Marine Environmental Research 120 (2016) 191–201

Contents lists available at ScienceDirect

Marine Environmental Research

journal homepage: www.elsevier.com/locate/marenvrev

Consistent patterns of variation in macrobenthic assemblages and environmental variables over multiple spatial scales using taxonomic and functional approaches

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ARTICLE INFO

Article history:
Received 6 June 2016
Received in revised form
17 August 2016
Accepted 23 August 2016
Available online 27 August 2016

Keywords:
Benthic ecology
Macrobenthic assemblages
Taxonomic composition
Functional groups
Environmental variables
Variability
Spatial scale
Nested design
Transitional water systems
Northeast Atlantic coast

ABSTRACT

Spatial variability of environmental factors and macrobenthos, using species and functional groups, was examined over the same scales (100s of cm to >100 km) in intertidal sediments of two transitional water systems. The objectives were to test if functional groups were a good species surrogate and explore the relationship between environmental variables and macrobenthos. Environmental variables, diversity and the multivariate assemblage structure showed the highest variability at the scale of 10s of km. However, abundance was more variable at 10s of m. Consistent patterns were achieved using species and functional groups therefore, these may be a good species surrogate. Total carbon, salinity and silt/clay were the strongest correlated with macrobenthic assemblages. Results are valuable for design and interpretation of future monitoring programs including detection of anthropogenic disturbances in transitional systems and propose improvements in environmental variable sampling to refine the assessment of their relationship with biological data across spatial scales.

1. Introduction

In most ecological systems, the composition of assemblages is the result of complex interactions between abiotic and biotic factors (Cisneros et al., 2011; Kraufvelin et al., 2011; Kraan et al., 2015). Moreover, natural assemblages are complex and integrally variable in space and time (e.g. Ysebaert and Herman, 2002; Fraschetti et al., 2005; Rubal et al., 2014). Dealing with this natural variability has been challenging when trying to understand ecological processes shaping the abundance and distribution of organisms (McGill, 2010). However, research has progressed from considering spatial variation of assemblages as "noise" to understanding that its knowledge is crucial because scales at which assemblages vary are also likely to be the scales at which ecological processes have great effects (Underwood et al., 2000; Kraufvelin et al., 2011; Valdivia et al., 2011). Therefore, the quantitative description and observation of patterns across a range of spatial scales is an essential step before explanatory models for patterns in assemblage structure can be proposed (Underwood et al., 2000; Hewitt et al., 2007). Indeed, they provide valuable insights about the mechanisms that probably strengthen diversity and affect the distribution of communities, supporting the development of conservation or environmental management strategies (McGill, 2010; Kraan et al., 2015).

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http://dx.doi.org/10.1016/j.marenvres.2016.08.011
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Insufficient knowledge of the scales at which relevant ecological processes act is a limitation to improve our understanding of biodiversity and ecosystem functioning and their underlying processes and often results in poor decision-making and environmental policy (Raffaelli and Friedlander, 2012; Yaffee, 1997).

Studies focused on determining spatial variability of assemblages have received wide attention in rocky intertidal systems (e.g. Valdivia et al., 2011; Veiga et al., 2013; Díaz et al., 2015). The general picture emerging from these studies is that variability is larger at smaller spatial scales (i.e. cm or meters), which seems to be pervasive in marine systems (see review by Fraschetti et al., 2005). In soft bottom ecosystems, studies on spatial variation of macrobenthos (e.g. abundance, diversity, species composition) have often focused on large scales (i.e. 100 s m to km), examining patterns apparently governed by conspicuous environmental gradients such as those defined by tidal regime or wave exposition (e.g. De la Huz and Lastra, 2008; Schlacher and Thompson, 2013; Veiga et al., 2014). Smaller scales (i.e. cm or meters) have, however, not been usually incorporated into large-scale studies (but see Olabarria and Chapman, 2001; Chapman and Tolhurst, 2004, 2007; Chapman et al., 2010), and thus losing information about variability at these scales, because in many cases macrobenthic replicates are pooled (e.g. Jaramillo et al., 1995; Schlacher and Thompson, 2013). However, many ecological processes and environmental features, such as sedimentary properties, hydrodynamics or bioturbation, change at smaller scales (mm to < 1 m), and can influence the distribution of fauna within large patchy habitats (e.g. Sun et al., 1993; Passarelli et al., 2012; Jungerstam et al., 2014; Díaz et al., 2015). This is especially evident in transitional water systems (i.e. estuaries, fjords, lagoons and rías) and archipelagos, which are highly dynamic in their physical-chemical and hydro-morphologic features, resulting in a mosaic of habitats at relatively short distances (i.e. <100 m; Sigala et al., 2012; Díaz et al., 2015).

