



Connectivity, neutral theories and the assessment of species vulnerability to global change in temperate estuaries



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ABSTRACT

One of the main adaptation strategies to global change scenarios, aiming to preserve ecosystem functioning and biodiversity, is to maximize ecosystem resilience. The resilience of a species metapopulation can be improved by facilitating connectivity between local populations, which will prevent demographic stochasticity and inbreeding. This investigation estimated the degree of connectivity among estuarine species along the north-eastern Iberian coast, in order to assess community vulnerability to global change scenarios. To address this objective, two connectivity proxy types have been used based upon genetic and ecological drift processes: 1) DNA markers for the bivalve cockle (*Cerastoderma edule*) and seagrass *Zostera noltei*, and 2) the decrease in the number of species shared between two sites with geographic distance. Neutral biodiversity theory predicts that dispersal limitation modulates this decrease, and this has been explored in estuarine plants and macroinvertebrates. Results indicate dispersal limitation for both saltmarsh plants and seagrass beds community and *Z. noltei* populations; this suggests they are especially vulnerable to expected climate changes on their habitats. In contrast, unstructured spatial pattern found in macroinvertebrate communities and in *C. edule* genetic populations in the area suggests that estuarine soft-bottom macroinvertebrates with planktonic larval dispersal strategies may have a high resilience capacity to moderate changes within their habitats. Our findings allow environmental managers to prioritize the most vulnerable species and habitats to be restored.

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1. Introduction

The most important direct drivers of global biodiversity loss and ecosystem service changes are habitat change, climate change, invasive alien species, overexploitation and pollution (Millennium Ecosystem Assessment, 2005). The undergoing destruction and degradation of natural habitats (Halpern et al., 2008) and, as a consequence, the increasing number of threatened species (He and Hubbell, 2011), are particularly severe at the coast, where human population is concentrated (Costanza et al., 1997; McGranahan et al., 2007) and the artificialization and urbanization is increasing at a greater rate than for inland areas (European

Environment Agency, 2006). Climate change is also considered as one of the major threats to coastal and estuarine ecosystems for the 21st Century (FitzGerald et al., 2008; Defeo et al., 2009; Reid et al., 2009; Philippart et al., 2011).

In this context, the conservation of estuarine biota is a priority. One of the main adaptation strategies to global change scenarios to preserve ecosystem functioning and biodiversity is to maximize ecosystem resilience (Mawdsley et al., 2009). The resilience is the system ability to absorb rapid environmental change (Heller and Zavaleta, 2009). The resilience of a species metapopulation can be improved by facilitating connectivity among local populations, which will prevent demographic stochasticity and inbreeding (Loew, 2000). Despite the fundamental role played by dispersal and population connectivity in determining the resilience of populations (e.g. Hastings and Botsford, 2006; Cowen et al., 2007; Bradbury et al., 2008; Cowen and Sponaugle, 2009), there is still

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a limited knowledge about the dispersal strategies of many marine species due to the difficulty of tracking the trajectory and fate of propagules (e.g. Shanks, 2009; Weersing and Toonen, 2009; Selkoe and Toonen, 2011). In the seascape, the connectivity among populations is mainly determined by the ocean currents and the dispersal capacity of organisms (e.g. Gawarkiewicz et al., 2007; Alberto et al., 2011; Coleman et al., 2011), as well as by the demographic prospects of reproduction, mortality and migration rate (Hubbell, 2001). In the particular case of ecotones such as estuaries, the movement of organisms or propagules can be very different between species depending on both habitat specificity and dispersal strategies (Boström et al., 2010). Thus, it is difficult to anticipate, for a given spatial scale, whether estuarine species circumvent habitat discontinuities, or on the contrary, are dispersal limited. The analysis of highly polymorphic molecular markers is a powerful tool for the study of connectivity among marine populations (e.g. Bradbury et al., 2008; Galindo et al., 2010; Selkoe et al., 2010; Alberto et al., 2011). Although dispersal limitation factors has been recognized to be a common process shaping both species and genetic diversity (Vellend and Geber, 2005), the first empirical evidence has been recently proved in aquatic beetles (Baselga et al., 2013).

Our main objective here is to estimate the degree of connectivity among the structural estuarine species (plants and macroinvertebrates) along the Basque coast (south-eastern Bay of Biscay), in order to assess community vulnerability in the face of global change scenarios. Basque estuaries have been radically transformed by anthropogenic activities during the 20th century (Cearreta et al., 2004; Chust et al., 2009), and they are expected to be impacted throughout the 21st century by a sea level rise of 29–49 cm (Chust et al., 2010), storm surges (Marcos et al., 2012), warming of surface air (especially heat wave episodes) and sea of 1.5–2.0 °C (Chust et al., 2011) and the intensification of extreme daily rainfall of 10% (Chust et al., 2011). Thus, the specific objectives are: 1) to determine and compare the connectivity between species communities across two estuarine taxa groups (i.e. plants of saltmarshes and intertidal seagrass meadows, and soft-bottom macroinvertebrates in intertidal and shallow waters); 2) to determine and compare the genetic connectivity between estuarine populations along the North Atlantic Iberian coast of two species with different dispersal strategies and life traits: the seagrass *Zostera noltei* and the bivalve cockle (*Cerastoderma edule*). Recent studies determining population genetic structure of sympatric marine species (e.g. Kinlan and Gaines, 2003; Selkoe et al., 2010) have provided valuable information on gene flow through the seascape. Estimating and understanding marine connectivity can also help environmental managers to guide and prioritize local restoration plans for both species and habitats, as well as to define strategies for climate change adaptation.

