Effect of long-term mechanical perturbation on intertidal soft-bottom meiofaunal community spatial structure

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ABSTRACT

Situated at the interface of the microbial and macrofaunal compartments, soft-bottom meiofauna accomplish important ecological functions. However, little is known of their spatial distribution in the benthic environment. To assess the effects of long-term mechanical disturbance on soft-bottom meiofaunal spatial distribution, we compared a site subjected to long-term clam digging to a nearby site untouched by such activities, in Bourgneuf Bay, on the Atlantic coast of France. Six patterned replicate samples were taken at 3, 6, 9, 12, 15, 18, 21 and 24 cm lags, all sampling stations being separated by 5 m. A combined correlogram–variogram approach was used to enhance interpretation of the meiofaunal spatial distribution; in particular, the definition of autocorrelation strength and its statistical significance, as well as the detailed characteristics of the periodic spatial structure of nematode assemblages, and the determination of the maximum distance of their spatial autocorrelation. At both sites, nematodes and copepods clearly exhibited aggregated spatial structure at the meso scale; this structure was attenuated at the impacted site. The nematode spatial distribution showed periodicity at the non-impacted site, but not at the impacted site. This is the first explicit report of a periodic process in meiofaunal spatial distribution. No such cyclic spatial process was observed for the more motile copepods at either site.

This first study to indicate the impacts of long-term anthropogenic mechanical perturbation on meiofaunal spatial structure opens the door to a new dimension of mudflat ecology. Since macrofaunal predator search behaviour is known to be strongly influenced by prey spatial structure, the alteration of this structure may have important consequences for ecosystem functioning.

1. Introduction

To date, the vast majority of the soft-bottom meiobenthic literature has dealt with descriptive aspects of the constituent taxa. Despite the paucity of ecological knowledge, however, there is nonetheless an awareness of the ecological importance of soft-bottom meiofauna to the marine ecosystem (Danovaro et al., 2007; Nascimeto et al., 2012; Pati et al., 1999; Watzin, 1983), especially in the intertidal, where meiobenthic populations are most abundant and productive (Giere, 2009; Vincx, 1996; Vranken et al., 1986). In particular, benthic meiofauna represent an important food source for higher trophic levels, to which more than 75% of their total production may be transferred (Danovaro et al., 2007). Due to their small size, high turnover and high abundance, meiofaunal organisms also constitute efficient environmental sentinels (Coull and Chandler, 1992; Moreno et al., 2008a, 2008b).

Given the ecological importance of soft-bottom meiofaunal communities, a research priority is the characterization of their spatial distributions, one of the fundamental features of community organization (Fortin and Dale, 2005; Legendre and Fortin, 1989; Legendre and Legendre, 2012; Underwood and Chapman, 1996). The characteristics of the spatial distribution of meiofauna are still poorly documented, but several studies have highlighted a heterogeneous distribution at various scales of study (Blanchard, 1990; Eckman and Thistle, 1988; Gallucci et al., 2009; Hulings and Gray, 1976; Sandulli and Pinckney, 1999). Understanding of these characteristics has begun to deepen with the development and utilisation of modern geostatistical techniques (Blanchard, 1990; Gallucci et al., 2009; Pinckney and Sandulli, 1990; Sandulli and Pinckney, 1999; Sun and Fleeger, 1991), such that it is now possible to more fully investigate meiofaunal spatial distribution at various scales and to turn our attention to the factors which may influence spatial distributions. Anthropogenic effects include mechanical perturbation, e.g. by fishing gear, whose effects on benthic macrofauna have been documented over the past few decades (Hermsen et al., 2003; Kaiser et al., 2001; Lambert et al., 2011; Thrush and Dayton, 2002; Thrush et al., 1998; Whomersley et al., 2010). To our knowledge, no studies have yet addressed the question of the effects of mechanical disturbance on meiofaunal spatial organization, and in particular the effects of protracted fishing in the intertidal zone, such as clam digging on soft-bottom intertidal zones in Europe, which has been practiced at least since the Neolithic (Dupont and Gruet, 2005).