The implementation of nested hierarchical designs that estimate variance components allows the examination of variability, both in univariate and multivariate contexts, at a range of spatial scales, from the sampling unit to geographical areas (Underwood, 1997; Underwood and Chapman, 1996, 1998a, b; Terlizzi et al., 2005; Kraufvelin et al., 2011). Analysis of variance tests the presence of significant variability at each scale but estimates of variance components also let us quantify the magnitude of variation for each scale independently of other scales (Morrisey et al., 1992). Hierarchical sampling designs are being increasingly used for studies of sedimentary systems, elucidating that abundance and diversity of macrobenthos show indeed considerable variability at different spatial scales (e.g. Morrisey et al., 1992; Ysebaert and Herman, 2002; Chapman and Tolhurst, 2004, 2007). However, many studies that have explored the relationship between environmental variables and benthic assemblages were based on environmental measures recorded from less sampling points compared with those for the fauna (e.g. De la Huz and Lastra, 2008; Kraufvelin et al., 2011; Veiga et al., 2011). This unbalanced design between environmental and biological data induces some error when an important amount of variability from biological data (different replicates) is linked to a single environmental measure (Kraufvelin et al., 2011). Despite this clear limitation, there are still few studies in sedimentary systems that examine multiple spatial scales of variability of both environmental variables and fauna (Chapman et al., 2010). In any case, the available literature has shown contradictory results. Some of them pointed out that physical features of habitats are sufficient to explain general patterns of benthos (Edgar and Barret, 2002; Ysebaert and Herman, 2002). On the contrary, others reported that those patterns are not clearly correlated with variation in environmental and sedimentary properties of the habitat (Tolhurst and Chapman, 2007; Chapman and Tolhurst, 2004, 2007; Chapman et al., 2010). Therefore, the link between spatial variation in environmental factors and biological patterns of soft bottom benthic assemblages is still poorly understood (Edgar and Barret, 2002; Ysebaert and Herman, 2002).

Macrobenthos plays an important role influencing the structure and functioning of ecosystems in transitional systems (Pratt et al., 2014). Most species display a sedentary lifestyle, intermediate trophic level positions, relatively long life-span, varying responses to changes in environmental conditions and importance in nutrient recycling. Because of that, macrobenthos may serve as an effective useful indicator of the ecological status of transitional water systems (Dauvin, 2007). In fact, macrobenthos is one of the biological elements described by the European Water Framework Directive (WDF, 2000/60/EC) to be used in defining ecological quality status in a water body. Therefore, macrobenthos has been a key element of many monitoring programmes. However, these programmes often have design issues. Firstly, they usually do not explicitly take into account distribution patterns at different spatial scales (Ysebaert and Herman, 2002). Secondly, most of them are mainly based on taxonomic composition and relative abundance of macrobenthic species. Nevertheless, the use of functional diversity (i.e. the diversity and range of functional traits present in the fauna of an ecosystem) is advocated because it is likely an imperative element of biodiversity for the ecosystem functioning (Hooper et al., 2005; Wright et al., 2006). In rocky shores, functional groups of macroalgae have been widely used, showing consistent spatial and temporal patterns with those found using species (e.g. Smale, 2010; Rubal et al., 2011; Veiga et al., 2013). However, whether this consistence occurs or not for macrobenthos in soft bottoms is yet poorly explored.

The first aim of this study was to detect and quantify significant spatial scales of variability in environmental variables (i.e. coastal water and sediment features) and macrobenthic assemblages in intertidal sediments of transitional water systems at scales ranging from 100s of cm to >100 km. These data were used to test the hypotheses that (1) spatial variability of macrobenthic assemblages obtained by using taxonomic composition would be consistent with that resulting considering functional groups and (2) environmental variables with patterns of variation similar to those of macrobenthos will be highly correlated with its structure.

2. Materials and methods

2.1. Study area

This study was done in the intertidal area of two transitional water systems: Ria de Aveiro and Ría de Vigo (Fig. 1). The Ría de Vigo is a partially stratified estuary on the NW coast of Spain. The combined effect of temperature and salinity results in the development of a strong stratification that leds to a positive circulation (Torres-López et al., 2001). Water residence time varies from a few days, during upwelling or strong rainy events in winter, to five weeks in the downwelling season (Prego and Fraga, 1992). It shows a funnel-like morphology with its central axis lying in a SW-NE direction, with the Cíes islands at the entrance, acting as a shelter against waves.

The Ria de Aveiro is located on the northwest coast of Portugal and connected to the Atlantic Ocean through an artificial inlet. It is classified as a bar-built estuary (Pritchard, 1967). It shows a rather complex topography with three main channels that radiate from the mouth with several branches, islands and mudflats resulting in extensive intertidal sand and mud flats (Dias et al., 1999). It has a length of 45 km and a maximum width of 10 km, thus covering an area of 43–47 km^2 at low and high tide, respectively. The hydrological circulation is dominated by marine influence.