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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 dataset, 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.

Keywords

Functional diversity, fish assemblage, Europe, tidal estuaries, habitat, glm

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 would constitute a starting point for better identifying estuarine fish assemblage reference conditions, 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

1 exploitation are assigned to the same functional group (Blondel, 2003). This functional
2 approach allows to reduce the complexity of fish assemblages and to focus on the use made
3 by fish of estuarine environments and, thus, on the ecological functions of estuaries (Garrison
4 and Link, 2000). In addition, categorization based on functionality rather than taxonomic
5 attributes, allows the comparison of fish assemblages belonging to different biogeographical
6 areas (Elliott et al., 2007). In the present study, functional groups related to fish ecological use
7 of estuaries and reflecting salinity preference and migration behaviour (Elliott et al., 2007;
8 Franco et al., 2008) were used to analyse the functional diversity of fish assemblages in 31
9 European tidal estuaries. From the ichthyofauna analysis of 17 European estuaries of the
10 eastern Atlantic seaboard, Elliott and Dewailly (1995) concluded that estuarine fish
11 assemblages typically consist of “a majority equally of estuarine resident, marine adventitious
12 and marine juveniles (25% each), with a small number of marine seasonal migrant,
13 diadromous and freshwater adventitious species”. Based on readjusted estuarine use
14 categories, Franco et al. (2008) found a similar pattern for 38 estuaries from the
15 Mediterranean to the Baltic regions. On the contrary, Selleslagh et al. (2009) used a
16 homogenous fish data set that allowed a quantitative analysis of 15 Atlantic French estuaries
17 and found that estuarine (54%) and marine migrant (33%) fish dominated assemblages in
18 autumn in terms of relative number of individuals. Based on a larger standardised data set, the
19 aim of the present paper was to check whether estuarine fish assemblages along the European
20 Atlantic coast fit with a functional pattern both in terms of number of species and fish density
21 per guild of estuarine use. The second objective was to identify the degree of variation in the
22 functional composition of fish communities in relation to large-scale abiotic descriptors of the
23 estuarine environment and to salinity gradients. In particular, the following questions are
24 addressed: Do larger estuaries shelter a higher species diversity (number of species and/or fish
25 densities per functional group) compared to smaller estuaries? Do species richness and
26 density patterns according to salinity estuarine zones are similar for different systems?

2. Materials and Methods

2.1. Acquisition and analyses of abiotic data

A total number 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 2500m² (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 caught fish 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) emphasized 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 thinlip 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 m²) were summed per functional group and per trawl

sample then, taking into account their underlying lognormal distribution, log-transformed 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 (m²) 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 1000m² 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 et al., 1987; Legendre and Andersson, 1999). The groups and distances to centroids were plotted on the first axes of a principal coordinate analysis (PCoA), using the function *betadisper[vegan]* on the R software (R Development Core Team, 2005). For each identified cluster of estuaries, the relative functional composition in density and species richness were analysed.

2.3. Statistical analyses of the link between abiotic descriptors and fish functional groups

1 Patterns in the standardized estimates of species richness and fish densities, globally and per
 2 functional group, averaged per season and estuary then per salinity class, were analysed to
 3 identify the degree of variation in the functional composition of a fish assemblage related to
 4 large-scale abiotic descriptors of the estuarine environment and to salinity gradients. The
 5 identification of best explanatory descriptors was based on generalised linear models.
 6 Preliminary graphic tests on data distribution showed that the Gaussian law was the most
 7 suitable to model both $SR/\ln(S_{sc})$ and $\ln(Dens+1)$ indices. To reduce the presence of zero-
 8 values while still keeping an ecological relevance, marine migrant and marine straggler
 9 species were pooled together as marine species (M) and catadromous and anadromous species
 10 as diadromous species (DIA, Table 1). Freshwater species, rarely present and in low densities,
 11 were not modelled.

12 Within models, we introduced factors related to the sampling procedure, when significant, in
 13 order to account for possible bias; these factors correspond to between-seasons and between-
 14 salinity-types variability. The between-years effect was not considered because most estuaries
 15 were sampled in one year only. This is the reason why, when an estuary was sampled over
 16 two years, data were averaged per season then per salinity class. Thereafter, abiotic
 17 descriptors (X_i) were added to the models, so that the GLM could be written as follows:

18 Indices = Season + SC + $X_1 \dots + X_i \dots + X_n$

19 The method used to select the best combination of abiotic descriptors was similar to Nicolas
 20 et al. (2010). Each preselected descriptor was first tested separately in models. To select the
 21 best explicative variables from among the significant ones, a stepwise procedure was used.
 22 The best final combination of descriptors was determined according to analyses of variance
 23 (Chi-square test at 5% level), Akaike Information Criterion (Sakamoto et al., 1986),
 24 ecological relevance and graphical analysis of residuals. The nature of the effect of the
 25 continuous explicative variables (i.e. positive or negative) on fish indices was identified from
 26 the sign of the corresponding coefficient(s). For the class factors, modalities were ordered

according to their corresponding coefficient and the difference between two adjoining modalities was checked with a student test (at 5% level).

3. Results

3.1. Abiotic contrasts among estuaries and preselection of potentially explanatory descriptors

The PCA plot based on abiotic data (60.2% of total inertia for the first two main components, Fig. 2) discriminated five distinct clusters of estuaries (hereafter referred as 'clusters'). Cluster A consisted of the smallest estuaries with a very narrow continental shelf, including the seven Spanish estuaries, the Goyen and Seudre (France), and the Mira (Portugal). Localised within the English Channel, estuaries from cluster B were characterized by low depth at the river mouth, high proportion of intertidal area and a very wide continental shelf. Cluster C pooled estuaries of intermediate size: three French estuaries in the Bay of Biscay and the two Scottish systems (the Forth and Tay). Cluster D consisted of the largest southern systems, characterized by mesotidal estuaries of moderate size associated with a huge watershed and a warm, dry climate. Last, the three widest French systems (cluster E) presented the highest river discharge.

