

Fine-scale spatial distribution of the temperate infaunal bivalve *Tapes* (= *Ruditapes*) *philippinarum* (Adams and Reeve) on fished and unfished intertidal mudflats

Peter G. Beninger*, Inna Boldina

Laboratoire de Biologie Marine, Faculté des Sciences, Université de Nantes, 2, rue de la Houssinière, 44322 Nantes Cedex France



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ABSTRACT

Temperate intertidal mudflats are important to both human and nonhuman foragers, the former for professional and recreational clam fishing, and the latter for food, especially for migratory shorebirds. Foraging strategy and success will depend to a large degree on the spatial distribution of the infaunal prey, which is very poorly-known at the scale at which these foragers exploit the resources. We characterized the fine-scale spatial distribution of the bivalve *Tapes philippinarum* on a chronically-fished and on an unfished (reference) mudflat, using autocorrelation, variogram, and fractal analyses. Two cohorts were identified at each site: one sub-legal and one legal size. Although both cohorts were clearly aggregated at the scale of ≤ 130 m, this aggregation was greatly attenuated at the fishing-impacted site, and most severely for the fished-size cohort. The fractal dimensions of the cohorts at the two sites corroborated the decreased spatial structure at the fishing – impacted site, and in particular for the fished-size cohort. Together with similar observations for other components of this mudflat ecosystem, these results underscore the need to incorporate the spatial aspect in assessments of both organism (prey or resource) distribution, its relationship to foraging strategies, and the effect of intertidal fishing on these processes.

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1. Introduction

There is increasing awareness of the importance of spatial structure in population and community ecology (Fortin et al., 2002; Legendre and Legendre, 2012). Ecological processes occur within a spatially-ordered context, and failure to properly take account of spatial structure can generate misleading data and erroneous conclusions (Kühn, 2007; Lennon, 2000). In particular, spatial structure is critical to understanding predator–prey relations (Benoit-Bird and McManus, 2012; Benoit-Bird et al., 2013a; Humphries et al., 2010; Reynolds and Rhodes, 2009; Sims et al., 2008).

The geo-statistical techniques available for the study of spatial structure are widely used in the fields of geology and forestry, yet they are much less familiar in marine ecology (Boldina et al., 2014). The few marine studies were initially concentrated on benthic spatial structure, especially on the very 2-dimensional intertidal mudflat habitat (Blanchard, 1990; Guarini et al., 1998; Kostylev and Erlandsson, 2001; Seuront and Spilmont, 2002; Weerman et al., 2011), although recent work has begun to extend this to 3 and 4-dimensional contexts (Benoit-Bird and McManus, 2012; Benoit-Bird et al., 2013a,b).

Initial studies in benthic marine spatial ecology focused on large-scale spatial structure, i.e. hundreds of meters or kilometers (Andrew and Mapstone, 1987; Kraufvelin et al., 2011; Legendre et al., 1997; Underwood et al., 2000). However, recent studies support early work which showed that spatial patterning is evident at scales closer to the size of the organisms studied, e.g. meters or tens of meters for macroscopic organisms, and centimeters for meiotic organisms (Blanchard, 1990; Boldina and Beninger, 2013; Boldina et al., 2014; Guarini et al., 1998; Seuront and Spilmont, 2002). In microphytobenthic communities, such patterning has been hypothesized to be the result of self-organization (Seuront and Spilmont, 2002; Weerman et al., 2010), and to be important for basic ecological processes such as feeding, reproduction, recruitment, and competition (Boldina and Beninger, 2013; de Jager et al., 2011) in marine animals. In particular, migratory shorebirds depend to a variable degree on infaunal bivalve resources (Beninger et al., 2011), and are considered to be sentinel species of environmental status (Huettmann and Czech, 2006; Piersma and Lindström, 2004).

To date, although fine-scale spatial studies on mudflats have covered the major ecological components of these ecosystems (Blanchard, 1990; Boldina and Beninger, 2013; Boldina et al., 2014; Guarini et al., 1998; Weerman et al., 2010), they are few in number, such that the knowledge base lacks sufficient depth to draw more general conclusions (Kraufvelin et al., 2011). Additionally, recent evidence suggests that

* Corresponding author.

