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Shifts from native to non-indigenous mussels: Enhanced habitat complexity and its effects on faunal assemblages

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ABSTRACT

Ecosystem engineers such as mussels may affect strongly both the structure of benthic assemblages and the ecosystem functioning. The black-pygmy mussel *Limnoperna securis* is an invasive species that is spreading along the Galician coast (NW Spain). Its current distribution overlaps with the distribution of the commercial native mussel species *Mytilus galloprovincialis*, but only in the inner part of two southern Galician rias. Here, we analysed the assemblages associated with clumps of the two mussel species and evaluated if the invasive species increased complexity of habitat. To measure complexity of clumps we used a new method modified from the "chain and tape" method. Results showed that the identity of the mussel influenced macrofaunal assemblages, but not meiofauna. *L. securis* increased the complexity of clumps, and such complexity explained a high percentage of variability of macrofauna. The shift in dominance from *M. galloprovincialis* to *L. securis* may alter habitat structure and complexity, affecting the macrofaunal assemblages with unpredictable consequences on trophic web relations.

1. Introduction

Invasion of non-indigenous species (NIS) mediated by anthropogenic pathways is a worldwide phenomenon that threats native communities (Davis, 2003). Such invasions have serious effects not only in the structure (i.e. species richness and abundances), but also in the functioning of ecosystems (Vitousek et al., 1997; Simberloff et al., 2013). Among ecosystems, coastal areas and estuarine environments are particularly vulnerable to invasions due to numerous introduction vectors and activities facilitating invasions (Ruiz et al., 1999). European coastal waters have historically experienced large human interferences and up to 1369 non native species have been introduced with consequent changes in habitats and biotic composition of resident communities (Katsanevakis et al., 2013).

Effects of invaders are frequently context-dependent, varying among habitats and across communities. Factors such as environmental heterogeneity (spatial, temporal and invader-driven), phase of invasion or invader's taxonomic distinctiveness within the recipient community may modulate the magnitude and direction of the impacts (Shea and Chesson, 2002; Ricciardi and Atkinson, 2004). For instance, NIS that become dominant in their communities and/or introduce new attributes to ecosystems are expected to have the most significant impacts (Shea and Chesson, 2002). Ecosystem engineers (*sensu* Jones et al., 1994) often have these characteristics (Sousa et al., 2009). They modulate the availability of resources for other species by building and modifying habitats causing important changes in structure and ecosystem functioning (Karatayev et al., 2007). Ecosystem engineering is very relevant in the context of invasions because invaders may bring novel functional traits to host ecosystems (Sax et al., 2007). Among the NIS that cause major ecological impacts are bivalves, whose activities can alter resource availability and ecosystem functioning (Crooks and Khim, 1999; Gutierrez et al., 2003). Shells introduce complexity and heterogeneity in the benthic environment and are important elements of habitat structure affecting processes at different levels from individual and population to ecosystems (Cole and McQuaid, 2010; Sousa et al., 2013). Complexity and heterogeneity of habitat are key factors controlling composition and species

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richness of associated assemblages (McCoy and Bell, 1991; Thompson et al., 1996). The most structurally complex habitats tend to harbour more abundant and diverse assemblages because among other effects, they provide a larger availability of surface for colonisation and refuges from predation (Thompson et al., 1996; Crooks, 2002). Complexity in ecology is a broader term with multiple interpretations and meanings (e.g. temporal complexity, spatial complexity). In our study, we define complexity as the tridimensional structure generated by the geometric aspects of mussel clumps, considered as ecological objects (Loehle, 2004).

Mussels are considered as important biodiversity hotspots by providing a biogenic complex structure, i.e. clumps or beds, which enhances diversity of associated fauna (Palomo et al., 2007; Buschbaum et al., 2009). They usually change the environment by forming dense aggregations attached to the substratum and conspecifics by byssal threads. Hence mussel beds provide highly complex habitats for a range of organisms, including algae, ascidians, amphipods, isopods, gastropods, crabs or polychaetes (Gutierrez et al., 2003; Norling and Kautsky, 2007; Palomo et al., 2007). Besides habitat provision, mussels also affect nutrient availability via biodeposition of faeces and pseudofaeces (Ward and Ricciardi, 2007), increasing microhabitat complexity on rocky substrata through biodeposition and sediment focusing in pits (Yager et al., 1993). By changing physical and biological properties they may significantly alter ecosystem structure and functioning (Palomo et al., 2007; Buschbaum et al., 2009; Sousa et al., 2009). However, such properties vary largely depending on diverse features, such as differences in the size, age, number or density of mussels, thickness of the clump, number of layers of mussels, identity of mussel species or size of a clump (Vaughn and Spooner, 2007; Ward and Ricciardi, 2007; Mermillod-Blondin, 2011). For example, more species are associated with older than younger mussels (Tsuchiya and Nishihira, 1986). Moreover, colonisation rates of algae and invertebrates on the sediment surrounding mussels and on mussel shells differ among mussel species (Spooner and Vaughn, 2006).

