Fine-scale spatial structure of the exploited infaunal bivalve *Cerastoderma edule* on the French Atlantic coast

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ABSTRACT

Investigations of biomass, production, and anthropogenic impact require knowledge of the spatial distribution of the species concerned. Studies of the spatial distribution of soft-sediment infauna are inherently difficult, because the organisms are generally not readily visible, necessitating painstaking excavation. Although the large-scale (tens of km) distribution patterns of infaunal bivalves have been studied previously, the fine-scale (1 to tens of meters) has received much less attention. We investigated the fine-scale spatial distribution of the edible cockle *Cerastoderma edule* at a fishing-impacted site and a non-impacted site on an intertidal mudflat in Bourgneuf Bay, France, in 2009–2010. A preliminary study using a 1 m spatial lag was performed to determine the optimum lags for a nested sampling design. Cohorts were identified using Bhattacharya-resolved size-frequency distributions and verification of isotropy, and the spatial characteristics of each cohort were determined using Moran's *I* auto-correlation coefficient. The non-impacted site presented one strongly-aggregated main cohort, C3, (Moran's *I* = 0.67 to −0.34, spatial range 16 to 20 m, inter-patch distance 41 to 51 m). The impacted site presented two main cohorts, C2 (1.31 cm mean shell length, SL) and C3 (2.11 cm SL) both of which also showed a patchy spatial distribution (C2: Moran's *I* = 0.7 to −0.72, spatial range 22 to 35 m; inter-patch distance 63 to 90 m; C3: Moran's *I* = 0.41 to −0.63, spatial range 36 to 58 m, inter-patch distance not defined). The C3 cohort was less aggregated than the C2; possibly due to the homogenizing effect of fishing, which typically proceeds via a Lévy walk foraging model.

Our results show that the spatial distributions of *C. edule* retained a strongly aggregated character over the 8 months of the study, suggesting that these characteristics are powerfully maintained by recruitment/post-recruitment processes, despite intense fishing pressure throughout the sampling period, and indeed for decades, prior to this study. These data also show that we cannot assume a random or a regular spatial distribution for this species in studies of biomass, production, trophic relations, or anthropogenic impact; rather, close attention must be paid to the spatial characteristics of studied populations in order to reduce the confounding effects of auto-correlation.

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1. Introduction

Most ecological processes are spatially structured and scale-dependent (Legendre et al., 1997); consequently, spatial characteristics are an important component of the conceptual framework of contemporary ecology in general (Fortin and Dale, 2005), and of marine ecosystems in particular (Andrew and Mapstone, 1987; Thrush, 1991; Underwood et al., 2000). Spatial distributions usually present some degree of pattern, and the detection of such patterns is often highly scale-dependant (Bergström et al., 2002; Legendre and Fortin, 1989; Thrush, 1991; Thrush et al., 1994). Most studies of the spatial organization of endobenthic ecological processes have concentrated on large-scale spatial patterns, due to the conventional wisdom that spatial distribution, and notably the distribution of intertidal species, are controlled essentially by large-scale physical factors (see

review by Chapman, 2000; Warwick and Davies, 1977). Nevertheless, distinct ecological processes (such as inter- and intra-specific interactions) also operate at small scales, generating spatial patterns not revealed at the larger scales (Norkko et al., 2001; Thrush, 1991). It is therefore important to investigate ecological processes over a range of different scales (Dayton and Tegner, 1984; Levin, 1992; Morrisey et al., 1992; Powell, 1995; Wiens, 1989). However, studies on the spatial distribution of soft sediment fauna often do not adequately include all of the relevant spatial scales (Morrisey et al., 1992).

Although it is well-known that there is an element of patchiness in the spatial distribution of intertidal infaunal invertebrates (Honkoop et al., 2006; Sutherland, 1982a), relatively few studies have incorporated the fine-scale component in the spatial distribution of soft-sediment infauna (Bergström et al., 2002; Hewitt et al., 1997; Huxham and Richards, 2003; Morrisey et al., 1992; Schneider et al., 1997), which are usually dominated by polychaetes and bivalves. In temperate European waters, these habitats often contain populations of the edible cockle *Cerastoderma edule*, which are exploited by both professional and recreational fishers

(Dare et al., 2004; Ferns et al., 2000; Kaiser et al., 2001; Piersma et al., 2001). Several recent studies report on the large-scale distribution of *C. edule* (Kraan et al., 2009; Ponsero et al., 2009), and to our knowledge only one study has touched upon the natural fine-scale spatial distribution of *C. edule* (Huxham and Richards, 2003). Here we use spatial autocorrelation analysis (Fortin and Dale, 2005; Legendre and Legendre, 1998) to investigate (1) the fine-scale (1 m–300 m) spatial distribution of *C. edule*, (2) evaluate the effects of clam digging on the characteristics, and (3) the eventual temporal stability of the characteristics of this distribution, in a population located on the French Atlantic coast.

