the flats were gradual, and could be adequately described by the range in heights and exposure times of the lowest and highest sampling stations at each subsites for average tide (see Table 5.1).

Wadden Sea
The Wadden Sea is wedged between the Frisian barrier islands and the northernmost mainland of The Netherlands. With a low tidal amplitude (1.5 m at neap to 3.5 m at spring tide), the intertidal flats of the Dutch part of the international Wadden Sea cover a total area of 890 km^2 (Wolff 1983; Van de Kam *et al.* 2004). The sediment consists of sand and muddy flats. We chose an area of 5.1 km^2 called Engelsmanplaat (53°26'N, 06°02'E), centrally located between the barrier islands of Ameland and Schiermonnikoog (Fig. 5.1). With a mean median grain size of 203 μm and a silt content of only 1.6 % (Table 5.1), the Engelsmanplaat subsite was the sandiest intertidal flat area included in this study. A second study area (Griend-East) was located 50 km further west and covered 17.3 km^2 of sandflat east of the islet Griend (53°16'N, 05°18'E). This flat was also uniformly sandy (average median grain size of 164 μm) with a very low silt content of 3.6%. At both Wadden Sea study sites we covered almost the whole width of the intertidal zone with a height difference (2.4 m) close to the

average tidal amplitude (Table 5.1). The difference of emersion times between the lowest and the highest points of the grid was consequently an important feature of every site (Table 5.1). Benthic life at Griend-East has been studied in similar ways before, but never in midwinter (Piersma *et al.* 1993c, 2001).

Wash

In the south-western part of the North Sea, the Wash is located in eastern England at the same latitude as the Wadden Sea (Fig. 5.1). It is one of the most important mud- and sand flat area in the British Isles (Davidson *et al.* 1991), it has a tidal amplitude of 3.4 m at neap tides and 6.5 m at spring tides, an intertidal area of 270 km^2 at ordinary spring tides and is composed of sandy and muddy areas divided by gully systems and river outflows into areas known as 'Sands'. We completely sampled two of the six Sands. The first, Stubborn Sand, is a sandflat in the north-eastern part of the Wash (7.8 km^2 sampled; 53°53'N, 00°27'E). Sediments were similar to those at Griend-East (median grain size of 172 μm, 6.2% silt; Table 5.1), but with four muddy stations at its southern tip along the outflow of the Wolferton Creek. The second site was Breast Sand (17.2 km^2 sampled; 53°50'N, 00°17'E) in the south-eastern corner of the Wash between the outflows of the Nene and Ouse Rivers. Breast Sand was the most hetero-geneous intertidal flat in this study. The western half of Breast Sand was non-homoge-neously sandy (median grain size of 153 μm, 17.7% silt). The eastern half was quite muddy (median grain size of 69 μm, 50.3% silt), with an uneven sediment surface of ridges and runnels. Height differences along the grid ranged from 2.9 m at eastern Breast Sand to 4.3 m at western Breast Sand (Table 5.1). The lower height differences at the eastern part was due to the presence of the deep outflow of the Ouse River where the slope was truncated, while on the western part the slope was regular across the tidal zone. The intermediate height difference (3.8 m) at Stubborn Sand was due to the presence of a dike/dune immediately edging the sandflat. This structure limited the width of the tidal zone such that only the lower shore levels with their associated longer immersion times were represented compared with bordered by saltmarshes where all shore levels were represented. The macrozoobenthos community of the Wash has been studied previously by Yates *et al.* (1993a, 1993b).

Mont Saint-Michel Bay

The Bay of Mont Saint-Michel is located on the coast the Channel Sea in the south-eastern part of the Gulf of Saint-Malo (Fig. 5.1). The sandy intertidal zone has the largest tidal amplitude in Europe (12 m on average, but with a maximum of 16 m) and covers 200 km^2 of mudflat. We selected two sectors. Cherrueix (28.0 km^2 sampled; 48°37'N, 01°41'W) is in the south-western part of the bay between the Guyoult River in the west, and an area with large tubeworm *Sabellaria alveolata* reefs in the east, salt marshes and a dyke in the south and mussel cultures to the north. Most of the inter-tidal flats of Cherrueix were uniformly sandy (median grain size of 162 μm, 19.4% silt). Some very coarse sands with median grain sizes of up 654 μm occurred at high parts of the intertidal, there were small muddy areas next to the *Sabellaria* reefs

(median grain size = 32 µm) and along the Guyoult river (median grain size = 50 µm). On the opposite side of the bay, a sandy area of 3.3 km^2 in front of the village of Saint-Pair was sampled (48°48'N, 01°35'W). At the bay-side, the flats were bordered by rocky outcrops. Saint-Pair was uniformly sandy with a median grain size of 168 µm and a silt content of 13.6%. The height differences covered by our grid were considerable at both sites (>6 m, Table 5.1), but never overlapped with mussel culture. Thorin *et al.* (2001) and Meziane & Retiere (2001) have previously made investigations of macrozoobenthos in these parts of Mont Saint-Michel Bay.

Aiguillon Bay
Aiguillon Bay (46°17'N, 01°10'W) is located exactly at the junction of the Charente and Vendée coastlines in the Gulf of Biscay and has a maximal tidal amplitude of 5–6 m. The bay is surrounded by salt marshes and two dykes in the north and south (Fig. 5.1) and it covers 28.7 km^2 of intertidal mudflats. The bay is divided into two by the Sèvre River that even holds water at low tide (Verger 2005). The upper and middle reaches of the intertidal zone are bare muddy flats, but the lowest parts are intersected by a fractional network of channels flowing into the Sèvre. We sampled the whole bay except the areas of oyster cultures in the southwest. With a mean median grain size of 8 µm and almost 90 % silt, Aiguillon Bay was homogeneous in sediment characteristics and by far the muddiest site examined here. The edges of the Sèvre River and of the channels were very soft with up to 95% silt, whereas the north-western part near Pointe de l'Aiguillon is sandier ('only' 85 % silt). Height differences across the sampled grid were small (2.7 m), especially in comparison with the mean tidal amplitude of 5 m due to the steep slopes of the edges of Sèvre River that limited sampling (Table 5.1). Emersion times are relatively long (11h) at the high sampling stations near the edge of the salt-marsh. We know of no published studies on the distribution and population structure of molluscs in Aiguillon Bay.

Marennes-Oléron Bay
Marennes-Oléron Bay (46°55'N, 01°10'W) is also on the Charente coastline; it is only 40 km south of Aiguillon Bay. The bay (150 km^2) has a tidal amplitude that ranges from 2.4 m (neap tide) to 5.1 m (spring tide) and is enclosed by Oléron Island in the west and the French mainland in the east, with intertidal areas bordering both the island and the mainland coast (Fig. 5.1). Two subsites were selected, the 4 km wide Moeze mudflats on the eastern mainland side and the flats of Oléron Island on the western side. The upper and middle mudflats of Moeze had a typical ridge and runnel structure, whereas the low lying mudflats (not sampled) were occupied by mussel-oyster culture or abandoned oyster farms. We confined our activities to the northern part, an area of 13.4 km^2. Moeze was a muddy subsite, although slightly less so than Aiguillon Bay (median grain size of 17 µm, 85.1% silt, but note that only two sediment samples were taken; Table 5.1).

The intertidal flats of Oléron were heterogeneous, a patchwork of muddy and sandy places covered by seagrasses *Zostera noltii* in the high and middle zones; the

lower part (not sampled) was covered by oyster culture. We sampled an area of open mudflat of 13.4 km². We encountered coarse sandy areas in the north (median grain size of 423 μm) and muddier areas in the south, especially near Chateau d'Oléron (median grain size of 60 μm). Height differences across the Oléron and Moeze grids were the smallest in this study (2.4 m and 2.0 m, respectively). This is because the local tidal amplitude is small, but also because the lowest areas were covered with oyster farms and not visited whereas the highest areas are cut off by dikes. Sauriau *et al.* (1989), De Montaudouin & Sauriau (2000) and Hautbois *et al.* (2002, 2004, 2005) have previously described the macrozoobenthic assemblages of this area.

Table 5.1. Description of intertidal study areas with references to time and extent of sampling (with numbers of samples analyzed for sediment characteristics indicated by N_{sed}), the relative numbers of samples collected on foot rather than by boat, and the tidal and sedimentary conditions at the sites.

Study sites	Study period	Number N (N_{sed})	Sampled on foot (%)	Tidal amplitude		Δ height (m)[a]	Emersion time[b]		Sediment characteristics	
				Neap Tide (m)	Spring tide (m)		Min (h)	Max (h)	Median grain size μm	Sediment <63μm (%)
Wadden Sea										
Engelsmanplaat	25 Nov to 4 Dec	356 (18)	72	1.5	3.5	2.5	1.5	11.0	203	1.6
	25 Nov to 27 Nov	79 (4)	35							
Griend East	30 Nov to 4 Dec	277 (14)	82			2.4	1.5	12.0	164	3.6
Wash				3.4	6.5					
Stubborn Sand	6 Jan to 14 Jan	381 (21)	100			3.8	1.5	8.5	172	6.2
Breast Sand	6 Jan to 11 Jan	117 (6)	100						114	32.1
Breast Sand East	8 Jan to 14 Jan	264 (15)	100			2.9	5.5	11.5	69	50.3
Breast Sand West						4.3	1.5	11.0	153	17.7
Mont Saint-Michel Bay	19 Jan to 27 Jan	502 (33)	100	6.0	12.7					
Cherrueix	19 Jan to 27 Jan	440 (30)	100			7.0	2.5	10.0	162	19.4
Saint-Pair	24 Jan to 26 Jan	62 (3)	100			6.7	0.5	8.0	168	13.6
Aiguillon Bay	7 Feb to 8 Mar	459 (9)	21	2.4	5.1	2.7	1.5	8.5	8	89.8
Marennes-Oléron Bay	18 Feb to 24 Mar	405 (14)	61	2.4	5.1					
Moeze	18 Feb to 22 Mar	196 (2)	19			2.0	4.0	9.0	17	85.1
Oléron	21 Feb to 24 Mar	209 (12)	100			2.4	4.5	8.0	132	39.3

[a] Difference between relative height of the highest and lowest sampling stations for each subsites
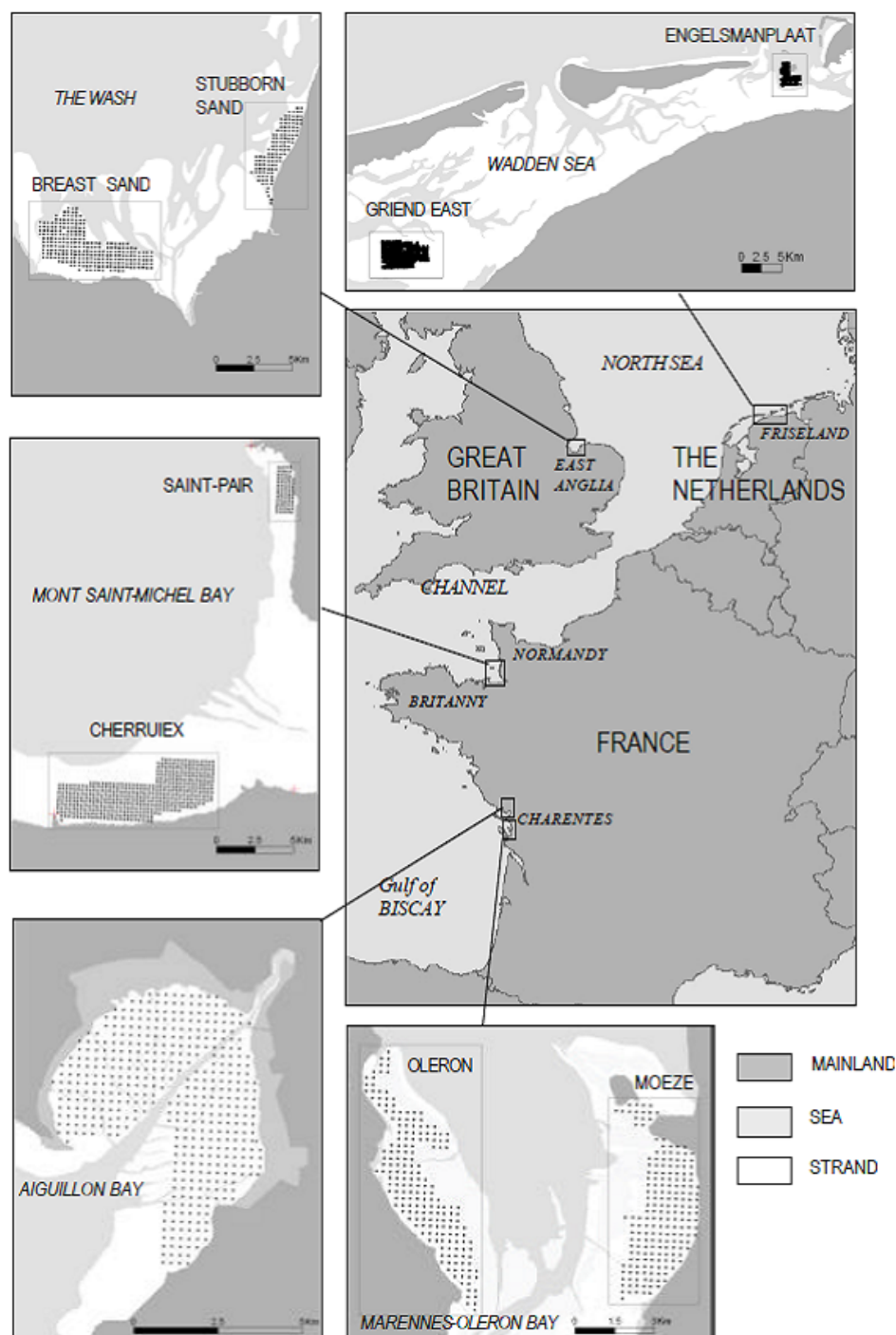[b] Minimal and maximal emersion time at respectively lowest and highest stations during the average

Figure 5.1. Map of the southern North Sea, Channel Sea and Gulf of Biscay, with maps of each of the five study sites, and the grid-map positions at the subsites when core samples were taken.

Materials and Methods

Distributions and densities of molluscs were determined by taking cores at predetermined stations, located by GPS (Garmin 45 and 12, using WGS84 as map datum), on a grid with points 250 m away from one another. Each sampling point is represented by dot in Fig. 5.1. At stations visited on foot, one sediment core (150 mm diameter) covering 0.018 (1/56) m^2 to a depth of 20–25 cm was taken. In some areas a part of the sampling was done from boats (inflatable zodiacs and other small vessels) when the tide covered the mudflats with 0.4–2.0 m of water. From the boat two sediment-cores (100 mm diameter) each covering 0.008 m^2 and to a depth of 20-25 cm each were taken, a total surface of 0.016 m^2. The core samples were sieved over a 1 mm mesh on site. Mudsnails, *Hydrobia ulvae*, were sampled by taking one additional core (70 mm diameter) of 0.0037 m^2 to a depth of 3 cm that was sieved over a 0.5 mm mesh. During the boat sampling, mudsnails were subsampled from an additional core that was sieved over a 0.5 mm mesh. All live molluscs were retained in a plastic bag and stored at –20°C for later analyses in the laboratory. At every 1 km intersection of the gridlines a sediment sample was taken with a 5 cm diameter core to a depth of 7-8 cm. These samples were stored frozen at –20°C in closed plastic bags.

From December 2003 to March 2004 a total of 2103 sampling stations were visited (Table 5.1). The intertidal areas in the Wash, Mont Saint-Michel Bay and the Oléron mudflats were exclusively sampled on foot, whereas the soft mud of Aiguillon Bay and Moeze were mainly sampled by boat. The Wadden Sea sites were done by either method. Sampling on foot and by boat yield identical density estimates (C. Kraan, personal observations); other relevant aspects of benthic sampling accuracy are discussed by Piersma *et al.* (1993c) and Durell *et al.* (2005). In the laboratory, the molluscs were identified and counted. Maximum length of the bivalves was measured with Vernier callipers to the nearest millimetre.

Median particle size and the percentage silt (fraction < 63 μm) of sediments were determined using a Coulter LS 230 particle size analyser. This apparatus measured particle sizes in the range of 0.04–2000 μm using laser diffraction. Before measurement in the Coulter Counter, they were treated in the same manner and sequence as described in detail by Van den Bergh *et al.* (2003).

Data were analysed statistically using *Systat* 11 software for *Windows*. Multidimensional scaling (MDS) ordination was achieved with *Primer 5*.

Results

Mollusc assemblages

In addition to the 12 bivalve species listed in Table 5.2, the *Ruditapes* spp. (Veneridae) found in the French sites comprised two cryptic species (*R. philippinarum* and *R. decussatus*) that were not distinguished. In addition, we found a single specimen of the deep water species *Pandoria inaequivalis* in Mont Saint-Michel Bay. Apart from the six

Table 5.2. Frequency of occurrence (Occ) and mean densities of mollusc species at each of the five main areas and the different subsites.

| Species | Wadden Sea | | | | Wash | | | | Mont Saint-Michel Bay | | | | Aiguillon Bay | | Marennes-Oléron Bay | | | |
| | Engelsmanplaat | | Griend East | | Stuborn Sand | | Breast Sand | | Cherrueix | | Saint-Pair | | | | Moeze | | Oléron | |
	Occ (%)	(ind/m²)	Occ (%)	(ind/m²)	Occ (%)	(ind/m²)	Occ (%)	(ind/m²)	Occ (%)	(ind/m²)	Occ (%)	(ind/m²)	Occ (%)	(ind/m²)	Occ (%)	(ind/m²)	Occ (%)	(ind/m²)
Bivalves																		
Crassotrea gigas	-	-	2.2	1.2	-	-	-	-	3.9	-	-	-	--	-	-	0.5	-	0.3
Mytilus edulis	-	-	0.7	0.6	-	-	2.3	33.9	-	5.5	-	-	-	-	-	-	5.3	4.6
Mysella bidentata	-	-	0.4	0.2	0.9	0.5	0.8	1.7	-	-	-	-	-	-	-	-	-	-
Cerastoderma edule	25.0	107.0	47.0	87.0	51.0	119.0	41.0	142.0	48.0	148.0	24.0	28.0	17.0	16.6	14.0	13.4	10.0	5.9
Ruditapes spp.	-	-	-	-	-	-	-	-	3.4	2.3	-	-	1.5	1.1	2.6	1.4	17.7	9.9
Macoma balthica	57.0	71.6	70.0	126.0	35.0	43.0	62.0	309.0	28.0	48.0	50.0	9.0	50.0	70.0	25.0	24.3	3.0	2.1
Tellina tenuis	1.3	0.7	-	-	2.6	1.4	0.8	0.4	0.2	0.3	6.5	3.6	-	-	-	-	-	-
Scrobicularia plana	0.4	2.1	-	-	-	-	20.0	19.9	3.0	2.7	-	-	36.0	126.0	29.0	83.4	31.0	41.5
Abra nitida	-	-	-	-	-	-	1.1	2.8	-	-	-	-	-	-	-	-	-	-
Abra tenuis	1.3	0.7	11.0	42.5	-	-	-	-	1.8	9.2	-	-	34.0	42.3	24.0	23.7	13.8	15.8
Ensis americanus	3.8	0.7	3.6	2.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Mya arenaria	1.3	5.7	8.7	5.9	0.9	0.5	1.9	1.1	-	-	-	-	-	-	-	-	-	-
Gastropods																		
Littorina littorea	-	-	0.4	0.2	-	-	-	-	-	-	-	-	-	-	-	-	3.8	4.0
Hydrobia ulvae	25.0	2826.0	23.0	1230.0	26.0	1362.0	34.0	1603.0	1.0	2.5	-	-	83.0	1664.0	93.0	2132.0	50.0	3324.0
Crepidula fornicata	-	-	0.4	0.4	-	-	-	-	0.9	1.4	-	-	-	-	-	-	0.5	15.0
Hinia reticulata	-	-	-	-	-	-	-	-	0.2	0.1	-	-	-	-	-	-	1.0	0.5
Retusa obtusata	-	-	0.4	0.2	-	-	0.4	0.2	-	-	-	-	0.7	0.4	1.0	0.6	-	-
Cyclope nereitida	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3.3	2.4

species of gastropods listed in Table 5.2, we found single specimens of both *Littorina saxatilis* and *Haminea navicula* on the Oléron sands. Two unidentified chitons were found at Mont Saint-Michel Bay. This gave us with a total of 15 bivalves, 8 gastropods and 2 chiton species. Most of the common species occurred throughout the range of study sites, but *Mysella bidentata*, *Ensis americanus* and *Mya arenaria* only occurred within the North Sea basin, whereas the *Ruditapes* spp. and *Cyclope nereitida* only occurred south of it (Table 5.2).

Two bivalve species, *Cerastoderma edule* and *Macoma balthica* were common at all sites, ranging from a few to several 100 specimens per square metre (Fig. 5.2). Mud-snails *H. ulvae* were only missing at the Saint-Pair sandflat in Mont Saint-Michel Bay. The bivalve *Scrobicularia plana* was found throughout the range at six of the nine subsites, whereas *Abra tenuis* was found in the north and the south, in the Wadden Sea, in the Channel Sea and south of Britanny. *Abra nitida* was found only in the Wash. Summarizing Table 5.2, we regard *Tellina tenuis*, *M. bidentata*, *E. americanus* and *Retusa obtusata* as uncommon or rare intertidal species and *Crassostrea gigas*, *Pandora inaequivalvis*, *Hinia reticulata*, *Crepidula fornicata* and *H. navicula* as accidental occurring low in the intertidal zone. *Littorina littorea*, *Mytilus edulis*, *Ruditapes spp.*, *M. arenaria* and *C. nereitida* had a very patchy distribution though they were locally abundant.

In the rest of the paper we will focus on the four most common and abundant bivalve species (and call them by their genus names *Cerastoderma*, *Macoma*, *Scrobicularia* and *Abra*, the latter referring to *A. tenuis* only) that together represented 96% of total individual bivalves collected, and on *Hydrobia* that comprised 99% of all collected gastropods. Densities of both *Cerastoderma* and *Macoma* were lowest at the sites south of Brittany (Fig. 5.2), being 'replaced' by *Scrobicularia* at the two study sites. *Hydrobia* was notably rare in Mont Saint-Michel Bay, but otherwise occurred in mean densities of comparable magnitude (1000–3000 ind./m^2) at other sites.

Between-species comparison of the mollusc fauna at different sites
We will now examine each of the study sites and summarize the general features of the occurrence and distribution of common molluscs.

Wadden Sea
At the two subsites, seven and eight bivalve species, and one and four gastropod species, were found (Table 5.2). At both subsites the bivalves were numerically dominated by *Cerastoderma* and *Macoma*, with much smaller numbers of *M. arenaria*. *Abra* occurred in high densities at Griend-East only. The mudsnail *Hydrobia* was common at both subsites. *Cerastoderma* distribution was rather dispersed at both Wadden Sea subsites (Fig. 5.3), whereas *Macoma* showed more distinct patterns of high density patch (Fig. 5.4). *Scrobicularia* was rare and appeared only on Engelsmanplaat (Fig. 5.5). *Abra* (Fig. 5.6, at Griend-East only) and *Hydrobia* (Fig. 5.7) showed also patterns of high density patches. At least at Griend-East, the latter three species co-occurred at the same central and slightly elevated 'ridge' northeast of the island, with the *Macoma-*
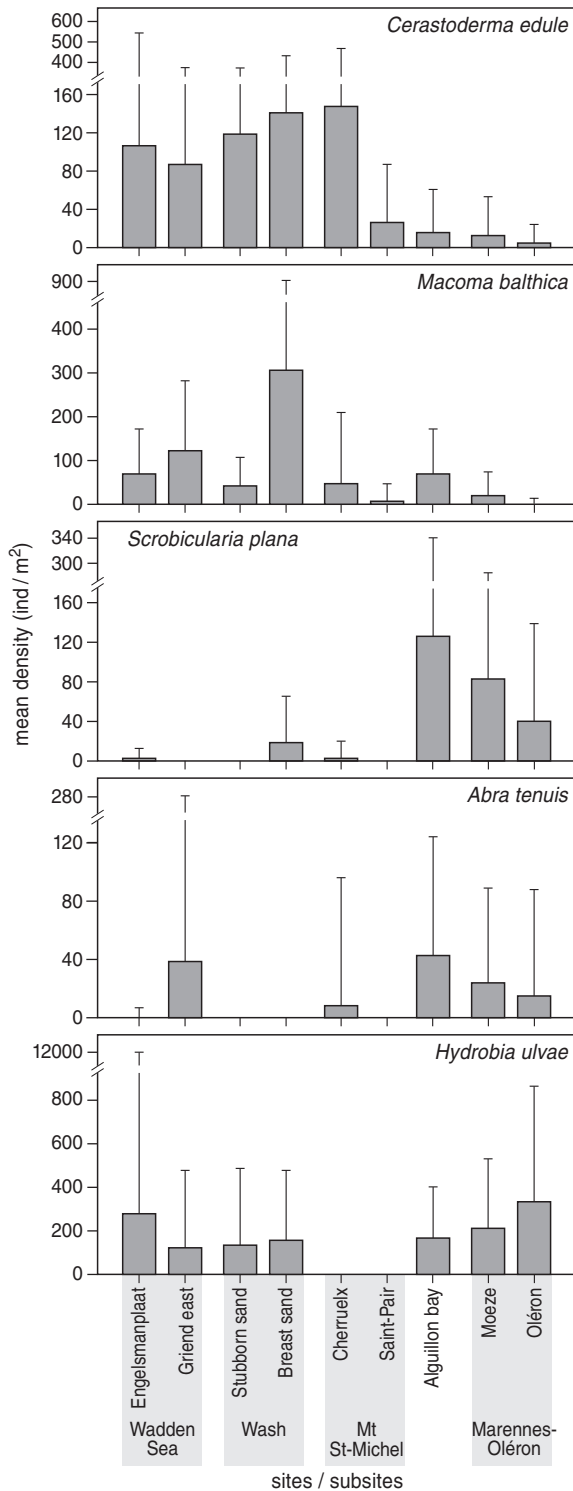
Figure 5.2. Overall average densities (ind/m^2 ± SD) of the four common bivalve species and of the single common gastropod *Hydrobia ulvae* encountered at the nine subsites of this study.

distribution also extending further north. At Engelsmanplaat, *Hydrobia* was found in the lee of the sandflat along the eastern channel.

The Wash

With five and eight bivalve species and one and two gastropods occurring at the two subsites (Table 5.2), and with *Cerastoderma, Macoma* and *Hydrobia* dominating the mollusc assemblage, the Wash was very similar to the Wadden Sea sites in terms of species composition. In the muddy east parts of Breast Sand, some banks of *M. edulis* were encountered and here *Scrobicularia* occurred in high densities. *Macoma* showed by far the most distinct distributional pattern at the Wash, occurring only at the upper shore half of Breast Sand and the higher area at the southern end of Stubborn Sand (Fig. 5.4). *Cerastoderma* occurred thinly spread out at the lower shore, especially at the western sandy parts of Breast Sand (Fig. 5.3). *Hydrobia*, again quite dispersed, covered the middle ground (Fig. 5.7).

Mont Saint-Michel Bay

With seven bivalves and three gastropods (Table 5.2), the Cherrueix subsite was much more biodiverse and rich in molluscs than Saint-Pair where only three species occurred in low densities. *Cerastoderma* and *Macoma* were the numerically dominant species. *Abra* was locally abundant at Cherrueix as was *T. tenuis* at Saint-Pair. Very few *Hydrobia* were found only at few uppershore sites at Cherrueix only. *Cerastoderma* showed the clearest zonation at Cherrueix occurring on the middle reaches of the intertidal sandflats (Fig. 5.3). The distribution of *Macoma* was rather spatially uncorrelated, with highest densities in the east (Fig. 5.4).

Aiguillon Bay

With five bivalves and two gastropods (Table 5.2), Aiguillon Bay had a similar number of species as all the other sites. Although *Cerastoderma* and especially *Macoma* were almost as common as at the more northern sites, *Scrobicularia* numerically dominated the bivalves here. Densities of *Abra* were as high as at Griend-East and *Hydrobia* was very common. Despite the uniform muddy sediments, the common bivalves showed distinct patterns of zonation. *Cerastoderma* (Fig. 5.3) occupied the lower parts of the Bay and overlapped with *Macoma* especially northeast of the Sèvre River (Fig. 5.4). Slightly more shoreward, there was a horseshoe-shaped pattern distribution with high densities of *Scrobicularia* (Fig. 5.5) and, a little higher still, of *Abra* (Fig. 5.6). Only Hydrobia occurred quite commonly right throughout the bay (Fig. 5.7).

