

Native and non-native fish across aquatic habitats in the Ebro Delta

Miguel Clavero^{1*}, Nati Franch², Verónica López^{2,3}, Quim Pou-Rovira⁴, Josep Maria Queral²

1. Estación Biológica de Doñana – CSIC. Americo Vespucio 26, 41092 Sevilla, Spain
2. Parc Natural del Delta de l'Ebre. Av. Catalunya 46, 43580 Deltebre, Tarragona, Spain
3. Institut d'Estudis Professionals Aquícoles i Ambientals de Catalunya (IEPAAC). 43540 Sant Carles de la Ràpita, Tarragona, Spain
4. Sorelló, estudis al medi aquàtic. Parc Científic de la UdG, 17003, Girona, Spain

* correspondence to migulclavero@ebd.csic.es

SUMMARY

We describe the variability in the composition of fish communities in the Ebro Delta (NE Iberian Peninsula) and report the habitat preferences of the most common species. The Ebro Delta is a large coastal wetland that has been intensively modified, mainly for rice cultivation involving the input of a large amount of low-conductivity waters into an originally brackish and saline system. We defined nine main habitat types within the Ebro Delta (the river, inflow channels, rice fields, outflow channels, springs, marshes, lagoons, lagoon mouths and bays) and sampled fish communities in them by establishing 376 sampling sites, in which we set 1431 fyke nets. We captured more than 120,000 fish belonging to 52 species, of which 37 were native and 15 were non-native. The ichthyofauna of the Ebro Delta is strongly structured in relation to habitat type, following variations in water salinity, and there is a clear segregation of native and non-native fish species. Native species are clearly dominant in the more saline habitats, namely bays, the lagoons, lagoon mouths and marshes, while non-natives dominate the aquatic habitats related to rice cultivation (inflow and outflow channels as well as rice fields). Freshwater springs are dominated by non-natives in terms of abundance, but not in terms of richness. Since the decline and loss of native fish species in the Ebro Delta seems linked to the massive inflow of low-conductivity waters for rice irrigation, fish conservation must focus in reducing the influence of those outflows on the remaining natural and semi-natural wetlands.

Keywords: coastal wetlands, biodiversity conservation, invasive species, threatened species, fyke nets, rice

Citation: Clavero M, Franch N, López V, Pou-Rovira Q, Queral JM (2021) Native and non-native fish across aquatic habitats in the Ebro Delta. *Fishes in Mediterranean Environments* 2021.002: 21p. <https://doi.org/10.29094/FiSHMED.2021.002>

INTRODUCTION

Wetlands are among the most threatened ecosystems worldwide. The loss of wetland area in the last century exceeds 50% and might approach 90% if the time window is expanded to the last 300 years (Davidson, 2014). This negative trend has accelerated in recent decades, with estimates of loss between 1970 and 2008 being around 30% globally and as high as 50% in Europe (Dixon et al., 2016). However, in some areas, wetland loss might have slowed down or even ceased recently due to public awareness and the implementation of policies aimed at their conservation (Keddy et al., 2009). In any case, the loss of wetland areas is just one of the components of the decline of these ecosystems, because many of the remaining wetlands often have a degraded ecological state (Brinson & Málvarez, 2002). While the mere existence of wetlands might have favoured the populations of some taxonomic groups in Mediterranean areas (e.g. waterfowl), other components of the wetland biota, including fish, are currently experiencing worrying declines (Balbo et al., 2017). In this context, it is critical to identify priority conservation areas among the surviving wetland systems, as well as within those same systems (Kingsford et al., 2016).

The Ebro Delta is a large (approx. 320 km²) coastal wetland formed by the deposition of sediments as the Ebro River enters the Mediterranean Sea (Ibáñez & Caiola, 2018; Fig. 1). The Delta has two sand spits, each one of which forms a semi-closed shallow bay. Until the late 19th and the early 20th century, the Ebro Delta lacked a stable human population, being largely considered a wasteland and exploited almost exclusively for extractive activities, such as hunting and fishing (Balada i Llassat, 1985; Curcó, 2006). Until that time, the Delta was also a highly dynamic territory, constantly growing due to the massive input of sediments transported by the Ebro River (Canicio & Ibáñez, 1999). This largely unexploited old Delta must have been a mosaic of saline and freshwater

wetlands and flooded meadows, with a wide variability in water salinities influenced by the seasonal dynamics of the Ebro River and the Mediterranean Sea (Benito et al., 2014), with a small influence of tidal cycles due to the small tidal range (around 20 cm). This system radically changed due to its stabilization through sediment retention in dams (Ibáñez et al., 1996) and to the introduction of rice-based agriculture. Rice cultivation started in 1860, when the inflow channel irrigating the right-hand hemidelta (i.e. the southern shore of the river) from the Xerta dam (some 30 km upstream from the Delta) started being operated (Balada i Llassat, 1985; Vilanova, 1992). The agricultural transformation of the left-hand hemidelta began in 1912, with the commissioning of the inflow channel irrigating that area (Vilanova, 1992). Almost two thirds of the Delta surface (some 200 km²) is nowadays devoted to irrigated rice culture (Clavero et al., 2015; Fig. 1). Within the Delta, the two principal inflow channels coming from the Xerta Dam form a complex network of smaller channels. From the rice fields the water is conducted either back to the river or to the sea through an equally complex network of outflow channels. The total channel network sums more than 1000 km in length (March & Cabrera, 1997). The low-conductivity water used for rice irrigation has huge impacts in the functioning of the aquatic systems of the Delta (Comín et al., 1987; Palacín et al., 1992), and negatively affects relevant elements of their biodiversity (Clavero et al., 2016). Semi-natural systems (lagoons and marshes) currently occupy only some 5% of the Delta surface, all of them being included in the Ebro Delta Natural Park, which protects an area of some 78 km² (Curcó, 2006).

The Ebro Delta has a very rich ichthyofauna, including more than 100 species, at least 43 of which can occupy freshwater habitats permanently or semi-permanently (López et al., 2012). Some of these species are globally threatened and have in the Ebro Delta one of their main strongholds, as

is the case of the Spanish toothcarp (*Aphanius iberus*) (Clavero et al., 2016). However, several native fish species have also suffered huge declines in, or even disappeared from the Ebro Delta, including migratory species, such as the Atlantic sturgeon (*Acipenser sturio*) or the sea lamprey (*Petromyzon marinus*), and primary freshwater ones, such as the Ebro nase (*Parachondrostoma miegii*) or the southern Iberian spined loach (*Cobitis paludica*) (López et al., 2012). In parallel with these generalized declines, and arguably driving several, if not most, of them, the Ebro Delta has suffered a spectacular and still ongoing process of invasion by non-native fishes. Up to 20 non-native fish species are established in the Ebro Delta (López et al., 2012), some of which were recorded for the first time in the

Iberian Peninsula in this wetland to later spread to other areas, such as the oriental weatherfish (*Misgurnus angullicaudatus*) (Franch et al., 2008) or the stone moroko (*Pseudorasbora parva*) (Caiola & de Sostoa, 2002; Dana et al., 2015). While most of the established non-native species are expanding their ranges within the Ebro Delta (see Franch et al., 2008), new ones are also arriving to and establishing in the area, most recently the mummichog (*Fundulus heteroclitus*) (Gisbert & López, 2007) and the European perch (*Perca fluviatilis*) (authors' unpublished data). This panorama is not exclusive of the fish fauna, with non-native species of other groups constantly arriving, establishing viable populations and expanding in the Ebro Delta (e.g. López & Quiñero, 2018).

