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Predicting coexistence and predominance patterns between the introduced Manila clam (*Ruditapes philippinarum*) and the European native clam (*Ruditapes decussatus*)

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In several European estuaries, the introduced Manila clam (*Ruditapes philippinarum*) has become a widespread and predominating species supplanting the native carpet shell clam (*Ruditapes decussatus*) whereas in other estuaries such as the Bay of Santander (Gulf of Biscay) this pattern has not been detected. Using this estuary as a case study, the potential coexistence/predominance patterns between these two species were explored with the objective of providing insight into the capacity of expansion of *R. philippinarum*. Firstly, the Ecological Niche Factor Analysis (ENFA) was applied to determine the niches of both species, using seven contemporary environmental variables, i.e. salinity, water depth, current velocity, and sediment sand, gravel, silt and organic matter content. Secondly, ENFA-derived habitat-suitability (HS) maps were simultaneously treated, using geospatial techniques and following HS index-based criteria, to determine the potential distribution patterns. Both species models performed well according to the cross-validation evaluation method. The environmental variables that most determined the presence of both clams were depth, current velocity and salinity. ENFA factors showed that *R. philippinarum* habitat differs more from the mean environmental conditions over the estuary (i.e. higher marginality) and has less narrow requirements (i.e. lower specialization). *R. philippinarum* dominated areas, determined by relatively lower current velocities and percentages of sand, higher organic matter contents and slightly shallower depths, were very reduced (i.e. 2.0% of the bay surface) compared to coexistence (47%) and *R. decussatus* predominance areas (7.4%). These results suggest that HS may regulate the expansion of *R. philippinarum*. ENFA, together with geospatial analysis of HS index, seems to be a valuable approach to explore the expansion potential of estuarine invasive or introduced species and thus support conservation decisions regarding native species.

1. Introduction

The natural or accidental invasions of marine non-indigenous species together with deliberate introductions can have significant impacts on native communities (Carlton, 1996; Ruiz et al., 1999). As rates of marine invasions continue to increase (Cohen and Carlton, 1998), pressure will tend to increase on managers to minimize the potential impacts of non-indigenous species, and on scientists to provide control measures (Bax et al., 2001). However, management decisions for the conservation of a native species or actions against a certain introduced or invasive species are often hindered by a lack of basic and essential ecological information. Therefore, the study of the potential distribution patterns of native and non-indigenous species is essential to identify priority areas for conservation and to establish specific zone-based management plans. This information is even more important when the studied species are commercial and a sustainable fisheries management is desired. Estimation of distributions of these species can be linked with the potential yield of the fishery (Vincenzi et al., 2006a,b) and thus zone-based management plans may establish different fishing strategies.

The Manila clam (*Ruditapes philippinarum*), native to the western Pacific Ocean (Scarlato, 1981), is one of the most world-widely introduced species for aquaculture purposes because of its high

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adaptability to various coastal environments and its suitability for aquaculture (Laing and Child, 1996; Usero et al., 1997). In several disturbed estuaries or lagoons of Europe such as Arcachon Bay (France) or the Lagoon of Venice (Italy), this species has supplanted the European native carpet shell clam (*Ruditapes decussatus*) by occupying similar ecological niches throughout its full range (Blanchet et al., 2004; Mistri, 2004; Dang et al., 2010). In the case of the Lagoon of Venice, it holds very high densities and has spread along the Adriatic coast at a rate of 30 km per year (Breber, 2002). This extreme domination pattern has not yet been detected in other estuaries, such as the Bay of Santander (Gulf of Biscay, N Spain) (Juanes et al., 2012). However, being aware of the large-scale decline of *R. decussatus* in several estuaries of Europe, to explore the potential expansion of *R. philippinarum* seems to be essential for the conservation of *R. decussatus*. The conservation of *R. decussatus* is ecologically relevant in terms of concern over the consequences of biodiversity loss on ecosystem processes and ecosystem function, which subsequently affect the provision of ecosystem goods and services, and ultimately affect human well-being (Diaz et al., 2006). Moreover, specific zone-based strategies towards the sustainable fishery of the native clam are particularly crucial, since it is a much slower growing species and less resistant to unfavourable environmental conditions than *R. philippinarum* (Breber, 1985, 1991; Usero et al., 1997).

The application of predictive models to obtain the potential distribution of marine species has increased, covering areas such as aquaculture (Longdill et al., 2008), fisheries management (Galparsoro et al., 2009), habitat management (Valle et al., 2011; Vasconcelos et al., 2013; Rinne et al., 2014) and conservation of a wide range of species such as cetaceans (Praca et al., 2009), migratory birds and turtles (Tian et al., 2008), polychaetes (Willems et al., 2008) and corals (Tittensor et al., 2009). With regards to bivalve species, habitat suitability predictions have been mainly focused on commercial species such as oysters and clams in order to improve management models or to restore habitats for aquaculture purposes (Soniat and Brody, 1988; Vincenzi et al., 2006a,b). Moreover, these techniques have also been used to predict spatial patterns of biological invasions and to prioritize locations for early detection and control of outbreaks of non-indigenous species (e.g. Inglis et al., 2006). Thus, these tools are now sufficiently mature to take on a larger role supporting conservation decisions, although linkage between research results and practice is still thin (Guisan et al., 2013).