E-mail address: Peter.Beninger@univ-nantes.fr (P.G. Beninger).

anthropogenic perturbation affects spatial patterning (Boldina and Beninger, 2013; Boldina et al., 2014), underscoring the need for further study.

The present work examines the fine-scale spatial structure of the Japanese littleneck clam, *Tapes* (= *Ruditapes*) *philippinarum*, on an intertidal mudflat subjected to long-term fishing pressure (and associated mechanical perturbation), as well as on a reference mudflat unaffected by clam fishing. A combined approach, using nested sampling, correlograms, variograms, and fractal analysis was used to obtain the most complete spatial characterization possible.

2. Materials and methods

2.1. Taxonomic clarification

Despite much meticulous research, the taxonomy and phylogenetic relations of the Veneroidea are neither completely resolved nor completely consensual (Bernard, 1983; Chiamenti, 1900; Costello et al., 2001; ITIS, 2014; Megerle, 1811; Mikkelsen et al., 2006; Philippi, 1836; WoRMS, 2013). Since it is necessary to designate the species of study, and since nomenclature of the Veneroidea in general, and this species in particular, are variously confused issues, it is first necessary to clarify the taxonomic situation.

Whether using morphological or molecular characters, classifications are always informed judgement calls, which may, and often are, disputed. These matters are either settled de facto by the emergence of a dominant name in the literature (appropriate or not), or remain unsettled due to the persistence of competing names. Such is the case for the species of the present study, for which an exhaustive list of scientific synonyms may be found in Fischer-Piette and Métivier (1971). There are several confounding issues in the nomenclature of this species, dating back to confusion in original descriptions by Linnaeus himself (recounted in Fischer-Piette and Métivier (1971)), concerning very subjective assessments of occasional internal shell color and anterior shell shape (and here compounded by an apparent error on the part of Fischer-Piette and Métivier themselves, mistaking the Latin *antice* – anterior – for the French ‘*arrière*’ – posterior). For the purpose of the present study, suffice it to say that there are two main issues with respect to the generic name, of which three versions are current: *Tapes*, *Ruditapes*, and *Venerupis* (Costello et al., 2001; ITIS, 2014; WoRMS, 2013). The first is whether the genus *Tapes* (as originally described in Megerle (1811)) is monophyletic (Bernard, 1983), whether it contains the subgenus *Ruditapes* (as may be surmised from Chiamenti (1900), who described *Ruditapes* as ‘*Appartengono a questa sezione quei tapes a superficie ruvida*’), or whether, beyond this greater external shell rugosity (*rudi* = rough), *Ruditapes* is a distinct genus, based on hinge characters (as in Fischer-Piette and Métivier (1971)).

The second major confounding issue with respect to the generic name is the confusing use of *Venerupis* (from *Venus* + *rupis* = rock Venus), listed on the Encyclopedia of Life website as the only ‘trusted’ name. On the contrary, it is without doubt the most questionable and least-suited generic name, because it firmly associates this genus with rocks, and, in particular, to a rock-boring life habit (originally placed in the Family ‘*Lithophaga*’ (Philippi, 1836)), which is absolutely erroneous for this sediment-dwelling species. Furthermore, there is additional confusion between the *Venerupis decussata* and the *Venus decussata* of Philippi (1836), which, although placed in different families, are undoubtedly different morphotypes of the same species. Moreover, this biologically-inappropriate genus name is clearly a minority appellation in the literature (Fischer-Piette and Métivier, 1971), and has been little used, and hence poorly-recognized, for decades.

With respect to the species name, it is possible that the Pacific species *philippinarum* was originally mistaken for the Atlantic *Venus decussata* by Linnaeus (Fischer-Piette and Métivier, 1971), such that the first reliable description of it as *philippinarum* was by

Adams and Reeve (in Gray et al., 1850), who maintained the generic name *Venus*. Of the specific synonymies compiled in Fischer-Piette and Métivier (1971, pp 32–33), it should be noted that *philippinarum* appears to be the dominant appellation.

In view of the foregoing, and since it is necessary to identify this species in some way (preferably the most appropriate), we have chosen the lesser of all the aforementioned evils, eschewing the very problematic generic name *Venerupis*, and using the readily-recognizable binomen *Tapes philippinarum*, while indicating the current competing generic synonym *Ruditapes*, and leaving the question of whether it really is a separate genus to the delight of future taxonomists. We further indicate the original authority Adams and Reeve (in Gray et al., 1850), following the rule of assigning authority to the first describers, regardless of the name used by them.

