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Functional diversity in European estuaries: Relating the composition of fish assemblages to the abiotic environment

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ABSTRACT

Based on a large standardised data set, the present study proposed a meta-analysis to describe general patterns in the functional diversity of estuarine fish assemblage in terms of both number of species and density along the European Atlantic coast. Fish species collected from 31 European estuaries from Portugal to Scotland were allocated to functional groups according to their ecological utilization of estuaries. A clustering analysis was performed to compare the overall functional structure of estuaries based on fish composition. Generalised linear models were computed to identify relationships between large-scale abiotic and intra-estuarine descriptors and functional attributes of estuarine fish assemblages. The total number of species, and more especially of marine species, was higher in larger estuaries with a wide entrance and, locally, in polyhaline waters. The total density was mainly related to the proportion of intertidal mudflats and, locally, was greater in mesohaline waters. In terms of relative density, northern systems were dominated by marine and catadromous species, while estuarine species were prevalent in the southern ones.

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1. Introduction

Estuaries constitute essential habitats for many fish species to complete their life cycle. While it is recognised that both diadromous and estuarine resident fish species truly depend on estuaries (Ray, 2005), most species originating from the marine environment (McLusky and Elliott, 2006) exploit these areas in a more opportunistic manner (Lenanton and Potter, 1987). Estuaries act temporarily as nursery and feeding areas, especially for marine juveniles, offering a highly nutrient rich environment and shallow turbid refuges suitable to their development (Blaber and Blaber, 1980; Potter et al., 1990). Man uses estuarine goods and services intensively, enhancing trophic resource depletion and habitat degradation, e.g. through fishing, embankments and organic and metal contaminations (Le Pape et al., 2007; Dauvin, 2008). As estuarine environments are naturally characterised by enrichment in organic matter and high variability of abiotic conditions, anthropogenic stresses are difficult to distinguish from natural ones (Elliott and Quintino, 2007). The sustainability of estuarine ecosystem functions relies on a good understanding of ecological processes and the choice of adequate and efficient management measures. Fish species present a wide diversity of biological cycles and ecological compartments, making them relevant integrated indicators to reflect estuarine conditions at multiple spatial and temporal scales (Whitfield and Elliott, 2002). Their life strategies related to their ecological use of estuarine habitats supposedly reflect the functioning of estuaries (Elliott et al., 2007). Relating the functional diversity in fish assemblages to the natural abiotic variability may constitute a starting point for identifying estuarine fish assemblage reference conditions, in order to analyse subsequently the human-induced impacts and to assess the ecological status of estuarine ecosystems (Coates et al., 2007; Courrat et al., 2009; Delpech et al., in press).

Functional attributes have been widely used to describe estuarine fish assemblages (e.g. Claridge et al., 1986; Potter et al., 1990; Elliott and Dewailly, 1995; Elliott et al., 2007; Franco et al., 2008). In such a classification, fish species that have similar features in resource exploitation are assigned to the same functional group (Blondel, 2003). This functional approach allows us to reduce the complexity of fish assemblages and to focus on the use made by fish of estuarine environments and, thus, on the ecological functions of estuaries (Garrison and Link, 2000). In addition, categorisation based on functionality rather than taxonomic attributes, allows the comparison of fish assemblages belonging to different biogeographical areas (Elliott et al., 2007). In the present study, functional

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groups related to fish ecological use of estuaries and reflecting salinity preference and migration behaviour (Elliott et al., 2007; Franco et al., 2008) were used to analyse the functional diversity of fish assemblages in 31 European tidal estuaries. From the ichtyofauna analysis of 17 European estuaries of the eastern Atlantic seaboard, Elliott and Dewailly (1995) concluded that estuarine fish assemblages typically consist of "a majority equally of estuarine resident, marine adventitious and marine juveniles (25% each). with a small number of marine seasonal migrant, diadromous and freshwater adventitious species". Based on readjusted estuarine use categories, Franco et al. (2008) found a similar pattern for 38 estuaries from the Mediterranean to the Baltic regions. On the contrary, Selleslagh et al. (2009) used a homogenous fish data set that allowed a quantitative analysis of 15 Atlantic French estuaries and found that estuarine (54%) and marine migrant (33%) fish dominated assemblages in autumn in terms of relative number of individuals. Based on a larger standardised data set, the aim of the present paper was to check whether estuarine fish assemblages along the European Atlantic coast fit with a functional pattern both in terms of number of species and fish density per guild of estuarine use. The second objective was to identify the degree of variation in the functional composition of fish communities in relation to largescale abiotic descriptors of the estuarine environment and to salinity gradients. In particular, the following questions are addressed: Do larger estuaries shelter higher species diversity (number of species and/or fish densities per functional group) compared to smaller estuaries, and are species richness and density patterns according to salinity estuarine zones similar for different systems?

