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Fine-scale spatial distribution of the common lugworm *Arenicola marina*, and effects of intertidal clam fishing

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ABSTRACT

Despite its ubiquity and its role as an ecosystem engineer on temperate intertidal mudflats, little is known of the spatial ecology of the lugworm *Arenicola marina*. We estimated lugworm densities and analyzed the spatial distribution of *A. marina* on a French Atlantic mudflat subjected to long-term clam digging activities, and compared these to a nearby pristine reference mudflat, using a combination of geostatistical techniques: point-pattern analysis, autocorrelation, and wavelet analysis. Lugworm densities were an order of magnitude greater at the reference site. Although *A. marina* showed an aggregative spatial distribution at both sites, the characteristics and intensity of aggregation differed markedly between sites. The reference site showed an inhibition process (regular distribution) at distances <7.5 cm, whereas the impacted site showed a random distribution at this scale. At distances from 15 cm to several tens of meters, the spatial distribution of *A. marina* was clearly aggregated at both sites; however, the autocorrelation strength was much weaker at the impacted site. In addition, the non-impacted site presented multi-scale spatial distribution, which was not evident at the impacted site. The differences observed between the spatial distributions of the fishing-impacted vs. the non-impacted site reflect similar findings for other components of these two mudflat ecosystems, suggesting common community-level responses to prolonged mechanical perturbation: a decrease in naturally-occurring aggregation. This change may have consequences for basic biological characteristics such as reproduction, recruitment, growth, and feeding.

1. Introduction

Temperate zone intertidal mudflats are characterized by high productivity and very dense populations of invertebrates (Whittaker, 1970; Pinckney and Zingmark, 1993; McLusky and Elliott, 2004; Kromkamp and Forster, 2006). They provide feeding and resting areas for large numbers of migratory shorebirds (Butler et al., 1987; Piersma and Jukema, 1990; Zwarts et al., 1990; Mawhinney et al., 1993), which feed on the meiofaunal and macrofaunal invertebrates (Piersma et al., 1998; Sutherland et al., 2000; Hamilton et al., 2006). Mudflats also provide nursery and feeding areas for commercially-important fish species (Gibson and Robb, 1992; Marshall and Elliott, 1997).

The deposit-feeding lugworm *Arenicola marina* is a dominant species of temperate-zone intertidal mudflats (Flach and Beukema, 1994), accounting for 10–20% of the total benthic biomass. Typical mean densities of 20–40 individuals m^{-2} are found in the Wadden Sea, with relatively constant population densities (Beukema, 1976; Volkenborn et al., 2007). An ecosystem engineer, *A. marina* transforms the intertidal mudflats habitat via bioturbation and its own physiological activity (Flach, 1992), consequently maintaining sediment permeability, stimulating nitrification (Hüttel, 1990), modifying carbon and sulfur dynamics (Kristensen, 2001; Nielsen et al., 2003) and inhibiting the succession to progressively finer sediment (Volkenborn et al., 2007). Bioturbation and feeding activities of *A. marina* also impact the biological community, e.g. meiofaunal and macrofaunal abundance and diversity (Flach, 1992, 1993; Volkenborn and Reise, 2006; Kuhnert et al., 2010), as well as microbial dynamics (Goñi-Urriza et al., 1999). *A. marina* is also used in pollution biomonitoring because of its bioaccumulation capacity (Casado-Martínez et al., 2007; Ramos-Gómez et al., 2011; Rodríguez-Romero et al., 2013).

Despite the importance of *Arenicola marina* in mudflat ecology, however, little is known concerning its spatial distribution within these habitats. Not only is spatial distribution one of the fundamental features of community organization, it is also essential to any serious sampling scheme in ecology (Legendre and Fortin, 1989; Underwood and Chapman, 1996; Fortin and Dale, 2005; Legendre and Legendre, 2012).

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Through its production of distinctive fecal casts at the sediment surface, *Arenicola marina* is probably the most conspicuous infaunal invertebrate. Early studies reported a non-uniform spatial distribution of *A. marina*, based on qualitative visual determination (Chapman and Newell, 1949). Later studies reported an over-dispersed distribution pattern within 30 × 30 m squares (Flach and Beukema, 1994), using the inadequate variance: mean method (Hurlbert, 1990; Dale et al., 2002). More refined work using nearest-neighbor analysis concluded that *A. marina* was randomly distributed at a scale of 0.5 m^2 (Retraubun et al., 1996). It is thus evident that both the methodology and the knowledge of *A. marina* spatial distribution require clarification. To our knowledge, no study to date has investigated the fine-scale spatial structure of *A. marina* using modern geostatistical methods.