Tapes philippinarum was introduced for aquaculture in France in 1972, and quickly supplanted the slower-growing native *Tapes decussatus*. It was extensively sown on natural mudflats, eventually dominating the venerid fauna of these habitats and becoming a main target species for intertidal clam fishing (Gouletquer, 1997; Hitier et al., 2010). It was the only species encountered at the two sites of the present study.

2.2. Study locations and sampling dates

The two study sites are located in Bourgneuf Bay on the French Atlantic coast, and have been described in Boldina and Beninger, 2013 and Boldina et al., 2014. The reference and the fishing-impacted sites were very similar in immersion regimes, sediment granulometry, temperature, and salinity. Although the primary objective of the present study was to determine whether *T. philippinarum* presents non-random spatial patterning within the relatively uniform mudflat habitat, the fact that virtually all sites accessible on foot are subject to clam fishing, presented the opportunity to compare the two types of sites. Although ideally, several impacted sites should be compared with several non-impacted sites, to control for site-specific effects, 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 Wilson, 1997). 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, thus eliminating recreational fishers, and too sparsely-populated by target species to be profitable for professional clam diggers. *Since when within-study 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), we thus compared a heavily fishing-impacted site with a non-impacted (reference) site.

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 methods is given in Boldina and Beninger (2013) and Cosquerie-Boldina (2011). The reference site was located nearby at 49.967°N, 2.152°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 on the impacted site was conducted on 3 May 2011 after the spike in fishing activity over the Easter holiday period. Sampling on the reference site was carried out on the following day, 4 May 2011.

2.3. Sampling strategy

Several parameters must be selected correctly to characterize a spatial pattern: sample size (number of sampling points), sampling grain (size of the sampling unit) and spatial lag (distance between sampling points) (Dungan et al., 2002; Fortin and Dale, 2005). As a starting-point, we chose the same spatial parameters as for *Cerastoderma edule* (Boldina

and Beninger, 2013): the sampling grain was 0.1 m² (0.4 × 0.25 m), a size frequently used in benthic macrofaunal studies (McIntyre et al., 1984; Southwood and Henderson, 2000). Although the minimum number of sampling points necessary to capture the spatial structure is 20, a greater number of sampling points may allow finer resolution, especially in cases where the spatial pattern is not very clear. The number of sampling points need not be the same for all sampling sites (Fortin and Dale, 2005). In total, 96 stations (= sampling points) were sampled at the reference site and 89 stations were sampled at the impacted site.

The same sampling strategy was used for both sites. Samples were collected using an iterative scheme of 5 m, then 1 m intervals. Transects were performed 100 m from low water mark. At each sampling station, 0.1 m² of sediment was excavated with a spade to – 15 cm, immediately sieved through a 1 mm mesh and put in containers for subsequent counting and size determinations.

2.4. Biometric measurements

To determine whether any eventual spatial patterning was age-specific, each sampled individual was measured along the maximum antero-posterior axis to the nearest 0.2 mm using Vernier calipers, for subsequent cohort analysis. A total of 2763 individuals were sampled and measured.

2.5. Statistical analysis

2.5.1. Cohort analysis

Deconstruction of sample size distributions into age classes (cohort analysis) was achieved using mixtures of probability distributions (Hasselblad, 1966). In the resulting probability density histograms, the area of each bar represents the probability density of each size class. The entire histogram has a total surface area of 1.

Cohort analysis was performed with the R package ‘mixtools’ (Benaglia et al., 2009). The size distribution was decomposed into separate normal components using the Iterative Expectation Maximization (IEM) algorithm (Benaglia et al., 2009).

2.5.2. Autocorrelation analysis

Plots of Moran's/autocorrelation coefficient vs lag distance (= correlograms), are frequently used in spatial ecology because they are relatively easy to interpret (although care must be taken to remain within the constraints of the technique), and in particular, they allow determination of patch size and inter-patch distance, as well as being amenable to significance testing (Fortin and Dale, 2005; Legendre and Legendre, 2012). To construct the autocorrelograms, we used the same distance classes as for the variograms. The patch size was determined as the distance corresponding to 0 value of Moran's *I* (Fortin and Dale, 2005; Sandulli and Pinckney, 1999).

