

Site-specific distribution of the bivalve *Scrobicularia plana* along the European coast

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ABSTRACT: The development and maintenance of spatial patterns and the way they affect the dynamics of populations and ecosystems is a key issue in ecology. Since each individual and each species experiences the environment on a unique range of scales, it is vital to determine the spatial scales across which organisms interact with each other and the structuring influence of their environments, which can be achieved by analyzing species' distribution patterns. Here, the spatial variation in the distribution of *Scrobicularia plana* is described for 4 intertidal areas along the species' distributional range. Spatial autocorrelation correlograms based on Moran's coefficient reveal that while the Trondheim (Norway) population was randomly distributed, at Minho (Portugal), the Westerschelde, and the Wadden Sea (both in The Netherlands) populations were aggregated. Patch diameter varied from 150 to 1250 m, in Minho and Westerschelde, respectively; while in the Wadden Sea, patches of 4 to 10 km were detected. Comparisons of spatial patterns with those of other co-occurring bivalve species (*Abra tenuis*, *Cerastoderma edule*, and *Macoma balthica*) revealed that *S. plana*'s distribution was generally patchier. The distribution of *S. plana* was correlated with sediment type at Westerschelde and Trondheim, but not Minho. The observed differences in distribution patterns and their correlation with environmental factors reveal that spatial patterns of *S. plana* are site-specific rather than species-specific.

KEY WORDS: Distribution · Intertidal · Larval settlement · Moran's *I* · Patchiness · Sediment type · Spatial autocorrelation analysis

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INTRODUCTION

Intertidal mudflats are valuable ecological entities that support large populations of birds (e.g. Beukema et al. 1993, Zwarts & Wanink 1993, Ens et al. 1994, Leguerrier et al. 2003, van de Kam et al. 2004), and act as nursery and feeding areas for fish and crustaceans (Martinho et al. 2007, Campos et al. 2010). Macrobenthic communities are key elements of intertidal ecosystems, playing an important role in the

food web and system dynamics (Herman et al. 1999). Spatial patterns of macrobenthic invertebrates are shaped not only by environmental variation, but also by biotic interactions among species and the diversity of the assemblages (Underwood et al. 2000). Identification and quantification of spatial patterns at several spatial and/or temporal scales are, therefore, essential to help understand the factors and processes shaping these soft-sediment communities (Ellis & Schneider 2008), a prerequisite for a sound

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implementation of integrated management, as it will allow for better predictions regarding communities' responses to future environmental changes.

The spatial pattern of a population is the result of a balance between dispersal and aggregation (Heip 1975, Meire et al. 1989, Folmer et al. 2010). Spatial patterns can be characterized by 2 aspects: intensity and form (Andrew & Mapstone 1987). Intensity, which relies on the distribution of density estimates, sorts distributions into 3 types: uniform, random, and aggregated (Meire et al. 1989, Thrush et al. 1989, Thrush 1991). A uniform pattern means that individuals are arranged in a regular way, likely due to intraspecific competition; while in the random pattern the space occupied by an individual is independent of the space occupied by others. In the aggregated pattern, individuals are clumped together as a result of environmental heterogeneity, predation pressure, competition or reproductive behavior (Heip 1975, Meire et al. 1989). As for the form of the spatial pattern, it corresponds to the size of patches and can be assessed with spatial autocorrelation which analyzes the degree of dependency among observations in relation to the arrangement of individuals in space (Thrush et al. 1989, Thrush 1991, Kraan et al. 2009).

Since the majority of natural environments are patchy and environmental heterogeneity tends to cause aggregated distributions, most populations are aggregated to some extent (Levinton 1972, Heip 1975, Barry & Dayton 1991, Kraan et al. 2009). Spatial aggregation can occur on different scales, e.g. from the geographical distribution of a species to the physical structure of the sediment (de Wolf 1989, Underwood & Chapman 1996, Kraan et al. 2010) and, as a consequence, ecological variables and processes tend to be scale-dependent (Legendre & Fortin 1989). Since organisms may respond to more than one of these levels (Hewitt et al. 1996), analysis of the hierarchical structure of factors affecting patchiness is essential to understand its responses.

Highly patchy spatial distributions are typical for many hard substrate invertebrates and also, for example, reef forming bivalves such as mussels, while soft bottom infauna is generally more evenly distributed (Meire et al. 1989). Nevertheless, a patchy distribution has been recorded in several co-distributed soft bottom bivalves such as *Mya arenaria* (Strasser et al. 1999, Bocher et al. 2007), *Macoma balthica*, and *Cerastoderma edule* (Meire et al. 1989, Kraan et al. 2009), and *Scrobicularia plana* (Hughes 1970, Langston 1986). Local distribution patterns of intertidal molluscs, however, may vary between sites and only by comparing the spatial patterns from

different areas can we determine if patterns are species- or site-specific (Bocher et al. 2007). While species-specific patterns suggest that spatial distributions are mainly determined by the characteristics of the species, site-specific patterns must be explained by interactions between species' characteristics and local factors. The later, therefore, emphasizes the need for site-specific studies for a better understanding of the factors determining the observed spatial patterns.