2. Materials and methods

2.1. Description of the study locations

The two study sites are situated in Bourgneuf Bay (Fig. 1). Bourgneuf Bay is characterized by a macrotidal semidiurnal regimen with a 6 m maximum tidal amplitude, high turbidity, annual mean water temperatures varying between 12.5 °C and 14.5 °C, and salinity from 29 to 31 (Dutertre et al., 2010).

It was not possible to choose the same location for both study sites, since all areas accessible on foot are susceptible to exploitation. We therefore chose one exploited site accessible on foot, and one unexploited site accessible only by boat. The intertidal sediment characteristics, immersion regimens, and salinity of the two sampling sites were quite similar. The unexploited site was located at 46°58′ 25″N, 002°11′ 010″W; it is hereafter referred to as the non-impacted site. The exploited study site (Passage du Gois) was located at 46° 55′15″ N, 2° 9′004″W, and is heavily fished by recreational clam diggers. Harvesting is manual, not only using standard regulation rakes, but also a variety of non-authorized gear.

2.2. Sampling dates

The study was conducted from December 2010 to August 2011. A pilot study was carried out at the non-impacted site on 6 and 7 December 2010 to determine the most appropriate sampling strategy for detecting fine-scale spatial processes. In total, 221 stations were sampled at the impacted site and 423 stations (including 160 points for the pilot study) were sampled at the non-impacted site. Subsequent samplings at the non-impacted site were conducted on 21 and 22 December 2010 and 3 and 4 January 2011, and the sampling was repeated eight months later on 18 August in order to establish whether the spatial distribution had changed significantly over time.

At the impacted site, fishing pressure is irregular throughout the year. Based on prior observation of fisher density on the mudflats, maximum fishing pressure is exerted from spring to autumn, especially during spring tides, school vacation periods (every 6 weeks in France), and is light to moderate during the winter. The first sampling of this site was carried out on 7 April 2011, and repeated on 2 and 3 May, after the spike in fishing activity over the Easter holiday period. The final sampling was performed on 19 August 2011.

It was not possible to visually assess cockle distribution for most of the year; however, on 18 and 19 August live cockles were visible at the surface of the sediments at both sites. This coincided with an extended period of high temperatures, and a decrease in the depth of the oxidized layer. It was thus possible to target cockle patches for spatial sampling at these sites on these dates.

2.3. Sampling strategy

Several parameters must be selected correctly in order to characterize a spatial pattern: sample size (number of sampling points), grain (size of the sampling unit) and spatial lag (distance between sampling points) (Dungan et al., 2002; Fortin and Dale, 2005). The minimum recommended sample size is 30 (Fortin and Dale, 2005; Legendre and Fortin, 1989), but a greater number of points may be needed to detect certain spatial processes, or, on the contrary, 20 points may be sufficient to capture spatial variability if the spatial pattern is very clear (Fortin and Dale, 2005). Our transects comprised at least 60 sampling points, with the exception of the August 19 sampling (26 points), due to
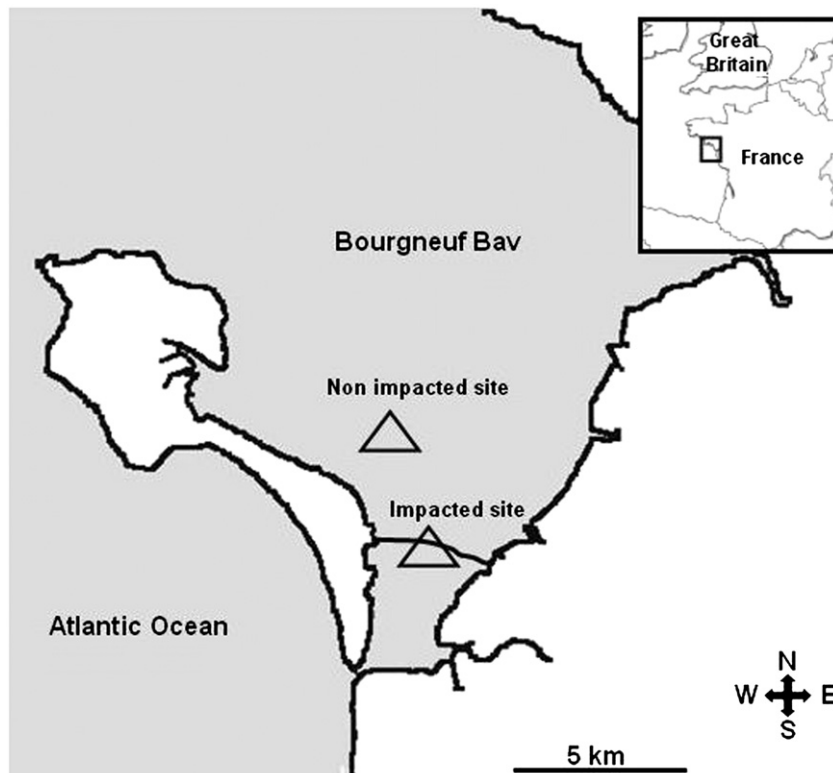