2.5.3. Variogram analysis

Variogram analysis is one of the most widely-used spatial statistic tools in ecology (Fortin and Dale, 2005). The mathematical background for these techniques is described in Haining (2003); Fortin and Dale (2005), and Legendre and Legendre (2012). Briefly, the semivariance measures the dissimilarity between two values of the same variable (i.e. evaluation of the degree of spatial dependence between measurements). An experimental semivariance is defined as:

$$\gamma(h) = \frac{1}{2N(h)} \sum_{i=1}^{N(h)} [Z(x_i) - Z(x_i + h)]^2$$

where $\gamma(h)$ is the semivariance, h is the lag distance between sampling points, $Z(x)$ is the number of individuals in the location x , $N(h)$ the number of pairs separated by distance h .

Among the uses of variogram analysis, a plot of semivariance versus lag distance (i.e. experimental semivariogram or variogram) enables the subsequent calculation of fractal dimensions, as outlined below (Kiinkenber, 1994).

2.5.4. Fractal dimension

The fractal approach is very useful in the analysis of spatial structure, because (1) it can be applied across all spatial scales and (2) it characterizes the spatial distribution with a single parameter independent of the magnitude of the measured variable (here, the density of organisms) (Burrough, 1981; Davies and Hall, 1999; Pitt and Ritchie, 2002).

A variety of methods exist for estimating the fractal dimension (Kiinkenber, 1994). The choice of methods is somewhat arbitrary, but depends to a certain extent on the nature of the data (Kenkel and Walker, 1993). In the present work we used the semivariogram method (Mark and Aronson, 1984), which is considered both reliable and consistent (Gneiting et al., 2012; Kiinkenber, 1994). The fractal dimension was calculated from the slope of a double logarithmic plot of the semivariance, $\gamma(h)$, versus the lag distance, h . Distance classes were spaced evenly, in order to avoid the post-log transformation scatter of data points (Kiinkenber, 1994). Only the linear portion of the log–log variogram (i.e. the distance at which autocorrelation is present, Fig. 4) was used for calculating the fractal dimension (Burrough, 1986; Carr, 1995; Seuront, 2010), using the formula:

$$D = 2 - S/2,$$

where S is the slope estimated from the log–log plot of the experimental variogram.

All statistical analyses were performed in R (2008) software. A frequentist-type NHST approach (see Beninger et al., 2012) is used to determine statistical significance of the graphical point values and slopes, as well as the fractal dimensions; in the absence of any previous, independent information on the consequences of a Type 1 error for the type of context of this study, we chose an $\alpha = 0.05$ level to indicate a sufficiently high probability that a given result is close to the true state. Given the nature of spatial correlograms, characterized by decreasing reliability with increasing distance, power calculations were not considered useful, and indeed, the correlogram shapes and statistical significance at $\alpha = 0.05$ of the point values, support this reasoning.

3. Results

3.1. Demographic structure of *T. philippinarum*

The deconstructed cohorts are shown in Fig. 1 for each site (mean $L \pm SD$, since the parameter of interest is dispersion about the mean (Beninger et al., 2012)). Two cohorts were identified at the reference site: 2.17 ± 0.2 cm (C2) and 3.29 ± 0.28 cm (C3) (Fig. 1. A). At the impacted site, three cohorts were identified: 1.35 ± 0.47 cm (C1), 2.46 ± 0.19 cm (C2), and 3.29 ± 0.28 cm (C3) respectively (Fig. 1. B). The latter two cohorts were abundant enough to allow statistical characterization of their spatial distribution (i.e. when organizing the data for calculation of distance classes, there were few or no zero-values).