2. Materials and methods

2.1. Acquisition and analyses of abiotic data

A total of 31 European tidal estuaries from Portugal to Scotland (Fig. 1) were described by large-scale abiotic descriptors using an ecohydrology approach (Nicolas et al., 2010). Estuaries were characterised by several types of descriptors (Table 1): latitude; five continuous geomorphological quantitative variables (watershed area, estuarine water area, estuary mouth width and depth and continental shelf width); three geomorphological class factors (intertidal area type, main nature of littoral substrate and wave exposure), and two hydrological continuous variables (tidal range and mean annual river discharge).

A normed principal component analysis (PCA) combined with a hierarchical clustering procedure was performed on all of these abiotic descriptors (Nicolas et al., 2010). Annual river discharge, watershed area and estuary area were log-transformed to lessen the influence of the few higher values on the many lower ones. The aim of this analysis was to highlight groups of estuaries with similar physical characteristics and select synthetic and uncorrelated variable(s) to describe fish communities.

2.2. Fish data

2.2.1. Collection, classification and selection of fish data

As specified by Nicolas et al. (2010), a large fish data set based on sampling surveys in the scope of the European Water Framework Directive (WFD, European Council Directive, 2000) was stored in a database. The present study only focuses on beam trawl surveys (i.e. 1 estuary \times 1 year \times 1 season) carried out in spring and autumn between 2005 and 2007, during which salinity was measured and a total area of at least 2500 m² (Nicolas et al., 2010) was sampled. A total of 878 trawls from 48 surveys were selected. These samples were categorised into three salinity classes (SC): oligohaline

(salinity <5), mesohaline (salinity between 5 and 18) and polyhaline (salinity >18), as simplified from the Venice classification system (Courrat et al., 2009).

Each fish caught was identified at species level. In Spanish Basque systems, Gobiidae species from Pomatoschistus genera were not determined and could correspond to different species. To counteract this bias, all *Pomatoschistus* were considered to represent one unique estuarine resident species. Each of the other species was assigned to a category related to their estuarine use. Elliott et al. (2007) emphasised the need for a standardisation of functional typologies and proposed an estuarine use functional group that may be applied to any parts of the world. Our functional classification corresponded to the one adapted by Franco et al. (2008) from Elliott et al. (2007) to the European estuarine waters. The different categories were: estuarine species (ES); marine migrants (MM); marine stragglers (MS); anadromous species (AN); catadromous species (CA) and freshwater species (FS). The allocation of a species to one specific category was based on both previously mentioned sources and local expert knowledge (Table 2). Some allocations were not straightforward, especially for the European flounder Platichthys flesus and the thin lip grey mullet Liza ramada. While P. flesus was classified either as catadromous (Lobry et al., 2003; Kottelat and Freyhof, 2007), marine migrant (Thiel et al., 2003; Franco et al., 2008) or estuarine resident (Elliott and Dewailly, 1995; Selleslagh et al., 2009), L. ramada was either catadromous (Elliott and Dewailly, 1995; Franco et al., 2008; Selleslagh et al., 2009) or marine migrant (Potter and Hyndes, 1999). These species can spend a long lifetime within estuaries (Potter and Hyndes, 1999; Elliott et al., 2007). However, since they were observed to spawn at sea and to be able to enter freshwater (Kottelat and Freyhof, 2007), they were grouped in the catadromous category together with the European eel Anguilla anguilla (Tsukamoto et al., 2002).

2.2.2. Calculation of fish assemblage descriptors

Abundances were divided by the corresponding trawl sampled surface. These resulting densities of individuals (ind. 1000 m⁻²) were summed per functional group and per trawl sample then, taking into account their underlying lognormal distribution, logtransformed to reduce the influence of exceptionally high densities. These log-transformed densities ln(Dens + 1) per functional group were averaged per survey then per estuary (pool of seasons and years) to compare the overall functional structure among estuaries. In a second approach analysing intra-estuarine processes, these indices were averaged at the salinity class scale (three classes per survey quite systematically, per season and estuary). Similarly, the total number of species (SR for species richness) was calculated per functional group and per survey and the same operation was carried out at the scale of the salinity class. Next, the number of species was divided by the log-transformed total sampled surface (m^2) carried out during a survey (S) or per salinity class (S_{sc}) to standardise species richness in relation to sampling effort (Nicolas et al., 2010). Consequently, indices based on species richness were referred to as SR/ln(S) or $SR/ln(S_{SC})$. To compare standardised values of species richness between estuaries, the number of species is expressed for a theoretical 1000 m² trawl haul.

2.2.3. Clustering analyses of estuaries based on fish assemblage descriptors

Analyses were carried out in terms of both number of species and density of individuals per functional group per estuary (pool of seasons and years). Groups of estuaries displaying similar functional composition were highlighted through a hierarchical clustering analysis using the Ward agglomerative method based on square-root-transformed Bray—Curtis similarity matrices (Faith

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