As there is some heterogeneity in the definition of the various scales of study, we have adopted the following terminology with respect to

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meiofauna: fine scale <3 cm, meso-scale <50 cm, large scale >50 cm. In the present study, we document the natural meso-scale spatial distribution of meiofauna on an intertidal mudflat on the French Atlantic coast. We also present the meso-scale spatial distribution of meiofauna on an intensely-fished intertidal mudflat, in order to obtain an indication of potential changes associated with long-term perturbation.

2. Materials and methods

2.1. Study locations and sampling dates

In order to investigate the effect of long-term intertidal clam fishing on associated meiofauna, it was of course necessary to investigate soft-bottom intertidal sites which were comparable in most respects except for anthropogenic impact. Ideally, in a study of the eventual ecological impact of intertidal fishing, several impacted sites should be compared with several non-impacted sites, to control for site-specific effects. However, in ecosystem effect studies, especially those on the effect of 'press' perturbation in strongly anthropized ecosystems, it is sometimes impossible to find a single non-impacted site (Brown and Herbert Wilson, 1997). The only possible solution in this case is to carry out a comparison between sites with different levels of perturbation. The number of sites with a low perturbation level may also be insufficient to make a true replication, as in Aspden et al. (2004). When replication is not feasible but the effect size is assumed to be large, clear demonstration of this effect may be considered an indication of real effect (Cleary, 2003; Oksanen, 2001).

Despite the ubiquitous intertidal fishing on the French Atlantic coast, in the present study we were able to locate a site which was not fished intertidally because it was not accessible on foot, and it was too small to be profitably fished by professional clam diggers. We thus compared a fishing-impacted site with a non-impacted site.

The two study sites were located in Bourgneuf Bay on the French Atlantic coast (Fig. 1). The abiotic characteristics of the two intertidal mudflats were quite similar (Table 1), characterized by a semidiurnal macrotidal cycle, high turbidity, seasonally variable water temperatures (4.4 °C to 20.4 °C), and seasonally variable salinity (30 to 31). Sediment profiles were obtained from 5 sediment cores to a depth of 5 cm, using laser granulometry and Gradistat software, using the size scale of Bott and Pye (2001); both sites were characterized by medium sand sediment, with very little difference in profile (Table 1). The impacted study site, situated at 46.929°N, 2.115°W, has been heavily exploited year-round by recreational clam diggers since the 1990s (Hitier et al., 2010) and probably since the construction of a submersible paved road in 1939 and the end of WWII. A succinct description of fishing

Table 1
Characteristics of two investigated sites and sediments.

Characteristics	Non-impacted site	Impacted site
Temperature	4.5 – 24.5 °C	4.5 – 24.5 °C
Salinity	30–31	30–31
Depth (m)a	3.1	3.0
Sediments		
Mean diameter µm	374.5 ± 25.7	426 ± 21.9
Sorting	Moderate	Moderate
Sediment fractions %		
Mud (<63 µm)	1.4 ± 0.3	0.7 ± 0.2
V. fine sand (63 µm – 125 µm)	1 ± 0.5	0 ± 0.3
Fine sand (125 µm – 250 µm)	25.2 ± 10.1	14.2 ± 8.6
Medium sand (250 µm – 500 µm)	50.4 ± 8.4	55.4 ± 6.5
Coarse sand (500 µm – 1 mm)	22 ± 13.2	29.5 ± 9.7

[a] Depth at high tide, coefficient 120 (http://www.geoportail.gouv.fr).

methods is given in Cosqueric-Boldina (2011) and Boldina and Beninger (2013). The non-impacted site was located nearby at 49.973°N, −2.1861 °W, and was accessible only by boat, and thus out of the reach of recreational clam diggers; it is classified as a non-exploited site (Hitier et al., 2010).

Sampling was conducted at two low tides on 21 (impacted site) and 22 March (non-impacted site) 2012.

2.2. Sampling strategy

2.2.1. Terminology

The vocabulary of spatial analysis has been developed in two different disciplines, forestry and geology (Perry et al., 2002), so there is some instability in terminology (Fortin and Dale, 2005). To avoid confusion, the following terms will be used throughout:

Spatial lag - the distance between any two points
Sample lag - the distance between two sampling points. Sample lags are decided prior to the study, and do not change thereafter.
Distance class - a mathematical construct obtained from the data after the study, in order to produce the best possible resolution correlograms.
Spatial process - the biological process which produces an observed spatial pattern
Spatial pattern - the distribution of individuals in a given space, usually "…a 'single realization' or 'snapshot' of a process or of a combination of processes at one given time" (Fortin et al., 2002).