Fig. 1. Location of the two study sites in Bourgneuf Bay.

technical constraints (Table 1). The sampling grain was 0.1 m^2 (0.4 × 0.25 m), a size frequently used in benthic macrofaunal studies (McIntyre et al., 1984; Southwood and Henderson, 2000). The choice of spatial lag was more difficult because, to our knowledge, there are no firm data on the fine-scale spatial distribution of C. edule. Nevertheless, this choice is very important. If the spatial lag (inter-point distance) is too large compared to the patch size, the spatial distribution will appear to be uniform, even if in reality it is clustered (Fortin et al., 1989). The pilot study on 6 and 7 December 2010 was designed to determine the optimal trade-off between sampling effort and potential for identification of the spatial distribution. Samples were collected at 1 m intervals along two 80 m transects; one parallel to and one perpendicular to the tidal flow (160 sampling points). Based on these results, a 1 m lag nested within a 5 m lag, was used in the subsequent samplings.

At each site, perpendicular transects were sampled as above, in order to check for anisotropy (direction-dependent variation of spatial characteristics). At each sampling point, 0.1 m^2 of sediment × 15 cm depth was sieved through a 1 mm mesh. All live cockles were counted and their shell length was measured (anteroposterior axis) to the nearest 0.2 mm with vernier calipers to establish size-frequency distributions and subsequent cohort analysis.

2.4. Statistical analysis

The shell length data were divided into incremental 0.3 cm classes. Cohort analysis was performed by modal class progression analysis (FISAT software). The size-frequency distribution was decomposed into separate normal components as per Bhattacharya (1967), and refined using the NORMSEP method (Hasselblad, 1966; Pauly and Caddy, 1985), which is based on maximum likelihood estimation.

To define the strength of autocorrelation and to test its statistical significance, statistics that include information on the spatial locations of each sample point should be used (Dale et al., 2002). Two types of such spatial statistics are frequently used in ecology: the semivariance and Moran's I spatial coefficient (Fortin and Dale, 2005), the latter being an extension of the familiar Pearson correlation coefficient (Legendre and Legendre, 1998). The semivariance can be used to study processes that do not meet the assumption of second order stationarity, i.e. non-stationarity of the mean and variance (Glover et al., 2011). On the other hand, although Moran's I cannot be calculated for non-second-order stationarity processes, it is easily interpreted, it enables cross-comparisons with other studies (Kraan et al., 2009), and it can be tested for significance (Legendre and Legendre, 1998). To evaluate the spatial distribution of the cockles in this study, Moran's I spatial autocorrelation coefficient was chosen. All counts were transformed ($\log (x+1)$) prior to statistical analyses in order to satisfy both normality and second-order stationarity, and Moran's I autocorrelation coefficient was calculated for each distance class (Fortin and Dale, 2005; Legendre and Legendre, 1998) Before constructing the spatial autocorrelograms, the data were grouped into distance classes, and Moran's I autocorrelation coefficient was computed for each distance class (Dale et al., 2002). We followed the suggested procedure of Legendre and Legendre (1998): the choice of the number of distance classes was a trade-off between the resolution of the correlogram and the power of the test. Sturges' rule (Legendre and Legendre, 1998; Sturges, 1926) can be applied to approximately estimate the optimum number of distance classes: number of classes = 1 + 3.3 log (n), where n is the number of distances in half of a symmetric distance matrix. Two methods of establishing distance classes may be used: the equidistant approach, and the equal frequency approach (Fortin and Dale, 2005). In the present study, the equal-distance approach was used where the number of sampling points was sufficiently large; when the number was insufficiently large for this approach, we used the equal frequency method, in order to minimize information loss. In the latter case, the significance tests have the same power, even for the large distance classes (Legendre and Fortin, 1989; Legendre and Legendre, 1998). Moran's I varies from − 1 (negative autocorrelation) to + 1 (positive autocorrelation) (Legendre and Legendre, 1998).

To visualize the spatial autocorrelation, spatial correlograms were constructed by plotting the distance classes vs. the corresponding values of Moran's I (Fortin et al., 1989, 2002). The statistical significance of the value of Moran's I attained for each distance class was assessed by the Monte Carlo permutation test (Besag and Diggle, 1977; Diggle, 2003; Sawada, 1999). The null hypothesis was the absence of spatial autocorrelation, corresponding to the Moran's $I = -1/(n-1)$ which tends to zero as the sample size increases (Lichstein et al., 2002; Paradis, 2010; Zuur et al., 2007).

Although it has been argued that patch size (spatial range) should be set at the distance where the value of Moran's I corresponds to a random distribution, i.e. where the autocorrelogram crosses the expected value of Moran's I (at or near 0 for a large sample size − (Fortin and Dale, 2005), Kraan et al. (2009) suggested setting the patch size at the distance where the threshold value of Moran's I is 'biologically meaningful', for example 0.1. Nevertheless, by applying different threshold values of Moran's I, these authors showed that there is no difference in calculated patch sizes. In order to simplify the analysis of the correlograms, we therefore decided to set the spatial range at the distance that corresponds to the 0 value of Moran's I.