Here, we focus on the peppery furrow shell *Scrobicularia plana*, a common species in European intertidal soft-sediment communities (Bocher et al. 2007). *S. plana* seems to be characterized by an overall patchy distribution (Hughes 1970, Langston 1986), which appears to be determined by the existence of specific environmental conditions during settlement (Santos et al. 2011b). The species is an important food source for shorebirds and fish (e.g. Hughes 1970, Moreira 1997), and economically valuable, especially in southern Portugal and Spain (Langston et al. 2007). The species is present along the NE Atlantic coast, from the Norwegian and Baltic Seas in the north to Senegal in the south, and in the Mediterranean Sea (Tebble 1976). Although it can be found in areas of sand, clay or mud, rich in organic matter, it has a clear preference for muddy sediments (Casagrande & Boudouresque 2005, Bocher et al. 2007).

To determine whether the species' distribution is a species- or site-specific trait, we analyzed the spatial distribution of *Scrobicularia plana*, as well as several co-distributed bivalve species, at 4 sites and 2 spatial scales. Such descriptive results serve as a basis for hypotheses regarding the factors and processes determining the observed spatial structure, they can then be put to a test with additional observations and experimental approaches.

MATERIALS AND METHODS

Field sampling

Distributions and densities of benthic bivalves were determined for 3 smaller-scale intertidal areas along the European coast: Minho, Portugal (41° 51–52' N, 08° 49–50' E); Westerschelde, The Netherlands (51° 20–21' N, 03° 42–44' E); and Trondheim, Norway (63° 18–19' N, 10° 09–11' E), as well as one larger-scale area, the Dutch Wadden Sea (Fig. 1). In order to estimate temporal changes and spatial differences in abundance, while accurately estimating model autocorrelation parameters, the most effective

sampling design was a grid with additional random samples placed on the gridlines (Bijleveld et al. 2012). The distance between points varied between locations according to the total area of the sampling sites. In addition to the regular grid, ~10% (Wadden Sea) to 25% (remaining 3 locations) extra cores were collected at random positions to account for auto-correlations at smaller distances (for the rationale of this approach, see Bijleveld et al. 2012). Description of the dimensions and number of points sampled in each grid can be found in Table 1.

At each sample point, identified using GPS coordinates, a sediment core (15 cm diameter, to a depth of 20–25 cm) was taken. The core samples were sieved, on site, over a 1 mm mesh and all organisms were collected and stored at -20°C for later analysis. A second core (6 cm diameter, to a depth of 5 mm) was taken in order to determine grain size composition of the sediment surface layer. Samples were stored at -20°C until further analysis.

Laboratory analyses

All bivalves collected were identified and counted. Sediment samples were freeze-dried (Christ Alpha 1–4 LD plus) and then treated to remove organic matter and carbonate material, as described by Van den Bergh et al. (2003). Analysis of median particle size and the percentage of silt (fraction $<63\ \mu\text{m}$) of sediment samples was performed using a Coulter LS 13320 particle size analyzer and autosampler.

Statistical analyses

The analyses were performed in 2 steps. Small-scale patchiness of *Scrobicularia plana* and a number of co-occurring bivalve species was analyzed for Minho, Westerschelde and Trondheim. A larger-scale analysis for *S. plana* was conducted in the Dutch Wadden Sea.

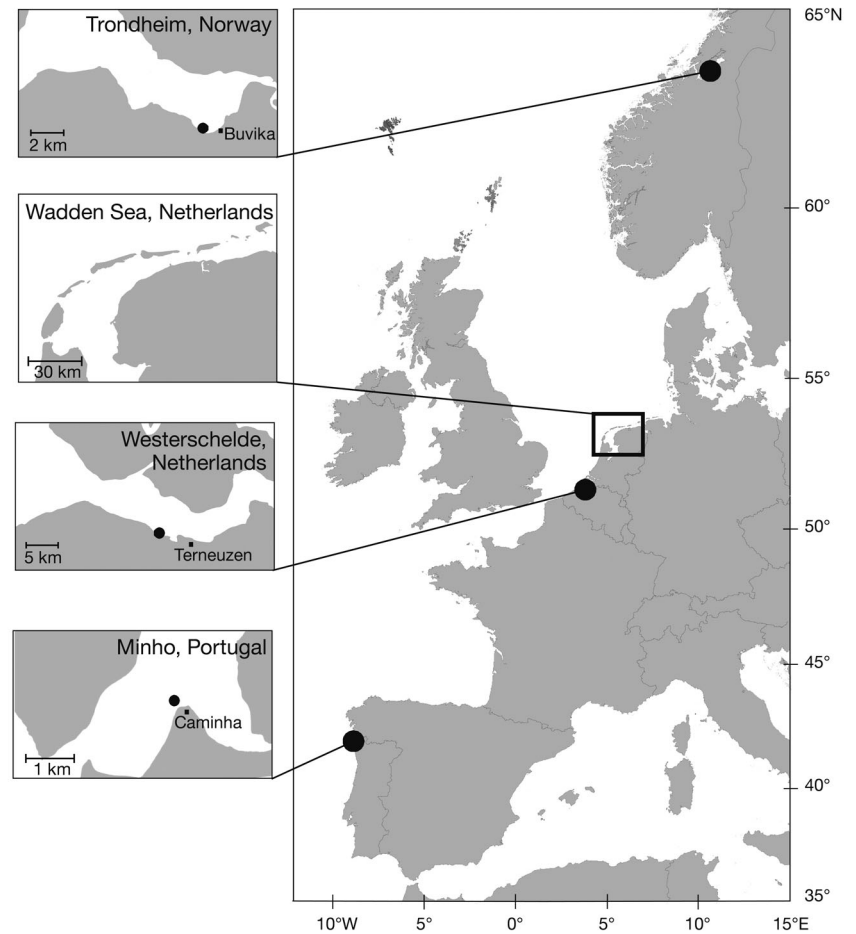


Fig. 1. Sampling locations of *Scrobicularia plana* along the European coast

Table 1. Dimensions and number of points sampled in each sampling grid. Number of sample points corresponds to total number of points sampled, i.e. including regular grid points as well as ~10% (Wadden Sea) to 25% (remaining 3 locations) of randomly placed points along the gridlines