The mussel *Limnoperna securis* (Lamarck, 1819) is a NIS that is spreading along the Galician coast (NW Spain) (Garci, 2007; Gestoso et al., 2012). This species is endemic to the brackish waters of New Zealand and Australia and has been introduced to Europe and Japan in the last two decades (Adarraga and Martínez, 2012 and references therein). Currently, it overlaps distribution with the commercial native species *Mytilus galloprovincialis* (Lamarck, 1819), forming mixed beds of patchy aggregations, i.e. clumps, on rocky intertidal shores in the inner part of two Galician rias (Garci, 2007; Gestoso et al., 2012). This habitat-modifying species may have unpredictable effects on associated biota by creating a new habitat in the invaded environment (Norling and Kautsky, 2007; Ward and Ricciardi, 2007). In addition, a recent study has confirmed the ability of *L. securis* to colonise both natural and artificial substrates from muddy/soft bottoms to hard rocks in the Ria de Vigo (Gestoso et al., 2012). This pattern of colonisation implies more heterogeneous and wider impacts on the invaded areas via interactions with the effects that these distinct substrates may generate in the settlement of assemblages (Chapman et al., 2005; Bulleri, 2005). Diverse studies have shown that patterns of colonisation of diverse organisms vary between artificial and natural substrates because of their intrinsic differences in physical features (e.g. Bulleri, 2005). For example, differences in topographic features between artificial and natural substrates, through influencing hydrodynamic conditions at small scale, could cause differences in patterns of colonisation of diverse invertebrates (Taylor and Schiel, 2003). Changes in abundance of predators between both types of substrates might also affect recruitment and post-recruitment processes (Bulleri, 2005). It is thus very likely that faunal assemblages associated with clumps may differ between natural and artificial substrates.

By supplying a new additional habitat for the native fauna and modifying the composition of native mussel beds, *L. securis* is likely changing associated assemblages. To date no studies have examined such effects. In this study, macro- and meiofauna associated with different types of mussel clumps, i.e. *M. galloprovincialis*, *L. securis* and mixed clumps, were examined. We tested the hypotheses that (1) there would be differences in composition and structure of macro- and meiofaunal assemblages associated with the different types of clumps, (2) pattern of variability of fauna associated with the different clumps would differ between types of substrates (i.e. natural *versus* artificial structures), (3) the different types of clumps would show differences in structural complexity, and such differences would explain in part the variability of macro- and meiofaunal assemblages.

2. Material and methods

2.1. Study area and sampling procedure

The study area was located in the inner part of Ria de Vigo, NW, Spain (42° 18′ 43″ N; 8° 38′ 9″W), where both mussel species overlap (Fig. 1). Three sites 1.3–9.1 km apart that presented both artificial and natural substrates were chosen. Artificial substrates were vertical seawalls made of granitic blocks and natural substrates were gently sloping granitic rocky platforms interspersed with particulate substrata, from pebbles to sand and mud.

At each site, clumps from three replicate 10 × 10 cm-quadrats were sampled on each type of substrate (rocky shore and seawall) at the same height on the shore (i.e. low shore, 0.4–0.8 m above the

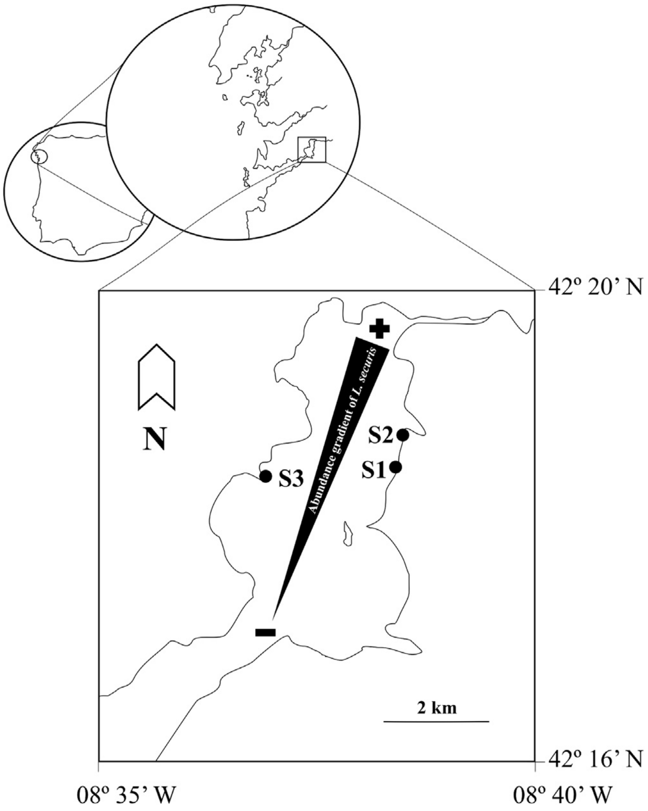

Fig. 1. Location of the study area and sampling sites in the inner part of Ria de Vigo (NW Spain). The gradient of abundance of *Limnoperna securis* is also indicated. S1 – Cesantes; S2 – Soutoxusto; S3 – Santa Cristina.