The potential presence of anisotropy was checked by constructing bearing correlograms for perpendicular directions (Perry et al., 2002; Rosenberg, 2000). When the spatial process was found to be isotropic, all-directional spatial autocorrelograms were calculated for the subsequent analyses. Bearings were obtained using a Silva forester's compass.

The shape of an autocorrelogram only provides information on average spatial pattern; autocorrelograms with similar shapes and spatial characteristics do not necessarily reflect geographical overlap in underlying spatial processes (Hewitt et al., 1996; Sokal and Oden, 1978), e.g. the distributions of cohorts C2 and C3. In order to verify this, the correlation in densities of C2 and C3 must be studied using the Pearson correlation coefficient. When studying the correlation between variables which are themselves spatially autocorrelated, standard statistical testing cannot be applied because the assumption of independence of samples is not respected (Fortin and Payette, 2002; Legendre et al., 2002; Liebhold and Sharov, 1998), resulting in an increased probability of Type I significance error (Fortin and Payette,

Table 1
Summary of sampling dates and corresponding spatial characteristics at the two study sites in Bourgneuf Bay. Normal type = C2 cohort, bold type = C3 cohort.

Date of sampling	Site	Number of sampling points	Cohorts	Mean density ± SE (m^{-2})	Spatial range (m)	Inter-patch distance (m)	Statistically significant Moran's I values, max and min
21,22 December 2010; 3,4 January 2011	Non impacted site	203	**C3**	**99 ± 77**	**20**	**41**	**0.67 to − 0.34**
18 August 2011	Non impacted site	60	**C3**	**85 ± 84**	**16**	**51**	**0.57 to − 0.31**
7 April 2011	Impacted site	106	C2	280 ± 156	22	68	0.47 to − 0.67
			C3	**54 ± 37**	**–**	**–**	**–**
2 and 3 May 2011	Impacted site	89	C2	167 ± 159	35	90	0.7 to − 0.72
			C3	**141 ± 122**	**58**	**–**	**0.41 to − 0.54**
19 August 2011	Impacted site	26	C2	223 ± 173	27	63	0.68 to − 0.73
			C3	**17 ± 21**	**36**	**–**	**0.41 to − 0.63**

2002). In some cases, when only one studied variable is auto-correlated, the classical correlation significance test can be applied (Lennon, 2000). However, in our study, both variables were spatially autocorrelated, so we used Dutilleul's modified *t*-test for a Pearson correlation coefficient, which adjusts the degrees of freedom according to the amount of autocorrelation in the data (Dutilleul, 1993; Legendre et al., 2002).

The statistical package PASSaGE (Pattern Analysis, Spatial Statistics and Geographic Exegesis) was used for all spatial analyses.

3. Results

All mean values are reported with standard deviations ($\pm$ SD).

3.1. Cohorts

At the non-impacted study site only one cohort with a mean size of 2.57 cm $\pm$ 0.280 (C3) was abundant enough to study its spatial distribution (See Fig. 2A).

At the impacted site, three cohorts were identified with mean lengths of 0.58 cm $\pm$ 0.150 (C1), 1.31 cm $\pm$ 0.159 (C2), and 2.11 cm $\pm$ 0.264 (C3) respectively (Fig. 2B). The latter two cohorts were abundant enough to assess their spatial distribution and to test the existence of autocorrelation in their distribution.

3.2. Isotropy

Sufficient numbers of cockles were found to enable verification of isotropy for the C3 cohorts at the non-impacted site and for the C2 cohort at the impacted site. The results of the perpendicular transect samplings revealed an isotropic spatial distribution at both sites (Fig. 3A, B).

3.3. Characteristics of spatial distribution — non-impacted site

Evidence of spatial pattern is deduced from both the Moran's *I* values and the shape of the correlogram (Legendre and Fortin, 1989). All values at the non-impacted site were statistically significant for all distance classes; although this in itself does not indicate biologically significant autocorrelation, especially in the case of the smallest Moran's *I* values, (due to the large number of pairs in each distance class), the shape of the autocorrelogram and amplitude of the Moran's *I* values (0.67 to $-$0.34) demonstrate very strong auto-correlation (Fig. 4A).

The observed spatial range at the non-impacted site was 20 m. The second peak of the correlogram, at a distance of 70 m, indicated that there was more than one patch detected within the sampled

Fig. 2. A. *Cerastoderma edule*, non-impacted site. Length-frequency distribution, December 2010–January 2011. B. *C. edule*, impacted site. Length-frequency distribution, April 2011.

area (Fortin and Dale, 2005). The distance between patches was approximately 41 m and the mean density of cockles was 99 $\pm$ 77 m^{-2}.