The correlation circle (Fig. 2) highlighted the strong positive correlations between mean annual river discharge, watershed area and estuary area ($0.68 < r < 0.92$, $p\text{-value} < 0.0001$) and between estuary area and entrance width ($r = 0.69$, $p\text{-value} < 0.0001$). Mean annual river discharge, which reflected the overall system size, was selected for further tests of the effect of system size on fish assemblage attributes. Entrance width, which informed on the connectivity of the estuary with the marine environment, was used as an indicator of marine influence. Latitude, continental shelf width and tidal range were also positively correlated ($0.61 < r < 0.76$, $p\text{-value} < 0.0001$): continental shelf width and tidal range increased from the southern Portuguese coast towards the northern English Channel (Fig. 1). Continental shelf

width was selected for further analyses of fish assemblages. The semi-quantitative intertidal class factor, which was negatively related to the entrance depth variable, ($r = -0.4$, $p\text{-value} < 0.05$), was the last selected descriptor. As most estuaries (58%) were well protected against waves, the wave exposure factor did not discriminate estuaries. Finally, the littoral substrate class factor was redundant with the continental shelf width effect.

3.2. Relative functional composition of estuarine fish assemblages

Over the entire study area, a total of 109 species from 42 different families were identified: among them 35% were marine straggler, 30% marine migrant, 15% freshwater, 12% estuarine, 5.5% anadromous and 3% catadromous species (Table 2).

Regarding the functional composition in terms of number of species, estuaries were categorised into three clusters (hereafter referred as ‘groups’, Fig. 3). Group I, which comprised most of the largest systems classed in clusters D and E (except the Douro estuary, Fig. 2), had the greatest number of species (with an average \pm confidence interval of 13 ± 1 for a 1000m² trawl haul), while the group III, comprising five small systems from clusters A and B, had the lowest species diversity ($SR = 5 \pm 2$ species). On average, estuarine fish assemblages in both groups I and II included all functional modalities and were largely dominated by marine species (i.e. MM and MS, on average 60.4% in relative proportion), and more particularly by marine migrant species ($38.6 \pm 2.4\%$ of the total number of species). On the contrary, group III was characterised by the absence of species with a freshwater origin, i.e. anadromous and freshwater species, and was rather mainly occupied by estuarine species ($60.6 \pm 20\%$).

In terms of density, two groups were distinguished among the estuaries (Fig. 4). All functional attributes were represented in the estuaries of the first group, while in the second, species with a freshwater origin (FS and AN) were lacking. In group I (Fig. 4), individuals from marine migrant species and catadromous species were the major contributors to total

density with a relative proportion of $31.7 \pm 3.7\%$ and $21.7 \pm 4.1\%$, respectively. By contrast, estuaries categorised in group II were largely dominated by the density of estuarine species ($45.8 \pm 9.5\%$). Group II consisted of ten of the smallest systems (clusters A and B, Fig. 2) and the three largest southernmost systems (cluster D). Anadromous species were present in half of the studied estuaries and were best represented in terms of density in the northernmost Tay (24%) and Forth (32.2%) estuaries. Freshwater species were found in eleven French systems, where they were low both in number (on average $SR = 1.4 \pm 0.7$ freshwater species per 1000m²) and in density of individuals ($14.6 \pm 5.4\%$ of total catch).

3.3. Links between the functional composition of fish assemblage and the abiotic estuarine environment

Salinity class significantly influenced total species richness in estuaries (Table 3a). The polyhaline area displayed on average the highest total number of species ($SR = 80 \pm 11$ for a 1000 m² trawl haul) compared to the oligo- and mesohaline areas (50 ± 8 species). Contrary to marine and estuarine species, the diadromous species were more numerous in oligo- and mesohaline areas ($SR = 14 \pm 3$ species) than in the salty downstream (10 ± 3 species, Table 3a). Most of the freshwater individuals (84%) were caught in the oligohaline area. The annual mean river discharge further explained the total number of species and the number of marine species with a positive effect (Table 3a). The three largest systems categorised in cluster E of Fig. 2 had a much higher total number of species ($SR = 15 \pm 3$ species) than the small estuaries grouped in cluster A (6 ± 2 species). In addition, entrance width was positively related to the total number of species and to the number of diadromous species (Table 3a). Fish density in the mesohaline area (64 ± 42 ind.1000m⁻²) was significantly higher, particularly for marine species, than in the oligohaline (36 ± 22) and polyhaline areas (22 ± 7 , Table 3b). Density of diadromous fish was higher both in oligo- and mesohaline areas ($16.5 \pm$

9.5 ind.1000m⁻²) than in polyhaline areas (3.7 ± 1.3 ind.1000m⁻², Table 3b). The relative intertidal area also explained a statistically significant part of variability in the total fish density and more especially the density of marine and estuarine species (Table 3b). Estuaries with the greatest proportion of intertidal mudflats (80-100% of total estuary area) had the highest densities (61 ± 31 ind.1000m⁻²), in particular with comparison to estuaries with less than 20% of intertidal mudflats (20 ± 15 ind.1000m⁻²). Entrance width had a further positive effect on the total density, the density of marine species and the density of diadromous species (Table 3b). Finally, continental shelf width also had a positive effect on diadromous species density (Table 3b), which was four times higher in the eastern Channel estuaries (25.7 ± 23.8 ind.1000m⁻²) than elsewhere (6.2 ± 2.2 ind.1000m⁻²).

4. Discussion

4.1. Prerequisites for a large-scale comparison of estuarine fish assemblages

A relevant and consistent comparison of estuarine fish assemblages on a large scale requires standardised fish data in relation to the type of fishing gear used, the sampling effort and the sampling period. Compared to the previous large scale qualitative analyses of European estuarine fish assemblages (Elliott and Dewailly, 1995; Franco et al., 2008), the present data set, based solely on beam trawl samples, was more homogenous. However, differences in the dimensions of the net, mesh size and weight exist between the beam trawls used for different surveys, according to the country and the size of estuaries (Nicolas et al., 2010). Trawl samples could also differ due to haul duration and speed. Thus, this absence of a standardised sampling protocol within the WFD framework still enhances heterogeneity problems for statistical analyses and dampens accuracy of the analysis. Nonetheless, by applying a transformation to both species richness (Nicolas et al., 2010) and abundance data based on the sampled surface, these differences were partly taken into account and our data were estimated

1 sufficiently standardised to compare fish assemblages in both qualitative and quantitative
2 terms.