Marennes-Oléron Bay

Although as biodiverse as the other sites (five and seven bivalves and two and five gastropods; Table 5.2), at Marennes-Oléron densities of *Cerastoderma* and *Macoma* were very low, whereas densities of *Scrobicularia* and *Abra* were high. *Ruditapes* spp. reached high densities at the Oléron subsite, and patches of *M. edulis* were found here too. Densities of *Hydrobia* were very high, with the Oléron subsite harbouring the
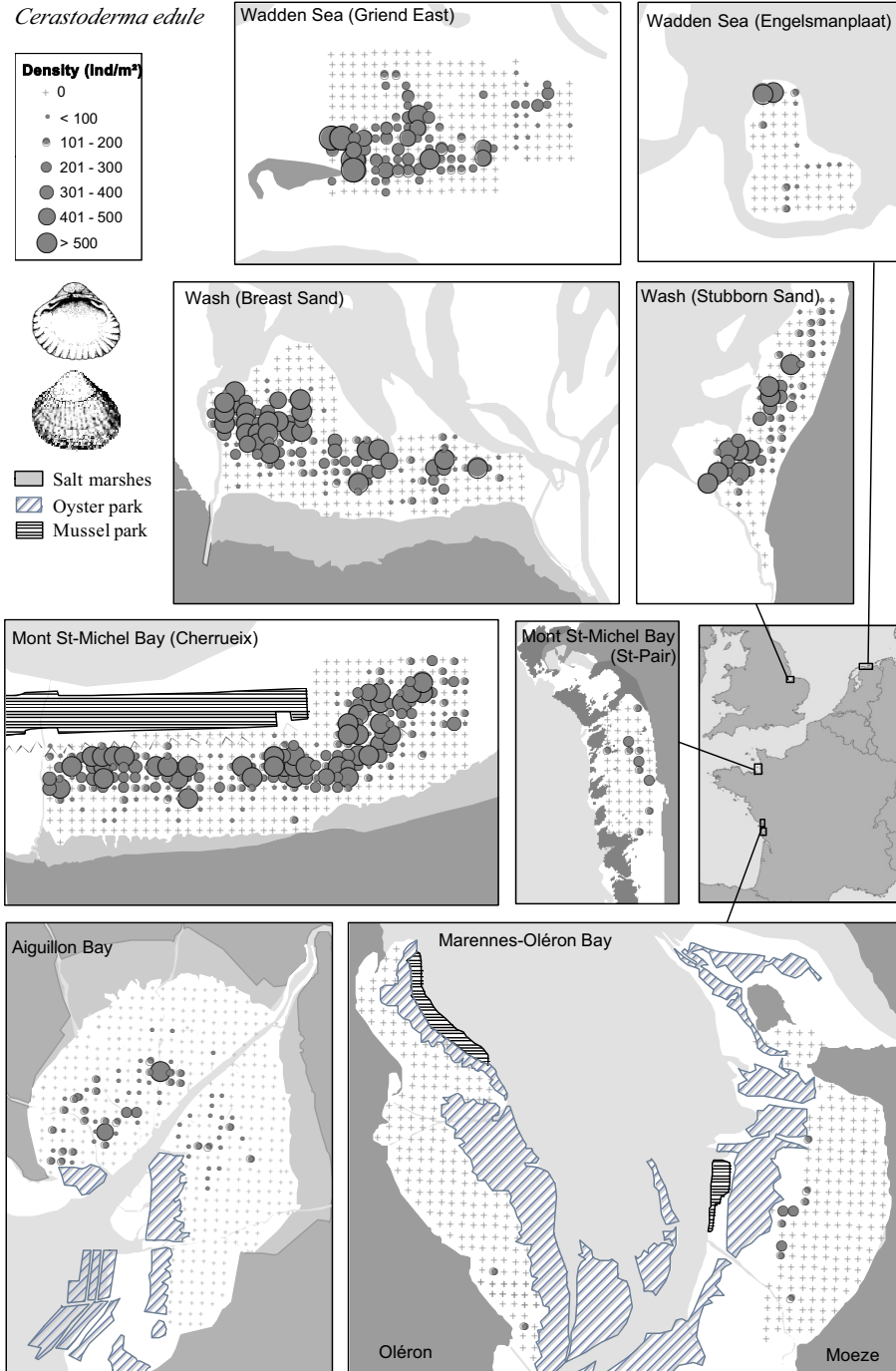
Figure 5.3. Numerical distribution of *Cerastoderma edule* over all subsites, from the Wadden Sea and the Wash in the north to the Marennes-Oléron area in the south. All grid maps are scaled identically and the degree of patchiness can be directly assessed.
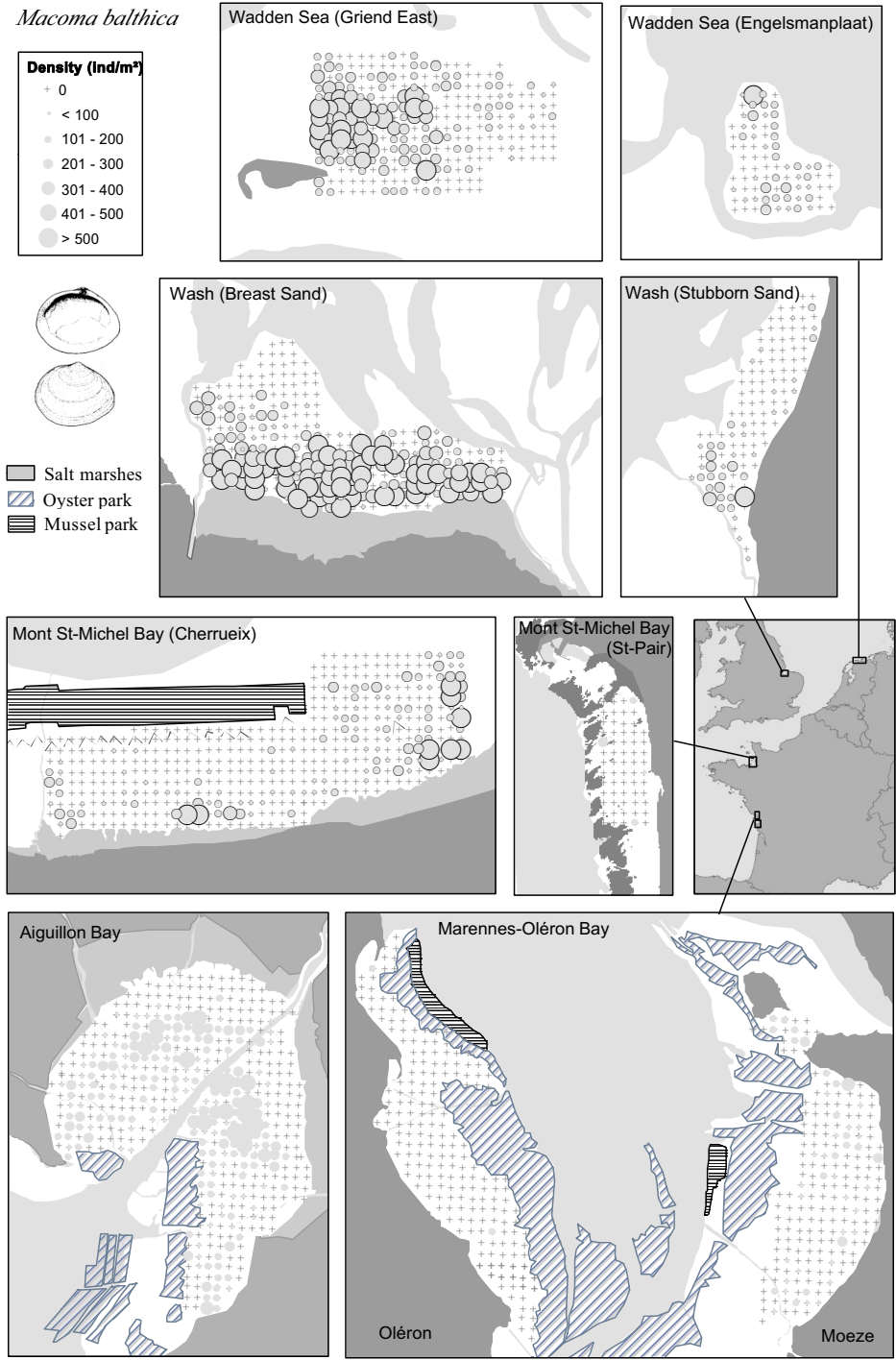
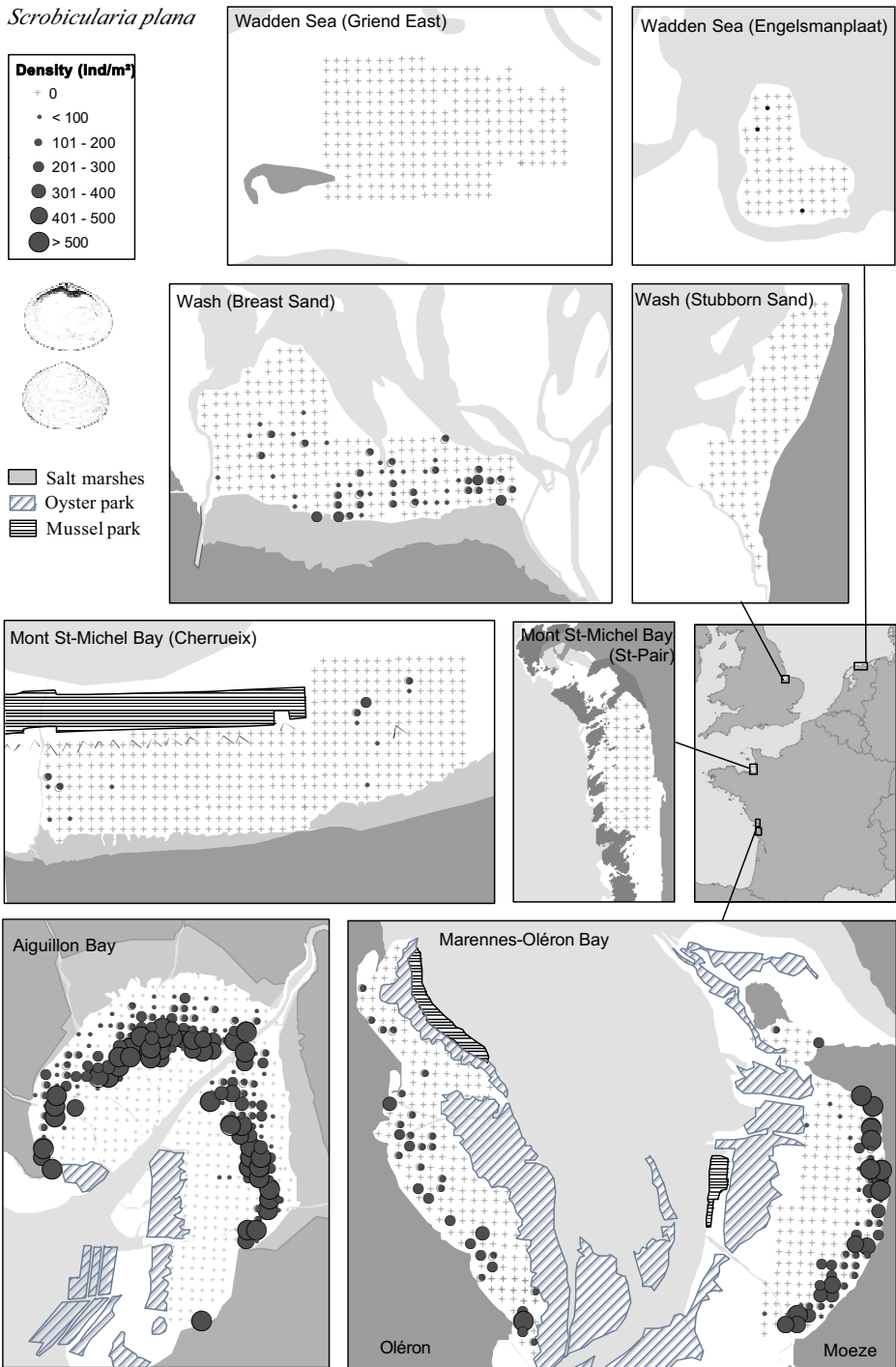**Figure 5.4.** Numerical distribution of *Macoma balthica* over all subsites.

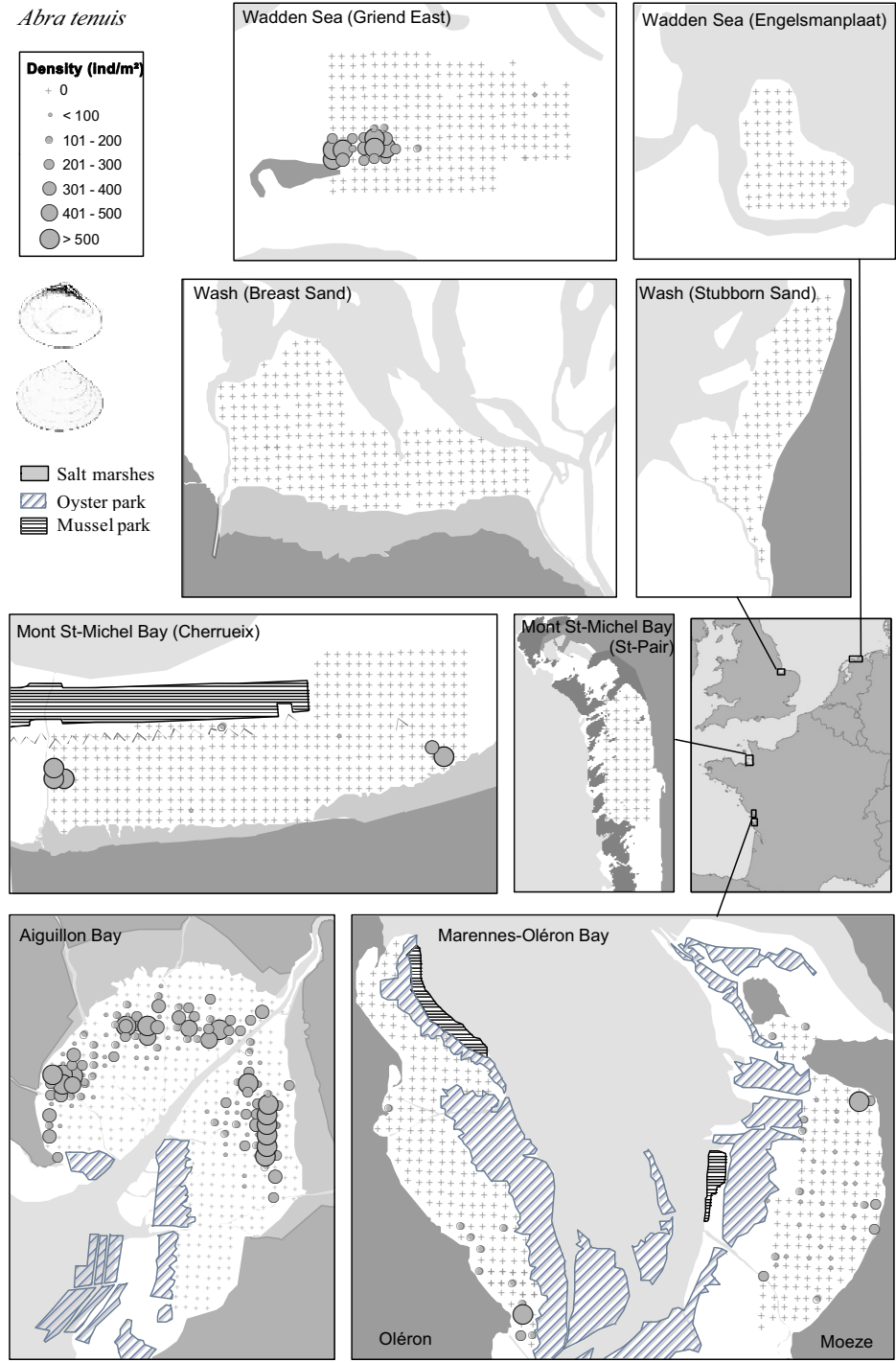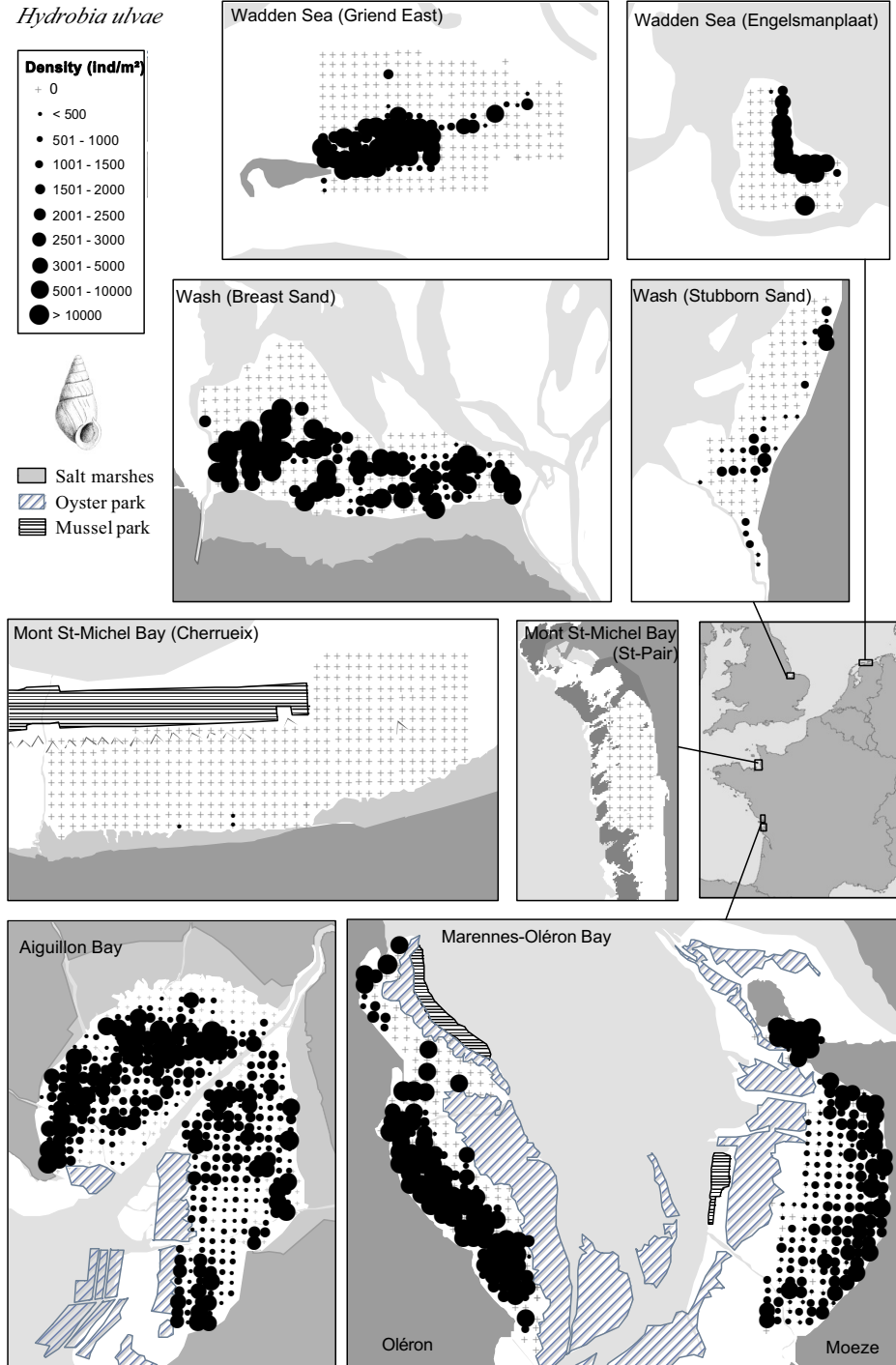**Figure 5.5.** Numerical distribution of *Scrobicularia plana* over all subsites.

Figure 5.6. Numerical distribution of *Abra tenuis* over all subsites.

Figure 5.7. Numerical distribution of *Hydrobia ulvae* over all subsites.

highest densities of any site in this study. Densities of *Cerastoderma, Macoma* and *Abra* were low and patterns of patchiness indistinct. However, *Scrobicularia* (Fig. 5.5) was clearly limited to the nearshore muddy sands (at Oléron) and muds (at Moeze). *Hydrobia* was somewhat more widely distributed (Fig. 5.7), but also had their point of distributional gravity near the shore, especially at Moeze (Fig. 5.7).

Between-site comparisons of common mollusc species
Here we will discuss similarities and differences in distributions and mean lengths of the common molluscs between sites.

Cerastoderma edule
Occurring at all sites, mean densities ranged from 5.9 (Oléron) to 148 ind/m^2 (Cherrueix) and were significantly different between all subsites (1-way ANOVA, $F_{8,2095} = 38.9$, $p < 0.001$). It was the numerically dominant bivalve species at Engelsmanplaat, Stubborn Sand, Cherrueix and Saint-Pair (Table 5.2). The species were present in almost half of all the sampled stations at the North Sea and Channel Sea subsites, except for Engelsmanplaat and Saint-Pair where they occurred in roughly one quarter of the stations. In southern subsites the species occurred at a maximum of 17% all stations. Sampling stations with densities up to 4928 (Cherrueix), 4144 (Engelsmanplaat), 3528 (Griend-East) and 2648 ind/m^2 (Breast Sand) were recorded.

   Cerastoderma occurred rather spread out at both North Sea study sites, but with the highest densities at the highest tidal levels in the Wadden Sea, and towards the lowest levels in the Wash (Fig. 5.3). Instead, they showed clear zonation at the French sites, occurring at the sandy middle levels in Mont Saint-Michel Bay and exclusively on the lowest (and very muddy) parts in Aiguillon Bay and Moeze. Shell length for the five sites varied from 1 to 39 mm, but never exceeded 24 mm at the study sites of south Britanny (Table 5.3). Mean lengths ranged from 11.1 mm in Aiguillon Bay to 18.1 mm at Saint-Pair, but the highest were found in two southern North sea sites (14.6–16.3 mm), smaller *Cerastoderma* occurring further south (11.1–12.7 mm).

Macoma balthica
Occurring at all study sites, mean densities of *Macoma* varied from 2.1 (Oléron) to 309 ind/m^2 (Breast Sand) and varied significantly between all subsites ($F_{8,2095} = 65.1$, $p < 0.001$). It was the numerically dominant bivalve at Griend-East and Breast Sand (Table 5.2). It occurred in up to 70% of sampled stations at Griend-East, but had a rather low presence at French sites (ca. 25%), except for Aiguillon Bay where it was present at half the stations. We recorded maximum densities of 3136 (Breast Sand) and 2632 ind/m^2 (Cherrueix), but nowhere else densities exceeded 1,000 ind/m^2. The distribution showed strong patchiness at all sites where *Macoma* occurred in good numbers (Fig. 5.4): it tended toward the highest parts of the intertidal flats in the Wadden Sea, the Wash and Mont Saint-Michel Bay, but avoided the high nearshore mudflats of Aiguillon Bay. Mean lengths of Macoma ranged from 7.9 mm at Griend to 15.4 mm at Saint-pair while the Wadden Sea and Mont Saint-Michel Bay harbouring

Table 5.3. Shell length of main mollusc species and shell height of Hydrobia ulvae for each subsite.

Study sites	Cerastoderma edule	Macoma balthica	Scrobicularia plana	Abra tenuis	Hydrobia ulvae
Wadden Sea					
Engelsmanplaat	17.1 ± 5.5 (2-39) *n* = 151	12.2 ± 5.3 (3-22) *n* = 99	34.5 (22-41) *n* = 2	-	2.3 ± 0.9 (1-6) *n* = 881
Griend East	16.3 ± 5.3 (1-38) *n* = 426	7.9 ± 5.0 (3-24) *n* = 621	-	5.5 ± 0.9 (3-8) *n* = 212	3.6 ± 1.1 (1-8) *n* = 1271
Wash					
Stubborn Sand	12.4 ± 5.8 (3-31) *n* = 249	10.2 ± 4.1 (4-19) *n* = 76	-	-	1.4 ± 0.7 (1-4) *n* = 596
Breast Sand	14.6 ± 6.3 (3-31) *n* = 662	8.9 ± 3.2 (3-25) *n* = 1441	14.7 ± 7.6 (5-41) *n* = 91	-	2.9 ± 1.0 (1-8) *n* = 1598
Mont Saint-Michel Bay					
Cherrueix	13.9 ± 4.0 (1-39) *n* = 1168	10.2 ± 5.2 (2-25) *n* = 382	-	4.1 ± 1.6 (1-8) *n* = 69	-
Saint-pair	18.1 ± 3.7 (3-28) *n* = 32	15.4 ± 4.2 (9-22) *n* = 10	-	-	-
Aiguillon	11.1 ± 4.1 (3-20) *n* = 178	8.3 ± 2.8 (2-27) *n* = 644	21.3 ± 9.2 (1-43) *n* = 1050	4.2 ± 1.7 (1-10) *n* = 577	3.3 ± 1.0 (1-6) *n* = 5903
Marennes-Oléron Bay					
Moeze	11.9 ± 4.1 (3-21) *n* = 69	10.5 ± 3.6 (4-18) *n* = 88	17.8 ± 8.3 (3-33) *n* = 347	5.0 ± 1.1 (2-7) *n* = 83	3.4 ± 1.1 (1-6) *n* = 2643
Oléron	12.7 ± 6.0 (5-24) *n* = 14	9.9 ± 2.8 (5-13) *n* = 7	17.4 ± 7.4 (4-29) *n* = 109	4.2 ± 1.0 (2-6) *n* = 58	3.9 ± 1.2 (1-6) *n* = 2502

Values are means ± SD with ranges in parentheses

the largest specimens. Nevertheless individuals over 20 mm length were nowhere common (Table 5.3).

Scrobicularia plana

This species was most abundant at the southern study sites, with mean densities ranging from 2.1 (Engelsmanplaat) to 126 ind/m^2 (Aiguillon Bay) ($F_{5,1641} = 49.9$, p < 0.001) At the subsites south of Brittany, *Scrobicularia* was found at around one-third of the stations (Table 5.2). North of Brittany they were only found in similarly high densities at Breast Sand. Maximum densities were reached in Aiguillon Bay (3055 ind/m^2), with peak densities of ca. 1000 ind/m^2 occurring at Moeze and Oléron. At Breast Sand, *Scrobicularia* was limited to the muddy eastern half without a strong pattern or zonation (Fig. 5.5). However, at the sites south of Brittany they only occurred in good numbers at the middle and upper levels of the mudflat (Aiguillon Bay) or close to the shore or dyke (Marennes-Oléron). *Scrobicularia* reached lengths slightly over 40 mm at Engelsmanplaat, Breast Sand and in Aiguillon Bay (Table 5.3). Mean lengths ranged from 14.7 mm (Breast Sand) to 21.3 mm (Aiguillon Bay).

Abra tenuis

Abra was also most abundant at the sites south of Brittany, though it occurred in quite high numbers at the east-tip of Griend Island (Fig. 5.6). Mean densities ranged from 0.7 at Engelsmanplaat to 42.5 ind/m^2 at Griend-East and were significantly different between all subsites ($F_{5,1654} = 41.0$, $p < 0.001$). *Abra* was the second most common bivalve species at Marennes-Oléron and the third most common in Aiguillon Bay (Table 5.2). The highest density per station was reached at Griend-East (3136 ind/m^2) but densities never exceeded 1000 ind/m^2 at other sites. *Abra* were never longer than 10 mm (Table 5.3). With a mean length of 5.5 mm, individuals were largely largest in the Wadden Sea compared to Aiguillon Bay and Moeze-Oléron with mean of 4.2 mm and 5.0 mm, respectively (Table 5.3).

Hydrobia ulvae

Mudsnails occurred commonly and in comparable densities at all study sites except Mont Saint-Michel Bay (Table 5.2). Mean densities ranged from 1230 (Griend-East) to 3324 ind/m^2 (Oléron) and were significantly different between all subsites ($F_{5,1594} = 62.2$, $p < 0.001$). They occurred on 23-34% of the stations at the North Sea sites, on half of the stations at Oléron and were present at almost all stations on the muddy flats of Aiguillon Bay and Moeze (Fig. 5.7). Maximum densities of more than 40000 ind/m^2 were recorded at Engelsmanplaat and in Aiguillon Bay and of 30000 ind/m_ at Oléron. In the Wadden Sea *Hydrobia* showed a high degree of spatial autocorrelation and densities were highest at the highest tidal levels. They were much more dispersed in the Wash and Aiguillon Bay, but occurred in well-defined bands in the middle and upper tidal zone at Marennes-Oléron Bay (Fig. 5.7).

Discussion

Latitudinal distribution and preferred sediment characteristics

Out of the 50–100 available coastal mollusc species, only five species were abundant and common at each of the five intertidal soft-sediment areas in north-western Europe. For example, at Marennes-Oléron a total of 37 gastropod species and 54 bivalve species have been found for the entire bay (De Montaudouin & Sauriau 2000), but only five gastropod and eight bivalve species were found during the present widely ranging quantitative assessment.

Cerastoderma and *Macoma* were the most widespread bivalves. Although species composition remained remarkably stable over the 900 km distance and 8° latitudinal range, there was a clear trend for *Scrobicularia* and *Abra* to be more abundant south of Brittany, perhaps ecologically 'replacing' *Cerastoderma* and *Macoma* that were so common north of it. *Cerastoderma* is a widespread bivalve species in Europe with a northern limit in the Barents Sea and in Iceland while reaching its southern limit in Mauritania (Hayward & Ryland 1990; T. Piersma personal observation). According to the present study, *Cerastoderma* appeared to be as much a 'northerner' as *Macoma*. However, the low densities in Aiguillon Bay and at Marennes–Oléron could be due to the muddy sediment there, since *Cerastoderma* clearly prefers sandy sediments (Huxham & Richards 2003; Carvalho *et al.* 2005). Not surprisingly, it was only found in the sandiest part of Aiguillon Bay. Further south, *Cerastoderma* occurs abundantly in Arcachon Bay (with densities up to 516 ind/m^2 and individuals of 30+ mm long; de Montaudouin 1996), 150 km south of Marennes-Oléron Bay. *Cerastoderma* was also recorded as the main non-cultured bivalve at Marennes-Oléron in spring 1984 (Sauriau *et al.* 1989). The low densities recorded by us could be due to high year to year variability in recruitment (Jensen 1992a; Guillou & Tartu 1994; Beukema *et al.* 2001; Flach 2003), combined with a relatively short lifespan.

Macoma is a clear 'northerner', reaching its southern distributional limit in the Gironde Estuary, just 15 km south of Marennes-Oléron (Bachelet 1980; Hummel *et al.* 1998; Drent *et al.* 2004). While *Macoma* is abundant on muddy-sand sediments (Azouzy *et al.* 2002; Huxham & Richards 2003; Poulton *et al.* 2004), it can be relatively abundant at very soft sediments like Aiguillon Bay. The very high densities of *Macoma* at Breast Sand are due to the presence of high numbers of spat at the higher sampling points.