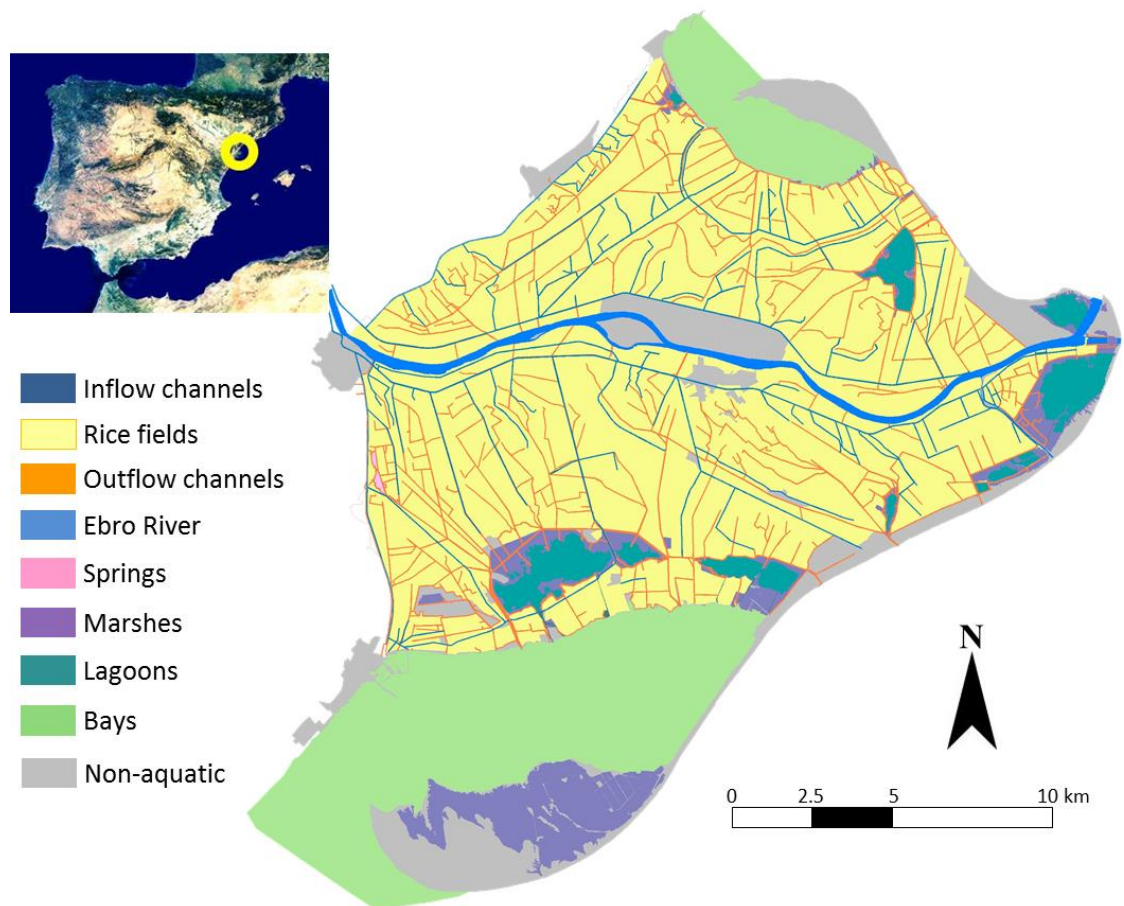


Figure 1. Maps situating the Ebro Delta within the Iberian Peninsula and indicating the distribution of the main habitat types defined within the Ebro Delta for this study. The habitat “mouths” (see Table 1) is not indicated due to the small size of the mouths connecting lagoons with the sea, the bays or the river. Non-aquatic habitats are mainly urban areas and sand beaches.

This work reports the results of an extensive survey of fish populations in the Ebro Delta, covering all main aquatic habitats included in it, originally designed to generate baseline data for the Atlas of Fish of this area (López et al., 2012). We specifically describe the habitat preferences of the most common fish species, relating them to their native or non-native status, as well as the patterns of variation in the structure of fish communities across habitats. Our ultimate objective was to provide useful information for the conservation of the rich ichthyofauna of the Ebro Delta.

METHODS

Fish sampling

We used fyke nets to sample fish communities in 376 sites distributed across the Ebro Delta. At all sites we used two-funnel, small fyke nets (98 cm long, 30 cm high, with a 95 cm wing and a 3.5 mm mesh), usually setting three of them (mean = 2.6, range = 1-10) for one day (mean = 22.5 hours, range = 10-43 hours). At half of those sites (N = 184; 49%), we also used three-funnel, large fyke nets (192 cm long, 43 cm high, with a 110 cm wing and a 7 mm mesh), usually setting three of them per site (mean = 2.4, range = 1-10). Overall, we used 1431 fyke nets, 998 small and 433 large ones. Since the catchability of fish species and size-classes within species can vary among different types of fyke nets (Clavero et al., 2006), we considered the results of the small and large fyke net sampling as different sampling events, what resulted in a total of 560 events.

We intended to cover as much as possible of the environmental variability of the Ebro Delta by stratifying our survey using a nine-level habitat classification (Fig. 1; Fig. 2; Table 1). At all sampling sites we measured water conductivity, as a surrogate of water salinity, using a portable device. All captured fish were identified to the lowest possible taxonomic level in the field (most often, directly to species) and released

at the same sampling site. We also identified captured individuals of other taxonomic groups, of which, for the aims of this work, we used the catch data of large decapod crustaceans (see below).

Data analyses

We first analysed fish catch data at the species level to then focus at community characteristics. We analysed the habitat preferences using presence-absence data of the most frequent species (the 18 fish species detected in at least 25 sampling events). To do so, we applied the Ivlev's electivity index (D) with Jacobs' modification (Jacobs 1974), an index that takes into account the proportional availability of a resource and the proportional use that each species does of that resource. We calculated the index by categorising sampling events under two criteria: i) conductivity classes (six classes; i.e. $< 2 \text{ mS} \times \text{cm}^{-1}$, $2-5 \text{ mS} \times \text{cm}^{-1}$, $5-10 \text{ mS} \times \text{cm}^{-1}$, $10-30 \text{ mS} \times \text{cm}^{-1}$, $30-60 \text{ mS} \times \text{cm}^{-1}$, and $> 60 \text{ mS} \times \text{cm}^{-1}$) and ii) habitat types (Table 1, Fig. 2). The Ivlev's electivity index ranges from -1 (total avoidance) to 1 (absolute preference), with values around 0 indicating the absence of selection, and is formulated as:

$$D = (r - p) / (r + p - (2 \times r \times p))$$

where "D" is the electivity measure, "r" is the proportion use of the resource by species X (i.e. the proportion of events with presence of species X in a conductivity category or habitat type, in relation to all presences) and "p" is the proportional availability of that resource (i.e., the proportion of sampling events in that conductivity category or habitat type).

For each sampling event we recorded fish species richness and fish abundance (estimated as catch-per-unit-of effort, CPUE, as individuals per fyke net per day, correcting for the time that each fyke net was set). Richness and abundance values were calculated both for the whole fish community as well as separately for native or non-native species. Richness and abundance values were compared across habitat types through one-way ANOVAs.

Native and non-native fish in the Ebro Delta
DOI: 10.29094/FiSHMED.2021.002

Table 1. The nine main habitat types defined for the Ebro Delta for the development of this study, specifying their local name (in Catalan) and adding a brief description of them. The table indicates the number of sampling events performed at each habitat type and the number of fyke nets used in them, the average water conductivity values recorded (in mS×cm⁻¹) and the number of native and non-native species captured.

Habitat	Local name	Description	Sampling events	Fyke nets	Conduct.	Native spp	Non-nat spp
Inflow channels	<i>Canals</i>	Network of channels taking the water from the Ebro River to the rice fields. The vast majority are made of concrete, lacking aquatic vegetation	43	110	1.18	4	11
Rice fields	<i>Arrossars</i>	Rice fields, irrigated through inundation	33	64	1.38	2	7
Outflow channels	<i>Desguassos</i>	Channels taking the water from the rice fields to the river, bays or the sea. Non-concreted, silty bottoms	149	333	4.65	16	13
Ebro River	<i>Riu</i>	Final stretch of the Ebro River	13	36	3.20	5	3
Springs	<i>Ullals</i>	Springs fed by groundwater upwelling, with outflows diverted through channels with ground bottom	62	86	2.11	7	8
Marshes	<i>Maresmes</i>	Shallow-water vegetated habitats surrounding lagoons and bays and along the Delta coastal line, featuring a wide range of salinities	99	221	35.95	19	9
Lagoons	<i>Basses</i>	Littoral lagoons with a well-developed shore vegetation. The salinity is variable among lagoons and is influenced by water inputs from the rice irrigation system	67	219	13.75	16	7
Mouths	<i>Provederos</i>	Wide channels connecting the lagoons with the sea or the bays. Some of them feature floodgates and structures for commercial fisheries	35	84	20.48	10	4
Bays	<i>Badies</i>	Semi-closed bays formed by the sand spits to the north and the south of the Delta	59	278	46.30	29	5

Native and non-native fish in the Ebro Delta
DOI: 10.29094/FiSHMED.2021.002



Figure 2. Images of the nine habitat types defined for this study. From left to right and from top to bottom: Inflow channel, Rice field, Outflow channel, Ebro River, Springs, Marshes, Lagoon, Mouths, Bays