3 Latitudinal variability in fish reproduction and recruitment peaks together with seasonal
4 patterns in migratory activities was expected to influence results (Potter and Hyndes, 1999;
5 Selleslagh et al., 2009). Nevertheless, among the 31 studied estuaries, the between-season
6 variability was never found significant in the models. Pooling spring and autumn in the
7 present comparative analyses appeared relevant and enabled us to consider a large data set,
8 since only 42% of the estuaries were sampled at both seasons.

9 Regarding the functional description of fish species, such large-scale comparison requires
10 clear definitions of the chosen functional groups and standardised allocations for each species
11 (Elliott et al., 2007). Nonetheless, as detailed for *P. flesus* and *L. ramada* species in the
12 Materials and Methods section, the allocation of some species to a specific functional group
13 can differ greatly from an author to another. Moreover, because of local fish behavioural
14 adaptations, Franco et al. (2008) recommended the use of flexible allocations for one species
15 to account for its associated geographical variability. For most of the identified fish species,
16 especially when they are of no fisheries interest, further research on their biology is required
17 at local level to allocate species to guilds according to region. As a consequence, these
18 inconsistencies in functional attributions may have a marked influence on the results. For
19 instance, Selleslagh et al. (2009), found for the three French Eastern English Channel Canche,
20 Authie and Somme estuaries, a mean relative proportion of estuarine individuals of 43%. But,
21 when allocating *P. flesus* as catadromous and not as estuarine species as done Selleslagh et al.
22 (2009), this proportion was reduced by 10%. Nevertheless, even if these problems of
23 allocation generate uncertainty, general patterns can be inferred from the present study.

24 25 **4.2. The functional diversity of European estuarine ichthyofauna: general patterns**

1 Like the composition of fish assemblages found by Elliott and Dewailly (1995), the present
2 estuarine fish assemblages were composed of a small number of diadromous and freshwater
3 species and a majority of marine migrant, marine straggler and estuarine species. The large
4 proportion of marine, and more precisely marine migrant species, and especially their juvenile
5 stage, emphasised the great importance of estuaries as fish nursery grounds (e.g. Elliott and
6 Dewailly, 1995; Potter and Hyndes, 1999; Laffaille et al., 2000; Franco et al., 2008; Courrat
7 et al., 2009) and their role in maintaining coastal stocks (Rochette et al., *in press*).
8 Nonetheless, contrary to Elliott and Dewailly's study (1995), these marine and estuarine
9 species were not present in equal proportions in all estuaries. Although Elliott and Dewailly
10 (1995) advanced 'common patterns of estuarine usage irrespective of the differences between
11 the estuaries', the present analyses highlighted different patterns among estuaries in terms of
12 both number of species and density. Large-scale abiotic gradients were shown to significantly
13 influence the functional diversity of fish assemblages:

14 ***4.2.1. The effect of system size and entrance width on species richness***

15 In terms of number of species, the clustering analysis emphasised that larger systems
16 presented a higher functional diversity and a higher total number of species. This relationship
17 between species richness and system size was confirmed by the GLM analyses and has
18 already been reported in other worldwide studies (Monaco et al., 1992; Pease, 1999; Harrison
19 and Whitfield, 2006; Nicolas et al., 2010). Nevertheless, while system size slightly influenced
20 the number of marine species, it did not explain the number of estuarine or diadromous
21 species. The increase in the total number of species according to the size of the estuarine
22 system is often related to a diversity of habitats (Monaco et al., 1992; Wootton, 1998; Nicolas
23 et al., 2010). However, this hypothesis requires further tests to determine whether the
24 heterogeneity of estuarine habitats influences the total number of species (Pihl et al., 2002).
25 Here, the width at the mouth further promoted total species richness, which tends to confirm
26 that the enhancement of high-salinity habitats favoured the exploitation of the estuary by

more different species (Nicolas et al., 2010). Furthermore, the positive influence of entrance width on the density of marine species suggests that further seawater penetration raises the migration and concentration of some marine individuals into estuaries. The entrance width also promoted diadromous migrant species both in terms of number of species and of density, probably due to the attraction of diadromous species for large fluvial plumes (Boehlert and Mundy, 1988; Tosi et al., 1990; Tosi and Sola, 1993). Nonetheless, as confirmed from the present analysis, the distribution of diadromous species, and more especially of anadromous species, are also related to biogeographical aspects, including homing and population decline (McDowall, 1988).

4.2.2. The contrast between northern and southern estuaries in terms of density

In terms of relative density, the clustering analysis revealed that northern systems sheltered fish of all estuarine use categories and were dominated by marine and catadromous species (group I, Fig. 4), while southern systems were dominated by estuarine species (group II, Fig. 4). The GLM analyses also revealed higher densities of diadromous species in northern estuaries and more particularly in the eastern English Channel compared to southern systems. However, these analyses did not demonstrate a latitudinal contrast in the density of estuarine species. Models showed that estuaries in the English Channel, which generally display a high percentage of intertidal area, exhibited among the highest densities in both marine and estuarine species. Thus, although southern estuaries were dominated by estuarine species, the density of these species appeared nonetheless higher in northern English Channel systems. Claridge et al. (1986) found that estuarine species represented only 0.6% of the total catch in the inner Severn estuary. Potter and Hyndes (1999) presumed the situation was similar in all macrotidal holarctic estuaries and explained this low representation of estuarine species as a result of their strong hydrodynamics that prevent the eggs and larvae being able to remain inside the estuary. However, the present dataset showed that even in the widest megatidal Loire and Seine estuaries, estuarine species were well represented, with 11 and 14.5%

1 respectively of the total catch, moreover for high total densities in these systems. Moreover,
 2 southern systems (group II, Fig. 4) were clearly dominated by estuarine species which
 3 represented on average 45% of total species richness (from 31% in the Mira estuary to 100%
 4 in the Urumea estuary). In contrast to the northern systems, these southern systems were
 5 characterised by a reduced freshwater influence due to a warmer and drier climate and by
 6 small tidal exchanges. This higher hydrological steadiness associated with high salinity values
 7 appears to provide a more favourable environment for the recruitment of resident species
 8 (Potter and Hyndes, 1999). This may explain the high representation of estuarine individuals
 9 in southern estuaries and the low number of species with freshwater affinities, i.e.
 10 anadromous and freshwater species. Accordingly, comparing sampling surveys carried out in
 11 the Tejo estuary between 1979 and 2002, Costa et al. (2007) showed that the density of
 12 estuarine species and marine species was higher in dry years than in wet ones. Martinho et al.
 13 (2007) reported that a severe drought occurred between summer 2003 and June 2006 in
 14 Portugal and observed subsequently an increase in marine stragglers in the Mondego estuary.
 15 Consequently, higher temperatures appeared to promote species with marine affinities (i.e.
 16 marine and estuarine species, Potter and Hyndes, 1999; Costa et al., 2007). In future analyses,
 17 it would be interesting to test the effect of both water temperature and river discharges on a
 18 more simultaneous temporal scale.