Scrobicularia reached highest densities in Aiguillon Bay and in Marennes-Oléron Bay, which reflects the known pattern of abundance peaks between the Gironde Estuary (Bachelet 1979) and Morocco (Bazaîri *et al.* 2003), with an emphasis on the Iberian Peninsula (Sola 1997; Verdhelos *et al.* 2005), although occurring all the way from Norway to Senegal (Hayward & Ryland 1990). *Scrobicularia* were already known to show a preference for muddy or sandy-mud flat habitats (Hughes 1969a, 1969b; Sola 1997).

Abra occurs over a large range, from estuaries in Scotland and the Wadden Sea to Mauritania (Hayward & Ryland 1990). It typically lives in relatively muddy intertidal

areas (Gibbs 1984; Dekker & Beukema 1993), with Aiguillon Bay and Marennes-Oléron Bay being good examples. In the Wadden Sea, the northern boundary of its distribution appears to be restricted by winter temperatures (Dekker & Beukema 1999). Nevertheless, our study shows that even in the Wadden Sea *Abra* can build up high population densities.

Our results confirm that *Hydrobia* is one of the most common mollusc species inhabiting East Atlantic intertidal mudflats from Norway to Senegal (Hayward & Ryland 1990). That *Hydrobia* was absent from Mont Saint-Michel Bay confirms the findings by Thorin *et al.* (2001). Although *Hydrobia* may prefer muddy sediments (Sola 1996; Blanchard *et al.* 2000; Haubois *et al.* 2005), their occurrence at sandy areas like Engelsmanplaat or Stubborn Sand (see Barnes 1981) suggests that some other factors than sediment characteristics restricts their striking absence from Mont Saint-Michel Bay. Instead, we suggest that *Hydrobia* is very sensitive to hydrodynamic factors (Vader 1964; Barnes 1981), and that this explains their absence from the single true macrotidal site in this study (Mont Saint-Michel Bay) and their occurrence in areas in the Wadden Sea where incoming tidal 'waves' come to a halt.

Population structures, only based in this study, on the mean size of the common molluscs were highly variable between sites, without clear north-south gradients. This could indicate little correspondence between the growth and age-composition characteristics of species found at particular sites. This variability is particularly striking for *Cerastoderma* with mean size appearing shorter in muddy sites like Aiguillon Bay and Moeze, which may relate to the clogging of the digestive systems by mud particles in this strict suspension feeder (Kamermans 1993; Urrutia *et al.* 2001). Differences recorded in mean sizes of *Macoma* also suggest considerable differences in reproductive cycles and growth characteristics between sites. Growth rates may be lower at muddy sites such as in Aiguillon Bay and at Breast Sand (where they only occurred in the muddy parts). So, apart from factors such as tidal immersion time (Vincent *et al.* 1994), water temperature (Beukema *et al.* 1985), food resources (Hummel 1985) and sediment characteristics could be an important determinant of the growth rate of *Macoma* and consequently their size (see Drent *et al.* 2004). Like for other species, the absence of clear north-south patterns in average sizes appears for *Scrobicularia* and *Hydrobia*. This confirms that growth rates and lifespan are different according to local characteristics for each species.

We can summarize aspects of these patterns in a multidimensional scaling (MDS) ordination based on the basis of densities of the five main molluscs at the nine study subsites (Fig. 5.8). Three clear different groups appeared (stress value = 0.01). The subsites of Oléron and Moeze and the site of Aiguillon Bay formed a distinct group with high densities of *Scrobicularia*, whereas the subsites of Wadden Sea and the Wash showed great similarity with comparable densities of *Cerastoderma* and *Macoma*. The two subsites of Mont Saint-Michel Bay were quite dissimilar as a consequence of the near-absence of *Hydrobia*. Mollusc community composition appeared clearly similar within than between the regions north and south of the Brittany Peninsula.
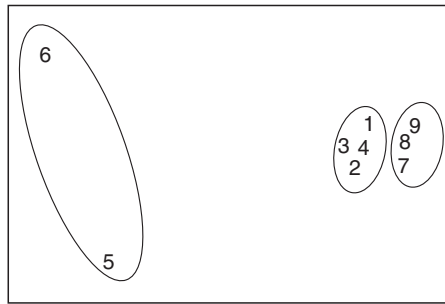
Figure 5.8. Two-dimensional MDS configurations for the densities of the five main mollusc species of the nine study subsites (stress value = 0.01). 1 = Engelsmanplaat, 2 = Griend east, 3 = Stubborn Sand, 4 = Breast sand, 5 = Cherrueix, 6 = St-Pair, 7 = Aiguillon, 8 = Moeze, 9 = Oléron.

Local distribution patterns

The distribution and abundance of intertidal molluscs is influenced by a host of environmental factors, including temperature, salinity, immersion time, current velocity, substrate type, food availability, water turbidity, occurrence of competitors, predators or parasites (Ysebaert *et al.* 2002; Gosling 2003). This study was not set up to establish correlations between all these factors and the distribution of molluscs. Instead, its strength is the possibility to make comparisons between the different local distribution patterns. The answer to the central question, whether mollusc distribution patterns are predominantly site- or predominantly species-specific, seems clear: on the basis of a subjective comparison of distribution maps, the distributional patterns appear site-rather than species-specific. For example, in the Wadden Sea *Cerastoderma* and *Macoma* showed a tendency to use relatively high sites while in the Wash *Cerastoderma* tended to occur in the low parts of the tidal flats, whereas *Macoma* rather used the high areas here. At the French sites both species occurred at intermediate tidal levels. *Hydrobia* occurred in high density bands in the Wadden Sea and at Marennes-Oléron, but was quite dispersed in the Wash and in Aiguillon Bay. Only the 'southern' species *Scrobicularia* and *Abra* were rather consistent in their distributions: they were most common in the high parts of the mudflats, where inundation times were short.

The site-specific distribution patterns must thus be explained by interactions between local factors and characteristics of the species (which can have a local component as well; see Drent 2004). At Stubborn Sand, Moeze and Oléron, sampled gradients were strictly limited at the higher range by dykes, and in the case of Saint-Pair by a cliff. At these sites artificial barriers can truncate the pattern of distribution. This appears clearly in Moeze and Oléron, where the highest densities of *Scrobicularia* and *Hydrobia* occur at the highest (nearshore) levels. The same phenomenon is illustrated by the horseshoe-shaped distributions of *Scrobicularia* (Fig. 5.5) and *Abra* (Fig. 5.6) in Aiguillon Bay where they extend to close to the shoreline in the northern-western part of the bay where saltmarshes are absent and a dike constitutes the artificial limit.

Particular to the French study areas is the presence of abandoned or active oyster or mussel cultures on the lower parts of the intertidal. The presence of very high densities of these commercial/tame bivalves may limit the settlement and growth of common non-cultivated bivalves (Ramon 1996).

Conclusions

This study is the first single winter comparison of the densities and distributions of mollusc populations at several intertidal soft-sediment areas in northwest Europe. The study demonstrated that: (a) *Cerastoderma* and *Macoma* are the most widespread and commonly occurring bivalve species over the five study sites. Although species composition remained remarkably stable over the 8º latitudinal range, there was a clear trend for *Scrobicularia* and *Abra* to be more abundant in the south and *Cerastoderma* and *Macoma* to be more common in the north; (b) Size of the common molluscs were highly variable between sites but without clear north-south gradients; (c) mollusc distribution patterns at the five study sites were predominantly site-specific, with little evidence for species-specific patterns recognisable throughout the range, the confinement of *Scrobicularia* and *Abra* to high muddy substrates throughout the range being the exception.

Dredging for edible cockles (*Cerastoderma edule*) on intertidal flats: short-term consequences of fisher patch-choice decisions for target and non-target benthic fauna

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Abstract

Intertidal flats in the Dutch Wadden Sea are protected by national and international treaties. Still, mechanical dredging for edible cockles *Cerastoderma edule* was allowed in 74% of 1200 km^2 of intertidal flats. Cumulatively, between 1992 and 2001, 19% of the intertidal area was affected by mechanical cockle dredging at least once. Based on a grid of 2650 stations sampled annually, we evaluate the extent to which cockle-dredging from 1998 to 2003 was selective with respect to non-target macrozoobenthic intertidal fauna. In all 4 years that comparisons could be made, to-be-dredged areas contained greater diversity of macrobenthic animals than areas that remained undredged. Targeted cockles were 2.5 times more abundant in areas that were to be dredged shortly, but other species also occurred in higher densities in these areas. Small amphipods and some bivalves occurred less in to-be-dredged areas than elsewhere. In terms of short-term responses to dredging, four non-target species showed a significant decrease in abundance one year after dredging. Only *Tellina tenuis* showed an increase a year after dredging.

Introduction

Large-scale industrial fishing such as trawling or dredging for demersal marine fauna is increasingly seen as a threat to the world's marine biota (Roberts 1997; Watling & Norse 1998; Jackson 2001; Coleman & Williams 2002; Dayton 2003; Rosenberg 2003; Blundell 2004). There is considerable evidence for short- and long-term negative effects of trawling and dredging on populations of target and non-target species (Jones 1992; Dayton *et al.* 1995; Jennings & Kaiser 1998; Collie *et al.* 2000; Piersma *et al.* 2001; Kaiser *et al.* 2006). However, management of such fisheries is often based on sustainable use of the stock of the target species only, without application of a more comprehensive ecosystem approach that includes non-target species (Turner *et al.* 1999; Murawski 2000).

Since the late 1980s and as a continuation of old fishing rights, in most years industrial harvesting of edible cockles (*Cerastoderma edule*) and blue mussels Mytilus edulis was allowed in 75% of the intertidal flats in the Dutch Wadden Sea, a 2400 km_ area of barrier islands, shallow waters and intertidal flats (Abrahamse *et al.* 1976; Van de Kam *et al.* 2004). These areas have been designated by the Dutch government as a State Nature Monument and Protected Nature Area. The Wadden Sea as a whole is protected under the European Commission's Bird and Habitat Directives, has Ramsar as well as Man and Biosphere (United Nations Educational, Scientific and Cultural Organization) status, and is a Particular Sensitive Sea Area under the International Maritime Organization of the United Nations. Although the scientific community voiced concern (Piersma *et al.* 1993b, 2001; Piersma & Koolhaas 1997; Kareiva & Laurance 2002; and see Swart & Van Andel 2008, for a historical review of the conflict), the government of The Netherlands assessed single-species stock status only (Kamermans & Smaal 2002; Smit *et al.* 1998).

Here, we document 'patch-choice decisions' by mechanical cockle-dredgers, at the scale of the actual fisheries, not only with respect to the target species (*C. edule*), but also for non-target macrobenthic species. Our assessment is based on six benthic surveys carried out between 1998 and 2003 that were done just before the cockle-dredging season, covering >170 km^2 of intertidal flats in the western Dutch Wadden Sea. Further, we evaluate short-term effects (1 year later) on local density by way of paired comparisons between neighbouring dredged (impact) and undredged (control) areas.

By matching neighbouring impact and control areas on the basis of abiotic characteristics, the absence of randomly appointed treatment and control areas, because of the non-random distribution of dredging-effort, was controlled for. In this way, spatial and temporal variation between control and impact area were (as far as possible) minimized. Finally, we examine whether changes in the abundance of various benthic species attributable to dredging is proportional to the selectivity exerted on them by the cockle-dredgers.

Dutch cockle-dredging

From 1993, following serious winter starvation of common eiders (*Somateria mollissima*) and European oystercatchers (*Haematopus ostralegus*) (Smit *et al.* 1998), 26% of the intertidal area in the Dutch Wadden Sea was closed to mechanical cockle-dredgers, with an additional 5% closed between 1998 and 2001. Reflecting the abundance or scarcity of cockles, the number of ships actively employed varied between a maximum of 22 and a minimum of 3 (in 2003).

Suction-dredging takes place when the mudflats are covered with a minimum of 80 cm of water (Fig. 6.1A). The dredges (75 cm or 125 cm wide) have a water jet in the
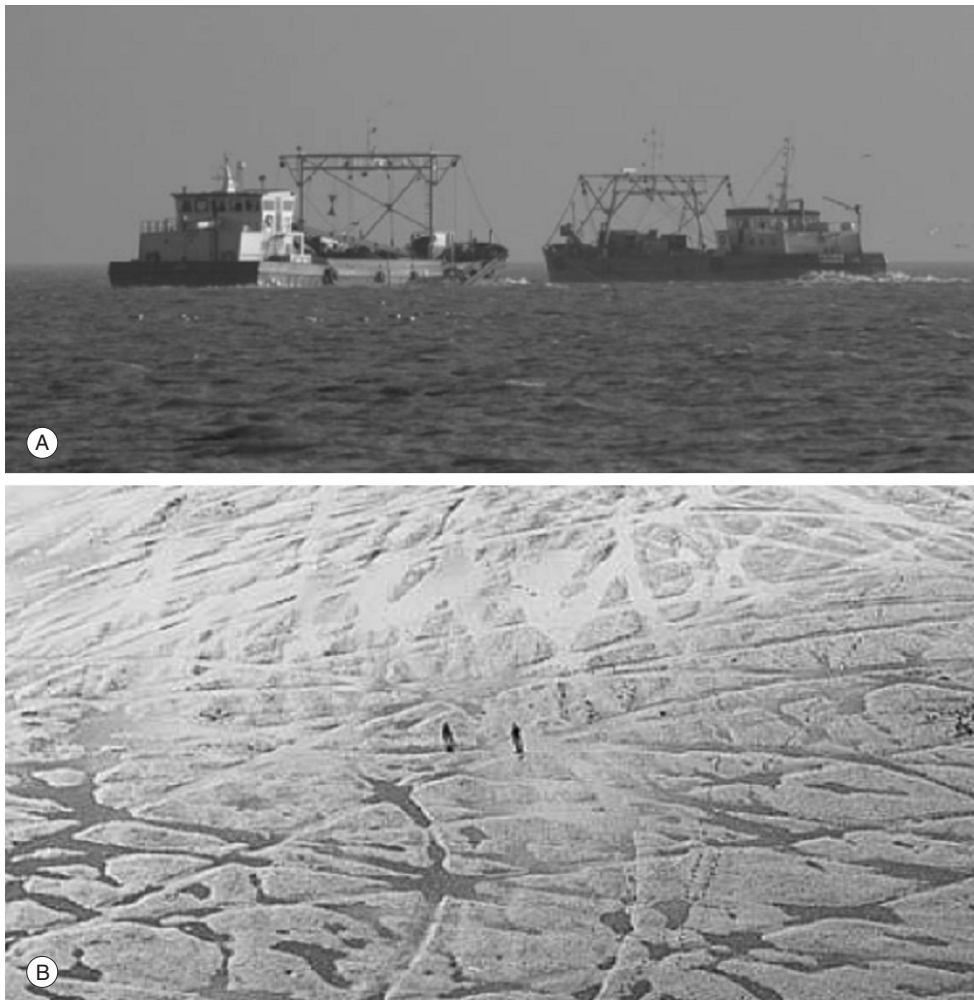
Figure 6.1. (A) Cockle dredgers in action near Vlieland, November 2002 (photo M. de Jonge). (B) Aerial view of the surface scars of cockle-dredging. For scale, note the two human figures (photo J. de Vlas).

front to loosen the top layer of the sediment, which is then scraped off by a blade at a depth of ~5 cm. Within the dredge, a strong water flow ensures that objects with a diameter <15 mm are pushed through a screen. The remaining larger objects are sucked on board the ship for further cleaning and handling. Cockle-dredgers aim at cockles >19 mm, the minimum size for consumption. After dredging, the intertidal flats appear 'scarred' (Fig. 6.1B), and can remain so for a whole winter period (De Vlas 2000; Ens *et al.* 2004).

To record position and fishing activity, mainly as an internal control, a 'black-box' system (a GPS logger) was operated on board every vessel by the Association of Mechanical Cockle Dredgers based in Kapelle (Kamermans & Smaal 2002). Cumulative seasonal data from the black boxes are screened and edited internally by the Association, which then releases maps with coloured blocks of 0.1' of latitude by 0.5' of longitude. Blocks are only coloured if >2% of the surface is touched by the dredge. Therefore, in many cases, sampling points to be dredged would not have been touched. This means that our assessment of dredging effects is conservative; i.e. a lack of statistical effects does not necessarily imply lack of ecological effects.

The Association presents an annual value for the total surface area of the tracks, a value corrected for overlap. On average, 4.3% of the 1200 km^2 of intertidal flats in the Dutch Wadden Sea (Wolff 1983) was reported to be affected annually by dredging from 1998 to 2000 (Donkers 1998, 2000; Huijssen 2001). When converted to actual fishing tracks, an average of 1.3% of the surface of intertidal flats would have been dredged each year (Kamermans *et al.* 2003). Cockle beds were often dredged in consecutive seasons; 54% of all dredged stations examined here ($n = 710$) were dredged once between 1998 and 2003, but 25% were dredged twice during the period, 14% three times, and 7% were dredged every year.

Materials and methods

Study area

The study area covers a large part of the western Dutch Wadden Sea (Fig. 6.2). With a tidal amplitude of 1.5 m at neaps, to 2 m at spring tides, it emcompasses an area of 890 km^2 of intertidal flats. The area is partitioned by three main tidal channels separating the mainland and the barrier islands of Texel, Vlieland, and Terschelling. The sediment consists of sands and muddy sands, with median grain sizes ranging from 140 to 200 μm (Piersma *et al.* 2001; Zwarts *et al.* 2004). Between 1989 and 1991, all natural beds of mussels were removed mechanically from the study area (Piersma *et al.* 1993c; Smit *et al.* 1998; Ens 2003).

Some 170 km^2 of the study area is covered with a grid of fixed sampling stations 250 m apart (Fig. 6.2). Except for a nearshore area just south of Vlieland that was closed in 1999 and re-opened in 2002, mechanical dredging was allowed everywhere. In 1998, 2000, 2001, and 2002, respectively 14.9%, 11.5%, 15.4%, and 8.0% of our sampling stations were dredged (Fig. 6.2). In 1999, virtually all fishing was in the

Figure 6.2. Sampling grid in the western Dutch Wadden Sea and the extent of mechanical cockle-dredging in autumn of 1998, 2000, 2001, and 2002. Dredged sampling stations are indicated by a filled dot, sampling stations not potentially affected by mechanical dredging by open circles. For each year, paired sampling areas with dredged and undredged quadrants, used to determine species' response to dredging, are indicated by boxes. Year 1999 is not shown, although benthic sampling was carried out, because that year all commercial dredging took place in the eastern Wadden Sea.

eastern part of the Dutch Wadden Sea. The cumulative area affected by dredging from 1992 to 2001 was 19% of the whole Dutch Wadden Sea (Kamermans *et al.* 2003); in our study area, this was 24.6% from 1998 to 2002.

Sampling routines

Sampling stations were visited either on foot or by boat once a year between mid-July and early September. Although fishing was permitted from mid-August on, dredging never started before early September and continued to December (or even as late as January/February in the 2002/2003 season). From 1998 to 2003 we sampled, respectively, 2326, 2539, 2731, 2749, 2762, and 2680 stations. These surveys, carried out independently of the fishery, aimed at documenting benthic food abundance to gain an understanding of shorebird distributions (Van Gils *et al.* 2005c, 2006c).

Sampling stations were found with hand-held GPS (Garmin 45 and 12, using WGS84 as map datum), and at each station one (on foot) or two (by boat) sediment cores, covering 0.018 m^2 in total, to a depth of 20–25 cm were taken. The cores were sieved over a 1 mm mesh and numbers of all species were recorded; for bivalves, the age/size classes were also noted. All crustaceans and molluscs were collected and stored at –20°C for later analysis in the laboratory (see Piersma *et al.* 1993c; Van Gils *et al.* 2006b, 2006c for details). On average, 56% of the samples were taken by boat and 44% on foot. Both methods, based on comparisons between benthos densities at 165 adjoining positions (excluding Hydrobia ulvea), that were either sampled by boat or on foot between 1998 and 2004, yield similar results (unpublished data).

An invasion of the exotic polychaete *Marenzelleria viridus* began about 1998, but quantitatively we only trust and subsequently use observations from 2000 on. Rare species such as the tube-living polychaete *Lagis koreni* were excluded from analysis. Their scarcity made comparisons between control and impact areas impossible. The mudsnail *H. ulvae* was also excluded, because numbers were not sampled quantitavely by boat. Note that cockles were separated into two size classes, ≤19 mm and >19 mm, and subsequently treated as separate species in the analysis.

Statistical analysis

We test for differences in the number of species per station (target-sized cockles excluded) between the to-be-dredged area and the undredged area for the whole western Dutch Wadden Sea, Student's *t*-tests on log-transformed data. This procedure assumes that cores taken 250 m apart are independent samples. Data from four dredging seasons (1998, 2000, 2001, and 2002) were included.

We also determined whether cockle-dredging led to changes in the abundances of macrozoobenthic species, *a posteriori* matching dredged (impact) areas with undredged neighbouring ones (control areas). We made sure that paired areas were similar in terms of tidal height, water coverage during high tide, and sediment composition, to ensure that temporal as well as spatial effects would be accounted for statistically (Fig. 6.2). Historically, industrial cockle-dredging already started in the 1950s, with strong growth in the 1970s (Dijkema 1997). Therefore, undredged areas only

refer to areas not dredged during this study. However, all areas are likely to have been affected by dredging in the previous 20 years (Zwarts *et al.* 2004). The relative occurrence of a particular species before dredging (Table 6.1) is computed as the ratio of the density in to-be-dredged to undredged areas (Fig. 6.2), N_{d0}/N_{c0}, where N denotes average density (averaged over all areas) of the focal species, and d and c designate dredged or control areas. Zero indicates before dredging and a numeral 1 to the densities 1 year after dredging.

Table 6.1. Relative occurrence averaged over all dredging seasons of target (large *C. edule*) and 20 non-target species (including *C. edule* ≤19 mm as a category) at intertidal sampling stations in the western Dutch Wadden Sea, based on the paired control and impact areas shown in Fig. 6.2.

Species	Taxon	Relative occurrence (dredged/ undredged)	Density-change direction attributable to dredging	*p*-value
Target species				
Cerastoderma edule >19 mm	Bivalvia	2.52	–	0.005*
Non-target species				
Mytilus edulis	Bivalvia	12.81	–	0.004*
Heteromastus filiformis	Polychaeta	1.77	–	0.003*
Phyllodoce mucosa	Polychaeta	1.58	+	0.32
Nereis diversicolor	Polychaeta	1.41	–	0.13
Nephtys hombergii	Polychaeta	1.37	–	0.17
Ensis americanus	Bivalvia	1.28	–	0.02*
Arenicola marina	Polychaeta	1.24	+	0.22
Macoma balthica	Bivalvia	1.17	–	0.24
Crangon crangon	Decapoda	1.10	–	0.025*
Lanice conchilega	Polychaeta	1.08	0	0.54
Carcinus maenas	Decapoda	0.98	–	0.21
Eteone longa	Polychaeta	0.95	0	0.83
Cerastoderma edule ≤19 mm	Bivalvia	0.87	+	0.07
Marenzelleria viridus	Polychaeta	0.85	–	0.10
Mya arenaria	Bivalvia	0.78	0	0.71
Scoloplos armiger	Polychaeta	0.72	0	0.67
Gammarus locusta	Amphipoda	0.71	+	0.27
Urothoe sp.	Amphipoda	0.69	0	0.63
Corophium volutator	Amphipoda	0.48	–	0.39
Abra tenuis	Bivalvia	0.27	–	0.47
Tellina tenuis	Bivalvia	0.11	+	0.001*

Non-target species were arranged according to the value of the ratio of dredged to undredged. The direction of change, increase (+), decrease (–), no change (0), is shown. Changes in density over 1 year are tested by bootstrapping. The asterisks indicate significance.

To detect changes in density atributable to cockle-dredging, we examined densities in paired areas after dredging, i.e. using the benthic data up to and including 2003. The changes in density attributable to dredging in autumn 1998 were then calculated with data from 1999, using stations sampled in both years only. This fisheries effect was calculated as $\ln (N_{d1}/N_{c1})$. In the absence of any effect of cockle-dredging, the relative occurrence and the fishery effect are expected to be the same, i.e. $\ln N_{d0}/N_{c0} = \ln N_{d1}/N_{c1}$. The null hypotheses of no fishery effect was tested with 1000 bootstrap samples (Manly 1997) of paired control (N_{c1}) and impact (N_{d1}) average densities after dredging and before dredging (N_{d0} and N_{c0}). This generated 1000 combinations of dredging-related alterations and the accompanying selectivity index (N_{d0}/N_{c0}) for each species. Average densities were based on paired area combinations; 25 in total over all years (see Fig. 6.2). Observed values were then compared with bootstrapped values (Manly 1997). Statistical analyses were performed with either *SYSTAT* or *R* (R Development Core Team 2006).

Results

Sampling points that were to be dredged had on average 25% more macrozoobenthic species (target-sized cockles excluded) than eventually undredged stations (Fig. 6.3) (Student's *t*-test, $t = 4.65$, d.f. $= 8$, $p < 0.01$). The Shannon–Wiener index, based on $\log(x + 1)$-transformed abundances, gave similar results ($p < 0.01$), with mean values for to-be-dredged areas between 0.48 and 0.53, and for undredged areas varying between 0.37 and 0.43. This means that from 1998 to 2002, cockle-dredgers concen-
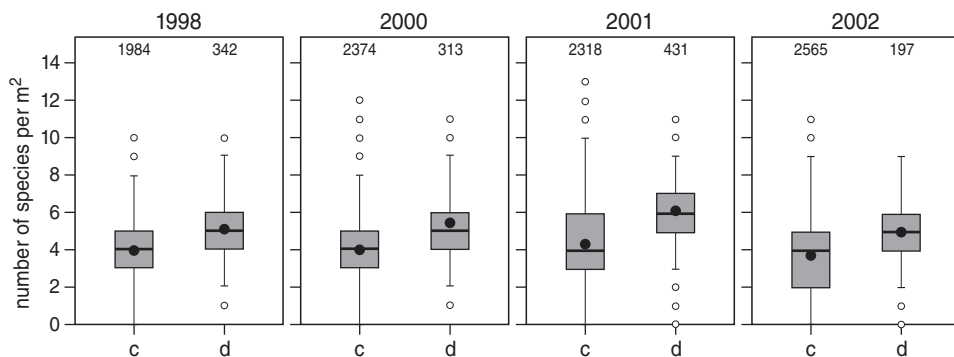

Figure 6.3. Total number of species of macrozoobenthic animals at sampling stations (consumption-size cockles not included) in intertidal flat areas in the western Dutch Wadden Sea in 1998, 2000, 2001, and 2002, either (d) or not affected (c) by mechanical cockle-dredging (see Table 6.1 for species composition). The numbers on top of each box indicate the number of samples taken. Average (dot), median (horizontal line) and outliers (circle) are shown in the box-plot.
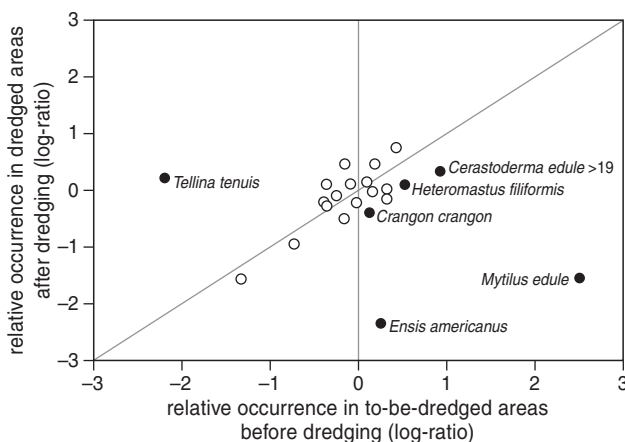
Figure 6.4. Responses of intertidal benthic species to mechanicalcockle-dredging a year after being dredged. The relative occurrence in paired dredged and undredged areas is plotted against the relative occurence in the same areas before dredging. Relative occurrence is expressed as the log-ratio of the average densities. Statistically significantly affected species are labelled (see Materials and methods for statistical approach). The diagonal line differentiates the fisheries effect; species significantly below the line are negatively affected by fisheries. The vertical line indicates equal relative occurrence in to-be-dredged and undredged areas.

trated their fishing in intertidal areas with relatively high macrozoobenthic species diversity.

Using the paired comparisons between undredged and to-be-dredged parts of the otherwise similar intertidal areas (Fig. 6.2), targeted *C. edule* (>19 mm length) were 2.5 times more abundant in the area to be dredged later that season (Table 6.1). *Mytilus edulis* was 12.8 times more abundant, *Nereis diversicolor* 1.4 times, *Ensis americanus* 1.3 times, and *Macoma balthica* 1.2 times (Table 6.1). Species that occurred less in to-be-dredged areas than elsewere were mainly small amphipods, polychaetes such as *Scoloplos armiger*, and the bivalves *Abra tenuis* and *Tellina tenuis* (Table 6.1).

Mechanical dredging for cockles had a significant negative short-term effect on the abundance of five species and a positive effect for one species, which corresponds to 27% of the intertidal benthic species examined (Table 6.1; Fig. 6.4). However, the relationship between fishery effect and relative occurrence could be characterized as fuzzy (Fig. 6.4). The abundance of most species seemingly neither increased nor decreased after 1 year proportional to their relative occurrence in dredged areas. Not surprisingly, consumption-size cockles showed a density reduction by cockle-dredging on top of natural mortality. The same effect was present for *M. edulis, Heteromastus filiformis, Crangon crangon* and *E. americanus*, even if the last three were not in particularly high densities in dredged areas. Small cockles (≤19 mm), *Carcinus maenas* and the polychaete *M. viridus* revealed no additional negative or positive fishery effect. Only *T. tenuis* demonstrated a significant increase in abundance after dredging.