We summarized the variability in the structure of fish communities by means of multivariate ordination methods. To reinforce the strength of this analysis we also took into account the information on four decapod taxa: i) the Mediterranean green crab (*Carcinus aestuarii*), ii) the stripped prawn (*Meliceratus kerathurus*), iii) shrimps (*Palaemon spp*), and iv) the invasive red swamp crayfish (*Procambarus clarkii*). We run a principal components analysis (PCA) with an input matrix having as columns the CPUEs of the 18 most common fish species (Fig. 3) plus the four most common decapod species and 552 sampling events as rows (i.e. excluding eight sampling events with no catch of those 22 species). We first run the PCA to select the number of principal components to be retained, attending at the sedimentation graphic of eigenvalues (i.e. the screen-plot criterion. McGarigal et al., 2000). After that, we rerun the PCA limiting the number of extracted PCs and applying a normalized varimax rotation to make easier the interpretation of the variability gradients represented by the PCs (McGarigal et al., 2000). The scores of each sampling event along the selected PCs were compared across habitat types through one-way ANOVAs and were related to conductivity and to the abundances of native and non-native species through Pearson's correlation. Results of these correlation analyses, as well as others presented throughout the paper are given in terms of effect size and direction of the relationships (focussing at the Pearson's correlation coefficient, r) and not attending at statistical significance, since biological meaningless relationships can be significant with high sample sizes. Thus, we only treated correlations as relevant when the absolute values of r , either for negative or positive correlations, was higher than 0.33.

All CPUE values were log-transformed ($\log_{10}(X+1)$) prior to any analysis. Conductivity values (in $\mu S \times cm^{-1}$) were also log-transformed ($\log_{10}(X)$).

RESULTS

Catch summary

Overall, we caught 120,484 fish belonging to 52 species, of which 37 are native to the Ebro Delta and 15 are non-native (Table 2). Among the non-native species, only one (the Iberian gudgeon *Gobio lozanoi*) is native to other areas in the Iberian Peninsula, the rest being also non-native to Iberia. More than eight out of every 10 individuals caught belonged to one of the three most abundant species, these being the globally threatened Spanish toothcarp and the non-natives Eastern mosquitofish (*Gambusia holbrooki*) and stone moroko. However, the most widespread species was the critically endangered European eel (*Anguilla anguilla*), which was caught in more than half of the sampling events. According to Fishbase (Froese & Pauly, 2009) almost all native fish present in the Ebro Delta (32 out of 37) are marine or are able to live in marine waters, while less than half (17 out of 37) live permanently or may live temporarily in freshwaters. Contrastingly, all 15 non-native species live or may live in freshwaters and only one of them (the mummichog) is able to live in marine waters (Table 2).

Species habitat selection

The general environmental requirements reported by Fishbase for the species caught in the Ebro Delta (Table 2) are mirrored on the environmental preferences of the 18 most common fish species within the Delta (Fig. 4). All six non-native fish species positively selected the waters with the lowest conductivity values and consistently avoided waters with conductivity above 5 $mS \times cm^{-1}$. This selection pattern was evident even for species known to withstand wide conductivity ranges, as are the common carp (*Cyprinus carpio*) and the Eastern mosquitofish. Of the native species, only the three-spined stickleback (*Gasterosteus aculeatus*) and the Ebro barbel (*Luciobarbus graellsii*) avoided high conductivity habitats, while all others showed moderate to

strong preference for these habitats. On the other hand, very few species exhibited a preference for the waters with the highest conductivities with the study area (i.e.

above 60 mS×cm⁻¹), this preference being clear only in the cases of the Spanish toothcarp and the golden grey mullet (*Chelon aurata*) (Fig. 4).



Figure 3. Images of the 18 most common fish species caught during this study, indicating their native (blue dot) or non-native (red dot) status in the Ebro Delta. From left to right and from top to bottom: Wels catfish, three-spined stickleback, Ebro barbel, stone moroko, oriental weatherfish, pumpkinseed sunfish, common carp, eastern mosquitofish, thinlip grey mullet, European eel, European seabass, flathead mullet, common goby, big-scale sandsmelt, Spanish toothcarp, golden grey mullet, peacock blenny, black goby..

Native and non-native fish in the Ebro Delta
DOI: 10.29094/FiSHMED.2021.002

Table 2. Fish species captured in this study, indicating their status (native or non-native) in the Ebro Delta, the global conservation status of the native species, according to the IUCN Red List (www.iucnredlist.org; * species not threatened globally but threatened in Spain), the environments they occupy, according to FishBase (www.fishbase.org; M, marine; F, freshwater; B, brackish), the number of sampling events in which each species was detected and the total number of individuals caught.

Species	English name	Status	Red List	Environ.	Sampling events	Indiv.
<i>Anguilla anguilla</i>	European eel	Native	CR	M, F, B	305	1411
<i>Gambusia holbrooki</i>	Eastern mosquitofish	Non-nat		F, B	251	47933
<i>Pseudorasbora parva</i>	Stone moroko	Non-nat		F	225	24117
<i>Atherina boyeri</i>	Big-scale sand smelt	Native	LC	M, F, B	142	6427
<i>Pomatoschistus microps</i>	Common goby	Native	LC	M, F, B	142	2966
<i>Aphanius iberus</i>	Spanish toothcarp	Native	EN	F, B	138	29891
<i>Chelon ramada</i>	Thinlip grey mullet	Native	LC	M, F, B	118	1083
<i>Misgurnus anguillicaudatus</i>	Oriental weatherfish	Non-nat		F	92	1432
<i>Cyprinus carpio</i>	Common carp	Non-nat		F, B	86	1057
<i>Luciobarbus graellsii</i>	Ebro barbel	Native	LC	F	84	402
<i>Silurus glanis</i>	Wels catfish	Non-nat		F, B	54	118
<i>Gasterosteus aculeatus</i>	Three-spined stickleback	Native	LC*	M, F, B	53	996
<i>Salaria pavo</i>	Peacock blenny	Native	LC	M, B	41	184
<i>Gobius niger</i>	Black goby	Native	LC	M, B	33	88
<i>Dicentrarchus labrax</i>	European seabass	Native	LC	M, F, B	31	54
<i>Mugil cephalus</i>	Flathead mullet	Native	LC	M, F, B	30	67
<i>Chelon aurata</i>	Golden grey mullet	Native	LC	M, F, B	30	265
<i>Lepomis gibbosus</i>	Pumpkinseed sunfish	Non-nat		F, B	26	397
<i>Carassius auratus</i>	Goldfish	Non-nat		F	23	41
<i>Sparus aurata</i>	Gilt-head seabream	Native	LC	M, B	18	26
<i>Alburnus alburnus</i>	Bleak	Non-nat		F, B	17	430
<i>Mullus surmuletus</i>	Striped red mullet	Native	LC	M	17	57
<i>Syngnathus abaster</i>	Black-striped pipefish	Native	LC	M, F, B	15	27
<i>Chelon saliens</i>	Leaping mullet	Native	LC	M, B	13	80
<i>Scardinius erythrophthalmus</i>	Rudd	Non-nat		F, B	11	53
<i>Mullus barbatus</i>	Red mullet	Native	LC	M	11	108
<i>Salaria fluviatilis</i>	Freshwater blenny	Native	LC*	F, B	9	15
<i>Gobio lozanoi</i>	Iberian gudgeon	Non-nat		F	7	12
<i>Syngnathus typhle</i>	Broadnosed pipefish	Native	LC	M, B	7	10
<i>Sander lucioperca</i>	Pikeperch	Non-nat		F, B	6	8
<i>Valencia hispanica</i>	Valencia toothcarp	Native	CR	F	6	147
<i>Syngnathus acus</i>	Greater pipefish	Native	LC	M, B	6	8
<i>Fundulus heteroclitus</i>	Mummichog	Non-nat		M, F, B	5	50
<i>Gobius paganellus</i>	Rock goby	Native	LC	M, F, B	5	9
<i>Lithognathus mormyrus</i>	Sand steenbras	Native	LC	M, B	5	16
<i>Solea solea</i>	Common sole	Native	DD	M, B	5	5
<i>Diplodus vulgaris</i>	Common two-banded seabream	Native	LC	M	4	6
<i>Engraulis encrasicolus</i>	European anchovy	Native	LC	M, B	4	4
<i>Rutilus rutilus</i>	Roach	Non-nat		F, B	3	456
<i>Cobitis paludica</i>	Southern Iberian spined loach	Native	VU	F	3	3
<i>Sarpa salpa</i>	Salema	Native	LC	M, B	3	4
<i>Gobius cobitis</i>	Giant goby	Native	LC	M, B	2	2
<i>Chelon labrosus</i>	Thicklip grey mullet	Native	LC	M, F, B	2	2
<i>Parablennius sanguinolentus</i>	Rusty blenny	Native	LC	M	2	2
<i>Symphodus cinereus</i>	Grey wrasse	Native	LC	M, B	2	3
<i>Micropterus salmoides</i>	Largemouth bass	Non-nat		F	1	1
<i>Xiphophorus maculatus</i>	Southern platyfish	Non-nat		F	1	5
<i>Gobius cruentatus</i>	Red-mouthed goby	Native	LC	M	1	1
<i>Boops boops</i>	Bogue	Native	LC	M	1	2
<i>Diplodus sargus</i>	White seabream	Native	LC	M, B	1	1
<i>Nerophis ophidion</i>	Straightnose pipefish	Native	LC	M, F, B	1	1
<i>Syngnathus phlegon</i>	Pelagic spiny pipefish	Native	DD	M	1	1