Preliminary trials using a multiple corer at the impacted site failed to properly sample sediment; we therefore decided to sample at both sites using individual corers, which performed flawlessly. In addition, preliminary trials of samplings at increasing distances from an initial sampling showed that nematode escape (burrowing) behavior was extremely rapid, but could be avoided by ensuring a distance of 5 m between sampling stations (unpublished data available on request). We therefore approached sampling sites as quickly and noiselessly as possible (long, low strides, minimum benthic-pedal surface contact), and sampled the sediment immediately upon arrival. Six samples were collected simultaneously by 3 human samplers using 2 cm diameter plastic tube cores to a depth of 5 cm. Although the anoxic-sulfide zone (black sediment) was located within 1–2 cm of the sediment surface, the 5-cm depth was chosen in order to ensure maximum capture, including any escaping nematodes (Fegley, 1987). The following sample lags were used: 3, 6, 9, 12, 15, 18, 21, and 24 cm (Fig. 2). This sampling scheme was repeated 6 times, separated by 5 m intervals, for each distance class, for a total of 288 sediment cores at each site (Fig. 2). The total sampled area was 11 m².
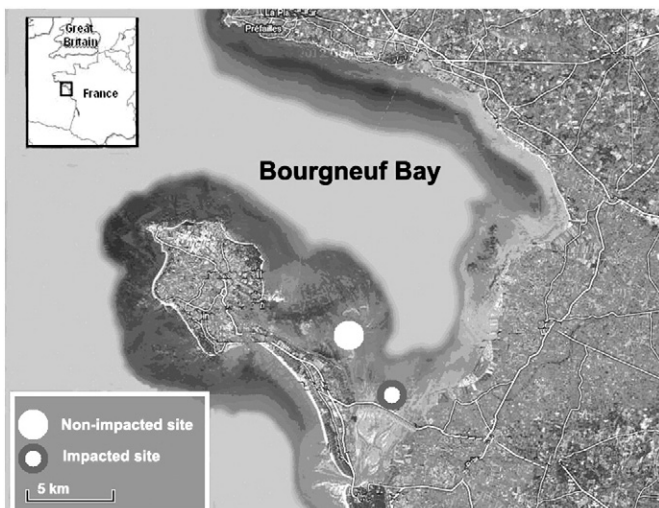

Fig. 1. Location of the two study sites in Bourgneuf Bay.

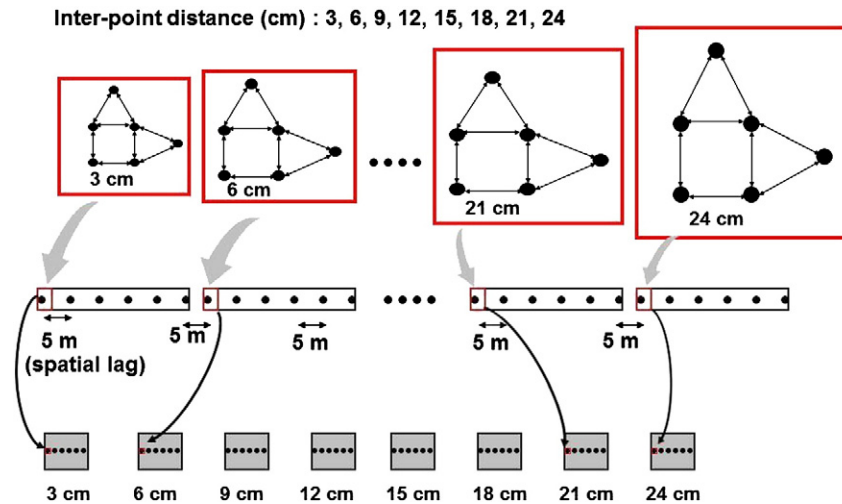**Inter-point distance (cm) : 3, 6, 9, 12, 15, 18, 21, 24**

Fig. 2. Meiofauna sampling protocol.