Location	Year	Grid length (easting, km)	Grid width (northing, km)	Total area (km ²)	Distance between points (m)	No. of sample points
Minho, Portugal	2009	1.6	1.6	2.6	50	137
Westerschelde, The Netherlands	2009	3.2	1	3.2	100	161
Wadden Sea, The Netherlands	2008	–	–	1500	500	4376
	2009	–	–	1500	500	4771
Trondheim, Norway	2008	1.3	0.7	0.9	50 × 100 ^a	79

^aEach point was sampled at a distance of 50 m northward and 100 m eastward

Distribution and density were plotted using the ggplot2 Package (Wickham 2009), in R v. 2.13.1. Spatial autocorrelation (SAC) between abundance and distance was calculated for *Abra tenuis*, *Cerastoderma edule*, *Macoma balthica*, *Mya arenaria*, and *Scrobicularia plana* using Moran's index (I), also in R. This index compares geographic neighbors in terms of their deviation from the mean of all observations, estimating an autocorrelation coefficient that varies between -1.0 (negative autocorrelation) and 1.0 (positive autocorrelation), with values near zero indicating no spatial autocorrelation. Where correlations are found, the cross point of the zero line is considered a rough measure of patch diameter.

Partitioning geographic distances into discrete *a priori* classes must be evaluated. Classes containing too few pairs of locations will produce less reliable Moran's I values, whereas coarser classes (encompassing a larger increment of geographic distance), while statistically reliable, will sacrifice resolution of the actual distance (patch) size. The number of distance classes (or lags) was calculated using Sturges' rule (Sturges 1926). The width of each distance class was determined as the maximum geographic distance divided by 2 (Rossi et al. 1992) and then subdivided by the number of distance classes. Once distance classes were determined, significance was tested by a Monte Carlo randomization test with 999 permutations, under a one-tailed test for positive autocorrelation (Legendre & Legendre 1998), using the spdep R Package (Bivand et al. 2011). As the pattern of a correlogram may be affected by the lag distances selected, the consistency of patterns was tested by altering the lag distance.

Correlograms, in which Moran's I coefficients are plotted against spatial distances, were generated in the ncf R package (Bjornstad 2009). Correlograms were globally significant only when at least one of its Moran's I values was significant at the Bonferroni corrected level (Oden 1984, Legendre & Legendre 1998). Within each correlogram, the significance of Moran's I for each distance class was tested using Holm's correction for multiple comparisons (Holm 1979). A requirement for this analysis is second-order stationarity, i.e. the mean and variance are constant and the autocorrelation function depends only on the distance between observations (Legendre & Legendre 1998). Therefore, in order to stabilize the mean and variance and avoid deviations that may result in violation of stationarity, frequency data were log-transformed $x' = \log(x + 1)$ prior to analysis (Zar 1996).

The relationship between sediment type, i.e. median particle size and the percentage of silt (fraction

$<63 \mu\text{m}$), and the distribution of *Scrobicularia plana* was determined with a partial Mantel test (Mantel 1967) implemented in the cluster (Maechler et al. 2011) and vegan (Oksanen et al. 2011) R packages. Significance was tested using 10 000 permutations. Probability levels were adjusted using the False Discovery Rate (FDR) correction procedure (Benjamini & Hochberg 1995), which controls the expected proportion of incorrectly rejected null hypotheses (type I errors).

RESULTS

Distribution and spatial autocorrelation in *Scrobicularia plana*

The numerical distribution of *Scrobicularia plana* over the 3 smaller-scale sampling sites (Fig. 2) shows that densities (means \pm SE) varied between 43 ± 5.49 ind. m^{-2} , in f to 72 ± 13.81 ind. m^{-2} , in Trondheim; while a value of 56 ± 6.87 ind. m^{-2} was registered for the Westerschelde.

The SAC analysis determined the number of distance classes calculated for each sampling site which varied only slightly, with 13 in Trondheim, 14 in Minho, and 15 in the Westerschelde. Lag distance was defined as 75, 114, and 60 m, for Minho, Westerschelde and Trondheim, respectively. A distance-based, spatial weights matrix was created for each location, using the defined lag distance as the upper distance bound. Only lags including >30 pairs of points were considered (Rossi et al. 1992) and, as a result, while all 15 lags were included in the analysis at Westerschelde, lags 14 for Minho and 7–13 for Trondheim were not analyzed. Tests of significance of the Moran's I for each lag revealed that, for *Scrobicularia plana*, lags 1, 2, 6, 8, 12, and 13 from Minho had a significant positive correlation coefficient. For the Westerschelde, lags 1–11 were significantly correlated, while in Trondheim only lag 5 was significant.

