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

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ABSTRACT: 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. The present study aimed to: (1) describe landscape scale spatial patterns of benthic infauna after evaluating 3 methods for analyzing autocorrelations (Moran's I, semivariance and fractals), (2) compare the benthic patterns with patterns described for other organisms, and (3) highlight shared characteristics. During 4 consecutive years (2002 to 2005) we assessed spatial structuring of 4 intertidal benthic invertebrates (*Cerastoderma edule*, *Macoma balthica*, *Nereis diversicolor* and *Nepthys 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 the least 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.

KEY WORDS: Cryptic macrozoobenthos · Intertidal · Landscape scale · Patch size · Spatial structure · Wadden Sea

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 openness 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. 1993) and have not yet returned, which can be credited partially to another benthic 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. 1993, Zwarts & Wanink 1993, Flach 1996, 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. 2006a, 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 few that combine a large sampling area (>1 km^2) with a large number of samples (>1000 samples) (Fig. 1, Table 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 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
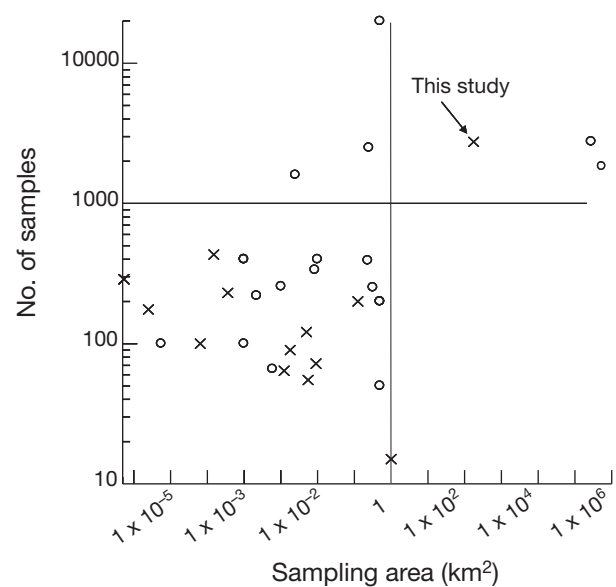

Fig. 1. Numbers of samples taken and the total area covered (km^2) in published spatial papers. (✕): marine studies; (○): terrestrial. The vertical line denotes a sampling area of 1 km^2, whereas the horizontal line divides studies with more than 1000 samples from studies with fewer samples

patterns. The simulated patterns were used to examine the behaviour of Moran's *I* (Moran 1950, Sokal & Oden 1978, 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 to 5° E) (Fig. 2) covered a surface of approximately 225 km^2. The area mainly consists of gullies, intertidal and subtidal mudflats, and is bordered to the west and north 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 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. 1993, Zwarts et al. 2003).

Table 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 & microalgae	Marine	USA	5.42×10^{-8}	288	Pinckney & Sandulli (1990)
Meiofauna & microalgae	Marine	USA	5.42×10^{-8}	288	Sandulli & Pinckney (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	Huxam & Richards (2003)
Macrozoobenthos	Marine	New Zealand	5.50×10^{-3}	55	Hewitt et al. (1997b)
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)

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. 1993, 2001, van Gils et al. 2006a). Measured densities of benthic fauna do not demonstrably change over this 2 mo sampling period (Piersma et al. 1993). We collected samples over a predetermined 250 m grid that covered the intertidal mudflats (Fig. 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 at each station. 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 sam-

pling 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. 1993, van Gils et al. 2006a,b).

