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Life-history, substrate choice and Cytochrome Oxidase I variations in sandy beach peracaridans along the Rio de la Plata estuary

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ABSTRACT

Life-history, substrate choice and Cytochrome Oxidase I (COI) sequences were analysed in populations of two peracaridans, the supralittoral talitrid *Atlantorchestoidea brasiliensis* and the intertidal cirolanid *Excirolana armata*. Three populations of each species, from beaches with similar grain size and located at different points along the natural gradient generated by the Rio de la Plata estuary were analysed. Abundance of *E. armata* increased with distance from the estuary, while the opposite trend was observed for *A. brasiliensis*. The proportion of females decreased towards high salinities for both species, significantly for *E. armata*. A test on substrate salinity preference revealed the absence of patterns due to active choice in *E. armata*. By contrast, *A. brasiliensis* showed no preference for the population closer to the estuary, while individuals from the other two sites significantly preferred high salinity substrates. Mitochondrial COI sequences were obtained from *A. brasiliensis* specimens tested for behaviour. Sequence analysis showed the population from the intermediate site to differ significantly from the other two. No significant genetic differentiation was instead found between populations from the two most distant sites, nor between individuals that expressed different salinity preference. Results showed that diverse sets of traits at the population level enable sandy beach species to cope with local environmental changes: life-history and behavioural traits appear to change in response to different ecological conditions, and, in the case of *A brasiliensis,* independently of the population structure inferred from COI sequence variation. Information from multiple traits allowed detection of population profiles, highlighting the relevance of multidisciplinary information and the concurrent analysis of field data and laboratory experiments, to detect responses of resident biota to environmental changes.

1. Introduction

The functionality of individuals, allowing their existence within the environment, can be expressed as traits that include behavioural, reproductive and morphological characteristics (McGill et al., 2006). Both genes and environment contribute to shaping an organism's traits, making "traits" a unit of considerable evolutionary relevance (Piersma and Drent, 2003), capable of detecting changing ecological scenarios (Williams et al., 2008; Gibert et al., 2015). Within species, traits can be identified, quantified and compared with other populations subject to different ecological pressures, focusing on local matches between populations and their local environment (Begon et al., 2006). Within a population, some traits can present high heritability, while others are more related to the organism's phenotypic plasticity in response to the environment (Sih et al., 2011). Thus, multiple (and non-mutually exclusive) causation can be assumed to have an effect on life-histories (Stearns, 1977). Such a mosaic has to be considered when approaching integrative species-environment studies, especially those targeting the effects of environmental changes on populations.

In this study, changes in behavioural, demographic and

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molecular traits were assessed in peracaridan populations from sandy beaches subject to different salinity conditions due to the estuarine gradient generated by the Rio de la Plata, the widest estuary worldwide. The Rio de la Plata begins at the confluence of the Uruguay and Paraná rivers and flows eastward into the South Atlantic Ocean. No clear physical boundary marks the river's eastern end. However, the International Hydrographic Organization defines the eastern boundary of the Rio de la Plata in the Uruguayan coast at Punta del Este (Fig. S1). The Rio de la Plata can be divided into inner and outer regions based on their morphology and dynamics. The inner, fluvial system presents high turbidity whereas the outer region is a mixohaline system with less turbidity (Martínez and Ortega, 2015). Along the macroscale salinity gradient (4.0–34.1, Lercari and Defeo, 2015) generated by the Rio de la Plata estuary, peracaridan crustaceans are dominant in abundance. They are direct developers and mostly linked to the mesoscale dimension (i.e. within a single beach, McLachlan and Brown, 2006), allowing one to consider these species as useful bioindicators of change (Colombini et al., 2011). Along the Uruguayan coast affected by an estuarine gradient, the supralittoral talitrid amphipod *Atlantorchestoidea brasiliensis* (Dana, 1853) and the intertidal cirolanid isopod *Excirolana armata* (Dana, 1853) represent the most abundant components of sandy beach biota (Lercari and Defeo, 2015). *Atlantorchestoidea brasiliensis* is found on a broad range of beach types across a wide latitudinal gradient (Cardoso and Veloso, 1996), whereas *E. armata* inhabits a wide biogeographic range, partly overlapping with the one of *A. brasiliensis*, but it is found only in fine sands and close to the intertidal zone (Defeo et al., 1997; Cardoso and Defeo, 2004).