Correlograms of *Scrobicularia plana* (Fig. 3) were globally significant at the Bonferroni corrected level for Minho and Westerschelde, which indicates that the species is patchily distributed at these locations, but not for the Trondheim sampling site. Indeed, densities showed positive autocorrelations at the smallest distance-classes, followed by random oscillations around zero and, in some cases, significantly negative correlation (i.e. dissimilar values appear in close association). *S. plana* in Minho was spatially correlated up to a distance of 150 m. In the Westerschelde, positive spatial correlation was observed for dis-

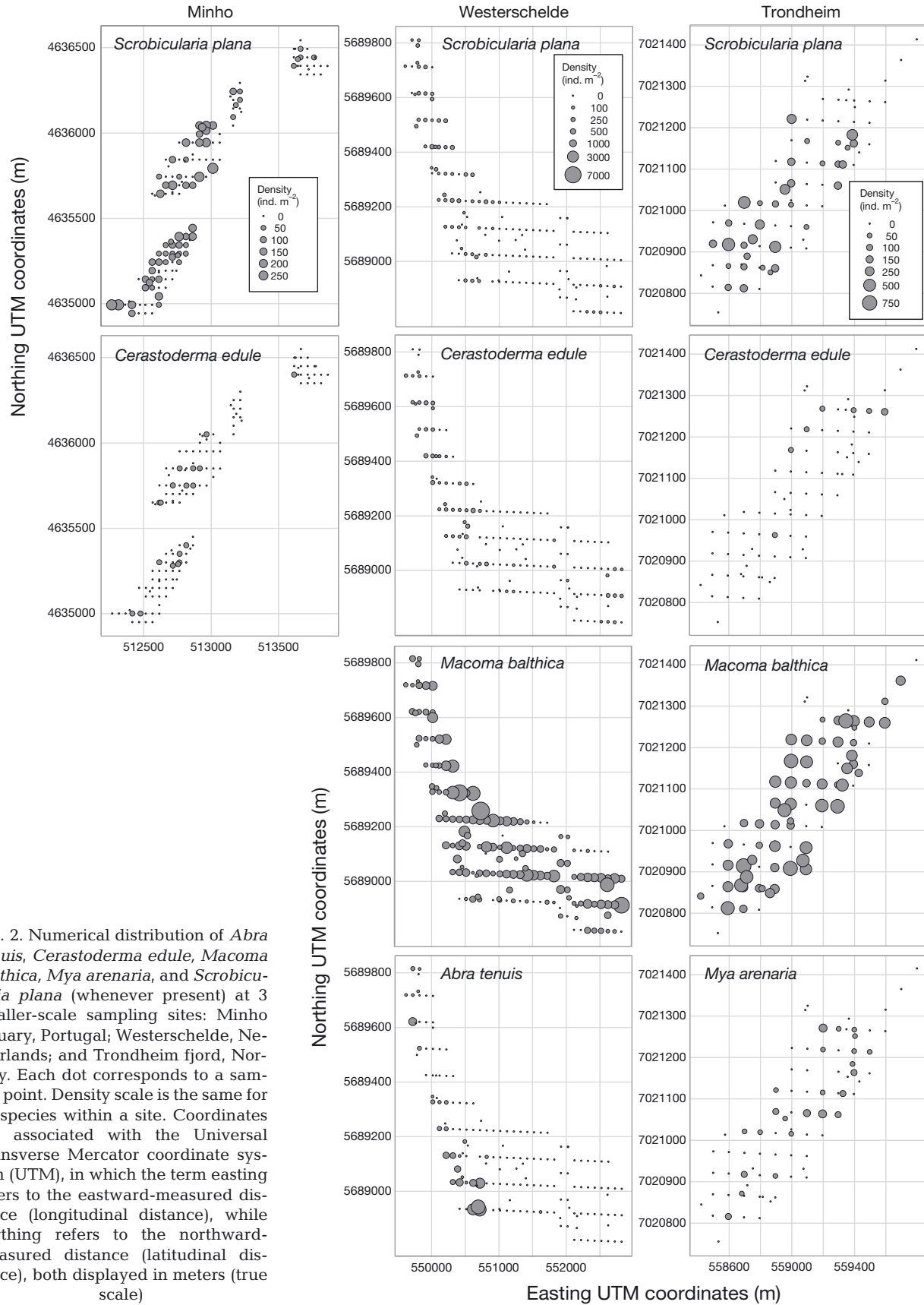


Fig. 2. Numerical distribution of *Abra tenuis*, *Cerastoderma edule*, *Macoma balthica*, *Mya arenaria*, and *Scrobicularia plana* (whenever present) at 3 smaller-scale sampling sites: Minho estuary, Portugal; Westerschelde, Netherlands; and Trondheim fjord, Norway. Each dot corresponds to a sample point. Density scale is the same for all species within a site. Coordinates are associated with the Universal Transverse Mercator coordinate system (UTM), in which the term easting refers to the eastward-measured distance (longitudinal distance), while northing refers to the northward-measured distance (latitudinal distance), both displayed in meters (true scale)