Simulations. Spatial structures were simulated using a 20 × 20 lattice with cell values ranging between 1 and 10 (see Fig. 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 (see Fig. 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
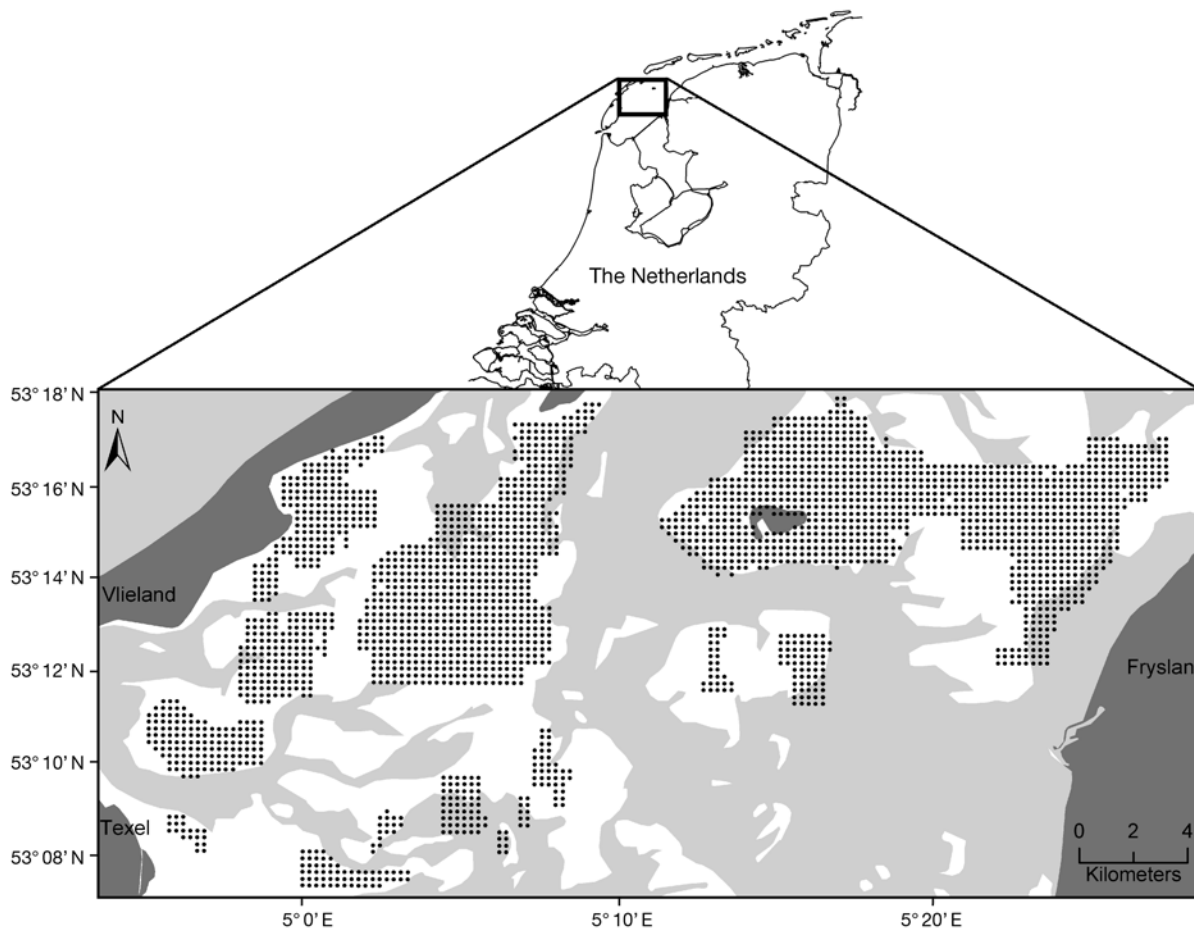
Fig. 2. Benthic sampling stations (•) on a 250 m grid in the western Dutch Wadden Sea. White areas indicate mudflats exposed during low low-water at spring tides, light grey areas indicate water and the dark grey area indicates land