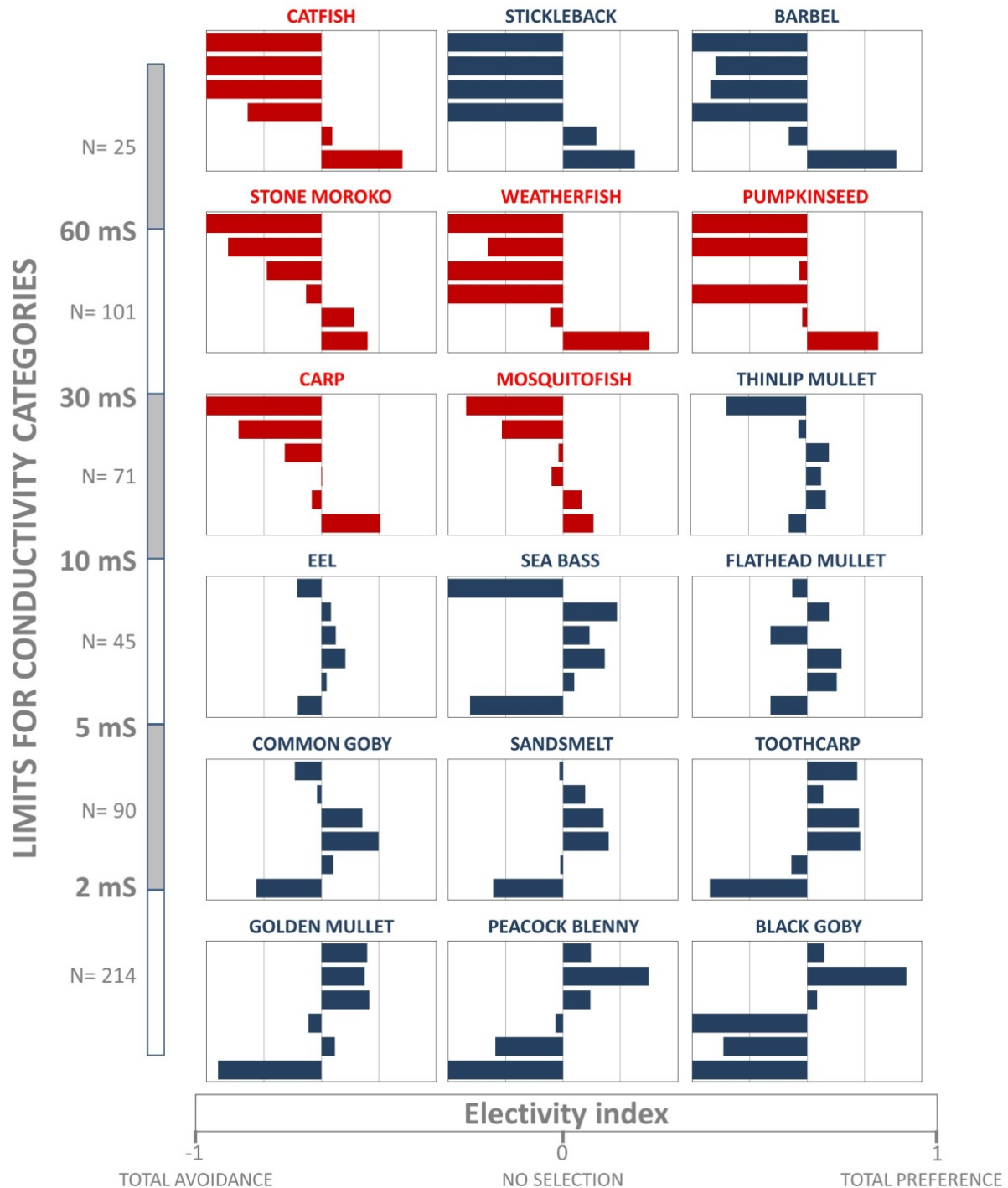


Figure 4. Electivity of the 18 most commonly recorded fish species for different water conductivity levels. Blue letters and bars denote native species and red letters and bars denote non-native ones. Species are ordered in decreasing order of preference for waters with higher conductivity. The electivity index is the Jacobs modification of the Ivlev's index, which ranges from -1 (denoting total avoidance) to +1 (total preference), with values around zero implying the lack of selection (i.e. used as expected from availability). The column in the left indicates the thresholds used to limit the six water conductivity categories as well as the number of localities included within each one of them.

The most common non-native fish species exhibited a consistent preference for the habitat types associated with rice cultivation (inflow and outflow channels and rice fields themselves) (Fig. 5). Avoidance of habitat types outside this irrigation systems was in general high or complete among non-native species, with the Eastern mosquitofish being the only non-native species that showed preference for non-agricultural habitats (mainly freshwater springs). The rice irrigation system was avoided by all native species except for the Ebro barbel, which was strongly linked to it, and for the flat-head (*Mugil cephalus*) and thinlip (*Chelon ramada*) grey mullets, which showed a preference for outflow channels, while being absent (i.e. total avoidance) from the inflow ones. The preference for low-conductivity waters shown by the three-spined stickleback (Fig. 4) is reflected in its almost exclusive occupation of freshwater springs (Fig. 5).

Among the common native species, the peacock blenny (*Salaria pavo*) and the black goby (*Gobius niger*) were the only ones showing clear preference for the Bay habitat, both of them, together with the seabass (*Dicentrarchus labrax*), displaying also a positive selection for mouth habitats (Fig. 5). Spanish toothcarp, common goby (*Pomatoschistus microps*) and big-scaled sand smelt (*Atherina boyeri*) exhibited a strong preference for lagoon habitats, while toothcarp also preferred marsh habitats, a preference shared with the three grey mullet species. It is remarkable that the European eel showed in general low selection values (either negative or positive), with the exception of its avoidance of rice fields, a generalist pattern that is also evident when analysing the use of made by this species of the various water conductivity categories (Fig. 4).

Patterns in community structure

Average native species richness per sampling event was highest in bays and lagoons (four species per sampling event), reaching also high figures in marshes and, to a lesser degree, in mouths and outflow

channels (Fig. 6). Native species richness was very low in rice fields, and also low in inflow channels, in the river and in springs. The low values of the river could be however related to methodological constraints (see beginning of the discussion). The variation in the abundance of native species across habitats was similar to that of richness, with the exception of the low abundance values in bays (Fig. 6). Average richness of non-native species was high in habitats linked to rice cultivation, the only ones in which these values were higher than the figure for native species. The average abundance of non-native species was highest in outflow channels, but also peaked in springs and marshes in spite the fact that richness values were low in these two habitats (Fig. 6).

Average water conductivity in the different habitats strongly determined average species richness found in them, with the direction of this relationship being opposite for native (positive) and non-native (negative) species. A similar pattern was also observed for average abundance values, although the strength of the relationships was weaker (Fig. 6).