Discussion

Most research dealing with fisheries effects necessarily describes ecological effects at spatial and temporal scales smaller than that of the actual fisheries (Collie *et al.* 2000; Kaiser *et al.* 2000; but see Thrush *et al.* 1998). Contrasting scales potentially obscure changes in benthic communities directly related to these fisheries. Our research is based on a long-term benthic research programme that happened to correspond to the actual extent of cockle-dredging in the western Dutch Wadden Sea (Fig. 6.2; Piersma *et al.* 2001; Van Gils *et al.* 2006b).

The experimental design that compared paired undredged and later dredged areas before and after dredging (Fig. 6.2) to the best of our knowledge has not been used before on such a large scale and should allow assessment of short-term fishery effects. The paired areas were matched by location, height in the intertidal zone and sediment characteristics, with the aim to minimize possible effects attributable to the non-random choice of fisheries locations. However, the possibility that areas selected by fisheries changed in a different way than unfished areas for other reasons than the fisheries itself cannot be excluded; changes may simply be related to the fact that the areas were biologically richer. Yet, under this constraint, we believe that our design is the best possible approach. The present analysis disentangled fisheries and natural mortality, and only the density change attributable to fisheries mortality is considered in relation to relative occurrence. This means that, in the absence of an effect of cockle-dredging, the relative occurrence and the fishery effect are the same ($\ln N_{d0}/N_{c0} = \ln N_{d1}/N_{c1}$). To express the fisheries effect as the ratio of dredged-to-undredged densities before and after dredging ($\ln N_{d0}/N_{c0} - \ln N_{d1}/N_{c1}$), though appealing, would produce spurious correlations when combined with relative occurrence (N_{d0}/N_{c0}). This is because density changes consist of natural mortality plus recruitment in the undredged area and additional dredging mortality in the dredged area. Both these independent mortalities would be incorporated in the error of the relative occurrence and the fisheries effect.

Contrary to the general impression at the time (and see Beukema *et al.* 1998, who refer to distinct cockle beds), mechanical dredging in the late 1990s focused on intertidal areas with the greatest abundance of large cockles (>19 mm) and the highest species diversity. Species targeted by shorebirds for food (*M. edulis, N. diversicolor, A. marina* and *M. balthica*) were in greater densities in to-be-dredged than in undredged areas.

Although some species we observed were only present in modest density in areas targeted by cockle-dredgers, short-term effects of dredging were noted. Because our estimates of short-term dredging disturbance are conservative, because of the rough assignments of dredged and non-dredged sampling locations (see Dutch cockle-dredging), and because we did not perform a random search for correlations but rather evaluated species one by one, we believe that application of a correction for multiple testing would lead to an unreasonable increase of type-II error (Nakagawa 2004; Garamszegi 2006). On longer time-scales, the dredged areas were characterized

by reduced settlement of cockles (and *M. balthica*), which may relate to loss of fine silts and an increase in median grain size (Piersma *et al.* 2001; Zwarts *et al.* 2004). Changes in sediment composition influence the feeding performance of deposit-feeding bivalves (Drent *et al.* 2004), including small cockles (Kang *et al.* 1999; Rossi *et al.* 2004). Such change in the sediment may also explain the increase in abundance of *T. tenuis* a year after being dredged. *T. tenuis* prefers very coarse sediments, often near the low water mark (Dekker & Beukema 1999; own data). A previous meta-analysis on the impact of mechanical fisheries on non-target species also noted that species from coarser sediments were less likely to be affected (Collie *et al.* 2000).

Using an overlapping dataset (1998-2002 rather than 1998-2003), but with different spatial resolution (272 km^2 blocks, rather than the 25 paired area comparisons used here), statistical technique and size assignment (≤16 mm in Van Gils *et al.* 2006b, ≤19 mm here), Van Gils *et al.* (2006b) also found densities of small cockles to remain stable in dredged blocks (note that we found a non-significant density increase; Table 6.1). Those authors showed that the detrimental effects of cockle-dredging on top predators such as red knots (*Calidris canutus*) was due to loss of body condition of cockles of edible size rather than than to density changes.

Decreases of *C. edule* and *M. balthica*, attributable to a single-dredging event, occurred over many rather than single years, and were a consequence of decreased spatfall in the years following dredging and increases in median grain size in the dredged area (Piersma *et al.* 2001). The absence of a short-term dredging effect on *M. balthica*, as we found in our study, is indeed consistent with this. That these species continued to decline up to 8 years after dredging (Piersma *et al.* 2001) suggests that single and multiple dredging events may reduce the system's resilience and shift inter-tidal soft-sediments to alternative states of reduced species richness (Scheffer *et al.* 2001). The failure of seagrass (*Zostera noltii*) to re-establish, the ongoing decline of *M. balthica* numbers in the western Dutch Wadden Sea (own data), and the absence of recovery of bivalve stocks after intensive cockle-dredging south of Vlieland and Richel (see Piersma *et al.* 2001) might be symptomatic of this state-shift.

To allow cockle-dredging, the Dutch government through its Ministry of Agriculture, Nature Conservation and Food Safety, had to give exemption from nature conservation laws, with due recognition of the precautionary principle and Ramsar's wise use principle. The compromise reached in parliament was that dredging for cockles should be allowed when more than 70% of the predicted energy intake of common eiders and European oystercatchers could be covered by the sum of the estimated availability of edible cockles, blue mussels, and trough shells (*Spisula subtruncata*) in the Wadden Sea and the nearshore waters of the North Sea. This requirement assumes that all biomass is harvestable (which it is not; Zwarts & Wanink 1993), that birds are omniscient (which they may be; Van Gils *et al.* 2006c) and free of travel costs (which they are not; Goss-Custard *et al.* 2004; Van Gils *et al.* 2006c), and that 30% of the required intake can be covered by other food sources (not a robust assumption according to Smit *et al.* 1998; Camphuysen *et al.* 2002; Atkinson *et al.* 2003). These mollusc-eating birds are in greatest numbers in the Wadden Sea in their non-breeding

season, which they have to survive in good condition to be able to complete their migration back to the breeding sites the following spring (Goss-Custard *et al.* 2004; Van de Kam *et al.* 2004).

The clear outcome of this work is to support the application of a whole ecosystem approach to fisheries management (e.g. Kaiser *et al.* 2000; Murawski 2000; Scheffer *et al.* 2005), with application of the wise use principle as advocated by European legislation. This principle states that any economic activity should prove itself harmless before it is allowed. The following example is relevant for the Wadden Sea. The approval of cockle-dredging decreased numbers of small mussels *M. edulis* in the dredged intertidal areas (Fig. 6.4). Consequently, the re-establishment of mussel beds in the western Dutch Wadden Sea was prevented (see also Herlyn & Millat 2000; Hiddink 2003), even though it represented a long-term conservation goal of the Dutch government (LNV 1998).

7

Landscape-scale experiment demonstrates that Wadden Sea intertidal flats are used to capacity by molluscivore migrant shorebirds

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Abstract

Whether intertidal areas are used to capacity by shorebirds can best be answered by large-scale manipulation of foraging areas. The recent overexploitation of benthic resources in the western Dutch Wadden Sea offers such an 'experimental' setting. We review the effects of declining food abundances on red knot *Calidris canutus islandica* numbers, based on a yearly large-scale benthic mapping effort, long-term colour-ringing and regular bird-counts from 1996 to 2005. We focus on the three-way relationships between suitable foraging area, the spatial predictability of food and red knot survival. For each benthic sampling position, red knot intake rate (mg AFDM s^{-1}) was predicted by a multiple prey species functional response model, based on digestive rate maximisation (this model explained diet and intake rate in earlier studies on red knots). This enabled us to derive the spatial distribution of the suitable foraging area, which in each of the 10 years was analysed with a measure of autocorrelation, i.e. Moran's *I*. Over the 10 years, when accounting for a threshold value to meet energetic demands, red knots lost 55% of their suitable foraging area. This ran parallel to a decrease in red knot numbers by 42%. Although there was also a decrease in patchiness (i.e. less information about the location of the suitable feeding sites), this did not yet lead to additional loss of birds. To cope with these landscape-scale declines in food stocks, an increase in the capacity for instantaneous food processing would be required. Although we show that red knots indeed enlarged their muscular gizzards, the increase in gizzard size was not enough to compensate for the decreased feeding area. Survival of *islandica* knots in the western Dutch Wadden Sea, based on colour-ring resightings, declined from 89% in the first half of our study period to 82% in the second half of our study period and could account for almost half of the decline in red knot numbers; the rest must have moved elsewhere in winter. Densities of red knots per unit suitable foraging area remained constant at 10 knots ha-1 between 1996 and 2005, which suggests that red knots have been using the Dutch Wadden Sea to full capacity.

Introduction

Whether habitats are used to capacity by their inhabitants, i.e. 'carrying capacity', is a question that has long occupied research agendas of workers in intertidal areas. This focus was a response to societal concerns about the continuing loss of extent and quality of wetland areas, and concerns about the fates of shared international resources, i.e. the migrant shorebirds using these habitats in the non-breeding season (e.g. Goss-Custard 1977; Goss-Custard & Moser 1988; Van de Kam *et al.* 2004; Verhulst *et al.* 2004; Burton *et al.* 2006). Often, an area's carrying capacity is expressed as the maximum number of bird-days, or the maximum numbers to survive winter, given the total food stocks available (Goss-Custard 1985; Sutherland & Anderson 1993; Goss-Custard *et al.* 2002, 2003; Van Gils *et al.* 2004).

Yet, besides the size of the stocks of suitable food, numbers of foragers also depend on the ways that food is distributed. Clear spatial patterning of prey enables foragers to distinguish among different prey densities more accurately and to optimize their movements by spending most time in rich areas (Benhamou 1992; Walsh 1996; Klaassen *et al.* 2006a, 2007; Van Gils *et al.* 2006c; Van Gils 2009). For example, positive spatial autocorrelation implies that high-density areas are found close to other high-density areas (Legendre 1993; Fortin & Dale 2005). However, if the degree of recognizable patchiness correlates with overall food abundance, this may have additional consequences. Taking a decline in shellfish-stocks in intertidal areas as an example: (i) the size of shellfish-patches could be getting smaller, down to a point where they are no longer recognized by a forager, i.e. they are below the 'grain' (Kotliar & Wiens 1990; Schmidt & Brown 1996); (ii) the distribution of shellfish could become more random (i.e. spatially unpredictable), implying that the strength of the autocorrelation for a given distance declines, which makes shellfish more difficult for foragers to find (Iwasa *et al.* 1981; Mangel & Adler 1994; Olsson & Holmgren 2000; Van Gils 2009). Declining prey-stocks might result in a decreasing abundance of foragers. In time, there might not be enough foragers to gather foraging information from and, consequently, the last suitable foraging areas become more difficult to discover (e.g. Templeton & Giraldeau 1996), leading to an Allee effect because of limited information sharing (Courchamp *et al.* 1999; Stephens & Sutherland 1999; Stephens *et al.* 1999; Jackson *et al.* 2008).

Field studies experimenting with landscape-scale declines of food stocks are impractical and unethical (Courchamp *et al.* 1999). However, in the Dutch Wadden Sea, as a result of intensive exploitation of natural resources in this protected nature reserve, such an 'experiment' has now been carried out (e.g. Piersma *et al.* 2001; Lotze *et al.* 2005; Van Gils *et al.* 2006b; Kraan *et al.* 2007; Swart & Van Andel 2008). The mechanical harvesting of cockles *Cerastoderma edule*, allowed in three-quarters of the intertidal flats, has decreased both the quality (flesh-to-shell ratio) and the abundance of available cockles for red knots *Calidris canutus* (Van Gils *et al.* 2006b). Note that fisheries impact shorebirds not only in the Wadden Sea, but in coastal areas worldwide (e.g. Atkinson *et al.* 2003; Baker *et al.* 2004). Here we examine the three-way rela-

tionships between food, predictability of food and population changes of molluscivore shorebirds, capitalizing on the experimental habitat modifications carried out between the late 1980s and 2003 (Piersma *et al.* 2001; Van Gils *et al.* 2006b; Kraan *et al.* 2007).

Our study is based on a high resolution benthic mapping programme (Bocher *et al.* 2007; Van Gils *et al.* 2009a; A.I. Bijleveld, J.A. van Gils, J. van der Meer, A. Dekinga, C. Kraan, H.W. van der Veer & T. Piersma, unpublished data), long-term colour-ringing efforts (Piersma & Spaans 2004; Van Gils *et al.* 2006b), and comprehensive high-tide bird-counts (Van Roomen *et al.* 2006). The focal species, red knots of the *islandica* subspecies, are long-distance migrants that socialize in large flocks outside the breeding season in the Wadden Sea (Piersma *et al.* 1993c; Nebel *et al.* 2000; Piersma 2007a). An estimated one-third to half of the population visits the area at some stage during winter (Nebel *et al.* 2000; Van Gils *et al.* 2006b), whose total population number dropped by 25% between 1997 and 2003 to c. 250000 (Van Gils *et al.* 2006b). As the diet of red knots consists of a number of prey species (e.g. Piersma *et al.* 1993c; Van Gils *et al.* 2005a), we use a multiple prey species functional response model, the so-called 'digestive rate model' (DRM) (Verlinden & Wiley 1989; Hirakawa 1995; Farnsworth & Illius 1998; Van Gils *et al.* 2005a), to express food abundance in a single dimension, i.e. (predicted) intake rate (mg AFDM s^{-1}). This model exploits prey selection on the basis of digestive quality (energy content over ballast mass), while respecting a digestive constraint, to maximize the average long-term energy intake (Hirakawa 1997; Van Gils *et al.* 2003b). Red knots typically exploit prey in accordance with the DRM (Van Gils *et al.* 2005a, 2005c; Quaintenne *et al.* 2009), rather than adhering to the classical prey-selection model, the so-called 'contingency model' (Charnov 1976; Stephens & Krebs 1986).

Materials and methods

Prey data

Intertidal macrozoobenthic prey was sampled between July and early September each year from 1996 to 2005 in our study area, the western Dutch Wadden Sea. Sampling stations were arranged in a fixed grid with 250 m intervals, covering most, if not all, of the intertidal area used by red knots roosting on Griend and Richel (Piersma *et al.* 1993c; Van Gils *et al.* 2006c), i.e. 225 km2 (Fig. 7.1). From 1996 to 2005 we sampled between 1807 (minimum) and 2762 (maximum) stations annually, either on foot (*n* = 10252) during low tide or by boat (*n* = 14980). The first year of full coverage was 1998 (Fig. 7.1); in 1996 and 1997 the sampling scheme was still expanding.

Sampling locations were found with handheld GPS (Garmin 45 and 12, using WGS84 as map datum) and at each station 1/56 m^2 was sampled to a depth of 20–25 cm. To distinguish accessible from inaccessible prey, for samples collected on foot, the top 4-cm (maximum bill-length) was separately sieved. The cores were sieved over a 1-mm mesh, and individuals were counted and recorded per species. Mudsnails *Hydrobia ulvae* were sampled on foot only, using a smaller core (1/267 m^2) to a depth

Figure 7.1. Distribution of predicted intake rate (mg AFDM s^{-1}) for 1998 (upper map) and for 2005 (lower map). Sampling stations that provide sufficient intake rate (≥ 0.3 mg AFDM s^{-1}) are black and grey otherwise. Light grey areas indicate mudflats exposed during low low-tide, dark grey areas indicate water, and land is represented by the white areas.

of 4 cm and sieving the sediment with a 0.5-mm mesh. All crustaceans and molluscs were collected and stored at –20°C for later analyses in the laboratory (see Piersma *et al.* 1993c; Van Gils *et al.* 2006b, 2006c, 2009a; Kraan *et al.* 2007), where size classes (to the nearest mm) were noted, enabling the determination of the ingestible fraction (Zwarts & Wanink 1993). We used a species- and length-specific proportion of prey

present in the top-layer of walking points to calculate the available prey fraction in stations sampled by boat.

From density to intake rate

We predicted the intake rate (mg AFDM s^{-1}) for every sampled position in each year, using the DRM (Verlinden & Wiley 1989; Hirakawa 1995; Farnsworth & Illius 1998; Van Gils *et al.* 2005a). Prey types are included in the predicted diet depending on energy content, amount of ballast mass, handling time, as well as the density of other high quality prey. Prey types are defined as any unique combination of energy content and ballast mass. Prey species, constituting a multitude of prey types, their characteristic, size-specific handling times and knot searching efficiencies, as well as other model details are presented in Piersma *et al.* (1995) and Van Gils *et al.* (2005a, 2005c, 2006c).

Predicted intake rate does not only depend on the density and digestive quality of prey, but also on the size of the gizzard, as processing capacity is determined by gizzard size (Van Gils *et al.* 2003a). Based on ultrasonographic 'field' measurements of gizzards (see Dietz *et al.* 1999; Dekinga *et al.* 2001), we used a 6-g gizzard (fresh mass) to predict intake rates for satisficing *islandica* knots (Van Gils *et al.* 2003a, 2005b).

To meet their demands on daily intake, which is limited by the time available for foraging combined with the attainable intake rate (Van Gils *et al.* 2007), *islandica* knots require a minimum intake rate of 0.3 mg AFDM s^{-1} to maintain a daily energy balance (Piersma *et al.* 1995).

A binary approach was chosen to deal with stations that did or did not meet the required minimum intake rate. Sampling stations with a predicted intake rate of at least 0.3 mg AFDM s^{-1} were given a value of 1 and a 0 otherwise [see Piersma *et al.* (1995) and Van Gils *et al.* (2006c) for validations of this approach]. In the Results section we present a sensitivity analysis of the effects of changing this threshold value.

Spatial analyses of benthos

To describe changes in the spatial predictability of food abundance, we analysed the spatial distribution of intake rates with Moran's *I* (Cliff & Ord 1981; Legendre & Fortin 1989; Fortin & Dale 2005). For each year, we determined the spatial patterning of the predicted intake rates, with due consideration of a threshold value to meet the demands on daily intake, using the before mentioned binary approach. The spatial structure intrinsic to the physical shape of the intertidal mudflats, the so-called 'background autocorrelation', was analysed as well (Kraan *et al.* 2009a).

Significance was determined by bootstrapping with 1000 runs (Manly 1997), but due to the large number of pairs in each distance-class, nearly all values were significantly different from random. To be able to describe biologically meaningful spatial patterns, we put an arbitrary significance-threshold at $I = \pm 0.1$ (Kraan *et al.* 2009a). This means, for example, that patch-sizes or range (e.g. Robertson 2000; Fortin & Dale 2005) are defined as the distance where the value of Moran's *I* crosses the ± 0.1 threshold. An example is presented in Fig. 7.2, where the correlogram (see Legendre &
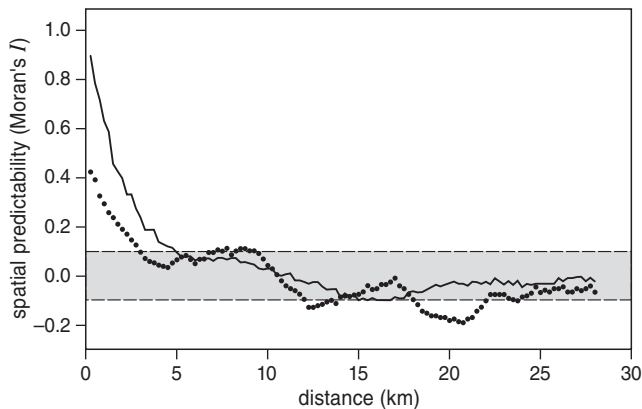
Figure 7.2. Correlogram based on the presence/absence of sufficient intake rate for red knots in 1996. x-axis shows the distance-interval (m), whereas the y-axis shows the value for Moran's *I*. The background autocorrelation (solid line), shaped by the intrinsic contour of the intertidal habitat itself, differs from the spatial patterns of intake rate (squares). The grey band mark the significance threshold.

Fortin 1989) of the suitable sites for *islandica* knots in 1996 is shown. To review changes in spatial predictability we used the amplitude of Moran's *I* at the first distance-class (250 m), i.e. the so-called 'structural variance' used in semi-variance analyses (Robertson 2000; Fortin & Dale 2005; Kraan *et al.* 2009a), as the information parameter. Spatial analyses were done with SAM (Rangel *et al.* 2006).

Bird counts
Since 1975/1976, regular bird-counts have been made during high-tide in the Dutch Wadden Sea. The count-data, consisting of two types, are analysed together and presented as a monthly average (Van Roomen *et al.* 2005). These two types are: (i) up to five simultaneous high-tide counts per season across the whole area; (ii) counts done on a monthly basis in a subsection of sites (Van Roomen *et al.* 2005). Missing count-data are imputed with a model taking into account a site, month and year factors (see Underhill & Prys-Jones 1994; Bell 1995).

In the present analyses for the seasons 1996/1997-2005/2006, we used September-April counts only, as other months' counts include both the *islandica* and the *canutus* subspecies of red knot. *Canutus* knots use the Wadden Sea as their (re)fuelling-site in August before continuing to western Africa and some might summer in the Wadden Sea after their return from the wintering areas (Piersma *et al.* 1993c; Nebel *et al.* 2000). Also, only counts from the western part of the Dutch Wadden Sea, i.e. the area between Texel, Terschelling and the Frisian mainland coast, were used. This area overlaps with the extent of our research area and has previously been shown to be used by red knots as a single 'functional unit' (sensu Tamisier 1979; Tamisier & Tamisier 1981; see Piersma *et al.* 1993c; Van Gils *et al.* 2006c).

Survival of red knot

Islandica knots were caught in the Wadden Sea with mistnets from the 1998/1999 to the 2005/2006 season. All birds were individually colour-marked to enable survival analyses based on resightings of these individuals (Brochard *et al.* 2002; Piersma 2007a). In this way, 3694 red knots were marked in total, varying between 175 and 686 per season. Nine seasons of colour-ring resightings (1998/1999-2006/2007), where a season lasts from one summer to the next, allowed survival to be estimated for eight successive seasons. We applied the standard Cormack-Jolly-Seber method in the *MARK*-programme (White & Burnham 1999) to estimate the annual survival (Phi) with a correction for the slight overdispersion of the data ($ĉ = 1.41$). This resulted in a division of survival in two time periods (see Results section): Phi$_{(period\ 1)}$ for the period before the 2002/2003 season, and Phi$_{(period\ 2)}$ from then on. Furthermore, the predicted suitable foraging area matched the same partitioning in periods (see Results section). Therefore, this division was also continued in the analyses of carrying capacity (see Results section). The relative support for each different model, i.e. model fit when varying the breakpoints and the comparison with a linear model excluding a breakpoint, was based on log-likelihood (e.g. Johnson & Omland 2004; Crawley 2007).

Results

A visual comparison between the first year of full grid coverage (1998) and the last year (2005) of the study period revealed the considerable changes in the extent of sampling stations that fulfilled the minimum intake requirements for *islandica* knots (Fig. 7.1). There was a significant decrease of 55% in the area suitable for foraging (Fig. 7.3A; GLM log-transformed data; $F_{1,8} = 45.68$; $p < 0.01$; log-likelihood = 12.61; from 5775 ha in 1996/1997 to 2581 ha in 2005/2006). However, a better fitting model was obtained by introducing a breakpoint in the GLM, thereby dividing the study period in two periods, i.e. 1996/1997-2001/2002 and 2002/2003-2005/2006 (Fig. 7.3A; log-likelihood = 16.39).

Between 1996 and 2005 the spatial predictability of intake rate, i.e. the structural variance, based on the amount of autocorrelation in the first distance-class (250 m), declined (Fig. 7.3b; GLM log-transformed data; $F_{1,8} = 15.91$; $p < 0.01$; log-likelihood = 9.59). All spatial patterns differed from the background (habitat-based) autocorrelation (Fig. 7.2). The best fitting model was obtained by treating 1996/1997-2003/2004 as a separate period from the years thereafter (Fig. 7.3B; log-likelihood = 13.00). The reduction of patch-size, i.e. the range, from 3000 (1996) to 1500 m (2005) was not significant at the 5% level, however (GLM log-transformed data; $F_{1,8} = 3.29$; $p = 0.11$).

The abundance of *islandica* knots decreased in the course of our study period (Fig. 7.3C; GLM log-transformed data; $F_{1,78} = 15.64$; $p < 0.01$; log-likelihood = 5.14). However, a model with a breakpoint indicated a break in trends after the winter of 2000/2001, and this was the superior model (Fig. 7.3C; log-likelihood = 7.23). From 1996/1997-2000/2001 on average 60209 red knot were encountered in the western
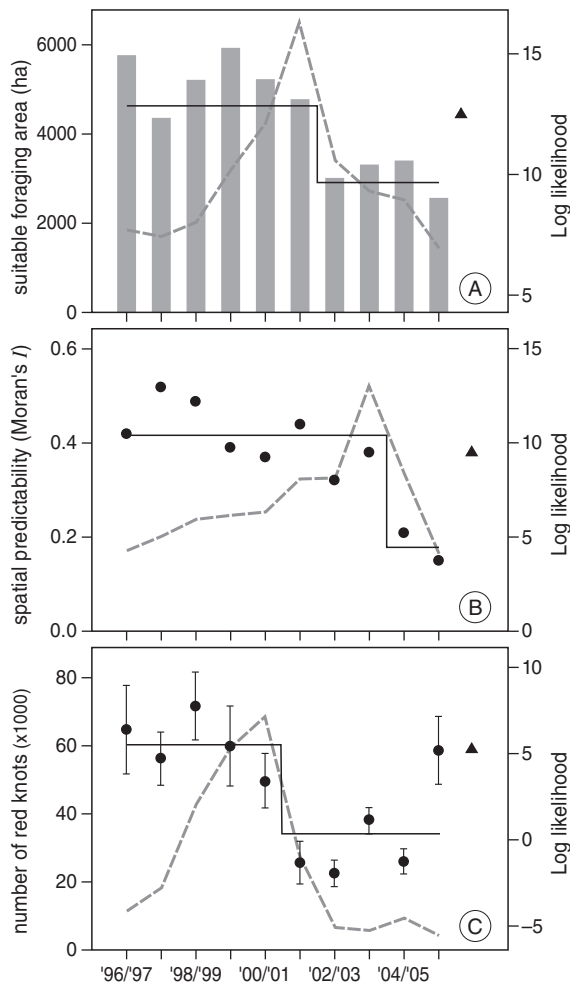
Figure 7.3. (A) Part of the sampling area (ha) that offered sufficient intake rate (≥ 0.3 mg AFDM s⁻¹). (B) Predictability of intake rate, expressed as the amplitude of Moran's *I* in the first distance-class (250 m). (C) Abundance of red knots (mean ± SE) in the western Dutch Wadden Sea during winter (September–April) from 1996/1997 to 2005/2006. Model fit (scaled on right axis) is shown for GLM with (dark grey line) or without (triangle) breakpoint that divides the data in two periods. Based on the best model, the mean (solid black line) for the two periods is shown.

Dutch Wadden Sea between August and April, whereas thereafter this number was 34007 (Fig. 7.3C). This means that the number of red knots decreased by 44% within a decade.

When the suitable foraging area and the number of *islandica* knots between both periods were compared, it was shown that both declined by about the same amount (Figs. 7.4A-B; comparison of averages ± SE between both periods; log suitable area:
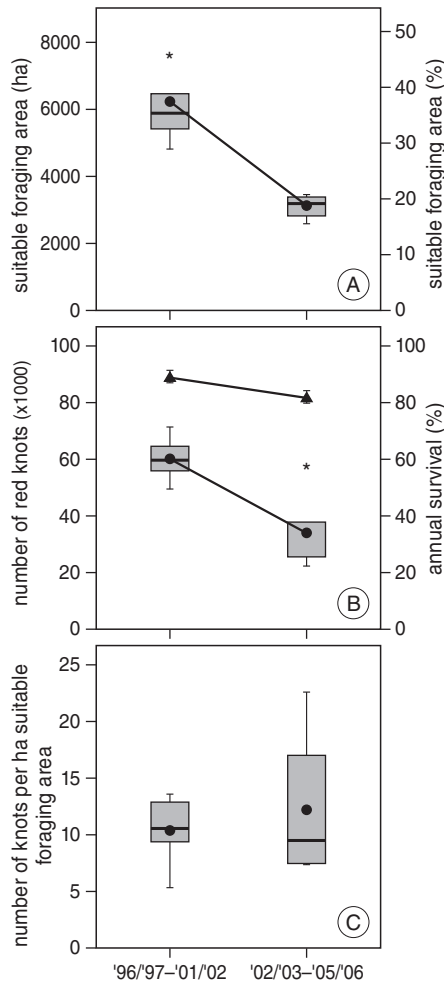
Figure 7.4. (A) Decrease of suitable foraging area between 1996/1997–2001/2002 and 2002/2003–2005/2006 (left axis: suitable foraging area expressed in ha; right axis: suitable foraging area in % of total area). (B) Decline of red knot-numbers (box plots scaled on left axis) and annual survival [mean (triangle) ± SE scaled on right axis] between both periods. (C) Because the 'slopes' in (A) and (B) are similar, the average number of red knots per ha suitable foraging area remained constant. Box-and-whisker plots give the mean (large dot), median (horizontal line inside the box), interquartile range (box), range (bars), and outliers (asterisk).