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 value of 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. 4 to 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 1978). 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. 3a), none of the 3 methods showed significant autocorrelation, indicating the absence of spatial structure. The double-log variogram (Fig. 3a) indicated that species distribution was a constant function of scale; it was completely self-similar. When values were structured along a gradient (Fig. 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 semi-variogram, 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. 3c) gave significant positive auto-correlations 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. 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 trough 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 repetitive 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. 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. 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 (Fig. 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 relationship 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. 4 to 7 for comparison with the spatial characteristics of the distribution of benthic species (see 'Materi-
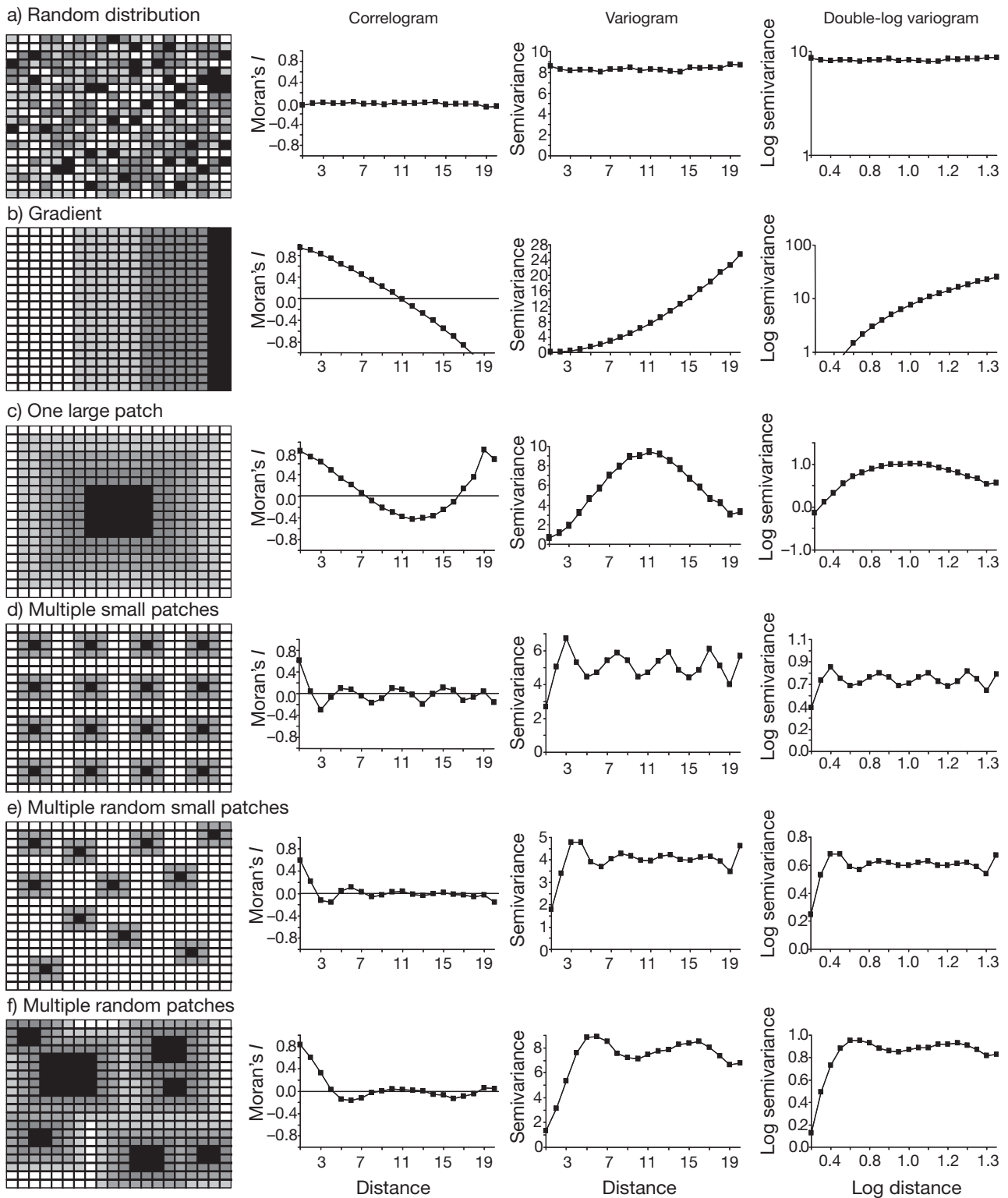
Fig. 3. Simulated spatial patterns where the value increases from 1 (white) to 10 (black), analyzed with Moran's *I* (correlogram), semivariance (variogram) and fractal dimension (double-log variogram). The complexity of the simulated pattern increases from top to bottom