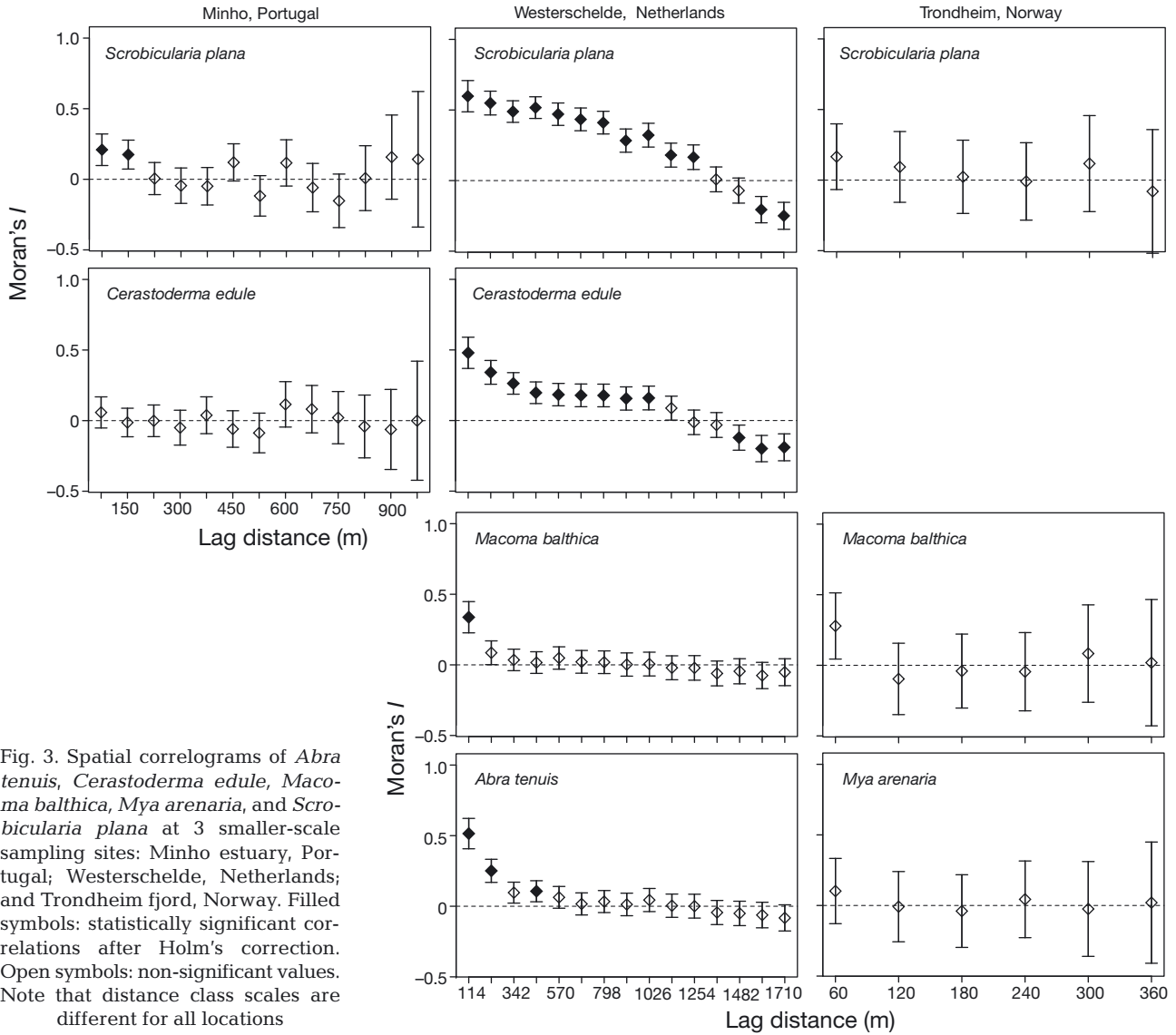


Fig. 3. Spatial correlograms of *Abra tenuis*, *Cerastoderma edule*, *Macoma balthica*, *Mya arenaria*, and *Scrobicularia plana* at 3 smaller-scale sampling sites: Minho estuary, Portugal; Westerschelde, Netherlands; and Trondheim fjord, Norway. Filled symbols: statistically significant correlations after Holm's correction. Open symbols: non-significant values. Note that distance class scales are different for all locations

tances up to ~1250 m, while significantly negative correlation was detected at distances >~1600 m. No spatial correlation was found for *S. plana* in Trondheim. Lag distances of 50 and 100 m for Minho and Trondheim, and of 100, 150, and 200 m for Westerschelde were tested, with no changes on the patterns in the correlograms.

The larger-scale analysis of the Wadden Sea data provided information on SAC of *Scrobicularia plana*, while the comparative sampling over 2 yr also provided an indication of pattern stability and uniformity (Fig. 4). Twenty-four lags were defined at 1 km distances. Moran's *I* values were statistically significant for lags 1–6, 8, 10–11, and 15–24 in 2008, and only lags 1–3 in 2009. Correlograms were globally significant at the Bonferroni corrected level (Fig. 5). After

Holm's correction, positive correlation was observed for distances of up to 6 km, with a second patch between 10 and 11 km in 2008, and at distances <4 km as well as at 24 km in 2009. However, patterns were not stable when lag distances were changed. Considering a lag distance of 2 km, a single patch was detected in 2008 at distances of up to 10 km; while for 2009, 2 patches were detected at up to 4 and 14 km, respectively.

