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Worldwide patterns of fish biodiversity in estuaries: Effect of global vs. local factors

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ABSTRACT

The main ecological patterns and the functioning of estuarine ecosystems are difficult to evaluate due to natural and human induced complexity and variability. Broad geographical approaches appear particularly useful. This study tested, at a worldwide scale, the influence of global and local variables in fish species richness in estuaries, aiming to determine the latitudinal pattern of species richness, and patterns which could be driven by local features such as estuary area, estuary mouth width, river flow and intertidal area. Seventy one estuarine systems were considered with data obtained from the literature and geographical information system. Correlation tests and generalized linear models (GLM) were used in data analyses. Species richness varied from 23 to 153 fish species. GLM results showed that estuary area was the most important factor explaining species richness, followed by latitude and mouth width. Species richness increased towards the equator, and higher values were found in larger estuaries and with a wide mouth. All these trends showed a high variability. A larger estuary area probably reflects a higher diversity of habitats and/or productivity, which are key features for estuarine ecosystem functioning and biota. The mouth width effect is particularly notorious for marine and diadromous fish species, enhancing connectivity between marine and freshwater realms. The effects of river flow and intertidal area on the fish species richness appear to be less evident. These two factors may have a marked influence in the trophic structure of fish assemblages.

1. Introduction

There is currently a global concern about biodiversity, especially its loss due to human impacts, as well as its impact in ecosystems goods and services (Díaz et al., 2006; Cardinale et al., 2012). Although there is a very large literature on this subject, most of it focuses on small spatial or temporal scales. Some contributions evaluated patterns and processes at wider scales (e.g. Oberdorff et al., 1995; Francis and Currie, 2003; Vinson and Hawkins, 2003), but for marine environments, and especially transitional ecosystems such as estuaries, these studies are extremely scarce (e.g. Attrill et al., 2001; Harrison and Whitfield, 2006a). In these studies, biodiversity is usually measured as the number of species observed or estimated to occur in an area (species richness; Gaston, 2000), which is also a simplistic approach to the role of biodiversity in ecosystem functioning.

In estuarine ecosystems, typically highly stressed by strong variations of environmental factors, ecological communities are naturally characterized by a restricted number of species, well adapted to such harsh conditions (McLusky and Elliott, 2007). The distribution patterns of fish species richness emerged in studies conducted in different parts of world (Australia, United-States of America, South Africa, Brazil, Mediterranean and Europe), and seem to be driven by local features, particularly linked to the system size and to the connectivity with the marine system (e.g. Monaco et al., 1992; Edgar et al., 1999; Pease, 1999; Araújo and de Azevedo, 2001; Ley, 2005; Harrison and Whitfield, 2006a; Franco et al., 2008; Nicolas et al., 2010b). However, no studies on estuarine fish assemblages were made at a worldwide level. The present work aims to address this topic at a global scale and to perform an analysis considering data from published studies providing a list as

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complete as possible of fish species including all the ecological guilds (cf. Elliott et al., 2007).

It is widely admitted on terrestrial and marine systems that the number of species follows a parabolic relationship according to the latitude, i.e. increasing number of species from the poles to the equator (e.g. Rex et al., 1993; Wright et al., 1993; Macpherson and Duarte, 1994; Blackburn and Gaston, 1996; Gaston, 1996; Roy et al., 1998). In estuaries, these trends were scarcely studied, being almost unknown the influence of global vs. local features on fish species richness. Three main estuarine properties, influencing fish assemblages at a local scale, emerged from the analysis of existing literature. One is the capacity to provide space, which can be described by the estuary size and induces an increase of total fish abundance and species richness with area (e.g. Whitfield, 1999; Franco et al., 2008; Nicolas et al., 2010b). The second is the capacity to recruit fish mainly for marine species but also for diadromous and freshwater fish, being this property often correlated with river flow and connectivity with the marine system (usually expressed as the estuary mouth width) (Potter et al., 1990; Martinho et al., 2007; Vinagre et al., 2009; Dolbeth et al., 2010; Robins et al., 2013). Finally, the trophic availability constitutes a major role in supporting fish populations and in particular the intertidal areas constitute important feeding areas (Costa and Elliott, 1991; Nicolas et al., 2010a). Thus, estuary size, river flow, mouth width and proportion of intertidal area were the selected drivers in this study, and together with latitude were evaluated as potential factor determining fish species richness in estuaries.