3.4. Characteristics of spatial distribution — impacted zone

For the site impacted by clam digging, it was possible to assess the spatial distribution of 2 of the 3 cohorts: C2 and C3 (insufficient N for C1 — Table 1, Fig. 2B).

The first sampling on the impacted site was carried out on 7 April 2011. As illustrated in Fig. 5A, the spatial autocorrelation coefficients were statistically significant only for the C2 cohort, with a spatial range of 22 m and an inter-patch distance of 68 m. The mean density of C2 cohort cockles was 280 $\pm$ 156 individuals m^{-2}. Moran's *I* values for the C3 cohort oscillated around zero and the mean density of cockles of this cohort was only 54 $\pm$ 37 individuals m^{-2} (Table 1).

For the samplings on 2 and 3 May 2011, both cohorts displayed spatial autocorrelation. The spatial autocorrelogram for C2 presents maximum and minimum Moran's *I* values of 0.7 and $-$0.72, and these were statistically significant for all distance classes except for the 7th and largest distance classes. The spatial range was 35 m, the inter-patch distance was 90 m, and the mean density ($\pm$ SD) was 167 $\pm$ 159 individuals m^{-2}. For the C3 cohort, significant positive autocorrelation occurred only in the first two distance classes, corresponding to a distance of 30 m; at approx. 80 m, the correlation became negative and statistically significant (Fig. 5B). The spatial range for C3 was 58 m. The absence of a second peak on the correlogram, indicates that the inter-patch distance was greater than the transect length (230 m). The mean C3 density was 141 $\pm$ 122 individuals m^{-2} (Table 1).

3.5. Temporal stability of spatial characteristics

The non-impacted zone was sampled 8 months later on 18 August. The spatial characteristics, i.e. patch size, the distance between patches, and amplitude of autocorrelation, remained quite similar to the results 8 months earlier: spatial range 16 m vs 20 m, inter-patch distance 51 m vs 41 m, and mean density 85 $\pm$ 84 individuals m^{-2} vs 99 $\pm$ 77 m^{-2}. The loss of statistical significance was due to fewer sampling points: 60 in August vs 203 in January (Fig. 4B).

At the impacted site, we were able to investigate the temporal stability of the spatial characteristics of two cohorts of *C. edule* (C2 and C3). The spatial autocorrelograms calculated for the impacted site on the sampling date of 19 August demonstrated significant spatial autocorrelation for the C2 cohort with a spatial range of 27 m, an inter-patch distance of 63 m and a mean density of 232 $\pm$ 173 m^{-2} (see Fig. 5C).

The analysis of the spatial pattern of the C2 cohort revealed very similar characteristics for the three sampling dates. The spatial range was 22 m, 35 m and 27 m, respectively, and the inter-patch distance was 68, 90, and 63 m, respectively. Moran's *I* autocorrelation coefficient was strong in all cases for most of the distance classes (Table 1).

The C3 distribution from the Aug 19 sampling was also spatially autocorrelated, but the spatial pattern was less conspicuous, due to the lower mean density (17 $\pm$ 21 m^{-2} vs 223 $\pm$ 173 m^{-2} for C2). The correlogram displayed statistically significant spatial correlation only at the smallest distance class (less than 20 m) with a value of Moran's *I* of 0.41, and statistically significant negative autocorrelation for the 5 and 6 distance classes between 50 and 75 m.

We were able to assess the temporal stability of spatial patterns for the C3 cohort for two sampling dates only (2–3 May and 19 August). The transects of 7 April were situated completely outside of C3 patches, the transects of 2 and 3 May were situated partially within patches (determined a posteriori from the data) as was the 19 August transect (determined a priori from the abundance of emerged cockles, see
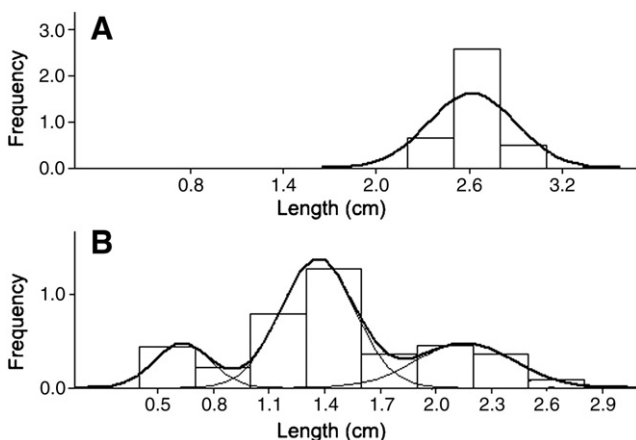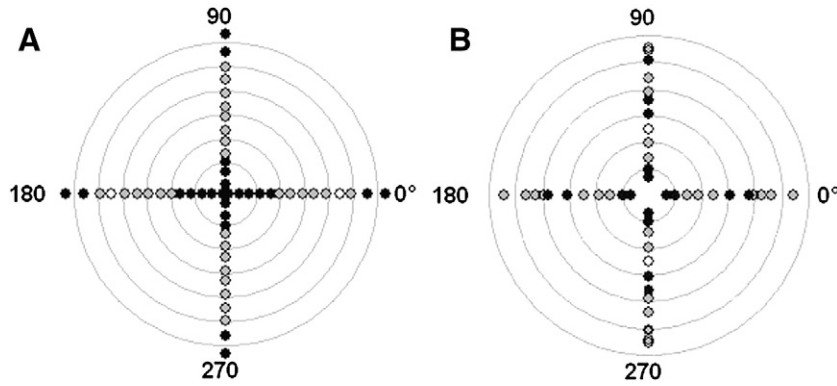
Fig. 3. A. *Cerastoderma edule*. Bearing correlogram for distribution of C3 cohort at the non-impacted site using 15 equidistant classes, December 2010–January 2011. B. Bearing correlogram for distribution of C2 cohort at the impacted site using 12 equidistant classes. Black circles indicate significant positive correlation; gray circles indicate significant negative correlation, white circles indicate statistically non-significant correlation. April 2011.