We extracted three PCs (PC 1 to 3) from the PCA, which altogether explained 32% of the variability contained by the original dataset (Fig. 7). PC1 (eigenvalue= 2.74) defined a gradient running from sampling events with high abundances of stone moroko, oriental weatherfish, red swamp crayfish and common carp, characteristic of the rice culture system and placed towards the negative end, to communities with high abundances of common goby, big-scale sandsmelt, Spanish toothcarp and shrimps, characteristics of lagoons, marshes and springs. Water conductivity increased along PC1 ($r=0.41$), which was also positively correlated with the abundance of native species ($r=0.46$) and negatively with that of non-native ones ($r=-0.39$). PC2 (eigenvalue= 2.10) separated sampling events in marsh and lagoon areas from those in other habitats, the former being characterised by thinlip and golden grey mullets, Spanish toothcarp, European eel and shrimp. The

abundance of native fish species clearly increased towards the positive end of PC2 ($r=0.58$). PC3 (eigenvalue= 2.14) was negatively correlated with water conductivity ($r=-0.50$), having to its negative extreme communities dominated by marine-dwelling species, such as the Mediterranean green crab, the peacock blenny, the black goby and the seabass, typical of bay and mouth habi-

tats, while freshwater spring habitats with stickleback, eastern mosquitofish, stone moroko and wels catfish (*Silurus glanis*) were placed towards its positive extreme. The abundance of non-native species had a strong, positive relationship with the scores of the different sampling events along PC3 ($r=0.67$).

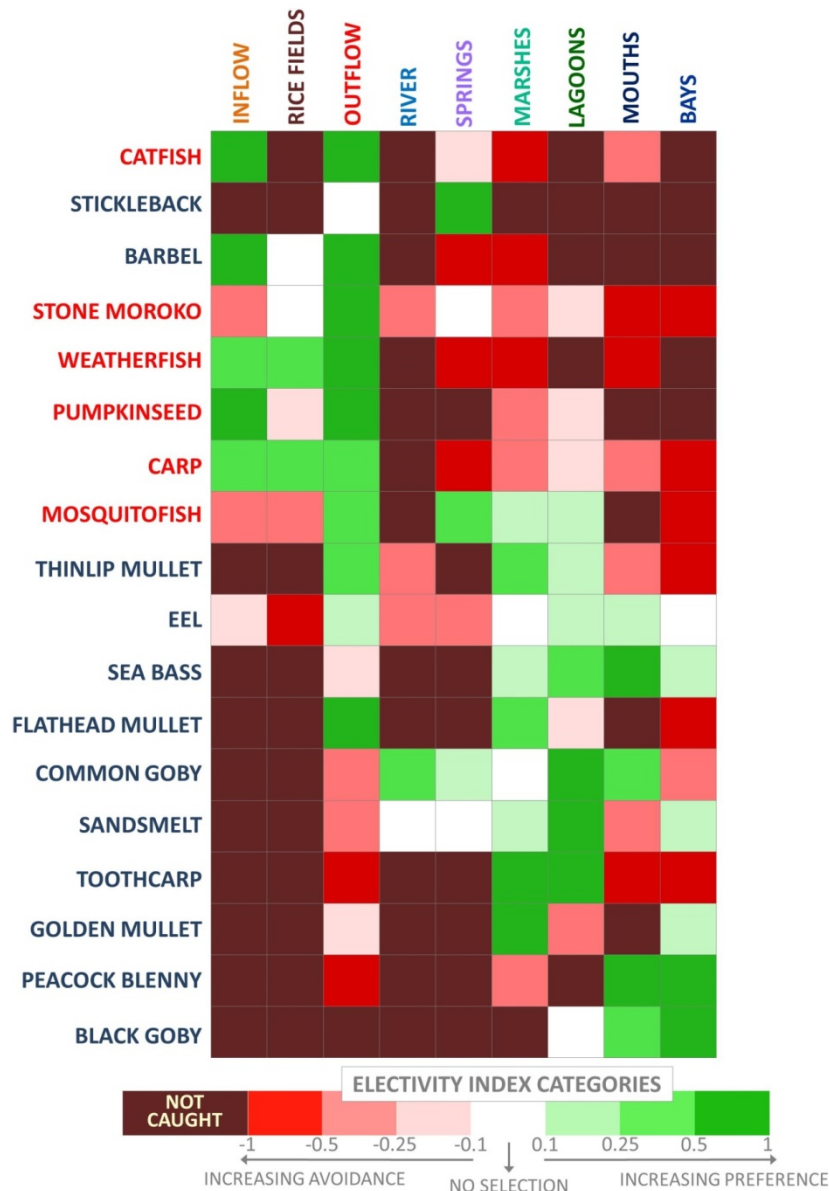


Figure 5. Electivity of the 18 most commonly recorded fish species for the nine main aquatic habitats of the Ebro Delta. Blue lettering denotes native species and red lettering denotes non-native ones. Species are ordered as in Figure 4. The electivity index is the Jacobs modification of the Ivlev's index, which ranges from -1 (denoting total avoidance) to +1 (total preference), with values around zero implying lack of selection (i.e. used as expected from the sampling effort applied to each habitat). The codification of the index values into categories is explained at the lower part of the graph.

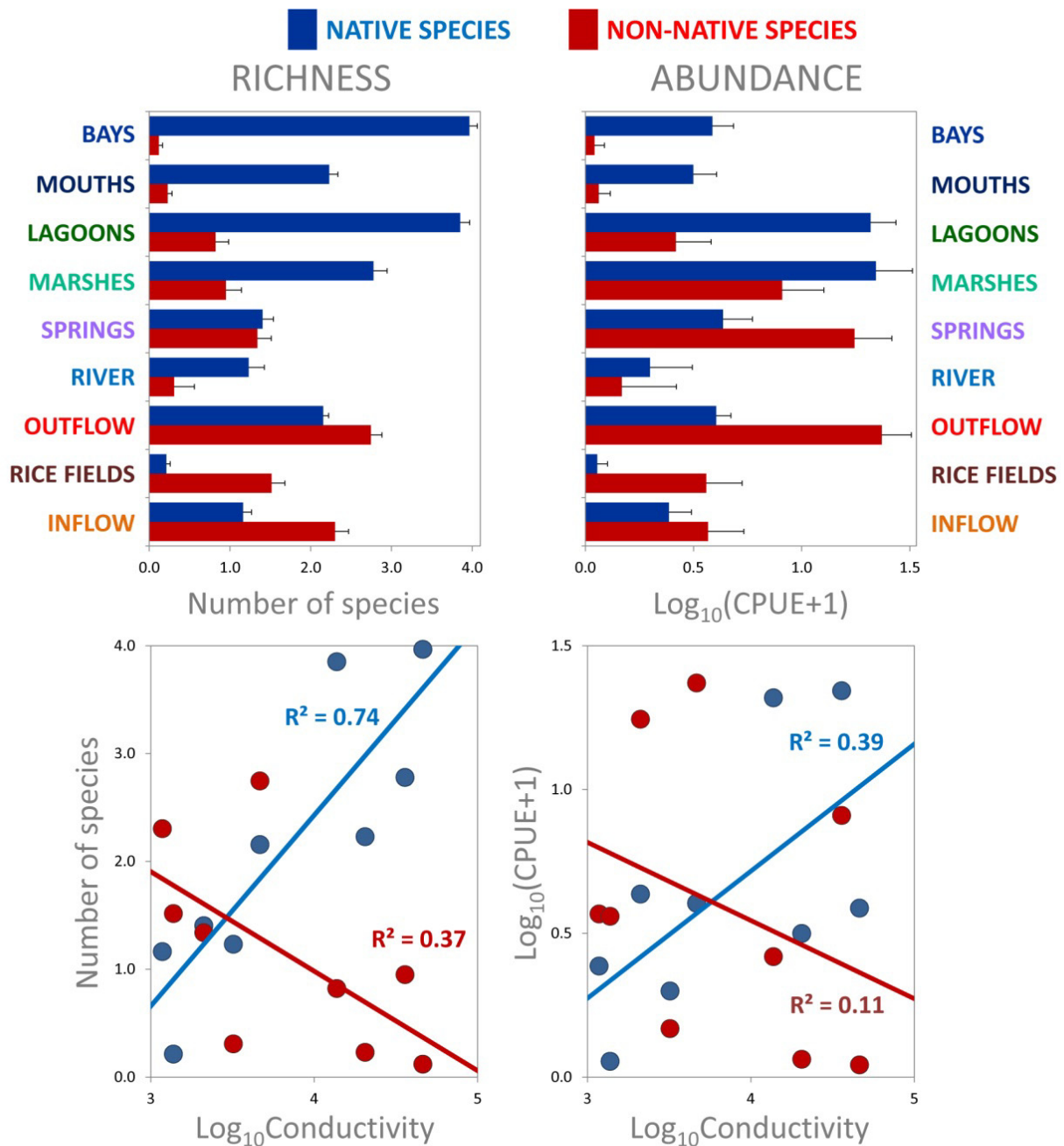


Figure 6. Variation in species richness and abundance of native (blue bars) and non-native (red bars) fish species across the nine main aquatic habitats of the Ebro Delta. Bars are mean values and whiskers are 95% confidence intervals. Lower panels show the relationships between richness and abundant figures with the average water conductivity recorded at each habitat, presented independently for native (blue dots) and non-native (red dots) species.