20 ***4.2.3. The effect of intertidal area on density***

21 The intertidal area type was the factor that accounted for the greatest deviance in total density,
 22 and more especially in density of marine and estuarine species. Elliott and Taylor (1989a;
 23 1989b) found in the Forth estuary that the biomass and the production of macrofauna per unit
 24 area were higher in the intertidal mud-flats than in the subtidal area. Most fish in estuaries
 25 have been shown to feed on benthic invertebrates (de Sylva, 1975; Elliott and Taylor, 1989b;
 26 Costa and Elliott, 1991); the intertidal areas constitute the dominant feeding area for the

1 estuarine fish populations (Costa and Elliott, 1991) and promote fish density. Both estuarine
 2 and marine species, and more particularly juveniles, preferred shallow systems with extensive
 3 intertidal mudflats, generally turbid, where they can find great food availability and reduced
 4 predation pressure (Blaber and Blaber, 1980). This also underlined the fact that small
 5 estuaries with a high proportion of intertidal flats could be as important as larger systems for
 6 their nursery function, displaying on average higher fish density per unit area (e.g. 44.9 ± 15.1
 7 ind.1000 m⁻² in the Authie estuary vs 4.5 ± 1.2 ind.1000 m⁻² in the Gironde estuary). The loss
 8 of intertidal area through channelization or land reclamation in these estuaries might thus
 9 have a heavy impact on fish production, as demonstrated in the Forth (McLusky et al., 1992)
 10 and the Seine (Rochette et al., *in press*) estuaries.

12 ***4.3. Intra-estuarine organisation of fish assemblages: the effect of the salinity gradient***

13 The present study highlighted the intra-estuarine structure of the fish assemblages in terms of
 14 both number of species and density. While the upper low-salinity estuary areas were
 15 dominated by freshwater and diadromous species, the lower high-salinity parts contained a
 16 majority of marine and estuarine species. As expected, and highlighted in other studies (Potter
 17 et al., 1990; Thiel et al., 1995; Pease, 1999), a high-salinity area promoted species richness.

18 This result further emphasises that large estuaries, which often present the entire range of
 19 haline habitats, may exhibit greater total species richness (Nicolas et al., 2010).

20 On the other hand, the total maximum fish density was observed in the middle mesohaline
 21 parts of estuaries, where intertidal mudflats that display a high carrying capacity (Elliott and
 22 Taylor, 1989b; Costa and Elliott, 1991) might predominate. Indeed, in estuarine mesohaline
 23 areas, where the environmental conditions are especially harsh (i.e. high variability in
 24 hydrodynamics, salinity, turbidity and sediment erosion/deposition), few species are
 25 physiologically able to colonize, inducing a low biological competition but high abundances
 26 (McLusky and Elliott, 2006). Furthermore, this reduced salinity area is often associated with

1 the presence of fine sediment particles (Harris and Heap, 2003; McLusky and Elliott, 2006)
2 with a high content of organic matter, which are particularly suitable for the development of
3 benthic invertebrates (Moore, 1978; Elliott and Taylor, 1989b; Eisma and Cadee, 1990).
4 These great abundances of benthic preys may be the origin of the observed location of the
5 high fish density (Nicolas et al., 2007). The high density of marine species in the same
6 mesohaline parts may also be partly related to a reduction in osmoregulation energy cost for
7 lower salinities (Potter et al., 1990). In contrast, the density of estuarine species, which are by
8 definition well-adapted to the high variability of the estuarine environment, appeared not to be
9 influenced by salinity, as found in other single-site studies (Henderson and Holmes, 1991;
10 Power et al., 2000). The density of diadromous species, able to osmoregulate, was higher in
11 both meso- and oligohaline estuary areas, while, as expected (Franco et al., 2008), the
12 freshwater species were restricted to the oligohaline areas.

14 5. Conclusions

15 The present study highlighted four main trends in the functional diversity of fish assemblages:
16 (1) system size and entrance width, which facilitate seawater penetration, promoted functional
17 diversity and the total number of species by enhancing density and number of marine species;
18 (2) northern estuaries were dominated by marine and catadromous species, while estuarine
19 resident species were prevalent in southern estuaries, potentially due to more stable hydrology
20 and higher temperature; (3) estuaries consisting for the most part of intertidal mudflats were
21 further highlighted as having a crucial role of nursery and trophic support for juvenile fish; (4)
22 fish assemblages were structured by the salinity gradient: high-salinity habitats concentrated
23 maximum species richness, consisting mainly of marine and estuarine species, mesohaline
24 habitats exhibited the greatest total density and especially the greatest density of marine
25 species; low-salinity habitats had the greatest density of diadromous species and could also
26 present some freshwater species.

1 Finally, despite the highly variable and complex functioning of estuaries that tends to hide
2 anthropogenic impacts (the estuarine quality paradox, Elliott and Quintino, 2007), general
3 patterns in fish assemblages reflecting natural variability can be distinguished. As a result,
4 when developing fish indicators to assess the level of anthropogenic pressures in estuaries
5 (Courrat et al., 2009; Delpech et al., *in press*), considering significant natural explanatory
6 descriptors such as system size, entrance width and salinity would greatly improve pressure-
7 impact models and the precision of fish-based indicators. Moreover, these descriptors are, for
8 most of them, easily available. Nonetheless, to improve the understanding of the relationship
9 between fish and their environment, more precise investigations at a smaller habitat scale
10 should be carried out.

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14
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Table 1: List of the abiotic attributes used to describe the estuarine environment, with their abbreviation and their ranges (minimum – maximum) and their units for quantitative variables or their classes for class factors.

Table 2: List of fish species caught during the 48 selected European surveys with the estuarine use functional group they were allocated in, their occurrence in percentage and their mean density value (\pm confidence interval) in number of individuals per 1000m².

