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Invasion of *Sargassum muticum* in intertidal rockpools: Patterns along the Atlantic Iberian Peninsula

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ABSTRACT

Spatial patterns of non-indigenous species show scale-dependent properties. *Sargassum muticum* is an invasive macroalga widely distributed along the Atlantic Iberian Peninsula. Despite being quite abundant from Norway to South Portugal, there is little information about its patterns of distribution, particularly at a large spatial scale (i.e. thousands of kilometres). Here, we examined the spatial variation in the invasion success of *S. muticum* from rockpools at multiple spatial scales using a hierarchical design. In addition, we analysed how the richness of native assemblages was related to its invasion success and how this relationship changed over different scales. Most of the variation in the invasion success was found at the smallest scales of pool and plot. Furthermore, the invasibility of native macroalgal assemblages was related to the native species richness, but causes that determined invasion success could not be separated from the effects provoked by the invader. Results suggest that small-scale (centimetres to metres) processes contribute considerably to the heterogeneity of *S. muticum* invasion success.

1. Introduction

Spatial scale not only influences the patterns that we observe, but also ecological processes and mechanisms differ at different spatial scales (Levin, 1992). While biotic processes and behaviour are usually implicated in the maintenance of small- to meso-scale spatial patchiness, oceanographic conditions and climate largely dictate regional, large-scale patterns (Underwood and Chapman, 1996). Spatial distributions of rocky intertidal organisms are scale-dependent and closely related to the trophic level and mode of reproductive dispersal (Burrows et al., 2009). In general, lower-trophic-level species, e.g. macroalgae, show more variability at large scales because their distributions tend to be controlled by spatially autocorrelated bottom-up processes, e.g. nutrients, light, and temperature (Broitman and Kinlan, 2006). Moreover, species with short-range dispersal may show more variability on smaller spatial scales than those with long-range dispersal (Johnson et al., 2001).

Non-indigenous species (NIS) are not the exception and, therefore, their patterns and processes show scale-dependent properties, e.g. invasion patterns, impacts or dispersal modes (Pauchard and Shea, 2006). Only a small fraction of the NIS are able to invade and thrive in new habitats since the invasion process depends on the traits associated with the non-indigenous organism (invasiveness), the propagule pressure (or introduction effort, i.e. the number of individuals introduced at a given location), and the characteristics of the recipient community (community invasibility) (Lonsdale, 1999). Invasion success has been related to abundance and distribution in the native range, and just as some NIS are more successful invaders than others, some communities are more susceptible to invasion than others (Stachowicz et al., 2002). Although diversity, number

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and identity of functional groups have been proposed as key factors controlling resistance to invasion of native communities (Elton, 1958; Arenas et al., 2006), the magnitude and direction of the relationship between diversity and susceptibility to invasion are scale-dependent, which constitutes the so-called "invasion paradox" (Fridley et al., 2007). The diversity–invasibility relationship takes various forms in observational studies of natural communities at large spatial scale, but it is generally negative in experimental studies at small-scale (Lonsdale, 1999). Factors such as propagule pressure, disturbance levels, climate, or resource heterogeneity simultaneously increase both native and non-indigenous diversity, and thus, positive relationships among native and non-indigenous diversity may occur (Stachowicz and Byrnes, 2006). However, at smaller spatial scales, the negative relationship results from the competitive interactions among native and NIS, recruitment and post-settlement processes or disturbance events (Fridley et al., 2007). For example, canopy and subcanopy macroalgae are habitat-forming species that may efficiently compete for light and substrate availability, showing strong effects on the presence and abundance of other taxa at scales of centimetres (Arenas et al., 2006). Such interactions are, however, likely to change depending on the habitat and the stage of the invasion. That is the case of the canopy species *Bifurcaria bifurcata* that inhibits recruitment of *Sargassum muticum* (Sánchez and Fernández, 2006), but it can be negatively affected by the invader when well-established (Viejo, 1997).

One of the most successful invaders along European coasts is the brown macroalga *S. muticum* (Yendo) Fensholt. This species was first detected in Europe in the early 70s (Farnham et al., 1973) and spread quickly across the European Atlantic seashores. In the Iberian Peninsula, it was first recorded in the 80s both in the Basque Province and in the Galician coast (see Pérez-Cirera et al., 1989), reaching recently the southern coast of Spain (Bermejo et al., 2012). However, its patterns of distribution and abundance are highly variable at different scales along the Iberian Peninsula (Engelen and Santos, 2009; Olabarria et al., 2009; Incera et al., 2011). Several factors have been pointed out as potential drivers of such variability. Environmental factors acting at large and/or meso-scales, such as seawater and air temperature, variability in hydrodynamic conditions or topography, may influence its reproductive patterns and dispersal rates (Incera et al., 2011). In fact, growth and reproduction of this species is enhanced by relatively warm water (up to around +25 °C) (Hales and Fletcher, 1990), although high air temperatures and large number of sun hours may negatively affect egg release in rockpools (Engelen et al., 2008). Competition with dominant native canopy forming species is an important factor causing variability in the rates of population growth of *S. muticum* at scale of metres, i.e. among intertidal rockpools from the same shore, especially during the establishment or early post-settlement phases (Britton-Simmons, 2006; Engelen and Santos, 2009). Other functional groups (crustose and turfy algae) are, however, important regulators of the recruitment of *S. muticum* through reduction of space availability (Britton-Simmons, 2006).