Distribution and spatial autocorrelation of other species

SAC analyses (Fig. 3) of the distribution of co-occurring bivalve species (Fig. 2) revealed that *Abra*

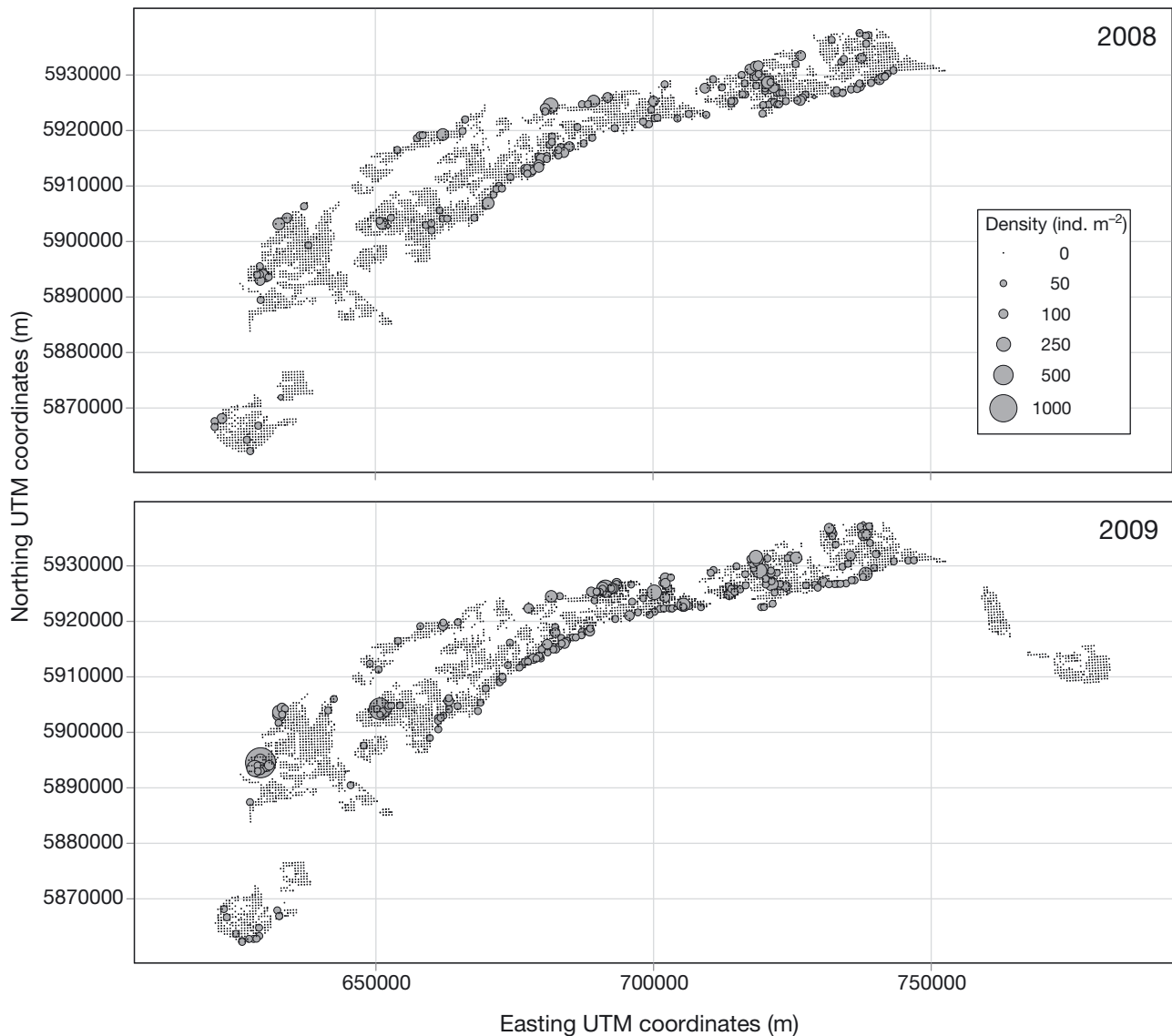


Fig. 4. *Scrobicularia plana*. Numerical distribution in the Dutch Wadden Sea. Each dot corresponds to a sample point. Density scale is the same for both years. See Figs. 1 & 2 for location of the Wadden Sea within the Netherlands and explanation of UTM coordinates, respectively

tenuis, which was only found in the Westerschelde, showed a significant correlation coefficient for lags 1–2. For *Cerastoderma edule*, lag 8 and lags 1–10 were significant in Minho and the Westerschelde, respectively. *C. edule* was also found in Trondheim, but was not included in the analysis given the extremely low densities. *Macoma balthica* was present in the Westerschelde where lags 1–3 were significant, and in Trondheim where it showed no correlation at all. Finally, no significant correlations were found for *Mya arenaria* in Trondheim. In Trondheim (*M. balthica* and *M. arenaria*) and in Minho (*C. edule*), correlograms were non-significant, which

indicates a random distribution. In contrast, all bivalve species in the Westerschelde showed globally significant correlograms. For these, a patch size of 1000 m was observed for *C. edule*, while smaller patches of 115 m and up to 230 m were observed for *M. balthica* and *A. tenuis*, respectively.

Relationship with sediment type

No significant correlation was observed between sediment type and the spatial distribution of *Scrobicularia plana* in Minho. Significant values were found