2.3. Extraction - identification

The entire sediment core was immediately fixed in 4% buffered formaldehyde–seawater solution. The sediments were later rinsed with tap water (previously checked for absence of meiofauna). The fraction remaining on a sieve of 63 μm mesh size was decanted and the meiofauna extracted from the sediment by centrifugation with Ludox HS 40®, density 1.15. The centrifugation was repeated twice (at 1300 g for 8 min and 5 min); with a measured efficiency of ≥ 97% (verified prior to the counting procedure). The extracted meiofauna were stored in 4% buffered formaldehyde–seawater solution, stained with Rose Bengal, and the number of nematodes and copepods (by far the dominant taxa) was counted in a transparent counting cell (110 x 600 mm, containing 200 cells) using an Olympus SZX7 stereo-microscope. Taxonomic determinations at lower levels were not performed, since this would reduce the number of individuals for each sampling point, and hence the statistical power of spatial tests (Fortin and Dale, 2005), and because we aimed to document community spatial distributions, rather than community compositions.

2.4. Statistical analysis

At present, the semivariance and Moran's *I* autocorrelation coefficient are the most widely-used spatial statistics tools in ecology (Fortin and Dale, 2005). The mathematical background for these techniques is described in Haining (Haining, 2003), Fortin and Dale (2005), and (Legendre and Legendre, 2012). Briefly, Moran's *I* measures the similarity between two values of the same variable, and the semivariance measures the dissimilarity. A plot of Moran's *I* coefficients vs distances separating the measures (lag distance) is referred to as a correlogram, whereas a plot of semivariance versus lag distance is called an experimental semivariogram or variogram.

The correlogram and variogram methods are complementary; under certain conditions we can consider correlograms and variograms as different descriptions of the same thing. The main assumption for the use of correlograms is second-order stationarity, i.e. the mean and variance remain constant over the entire study area (Fortin and Dale, 2005; Legendre and Legendre, 2012). The correlogram shape indicates the patch sizes and the spatial lags with negative and positive autocorrelation.

Moran's *I* can also be tested for significance (Legendre and Legendre, 2012), and permits comparisons between different data sets (Kraan et al., 2009). However, this method can be greatly biased by the presence of outliers (Fortin et al., 2002).

Contrary to correlograms, variograms can be computed for spatial processes that only satisfy the intrinsic hypothesis, i.e. the mean is constant over the study area, and the increment of variance between two different locations depends only on the distance between locations (Oliver et al., 1989), which is a less restrictive assumption than second-order stationarity (Fortin et al., 1989). Furthermore, the theoretical variogram obtained by modelling the experimental variogram allows us to predict the spatial structure of unsampled areas of the studied space.

For some kinds of data, correlograms and variograms can be different (Schiemann et al., 2010), and this is especially true when the spatial process lacks second-order stationarity. Hence, simultaneous use of correlograms and variograms yields a more exact description of the spatial structure (Rossi et al., 1992), and this approach was followed in the present study. Omnidirectional spatial autocorrelograms were used to evaluate the strength of autocorrelation and to compare the patch sizes at both study sites. The statistical significance of the value of Moran's *I* attained for each distance class was assessed using the Monte Carlo permutation test (Besag and Diggle, 1977; Diggle, 2003); in the absence of information on the consequences of false positive/negative results, an α level of 0.05 was chosen for all significance tests (Beninger et al., 2012). H_0 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; Zuur et al., 2007). We set the spatial range (patch size) at the distance that corresponded to the 0 value of Moran's *I* (Fortin and Dale, 2005; Sandulli and Pinckney, 1999). Addition of diagonal distances for each sampling lag results in a wider range of possible 'distance classes' (3 – 33.9 cm), which were used in statistical analysis and results presentation. The distance classes were chosen as explained in Boldina and Beninger (2013).