Previous studies about the distribution of this invader have been usually performed on emergent substrata (but see Viejo, 1997), and generally covered small- and meso-scales, i.e. ranging from metres to kilometres (Olabarria et al., 2009; Incera et al., 2011). Here, we covered a larger spatial scale of about 1000 km, focussing on invasion in rockpool habitats because these habitats seem to be among the most heavily invaded in these coastal areas. In addition, we explored the relationships between the richness of native macroalgal assemblages and the invasion success of *S. muticum* and how these relationships changed at different scales.

Our study took place along the north and west coasts of the Iberian Peninsula (Fig. 1). The area of study is particularly relevant because of its location within the broad transitional zones between cold- and warm-water species (Tuya et al., 2012) with upwelling processes dominating on the northwestern part of the area (Bode et al., 2002). Latitudinal gradients in ocean conditions, particularly year-round seawater temperature, nutrient concentration and chlorophyll a, have been described along these coasts (Gómez-Gesteira et al., 2008; Tuya et al., 2012). Moreover, environmental conditions in rockpools along the geographical gradient differ in thermal stress due to differences in air temperature and number of sun hours (Engelen et al., 2008).

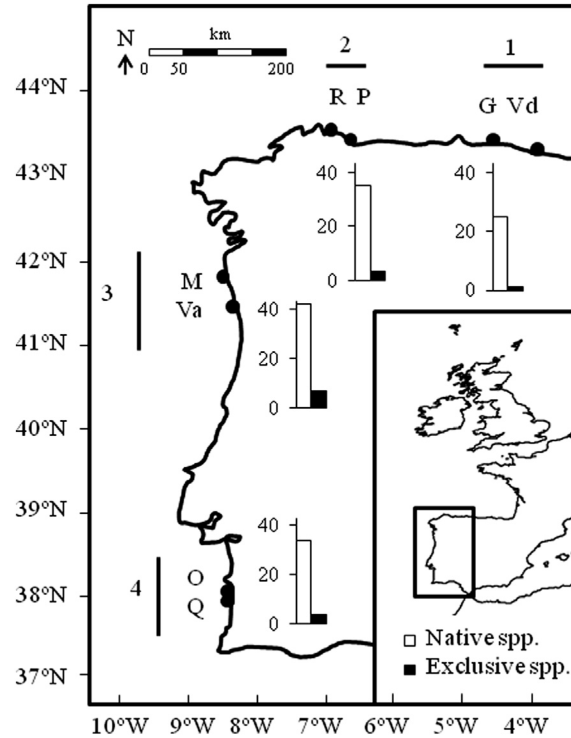

Fig. 1. Map showing study area (Region 1, northern Iberian Peninsula; Region 2, northwestern Iberian Peninsula; Region 3, central-western Iberian Peninsula and Region 4, southwestern Iberian Peninsula) and locations within each region (G, La Griega; Vd, Vidiago; R, Rocas Blancas; P, Peizás; M, Moledo; Va, Viana; O, Oliveirinha and Q, Queimado). Native species richness and number of exclusive species (native species appearing exclusively in that region) are indicated for each region.

Specifically, we analysed the spatial variability of the invasion success of *S. muticum* in mid-shore rockpools, measured in our case as percentage cover, biomass, length and density of the species, along four different regions located on the north and west coasts of the Iberian Peninsula. The study included a nested design with four regions (hundreds of kilometres apart), two locations within each region (tens of kilometres apart), 24 pools within each location (metres apart) and 3 plots within each (centimetres apart). Furthermore, we explored the relationship between the invasion success and the native richness of macroalgal assemblages, and analysed the possible role of canopy and subcanopy-forming species in the success of the invader. We examined in our study only invaded rockpools to avoid that our findings and patterns were biased by the fact that not all the rockpools might be a suitable habitat for *S. muticum*.

2. Material and methods

2.1. Environmental conditions in the study area and sampling design

The study area encompassed almost 1000 km of temperate coast (from 43°24′ to 37°53′ N) along the Atlantic Iberian Peninsula. Four