3.2. Autocorrelation analysis

3.2.1. Reference site

The shape of the autocorrelograms and the amplitude of the Moran's *I* values (0.6–0.5 for C2 and 0.57–0.53 for C3, Fig. 2. A) demonstrated strong spatial autocorrelation. Moran's *I* autocorrelation coefficient was statistically significant for most distance classes. The patch size was approximately 38 m for C2 and 27 m for C3. The presence of the second peak on both correlograms indicates that

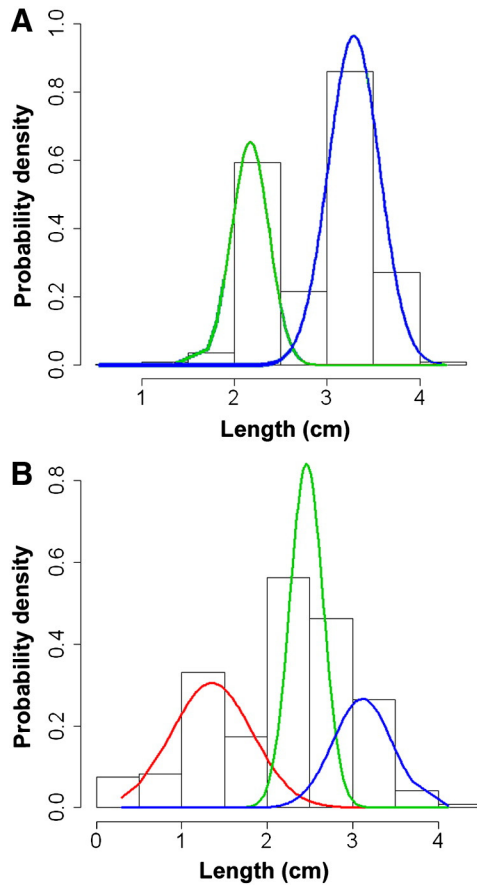


Fig 1. *Tapes philippinarum*. Length - probability density distributions. A. Reference site. B. Impacted site.

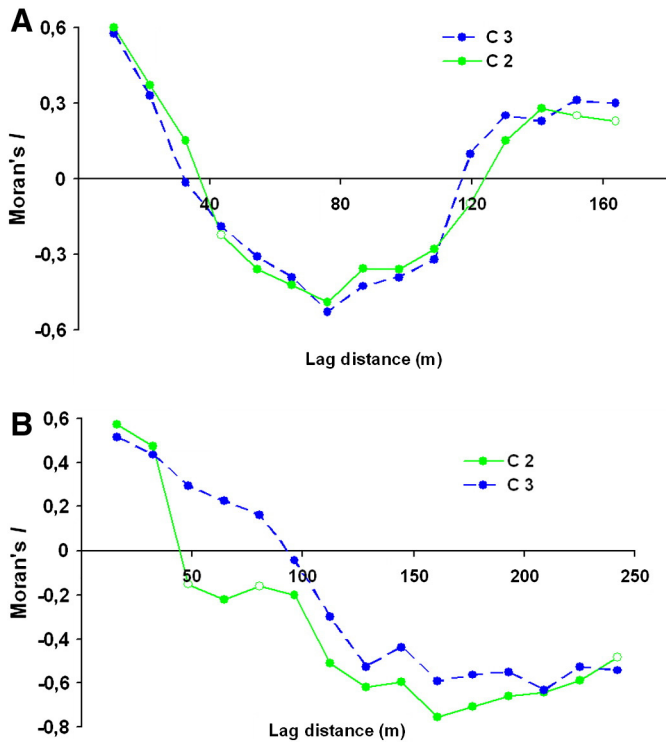


Fig 2. Spatial autocorrelograms for *T. philippinarum* densities. A. Reference site. B. Impacted site. C2 is presented by solid line, C3 by dashed line. Significant values are represented by solid circles, non-significant values are represented by empty circles.

there was more than one patch detected within the sampling transects. The observed inter-patch distances were almost identical for C2 and C3: 87 and 86 m, respectively.

3.2.2. Impacted site

The amplitude of the Moran's *I* values (0.57–0.76 for C2 and 0.5–0.63 for C3) demonstrated strong spatial autocorrelation. The patch size was approximately 45 m for C2 and 86 m for C3. The absence of a second peak on the correlograms indicates that the inter-patch distance was greater than the lengths of the transects (Fig. 2. B).

3.3. Variogram analysis and fractal dimension

3.3.1. Reference site

The points used for the calculation of fractal dimension from the variogram are shown in Fig. 3.

The spatial structure of *T. philippinarum* showed strong scaling behavior over the range < 80 m ($R^2 = 0.99$ and 0.98 for C2 and C3 cohorts respectively). A statistically significant difference of slopes of regression lines of the log-log plots of semivariance vs lag distance was not detected. In fact, the fractal dimension was nearly identical for both cohorts: 1.65 for C2 and 1.64 for C3 (Fig. 4).