$t = 5.80$; df = 8; $p < 0.01$; log knot-numbers: $t = 3.38$; df = 8; p = 0.02). It follows that the average number of knots per ha suitable foraging area remained constant between both periods at $c.$ 10 birds ha^{-1} (Fig. 7.4C; $t = -0.424$; df = 8; p = 0.683). Shifting the breakpoint in knot numbers one season ahead, thus matching the partitioning in periods of suitable foraging area, did not change this conclusion ($c.$ 10 birds ha^{-1}; $t = -1.131$; df = 8 ; $p = 0.291$).
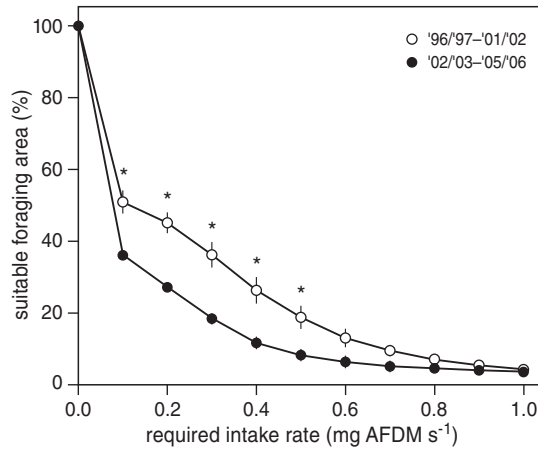
Figure 7.5. Decrease of suitable foraging area (mean ± SE) with increasing required predicted intake rates (mg AFDM s⁻¹) to maintain a daily energy balance. Open dots indicate the period 1996/1997–2001/2002, whereas the closed dots indicate 2002/2003–2005/2006. Asterisks mark significant differences.

Table 7.1. (A) Model selection and (B) real function parameters, for the best fitting model of the red knot survival analysis. AICc denotes AIC corrected for small-sample bias.

	AICc	Delta AIC	AICc weight	Model likelihood	No. parameters	Deviance
(A) Model selection						
phi(2periods)p(year)	5766.10	0.00	0.58221	1.0000	10	336.757
phi(year)p(year)	5768.01	1.91	0.22438	0.3854	15	328.586
phi()p(year)	5768.3	2.20	0.19341	0.3322	9	340.973
phi(year)p()	5823.6	57.59	0.00000	0.0000	9	396.359
phi()p()	5845.40	79.30	0.00000	0.0000	2	432.115

	Estimate	Standard Error	95% CI
(B) Parameters			
Phi (period 1)	0.890	0.016	0.854-0.918
Phi (period 2)	0.820	0.023	0.770-0.861
P (1998/1999)	0.346	0.049	0.257-0.446
P (1999/2000)	0.108	0.017	0.079-0.146
P (2000/2001)	0.344	0.024	0.299-0.392
P (2001/2002)	0.213	0.018	0.180-0.250
P (2002/2003)	0.270	0.020	0.232-0.311
P (2003/2004)	0.330	0.023	0.286-0.376
P (2004/2005)	0.348	0.028	0.296-0.404
P (2005/2006)	0.277	0.026	0.229-0.330

Period 1 refers to 1998/1999-2001/2002; period 2 to 2002/2003-2005/2006.

Whether a location is suitable for foraging is based on a binary division of predicted intake rates, where an intake rate of 0.3 mg AFDM s^{-1} acts as barrier. To estimate the sensitivity of this barrier, we varied the threshold values to assess the suitable foraging area in both periods, i.e. 1996/1997-2001/2002 and thereafter (Fig. 7.5). With increased required intake rates, the suitable foraging area decreases (Fig. 7.5), as fewer locations can provide the necessary amount of food. However, the differences between both periods were maintained until the outlying (and unlikely) values of required intake rates were reached (Fig. 7.5).

The model in which we distinguished between the annual survival of *islandica* knots in two periods (see Methods section) fitted better than a model with a year-dependent survival and was significantly better than the reduced model [Phi()p(year)] without a difference in annual survival between the periods or years (Likelihood Ratio Test; χ^2 = 4.22; p = 0.04) (Table 7.1A). The annual resighting probability was 28% on average (SE = 3%) and varied between 11% (SE = 2%) in the 1999/2000 season to 35% (SE = 5%) in the 1998/1999 season (Table 7.1B). During 1996/1997-2001/2002 annual survival $\pm$ SE was estimated at 89 $\pm$ 2%, whereas in 2002/2003-2004/2005 it was 82 $\pm$ 2%.

Discussion

Capitalizing on an 'experiment' resulting from government-facilitated shellfish-over-exploitation in formally fully protected intertidal flats in the western Dutch Wadden Sea (Piersma *et al.* 2001; Lotze *et al.* 2005; Van Gils *et al.* 2006b; Kraan *et al.* 2007; Swart & Van Andel 2008), we examined changes in the three-way relationships between suitable foraging area, spatial predictability of food, and red knot survival. *Islandica* knots visiting the area to winter after their arctic breeding season in the period 1996-2005 (Piersma *et al.* 1993c; Nebel *et al.* 2000), were faced with a decline in the extent of suitable foraging area, especially from 2002 onwards (Fig. 7.3A), and a decline in the spatial predictability of their food (Fig. 7.3B). For such a benthivorous predator, which also has to deal with tidal cycles (Van Gils *et al.* 2005c, 2006c, 2007), interference competition (Van Gils & Piersma 2004; Vahl *et al.* 2005), and predation by raptors (Piersma *et al.* 1993c; Van den Hout *et al.* 2008), these landscape scale changes have population-level impacts.

Declining suitable foraging area
The decline of suitable foraging area and the decline of *islandica* knots ran parallel (Fig. 7.4A-B), and the mean density of birds remained stable at *c.* 10 individuals per ha suitable foraging area before and after 2002 (Fig. 7.4C). This not only strongly indicates that the available suitable foraging area regulates red knot numbers in the western Dutch Wadden Sea, but also that the intertidal areas are used to full capacity by red knots (Goss-Custard 1977, 1985).

In addition to the absolute decrease of sites that are above the threshold predicted intake rate, also the spatial arrangement of the remaining area that still provided suffi-

cient food is of importance. Red knots follow strategic itineraries across the intertidal landscape, utilizing a west-east gradient in exposure-time, to be able to fulfil their energetic demands (Van Gils *et al.* 2005c, 2006c). For example, satisficing *islandica* knots extend their working day routinely beyond 12 hours, up to 17 hours, to sustain their energy requirements (Van Gils *et al.* 2005c, 2007). However, the intertidal areas that would allow such an extension of the feeding day, when taking the energetic requirements into account, now no longer provide sufficient foraging opportunity simply because suitable sites are not lined-up in a west-east gradient anymore (compare Fig. 7.1, lower panel, with Fig. 6 in Van Gils *et al.* 2005c). Tidal flats that would enable an extension of the working day beyond 14 hours (3 hours shorter than what was sometimes necessary in 1997-2000) were nearly devoid of suitable foraging sites in the second period (Fig. 7.1, lower panel, compared with Fig. 6 in Van Gils *et al.* 2005c), which raises the question if it would still have been profitable to go that far east in the second period.

Although red knots may recently have been unable to extend their feeding day by moving along a west-east axis, they would have been able to boost their digestive capacity. For example, increasing gizzard size from 6 g to 8 g, which increases the digestively constrained intake rate, would lead to an increase in suitable foraging area for red knots with undersized gizzards (Fig. 7.6A). For the period 2002/2003–2005/2006 this would amount to *c.* 1000 ha. Indeed, average gizzard size of *islandica* knots increased in the second period (Fig. 7.6B). However, even though the increase in gizzard size between the two periods was small (0.4 g), it was significant [GLM using 125 measured gizzards between September and April and YEAR nested within PERIOD (in 1996 and 2005 no gizzards were measured); $F_{3,121} = 5.76$; $P = 0.001$]. Yet, it would only have lead to an increase in suitable foraging area of *c.* 225 ha (Fig. 7.6A). That red knots only partially increased gizzard size may indicate that they minimize the overall rate of energy expenditure by carrying the smallest possible gizzard for the energy budget to be in balance (Van Gils *et al.* 2003a, 2007). Enlarging gizzard size increases a number of cost factors that we did not account for, as, for example, growing and maintaining such a large gizzard increases the average daily metabolic rate (Van Gils *et al.* 2003a) and affects manoeuvrability when escaping from predators (Dietz *et al.* 2007).

Decline of foraging information

When food abundance decreases (Figs. 7.1 & 7.3A), spatial patterns of food distributions change as well (Fig. 7.3B). The observed decline in structural variance, implying a more random distribution of food, reduces the amount of available foraging information. This is particularly unfavourable for predators foraging on prey that are hidden, e.g. covered in snow or beneath a layer of mud. Such animals, including bison *Bos bison* (Fortin 2003), tundra swans *Cygnus columbianus bewickii* (Klaassen *et al.* 2006a), mallard *Anas platyrhynchos* (Klaassen *et al.* 2007), and red knots (Van Gils *et al.* 2003b), adjust their foraging behaviour to spatial structuring of their cryptic prey. To maximize their long-term intake rate, they stay longer in rich areas and reside
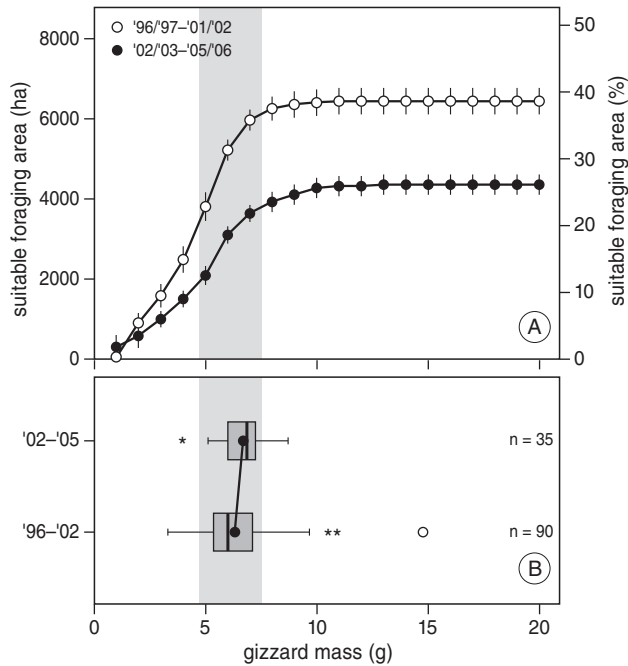
Figure 7.6. (A) Suitable foraging area (ha; mean ± SE) during 1996/1997–2001/2002 (upper line) and 2002/2003–2005/2006 (lower line) for a minimally required intake rate of 0.3 mg AFDM s^{-1} as a function of gizzard mass (left axis: suitable foraging area expressed in ha; right axis: suitable foraging area in % of total area). (B) Distribution of gizzard masses (g) in 1996/1997–2001/2002 and 2002/2003–2005/2006. Grey bar indicates the mean ± SD gizzard mass from 1996 to 2005. Box-and-whisker plots as described for Fig. 7.4. The open circle marks an outlier.

shorter in poor foraging sites by using foraging success as an indicator of prey density (Olsson & Holmgren 1998). Loss of spatial predictability of food and therefore adhering a more random distribution, as encountered by red knots in the western Dutch Wadden Sea (Fig. 7.3b), means that food might be more difficult to find (Mangel & Adler 1994) and that patch sample information is less reliable, which increases the assessment error and time needed to detect that the area is poor (Iwasa *et al.* 1981; Olsson & Brown 2006). An increasing amount of time has to be devoted to the actual searching of cryptic prey, reducing the daily energy intake further. In addition, longer foraging periods lead to higher risks (e.g. predation risk), as described elsewhere (Van Gils *et al.* 2006c, 2007).

The decline of red knots should have been more rapid than the loss of suitable foraging area to be indicative of an Allee effect. In the latter case, the population size would have been below a critical threshold, upon which the inverse density dependence would become visible (Courchamp *et al.* 1999). Note however that, if the decline of red knots would be more rapid than the decline of suitable foraging area, an alter-

native explanation might also hold: at low prey densities interference competition would increase, which would lead to lower forager-to-prey ratios as predicted by some of the models considered by Van der Meer & Ens (1997). Predictability of good foraging sites over time, i.e. high temporal autocorrelation, may play a yet undetermined role as well. Untying these possible effects remains a challenge for the future.

Population level changes

Following the joint decline of suitable foraging area and loss of information about their prey, survival of *islandica* knots decreased from 89% to 82%. As the mean life span (MLS) is a function ($-1/\ln[\varphi]$) of annual survival (φ), we can express the difference in survival as a difference in MLS. MLS of birds with an annual survival of 89% is 8.6 years, whereas it is 5.0 years for birds with a survival rate of 82%. Therefore, the average MLS of *islandica* knots wintering in the western Dutch Wadden Sea shortened by 42% in the period 1996-2005.

Under the assumption that survival was at equilibrium with reproduction between 1996/1997–2001/2002 but not thereafter, we expect an annual decrease in population size of the locally wintering red knots during the second period of (89% – 82%) / 89% = 8%. In terms of numbers, we would then expect an average number of 49093 (SD = 5278) red knots during 2002/2003–2005/2006 [derived from the 1996/1997–2001/2002 counts with 60 209 as the average number of red knots, ($\sum_{t=1}^{4}60209(1-0.08^{t})/4$, over the 4 years from 2002/2003 to 2005/2006].

The actual average number in the area was 34007 (SD = 14877), which means that reduced survival (with constant recruitment) only explained 100% * (60209–49093)/ (60209–34007) = 42% of the loss in numbers: more red knots 'disappeared' from the Dutch Wadden Sea than could be explained by the increased mortality (e.g. Van Gils *et al.* 2006a). Apparently, many surviving red knots emigrated permanently out of this Marine Protected Area [note that the Wadden Sea harbours one-third to half of the total *islandica* wintering population (Van Gils *et al.* 2006b)], and reduced food abundance may have indirectly lead to reduced breeding success (Ebbinge & Spaans 1995; Baker *et al.* 2004; Morrison *et al.* 2007). In any case, the reduced annual survival clearly supports the suggestion that the Wadden Sea was filled to capacity in the decade during which this study took place (cf. Goss-Custard 1985; Goss-Custard *et al.* 2002).

Why Afro-Siberian red knots *Calidris canutus canutus* have stopped staging in the western Dutch Wadden Sea during southward migration

Casper Kraan, Jan A. van Gils, Bernard Spaans, Anne Dekinga, and Theunis Piersma

Summary

Afro-Siberian red knots *Calidris canutus canutus* use the western Dutch Wadden Sea as a refuelling area during southward migration from Taymyr to West Africa. Here we document the decline of their food stocks in this area, based on a yearly large-scale benthic mapping effort, from 1996 to 2005. For each benthic sampling position, intake rate (mg ash-free dry mass s^{-1}) was predicted by an optimal diet model based on digestive rate maximization. Over the 10 years, when accounting for a threshold value to meet energetic fuelling demands, *canutus*-knots lost 86% of their suitable foraging area, in no small measure due to extractive shellfishing. Over this period, the proportion of probable *canutus*-knots in mistnet catches in July-August declined relative to overwintering *islandica*-knots (for which we could show a food-explained decline in numbers). We discuss the possible direct causality between a decline in the quality of intertidal mudflats in the Dutch Wadden Sea and population declines in their West-African wintering quarters.

Introduction

Several wader populations visiting the Wadden Sea during migration or in winter are in decline (Stroud *et al.* 2004; Van Roomen *et al.* 2005; Delany *et al.* 2009). Most strikingly, especially the East-Atlantic Flyway species and populations that most depend on the Wadden Sea show the steepest declines (Davidson 2003; Stroud *et al.* 2004). This suggests that these populations are bottlenecked in the Wadden Sea (Davidson 2003; Van Gils *et al.* 2009b). Previous analyses have confirmed that the quality and extent of intertidal foraging areas in the Wadden Sea has declined, especially for molluscivore shorebirds (Verhulst *et al.* 2004; Van Gils *et al.* 2006b; Kraan *et al.* 2009b).

Based on a long-term benthic mapping programme and ongoing research on the distributional ecology of red knots *Calidris canutus* in the western Dutch Wadden Sea (Piersma *et al.* 1993c; Van Gils *et al.* 2006b; Kraan *et al.* 2009b), the three-way relationships between abundance of *islandica*-knots, declining benthic food stocks and survival has recently been demonstrated (Kraan *et al.* 2009b). The carrying capacity for *islandica*-knots (breeding in the Nearctic, wintering in Western Europe; Davidson & Piersma 2009) depends on the extent of intertidal mudflats that is of sufficient quality: only areas offering a predicted intake rate (Van Gils *et al.* 2005a) of at least 0.3 mg AFDM s^{-1} (Piersma *et al.* 1995) to meet the daily energy demands within two low tide periods are acceptable. Changes in this extent closely correlated with wintering numbers (Kraan *et al.* 2009b).

Canutus-knots, the other subspecies making use of the Dutch Wadden Sea, pass through the area during southward migration to West Africa (Piersma *et al.* 1992, 1993c; Nebel *et al.* 2000; Piersma & Davidson 2009). From the early 1980s to the mid 1990s their population has decreased with 34% to 339000 birds (Stroud *et al.* 2004). However, due to difficulties in separating *canutus*- and *islandica*-knots staging in the Wadden Sea (Piersma *et al.* 1993c; Nebel *et al.* 2000), information about presence and refuelling rates at this critical time during their annual cycle is scarce (but see Piersma *et al.* 1993c; Nebel *et al.* 2000). Here we aim to fill that gap by illustrating the decreasing refuelling opportunities for *canutus*-knots between 1996 and 2005 based on our annual large-scale benthic mapping in the western Dutch Wadden Sea.

Materials and methods

The western part of the Dutch Wadden Sea (53°N, 4-5°E), surveyed by us each year from 1996 to 2005, is bordered by the barrier islands of Texel, Vlieland and Terschelling at the north and the mainland coast of Friesland in the south and spans about 225 km^2 (Fig. 8.1). This area covers most, if not all, of the intertidal mudflats used by red knots roosting on Griend and Richel (Piersma *et al.* 1993c; Van Gils *et al.* 2006c).

Intertidal macrozoobenthic prey was annually sampled between July and early September. Sampling stations were arranged in a fixed grid with 250 m intervals (Fig. 8.1) and were visited either on foot during low tide or by rubberboat during high tide.

Figure 8.1. Distribution of predicted intake rate (mg AFDM s^{-1}) for 1998 (upper map) and for 2005 (lower map). Sampling stations that provide sufficient intake rate ($\geq$ 0.6 mg AFDM s^{-1}) are black and grey otherwise. Light grey areas indicate mudflats exposed during low low-tide, dark grey areas indicate water and land is represented by white areas.

To distinguish accessible from inaccessible prey, for samples collected on foot, the top 4-cm (maximum bill length of red knots) and the bottom 4–20 cm were sieved separately. The cores were sieved over a 1-mm mesh and identified individuals were counted. Mudsnails *Hydrobia ulvae* were sampled on foot only, using a smaller core (1/267 m^2) to a depth of 4 cm and sieving the sediment with a 0.5-mm mesh. Crustaceans and molluscs were collected and stored at –20°C for later analyses in the laboratory (Piersma *et al.* 1993c; Van Gils *et al.* 2006b, 2006c; Kraan *et al.* 2009b), where size classes (to the nearest mm) were noted, enabling the determination of the

ingestible fraction (Zwarts & Wanink 1993). To determine the ash-free dry mass and shell mass of prey, the fleshy parts were removed from the shell and both shell and flesh were dried to constant mass in a ventilated oven at 55-60°C. Dry mass of both shell and flesh were determined. Then, the dried flesh was incinerated at 550°C for 5 h, after which the remaining ash-mass was subtracted from dry mass to determine AFDM-flesh. We used a species- and length-specific proportion of prey present in the top-layer of walking points to calculate the available prey-fraction in stations sampled by boat.

As the diet of red knots consists of a number of prey species of variable size (e.g. Piersma *et al.* 1993c), we used an optimal diet model to predict intake rate (mg AFDM s^{-1}) for every sampled position in each year. This particular model, the so-called digestive rate model (Hirakawa 1995; Van Gils *et al.* 2005a) exploits prey selection on the basis of digestive quality (energy content over ballast mass), such that the average long-term energy intake is maximized under a digestive constraint (Hirakawa 1997). Red knots typically exploit prey in accordance with the digestive rate model (Van Gils *et al.* 2005a, 2005b, 2006c; Quaintenne *et al.* 2009).

As processing capacity is determined by gizzard size, predicted intake rate not only depends on the density and the digestive quality of the prey, but also on the size of the gizzard. We used a 6-g gizzard to predict intake rates for net rate-maximizing *canutus*-knots passing through the Dutch Wadden Sea in autumn. This gizzard size is based on 52 red knots caught and colour-ringed in the Dutch Wadden Sea, of which the gizzards were non-invasively measured (Dietz *et al.* 1999; Dekinga *et al.* 2001) in the period 1998-2004; these particular birds being re-sighted on the Banc d'Arguin afterwards ensured their correct subspecific identity.

To fuel up at maximum rates, *canutus*-knots require an instantaneous intake rate of 0.6 mg AFDM s^{-1}, which is based on the maximum daily amount of energy of 544 kJ

Table 8.1. Number and average biometrics of red knots captured during July-August in 1995–2005 in the western Dutch Wadden Sea.

| Year	Catching period	*n*	Mass (g)		Bill-length (mm)	
			Mean	Range	Mean	Range
1995	27 July - 29 Aug.	49	144	112 - 194	34	30 - 38
1996	17 July - 21 Aug.	28	144	100 - 197	34	29 - 38
1997	04-21 Aug.	72	142	97 - 197	33	28 - 38
1998	28 July - 31 Aug.	175	136	99 - 188	33	28 - 39
1999	10-13 Aug.	256	138	99 - 211	34	27 - 39
2000	31 July - 31 Aug.	136	143	109 - 207	34	28 - 39
2001	03 July - 20 Aug.	260	134	102 - 194	34	27 - 38
2002	No catching	-	-	-	-	-
2003	29 July - 30 Aug.	242	135	99 - 197	34	29 - 40
2004	20 July - 27 Aug.	122	135	108 - 204	34	29 - 39
2005	07 Aug.	29	135	116 - 157	34	30 - 37
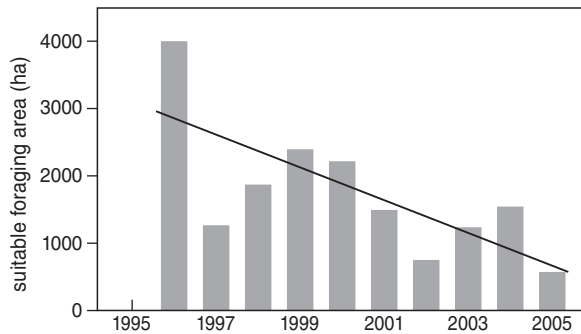
Figure 8.2. Plotted for each year, that part of the sampling area (ha) offering sufficient intake rate (≥ 0.6 mg AFDM s^{-1}) for fuelling *canutus*-knots. Note that the suitable foraging area was standardized to the total area covered during 2002, when the largest number of samples (2762) was taken.

that red knots can assimilate (irrespective of gizzard size; Kvist & Lindström 2003; Van Gils *et al.* 2003a), the energetic density of their food of 22 kJ per g AFDM (Zwarts & Wanink 1993), and an average working day of 12 h (Van Gils *et al.* 2005c).

To indirectly assess the proportion of *canutus*-knots using the Dutch Wadden Sea, we used data on body mass, primary moult and bill length from red knots captured in mist-nets in July-August 1995-2005 (Table 8.1). As *canutus*-knots on average have a higher body mass because they fatten-up, do not moult their primaries until reaching the wintering grounds, and are longer-billed than *islandica*-knots (Nebel *et al.* 2000), these variables can indicate the relative occurrences of the two subspecies.

Results

A visual comparison between the first year of full grid coverage (1998) and the last year (2005) of the study period reveals the considerable changes in the extent of intertidal mudflats that fulfilled the minimum intake requirements for *canutus*-knots (Fig. 8.1). The suitable foraging area decreased with 86% from 3996 ha in 1996 to 576 ha in 2005 (Fig. 8.2; GLM log-transformed data: slope = –0.058, $F_{1,8}$ = 4.477, p = 0.02).

The relationship with numbers of *canutus*-knots can not be drawn, but the biometric data from mist-netted red knots shows that the proportion of red knots without primary moult has declined (Fig. 8.3A; GLM arcsine-transformed data: slope = –0.046, $F_{1,8}$ = 5.507, p = 0.047), as has the proportion of red knots with body mass values higher than 150 g (Fig. 8.3B; GLM arcsine-transformed data: slope = –0.031, $F_{1,8}$ = 13.043, p = 0.007). The proportion of long-billed red knots ($\geq$ 35.5 mm) did not change (Fig. 8.3C; GLM arcsine-transformed data: slope = 0.001, $F_{1,8}$ = 0.031, p = 0.865). None of these yearly average biometric values (Fig. 8.3) correlated directly with the yearly extents of suitable foraging area (Fig. 8.2).
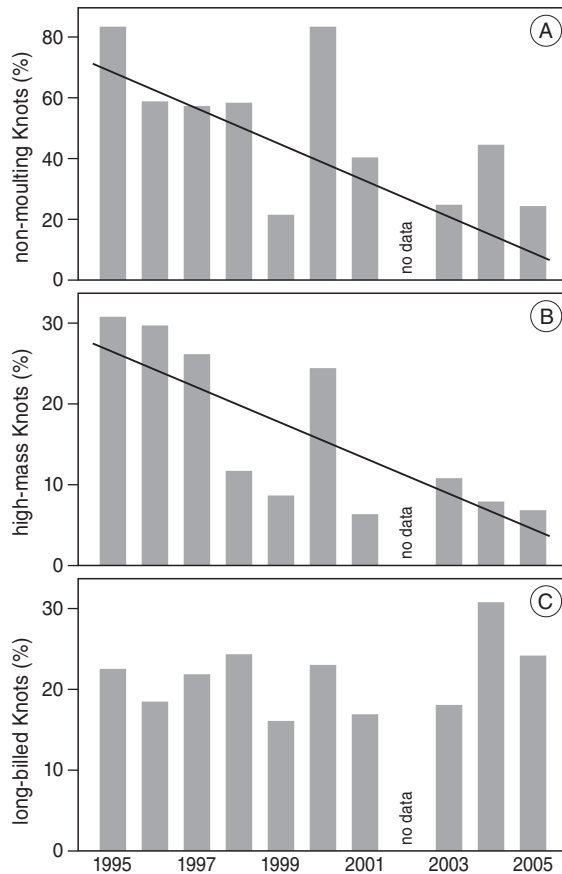
Figure 8.3. (A) Percentage of red knots without primary moult, (B) with a body mass equal to or above 150 g and (C) with a bill length >= 35.5 mm in mist-net catches in July–August 1995-2005 (see Table 8.1).

Discussion

The data on body mass and moult indeed suggest that *canutus*-knots have been in decline over the last decade, especially accounting for the fact that over this period *islandica*-knots showed a numerical decline with 44% (Kraan *et al.* 2009b). Because *canutus*-knots are storing extra fuel, during July-August, they require a higher intake rate (≥ 0.6 mg AFDM s^{-1}) than *islandica* knots (≥ 0.3 mg AFDM s^{-1}). Therefore, they must find areas offering more food and/or of better quality, which have become increasingly sparse (Figs. 8.1–8.2). The area of sufficient quality for *canutus*-knots declined with 86% (Fig. 8.2), whereas *islandica*-knots' feeding area 'only' declined with
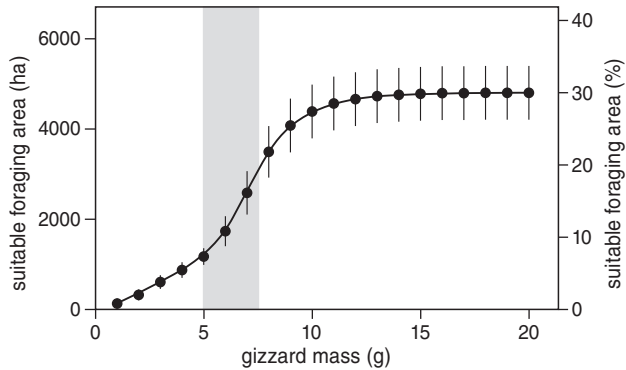
Figure 8.4. Suitable foraging area (ha; mean ± SE) during 1996-2005 for a minimally required intake rate of 0.6 mg AFDM s^{-1} as a function of gizzard mass (left axis: suitable foraging area expressed in ha; right axis: suitable foraging area in % of total area). Grey bar indicates the mean ± SD gizzard mass from 1998 to 2004.

55% from 5775 ha to 2581 ha between 1996 and 2005 (Kraan *et al.* 2009b). Analyses of spatial patterns in benthic richness with respect to bottom-disturbance by shellfish-dredging has indicated that these declines in no small part may be due to these economic activities in an otherwise protected nature reserve (Piersma *et al.* 2001; Van Gils *et al.* 2006b; Kraan *et al.* 2007).

To increase their digestive capacity, and thereby the range of sampling stations theoretically yielding suitable feeding conditions (Kraan *et al.* 2009b), red knots could increase their gizzard size (Fig. 8.4). However, 52 gizzards of *canutus*-knots caught in the Dutch Wadden Sea and resighted on Banc d'Arguin later showed that *canutus*-knots in fact slightly decreased gizzard size between 1998 and 2004 (average ± SD = 6.2 ± 1.3 g; GLM log-transformed data: slope = -0.025, $F_{1,50}$ = 5.502, p = 0.023). This is consistent with previous conclusions that during refuelling stages during migration red knots try to maintain the smallest possible gizzards (Van Gils *et al.* 2003a, 2007). Enlarging their gizzards would increase a number of cost factors. For example, growing and maintaining such a large gizzard increases the average daily metabolic rate (Piersma *et al.* 2003; Van Gils *et al.* 2003a) and affects manoeuvrability during escapes from predators (Dietz *et al.* 2007).

Although we are unable to determine the precise decline in numbers, in parallel with what we have shown for wintering *islandica*-knots (Kraan *et al.* 2009b), we would expect the decline in *canutus* to amount to over 86%. On the Banc d'Arguin, Mauritania, where 3/4 of the population winters (Stroud *et al.* 2004), numbers have declined over the last two decades (Van Gils *et al.* 2009b). During this time food densi-ties have actually increased (Van Gils *et al.* 2009b), suggesting that the declines are not due to local changes at the wintering sites. Major population declines also occurred further south: in Guinea-Bissau (Stroud *et al.* 2004), in Namibia (Wearne & Underhill

2005) and at Langebaan Lagoon, South Africa, where the population decreased from 2800 knots in 1975-1986 to 374 in 1998-2005 (Wearne & Underhill 2005). We suggest that the decline in suitability of the western Dutch Wadden Sea as a refuelling site during southward migration led to decreases in the relatively unspoiled wintering areas in West- and southern Africa (see also Van Gils *et al.* 2009b).