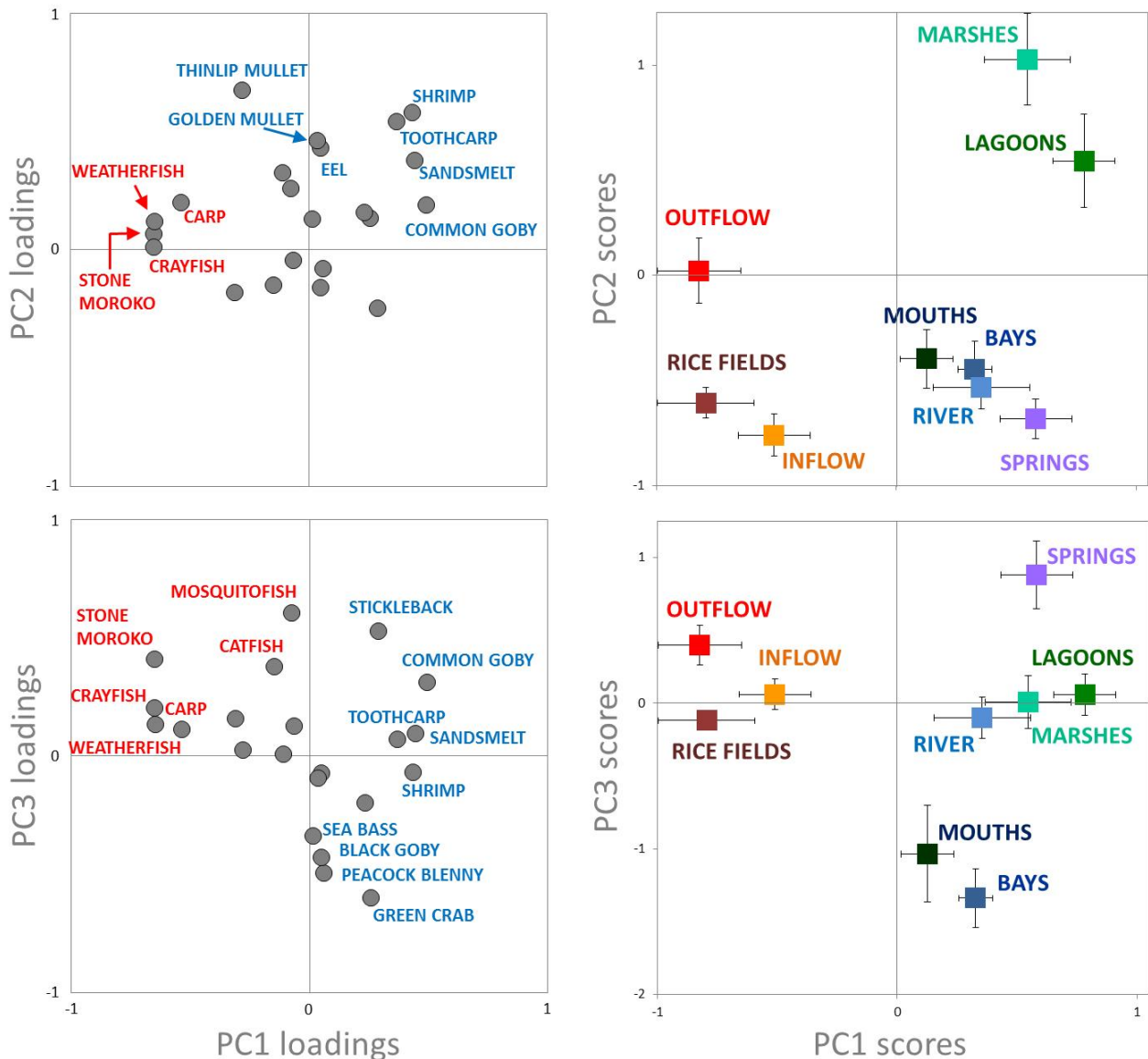


Figure 7. Results of the principal components analysis (PCA) summarizing the variability in the catch of fish and large crustaceans species in 552 localities distributed across the Ebro Delta and covering its main aquatic habitats. Left panels: loadings of the original input variables (i.e. Log₁₀-transformed CPUEs of fish and crustacean species recorded in at least 25 occasions) for the 3 principal components extracted from the PCA. In order to facilitate the interpretation of the principal components, in each panel signalled species are those having a loading with an absolute value larger than 0.33 in at least one of the principal components. Right panels: mean (±SE) position of the different aquatic habitats in the spaces defined by the 3 principal components resulting from the PCA.

DISCUSSION

On the limitations of the sampling strategy

Fish communities can be studied through a wide variety of methodological approaches, all of which has relevant limitations related both to the species involved and the environmental characteristics of the water masses (e.g. Murphy & Willis, 1996; Portt et al., 2006). Different methods can differ in their efficiency in different habitats, while in the same site they can give contrasting images of the fish community, due to the differential catchability among fish species and among size classes within species. The high fish species richness and the diversity of aquatic environments of the Ebro Delta represented thus a challenge for studying the fish communities of that area. A variety of methods were employed to collect data for the Fish Atlas of the Ebro Delta (boat and foot electrofishing, trammel and gill nets and different types of traps and nets; López et al., 2012), but direct comparisons of the results from different fishing methodologies may be misleading. Fyke nets were the most widely applicable methodology across the Delta, and thus, for the sake of result comparability, here we focussed on the analyses of the fyke net catch. However, we must acknowledge that the efficiency of fyke nets seems low for some species (e.g. the different mullet species) and, especially, in some habitat types. Fyke nets can be inefficient in large water masses (e.g. Laponte et al., 2006), as is the case of the Ebro River, the mouths or the bays, for which we obtained either lower species richness than expected (in the river) or low fish abundances (in all three cases). In these environments fyke nets would arguably fail in capturing fish species not associated to the bottom. In the inflow channels, fyke net setting was limited by the concrete channel structure (see Fig. 2) and the strong water current, possibly hindering fish catch. Notwithstanding these limitations, the strength of the ecological patterns presented here support the use of fyke nets as a generalist methodology to characterise fish popula-

tions and communities (e.g. Clavero et al., 2006; Clavero et al., 2009). However, we recommend the development of studies using alternative fishing gears to describe fish communities in some important habitats within the Ebro Delta, especially the Ebro River and the two semi-closed bays.

Native vs non-native species across habitats

We have shown that the rich ichthyofauna of the Ebro Delta is strongly structured across the main types of aquatic habitats, following variations in water conductivity. Furthermore, this structuring involves a generalized segregation of native and non-native fish species. Native species are clearly dominant, both in terms of richness and abundance in the bays, the lagoons and their mouths and in marsh habitats, while non-natives dominate the aquatic habitats related to rice cultivation (inflow and outflow channels as well as rice fields). Freshwater springs are also dominated by non-natives in terms of abundance, but not when attending to richness, since the figures were similar for native and non-native species.

Very little is known about how the fish fauna of the Ebro Delta looked like before the start of rice culture, with its associated massive inflow of freshwater, and the building of the large dams of the lower Ebro River. The river was certainly important for several migratory fish species, including shads (*Alosa* spp.), the sea lamprey and the Atlantic sturgeon, which could go up the Ebro for more than 400 km (Fernández-Colomé & Farnós, 1999). These fish were cited as common along the lower Ebro River in the geographical dictionary edited by Pascual Madoz in the mid-19th century (Madoz, 1845-1850; see Clavero and Hermoso, 2015 for details on this source), which also cited frequently the presence of eel, barbel and nase (arguably Ebro nase). The information is much scarcer on the fish communities occupying the wetlands of the alluvial plain prior to the main human impacts. It can be assumed, however, that these would be composed by a mixture of the riverine fau-

na, marine elements, and proper wetland (e.g., toothcarp) and estuarine taxa (e.g., grey mullets, sandsmelt).