3.3.2. Impacted site

The spatial structure of *T. philippinarum* showed scaling behavior over the range < 125 m ($R^2 = 0.97$ and 0.95 for C2 and C3 cohorts respectively) (Fig. 6). The points used for the calculation of fractal dimensions from the variogram are shown in Fig. 5. The resulting fractal dimensions were 1.78 (C2) and 1.83 (C3) (Fig. 6).

The fractal dimensions of C2 and C3 cohorts were significantly higher for the impacted site compared to the reference site (covariance analysis, $F = 65.08$, $P = 6E - 06$ and $F = 75.62$, $P = 2E - 06$ respectively) indicating that the spatial structure of the C2 and C3 cohorts at the impacted site was more homogeneous than that of the reference site. Furthermore, there was a much greater difference between the fractal dimensions of the sub-legal (C2) and legal – size cohorts (1.78 vs 1.83), compared to the nearly identical fractal dimensions of the reference site (1.65 and 1.64).

4. Discussion

T. philippinarum showed a clearly aggregated spatial distribution for both sites at distances < 130 m. Not surprisingly, this result contradicts the 'random' 2-dimensional spatial distribution previously reported for *T. philippinarum* (Lee, 1996), using the highly inadequate variance:mean method (Dale et al., 2002; Hurlbert, 1990). Aggregative prey spatial distributions can have effects disproportionate to the biomass of organisms in them, underscoring the importance of their detection and characterization in ecological studies (Benoit-Bird and McManus, 2012).

The high values of Moran's *I* autocorrelation coefficient for *T. philippinarum* on the impacted site fail to tell the complete

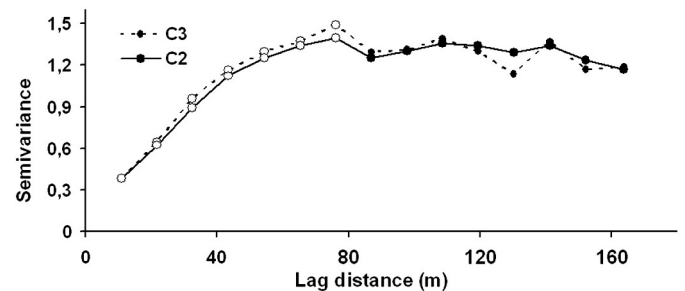


Fig 3. *Tapes philippinarum*, reference site. Experimental variograms for C2 and C3 cohorts. Open circles show the points used for calculating the fractal dimension.

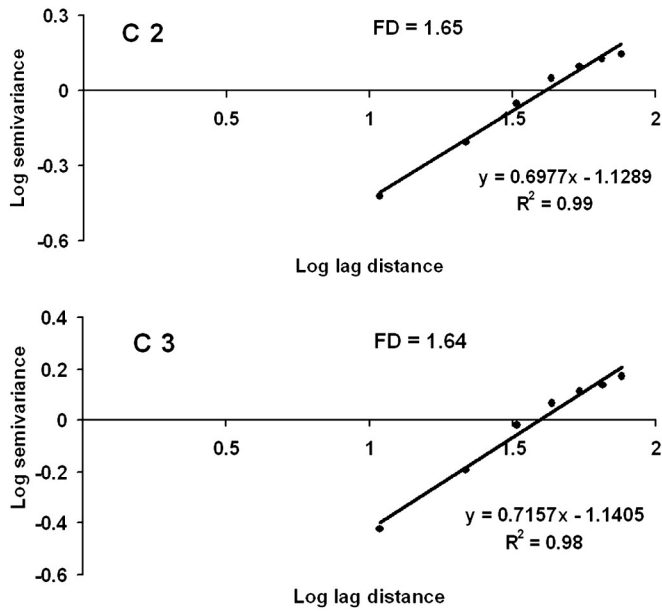


Fig 4. *Tapes philippinarum*, reference site. Variogram data on log-log scale for C2 and C3 cohorts. FD, fractal dimension.

story. The patch number was reduced within the transects studied, and patch size increased with respect to the reference site, especially for the fished – size C3 cohort (86 vs. 27 m), indicating an attenuation of aggregation in the *T. philippinarum* spatial distribution at the fishing-impacted site, especially for the fished-size C3 cohort, compared to the reference site.