[Materials and methods](); it was thus possible to assess the spatial distribution of this cohort on these dates.

The spatial range was 58 m and 36 m, respectively, for two sampling dates. The distance between patches of the C3 cohort was not defined in any case because it was greater than our transects (maximal length of transects was 250 m).

3.6. Relationship between adults and juveniles

Despite the different spatial ranges of C2 and C3 for the 2–3 May sampling data, there was a significant correlation between the distributions (geographical overlap) of these two cohorts. Dutilleul's modified *t*-test showed a correlation coefficient of 0.63 with a conventional P value of 0.0002, and a spatial correlation-corrected P value of 0.03. Although a loss of statistical significance due to the reduced effective sampling size used in Dutilleul's modified *t*-test was noted, the correlation in the spatial distribution of juvenile and adult cockles remained significant.

The correlation in the spatial distribution of juvenile and adult cockles for the 19 August sampling data is not statistically significant.

The correlation between the spatial distributions of C2 and C3 was assessed at a correlation coefficient of 0.67 with a conventional P value of 0.00021; Dutilleul's modified *t*-test yielded a corrected P value of 0.14, thus there was a considerable loss of statistical significance.
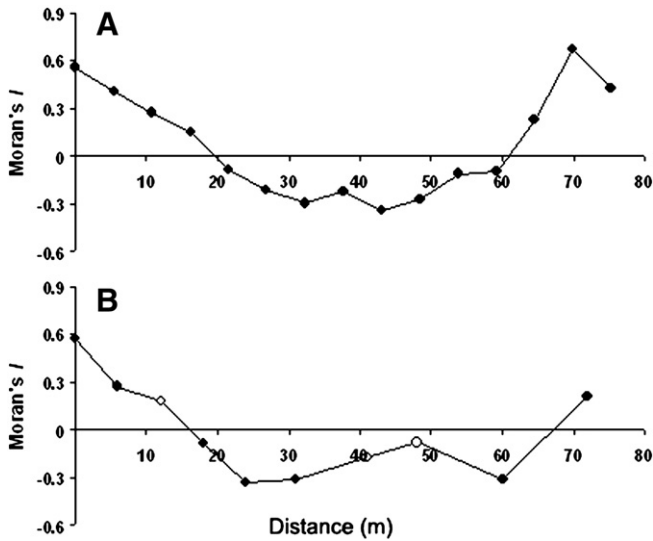

Fig. 5. A. *C. edule*. All-directional spatial autocorrelogram for cockle densities using 12 equidistant classes. Impacted site, 7 April 2011. C2 cohort is presented by solid line and circles; C3 by dashed line and triangles. Significant values are represented by black symbols; non-significant values are represented by empty symbols. B. *C. edule*. All-directional spatial autocorrelogram for cockle densities using 12 equidistant classes. Impacted site, 2 and 3 May 2011. C2 cohort is represented by solid line and circles; C3 by dashed line and triangles. Significant values are represented black symbols, and non-significant values are represented by empty symbols. C. *C. edule*. All-directional spatial autocorrelogram for cockle densities using 9 equidistant classes, Impacted site, 19 August 2011. C2 cohort is represented by solid line and circles; C3 by dashed line and triangles. Significant values are represented by black symbols, and non-significant values are represented by empty symbols.