There is a solid data background regarding the influence of the Rio de la Plata estuary on the resident fauna of sandy shores, identifying salinity as a key variable affecting diversity patterns over geomorphological differences (beach morphotypes: Defeo and McLachlan, 2013). Recently, a threshold value -rather than a gradient-was suggested as a trigger of biotic patterns (Bozzeda et al., 2016), thus pointing to non-linear dynamics acting on the system. Previous macroscale studies on these species showed that population characteristics such as senescence, fecundity, embryos size, weight of brooding females, size at maturity and sex ratio of *A. brasiliensis* were related to reproductive strategies defined by salinity variations (Gómez et al., 2013), whereas seawater salinity and sand grain size were relevant explanatory variables of variations in occurrence and abundance of *E. armata* (Lozoya et al., 2010).

Talitrid amphipods and cirolanid isopods display behavioural adaptations to daily and seasonal variations in the environment. Behavioural adaptations to a local beach morphotype and exposure (Yannicelli et al., 2002; McLachlan and Dorvlo, 2005; Fanini and Lowry, 2014), paired with high behavioural plasticity (Brown, 1996), are relevant in peracaridans to cope with a changing environment. Behavioural traits are considered the most plastic among phenotypic characteristics (Blomberg et al., 2003) and provide important clues of ongoing processes across populations. Nevertheless, only those behavioural features that can effectively enable the population to cope with environmental variations are found to be plastic (Scapini, 2014), and this is likely related with the cost of plasticity (Blomberg et al., 2003).

While a genetic component of phenotypic traits is generally assumed, few studies have combined molecular profiles with different phenotypes in peracaridan populations inhabiting sandy beaches. Mitochondrial Cytochrome Oxidase subunit I (COI) sequence analysis has been frequently used to infer population structure at both meso- and macroscales. Geographical distance in many cases results in detectable molecular differentiation (Palumbi, 1994) in intraspecific studies. COI analysis of talitrid (Pavesi et al., 2013) and cirolanid (Spooner and Lessios, 2009) populations, allowed to highlight geographic patterns of differentiation. COI sequence data has been found especially useful in providing new insights when combined with ecological or behavioural data: for instance the population structuring found in the Mediterranean sand-hopper *Talitrus saltator* on a scale of a few kilometres was found to match behavioural changes (Ketmaier et al., 2010).

The present study aims to merge in an integrated perspective the results from different fields (individual behaviour, population demography and genetics), usually tackled separately in most published studies. The traits considered were selected to include diversity at different levels (*sensu* Noss, 1990); they are likely non-independent from each other, but they might be differently affected by the same environmental pressure. Finally, they can be summarised at population level. Traits under investigation are also expected to change in response to the changes in environmental parameters found along the estuary, as follows: 1) inter-dependent population life-history traits such as abundance, fecundity and sex ratio are affected by the inclusion within the estuarine environment; 2) preference for substrate salinity is affected by the exposure to low salinity values; and 3) molecular variation is affected by geographical distance, and populations with different COI profiles express different substrate preference.

2. Materials and methods

2.1. Site selection

The beaches selected were assigned to arbitrary categories hereafter called “inner”, “intermediate” and “oceanic”, based on their geographical distance along the estuary (see Table 1 for toponyms and coordinates). The “inner” sites are included within the geomorphologically defined estuary (Martínez and Ortega, 2015). The incoming seawater has different salinities and broad seasonal fluctuations, that are more marked on the inner shores of the Rio de la Plata estuary (Lercari and Defeo, 2015, Table 1). It was also assumed that substrate salinity is related to local seawater salinity (Geng et al., 2016). For each of the two species under analysis (*A. brasiliensis* and *E. armata*) three beaches at different distances along the estuary were selected (Supplementary Material, Fig. S1) based on historical records of resident populations. Within the same category the geographically closest localities hosting *A. brasiliensis* and *E. armata* populations were chosen as study sites. The talitrid can be found on beaches with a variety of substrates, ranging from fine to medium sand, while the cirolanid is selective for fine to very fine sand (sand classes after Blott and Pye, 2001). The two species were found to be sympatric only on the oceanic beach (Table 1), characterised by fine sand.

Geographic distance from the inner site was selected as independent variable throughout the analysis of different traits. This was found the best option to optimize the issue of reporting results into scales meaningful to all traits analysed, often raising in the case of interdisciplinary studies (Oberg, 2010).

2.2. Population traits

The following population traits were considered: abundance (number of individuals per strip transect ind$\cdot$m^{-1}) following Defeo (1996), fecundity (juveniles/total), and sex ratio (males/females). Each beach was sampled every 2 months from August 1999 to May 2001. Samples were taken at each beach following a standard design: three transects were set perpendicular to the shoreline, and spaced 8 m apart, extending from the base of the dunes to the seaward limit of the isopod/amphipod distribution. Sampling Units (SUs) on each transect were extracted every 4 m with a 27 cm in