Acknowledgements

Shellfish dredging pushes a flexible avian top predator out of amarine protected area

Jan A. van Gils, Theunis Piersma, Anne Dekinga, Bernard Spaans, and Casper Kraan

Abstract

There is a widespread concern about the direct and indirect effects of industrial fisheries; this concern is particularly pertinent for so-called 'marine protected areas' (MPAs), which should be safeguarded by national and international law. The intertidal flats of the Dutch Wadden Sea are a State Nature Monument and are protected under the Ramsar convention and the European Union's Habitat and Birds Directives. Until 2004, the Dutch government granted permission for ~75% of the intertidal flats to be exploited by mechanical dredgers for edible cockles (*Cerastoderma edule*). Here we show that dredged areas belonged to the limited area of intertidal flats that were of sufficient quality for red knots (*Calidris canutus islandica*), a long-distance migrant molluscivore specialist, to feed. Dredging led to relatively lower settlement rates of cockles and also reduced their quality (ratio of flesh to shell). From 1998 to 2002, red knots increased gizzard mass to compensate for a gradual loss in shellfish quality, but this compensation was not sufficient and led to decreases in local survival. Therefore, the gradual destruction of the necessary intertidal resources explains both the loss of red knots from the Dutch Wadden Sea and the decline of the European wintering population. This study shows that MPAs that do not provide adequate protection from fishing may fail in their conservation objectives.

Introduction

Worldwide benthic communities of intertidal soft sediments are seriously threatened by bottom-touching fisheries such as dredging (Jackson *et al.* 2001). Not only do target species directly decline in numbers because of removal, but target and non-target species are also indirectly affected (Piersma et al. 2001; Hiddink 2003). In turn, predators such as migrant shorebirds, which make a living from benthic invertebrates, are declining in many parts of the world, and a link with commercial fishing activities seems evident (Atkinson *et al.* 2003, 2005; Verhulst *et al.* 2004). Until 2004, three-quarters of the intertidal flats of the Dutch Wadden Sea were open to mechanical dredging for edible cockles, despite the high-level conservation status, despite the concerns about the damaging effects of cockle dredging to intertidal ecosystems, and despite the limited economic value of cockle dredging (a total of only 11 license holders maintained a fleet of just 22 fishing boats [Kamermans & Smaal 2002]).

A direct, immediate effect of dredging is the complete removal of all organisms larger than 19 mm in the 5-cm top layer. Because the sites dredged are usually the most biodiverse (Kraan *et al.* 2007), dredging may also affect smaller cockles; other bivalves such as blue mussels (*Mytilus edulis*), Baltic tellins (*Macoma balthica*), and sandgapers (*Mya arenaria*); polychaetes; and crustaceans such as shorecrabs (*Carcinus maenas*). More indirectly and over longer time scales, sediments become coarser after dredging events, leading to reduced settlement success in both cockles and Baltic tellins (Piersma *et al.* 2001). Because grain size affects the feeding performance of bivalve mollusks (Drent *et al.* 2004), one expects prey condition or quality (defined as flesh-to-shell ratio [Van Gils *et al.* 2003a]) to be negatively affected by dredging activities. We may thus expect mechanical dredging to lead to both short- and long-term declines in quantity and quality of a variety of macrobenthic organisms.

Shellfish-eating shorebirds can cope with reductions in both prey density and in prey quality, as long as the reductions are not too large and do not occur simultaneously (Fig. 9.1). Red knots have been shown to flexibly adjust their digestive capacity to food quality so that food processing rates are just sufficient to obtain the daily amount of energy (i.e., flesh) required to maintain energy balance (Van Gils *et al.* 2003a, 2005b). Maintaining a larger digestive system would be costly in terms of maintenance and transport costs (Piersma *et al.* 2003). Therefore, a knot's intake rate is often constrained by a digestive bottleneck (Van Gils *et al.* 2003a; 2005c). This implies that a decline in prey density, although it may hamper maximum rates of prey collection (dictated by so-called 'short-term functional responses' such as Holling's type II disk equation), will often only marginally affect the digestively constrained intake rate over the full low-tide period (Fig. 9.1). Likewise, as the digestive system is flexible and can be adjusted rapidly (Dekinga *et al.* 2001), a decline in food quality can be compensated for by an increase in digestive capacity (Fig. 9.1). By contrast, once both density and quality decline simultaneously, the situation may become critical. In such cases, intake rate may become too low to maintain daily energy balance (Fig. 9.1).
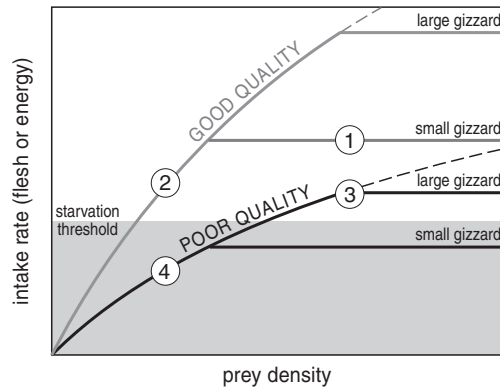
Figure 9.1. Holling's Type II functional response describes intake rate (be it flesh or energy) as a function of the density of either poor-quality (black lines) or good-quality (gray lines) prey. Digestive constraint limits shell-mass processing rate and is given for two gizzard sizes for each prey quality (horizontal cut-offs in functional response; digestively unconstrained intake rates continue as dashed lines). By knowing the threshold intake rate needed to avoid starvation (border between gray and white background), one can predict a bird's starvation chances on the basis of gizzard size and prey quality and density. (1) A small gizzard is sufficient to stay alive when prey is of good quality and occurs in high densities. Going from (1) to (2), prey density is reduced, which does not affect survival as intake rate remains above the critical threshold. Going from (1) to (3), prey quality (flesh-to-shell ratio) is reduced. To maintain a sufficient intake rate, the knot needs to increase its shell-mass processing rate, which requires a gizzard enlargement. Going from (1) to (4), the combined reduction in density and quality makes a gizzard enlargement no longer sufficient (as intake rate is now constrained by prey density), and the bird is bound to starve.

We studied dredging-induced changes in food quantity and quality and their effects on digestive physiology and survival in red knots (henceforth called knots) in the western Dutch Wadden Sea (53°14′N, 5°10′E). This site is of major importance for wintering *islandica* knots, and it is estimated that about 1/3–1/2 of the population stays or at least passes through the area each winter (Davidson & Wilson 1992; Nebel *et al.* 2000). In an area of roughly 250 km², we annually (1998–2002) sampled densities and qualities of knot food in great detail (Fig. 9.2A). Each year, mechanical dredging took place from early September into December, immediately after the completion of our sampling program. We used the exact locations of dredging to categorize 1-km² sample blocks as dredged or undredged (bearing in mind that this is not an ideal randomized block design, because blocks were selected by the fishermen). Because knots during our study period mostly consumed first-year cockles (mean percentage in diet ± standard error [SE] = 57.9 ± 2.8% of ingested flesh; *n* = 174 dropping samples), quantity and quality effects of dredging were studied with respect to newly settled cockles (≤16 mm) only.

We will make the point that shell fishing and shorebird conservation are incompatible. Marine Protected Areas (MPAs) are increasingly seen as a tool to manage

sustainable fisheries in coastal ecosystems (Gerber *et al.* 2003), which gives policy makers the feeling that they can achieve a win-win for both conservation and commercial exploitation. However, in practice, because nature conservation objectives are often fitted around the ongoing fisheries, conservation and commerce are not compatible (Jameson *et al.* 2002) as exemplified here in the case of knots and shell fishing in the Dutch Wadden Sea.

Results/Discussion

Densities of small cockles remained stable in areas mechanically dredged, whereas they increased by 2.6% per year in undredged areas (general linear model [GLM] with $n = 271$ blocks: $R^2 = 0.02$, $p = 0.04$) (Fig. 9.2B). Moreover, quality of small cockles declined by 11.3% per year in dredged areas and remained stable in undredged areas (GLM with $n = 59$ blocks: $R^2 = 0.07$, $p = 0.04$) (Fig. 9.2B). These results are consistent with a previous assessment (Piersma *et al.* 2001) that showed dredged areas to become unattractive areas for cockles to settle, a finding that was explained by dredged sediments losing silt and becoming coarser. In deposit-feeding bivalves such as freshly settled cockles (Kang *et al.* 1999; Rossi *et al.* 2004), coarser sediments may lead to worse feeding conditions (Drent *et al.* 2004) and therefore to reduced body condition, which, from the predator's point of view, equals reduced prey quality (Van Gils *et al.* 2006a).

To express changes in carrying capacity in relation to dredging activity, we calculated for each year the percentage of blocks that would yield insufficient intake rates for knots to maintain a positive energy balance (taking 4.8 W as the critical metabolizable energy intake rate [Piersma *et al.* 1995]). During our study period, the percentage of km2 blocks that were too poor for knots to feed increased from 66% in 1998 to 87% in 2002 (GLM with $n = 5$ years: $R^2 = 0.80$, $p = 0.04$) (Fig. 9.3A). This was entirely due to an increase in previously suitable blocks that were dredged (GLM with $n = 5$ years: $R^2 = 0.96$, $p = 0.003$) (Fig. 9.3a, dark gray bars). We calculated that of this 21% increase in unsuitability, 8% was due to a decline in prey densities alone, whereas the remaining 13% was due to the simultaneous decline in density and quality (note that these calculations include all potential prey species, not only cockles). In contrast, the percentage of unsuitable blocks that were never dredged before did not change (GLM with $n = 5$ years: $R^2 = 0.02$, $p = 0.80$ (Fig. 9.3A, light gray bars). As a consequence of the widespread dredging in the best areas, diet quality declined by 11.7% per year (GLM with $n = 174$ dropping samples: $R^2 = 0.05$, $p = 0.003$) (Fig. 9.3B), a similar rate of decline (11.3%) as shown by the quality of cockles, the knots' main prey, in dredged areas. To compensate for reductions in diet quality, knots should increase gizzard mass (Dekinga *et al.* 2001; Van Gils *et al.* 2003a). Indeed, in the course of the study period, gizzard mass increased by 3.4% per year (GLM with $n = 644$ birds: $R^2 = 0.02$, $p = 0.0001$) (Fig. 9.3C). This increase in gizzard mass exactly matches our quantitative expectations, because experimental results on shell mass processing rates (Van Gils *et al.* 2003a) imply that gizzard mass should vary inversely with the square root of prey
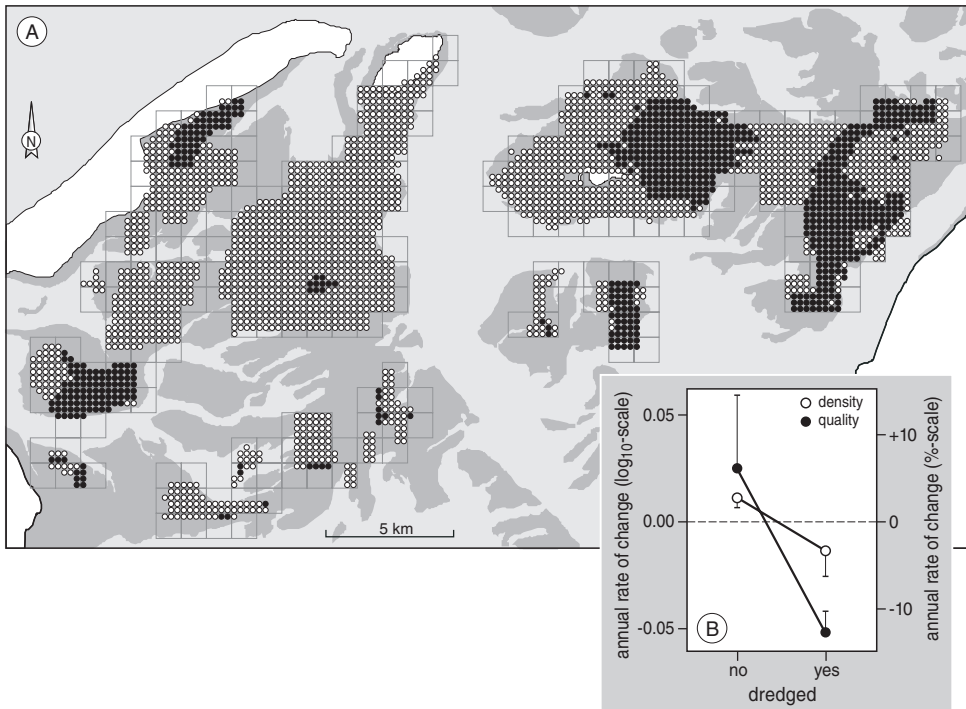
Figure 9.2. (A) Map of the study area with 2,846 sampling stations (dots) categorized into 272 square kilometer blocks (squares containing 16 stations at most). A dot is filled when a station has been dredged at least once in 1998-2002 and is open when the station was never dredged during that period. (B) Densities of available cockles remained stable in dredged blocks, but they increased (+3% year^{-1}) in undredged blocks (open dots ± SE bars). Quality of available cockles declined in dredged areas (-11% year^{-1}), whereas it remained stable in undredged areas (filled dots ± SE bars).

quality (i.e., square root of the annual 11.7% decline in prey quality = 3.4%). More specifically, gizzard masses do not deviate from the predicted gizzard masses required to balance the energy budget (predicted from yearly average prey quality values [Van Gils *et al.* 2003a, 2005b], $p > 0.1$, $n = 484$).

Nevertheless, resightings of individually color-banded birds, whose gizzards were measured before release, suggest that on average, birds not seen in our study area within the year after release had undersized gizzards ($p < 0.01$, $n = 362$), whereas individuals that we did see again had gizzards that enabled them to achieve a balanced daily energy budget ($p > 0.4$, $n = 122$) (Fig. 9.4A). That birds returning from the high-arctic breeding grounds with undersized gizzards (Piersma *et al.* 1999b) do not simply enlarge their gizzard may be explained by time and energy constraints (Piersma *et al.* 1999a; Dekinga *et al.* 2001). Birds arriving with too small a gizzard may need more time to adjust their gizzard than their fat stores allow them, and therefore they face starvation unless they leave the area (indeed we found that birds with a smaller gizzard
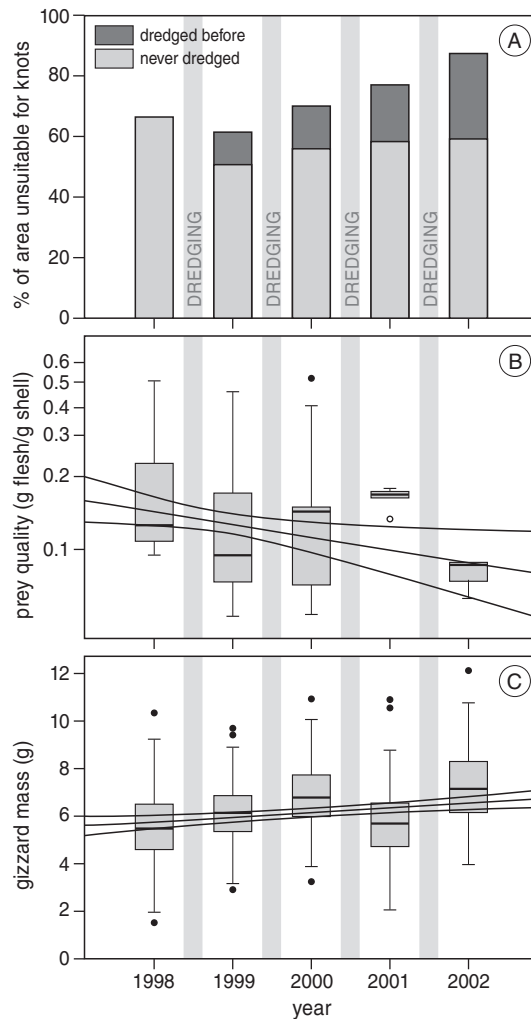
Figure 9.3. (A) The percentage of blocks that yielded insufficient intake rates (<4.8 W) increased over time due to an increase in unsuitable blocks being dredged in previous years (dark gray bars; as opposed to light gray bars indicating unsuitable blocks that were never dredged). (B) Quality of prey included in the diet has declined over time (box-and-whisker plot, line gives GLM ± 95% confidence intervals). (C) In response, gizzard mass has increased over time (boxes and lines as in [B]).

have a lower body mass; $R^2 = 0.06$, $p < 0.00001$, $n = 483$). This implies that the proportion of birds arriving with a gizzard large enough to survive increases as a function of food quality at the arrival destination (Fig. 9.4A-B). Indeed, local annual survival rate (calculated from resighting rates of color-banded birds) increased with food quality in the expected direction (Fig. 9.4C). When we estimated the distribution of gizzard masses upon arrival (by selecting only those birds caught in the Wadden Sea during

Figure 9.4. (A) Gizzard mass required to maintain energy balance declines as a function of prey quality (solid line). Gizzards of birds seen again after catching fit this relationship (mean ± SE), whereas gizzards of birds not seen again are significantly smaller (note that both groups almost entirely overlap in the poorest-quality year). (B) Observed gizzard masses upon arrival are distributed according to the left-most normal distribution. If there were no room f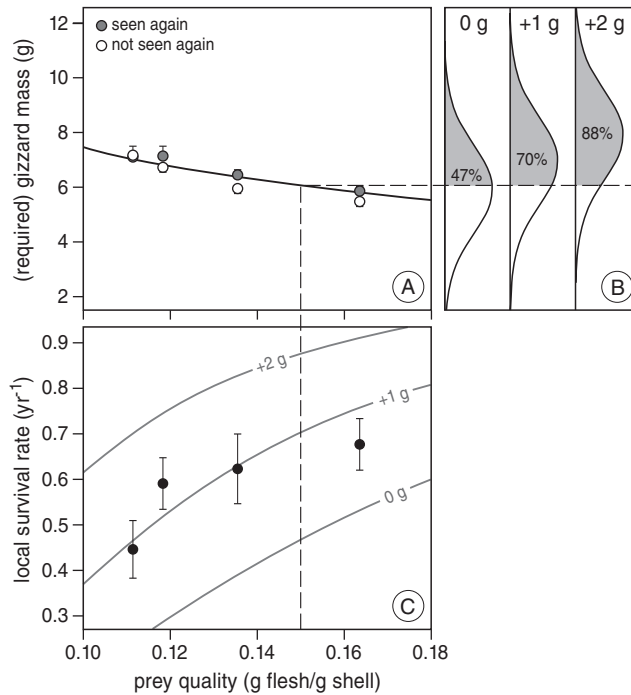or flexibly adjusting gizzard mass (0 g), only 47% of the arriving knots would be able to avoid starvation (shaded area) at an example prey quality of 0.15 g flesh per g shell (dashed line). If there were room for flexibility (+1 and +2 g in this example), a much larger proportion would be able to survive (respectively 70% and 88%). (C) Observed local survival rate (yr^{-1}; ± SE) increased as a function of prey quality and best matched with predicted survival in a +1-g flexibility scenario..

late July) and calculated, for various degrees of gizzard flexibility, the proportion of birds that would survive the critical gizzard-enlargement phase (Fig. 4B-C), the best fit with the actual survival data was obtained if knots had time to increase their gizzard by 1 g only (Fig. 9.4C).

Color-banded knots that disappeared from our study area may have died or, perhaps more likely for a wide-ranging migrant, emigrated to other areas such as the estuaries in the United Kingdom, where they probably paid a mortality cost due to the extra travel and/or due to uncertainties in the food supply at their new destination (where they also fed on hard-shelled prey, in the past [Prater 1972; Goss-Custard *et al.* 1977] and more recently [Atkinson *et al.* 2004; Stillman *et al.* 2005], and thus faced gizzard-related mortality; note that knots are 'forced' to feed on hard-shelled prey as

their pressure-sensitive bill tip can only detect hard objects buried in soft sediments [Piersma *et al.* 1998]). In any case, the declining numbers of knots wintering in the Dutch Wadden Sea (Van Roomen *et al.* 2005) can be explained as a response to declining food conditions. Moreover, the 25% decline of the entire northwestern European wintering population between 1997-1998 and 2002-2003 (from ~330000 to ~250000) (Austin G, Van Roomen M, Koks B, Piersma T, unpublished data) can be explained by measured decreases in local survival of the Wadden Sea segment of the population during the study period (using the observed local survival rates, we estimated an extra mortality of 58000 birds over the 5-y period). This study concludes that industrial forms of commercial exploitation of protected marine nature reserves in The Netherlands, by indirectly reducing food resource quality to such extents that changes can no longer be accommodated by adjustments of the digestive system, are directly responsible for the overall population decline of a fully protected shorebird species. This paper thereby adds to growing list of studies (Jameson *et al.* 2002; Caddy & Surette 2005) stressing the uselessness of declaring a marine area as protected whenever the species living in it are seriously affected by the ongoing but regulated human activities.

Materials and Methods

Sampling prey density and quality

From late July to early September 1998–2002, we sampled macrozoobenthos throughout the western Dutch Wadden Sea in a regular grid (250-m grid intersections; Fig. 9.2A). In total, we visited 2846 stations, of which the majority (75%) was sampled each year (89% in 4 out of 5 y). Stations were located using a handheld global positioning system (GPS) receivers (Garmin 45 and 12; Garmin Corporation, Lenexa, Kansas, United States) and were either visited during low tide (on foot) or during high tide (by rubber boat). At each station, a sediment core was taken (15-cm diameter; 20-cm deep) that was sieved over a 1-mm mesh. To distinguish accessible prey from prey living beyond the reach of a knot's bill (4 cm), we sieved the top layer (upper 4 cm) separately from the bottom layer (only the 'low-tide samples'). Mudsnails (*Hydrobia ulvae*) were sampled using a smaller core (7-cm diameter) and a finer mesh (0.5 mm). All potential prey items retained on the sieve were frozen (_20 °C) for later analyses. In the laboratory, items were identified with respect to species and size (to nearest mm; or, in the case of *H. ulvae*, to nearest 0.5 mm). Size classes were determined to distinguish ingestible prey from prey too large to be swallowed (Van Gils *et al.* 2005c). Methods to determine flesh and shell mass are explained elsewhere (Piersma *et al.* 2001; Van Gils *et al.* 2005a).

Mechanical dredging and its effects on cockle density and quality

During each of the 5 y studied, mechanical dredging took place after our sampling program; i.e., from early September into December. Exact locations of dredging were

known, because for reasons of internal control, every vessel had a GPS-logger onboard (Kamermans & Smaal 1998). Cumulative seasonal data on dredging locations were available in the form of fine-scaled maps (resolution of 0.1 min latitude by 0.5 min longitude).

We analyzed the effects of mechanical dredging on cockles that were actually available to knots (i.e., ≤ 16 mm, because larger ones cannot be swallowed [Zwarts & Blomert 1992]). We pooled sampling stations in 272 blocks measuring 1 km by 1 km each (Fig. 9.2A; many sampling stations did not have cockles available during multiple years making it impossible to study changes in quality at the spatial scale of stations). A block was considered dredged when at least one station was dredged in at least 1 y. Per block, we applied the following GLMs: $\log_{10}(\text{density} + 1)$ = constant + year and $\log_{10}(\text{quality})$ = constant + year. Subsequently, we tested whether significant variation in the coefficients for year could be explained by whether a block was ever dredged or not during 1998–2001 (again using GLM).

Suitability for knots

The measurements on (available) prey densities and qualities allowed us to predict for each station an intake rate for a knot with an average-sized gizzard (6-g fresh mass). We did so by applying the so-called 'digestive rate model', a multi-species functional response that takes rates of digestion into account (Hirakawa 1995), which accurately predicted diet choice, patch choice, and intake rate in both free-ranging and captive knots (Van Gils et al. 2005a, 2005c). Subsequently, after averaging these intake rates per block, we determined a block's suitability. A block was considered suitable when it yielded an intake rate sufficient to maintain energy balance when feeding for 10 h per day (corresponding to an intake rate of at least 0.3 mg dry flesh mass s^{-1}, which equals a metabolizable energy intake rate of at least 4.8 W; note that the energy contents of 1 g of flesh is more or less constant in mollusks [Zwarts & Wanink 1993]). This approach is widely used (Sutherland & Anderson 1993; Gill et al. 2001) and adequately predicted the distribution of knots in an earlier study (Piersma et al. 1995).

Diets, gizzard sizes, and observed and predicted survival rates

Diet quality was reconstructed by fecal analyses, following the procedures outlined by Dekinga & Piersma (1993). Dropping samples were collected during low tide at sites where flocks of knots had just fed. Across the 5 y of study, we analyzed 174 dropping samples, comprising 1–100 dropping(s) each (15 on average).

In order to estimate gizzard sizes and survival rates, we annually mistnetted knots from late July to late November, mostly near their main roost at Richel (an island located midnorth of our study area; Fig. 9.2A), but occasionally near the isle of Schiermonnikoog (±75 km ENE of Richel). Based on the presence or absence of active wing molt (Nebel et al. 2000), we determined subspecific identity and selected for the current analyses islandica individuals only (population numbers and survival rates are best known in this subspecies). Gizzard masses were estimated using ultrasonography (Pie 200 ultrasound, Pie Medical Benelux BV, Maastricht, The Netherlands; applied to

644 out of the 1069 individuals selected). This method has been extensively calibrated (Dietz *et al.* 1999) and has been successfully applied in earlier studies (Dekinga *et al.* 2001; Van Gils *et al.* 2003a, 2005a, 2005c). Furthermore, to estimate survival rates, each bird was given a unique combination of color bands. We used the Cormack-Jolly-Seber model of the MARK software package (Sandercock 2003) to estimate 'local survival', i.e., the actual survival during the first year after capture minus the (unknown) fraction of birds that emigrated permanently from our study area. In the model, annual survival rate was allowed to differ in the first year after capture and was assumed constant thereafter. This can be biologically interpreted as a variable proportion of birds becoming site faithful in each year. In case permanent emigration leads to death, the extra mortality equals the difference between first-year-after-capture global survival rate (mean = 0.73; SE = 0.03; calculated over all resightings, both inside and outside the Wadden Sea) and first-year-after-capture local survival rate. Assuming that each autumn, 100000 individuals 'try out' the Wadden Sea, this extra mortality in the NW-European wintering population as the result of emigration can thus be estimated. Note that we had 4 rather than 5 y of data, because our color-banding program started in 1998, yielding the first survival estimate for 1998–1999.

According to the following procedure, we predicted local survival rate for various degrees of gizzard flexibility (0-2 g) upon arrival in our study area (lines in Fig. 9.4C). Based on experimental results on shell mass processing rates as a function of gizzard size (Van Gils *et al.* 2003a), we calculated the minimal gizzard size required to avoid starvation as a function of prey quality (line in Fig. 9.4a). Using the observed distribution of gizzard masses upon arrival (the 0-g distribution in Fig. 9.4B, representing knots caught during late July only; n = 218; mean = 5.92; variance = 2.61), we then calculated the proportion of birds having a gizzard of at least this critical size, which would be the proportion of birds able to survive in our study area (47% at the example prey quality of 0.15 g flesh per g shell in Fig. 9.4). Assuming that knots upon arrival have the flexibility to increase their gizzard slightly (e.g., by +1 g), we calculated an updated 'effective' gizzard mass distribution upon arrival (i.e., a distribution that shifted by, e.g., +1 g; Fig. 9.4B), yielding an updated proportion of birds with a large enough gizzard, i.e., able to survive (70% for the +1-g example). We refer to Van Gils *et al.* (2003a, 2005b, 2006a) for more details on modeling gizzard masses.

10

General discussion: from spatial ecology to ecosystem resilience

Casper Kraan

The ecological world is spatially patterned and patchy (Legendre 1993; Sparrow 1999; Wagner & Fortin 2005). Such a world not only poses methodological and analytical challenges (e.g. Legendre *et al.* 2002, 2004; A.I. Bijleveld, J.A. van Gils, J. van der Meer, A. Dekinga, C. Kraan, H.W. van der Veer & T. Piersma, unpublished data), but also necessitates that we incorporate spatial patterning as a functional element of a species' ecology. The work presented in this thesis embraced this vision and explored the spatial distribution of benthic invertebrate communities at a landscape scale, using tools from spatial ecology, in intertidal ecosystems that are subject to multiple stressors such as fisheries for blue mussels (*Mytilus edulis*), edible cockles (*Cerastoderma edule*) and lugworms (*Arenicola marina*). We composed a benthic baseline (Chapter 2) for parts of the western Dutch Wadden Sea to be able to contrast the current benthic abundances with their former richness. Furthermore, we described the spatial distribution of benthic species and a number of environmental variables affecting their spatial distribution (Chapters 3-4) in this same area, but also scaled-up the geographical window by comparing the present benthic community in the Dutch Wadden Sea with those in a number of intertidal areas scattered across northwest Europe (Chapter 5). As another layer we determined the consequences of mechanical dredging for edible cockles on target and non-target benthic species and highlighted how this changed resource landscape affected carrying capacity and survival of a molluscivore avian top-predator, the red knot *Calidris canutus* (Chapters 6-9). In this final chapter we strive to link spatial ecology with ecosystem management, thus to broaden the current application of spatial statistics and propose avenues of future research to monitor the health of ecosystems.

What was natural in the Wadden Sea?