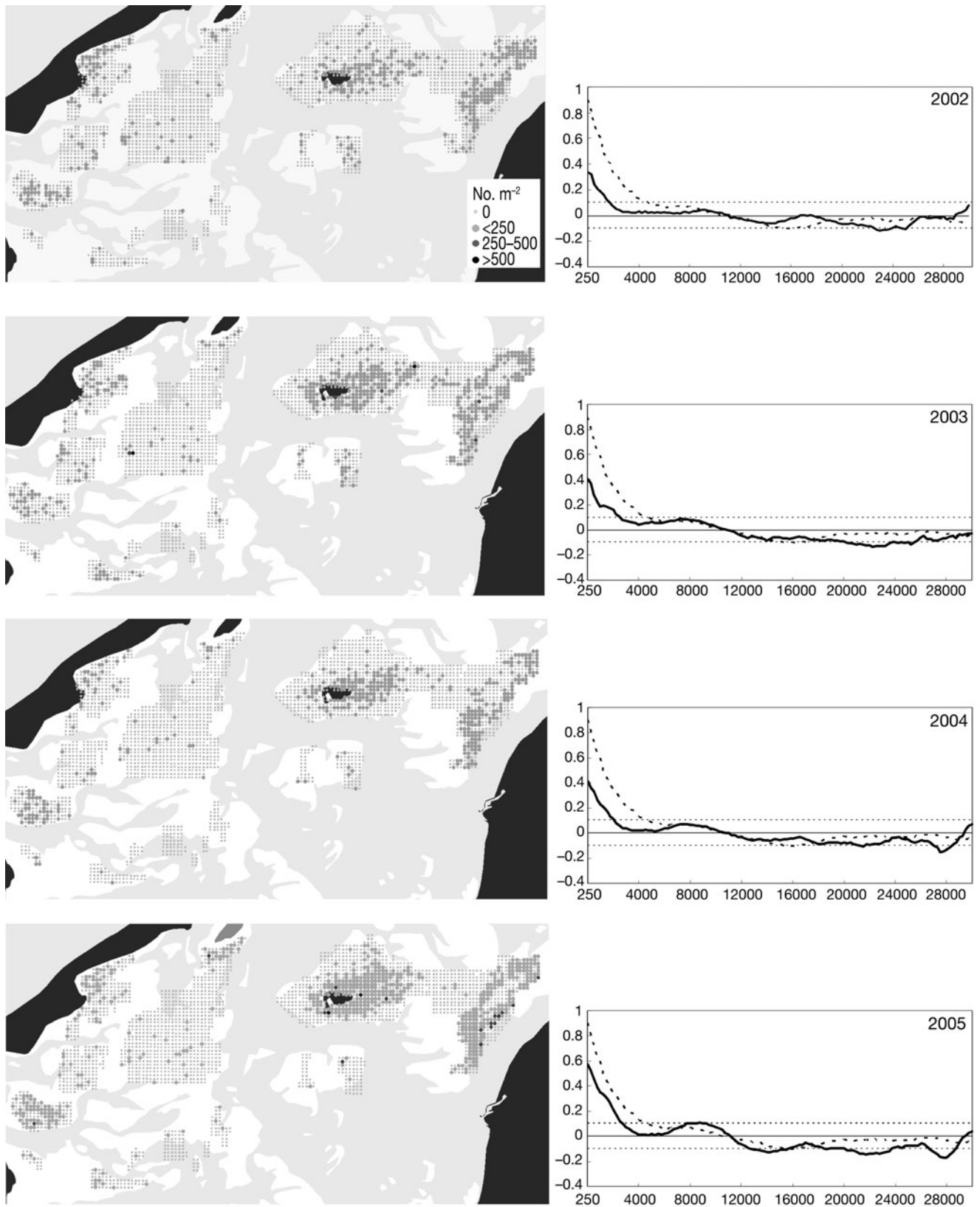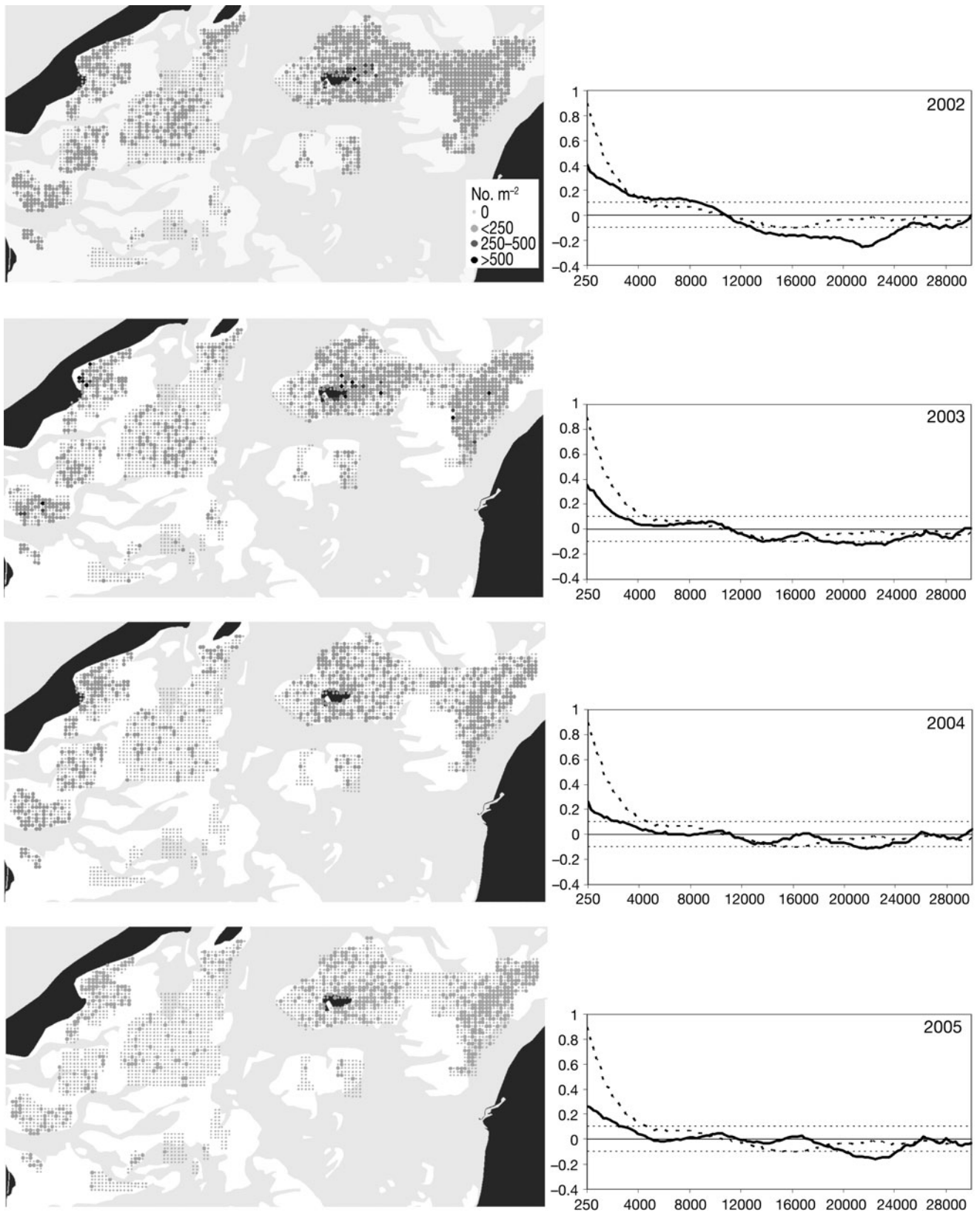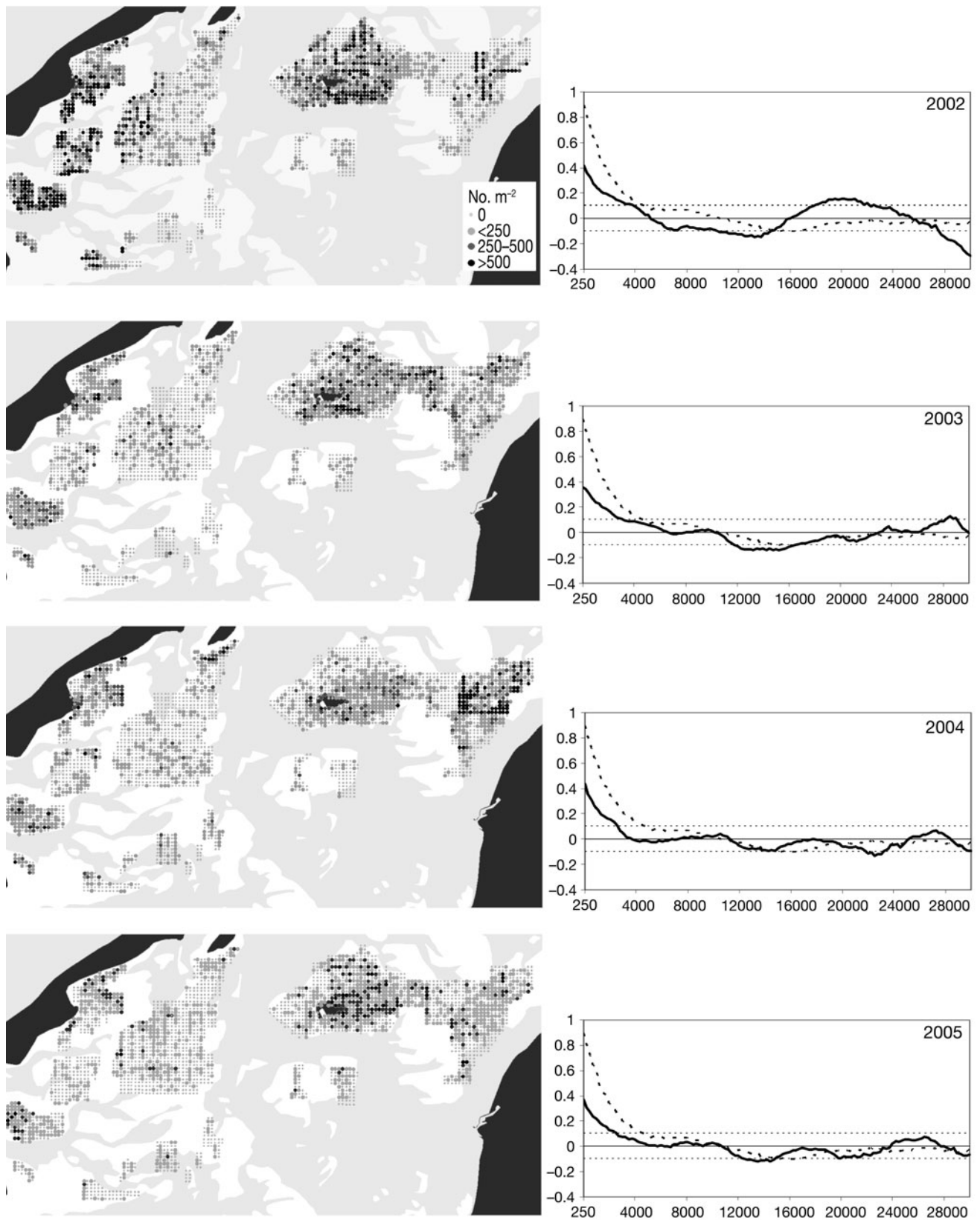
Fig. 4. *Cerastoderma edule*. Distribution from 2002 to 2005 (left panels) and the correlogram (solid line) of their spatial pattern; on the *x*-axis the distance (in m) and on the *y*-axis Moran's *I*. The dotted, horizontal lines in the correlogram indicate the 95% CI. The background autocorrelation, determined by the extent of intertidal flats, is represented by the dashed line