2. Materials and methods

2.1. Worldwide dataset

2.1.1. Estuary definition

The definition of estuaries proposed by Day (1980), in which an estuary is 'a partially enclosed coastal body of water which is either permanently or periodically open to the sea and within which there is a measurable variation of salinity due to the mixture of sea water with freshwater derived from land drainage' was chosen for this study. Estuaries selected under this definition included a diversity of geomorphological and hydrographic types such as permanently open estuaries, temporarily open/closed estuaries, estuarine lakes, estuarine bays and river mouths, corresponding to the main typologies defined by Whitfield (1992), based on the definition proposed by Day (1980).

2.1.2. Fish biodiversity dataset

Studies concerning the structure of fish communities in estuaries worldwide were compiled in a database. For each study, the fish species list and information relative to sampling protocol, i.e. fishing gear type, sampling effort, spatio-temporal scale, were included in the database.

The selection of studies and data to be analyzed was a critical issue in the present work. In order to allow comparisons, the selection criterion was established taking into account spatial and temporal scales and sampling techniques and effort. Inside estuaries, fish species richness presents a high variability due to salinity and temperature gradients (e.g. Marshall and Elliott, 1998; Lobry et al., 2006; Nicolas et al., 2010a). Thus, only studies with a wide spatial (i.e. sampling in all the main saline zones: oligo-, meso- and polyhaline zones) and temporal (sampling throughout the year) sampling were considered. Additionally, some recent studies (e.g. Franco et al., 2012; Pasquaud et al., 2012) also highlighted the effect of sampling techniques on species composition of the catch. In order to minimize this effect, only the estuaries subjected to intensive sampling, i.e. multi-gears (with a minimum of one passive and one active gear) but also with a high sampling effort, were included in the study. The application of these criteria resulted in a set of 71 estuarine systems (Fig. 1, Appendix), that were used in the data analyses.

2.1.3. Global and local features

Latitude (degrees) of the estuary was used as a measure of global feature, since it reflects biogeographic area, temperature and a wide number of macroclimate and large scale environmental variables. Geomorphological and hydrological characteristics, i.e. estuary area (km^2), the width of the estuary mouth (m), proportion of intertidal area (percentage of the total estuary area) and the mean annual river discharge ($m^3\ s^{-1}$), were used as measures of local features. The percentage of intertidal area was chosen instead of its absolute value because data exploration results showed a high level of correlation of this last one with the estuarine area. Latitude and mouth width were estimated using a Geographical Information System, and estuary area, percentage of intertidal area and mean annual river discharge were obtained from literature.

2.2. Data analyses

In order to identify eventual redundancies between environmental variables, correlations between each pair of variables were calculated, using Spearman correlation coefficients. In these analyses, latitude was transformed in absolute values as the main latitudinal pattern in biodiversity displays a linear relation from the poles to the equator. Generalized linear models (GLMs) were performed to identify the environmental (global and local) variables which best accounted for variability in fish species richness. Models based on a Gaussian distribution with an identity link function were chosen after preliminary tests on the data distribution. Analyses of variance (χ^2 test) were performed on each environmental variable in order to select the significant ones to be included in the models. Variables were ordered according to their decreasing significance for the explanation of the variability, and a stepwise procedure was carried out to test combinations of variables and their interaction, and to select the best model according to the Akaike Information Criterion (AIC; see Akaike, 1974 for details). The total deviance explained and relative contribution of each factor are evaluated for each model. Analyses are computed using the *stats* package of R software (R Development Core Team, 2008) and a significance level of 0.05 was considered in all test procedures.

3. Results

3.1. Relationships between species richness and global (latitude) factors

Fish species richness distribution according to latitude presented a parabolic trend with a maximum in regions between 5° and 20° N, although a high richness was also detected for an estuary located at approx. 35° S (Fig. 2a.). Nevertheless, a high variability was observed, particularly in low latitudes, with values varying between 62 and 153 species. The lowest values were registered at 40° S (24 and 27 species).

3.2. Relationships between species richness and local factors

An increasing trend between estuary area, mouth width and river flow with species richness were noticed (Fig. 2b, c and d). Despite these trends a high variability was also obtained and also an increasing variance for some variables (especially for mouth width). The relationship between species richness and percentage of intertidal area was not evident (Fig. 2e).