Fig. 4. A. *Cerastoderma edule*. All-directional spatial autocorrelogram for cockle densities using 15 equidistant classes. Non-impacted site, December 2010–January 2011. Data grouped for all transects. Statistically-significant values are represented by black circles. B. *C. edule*. All-directional spatial autocorrelogram for cockle densities using 10 distance classes with an equal numbers of observations. Non-impacted site, 18 August 2011. Significant values are represented by black circles, and non-significant values are represented by empty circles.
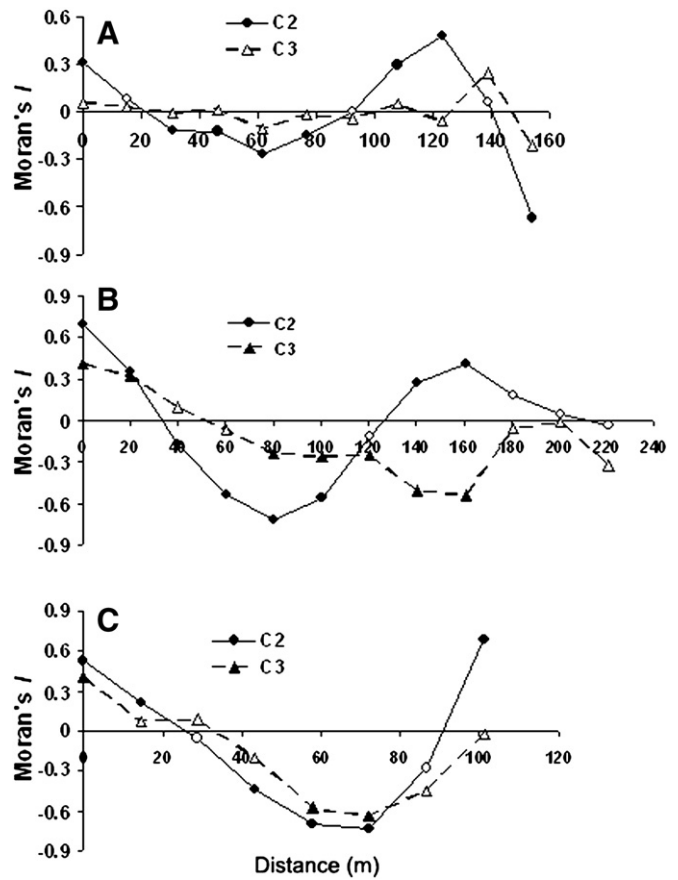
4. Discussion

4.1. Type of spatial distribution

The results of this study show that the spatial distribution of *C. edule* was clearly aggregated, with very similar fine-scale spatial patterns at both the non-impacted and impacted sites. The mean densities were spatially autocorrelated and statistically significant at a distance of <300 m, especially at distances between 0 and 60 m. These results are at variance with the assumptions of some previous studies, ie. that the fine-scale spatial distribution of suspension-feeding bivalves must be random, due to the absence of competition for food (Heip, 1975). Although Richardson et al. (1993) reported a random spatial distribution for *C. edule*, their study used a maximum scale of 1 m², which obviously could not detect patterns at larger (but nonetheless 'fine') scales such as the patterns observed in the present study (tens of meters). The results of the present study support and extend those of Huxham and Richards (2003) on a non-impacted *C. edule* population, which found one patch with a spatial range of 20 m². More definitive support for fine-scale spatial aggregation is provided when more than one such patch is identified, as was the case in the present study.

4.2. Temporal stability of spatial characteristics

The spatial characteristics, such as spatial range, inter-patch distance and the average density of cockles did not change substantially (there is no statistical test of significance for the former two characteristics) throughout the sampling period for the C3 cohort at the non-impacted site, and for the C2 and C3 cohorts at the impacted site. The maintenance of a grouped spatial distribution probably confers a reproductive advantage in non-motile, broadcast-spawning species (Coma and Lasker, 1997). The temporal stability of the fine-scale aggregated spatial patterns, observed in several bivalve species (Hewitt et al., 1996, 1997), and in the present study for adult cockles, may be partially explained by the limited locomotor ability of infaunal bivalves (Norkko et al., 2001; Richardson et al., 1993).

4.3. Influence of fishing pressure on C. edule spatial distribution

Of the cohorts observed at this site, only the largest, C3, could be directly impacted by recreational clam diggers. Despite the legal minimum size limit of 2.7 cm for *C. edule*, enforcement is largely lacking (Maison, 2009), such that most of the C3 cohort is subject to fishing pressure.

The Moran's *I* values and the correlogram for the C3 cohort on 2 and 3 May and 19 August show that fishing pressure tends to homogenize the spatial distribution of the C3 cohort compared to the C2 cohort, as well as to the C3 cohort at the non-impacted site (visual comparison of correlograms). Such homogenization cannot be the product of spatially-uniform fishing pressure, which would tend to accentuate existing spatial heterogeneity (Kawata et al., 2001).

Most top predators, including humans, unconsciously adopt a Lévy type foraging strategy, rather than a uniform search strategy (Viswanathan et al., 2011). For example, oystercatchers are able to discriminate the areas of highest cockle density and feed mostly in these areas (Sutherland, 1982b). Predators moving randomly in the absence of visible patches, but displacing directly to patches when they are detectable, are likely to follow a Lévy search pattern (Elliott et al., 2009). Ship-based fishers also adopt a 'Lévy walk' search strategy (Bertrand et al., 2005; Marchal et al., 2007). Brown et al. (2007) have shown that human hunter-gatherers employ a Lévy flight behavior, similar to that of the Lévy walk. It is thus likely that clam diggers also adopt this foraging strategy, and therefore more intensively fish the areas of high cockle density. This type of fishing pressure tends to homogenize the existing spatial structure,

and may have repercussions on subsequent population dynamics (de Roos et al., 1998).