Although fractals are typically associated with self-similarity, the fractal dimension, here derived from the variograms, is also a particularly informative descriptor of the degree of structural order (Davies and Hall, 1999; Gneiting et al., 2012; Seuront, 2010). A highly-ordered spatial structure may be of two very different types: an aggregative pattern, and an inhibition (i.e. regular) pattern.

The strength of the fractal dimension is a useful indicator of the degree of order in this pattern, with a minimum possible value of 1 (minimum occupied space, highly ordered structure) and 2 (maximum occupied space, total absence of spatial structure). A value of 1.5 denotes ideal self-similarity (identical repeating pattern) at all scales. The values of 1.64 and 1.65 at the reference site indicate a relatively high level of spatial organization, whereas the greater values of 1.78 and 1.83 at the fishing-impacted site clearly illustrate degradation in the aggregative spatial structure.

Real natural objects and processes rarely show fractal behavior over all scales, but rather over a restricted range of scales. Nevertheless, estimation of the fractal dimension over that limited range of scales is useful and informative, as it reflects the real properties of the process

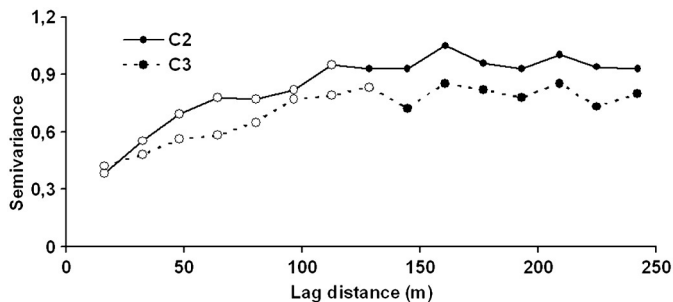


Fig 5. *Tapes philippinarum*, impacted site. Variogram data on log-log scale for C2 and C3 cohorts. Open circles show the points used for calculating the fractal dimension.

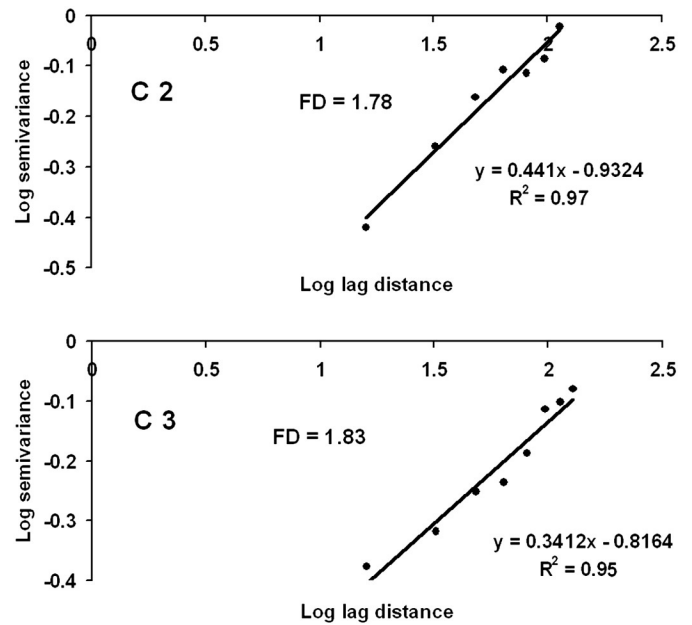


Fig 6. *T. philippinarum*, impacted site. Variogram data on log-log scale for C2 and C3 cohorts. FD, fractal dimension.

(Avnir et al., 1998; Bradbury et al., 1984). In the present study the fractal behavior is observed at scales < 130 m.

Although large-scale patterns are essentially structured by abiotic factors (Barry and Dayton, 1991), processes operating on small scales, throughout larger scales, may also influence spatial distribution at the larger scales (Thrush et al., 1997). This is likely to be the case for the species studied here, given the extent of intertidal clam fishing on the French Atlantic coast (up to 380% increase for some sites from 1997 to 2009 – (Hitier et al., 2010), 46,100 mean annual visits (Hitier et al., 2010, and in preparation).