Due to its ubiquity on mudflats, *Arenicola marina* populations often overlap with those of fished infaunal molluscs, such as clams. The potential effects of clam fishing on the spatial structure of this ecosystem engineer have not been investigated to date. Although there have been attempts to evaluate the effect of harvesting and human trampling on the abundance of *A. marina* (Beukema et al., 1995; Cryer et al., 1987; Rossi et al., 2007), we are not aware of any study investigating the effect of anthropogenic mechanical perturbation on the fine-scale spatial structure of *A. marina.*

In the present study, we use modern geostatistical methods for analyzing the fine-scale spatial structure of an unperturbed *Arenicola marina* population, and compare this with a site impacted by long-term clam digging.

2. Materials and methods

2.1. Terminology

Due to the both the relative novelty of geo-statistical techniques in marine ecology, and the instability of terminology in spatial analysis (Fortin and Dale, 2005), it is necessary to explain some of the key terms used in this approach. The following glossary is intended to provide sufficient detail for understanding of the rationale for each procedure or concept; for complete background, we direct the reader to the following seminal works: Fortin and Dale (2005), Illian et al. (2008). The terms are presented in a logical, rather than an alphabetical, order.

Spatial process is the underlying biological process which produces an observed spatial pattern.

A **Stationary spatial process** is one which is constant (i.e. individual density means and variances are constant) throughout the studied region.

Isotropic spatial process designates a spatial process which is invariant in all directions.

Spatial pattern is 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., 2003).

Autocorrelation is the correlation between data points themselves, rather than between data series. Autocorrelation may be positive (nearby points have more similar values than would be expected by random) and negative (nearby points have less similar values than would be expected by random). In the presence of autocorrelation sampled values are not independent from each other (Tobler, 1970). The kind of autocorrelation between values defines the type of spatial distribution.

Aggregation or aggregated (clustered, clumped, grouped) spatial distribution occurs when the spatial autocorrelation is positive, so individuals tend to occur in groups rather than in a random spatial distribution.

Inhibition or uniform (regular) spatial distribution occurs when the spatial autocorrelation is negative; individuals repel each other, maximizing the distance between themselves, so they are spaced more evenly than in a random spatial distribution.

Point pattern analysis studies the spatial distribution of individuals. Each point represents the position of individual.

First-order point pattern analysis is based on the density of points (individuals) across the studied area.

Second-order point pattern analysis is based on the distances between points across the studied area.

Kernel density estimation may be likened to a histogram based on probabilities rather than on data points.

Ripley's K is a function based on the comparison of average point density (i.e. density of individual animals) in a given area to average point density of circles of increasing radii, drawn around each data point, within this area (Fig. 1).

The average density of points within circles of increasing radius r is compared to the average point density of the total area (Fortin and Dale, 2005):

$$K(r) = \frac{1}{n}\sum_{i=1}^{n} Np_i(r)/\lambda$$

where p_i is the i-th point, and λ is the average density of points.

Ripley's K values vs. r plots reveal the inter-point distances where the spatial aggregation is statistically significant by comparing the actual K values with the K values of a random spatial point pattern of the same size and shape, simulated using a Monte Carlo method. An aggregated spatial distribution is present when the Ripley's K values of the data set are located above the simulated envelope of random point data. Ripley's K values located within the simulated envelope indicate a random spatial distribution, and Ripley's K values situated below the simulated envelope indicate a regular spatial distribution, itself indicative of inhibition (Illian et al., 2008). Since Ripley's K values may be biased at the edges of studied areas, an edge correction of Ripley's K is conventionally used (Illian et al., 2008).

Quadrat-based count data are obtained by dividing the studied area into quadrats, in which the number of individuals is counted (contrast with point pattern data, where individual data points are used). The obtained data may be analyzed with different geo-statistical methods, such as Moran's *I* correlograms, wavelets etc.

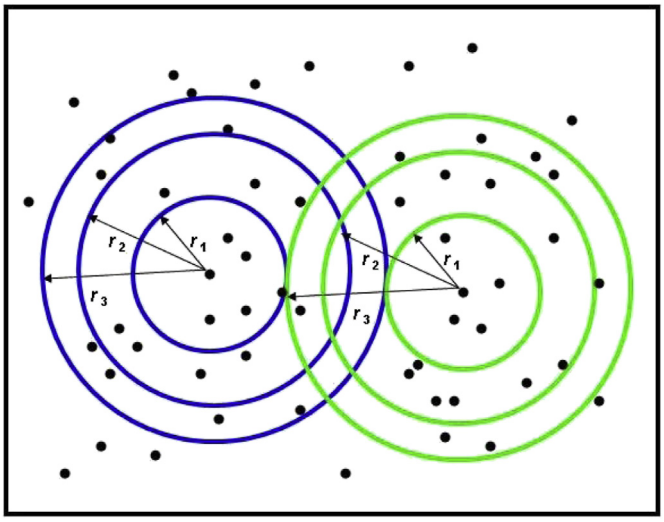

Fig. 1. Construction of a Ripley's K function. The circles of different radii (r_1, r_2, r_3 …) are drawn around every point (individual) of the studied area. For purposes of illustration, only three concentric circles drawn around two points are illustrated here.