The experimental variograms were normalized by the global variance in order to permit comparisons between sites (Khachatryan and Bisgaard, 2009). The resulting standardized experimental variograms were fitted by a theoretical model using ordinary least squares. The model with the lowest Akaike Information Criterion (AIC) value was considered the best-fitting variogram model (Akaike, 1981; Burnham and Anderson, 2002). The parameters for this model were estimated using the maximum likelihood approach (Diggle et al., 2003): the sill S (the asymptotic variance to which the function tends with increasing lag distance), the range r (distance at which the theoretical variogram reaches the sill, i.e. the distance beyond which the measured variable is no longer autocorrelated) and the nugget (variations at scales smaller than sample distances, and also the measurement error) (Rossi et al., 1992). Three theoretical models were initially tested: Gaussian, spherical, and exponential.

In cases where the experimental variogram presented periodic structure, i.e. the variance oscillated about the sill as a sine-wave, the hole-effect model was applied. The most often-used variogram model for describing the dampened-hole effect (when peaks and troughs alternate and attenuate gradually) is a multiplicative exponential–cosine composite model (Li et al., 2011; Ma and Jones, 2001; Pyrcz and Deutsch, 2003) which is a product of cosine and exponential functions and is expressed as:

$$\gamma = S\left(1 - exp\left(\frac{-3h}{r}\right)\cos(bh)\right)$$

Where γ is the semivariance, h: the distance, r: the range, S: the sill, and b: the angular frequency (b $= 2\pi/\lambda$, where λ is the wavelength). The cosine term describes cyclicity and the exponential term attenuates sinusoidal amplitudes. The exponential–cosine composite model was fitted as described in Ma and Jones (2001).

All statistical analyses were performed in R (2008) software.

3. Results

3.1. Characteristics of nematode spatial distribution

Nematodes on both impacted and non-impacted sites showed strong spatial autocorrelation (Fig. 3). Moran's *I* values for the nematodes of the non-impacted site oscillated between 0.4 and −0.22, presenting three distinct peaks, indicating the presence of several patches within the sampling area (Fortin and Dale, 2005). Moran's *I* values were statistically significant for the 1st, 4th, and 5th distance classes. The patch size was 7.9 cm, the inter-patch distance between 4 and 7 cm, and the mean density ($\pm$SD) was 185 $\pm$ 86 individuals cm^{-2}.

For the nematodes of the impacted site, the spatial autocorrelation was statistically significant only for the 1st distance class, although the values of Moran's *I* autocorrelation coefficient remained rather high and varied between 0.31 and −0.2. The loss of statistical significance may have been due to the reduced mean density at the impacted site. The patch size was 16.9 cm, the inter-patch distance 8 cm, the mean density ($\pm$SD) was 162 $\pm$ 50 individuals cm^{-2}.

The experimental variogram for nematode density at the non-impacted site shows strong cyclicity beginning at 8 cm, with attenuated amplitude at increasing lag distances (Fig. 4). The best-fitted theoretical model for this variogram is a combination of an exponential model, representing the variability at small distances, and the exponential–cosine composite model representing the cyclic variation at distances greater than 8 cm:

$$\gamma = \begin{cases} 0.29 exp\,(0.085h) & if \ \ h{<}8 \\ 0.1 + 1.05\left(1 - exp\left(\frac{-3h}{85}\right)\cos(1.025h)\right) & if \ \ h{\geq}8 \end{cases}$$
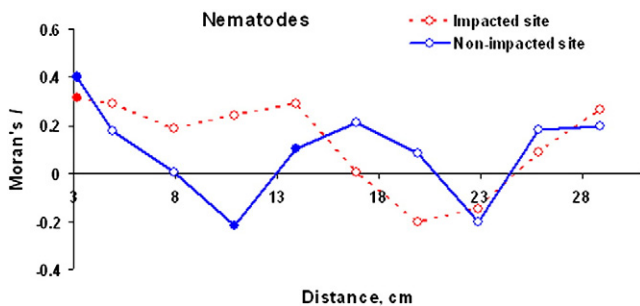
Fig. 3. Omnidirectional spatial autocorrelogram for nematode densities using 10 equidistant classes. Significant values are represented by solid symbols; non-significant values are represented by empty symbols.
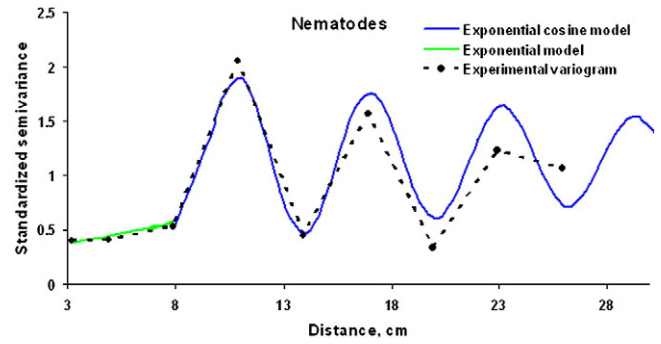
Fig. 4. Nematodes, non-impacted site. The standardized experimental variogram is presented by the dashed line and circles, the exponential model by the solid green, the exponential-cosine composite model by the solid blue line.