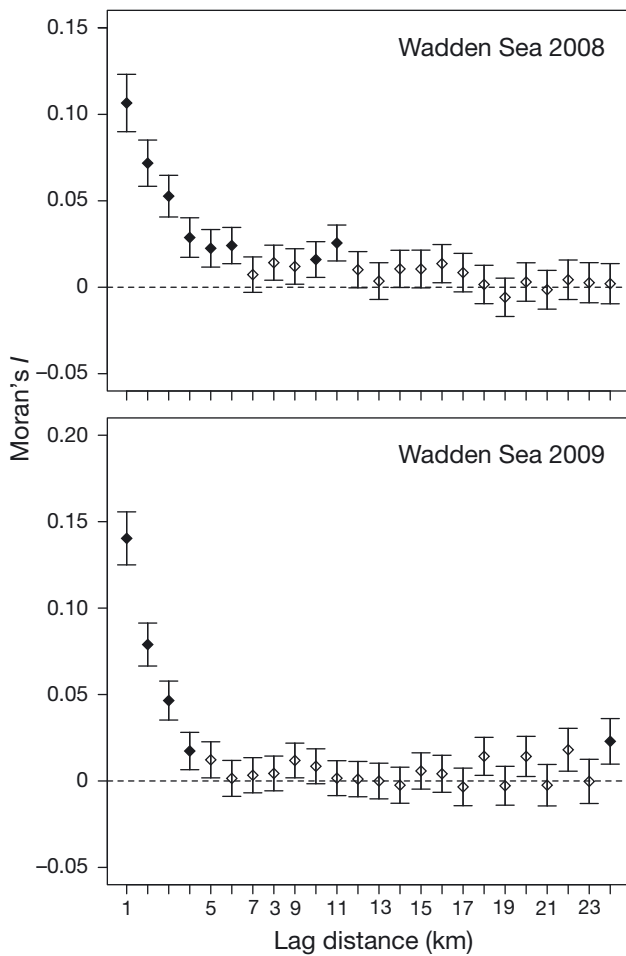


Fig. 5. *Scrobicularia plana*. Spatial correlograms in the Dutch Wadden Sea. Filled symbols: statistically significant correlations after Holm's correction. Open symbols: non-significant values

with both median particle size and percentage of silt in Westerschelde, and for percentage of silt in Trondheim (Table 2).

DISCUSSION

This study has provided insight into the small to large scale spatial patterns of *Scrobicularia plana* at 4 different sites along the species' distributional range. While in Minho and Westerschelde individuals showed an aggregated pattern, the Trondheim population was randomly distributed. These findings confirm previous statements (Hughes 1970, Langston 1986) that *S. plana* is characterized by patchy distributions.

A key point of the study was to analyze the shape of the correlogram since it is associated with particu-

Table 2. Partial Mantel test correlation coefficients (r) between sediment variables and frequency of *Scrobicularia plana* at 3 small-scale sampling locations. Probabilities have been FDR corrected and are expressed as: *** $p < 0.0003$; ** $p < 0.0033$; * $p < 0.0167$

Location	Sediment variable	r
Minho, PT	Median particle size	0.028
	Percentage of silt	-0.058
Westerschelde, NL	Median particle size	0.176***
	Percentage of silt	0.191***
Trondheim, NO	Median particle size	-0.019
	Percentage of silt	0.228**

lar types of spatial structures (Legendre & Fortin 1989). Results demonstrated that the spatial distribution of *Scrobicularia plana* varied between locations. The random pattern observed for the Trondheim population was also detected in a previous study in the Oosterschelde, The Netherlands (Meire et al. 1989). However, most populations appear to have some degree of aggregation. In Minho, positive auto-correlations at the smallest distances, with non-significant random variation from ~200 m onwards, suggested the presence of differently sized random patches (Kraan et al. 2009). This pattern is similar to the one detected in a population in north Wales (Hughes 1970), as well as the one inferred from the Westerschelde correlogram, with the difference being that negative values were observed at greater distances. The latter is the most commonly observed pattern for natural populations in which nearby sites have similar values and the most dissimilar localities are farthest apart (Sokal & Oden 1978). However, when increasing lag distance to 250 m, which allowed the coverage of a much larger area, values at the farthest distances became non-significant. The shape of the correlogram is, therefore, indicative of a single large patch as opposed to a gradient (Kraan et al. 2009).

Different spatial arrangements are expected to have major effects on species performance and population dynamics. For example, when conspecifics are aggregated, strong competitors perform poorly which can slow competitive exclusion, facilitating coexistence (Hart & Marshall 2009). On the other hand, if intraspecific competition is strong, most species are likely to benefit from being randomly distributed (Turnbull et al. 2007). An aggregated distribution can also be disadvantageous if energy is a limiting factor (Heip 1975). This may help explain the random distribution of the Trondheim population since food availability is generally lower at northern

latitudes. As the timing, duration, and composition of phytoplankton blooms are determined by temperature (e.g. Moline & Prézelin 1996), a relationship between spatial distribution of *Scrobicularia plana* at a larger scale and temperature is suggested by the observed patterns.

As most natural populations are, to some extent, patchy in their spatial pattern (Levinton 1972, Heip 1975, Barry & Dayton 1991), it is more important to determine the size of patches. Differences in patch size were observed between sites, indicating that patchiness occurs at different spatial scales. Analysis of the Wadden Sea data also provided information about the effects of temporal scale stability. Density and SAC were similar in both years, but size varied between 2008 and 2009. Variation in patch size may affect recruitment success and, ultimately, population dynamics, depending on the location of patches, as well as the dispersal ability of a species. If populations are self-recruiting from within patches, then larger patches should promote recruitment success.

Are distribution patterns consistent between species?