Selecting the adequate modelling technique for the available data and objective of the study is critical to be as accurate as possible when predicting the potential distributions (Elith et al., 2006). Most of the available methods are based on presence/absence data (i.e. GLM, GAM, classification and regression tree analyses, and artificial neural networks). Brotons et al. (2004) suggest that GLM predictions (e.g. Vasconcelos et al., 2013) are more accurate than those obtained with the presence-only methods, such as Ecological Niche Factor Analysis (ENFA) (Hirzel et al., 2002), when species were using available habitats proportionally to their suitability, making absence data reliable and useful to enhance model calibration. However, absence data could be often of limited use because certain areas within the study site may be suitable, but has not yet been colonized by the invasive or introduced species (Hirzel et al., 2002). This suggest that pure presence-only methods are more likely to predict potential distributions that more closely resemble the fundamental niche of the species, whereas presence-absence modelling is more likely to reflect the present natural distribution derived from realized niche (Zaniewski et al., 2002). Therefore, ENFA may be particularly suitable when the objective is to predict the potential expansion of an introduced species and not the current status of colonization. This approach has proven to be a valuable tool for predicting habitat suitability of marine benthic species (e.g. Willems et al., 2008; Galparsoro et al., 2009; Valle et al., 2011) and for monitoring the potential spread of invasive or introduced species in terrestrial habitats (e.g. Hirzel et al., 2004a).

Within this context, ENFA was applied for *Ruditapes decussatus* and *Ruditapes philippinarum* in the Bay of Santander (N Spain, Gulf of Biscay) in order to (1) examine the influence of several ecologically relevant environmental variables in determining suitable habitats for both species and (2) explore potential coexistence and predominance patterns. The development of these objectives allowed testing the hypothesis that habitat suitability can play an important role in regulating the expansion and predominance of *R. philippinarum* over *R. decussatus*. To test this hypothesis, the following research questions concerning the distribution patterns between both species were posed: (1) is the habitat of the estuary more suitable for *R. philippinarum* than for *R. decussatus*? and (2) is *R. philippinarum* predominance area larger than that where *R. decussatus* predominates? Previous data indicate that *R. philippinarum* is abundant and widespread in this estuary but a clear predominance pattern over the native clam has not been detected yet. Therefore, a priori, it was expected that habitat suitability might be regulating its expansion. The method applied and results of this study are intended to serve as a tool for conservation and ecosystem management dealing with introduced or invasive species.

2. Material and methods

2.1. Study area

The study area is located in the Bay of Santander (Gulf of Biscay) (Fig. 1), the largest estuary in northern Spain with an area of 22.7 km^2. The intertidal zone represents 67% of the total area of the bay (1573 ha) and is mainly concentrated in the right margin of the bay. Shellfishing of *Ruditapes decussatus* and *Ruditapes philippinarum* is conducted in seven intertidal fishing zones (Fig. 1), using traditional techniques (i.e. hand rakes, knifes) (Juanes et al., 2012). A small *R. philippinarurm* farming area (~1 ha) is located in the tidal flat of Elechas (Fig. 1). Galván et al. (2010) classified this estuary as morphologically complex and dominated by intertidal areas and tidal dynamics. The substratum of this area varies from sandy (northern open areas) to muddy (southern and inner areas) (Fig. 2). Subtidal zones are dominated by shallow waters (<5 m), with maximum depths of 10–12 m along the navigation channel (Juanes et al., 2012). Hydrodynamic conditions are controlled by a semi-diurnal tidal regime and a 3 m mean tidal range, interacting with variable freshwater inputs coming mainly from the river Miera through the Cubas area with a mean flow of 8 $m^3 s^{-1}$ (Galván et al., 2010). Further details of this estuary and its sand flats are provided elsewhere (e.g. Puente et al., 2002; Juanes et al., 2012; López et al., 2013).

2.2. Clams presence data

Sampling surveys were conducted between April and May of 2010 to detect the presence of *Ruditapes decussatus* and *Ruditapes philippinarum*. Clams were collected at 39 stations (1 m × 10 m transects) by a professional shell-woman by hand raking of the sediment, following Juanes et al. (2012). Transects were located in intertidal and shallow subtidal zones, considering these species depth range (Vincenzi et al., 2006a,b; Albentosa and Moyano, 2009). Locations where presence was documented were marked with a GPS device. Taxonomic determination of individuals was carried out in the laboratory. Both species presence maps (Fig. 1)