Introduction

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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).](image)

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
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)fueling 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 km² 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 & Hobbis 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).

![Decision tree](image)

**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.

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