Where the sill is 1.05, the range 85 cm, and the angular frequency 1.025.

The experimental variogram for nematode density at the impacted site does not present the cyclic behavior described above, and the AIC shows that it is best explained by the Gaussian model:

$$\gamma = c + (s-c)\left(1 - \exp\left(\frac{-3h^2}{r^2}\right)\right)$$

Where the nugget c $= 0.42$, the sill s $= 1.207$, the range r $= 22.1$ cm, and h is the distance (Fig. 5).

The difference in spatial structure is clearly evident in the two variogram models presented in Fig. 6. The variograms for both sites present a noticeable nugget effect, i.e. there is spatial autocorrelation at distances smaller than our minimum scale (diameter of each sampling point, i.e. 2 cm).

3.2. Characteristics of copepod spatial distribution

The spatial distribution of copepods at the non-impacted site demonstrated significant autocorrelation (Fig. 7). The Moran's *I* auto-correlation coefficient varied between 0.05 and 0.89, with no negative values over the total sampling distance of 25 cm, which means that there was a single patch, with a size greater than the total sampling distance. Moran's *I* values were statistically significant for all but the first, the third and the last distance classes. The mean density ($\pm$SD) of copepods at the non-impacted site was 28 $\pm$ 15 individuals cm^{-2}.

The Moran's *I* values for copepods at the impacted site were not statistically significant for any distance class. It should be noted that the autocorrelation was negative for the first distance class, and increased subsequently. The mean density ($\pm$SD) of copepods at the impacted site was 22 $\pm$ 13 individuals cm^{-2}.
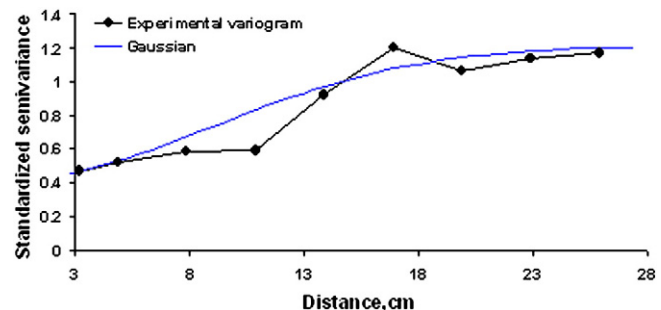
Fig. 5. Nematodes, impacted site. Standardized experimental variogram is represented by dashed line and circles, gaussian model by solid line.
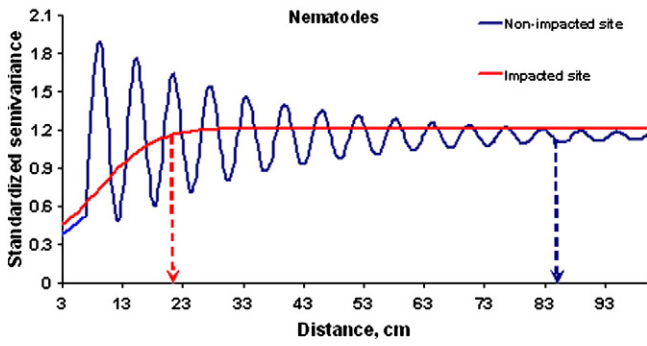
Fig. 6. Variogram models of nematode density vs distance (extrapolated) for the non-impacted and impacted sites.

The variograms for copepods are not presented, since they do not provide any additional information.