4.1. Implications for predator foraging strategy

Anecdotal observations indicate that *T. philippinarum* is preyed upon by a range of crustacean, fish, and shorebird predators. At low tide, the most conspicuous and dominant predators are humans and shorebirds. The importance of *T. philippinarum* to the Eurasian oystercatcher (*Haematopus ostralegus ostralegus*) was demonstrated by Caldow et al. (2007). Predator consumption rate greatly depends on the prey distribution, so the quantification of the spatial distribution of the prey species is important for foraging ecology (Humphries et al., 2010; Miramontes et al., 2012; Pitt and Ritchie, 2002; Reynolds and Rhodes, 2009; Ritchie, 1998; Seuront and Spilmont, 2002; Sims et al., 2008).

According to optimal foraging theory, predator foraging behavior will be greatly influenced by the probabilistic encounter rates (Krebs and McCleery, 1984). These will be determined by prey spatial distribution (including abundance) and predator detection capability (Humphries et al., 2010; Reynolds and Rhodes, 2009). When the prey species shows a patchy distribution and is easily detected by a predator (as in the eagle ray–bivalve relation (Hines et al., 1997), a nonlinear Lévy walk foraging response is predicted (Humphries et al., 2010; Reynolds and Rhodes, 2009; Sims et al., 2008). Regardless of detection ability, a non-patchy (random or regular) structure should produce a more random search strategy, approximated by Brownian motion or one of the forms of correlated random walks (CRW) (Humphries et al., 2010; Reynolds and Rhodes, 2009; Zollner and Lima, 1999). A patchy prey distribution with few or no available cues should produce the Lévy walk strategy in individuals which detect the patches, and a Brownian or CRW strategy in those which do not (e.g. dunlin–bivalve relation – Santos et al., 2009). It should be noted

that megafaunal predators (including humans) probably have a low detection efficiency for very small prey patches (Cummings et al., 1997; Santos et al., 2009; Whitlatch et al., 1997), so the Lévy walk strategy will probably only be observed at patch sizes such as, or greater than, those of the present study.

A low fractal dimension indicates a high level of aggregation with a small number of patches, and thus less space-filling, while a high fractal dimension means low aggregation and better space-filling (Pitt and Ritchie, 2002; Seuront and Spilmont, 2002). Given a moderate to high prey detection ability, such as in eagle rays or intertidal clam fishers, a Brownian or CRW strategy is most appropriate for prey spatial distributions with little aggregation and high space-filling (high FD – Seuront and Lagadeuc, 2001), whereas a Lévy walk strategy is best suited to patchy prey distributions with much less space-filling (low FD – Elliott et al., 2009). As FD increases, predators should show a shift from a Lévy walk to a more random strategy. We would therefore expect non-human *T. philippinarum* predators (e.g. shorebirds) to exhibit a Lévy walk strategy at unfished sites, and a more random strategy at the numerous fishing-impacted sites.

Incorporating the time dimension in spatial analysis and optimal foraging theory allows predictions of dynamic foraging strategy, based on resource depression and the marginal value theorem (Krebs and McCreery, 1984). In a predator–prey system characterized by a patchy prey distribution and moderate- to high predator detection ability, predation is expected to increase upon patch detection, and decrease as prey within the patch are depleted. The attenuation of *T. philippinarum* aggregation observed at the fishing-impacted site is therefore expected to reduce predation in non-human foragers, notably shorebirds, which actually rely on these resources for food. This effect may be accentuated by interference competition (Wahl et al., 2005). Human predators may, however, continue to prey, however inefficiently, upon depleted patches due to different motivations (e.g. recreation – unpublished survey data), further depleting the patches and rendering them extremely unprofitable for non-human foragers. Obviously, the implications for shorebirds and other predators should be carefully weighed by coastal management and conservation authorities.

In conclusion, intertidal *T. philippinarum* displays an aggregative fine-scale spatial distribution, and this pattern is greatly attenuated at the fishing-impacted site. Identical observations have been made for the sympatric *Cerastoderma edule* (Boldina and Beninger, 2013), as well as for the common lugworm *Arenicola marina* (Boldina and Beninger, 2014), and even for the associated meiofauna (Boldina et al., 2014). In addition to the potential consequences of such attenuation on feeding, reproduction, and recruitment, highlighted in these works, it is important to consider the implications for foraging in non-human predators such as shorebirds, which are major sentinels of environmental status (Huettmann and Czech, 2006; Piersma and Lindström, 2004).

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