The Wadden Sea has experienced over 1000 yrs of impact since the onset of human settlement (Reise 2005; Lotze *et al.* 2006). This included fishing, hunting, harvesting of natural resources, and land reclamation. In the last two centuries large-scale overfishing, eutrophication and chemical pollution have had strong cumulative effects on marine flora and fauna (De Jonge *et al.* 1993; Wolff 2000a, 2005a; Lotze 2005; Lotze *et al.* 2005). To illustrate the potential for ecosystem restoration, we depict the former richness of the Wadden Sea and contrast that with its current condition (Fig. 10.1). A sound knowledge of what was natural in the Wadden Sea might prevent what is called a 'shifting baseline syndrome' caused by 'historical amnesia', which leads to a perception of degraded ecosystems as being natural (Pauly 1995; Dayton *et al.* 1998; Lotze & Worm 2009).

    Not surprisingly, most historical information is limited to species that have or had economical value; therefore, the historical baseline will largely be restricted to 'edible' species in an exploitative context. In addition, detailed species accounts of intertidal macrozoobenthic species, besides some fisheries data (Hoek 1911), are only available from the first half of the 20th century onwards (e.g. Thamdrup 1935; Wohlenberg
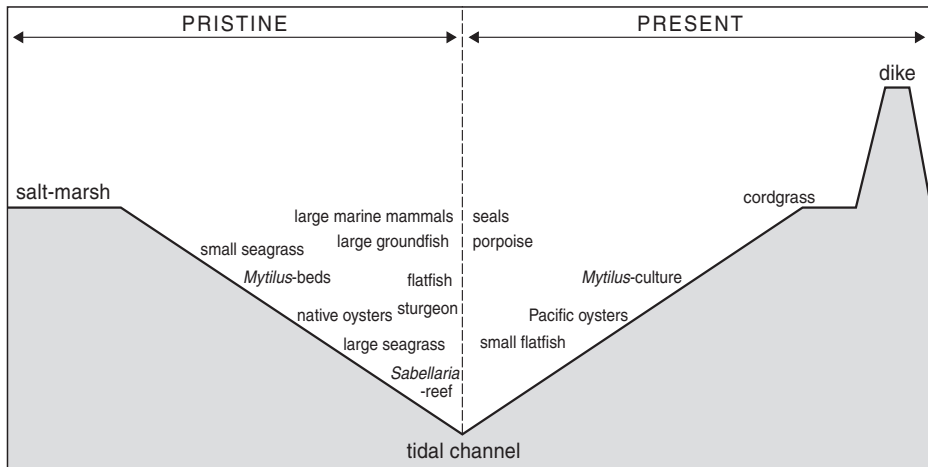
Figure 10.1. Schematic representation of pristine (left) and present (right) tidal areas extending from the saltmarsh or dike towards the gully. Cordgrass *Spartina anglica*, small seagrass consists of *Zostera noltii* and *Z. marina*, large seagrass *Z. marina* only, native oyster *Ostrea edulis*, Pacific oyster *Crassostrea gigas* and blue mussel *Mytilus edulis*. Inspired by and modified from Reise (2005).

1937; Linke 1939; Kreger 1940; Kuenen 1942). As mentioned in Chapters 1 and 2, for the Dutch Wadden Sea no past and present comparisons have been made, except assessments of extinctions and human exploitation of species (Wolff 2000a, 2005a; but see Chapter 2). Besides, only a few studies from the Danish and German parts of the Wadden Sea compared historical with recent benthic diversity (e.g. Reise *et al.* 1989; Jensen 1992b).

Birds

Archaeological evidence suggests that large birds like greater flamingo (*Phoenicopterus ruber*) and Dalmatian pelican (*Pelecanus crispus*) formerly occurred in the Wadden Sea (Lotze 2005; Lotze *et al.* 2005). Other species of waterfowl, terns and shorebirds such as common eider (*Somateria mollissima*) and cormorant (*Phalacrocorax carbo*) breeding in the area were reduced to very low numbers in the late 19th and early 20th centuries due to egg collecting and persecution (Swennen 1991). For example, in The Netherlands the squacco heron (*Ardeola ralloides*) became extinct *c.*1860, the common crane (*Grus grus*) disappeared in the early 19th century in Denmark (Wolff 2000b; Lotze 2005). However, not all is lost and there are also species that colonised the lost territory, e.g. great white egrets (*Egretta alba*) started to breed again in the Netherlands in 1978 after a 600-year absence and the white-tailed eagle (*Haliaeetus albicilla*) returned here in 2006. But note that many shorebird species using the area at some stage during their annual cycle continue to decline, particularly those species which depend most on shellfish resources in the Wadden Sea (Stroud *et al.* 2004; van

Roomen *et al.* 2005; Delany *et al.* 2009). In addition, beach breeding birds such as Kentish plover (*Charadrius alexandrinus*) and terns show declining populations as well (Lotze 2005).

Marine mammals
Historically the Wadden Sea harboured large marine mammals such as grey whales (*Eschrichtius gibbosus*) that probably used the area for calving, and northern right whales (*Eubalaena glacialis*) (Wolff 2000b; Lotze 2005). Smaller cetaceans such as harbour porpoise (*Phocoena phocoena*) and bottlenose dolphin (*Tursiops truncatus*) were regular to common visitors (see review by Holm 2005; Lotze 2005; Camphuysen & Peet 2006; Van der Meij & Camphuysen 2006). Both larger whales were exploited to extinction within the greater Wadden Sea area more than 340 yrs ago (Wolff 2000b; Lotze 2005). The harbour porpoise population, after going through a great depression in numbers in the 1940s and thereafter, is showing signs of recovery. Currently harbour porpoise are no longer exploited, but many drown in fishnets (Haelters & Camphuysen 2009). Bottlenose dolphins disappeared all together and currently are rare visitors (Lotze 2005). The disappearance of bottlenose dolphin coincided with the disappearance of its prey, Zuiderzee herring (*Clupea harengus*), after closing the Zuiderzee in the 1930s (Wolff 2000b). Nowadays, the most likely marine mammals to be encountered are grey seals (*Halichoerus grypus*) and harbour seals (*Phoca vitulina*). Harbour seals populations are rapidly recovering after hunting them for pelts was banned in 1962 and overcoming two successive viral epidemics, whereas grey seals slowly are colonizing the area after being locally extinct or extremely rare in the Wadden Sea for a long time (Wolff 2005a).

Fish
Large groundfish such as thornback ray (*Raja clavata*) and common skate (*Raja batis*) occurred commonly and were fished until the mid-20th century, after which these populations were depleted and extinct in the Wadden Sea (Lotze 2005, 2007). Anadromous fish such as Eurasian sturgeon (*Acipenser sturio*) and Atlantic salmon (*Salmo salar*) were very abundant and exploited until the 1930s, after which they became almost extinct (Lotze 2005). Similar population trends are described for various flatfish species like flounder (*Pleuronectes platessa*) and sole (*Solea solea*), or eel (*Anguilla anguilla*). Depletion of eel stocks increased markedly after 1932 when the Zuiderzee was closed and turned into a large freshwater lake, prohibiting the continuation of some fisheries (Wolff 2005a; De Leeuw *et al.* 2008).

Macrozoobenthos
Macrobenthic invertebrates were fished since human settlement on the coast. European oysters (*Ostrea edulis*) were among the first harvested species until the 1850s, after which fisheries were not economically viable anymore. Around the 1950s the European oyster disappeared completely (Dijkema 1997; Lotze 2005; Reise 2005). To overcome this economic loss, the exotic Pacific oyster (*Crassostrea gigas*) was intro-
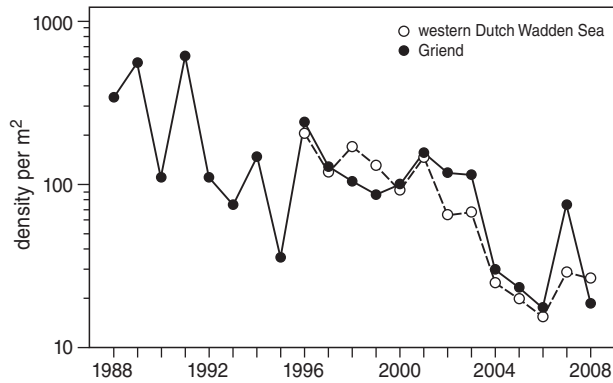
Figure 10.2. Density of Baltic tellin (*Macoma balthica*) from 1988 to 2008 around Griend, and the western Dutch Wadden Sea as a whole, Griend inclusive. Y-axis is log-scaled. Graph after Piersma *et al.* (2009).

duced in 1964 (Dijkema 1997; Wolff 2005b) and currently this species is spreading across the entire Wadden Sea in increasing abundances (Lotze 2005; Reise 2005; Wolff 2005b; own observations). See Wolff (2005b) for an extensive overview of non-indigenous species in the Dutch Wadden Sea. In addition, species like brown shrimp (*Crangon crangon*), blue mussel (*M. edulis*), edible cockle (*C. edule*), ragworm (*Nereis virens*), lugworm (*A. marina*) and common whelk (*Buccinum undatum*), were commercially fished in the 19th, 20th, and 21st centuries (e.g. Reise *et al.* 1989; Beukema 1995; Dijkema 1997; Smit *et al.* 1998; Piersma *et al.* 2001; Kamermans & Smaal 2002; Reise 2005; Wolff 2005a; Chapter 6). Other species, like the reef-forming tube-worm *Sabellaria spinulosa* ('sand coral') that occurred in tidal channels of the German Wadden Sea, were decimated as a side-effect of bottom-touching fisheries and only exist, if any, in small, localised patches at present (Reise 1982, 2005; Michaelis & Reise 1994; Wolff 2000a). Some bivalve species sharply declined as well, although not specifically exploited. The population of Baltic tellin *Macoma balthica*, for example, collapsed by 90% between 1997 and 2007 in the western Dutch Wadden Sea (Fig. 10.2; Piersma *et al.* 2009; Van Gils *et al.* 2009a).

Overall

Historical baselines offer new insights into past ecosystems and their inhabitants, and provide important context for contemporary management of intertidal ecosystems (Jackson *et al.* 2001; Lotze & Worm 2009). The former richness of the Wadden Sea, as presented here, illustrates the radical, mostly human induced, changes of the species community (Fig. 10.1; Chapter 2). The general emerging pattern is a loss of large organisms, loss of species that provide structure on the mudflats, reduced abundances of species that still occur (Lotze 2005; Chapter 2) and, to date, failed recovery of harvested benthic populations. However, opportunities for successful restoration of marine resources exist, if exploitation is reduced substantially (Worm *et al.* 2009). The

seascape has been simplified and homogenized, with a loss of three-dimensional habitats (Fig. 10.3; Lotze 2005; Chapter 2), comparable to large-scale clearcutting of forests (e.g. Watling & Norse 1998). For example, large natural mussel beds were fished, which altered intertidal areas into sandflats dominated by small infauna (Fig. 10.3; Chapter 2), and nowadays mussels, particularly in the western Dutch Wadden Sea, mostly are restricted to cultured plots (Dijkema 1997; Smit *et al.* 1998). The sequence of exploitation, starting with large marine mammals such as whales and gradually increasing efforts towards smaller and less valuable organisms such as shrimp (*C. crangon*) as a consequence of overexploitation of large animals, is a typical example of fishing down the food chain (Pauly *et al.* 1998; Pauly & Maclean 2003). At present, only 12% in 77 species of which data are available still are abundant (i.e. at least 90% of their historical abundance), and of the 26 commercially fished species, 88% have been depleted by 2000 (see review by Lotze 2007). The degrading of marine intertidal ecosystems is not unique to the Wadden Sea, but is a worldwide phenomenon (Jackson *et al.* 2001; Barrett *et al.* 2004; Lotze *et al.* 2006; Airoldi & Beck 2007). The Wadden Sea, however, is ranked among the most degraded overall and is in a state far from its historical baseline (Lotze *et al.* 2006; Chapter 2), which may forecast the fate of other intertidal ecosystems faced with human exploitation, but also that of offshore areas due to increasing depth of fisheries. As stated in Chapter 2, what is necessary for its former richness to be restored? And in parallel, what should be considered realistic or desirable?

Hidden spatial structure of intertidal fauna

Intertidal mudflats are often characterized as vast and featureless areas of mud and sand (Verwey 1952; Peterson 1991; Hewitt *et al.* 2005; Chapter 3) which is enhanced by the cryptic nature of many of their inhabitants that live hidden beneath the muddy or sandy surface (Peterson 1991; Thrush 1991). This view is amplified by the degrading of intertidal areas, which particularly reduces visible structural heterogeneity provided by, for example, mussel beds or *Sabellaria*-reefs (see previous section; Fig. 10.3). Therefore assessing spatial patterns in the distribution of species (Chapter 3), and the environmental parameters that shape these distributions (Chapter 4) is particularly interesting and important. They could inform us if we would strive for protection and restoration. Spatial structure reflects life-history factors, intra- or inter-specific interactions, and species-environment relationships (Thrush 1991; Legendre 1993). Given the large scale of our research, focus has been on the latter (see Figs. 1.1 & 1.3).

Summarizing our spatial results, spatial structuring was discernable at the scale of the western Dutch Wadden Sea for each benthic species highlighted in this thesis (Chapters 3-4). These patterns differed from the intrinsic autocorrelation imposed by the monitored points, which indicated that species distributions at a landscape-scale are shaped by processes other than the extent of mudflats (Chapter 3). Indeed, environmental variables, such as sedimentary characteristics and inundation time, deter-

Figure 10.3. Intertidal mudflats in the western Dutch Wadden Sea around ca. 1986 (top) and the same area in 2004 (bottom). The harbour of Oudeschild, Texel, is clearly visible in the background. Note the presence of musselbeds (*Mytilus edulis*) as recent as ca. 1986 (upper picture) and their absence in the more recent picture. Worth mentioning is the appearance of windmills recently (bottom photo). Photographs by Jan van de Kam (top) and Bernard Spaans (bottom).

mined large-scale species' spatial patterning in the Dutch Wadden Sea (Chapter 4). Although it is expected that species are not randomly distributed throughout the study area (e.g. Sparrow 1999; Wiens 2000; Klaassen & Nolet 2008) our work constituted the first use of spatially explicit analysis for macrozoobenthic fauna in the Dutch Wadden Sea (Chapters 3-4). These results also emphasize that accounting for autocorrelation is not only purely of theoretical interest, but should be included in any analyses dealing with spatial data (see Chapter 1 and references cited there).

Beyond landscape-scale: scaling-up to the northwest Atlantic coast
A comparison with patterns observed elsewhere would be timely. This only is possible with data collected in exactly the same way, i.e. the same sampling grain (see Kotliar & Wiens 1990; Levin 1992; Chapter 3). Fortunately, such unique data are available from a single winter sampling expedition in northwest Europe (Compton *et al.* 2008, 2009; Quaintenne *et al.* 2009; Chapter 5). We sampled benthic fauna, using the familiar 250 m grid (e.g. Van Gils *et al.* 2009a), in five intertidal areas, 9 sites, between December 2003 and March 2004 (details in Chapter 5). On this large geographical scale species' distributions were predominantly site-specific, rather than similar throughout, and community composition showed greater similarity within than between the northern and southern areas (Chapter 5). However, distribution patterns of species were visually assessed only. Spatially explicit distribution patterns have not been determined, up till now.

For two benthic species that were common at most sites, *M. balthica* and *C. edule*, respectively (Chapter 5), we analysed spatial patterns with Moran's *I* (e.g. Fortin & Dale 2005; Chapters 1 & 3). Surprisingly, all correlograms had a similar overall shape, i.e. short distance positive autocorrelation that gradually decreased with distance (Fig. 10.4; compare with Fig. 3.3E-F), despite the differences in environmental characteristics such as the median grain-size and tidal amplitude (Compton *et al.* 2008, 2009; Chapter 5). On closer inspection, *M. balthica* almost had a random distribution at Oléron and a very strong spatial pattern in the first few distance classes at Griend (Fig. 10.4A). *C. edule* showed remarkably similar patterns in all sites (Fig. 10.4B). For small-scale studies (≤ 6 m) the argument has been put forward that similar spatial patterns, but with differing environmental conditions, can be attributed to biological interactions (Hewitt *et al.* 1996; Bergström *et al.* 2002). For our own research this seems an unlikely explanation, given our scale of research (≥ 250 m). Which processes lead to these repeatable spatial patterns may even vary between systems (Thrush *et al.* 2005; Compton *et al.* 2009), and this therefore remains a question mark at present. This first attempt to seek generality and go beyond a landscape-scale clearly highlights the need for experimental work and cross-scale monitoring to gain more biological insight in what determines species' distributions and to be able to match pattern with process.

Next generation landscape-scale monitoring: SIBES
Based on the results of Chapters 3-5, a general impression of benthic species' spatial patterns, their relationship with environmental variables and patterns on even larger
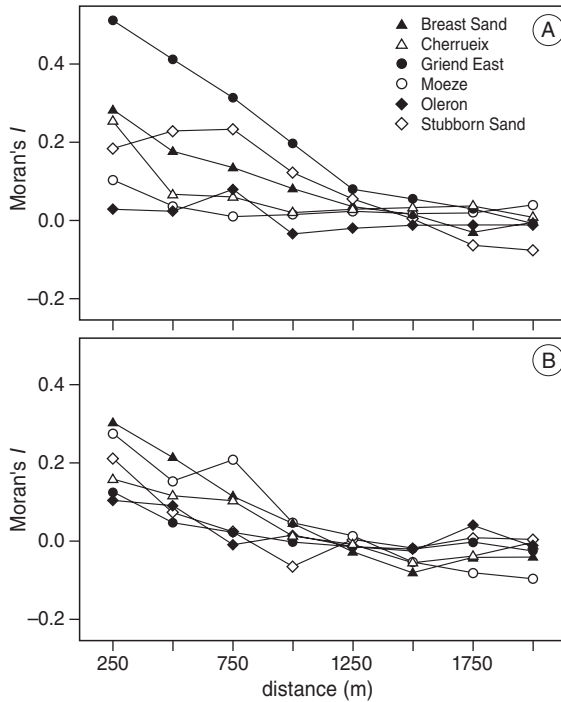
Figure 10.4. Correlogram of the spatial patterns of (A) *Macoma balthica* and (B) *Cerastoderma edule* based on the winter-sampling data of northwest Europe (Chapter 5); on the x-axis the distance (in m) and on the y-axis Moran's *I*.

geographical scales have been described. The question arises how to design a benthic monitoring programme or monitoring of any organism for that matter that allows complex spatial and temporal species-environment interactions to be estimated? In the following we summarize how our research group at NIOZ recently tackled these problems and currently is further improving the sampling grid applied throughout this thesis to a state-of-the-art monitoring programme: **SIBES** (**S**ynoptic **I**ntertidal **B**enthic **S**urvey of the Wadden Sea). This part draws heavily on work by A.I. Bijleveld, J.A. van Gils, J van der Meer, A. Dekinga, C. Kraan, H.W. van der Veer & T. Piersma (unpublished data) and upcoming joint efforts of Sander Holthuijsen, Job ten Horn, Anne Dekinga, Jeremy Smith, Geert Aarts, Theunis Piersma, Henk van der Veer, Maarten Brugge, Bernard Spaans, Jan van Gils and others.

Optimal sampling designs are first and mostly constrained by their expense (e.g. Andrew & Mapstone 1987; Van der Meer 1997). One complete grid-sampling season in the 'old-style', from preparing the first sheets until the final shell mass has been entered into the data-base, approximately required two man-years of effort and a lot of voluntary additional man-power. For maximum effectiveness at minimal costs and labour, optimisations of such monitoring efforts are critical. A monitoring
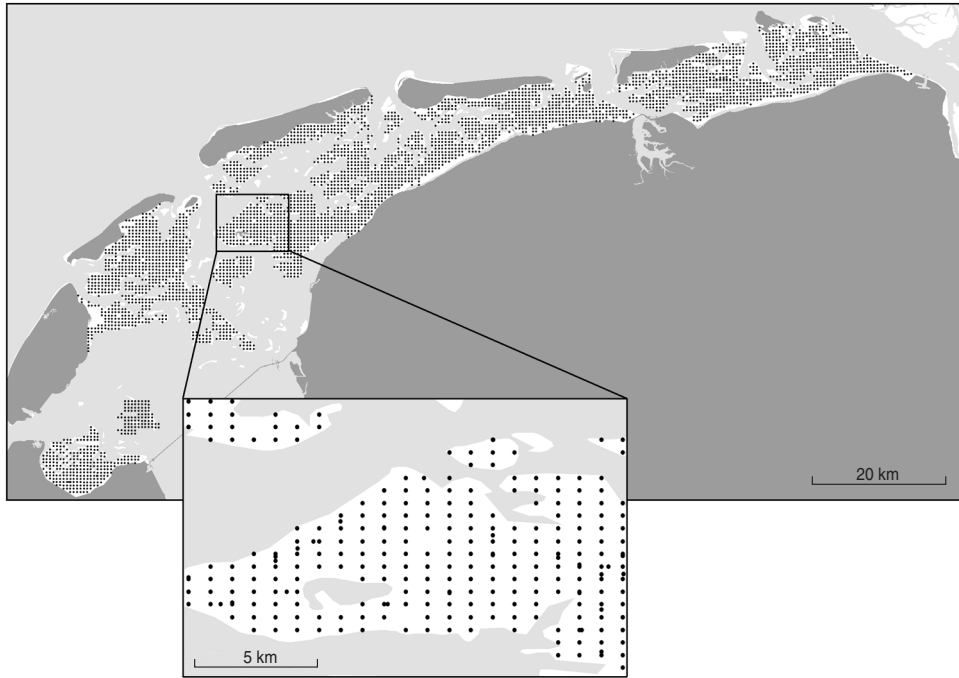
Figure 10.5. Map of the recently (2008) started **SIBES** (**S**ynoptic **I**ntertidal **B**enthic **S**urvey of the Wadden Sea) monitoring programme. All benthic sampling stations (black dots) on a 500 m grid are shown (large map). The inset shows a close-up of the benthic sampling stations and the 10% random stations at irregular intervals around Griend. White areas indicate mudflats exposed during low-water, intermediate grey areas indicate water, and land is represented by the darkest grey areas.

programme can have multiple objectives with conflicting demands on the optimal sampling design: (1) estimation of temporal changes and spatial differences in abundance, (2) mapping, i.e. prediction of abundances at unsampled locations. Since these predicted abundances are based on estimated autocorrelations, an additional objective is (3) determining how accurately autocorrelation of the model parameters is estimated (A.I. Bijleveld, J.A. van Gils, J van der Meer, A. Dekinga, C. Kraan, H.W. van der Veer & T. Piersma, unpublished data). There are numerous sampling designs commonly used to choose from. These include transect sampling and variations thereof (e.g. Beukema 1982; Yates *et al.* 1993a) or a number of grid-based sampling methods (e.g. Fortin *et al.* 1989; Legendre *et al.* 1997; Van Gils *et al.* 2009a; Chapters 3-5). Another complication is the effect of inter-sampling distance on the amount of autocorrelation (Fortin & Dale 2005). The larger this distance, the more dissimilar response variables will be and thereby the autocorrelation will be reduced. However, this also reduces the accuracy of interpolated predictions, since this is based on autocorrelation of the data (e.g. Koubbi *et al.* 2006).

Bijleveld and co-workers handled all these different options by simulating spatial data with an imposed, but naturally occurring, amount of autocorrelation for a number of common species. Then, based on minimum detectable difference in mean between two areas, the mean prediction error, and estimated bias of correlation parameters, the optimal sampling design was selected. The sampling design that best catered for all three objectives combined for the Wadden Sea intertidal flats was grid sampling at 500 m intervals with an additional number of random samples (10 %) placed on gridlines (Fig. 10.5). These random samples were included to be able to estimate autocorrelation between 0 and 250 m. Their positioning along gridlines, in stead of completely random, enhanced the actual implementation during sampling. Grid sampling with additional random sampling is considered an accurate and powerful tool with the largest effectiveness/cost-ratio for monitoring programmes that allows for: (1) estimates of population sizes, (2) monitoring of population trends, (3) comparisons of populations/trends between years or areas, (4) modelling autocorrelation, (5) mapping of species distributions with a complete coverage of intertidal areas and (6) further understanding of processes that structure species distributions. Especially the latter three are upgrades from the old-style grid. In the coming years, from 2008 onwards, this landmark sampling of more than 4000 benthic stations (Fig. 10.5) will be tested and carried out annually for at least five sequential years. Hopefully it will prove to be an optimal sampling design to monitor benthos in a changing Wadden Sea and allow detecting anthropogenic impacts on intertidal macrozoobenthos.

Molluscivore sentinels: a bird's eye view of benthos

Along the East-Atlantic Flyway, the Wadden Sea is a crossroad for migratory molluscivore and other shorebirds (Fig. 10.6; Van de Kam *et al.* 2004). These birds breed in the Canadian and Siberian Arctic, but winter in the Wadden Sea or make use of the benthic resources to fatten-up before continuing to their West African wintering grounds. In particular species that depend most on the benthic food-base showed the largest population declines (Stroud *et al.* 2004; Van Roomen *et al.* 2005; Delany *et al.* 2009), which suggests a bottleneck in the Wadden Sea (Davidson 2003; Van Gils *et al.* 2009b; Chapters 7-9). Building on more than a decade of research that focussed on benthic stocks (e.g. Piersma *et al.* 2001), foraging ecology and survival of red knots (e.g. Piersma *et al.* 1993c; Van Gils *et al.* 2006b) and their physiological flexibility (e.g. Dietz *et al.* 1999; Dekinga *et al.* 2001; Van Gils *et al.* 2005c, 2007), our research allowed a bird's eye view of benthos in a changing Wadden Sea (Chapters 6-9).

Fisheries of benthic prey stocks
In the Dutch Wadden Sea industrial harvesting of edible cockles (*C. edule*) and mussels (*M. edulis*) has been carried out since the late 1980s (Dijkema 1997; Smit *et al.* 1998; Piersma *et al.* 2001; Ens 2003; Chapters 6-7 & 9). Note that 'artisan' cockle fisheries already collected up to one third of the standing stock as early as 1949 (Verwey

Figure 10.6. The Wadden Sea's strategic location is rather like the neck of a funnel running from the extensive arctic tundra breeding grounds of North America and Eurasia (shown in black) down to the two large tidal areas of West Africa (Banc d'Arguin in Mauritania and the Achipelago dos Bijagos in Guinea-Bissau). This map shows the positions of other countries relative to the Wadden Sea, and from this perspective the directions shown are accurate. The distances displayed on the map are distances to that point from the Wadden Sea following great circle routes. Graph after Reneerkens *et al.* (2005) and Piersma (2007b).

1952). Accidental observations of such large-scale bottom-touching fisheries near Griend between 1988 and 1991 and the rare occurrence of foraging knots afterwards, but also delayed recovery (≥ 8 yrs) of benthic resources (Piersma *et al.* 1993b, 1993c, 2001; Piersma & Koolhaas 1997) invited analyses of effects of such fisheries by standardly collected data of our research group. The main aim was to better understand the impact of cockle dredging on shorebird prey and thereby improve forecasting the decisions foraging knots have to make for survival. Our publications, as well as published analyses of mass mortality of common eiders (Camphuysen *et al.* 2002) and oystercatchers *Haematopus ostralegus* (Atkinson *et al.* 2003) due to food shortage after fishing, raised controversy and public concern, which lead to two projects on the effects of cockle-dredging, EVA-I and EVA-II, respectively, carried out by several ministerial research institutes (Swart & Van Andel 2008). Thus far, the monumental efforts by Zwarts *et al.* (2004) within EVA-II, who reviewed and partly re-analysed all Wadden Sea sediment data from the 1950s (see Postma 1957) onwards and made them

available to the general public, proved an invaluable information source (e.g. Folmer *et al.* submitted manuscript-a; Chapter 2).

In a nutshell, our benthic sampling efforts, when combined with vessel monitoring fisheries data (see Chapter 6), allowed us to describe impacts across the landscape (Piersma *et al.* 2001; Chapters 6 & 9). Matching scales of impacts with those of the research is of critical importance to discern between, for example, actual recovery after impact or random recruitment events with short-term density increases (Thrush *et al.* 1996, 1998; Kaiser 2003). Cockle-dredging took place in the most biodiverse areas of the western Dutch Wadden Sea (Piersma 2007b; Chapter 6), which also contained the greatest abundances of food for shorebirds (Chapter 6). From one year to the next benthic species responded unpredictable to being dredged, highlighting the need to an ecosystem approach to conservation that includes target and non-target benthic fauna (Chapter 6). At longer time-scales, recruitment of cockles and Baltic tellins decreased in dredged areas, as did the body condition of suitably sized cockles for knots (Piersma *et al.* 2001; Chapters 6 & 9). Bottom-touching fisheries rendered habitats less suitable for macrobenthic fauna (Piersma *et al.* 2001; Thrush & Dayton 2002; Hiddink 2003; Kaiser *et al.* 2006), which might also explain the continuing decline of *M. balthica* (Fig. 10.2; Piersma *et al.* 2009; Van Gils *et al.* 2009a) and delayed recovery of mussel beds in the western Dutch Wadden Sea (Herlyn & Millat 2000; Chapters 2 & 6). Recently, mechanical cockle-dredging (but not hand-cockling [Van Leeuwe *et al.* 2008]) was banned from the Dutch Wadden Sea (from 2005 onwards; Swart & Van Andel 2008) and due to our ongoing benthic monitoring efforts it will be possible to track the extent and time-scale of recovery. Predicted recovery times after dredging vary between 1 to 30 yrs (Collie *et al.* 2000; Versteegh *et al.* 2004). If, however, the intertidal areas south of Vlieland (de Waardgronden; Chapter 2), provide a case of such recovery, then 30 yrs may even be an underestimation (see Chapters 2 & 6). After being dredged for cockles on numerous occasions in the late 1980s and early 1990s, the area is currently nearly devoid of shellfish (Chapter 2), so far without any sign of revival of benthic resources.