4. Discussion

4.1. Non-impacted site

The results of the present study show that nematodes and copepods clearly exhibit aggregated spatial structure at the meso-scale. These results are in accordance with previous studies that have demonstrated the presence of spatial aggregation at fine- (<3 cm) and meso-scales (<50 cm) (Blanchard, 1990; Blome et al., 1999; Gallucci et al., 2009; Johnson et al., 2007 and Sandulli and Pinckney, 1999). Taken together with the results of the present study, the emerging pattern from spatial distribution studies in mudflats, using contemporary autocorrelation techniques, is that despite the apparent homogeneity of the habitat, organisms are distributed aggregatively, at several scales of distance and organism size (Bergström et al., 2002; Boldina and Beninger, 2013; Hewitt et al., 1996; Kraan et al., 2009; Legendre et al., 1997).

Periodic spatial processes have frequently been reported in terrestrial systems (Ciollaro and Romano, 1995; Cohen et al., 1990; Curran, 1988; Iwasa et al., 1991; Pastor et al., 1998), but spatial process cyclicity has received much less attention in marine ecology (Blome et al., 1999; Rossi et al., 1992). Ignoring the presence of cyclicity may bias the resulting spatial models (Jones and Ma, 2001; Journel and Froidevaux, 1982; Journel and Huijbregts, 1978; Pyrcz and Deutsch, 2003), with significant implications for sampling design. A spatial process similar to the periodic spatial structure of nematode assemblages at the non-impacted site has previously been either inadvertently reported (Blanchard, 1990; Gallucci et al., 2009; Sun and Fleeger, 1991), or incompletely alluded to without modelling (Blome et al., 1999). The exponential–cosine composite model suggests that aggregation at the

meso-scale dampens progressively, beyond the meso-scale, to a distance of 85 cm. For the first distance classes, the experimental variogram is better modelled by an exponential variogram, characterised by near-linear behaviour close to the origin. Such cyclical structure in a spatial model indicates the presence of cyclicity in the underlying spatial process (Chou, 1995; Legendre and Fortin, 1989; Radeloff et al., 2000; Rossi et al., 1992).

Contrary to the nematodes, the copepod spatial aggregation was not periodic at the scale of the study, and only one patch, larger than the sampling distance, was detected (see above). This finding supports previous reports of a larger size of benthic copepod patches compared to nematode patches (Blanchard, 1990; Gallucci et al., 2009).

The spatial aggregation of meiofauna has been attributed to various factors such as: the complex spatial patterns of food resources of meiofauna and the attraction of the meiofauna by them (Blanchard, 1990; Fabiano and Danovaro, 1999; Gallucci et al., 2009; Gerlach, 1977; Neira et al., 2001; Ólafsson, 1992; Rice and Lambshead, 1994; Ullberg and Ólafsson, 2003), aggregation for reproduction (Steele et al., 2009), and foraging behavior of predator species (Lion and Van Baalen, 2008). In addition, weak re-suspending benthic-interface currents do not hinder the formation of spatial patches, because the re-settlement of marine nematodes is not a passive process (Gingold et al., 2011; Ullberg and Ólafsson, 2003). The more motile copepods may be more affected by wave- and current-induced dispersal processes, especially since they actively emerge from the benthos (Commito and Tita, 2002; Teasdale et al., 2004; Vopel and Thistle, 2011), and this may explain why their patches were larger than those of nematodes.

4.2. Impacted site

Nematodes at the impacted site had a larger aggregation structure than nematodes at the non-impacted site (patch size 16.9 cm vs. 7.9 cm). Additionally, the periodic behaviour observed for the nematode distribution at the non-impacted site was absent at the impacted site; in fact, the spatial characteristics were so greatly impacted that a Gaussian variogram model (parabolic behavior for the first distance classes and smoothly augmented variance for the larger distance classes) replaced the exponential/exponential–cosine composite model which characterized the non-impacted site. The attenuation of aggregative structure, as well as the lack of cyclicity observed at the impacted site, suggests that long-term mechanical perturbation via clam digging affects spatial aggregative characteristics at the meso-scale.

With respect to the meiofaunal copepods, a reduction in auto-correlation strength was also observed at the impacted site, again suggesting an effect of long-term clam digging.