Table 3: Analysis of deviances for the generalized linear models computed on both (a) number of species (SR) and (b) densities (Dens) of each functional group category used as response variables with regards to selected descriptors (Intro. Var.) of abiotic attributes of estuaries. Df: degrees of freedom; Expl. Dev.: explained deviance in percentage per introduced descriptor. Sig.: significance (Chi square test), *: when p-value <5%, **: <1%, ***: <0.1%. Slope: slope sign when the explicative descriptor was a quantitative variable; for the class factors, all modalities were presented in decreasing order according to their effect. When the difference between two adjoining modalities was significant (student test), the symbol “>” was applied. Abbreviations of descriptors are detailed in Table 1.

Table 1

Abbreviations	Abiotic attributes	Ranges and units or classes
Continuous explaining variables		
LAT	Latitude	37.2 - 56.5 decimal degrees
CSW	Continental shelf width	4 - 284 kilometres
LS	Main Littoral substrate	1: Mud; 2: Mud/Sand; 3: Sand; 4: Sand/Gravel; 5: Rock
TR	Tidal range	2.9 - 11.8 metres
RD	Mean annual river discharge	2 - 960 metres cube per second
WA	Watershed area	105 – 117 955 square kilometres
EA	Estuary area	0.5 - 533 square kilometres
EW	Entrance width	0.2 - 16 kilometres
ED	Entrance depth	0.5 - 29 metres
Categorical explaining factors		
IA	Intertidal area type	1: 0-20%; 2: 20-40%; 3: 40-60%; 4: 60-80%; 5: 80-100%
WE	Wave exposure	1: extremely exposed; 2: moderately exposed; 3: sheltered
SC	Salinity class	1: oligohaline; 2: mesohaline; 3: polyhaline
S _{sc}	Sampled surface per salinity class	1 000 – 174 155 square kilometres

Table 2

Species	Functional group	Occurrence (% among the 48 surveys)	Mean density
<i>Abramis brama</i>	FS	13	5.9 ± 3.1
<i>Agonus cataphractus</i>	MS	8	2.6 ± 2.2
<i>Alburnus alburnus</i>	FS	2	172.9 ± 643
<i>Alosa alosa</i>	AN	4	0.6 ± 0.2
<i>Alosa fallax</i>	AN	4	0.3 ± 0.1
<i>Ameiurus melas</i>	FS	13	0.9 ± 0.6
<i>Ammodytes tobianus</i>	MS	19	1.5 ± 0.4
<i>Anguilla anguilla</i>	CA	56	2.1 ± 0.4
<i>Aphia minuta</i>	MS	27	4.2 ± 1.0
<i>Argyrosomus regius</i>	MS	6	2.6 ± 0.5
<i>Arnoglossus imperialis</i>	MS	2	1.1 ± 0.0
<i>Atherina boyeri</i>	ES	2	1.0 ± 0.0
<i>Atherina presbyter</i>	MM	17	1.2 ± 0.3
<i>Barbus barbus</i>	FS	6	1.3 ± 0.9
<i>Blicca bjoerkna</i>	FS	10	11.1 ± 13.9
<i>Buglossidium luteum</i>	MS	6	5.3 ± 6.5
<i>Callionymus lyra</i>	MS	29	1.7 ± 0.7
<i>Callionymus maculatus</i>	MS	2	3.4 ± 0.0
<i>Carassius carassius</i>	FS	2	1.8 ± 2.3
<i>Chelidonichthys lucernus</i>	MM	10	0.9 ± 0.4
<i>Chelon labrosus</i>	MM	2	0.3 ± 0.0
<i>Ciliata mustela</i>	ES	13	1.0 ± 0.3
<i>Clupea harengus harengus</i>	MM	15	20.0 ± 16.5
<i>Conger conger</i>	MS	2	1.2 ± 0.1
<i>Crystallogobius linearis</i>	MS	2	0.3 ± 0.0
<i>Cyprinus carpio carpio</i>	FS	2	0.9 ± 0.0
<i>Dicentrarchus labrax</i>	MM	65	4.4 ± 0.8
<i>Dicentrarchus punctatus</i>	MM	13	0.6 ± 0.2
<i>Dicologlossa cuneata</i>	MM	4	0.3 ± 0.0
<i>Diplodus annularis</i>	MS	2	3.3 ± 1.8
<i>Diplodus bellottii</i>	MM	4	1.6 ± 0.5
<i>Diplodus cervinus cervinus</i>	MM	2	0.8 ± 0.0
<i>Diplodus sargus</i>	MS	19	3.8 ± 1.7
<i>Diplodus vulgaris</i>	MS	13	4.9 ± 1.7
<i>Echiichthys vipera</i>	MS	29	1.8 ± 0.7
<i>Engraulis encrasicolus</i>	MM	38	4.2 ± 1.3
<i>Entelurus aequoreus</i>	MS	4	0.9 ± 0.0
<i>Eutrigla gurnardus</i>	MM	2	1.4 ± 0.0
<i>Gadus morhua</i>	MM	2	1.1 ± 0.0
<i>Gaidropsarus vulgaris</i>	MS	2	0.5 ± 0.4
<i>Gasterosteus aculeatus aculeatus</i>	ES	15	0.8 ± 0.3
<i>Gobio gobio gobio</i>	FS	2	5.2 ± 7.3
<i>Gobius niger</i>	ES	40	6.0 ± 2.1
<i>Gobiusculus flavescens</i>	MS	2	6.5 ± 5.0
<i>Gymnocephalus cernuus</i>	FS	6	1.2 ± 0.8
<i>Halobatrachus didactylus</i>	MS	8	5.5 ± 1.7
<i>Hippocampus guttulatus</i>	ES	6	0.9 ± 0.7
<i>Hippocampus hippocampus</i>	ES	15	1.2 ± 0.4
<i>Hyperoplus immaculatus</i>	MM	2	3.7 ± 0.0
<i>Hyperoplus lanceolatus</i>	MS	4	1.1 ± 1.3
<i>Labrus bergylta</i>	MS	2	1.8 ± 0.0