Fig. 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. 4 for further explanation
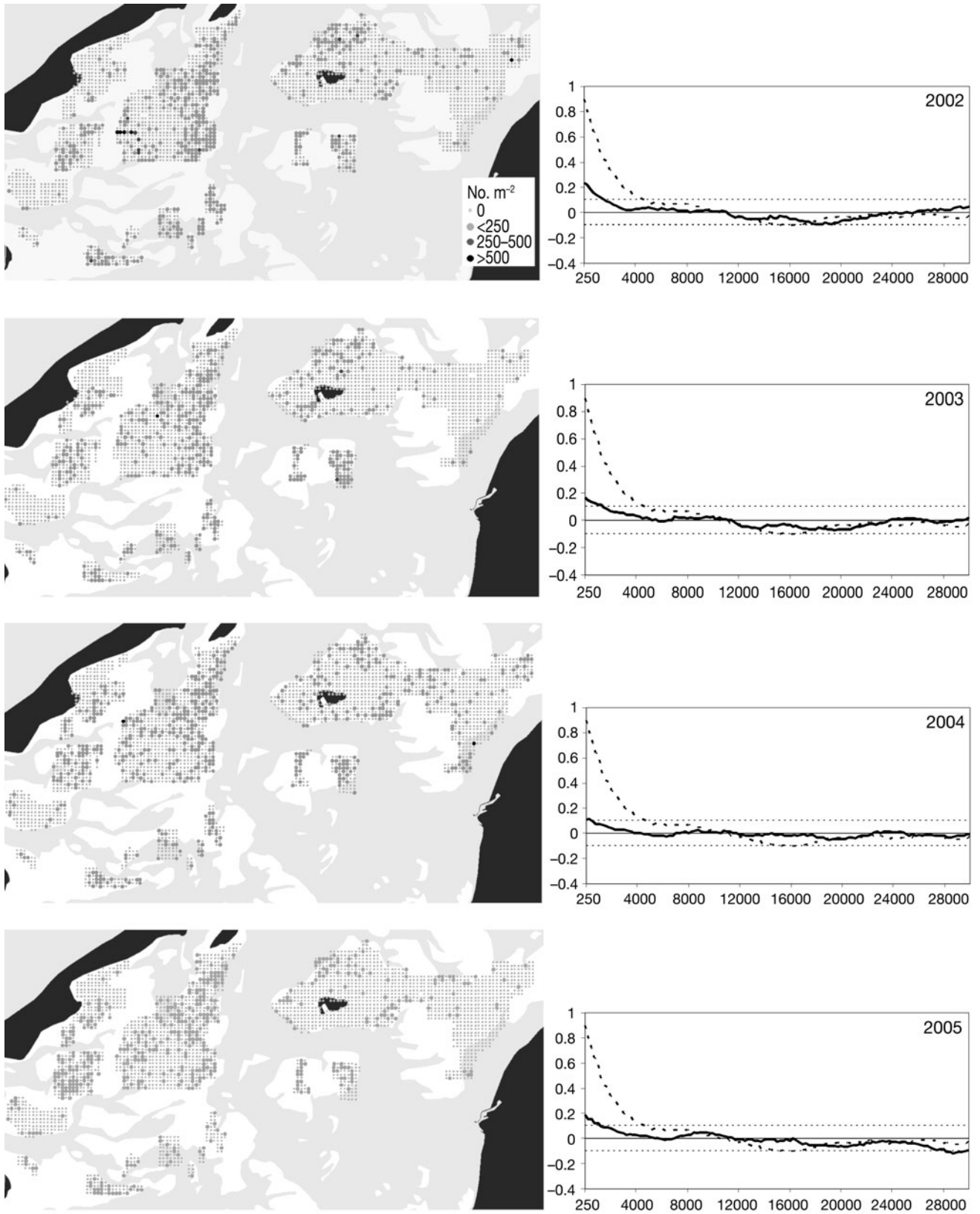
Fig. 6. *Nereis diversicolor*. Distribution from 2002 to 2005 (left panels) and the correlogram (solid line) of their spatial pattern; on the *x*-axis the distance (in m) and on the *y*-axis Moran's *I*. See Fig. 4 for further explanation