Although previous studies have described the negative impact of mechanical disturbance on meiofaunal density which, contrary to the macrofauna, is rather quickly established after short-term mechanical perturbation (Bolam et al., 2006; Ingole et al., 2005; Johnson et al., 2007; Sherman and Coull, 1980; Whomersley et al., 2009), no data has been available to date on the possible effects of long-term mechanical perturbation on meiofaunal spatial structure. Clam digging may attenuate the spatial aggregation of meiofauna due to acute mechanical disturbance and re-suspension, and subsequent inability of the meiofauna to settle close to its original location. Indeed, marine nematodes have been shown to be passively transported over large distances (to tens of meters) after energetic re-suspension (Gingold et al., 2011). Other characteristics of the meiofaunal community, such as taxonomic composition, are known to be impacted by natural or anthropic mechanical disturbance (Fiordelmondo et al., 2003; Schratzberger et al., 2002; Tita et al., 2000); the consequences of either type of alterations cannot yet be assessed from a standpoint of adequate knowledge of the functional roles of each taxon in the benthic community. However, for such small, non-broadcast-spawning organisms, spatial aggregation is clearly advantageous for sexual reproduction; in turn, spatial aggregation of meiofaunal prey is clearly advantageous for their macrofaunal predators,
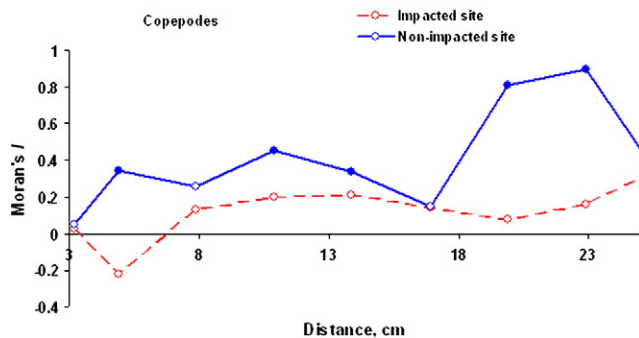

Fig. 7. Omnidirectional spatial autocorrelogram for copepod densities using 9 equidistant classes. Significant values are represented by solid symbols; non-significant values are represented by empty symbols.

which may exhibit a Levy walk-type predation strategy (Viswanathan et al., 2011). An attenuation of this spatial aggregation may therefore impact both meiofaunal population dynamics and trophic transfer to higher levels of the mudflat ecosystem.

4.3. Implications for sampling in meiofaunal studies

The present study demonstrates that despite apparent habitat homogeneity, mudflat meiofaunal organisms were distributed aggregatively, and sometimes periodically, at the meso-scale. These results have important consequences for sampling design, which in turn greatly influences estimates of biomass and production at larger scales (Chapman and Underwood, 2008). The conventional wisdom of spatial sampling design is that sampling variance decreases with the size of the sampling gear; hence, it has been suggested that in order to avoid bias from small-scale patchiness, the surface of meiofaunal sampling gear should be greater than the patch size (Giere, 2009). However, based on the data of the present study (autocorrelation persisting up to 80 cm at the meso scale), the sampling gear would have to be unrealistically large. A more realistic option would be to use either a blocked design (Dutilleul, 1993) or the genetic algorithm method (Ver Hoef, 2012) which, although requiring prior knowledge of the approximate patch size (the results of the present study may be used as a reference point) does not require the use of unwieldy or unrealistic sampling gear.

From the data of the present study, it is clear that the necessary integration of the spatial component into the study of meiofaunal ecology (e.g. to determine total meiofaunal biomass or production on a mudflat) requires a re-thinking of how we perform meiofauna sampling. The guidelines presented above are meant to assist in this effort.

4.4. Effect of fishing on meiofauna spatial distribution

The results of the present study describe not only the meso-scale spatial characteristics of meiofaunal communities which are not subjected to long-term anthropogenic mechanical perturbation, but also pinpoint the alterations of these characteristics in communities which are exposed to such perturbation: decreased aggregation and disappearance of cyclicity. These results underscore the need to more fully understand the effect of intertidal fishing (which is often the least-regulated form of fishing) on the ecology of meiofauna, and indeed, on the dependent higher trophic levels of mudflats.

Acknowledgments

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