It seems plausible that the fresh-water entering the Delta for rice cultivation would have favoured its occupation by native primary freshwater species. However, this putative positive effect would have been offset by the direct, negative impacts of non-native fish species (Hermoso et al., 2011), which thrive in the lower Ebro and are clearly favoured within the Delta by the rice irrigation system. In fact, several fresh-water species have dramatically declined both in the lower Ebro (e.g., the Catalan chub, *Squalius laietanus*, or the Ebro nase) and within the Delta (e.g., the spined loach, the three-spined stickleback or the fresh-water blenny, *Salaria fluviatilis*). All these declines can have been much larger than the actual data show, but their real dimension will remain unknown because the collection of information on fish communities started when some invasive fish were already present and widespread within the Delta (e.g., Sostoa, 1983). Nowadays, native freshwater species are scarce in the low-conductivity waters of the Delta, either having disappeared, or almost so, or being relegated to the more saline environments, apparently due to exclusion by non-natives. The only native species that widely coexists with non-natives in low-conductivity waters is the Ebro barbel, a pattern that is common in invaded fish communities across the Iberian Peninsula (e.g., Clavero et al., 2013). The freshwater springs of the Ebro Delta, locally known as *ullals*, had singular fish communities in the Iberian context, with the coexistence of spined loach, three-spined stickleback, common goby and probably Spanish and Valencia (*Valencia hispanica*) toothcarps. However, these unique environments have experienced major degradation due to agricultural activities involving the establishment of draining channels (Rodríguez-Capítulo et al., 1994) and the arrival and thriving of pervasive invasive fish species, such as mosquitofish, wels catfish or, more recently, the southern platyfish (*Xiphophorus maculatus*). As a consequence, the native communities of the *ullals* have

been definitely altered, and most of their elements are nowadays extremely rare or totally gone.

The fish communities of lagoons and marshes of the Ebro Delta are dominated by native species. But the presence and occasional dominance of non-native fish species in these habitats seems to be linked to low-conductivity water flowing through the rice irrigation system, arriving to marshes and lagoons as outflows from rice fields. In fact, the proportion of native species from all fish species detected across the different sampling events increased together with water conductivity both for lagoon ($r=0.37$) and marsh ($r=0.66$) samples. Most lagoons, and arguably of several marshes, have disrupted salinity regimes, with minimum conductivity values during summer, coinciding with the rice irrigation period, when values should peak in a naturally functioning Mediterranean coastal wetland (Comín et al., 1987). This disrupted salinity pattern has been shown to favour the occupation of lagoons by invasive fish species (Clavero et al., 2016), to reduce the richness and diversity of macroinvertebrates (Prado et al., 2014) and to alter the abundances of phytoplankton and zooplankton, favouring the former (Prado et al., 2017). Furthermore, outflows from rice fields also increase phosphorus concentration (Comín et al., 1987), which generates eutrophication and has been shown to induce changes in the characteristics of the lagoons, involving the disappearance of submerged macrophyte beds (e.g. Prado et al., 2013). This vegetation loss could increase the impairment of native fish species, such as the endangered Spanish toothcarp, in the presence of invasive fish (Magellan & García-Berthou, 2016).

The least invaded fish communities in the Ebro Delta are those occupying the two bays. Non-native species were detected in only four out of the 59 sampling events in bays, and always in low numbers. The mosquitofish was present in those four sites, coexisting in one of them with the stone moroko, the common carp and the goldfish (*Carassius auratus*), and also with the red

swamp crayfish, despite a rather high water conductivity ($48.5 \text{ mS} \times \text{cm}^{-1}$). Low-conductivity, nutrient-rich water coming from the rice fields has been shown to influence the biological communities of the bays (Palacín et al., 1992; Prado, 2018), but this influence is far from favouring the occupation of this marine habitat by freshwater non-native fish species. The bays of the Ebro Delta have for long been exploited by several activities, including professional and recreational fisheries and bivalve production, which arguably would have impacts on their fish communities. However, the evaluation of those impacts is hindered by the scarce information on the ichthyofauna of this habitat. Preliminary data show that this ichthyofauna is rich in species and has elements of high conservation value, such as up to seven Syngnathidae species (Franch et al., 2016). Further work on the Ebro Delta bays would improve the knowledge of their fish communities and promote their conservation through the identification of priority biodiversity areas and the regulation of productive and leisure activities.

Management and research prospects

We have shown that the loss of biotic integrity of the Ebro Delta fish fauna is linked to the massive inflow of low-conductivity waters for rice irrigation, which is favouring non-native fish species at the expense of native ones. Our results are in agreement with those of previous works developed in the same area and dealing with a variety of indicators and organisms (e.g. Comín et al., 1987; Prado et al., 2013, 2014, 2017; Clavero et al., 2016; Prado, 2018). Rice culturing was and is the cornerstone of human occupation of the Ebro Delta and its restriction is currently out of discussion, even in the face of severe future challenges as sea level rise (Prado et al., 2019). Thus, the conservation of the fish fauna of the Ebro Delta must focus in reducing the influence of the outflows of the rice irrigation system on natural and semi-natural wetlands. There have been management actions of this nature, such as the establishment of channels around the perime-

ter of some lagoons (Menéndez et al., 1995), but they seem to have been ineffective (Clavero et al., 2016). At the same time as reducing the connectivity between outflow channels and wetlands (mainly lagoons and marshes), management actions could also favour the connectivity of those same channels with marine waters, both in the bays and in the Mediterranean. This could be done by taking advantage of the sea intrusions during gales, or by creating such intrusions, and would in theory have a negative impact on the populations of non-native species.

Fish conservation in the Ebro Delta also requires research, monitoring and management actions focused either on specific species or habitats. In the case of species, it is worth pointing out the relevance of the Ebro Delta for the conservation of the Spanish toothcarp. It is important to maintain a long-term monitoring scheme of the main population nuclei of this species in order to describe the impacts of present threats, allowing management responses, and to anticipate future challenges, such as climate change impacts (Prado et al., 2019) or the expansion of new invaders (e.g. mummichog or the blue crab, *Callinectes sapidus*). But the conservation value of the Iberian toothcarp should not overshadow the conservation value other fish populations found in the Ebro Delta, such as those of the three-spined stickleback, the freshwater blenny, the Iberian spined loach or the Valencia toothcarp. All these species are monitored by the Ichthyological Centre of the Ebro Delta Natural Park, which also develops ex-situ breeding programs for some of them. However, the situation of some of these species (e.g. the spined loach) is critical and calls for the design and implementation of specific management actions. Monitoring is also required to evaluate the evolution of the populations of invasive species, very especially in the cases of those that have recently established in the Ebro Delta (e.g. platyfish, mummichog or perch).

Among the aquatic habitats of the Ebro Delta, the Ebro River's main channel and the two bays have not been efficiently

surveyed by us, due to our use of fyke nets. The fish communities of those systems have been scarcely studied, but the available information already highlights their singularity and conservation value. We thus advocate for the development of more research and monitoring work in both the river and the bays. The Life project Migratoebre (www.migratoebre.eu), implemented in the lower reaches of the river, will certainly lead to an improvement of our knowledge of its ichthyofaunal and of the management options for its conservation. Conservation actions are certainly needed in the ullals, which are currently highly degraded both structurally and in terms of biotic integrity, and where drastic declines in some native freshwater fish species have been recently recorded.

Finally, we want to highlight the uniqueness of the Ebro Delta as a natural laboratory to learn about fish ecology and fish conservation. In the Delta, the different aquatic habitats are in close and dynamic contact, being affected by human activities at different spatial scales, from the local (e.g. fisheries, agriculture) to the regional (depletion of sediment loads) and global (climate change). These numerous and complex human impacts acting upon an equally complex area constitute a challenge to plan and implement management schemes aimed at fish conservation. However, it is worth confronting those challenges in the light of

the conservation value of the Ebro Delta ichthyofauna.

ACKNOWLEDGEMENTS

We are grateful to Montse Garrido, Berto Gaya, Eloi Cruset and several students and volunteers for their help during the field work and to Josep Antoni Vidal "Jou", José Ventura, Paco Vidal, Josep Queral "Mondiu" and Raül Callau for letting us work in their rice fields. This work was funded by the Ebro Delta Natural Park (EDNP) as part of the "Atlas of fishes of the Ebro Delta" project. We thank the personnel of the EDNP, and especially Xavi Abril and Toni Curcó, for their constant help, support and advice. Also, special thanks to Mariano Cebolla (<https://www.marianocebolla.com/>), for allowing us to reproduce some of his photographs in Figures 2 and 3.