Fig. 7. *Nepthys 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. 4 for further explanation

als 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. 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. 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. 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 2002 ($I = 0.4$) and 2005 ($I = 0.3$) (Fig. 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 patch size (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. 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 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 *Nepthys hombergii* generally occurred in low densities throughout our sampling area (Fig. 7), with the 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.

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. 8), they also reveal higher amplitudes in the correlograms (Figs. 4 to 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 showed a significant relationship 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. 3f) and multiple random small patches (Fig. 3e), both characterized by short-distance positive autocorrelation and noise at larger distances.

DISCUSSION

Although spatially explicit analytical methods are common practice in plant and landscape ecology (e.g. Sokal & Oden 1978, Cliff & Ord 1981), with notable exceptions (Thrush et al. 1989, Hewitt et al. 1997a,b, 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),
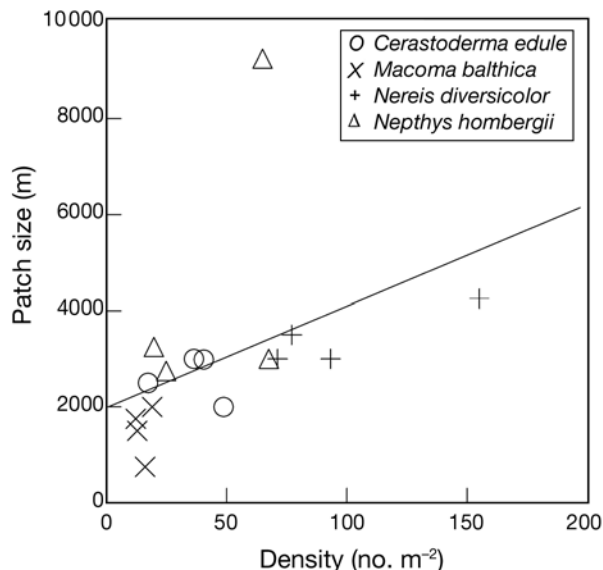

Fig. 8. Patch size in relation to the density of the 4 benthic species studied (*Cerastoderma edule*, *Macoma balthica*, *Nereis diversicolor* and *Nepthys hombergii*) from 2002 to 2005 (see Figs. 4–7)

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. 4 to 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. 1, Table 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. 4 to 7), reaching a diameter of up to 9000 m. These patterns, comparable to the simulated multiple random patches (Fig. 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. 4 to 7). Apart from McArdle & Blackwell (1989), also a marine study, the present study is the only one extending the analysis beyond a single snapshot 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 those 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 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 mathematical 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 could potentially enhance the ecological understanding of, for example, benthos–sediment relationships in intertidal areas within a spatially explicit framework.

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