<i>Lampetra fluviatilis</i>	AN	8	1.1 ± 0.7
<i>Lepadogaster lepadogaster</i>	MS	2	0.7 ± 0.0
<i>Lepomis gibbosus</i>	FS	2	1.6 ± 0.0
<i>Lesueurigobius friesii</i>	MS	4	2.1 ± 2.0
<i>Leuciscus leuciscus</i>	FS	2	6.6 ± 0.0
<i>Limanda limanda</i>	MM	4	2.8 ± 2.3
<i>Lithognathus mormyrus</i>	MS	4	1.1 ± 0.7
<i>Liza aurata</i>	MM	13	1.4 ± 0.7
<i>Liza ramada</i>	CA	31	3.0 ± 1.1
<i>Merlangius merlangus</i>	MM	15	2.3 ± 0.7
<i>Merluccius merluccius</i>	MS	6	0.4 ± 0.1
<i>Monochirus hispidus</i>	MS	2	4.0 ± 1.9
<i>Mullus barbatus barbatus</i>	MM	2	0.3 ± 0.0
<i>Mullus surmuletus</i>	MM	8	3.1 ± 3.3
<i>Myoxocephalus scorpius</i>	MM	2	2.2 ± 0.0
<i>Osmerus eperlanus</i>	AN	13	5.2 ± 1.7
<i>Pagrus pagrus</i>	MS	4	1.9 ± 1.1
<i>Parablennius gattorugine</i>	MS	4	0.9 ± 0.3
<i>Pegusa lascaris</i>	MS	4	2.8 ± 4.0
<i>Perca fluviatilis</i>	FS	4	8.3 ± 14.4
<i>Petromyzon marinus</i>	AN	2	0.2 ± 0.0
<i>Platichthys flesus</i>	CA	69	10.6 ± 2.5
<i>Pleuronectes platessa</i>	MM	44	6.8 ± 1.9
<i>Pomatoschistus spp</i>	ES	94	27.1 ± 6.6
<i>Psetta maxima</i>	MM	4	1.0 ± 0.7
<i>Raja clavata</i>	MS	13	0.7 ± 0.4
<i>Raja undulata</i>	MS	2	1.2 ± 0.2
<i>Rajella fyllae</i>	MS	2	0.3 ± 0.0
<i>Rutilus rutilus</i>	FS	13	5.8 ± 6.0
<i>Salmo trutta trutta</i>	AN	2	0.7 ± 0.0
<i>Sander lucioperca</i>	FS	6	2.3 ± 1.2
<i>Sardina pilchardus</i>	MM	6	0.7 ± 0.5
<i>Sardinella aurita</i>	MS	2	1.5 ± 0.0
<i>Sarpa salpa</i>	MM	2	1.2 ± 0.0
<i>Scophthalmus rhombus</i>	MM	10	1.2 ± 0.4
<i>Scorpaena notata</i>	MS	4	1.2 ± 0.0
<i>Silurus glanis</i>	FS	2	0.4 ± 0.0
<i>Solea senegalensis</i>	MM	27	2.3 ± 0.6
<i>Solea solea</i>	MM	73	6.3 ± 1.1
<i>Sparus aurata</i>	MM	2	1.0 ± 0.4
<i>Spinachia spinachia</i>	ES	4	0.9 ± 0.2
<i>Spondyllosoma cantharus</i>	MM	4	1.8 ± 0.9
<i>Sprattus sprattus sprattus</i>	MM	44	15.9 ± 6.4
<i>Squalius cephalus</i>	FS	4	7.2 ± 6.6
<i>Symphodus bailloni</i>	MS	8	2.3 ± 1.7
<i>Symphodus cinereus</i>	ES	2	7.3 ± 0.0
<i>Symphodus melops</i>	MS	2	4.6 ± 0.1
<i>Symphodus roissali</i>	MM	4	0.8 ± 1.0
<i>Syngnathus acus</i>	ES	38	2.0 ± 0.4
<i>Syngnathus rostellatus</i>	ES	25	1.6 ± 0.3
<i>Syngnathus typhle</i>	ES	4	1.5 ± 0.5
<i>Torpedo torpedo</i>	MS	4	1.6 ± 0.7
<i>Trachurus trachurus</i>	MM	8	0.7 ± 0.4
<i>Trigla lyra</i>	MM	2	0.2 ± 0.0
<i>Trisopterus luscus</i>	MM	21	4.7 ± 1.3
<i>Trisopterus minutus</i>	MS	6	7.9 ± 14.2

<i>Umbrina canariensis</i>	MS	4	1.0 ± 1.2
<i>Zoarces viviparus</i>	ES	2	1.1 ± 0.0

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Table 3

Intro. Var.	Df	Expl. Dev.	Sign.	Slope
(a) Models of species richness indices				
<i>Total SR/ln(S_{sc}) ~ SC + log(RD) + EW</i>				
SC	2	16.4	***	SC3 > SC2, SC1
+ log(RD)	1	16.8	***	+
+ EW	1	6.1	**	+
Residuals	90	60.7		
<i>SR_M/ln(S_{sc}) ~ SC + log(RD)</i>				
SC	2	36.7	***	SC3 > SC2 > SC1
+ log(RD)	1	9.7	***	+
Residuals	91	53.6		
<i>SR_ES/ln(S_{sc}) ~ SC</i>				
SC	2	17.9	***	SC3 > SC2 > SC1
Residuals	92	82.1		
<i>SR_DIA/ln(S_{sc}) ~ SC + EW</i>				
SC	2	9.1	**	SC1, SC2, SC3
+ EW	1	26.8	***	+
Residuals	91	64.1		
(b) Models of density indices				
<i>Total ln(Dens+1) ~ SC + IA + EW</i>				
SC	2	7.9	**	SC2 > SC1, SC3 > 0
+ IA	4	23.3	***	IA5, IA4, IA2, IA3 > IA1
+ EW	1	7.9	**	+
Residuals	87	60.9		
<i>ln(Dens_M+1) ~ SC + IA + EW</i>				
SC	2	7.1	*	SC2 > SC3, SC1
+ IA	4	17.4	***	IA5, IA4, IA3, IA2, IA1
+ EW	1	8.3	**	+
Residuals	87	67.2		
<i>ln(Dens_ES+1) ~ IA</i>				
IA	4	17.9	***	IA5, IA3, IA4, IA2, IA1
Residuals	90	82.1		
<i>ln(Dens_Dia+1) ~ SC + CSW + EW</i>				
SC	2	14.4	***	SC1, SC2 > SC3
+ CSW	1	17.3	***	+
+ EW	1	4.7	*	+
Residuals	90	63.6		

Figures

Fig. 1: Location of the 31 European tidal estuaries studied. The continuous line off the coast corresponds to the 150m deep limit of the continental shelf.