AUTHOR'S CONTRIBUTIONS

NF and VL planned the field sampling, which involved the work of all authors. MC led the analyses of data and the writing of the manuscript, aided by the inputs of all authors

CITED REFERENCES

- Balada i Llasat R (1985) El Delta de l'Ebre. *Treballs de la Societat Catalana de Biologia* 37: 29-44
- Balbo AL, Martinez-Fernández J, Esteve-Selma MA (2017) Mediterranean wetlands: archaeology, ecology, and sustainability. *WIREs Water* 2017, e1238
- Benito X, Trobajo R, Ibáñez C (2014) Modeling habitat distribution of Mediterranean coastal wetlands: the Ebro Delta as case study. *Wetlands* 34: 775-785
- Brinson MM, Málvarez AI (2002) Temperate freshwater wetlands: types, status and threats. *Environmental Conservation* 29: 115-133
- Caiola N, de Sostoa A (2002) First record of the Asiatic cyprinid *Pseudorasbora parva* in the Iberian Peninsula. *Journal of Fish Biology* 61: 1058-1060

- Canicio A, Ibáñez C (1999) The Holocene evolution of the Ebre Delta, Catalonia, Spain. *Acta Geographica Sinica* 54: 462-469
- Clavero M, Blanco-Garrido F, Prenda J (2006) Monitoring small fish populations in streams: a comparison of four passive methods. *Fisheries Research* 78: 243-251
- Clavero M, Pou-Rovira Q, Zamora L (2009) Biology and habitat use of three-spined stickleback (*Gasterosteus aculeatus*) in intermittent Mediterranean streams. *Ecology of Freshwater Fish* 18: 550-559
- Clavero M, Hermoso V, Aparicio E, Godino FN (2013) Biodiversity in heavily modified water bodies: native and introduced fish in Iberian reservoirs. *Freshwater Biology* 58: 1190-1201
- Clavero M, Hermoso V (2015) Historical data to plan the recovery of the European eel. *Journal of Applied Ecology* 52: 960-968
- Clavero M, López V, Franch N, Pou-Rovira Q, Queral JM (2015) Use of seasonally flooded rice fields by fish and crayfish in a Mediterranean wetland. *Agriculture, Ecosystems and Environment* 213: 39-46
- Clavero M, Franch N, Pou-Rovira Q, Queral JM (2016) Disruption of salinity regimes in Mediterranean coastal wetlands and its impact on the coexistence of an endangered and an invasive fish. *FiSHMED Fishes in Mediterranean Environments* 2016.001: 20p
- Comín FA, Menéndez M, Forés E 1987 Salinidad y nutrientes en las lagunas costeras del Delta del Ebro. *Limnetica* 3: 1-8
- Curcó A (2006) Aiguamolls litorals: el Delta de l'Ebre. Síntesi del medi físic d'una zona humida litoral. *L'Atzavara* 14: 55-72
- Dana ED et al. (2015) Primer hallazgo de *Pseudorasbora parva* (Temminck & Schlegel, 1846) (Cyprinidae) en la Cuenca Sur de España. *Limnetica* 34: 311-320
- Davidson NC (2014) How much wetland has the world lost? Long-term and recent trends in global wetland area. *Marine and Freshwater Research* 65: 934-941
- Dixon MJR (2016) Tracking global change in ecosystem area: the Wetland Extent Trends index. *Biological Conservation* 193: 27-35
- Fernández-Colomé JV, Farnós A (eds) (1999) *Els esturions (el cas del riu Ebre)*. Generalitat de Catalunya. Tarragona
- Franch N et al. (2008) On the establishment and range expansion of oriental weatherfish (*Misgurnus anguillicaudatus*) in NE Iberian Peninsula. *Biological Invasions* 10: 1327-1331
- Franch N et al. (2016) Fish fauna of the Ebro Delta Bays. Summaries book SIBIC 2016, VI Iberian Congress of Ichthyology. Murcia
- Froese R, Pauly D (2009) FishBase. www.fishbase.org [accessed July 2018]
- Gisbert E, López MA (2007) First record of a population of the exotic mummichog *Fundulus heteroclitus* (L., 1766) in the Mediterranean Sea basin (Ebro River delta). *Journal of Fish Biology* 71: 1220-1224
- Ibáñez C, Prat N, Canicio A (1996) Changes in the hydrology and sediment transport produced by large dams on the lower Ebro river and its estuary. *Regulated Rivers: Research & Management* 12: 51-62
- Ibáñez C, Caiola N (2018) Ebro Delta (Spain). Pages 1113-1121 in Finlayson CM, Milton R, Prentice C, Davidson NC (eds.), *The Wetland Book: II: Distribution, Description, and Conservation*. Springer
- Jacobs J (1974) Quantitative measurement of food selection: a modification of the forage ratio and Ivlev's electivity index. *Oecologia* 14: 413-417
- Keddy PA et al. (2009) Wet and wonderful: The world's largest wetlands are conservation priorities. *Bioscience* 59: 39-51

- Kingsford RT, Basset A, Jackson L (2016) Wetlands: conservation's poor cousins. *Aquatic Conservation: Marine and Freshwater Ecosystems* 26: 892-916
- Lapointe NW, Corkum LD, Mandrak NE (2006) A comparison of methods for sampling fish diversity in shallow offshore waters of large rivers. *North American Journal of Fisheries Management* 26: 503-513
- López V et al. (2012) *Atles de peixos del delta de l'Ebre*. Generalitat de Catalunya. Departament de Medi Ambient i Habitatge. Parc Natural del Delta de l'Ebre.
- López J, Quiñonero S (2018) El Delta del Ebro, un campo de batalla contra las invasiones biológicas. *Quercus* 387: 22-28
- Madoz P (1845-1850) *Diccionario geográfico, estadístico y histórico de España, y sus posesiones de ultramar*, 16 vols. P. Madoz. Madrid
- Magellan K, García-Berthou E (2016) Experimental evidence for the use of artificial refugia to mitigate the impacts of invasive *Gambusia holbrooki* on an endangered fish. *Biological Invasions* 18: 873-882
- March J, Cabrera J (1997) La infraestructura hidráulica, motor del desarrollo del Delta. *Revista de Obras Públicas* 3368: 73-82
- McGarigal K, Cushman S, Stařford S (2000) *Multivariate statistics for wildlife and ecology research*. Springer-Verlag, New York
- Menéndez M, Giménez E, De Cid R, Forés E (1995) Effects of decreasing water discharge as consequence of a circumvallation canal construction on salinity, nutrients and macrophytes in a coastal lagoon. Pages 953-964 in Özhan E (ed.) *Proceedings of the Second International Conference on the Mediterranean Coastal Environment: MEDCOAST 95*. Tarragona, Spain
- Murphy BR & Willis DW (eds) (1996) *Fisheries techniques*. American Fisheries Society, Bethesda
- Palacín C, Gili JM, Martin D (1992) Evidence for coincidence of meiofauna spatial heterogeneity with eutrophication processes in a shallow-water Mediterranean bay. *Estuarine, Coastal and Shelf Science* 35: 1-16
- Portt CB, Coker GA, Ming DL, Randall RG (2006) A review of fish sampling methods commonly used in Canadian freshwater habitats. *Canadian Technical Report of Fisheries and Aquatic Sciences*: 2604
- Prado P, Caiola N, Ibáñez C (2013) Spatio-temporal patterns of submerged macrophytes in three hydrologically altered Mediterranean coastal lagoons. *Estuaries and Coasts* 36: 414-429
- Prado P, Caiola N, Ibáñez C (2014) Freshwater inflows and seasonal forcing strongly influence macrofaunal assemblages in Mediterranean coastal lagoons. *Estuarine, Coastal and Shelf Science* 147: 68-77
- Prado P, Caiola N, Ibáñez C (2017) Water management alters phytoplankton and zooplankton communities in Ebro delta coastal lagoons. *Limnetica* 36: 113-126
- Prado P (2018) Seagrass epiphytic assemblages are strong indicators of agricultural discharge but weak indicators of host features. *Estuarine, Coastal and Shelf Science* 204: 140-148
- Prado P, Alcaraz C, Benito X, Caiola N, Ibáñez C (2019) Pristine vs. human-altered Ebro Delta habitats display contrasting resilience to RSLR. *Science of the Total Environment* 655: 1376-1386
- Rodrigues-Capítulo A, España A, Ibáñez C, Prat N (1994) Limnology of natural wells in the Ebro Delta (NE Spain). *Internationale Vereinigung für theoretische und angewandte Limnologie: Verhandlungen* 25: 1430-1433

Native and non-native fish in the Ebro Delta
DOI: 10.29094/FiSHMED.2021.002

Sostoa A (1983) *Las comunidades de peces del Delta del Ebro*. PhD dissertation. Universitat de Barcelona.

Villanova XR (1992) Inicio y consolidación del cultivo del arroz en el Delta del Ebro. *Narria: Estudios de artes y costumbres populares* 57: 16-21