To address these objectives, two proxies of connectivity have been used, based upon genetic and ecological drift processes and dispersal limitation factors (Vellend and Geber, 2005). Under a 'stepping stone model' of dispersal, in which populations tend to exchange migrants (or propagules) with nearest neighbours along the coastline, the Isolation By Distance (IBD) theory suggested that pairwise genetic variation (for instance the Wright's fixations index F_{ST}) will increase with the geographic distance between the pair of populations (Wright, 1943; Kimura, 1953; reviewed in Selkoe and Toonen, 2011). IBD assumes neutral alleles (not affecting fitness) and populations at equilibrium between dispersal and genetic drift (Hutchinson and Templeton, 1999). In contrast, in a metapopulation where all populations exchange migrants equally, F_{ST} is not correlated with geographic distance. Therefore, the slope of IBD is commonly used for estimating dispersal distance with genetic markers. The IBD theory is a central concept of the neutral theory of

molecular evolution (Kimura, 1983), which states that most of evolutionary changes at the molecular level is the result of randomly genetic drift acting on neutral alleles (not affecting fitness). In ecology, although disentangling whether the regional distribution of species arises from dispersal limitation (MacArthur and Wilson, 1967) or by niche adaptive processes (Hutchinson, 1957) have long debated, the emergence of the concept of neutrality (Hubbell, 2001) appeared more recently than in population genetics. The neutral theory of biodiversity developed by Hubbell (1997, 2001) is *neutral* because all individuals are assumed to have the same prospects for reproduction and death (Chave, 2004). Under Hubbell's model, where a metacommunity is composed by a set of communities exchanging individuals of different species with a migration rate, the variability in relative abundances across species is solely due to demographic stochasticity or 'ecological drift'. When migration rate is low in such a model (i.e. species are dispersal limited), species cross-site similarity (i.e. the opposite of β -diversity) is predicted to decline logarithmically with increasing geographical distance (Hubbell, 2001; Chave and Leigh, 2002). This pattern, named 'distance decay', has been observed for different taxonomic groups: rainforest trees (e.g. Condit et al., 2002; Chust et al., 2006a), coral reefs (Hubbell, 2001), marine bacteria (e.g. Martiny et al., 2011) and plankton (Irigoien et al., 2011; Chust et al., 2013; but see; Cermeño et al., 2010). The estimated correlation and rate of change (i.e. slope) in species similarity with increasing geographic distance, hence, can be used to compare the degree of dispersal limitation among different communities (Chust et al., 2006b). However, species distributions and environmental variables tend to be spatially autocorrelated (Legendre, 1993), hence distance decay might be a result from the relation between species composition and environmental niche factors. In such a case, appropriate statistical techniques need to be applied in order to disentangle both effects (e.g. Chust et al., 2013). Within this framework, our expectations in estuarine species is that the group of species more limited by dispersal at the community level should also have more fragmented genetic population structure, in accordance to recent findings in aquatic beetles (Baselga et al., 2013).

2. Material and methods

2.1. Study area

The study area is located within the Basque Country (Spain), in the southeastern part of the Bay of Biscay (Fig. 1). The total length of this section of the coast is ca. 150 km, with 13 main estuaries (Borja and Collins, 2004) (Fig. 1). The maritime climate along the Basque coast is related mainly to its location within the Bay of Biscay and the NE Atlantic (González et al., 2004). In relation to its location and orientation, this part of the coast is exposed to large storms from the NW, produced by evolution of the North Atlantic low pressure systems. Strong NW swell waves dominate and are the most common sea state within the study area. The tidal wave is semi-diurnal in character within the Bay of Biscay (Uriarte et al., 2004). Along the Basque coast, the mean tidal range is approximately 1.65 m on neap tides and 4.01 m on springs (Chust et al., 2010). Despite the importance of tidally-induced surface water fluctuations, the contribution of the tides to the generation of currents is somewhat modest (except within the estuaries) (Uriarte et al., 2004). The coast is dominated by rocky substrata with vertical cliffs intercalated with small estuaries and sandy beaches. The continental shelf in the Basque Country is characterized by its narrowness; it ranges from 7 km to 20 km (Galparsoro et al., 2010). As a consequence of this coastal configuration, salt-marshes are

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