Comparison of spatial patterns of co-occurring bivalve species allowed us to determine if distribution patterns differ (and to what extent) between species within the same area. All bivalve species from Trondheim showed a random distribution. It is possible, however, that aggregation at an even smaller spatial scale went undetected because samples were collected at distances >50 m. Similar to *Scrobicularia plana*, *Cerastoderma edule* showed a highly aggregated pattern in both the Westerschelde (present study) and the Wadden Sea (Kraan et al. 2009), although with a somewhat smaller patch size. Note, however, that Kraan et al. (2009) used a cut-off point in the Moran's *I* graphs of 0.1 instead of 0 and patch sizes of both species are very similar if a single cut-off point (0) is used. In contrast, in Minho, *C. edule* was characterized by a random distribution. Although both bivalve species are characteristic of the mid-tidal zone of the mudflats (Eltringham 1971) and are often found together in the same area (e.g. Ysebaert & Herman 2002, Dolbeth et al. 2003), *C. edule* is more common in sandy areas (Bocher et al. 2007), which could help explain the observed differences. The similar distribution patterns of *Abra tenuis* and *S. plana* in the Westerschelde (although at different scales) can also be related to the occupation of similar

niches, with both species being more abundant at southern sites and with a clear preference for muddy sediments (Bocher et al. 2007). Finally, *Macoma balthica* in the Wadden Sea (Kraan et al. 2009) showed a very similar pattern to the one observed in the present study for *S. plana*, but a smaller degree of aggregation in the Westerschelde. Differences may be explained by density-dependent processes as *M. balthica* shows higher densities at higher latitudes, while *S. plana* is more abundant in southern areas (Bocher et al. 2007).

Species composition differed between the sites studied, which probably affects *Scrobicularia plana*'s functional role in the macrobenthic community, in particular, density dependent processes related to predator-prey interactions and intraspecific competition. For example, the oystercatcher *Haematopus ostralegus*, one of the main predators of *S. plana* (Hughes 1970), also feeds on other bivalves, such as *Cerastoderma edule*, *Macoma balthica*, and *Mya arenaria* (Zwarts & Wanink 1993, Wanink & Zwarts 2001). If these species are absent from the community, the predation pressure on *S. plana* can increase, leading to higher mortality (Holt 1977). Prey switching in oystercatchers as a response to changes in abundance has been observed (Zwarts & Wanink 1993). As shorebirds concentrate their feeding efforts on particularly food-rich areas (e.g. van Gils et al. 2005), spatially heterogeneous predation pressure could in principle help explain patchy structures (Schneider 1992), such as those of *S. plana* (Jensen & Mouritsen 1992). At this moment, we lack the data to say whether shorebird predation played such a role in the studied systems.

In contrast, the absence of other bivalve species may have a positive effect on *Scrobicularia plana*, as the interspecific competition for food and space can result in a decrease in growth and the overall condition of the bivalves (e.g. Kamermans et al. 1992). However, as body condition of *S. plana* in Westerschelde is better than in Minho and similar to that of Trondheim (Santos et al. 2011a), and the larger patch size and higher species diversity in Westerschelde would suggest higher interspecific competition, this does not seem to be the case. Not only do the spatial patterns of *S. plana* differ among sites, but also those of the other co-occurring bivalve species. This suggests that the spatial distributions of all the species are site-specific, which is in agreement with a previous study from Bocher et al. (2007). Nevertheless, *S. plana* appears, overall, to be more aggregated than other co-distributed bivalve species.

Relating distribution patterns to environmental factors

Sediment composition is one of the factors that influences estuarine benthic assemblage structure and species distribution at local (smaller) spatial scales (Warwick et al. 1991, Ysebaert & Herman 2002, Bocher et al. 2007, Kraan et al. 2010). In our study, the distribution of *Scrobicularia plana* in the Westerschelde and in Trondheim was correlated with median particle size (Table 2), confirming that a muddy sediment type is an important environmental factor determining the species' settlement patterns and subsequent survival, as shown in previous studies (Casagrande & Boudouresque 2005, Bocher et al. 2007, Compton et al. 2009). For deposit-feeders, such as *S. plana*, the higher content of organic matter in muddy sediments (as compared to sandy sediments), is expected to provide higher quality habitat (Levinton 1972). Therefore, a coupling of feeding mode and sediment type is expected. If this is indeed the case, it suggests active habitat selection at the time of settlement with larvae actively settling in areas where the adults will do well in terms of feeding performance. Such an argument is strengthened by the observation that the spatial distributions of juvenile *S. plana* match those of the adults (Compton et al. 2009).

Active patch selection is expected when patches differ in habitat quality (Wiens 1976). The limited dispersal of adult *Scrobicularia plana* (Hughes 1970) implies, however, that the observed spatial patterns are unlikely to be a result of aggregative behavior of adults, but are instead caused by larval settling and post-settlement behavior (Underwood & Chapman 1996). Species with no (or short) pelagic stages tend to have strongly aggregated distributions as a result of low mobility, while a long pelagic phase allows the population to be distributed along a larger area (Johnson et al. 2001, Shanks et al. 2003). As the pelagic stage of *S. plana* can last for several weeks (Frenkiel & Mouza 1979), larvae should be able to disperse for distances of tens of km (Shanks et al. 2003), hence connecting the different patches. However, evidence is mounting that effective larval dispersal in marine populations is often limited (Cowen et al. 2000). As larvae are difficult to track directly, the extent of interpopulation connectivity can only be indirectly estimated using genetic methods. We have shown low interpopulation connectivity for *S. plana* (Santos et al. 2012), a strong indication of local larval retention.

In conclusion, the spatial distribution of *Scrobicularia plana* is site-specific rather than species-specific as a random distribution of *S. plana* is observed in

Norway, while populations from Portugal and the Netherlands show some degree of aggregation. Sediment composition is correlated to *S. plana*'s distribution in 2 of the sites, suggesting that it is an important factor influencing the species distribution. Therefore, at the local scale, aggregation patterns are greatly determined by abiotic factors, particularly sediment type which acts as a cue for larval settlement.

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