The fine-scale spatial aggregation of broadcast spawner species enhances gamete encounter probabilities and improves spawning synchrony (Pennington, 1985; Stokesbury and Himmelman, 1993; Young et al., 1992); this has been successfully modeled (Claereboudt, 1999). Since the reproductive success of broadcast spawning species depends, at least partly, on the density of adult individuals (Levitan et al., 1992) it would be worthwhile to investigate the effect of spatial homogenization on population reproductive success.

Although the number of C2 clams at the non-impacted site was too small to allow analysis, the aggregated character of their spatial distribution at the impacted site appears to be little affected by clam digging or associated trampling. This may be due to the limited damage to (Kaiser et al., 2001), and rapid re-burrowing ability of, small-sized cockles rejected on the sediment surface by diggers (McLaughlin et al., 2007) which protects them from being transported by tidal currents (Stanley, 1998) or from being consumed by scavenging birds (Coffen-Smout and Rees, 1999). This finding is in line with that of Rossi et al. (2007), which showed that trampling does not appear to modify the abundance of small-sized cockles.

4.4. Relationship between adults and juveniles at the impacted site

The observed patch size of the C3 cohort for every sampling period was always larger than that of the C2 cohort; this difference could be due to the homogenization effect of fishing pressure, as mentioned above.

With respect to the possible relation between adult and juvenile spatial distributions, a significant positive correlation was found for the 2 and 3 May samplings, but not for the 19 August sampling. The lack of positive association on this latter date may be due to the fact that strongly autocorrelated variables reduce the power of Dutilleul's modified test. In such a case, a sample size of at least 100 points is recommended (Legendre et al., 2002), whereas for the 19 August sampling, there were only 26 sampling points. This number was sufficient to characterize the spatial pattern of the patches which were visible on that date, but insufficient for Dutilleul's modified test, which reduced the effective sampling size from 26 to 7, resulting in loss of statistical significance. Where the sampling size was sufficiently large, therefore, the correlation analysis demonstrated the existence of a positive correlation between juvenile and adult *C. edule* fine-scale spatial distributions.

The formation of spatial patterns of adult and juvenile cockles is determined by two major factors: the recruitment rate and post-settlement processes. Attempts to quantify the relative importance of these two factors have produced conflicting results. Ólafsson et al. (1994) suggest that post-recruitment interactions may be more important than recruitment for population organization. This hypothesis drew support from field experiments where no statistically-significant correlation between adult cockle densities and settlement rate was found (de Montaudouin and Bachelet, 1996), except when recruitment could be depressed by high adult suspension-feeding bivalve densities (*C. edule* and *Mya arenaria* — André and Rosenberg, 1991; Bachelet et al., 1992). However, the lack of knowledge regarding fine-scale spatial distribution could be a confounding effect in these studies (David et al., 1997).

Several studies have shown the ability of juvenile *C. edule* and other infaunal bivalves to migrate over long distances by thread drifting after primary settlement (Armonies, 1994a, 1994b; Beukema, 1993; Commito et al., 1995; de Montaudouin and Bachelet, 1996); indeed, this may even be a regular mechanism of mass migration and secondary recruitment (Beukema and de Vlas, 1989). Larval behavior may favor the establishment of aggregated distributions, e.g. positive and negative attraction to adults, to already-settled juveniles, or chemical cues from potential food or habitat sources (Huxham, and Richards, 2003; Ólafsson et al., 1994; Richards et al., 2002; Thrush et al., 1996).

4.5. Importance of fine-scale spatial distribution in ecological studies of the mudflat habitat

The analysis of spatial autocorrelation in the study of ecological processes is crucial, and when it is ignored (as is often the case), the data generated can be very misleading, and even contrary to the real state of the process or the real causal associations (Kühn, 2007; Lennon, 2000). This can lead to the creation of a false hierarchy of explanatory factors of ecological processes determined by, but not recognized as due to, spatial autocorrelation strength (Lennon, 2000). Even a spatially-nested sampling design cannot completely mitigate this problem, so it is imperative to include spatial analysis in the study (Legendre and Fortin, 1989). Prior knowledge of spatial autocorrelation can significantly improve field sampling design, by using a computer-intensive genetic algorithm (Ver Hoef, 2012). The results of the present study could thus help to design more accurate methods of biomass and production estimations for *C. edule* and other endobenthic bivalve species (in preparation).

Beyond improvements in study techniques, the analysis of infaunal bivalve fine-scale spatial distribution has obvious and important consequences for studies of biomass, production, and anthropogenic impact. Of particular interest is the effect of fine-scale spatial distribution of infaunal bivalves on trophic relationships in the mudflat ecosystem, notably with respect to shorebird predation (Sutherland, 1982b; Wahl et al., 2005).

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