Fig. 2: Projection of the 31 estuaries on the first two main components of the PCA performed on abiotic variables (see Table 1 and Fig. 1 for abbreviations). The correlation circle of active abiotic variables was inserted in the bottom right part. The six clusters were obtained by clustering method using Ward criteria based on the matrix of Euclidean distance between pairs of sites.

Fig. 3: Relative presence of estuarine use categories among estuaries in terms of species richness. **a/** Ordination diagram for the principal coordinates analysis (PCoA) based on Bray-Curtis similarity matrices performed on the number of species per estuarine use categories, averaged per estuary. **b/** Barplot representing in the upper part the relative percentage of estuarine use categories in number of species and in the lower part the total number of species per cluster.

Fig. 4: Relative densities of estuarine use categories among estuaries. **a/** Ordination diagram for the principal coordinates analysis (PCoA) based on Bray-Curtis similarity matrices performed on the log-transformed densities of individuals per estuarine use categories, averaged per estuary. **b/** Barplot representing in the upper part the relative percentage of estuarine use categories in densities and in the lower part the total mean of log-transformed densities per cluster.

Fig. 1

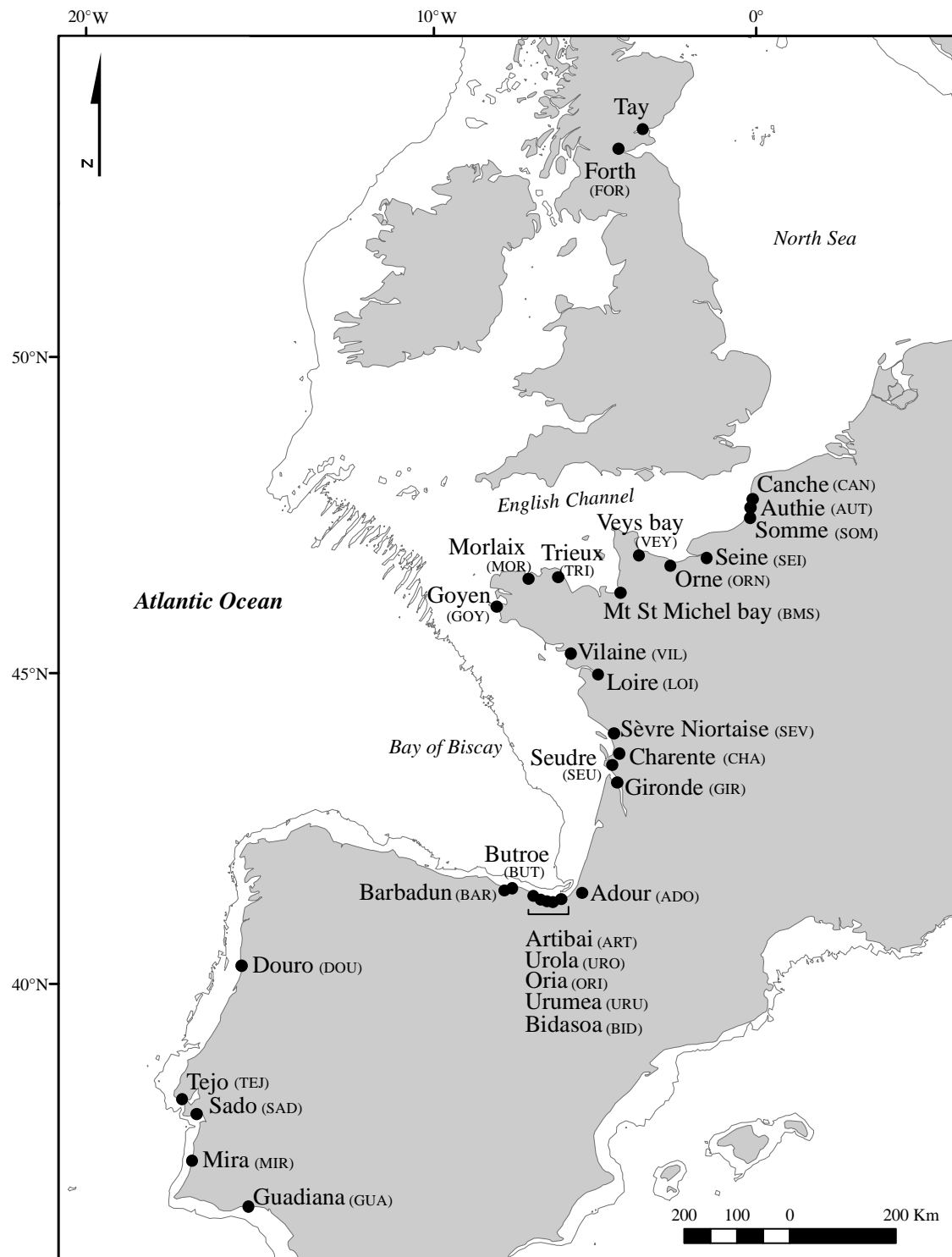


Fig. 2

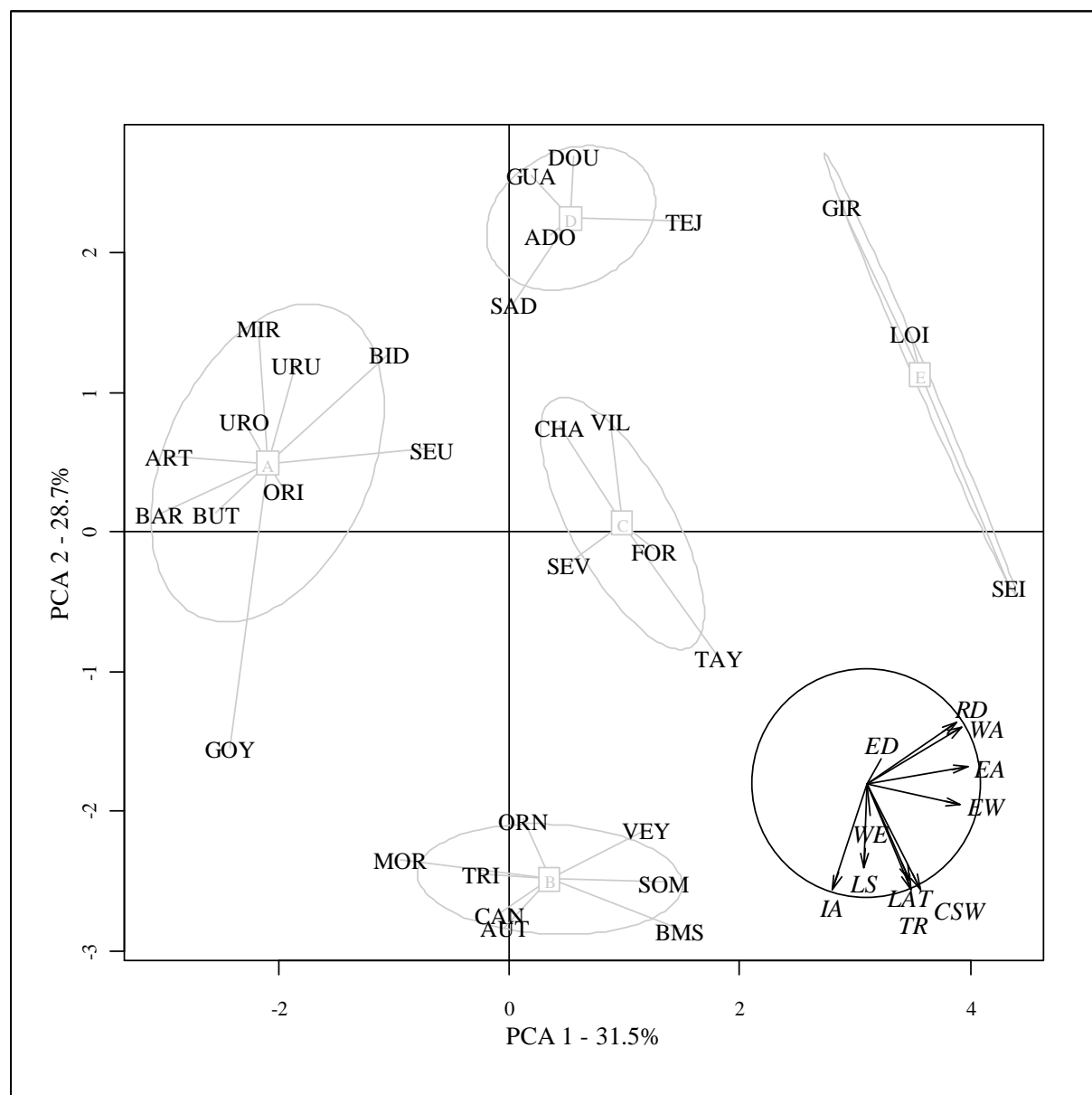


Fig. 3

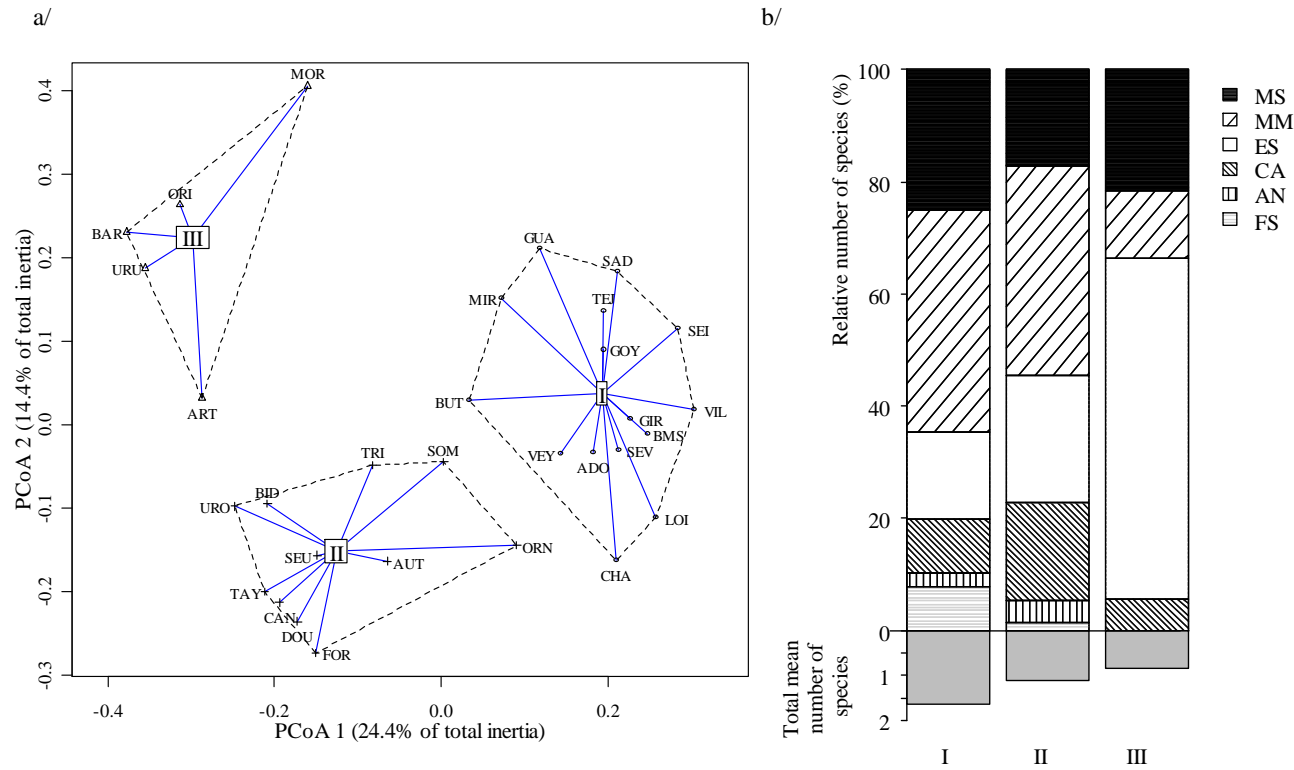


Fig. 4 :