Suitable foraging area, information and carrying capacity

To treat the overexploitation of benthic resources as an 'experiment' and describe the consequences from a bird's eye view, a translation from benthic stocks to resource landscape for molluscivore shorebirds is required. Such a crucial step was made possible by the digestive rate model (DRM; Hirakawa 1995, 1997), which was adjusted to and validated for knots by Jan van Gils and co-workers (Van Gils *et al.* 2005a, 2005c; Quaintenne *et al.* 2009; Chapters 7-9). This model summarizes all current knowledge about the foraging ecology of knots and predicts optimal diets that maximize long-term intake rate for knots at each benthic sampling position (Fig. 10.7). Knots indeed are an ideal model species for such analyses due to: (1) the ease with which their prey densities can be determined (Zwarts & Blomert 1992; Piersma *et al.* 1993c; Van Gils *et al.* 2006c; Chapters 7-9), (2) the ability to use droppings to reconstruct their diet (Dekinga & Piersma 1993; Van Gils *et al.* 2005a), (3) knots' suitability for living in
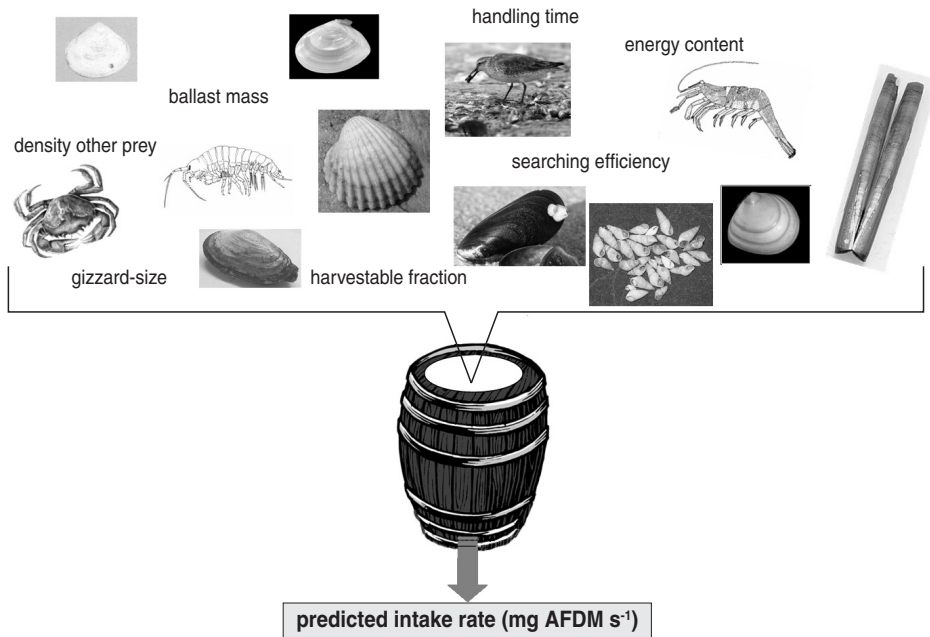
Figure 10.7. Schematic representation of the digestive rate model, the required inputs such as prey species and gizzard-size, and the final output: predicted intake rate (mg AFDM s^{-1}). This model was used in Chapters 7-9.

captivity and experimentally measure model parameters (Piersma *et al.* 1995; Van Gils *et al.* 2005a), (4) a measurable gizzard-size that reflects their state (Dietz *et al.* 1999; Dekinga *et al.* 2001; Van Gils *et al.* 2005b; Chapters 7-9), and in addition (5) their abundance is monitored in the Wadden Sea since the 1970s (Van Roomen *et al.* 2005; Chapter 7) and beyond (Piersma 2007a).

Between 1996 and 2005 the suitable foraging area for *Calidris canutus islandica*- and *Calidris canutus canutus*-knots in the western Dutch Wadden Sea declined between 55% (*islandica*; Chapter 7) and 86% (*canutus*; Chapter 8). Parallel to this, numbers of both subspecies declined as well; *islandica* declined by 42%, while for *canutus* we could illustrate a decline in mistnetted birds relative to the proportion caught *islandica* knots on the basis of biometrics (Chapters 7-9). The actual number of birds are not estimable for *canutus* knots in the Dutch Wadden Sea (see discussions in Nebel *et al.* 2000 and Chapter 8), but their proportional decline in catches hints at *canutus*-knots now skipping the area for staging during southward migration. To overcome the loss in suitable foraging area, knots could increase their muscular gizzard, thereby increasing the capacity of processing lower quality prey (Van Gils *et al.* 2005b). Interestingly, both subspecies maintained a gizzard that just satisfied fuelling or wintering demands on intake rate (Van Gils *et al.* 2003a, 2007; Chapters 7-9). Supporting a small as possible gizzard reflects a trade-off between having the ability to

forage in areas of poorer quality and, for example, escaping from predators (Dietz *et al.* 2007; Chapters 7-9). Indeed, each subspecies of knot, either migrating or fuelling along their flyway, have been shown to maintain a small as possible gizzard size in response to variations in prey quality and climate in order to balance energy budgets on a daily basis (Van Gils *et al.* 2005b).

The spatial information that predators obtain from their prey distributions enables them to optimize movements through the resource landscape and spend most time in rich areas (Benhamou 1992; Klaassen *et al.* 2006b; Van Gils 2009). Even when foraging on cryptic prey, such as tundra swans *Cygnus columbianus bewickii* feeding on submerged pondweed (*Potamogeton pectinatus*) tubers (Klaassen *et al.* 2006a), animals should behave as if they were foraging in a patchy resource landscape (Arditi & Dacorogna 1988; Kacelnik & Bernstein 1988). The pay-off of including spatial information about prey stocks in foraging decisions is a higher likelihood of survival (Van Gils 2009). Although the spatial information for knots in the western Dutch Wadden Sea has declined between 1996 and 2005, this did not yet lead to an additional loss of birds due to favourable feeding areas being undetectable (Chapter 7). Therefore, the decline of both knot populations can solely be attributed to a decline in both quality and extent of intertidal foraging areas (Chapters 7-9). Currently, new lines of research are being pursued that continue with the building blocks provided by the pioneering knot-work of our research group over the past decade and spatially explicit analysis. These projects extend optimal foraging models with the ecology of information use and include joint interactions between social attraction such as flocking behaviour and interference, but also spatially autocorrelated food distributions (Van Gils 2009; Folmer *et al.* submitted manuscript-a, submitted manuscript -b).

One of the key advances of highlighting changes in benthic stocks from a bird's eye view is the ability to show the consequences that landscape-scale declines in suitable foraging areas has on bird numbers (Chapters 7-9). Besides, by combining these two data-sets we were able to show parallel declines of knot numbers and hidden prey stocks at a landscape scale (Chapter 7), which could be translated to carrying capacity: on average 10 knots ha-1 suitable foraging area. Again this is made possible by our long-term benthic sampling efforts. Traditionally, carrying capacity is expressed as maximum number of bird-days or the maximum number of birds to survive winter (e.g. Goss-Custard 1985; Sutherland & Anderson 1993; Van Gils *et al.* 2004), which does not necessarily has a link with a foragers' resource landscape. Our integrative approach, although depending on much detailed data for its functioning, illustrated that the Dutch Wadden Sea has been used to capacity by knots (Chapters 7-8). In addition, based on an extensive knot colour-ringing programme, survival could be estimated for *islandica*-knots in the western Dutch Wadden Sea (Brochard *et al.* 2002; Piersma & Spaans 2004; Chapters 7 & 9). Survival declined from 89% to 82% between 1996 and 2005, and could account for almost half of the decline in *islandica*-knot numbers (Chapter 7).

Our efforts to monitor benthic prey stocks, describe effects of mechanical cockle-dredging on target and non-target fauna, catch and colour-ring knots, perform high-

tide counts of roosting knots and seek ways to connect these different information sources via outdoor and indoor experiments, modelling and combinations thereof, made it possible to describe landscape-scale decline of suitable foraging areas, declining number of knots, declining carrying capacity and reduced survival (Chapters 7-9). Molluscivore shorebirds indeed are suitable sentinels (*sensu* Piersma & Lindström 2004) to monitor the health of intertidal ecosystems.

Carry-over effects

Scaling-up these analyses to other species or even other flyways is not (yet) possible, mainly due to a lack of detailed information on benthic stocks, too little knowledge about the foraging ecology of species, other than perhaps their diet, and the absence of integrative monitoring programmes. Testing our models outside their training environment, i.e. validating so-called spatial, temporal and methodological 'model transferability' (Zharikov *et al.* 2009), therefore remains a future challenge. This again illustrates the unique possibilities created by our long-term investments in monitoring benthic stocks *and* shorebirds (Piersma *et al.* 1993a, 1993c; Van Gils *et al.* 2006c; Chapters 6-9). However, degrading impacts on marine intertidal ecosystems by man 'cascading down' from the benthic resources to shorebird predators, as shown by our work (Chapters 6-9), are likely to occur on a global scale. For example, declining refuelling rates and rapid population decline in red knots (*rufa*-subspecies) have been linked to overharvesting of horseshoe crab eggs (*Limulus polyphemus*) by fishermen in Delaware Bay, USA (Baker *et al.* 2004; Atkinson *et al.* 2007). Or, as another example, planned and partly executed reclamations of intertidal areas in South Korea, reduce the suitable foraging area in one of the main migratory crossroads in the East Asian-Australasian Flyway (Rogers *et al.* 2006). These areas are key migration sites for the highly endangered spoon-billed sandpiper (Eurynorhynchus pygmeus) and its fate therefore is not hard to forecast.

Nevertheless, we can scale-up within the East-Atlantic Flyway using the *canutus*-knots as case. Since 2002 our research group annually visits the Banc d' Arguin, Mauritania, to get better grips on the size and survival of the *canutus*-population and a better understanding of their behavioural ecology at this wintering site (e.g. Leyrer *et al.* 2006; Van den Hout *et al.* 2007; Jan van Gils, Jutta Leyerer, Matthijs van der Geest, Bernard Spaans and Theunis Piersma, unpublished data). The area harbours _ of the *canutus*-population (Stroud *et al.* 2004). However, the total population in their West African wintering quarters is declining (Stroud *et al.* 2004; Chapter 8), whereas benthic prey stocks are actually increasing there (Fig. 10.8; Van Gils *et al.* 2009b). This hints at a bottleneck prior to arrival at the wintering area (Davidson 2003), which constraints their population-size. Indeed, in the Wadden Sea, their main fuelling site before continuing migration to the Banc d'Arguin (Piersma *et al.* 1992; Nebel *et al.* 2000), the extent and quality of intertidal mudflats has declined (Chapters 7-9). This suggests that the carrying capacity of knots in their West African wintering quarters might be coupled to and limited by the carrying capacity of the Wadden Sea (Fig. 10.8; Van Gils *et al.* 2009b).
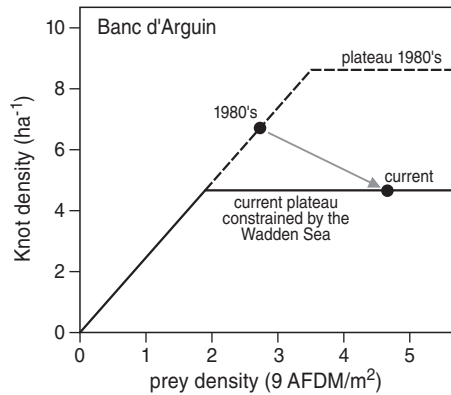
Figure 10.8. Hypothetical scenario which could explain why red knots wintering at Banc d'Arguin have declined, in spite an increase in their food supply. In the 1980s there was much more food available in the Wadden Sea than nowadays and therefore the number of knots wintering at Banc d'Arguin, Mauritania, was determined by the food abundance at Banc d'Arguin itself. Nowadays, the number of Banc-d'Arguin-wintering knots is regulated by the low food stocks in the Wadden Sea.

Avenues for future research: ecosystem resilience

Marine ecosystems are changing on a global scale due to human disturbances, such as exploitation and climate change. These changes are especially profound in coastal and estuarine ecosystems (Pauly *et al.* 2002; Lotze *et al.* 2006; Worm *et al.* 2006), with reductions in food web complexity, species diversity, habitat structure and a decrease in the body size of organisms (Thrush *et al.* 2006, 2009; Chapters 2, 6-9). When such drastic changes occur quickly they are often described as a regime shift (Scheffer *et al.* 2001; De Young *et al.* 2004, 2008; Folke *et al.* 2004; Thrush *et al.* 2009). The processes within an ecosystem that prevent such rapid change, although largely unknown, are commonly grouped under the term resilience (Scheffer *et al.* 2001; Folke *et al.* 2004; De Young *et al.* 2008; Thrush *et al.* 2009). In general, lowered resilience leads to increased risk of a regime shift. Scientific interest in regime shifts and resilience is the fastest growing discipline in ecology as a whole (Andersen *et al.* 2008), not in the least because most shifts negatively impact economy and society (Hughes *et al.* 2005).

Ecological resilience is the amount of disturbance a system can undergo and still retain the same structure, function and feedbacks (Gunderson 2000; Folke *et al.* 2004; Thrush *et al.* 2009); it describes long-term ecosystem recovery potential or self-repairing capacity. For the Wadden Sea this should minimally result in an ecosystem dominated by intertidal mussel-beds, seagrass (*Zostera*) meadows, and high densities of cockles (e.g. Kreger 1940; Van der Baan *et al.* 1957; Chapter 2) after recovery from human disturbance. In practice, however, we do not yet know how or even if we can measure ecological resilience directly. Recently, though, an increase in temporal auto-
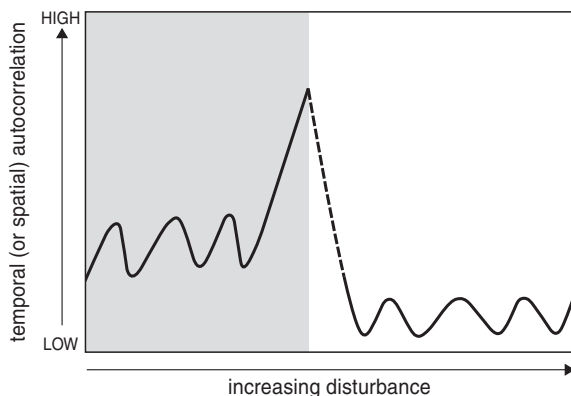
Figure 10.9. Conceptual graph showing how temporal (or spatial) autocorrelation monitors the disturbance of ecosystems. Temporal (or spatial) autocorrelation fluctuates within certain limits, and then, following continuing disturbance and the inability to recover, temporal (or spatial) autocorrelation sharply increases untill the limits of resilience. Under continued disturbance, a regime shift follows. The dotted line indicates the transition. After Dakos *et al.* (2008, in press).

correlation, defined as observations of, for example, species abundance being more similar in time than by random chance, has been proposed as a proxy to detect the limits of ecological resilience (Fig. 10.9; Dakos *et al.* 2008). This idea, which can be mathematically shown to indicate the proximity of a regime shift (Dakos *et al.* 2008; Scheffer 2009; Scheffer *et al.* 2009), is based on the notion that slowing down of recovery from disturbance leads to a lower rate of change in an ecosystem, and therefore the temporal autocorrelation increases. The state of the ecosystem at any given moment becomes more and more like its past state (Scheffer *et al.* 2009). Currently these shifts are only detected with hindsight (De Young *et al.* 2008; Thrush *et al.* 2009). However, there is growing awareness that better tools for forecasting loss of resilience or predicting regime shifts are required to assist management and protection of coastal ecosystems (Thrush *et al.* 2008, 2009).

A particularly important advance is the inclusion of both spatial and temporal heterogeneity (Thrush *et al.* 2008, 2009) as functional elements of benthic systems, since thus far resilience and regime shifts are temporal concepts that ignored the impact of human disturbance on ecosystems in a spatial context (Scheffer *et al.* 2009; Thrush *et al.* 2009). This requires a better understanding of the interaction between animal-environment relationships in spatially explicit frameworks (Sparrow 1999; Keitt *et al.* 2002; Fortin & Dale 2005; Wagner & Fortin 2005; Carl & Kühn 2007; Dormann *et al.* 2007; Carpenter *et al.* 2008; Chapter 4) and the degrading impact of multiple stressors on coastal ecosystems (Scheffer *et al.* 2001; De Young *et al.* 2008; Thrush *et al.* 2008, 2009). Understanding animal-environment relationships within a spatial framework is one of the main frontiers in ecology (Gaston 2000; Thrush & Dayton 2002; Scheffer & Carpenter 2003; Rietkerk *et al.* 2004; Witman *et al.* 2004). At

present the driving mechanisms of spatial and temporal variation in abundance of species are poorly understood (Gaston 2000; Hughes *et al.* 2005), which limits our ability to aptly monitor the health of an ecosystem and define baselines.

The prime novel avenue for future research is to use large-scale data from benthic monitoring programmes to describe species-environment relationships along gradients of disturbance with state-of-the-art spatially-explicit methods, such as GEE or GLMM (Carl & Kühn 2007; Dormann *et al.* 2007; Aarts *et al.* 2008; Chapter 4), and integrate these into the resilience framework. Spatial analysis are then used as an ecological tool to, for example, infer habitat preferences of species and highlight human-induced loss of such preferred habitats to aid conservation studies. This would increase the predictive capacity and possibly allows forecasting the boundaries of resilience, improving stewardship of ecosystems. Describing the boundaries of resilience with spatial data, as presented for temporal data (Fig. 10.9; Dakos *et al.* 2008), is a future goal. The first theoretical work on spatially explicit ecological models of alternative stable states has just been published (Dakos *et al.* in press), which suggests that increased spatial autocorrelation may be a leading indicator of a critical transition (Fig. 10.9), since cells close to a tipping point are more influenced by the dynamics of their neighbours and therefore behave in a more similar way (Dakos *et al.*, in press). In addition, spatial indicators might outperform temporal indicators (Guttal & Jayaprakash 2009; Dakos *et al.* in press). However, these proposed indicators have not been tested with field-data (Scheffer *et al.* 2009). Our approach, although depending on large amounts of data, would address fundamental knowledge gaps in both the resilience-regime shift and spatial ecology paradigm, and furthermore also connect these theoretical frameworks that thus far existed in isolation from each other.

Acknowledgements

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Nederlandse samenvatting

De verspreiding en aantallen dieren, zowel in ruimte als tijd, staan centraal in de ecologie. Inzicht in soortsverspreiding creëert niet alleen methodologische en analytische uitdagingen, maar vraagt ook dat we ruimtelijke autocorrelatie beschouwen als een functioneel onderdeel van de ecologie van een soort. Positieve ruimtelijke autocorrelatie of ruimtelijke patronen betekent dat aantallen dichtbij meer aan elkaar gelijk zijn dan aantallen verder weg (of omgekeerd in het geval van negatieve ruimtelijke autocorrelatie), wat statistische berekeningen beïnvloedt en kan leiden tot foutieve conclusies (indien autocorrelatie wordt genegeerd). Vanuit een ecologisch perspectief weerspiegelt ruimtelijke autocorrelatie reproductie, competitie, predatie, manier van voedselzoeken en voortbeweging en soort-omgeving relaties. Dit proefschrift bekijkt op landschapsschaal de gemeenschap van schelpdieren, wormen en kreeftachtigen, die net onder of op het oppervlak leven van droogvallende zand- en modder-vlaktes van de Nederlandse Waddenzee. Als voorbeeld gebruiken we een vogelperspectief van bodemlevend fauna (benthos) om veranderende voedselbronnen te koppelen aan draagkracht en overleving van een schelpdieretende vogel: de kanoet (*Calidris canutus*).

Doordat meerdere vormen van verstoring plaatsvinden, zoals toegenomen eutrofiëring, toegenomen menselijk ingrijpen of verhoogde erosie, wordt de Waddenzee beschouwd als één van de meest gedegradeerde ecosytemen wereldwijd. Om de huidige verspreiding en aantallen van macrobenthische bodemfauna in perspectief te kunnen plaatsen, hebben we een 'benthische basislijn' gereconstrueerd van twee gebieden: Posthuiswad en Staart van Schieringhals. In 1930–1960 hadden beide gebieden een hoge dichtheid aan soorten die droogvallende wadplaten van structuur voorzagen, zoals mossels (*Mytilus edulis*) en kokkels (*Cerastoderma edule*). In 1996 waren schelpdieren met een factor 10 afgenomen, zonder een teken van herstel tot ten minste 2005. Temporele trends toonden aan dat kreeftachtigen ook zijn afgenomen, terwijl wormbestanden stabiel gebleven zijn. Benthische levensgemeenschappen zijn verarmd gedurende de laatste halve eeuw, wat heeft geleid tot een vereenvoudigd en meer homogene zeebodem (**Hoofdstuk 2**).

In **Hoofdstukken 3-4** beschrijven we de ruimtelijke patronen op een landschapschaal van een aantal benthos soorten (*Macoma balthica, C. edule, Nereis diversicolor, Nephtys hombergii, Marenzelleria viridis, Scoloplos armiger, Corophium volutator* en *Urothoe poseidonis*), waarbij we in het bijzonder methodologische en analitische uitdagingen benadrukken. We vergelijken drie methodes om ruimtelijke autocorrelatie te analyseren: (1) fractalen, (2) variogrammen en (3) Moran's *I*. Op basis van gesimuleerde ruimtelijke patronen kozen we de laatste methode vanwege: (1) door standardisatie kunnen resultaten rechtstreeks worden vergeleken, (2) Moran's *I* is makkelijker te begrijpen doordat het verwant is aan de bekende Pearson's correlatie coëfficiënt, en (3) significantie kan gemakkelijk worden bepaald. Bijgevolg werd Moran's *I* gebruikt door dit hele proefschrift om ruimtelijke patronen te beschrijven. Voor elke soort waren ruimtelijke patronen op een landschapschaal onderscheidbaar. Door onze ongeëvenaarde landschapschaal bemonstering (225 km^2), in combinatie met het groot aantal monsterpunten (jaarlijks ongeveer 2750), was vergelijking met andere studies niet mogelijk (**Hoofdstuk 3**).

Vervolgens breiden we deze ruimtelijk expliciete analyses uit door middel van het analyseren van de omgevings processen die vorm geven aan soortverspreidingen. Momenteel worden drijvende mechanismen van ruimtelijke variatie in aantallen niet goed begrepen en vormt dit een van de belangrijkste speerpunten in de ecologie. Voortschrijdende wiskundige verfijning biedt gelukkig een uitweg: 'generalised estimating equations' (GEE). GEEs kunnen het best worden omschreven als regressie-modellen die expliciet rekening houden met ruimtelijke autocorrelatie in zowel de afhankelijke- als de verklarende-variabelen. GEEs bieden preciezere en statistisch gezien betrouwbaardere schattingen (groter betrouwbaarheids-interval) van de omgevings-variabelen die soortverspreidingen sturen. We hebben deze geavanceerde methode getest op de landschapschaal verspreiding van de voorafgaande soorten. Mediane korrelgrootte en overstromingsduur werden gebruikt als typische verklarende omgevingvariabelen. GEEs verwijderden veel van de overblijvende ruimtelijke variatie, waardoor de invloed van mediane korrelgrootte en overstromingsduur als actoren in de soortsversvreiding op de schaal van het getijde gebied werd onderstreept. Ondanks dat we ons tot nog toe vooral hebben geconcentreerd op de methodolische puzzels die gepaard gaan met soort-omgeving relaties, kunnen we concluderen dat deze ruimtelijke aanpak de huidige kennis uitbreidt en een verbeterd begrip biedt van soortsversvreiding in een omgeving met ruimtelijke structuur. GEEs bieden de noodzakelijke methodologische vooruitgang om het verband tussen patroon en proces naar een hoger plan te tillen. Een praktisch probleem om aan te pakken zou de veronderstelde verplaatsing van de verspreiding van volwassen *M. balthica* in de westelijke Waddenzee kunnen zijn (**Hoofdstuk 4**).

Naast het benadrukken van de historische ontwikkelingen van benthische gemeenschappen in de westelijke Nederlandse Waddenzee die handvaten kunnen bieden voor ecosyteem herstel, hebben we onze geografische schaal uitgebreid tot Noord-West Europa in de vergelijking tussen huidige benthische gemeenschappen. Deze vergelijking is gebaseerd op een benthos-bemonstering tijdens de winter van 2003–2004 in de Waddenzee (Nederland), de Wash (Engeland), de baai van Mont Saint-Michel (Frankrijk) en twee baaien aan de centraal Atlantische kust in het zuiden van Brittanië (Frankrijk). Op deze grote schaal waren soorts aantallen voornamelijk gebied-specifiek, in plaats van overal gelijk (**Hoofdstuk 5**).

Degraderende effecten van mensen op marine getijde ecosystemen werken door van de benthische bewoners naar hun predatoren. Daarom hebben we de gevolgen van veranderende benthische voedselbronnen benadrukt op een landschapschaal voor kanoeten die buiten het broedseizoen de Nederlandse Waddenzee bezoeken. Hiermee verbinden we bestaande kennis van het voedselzoek-gedrag van kanoeten, hun fysiologische flexibiliteit en de ruimtelijke variatie in prooi aantallen. Eerst beschrijven we de mate waarin mechanische kokkelvisserij tussen 1998 en 2003 niet doel-soorten bevistte. Mechanische kokkelvisserij, die de top 5-cm van het sediment verstoort, behoort tot de meest destructieve vorm van bevissing. Kokkelvisserij in de westelijke Nederlandse Waddenzee vond inderdaad plaats in gebieden met de hoogste biodiversiteit, en deze bevatten ook de hoogste aantallen prooien voor steltlopers. De korte-

termijn reactie van de bodemfauna op bevissing was onvoorspelbaar. Dit benadrukt de noodzaak voor een ecosysteem-benadering voor bescherming die zowel doel- als ook niet doel-soorten bevat (**Hoofdstuk 6**).

Vervolgens behandelen we deze over-exploitatie van benthische voedselbronnen als een 'experiment' om het geschikte forageergebied, ruimtelijke voorspelbaarheid van voedsel en overleving van kanoeten van de *islandica*-ondersoort (*C. c. islandica*) tussen 1996 en 2005 te verbinden. Hierin wordt een verterings-model gebruikt om de voorraad bodemfauna naar een prooi-landschap voor kanoeten te vertalen. Dit model voorspelt optimale diëten die de lange termijn opname van voedsel maximaliseren, waarbij rekening gehouden wordt met een mogelijke beperking van de verteringssnelheid. Rekening houdend met een drempelwaarde om in de energie behoefte te voorzien, verloren kanoeten over de tien jaren 55% van het geschikte forageergebied. Dit verliep statistisch parallel aan eenzelfde afname in kanoeten-aantallen van 42%. Ook de overleving van kanoeten op basis van kleurringen nam af in dezelfde periode van 89% tot 82%. De afname van ruimtelijke patronen, dat wil zeggen de vermindering in informatie over de positie van geschikte forageer plekken, heeft nog niet geleid tot een extra afname van vogels. De aantallen *islandica*-kanoeten per eenheid geschikt forageergebied bleef constant op 10 kanoeten per hectare tussen 1996 en 2005. Dit suggereert dat ze de Nederlandse Waddenzee aldoor op volledige capaciteit gebruikt hebben (**Hoofdstuk 7**).

Het geschikte forageergebied van de andere ondersoort van de kanoet (*canutus*), die het gebied benutten tijdens hun zuidwaartse trek om op te vetten voordat ze doorgaan naar de West-Afrikaanse overwinteringsgebieden, nam sneller af dan dat van de *islandica*'s: tussen 1996 en 2005 werd 86 % van het gebied ongeschikt. Op basis van biometrie (lichaamsgewicht, slagpen-rui en snavellengte) konden we de proportionele afname in mistnet vangsten aantonen. Dit was een aanwijzing dat *canutus*-kanoeten de Nederlandse Waddenzee overslaan tijdens de zuidwaartse trek. Gegeven de grote afname van geschikt forageergebied in de Waddenzee, tegelijkertijd afnemende aantallen in de belangrijkste overwinteringsgebieden in westelijk Afrika en toenemende bodemfauna bestanden met prooien in deze overwinteringsgebieden, was dit een indicatie dat de Nederlandse Waddenzee het belangrijkste knelpunt was buiten het broedseizoen. Dit impliceerde dat de draagkracht van kanoeten in westelijk Afrika misschien gekoppeld is en beperkt wordt door de draagkracht van de Waddenzee (**Hoofdstuk 8**).

Om het verlies van geschikt forageergebied door industriële visserij te kunnen weerstaan zouden kanoeten de omvang van hun spiermaag kunnen vergrootten. Hierdoor wordt de capaciteit om voedsel van slechtere kwaliteit te kunnen verwerken groter. Inderdaad, kanoeten pasten hun maaggrootte aan, maar dit compenseerde niet voor het verlies van de omvang en kwaliteit van geschikte droogvallende forageergebieden. Bijgevolg nam ook de lokale overleving van kanoeten af. De afname van de noodzakelijke voedselbronnen in het getijde-gebied kan zowel de afname van kanoeten in de Waddenzee als de afname van de overwinterende populatie in Europa verklaren (**Hoofdstuk 9**).

Ten slotte worden de belangrijkste bevindingen van het werk in dit proefschrift in een bredere context geplaatst. Ik belicht een bijzonder interessante toekomstige onderzoeksrichting waarin ruimtelijke ecologie gekoppeld wordt aan ecosysteem-beheer om de status van ecosystemen te monitoren. Mijn voorstel omvat het gebruik van gegevens van grootschalige bodemfauna bemonsteringen om soort-omgevings relaties te beschrijven langs gradiënten van verstoring met de meest recente ruimtelijk expliciete modellen zoals GEE. Zulke analyses kunnen dan benut worden als hulpmiddelen om habitat voorkeuren van soorten te beschrijven en om het verlies van dat type habitat te benadrukken via het verlies van soorten. Hierdoor zou het voorspellend vermogen toenemen en het zou misschien mogelijk worden ecosysteem-veerkracht — het langetermijn vermogen van een ecosysteem om van een verstoring te herstellen — beter te begrijpen waardoor beheer van ecosystemen verbetert (**Hoofdstuk 10**).

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