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Trends in fish diversity in Portuguese estuaries in the past decades and predictions in face of global changes

P. Brandão [a,*], L.M. da Costa [b], J.L. Costa [a,b], H.N. Cabral [c], T.A. Marques [d,e], S. França [a,b]

[a] Departamento de Biologia Animal, Faculdade de Ciências, Universidade de Lisboa, Campo Grande, Lisboa, Portugal
[b] MARE - Marine and Environmental Sciences Centre/ ARNET - Aquatic Research Network, Faculdade de Ciências, Universidade de Lisboa, Lisboa, Portugal
[c] INRAE, UR EABX, Cestas, France
[d] Centre for Research into Ecological and Environmental Modelling, The Observatory, University of St Andrews, St Andrews, KY16 9LZ, Scotland, United Kingdom
[e] CEAUL - Centro de Estatística e Aplicações da Universidade de Lisboa, Departamento de Biologia Animal, Universidade de Lisboa, Campo Grande, Lisboa, Portugal

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ABSTRACT

Coastal transition ecosystems like estuaries are amongst the most productive aquatic ecosystems on the planet, recognized worldwide as a fundamental component of coastal areas in terms of biological relevance and anthropogenic use. Estuaries along the Portuguese coast differ in their geomorphological and hydrological characteristics. These systems play a crucial role in terms of nursery areas for economically important fish species. Although several authors have observed high specific variability in estuarine fish communities along the Portuguese coast, few studies explore the factors that influence it. Most of these studies focus on a single estuary and, when several are addressed, only a single factor is used to assess the specific variability of the communities. The presente work aims to analyze the ecological role played by these estuaries for fish communities, namely in terms of their species richness, using a 30 year historical database provided by the Portuguese Coastal Monitoring Network Research Infrastructure (CoastNet RI). To this end, a generalized additive model (GAM) was developed to analyze the variation of species richness as a function of a set of temporal, spatial and environmental characteristics from the nine principal estuarine systems on the Portuguese coast. A total of 142 species from 45 families were identified. The Tejo, Mira, and Sado estuaries had the highest species counts (92, 72, and 64 species, respectively), while Minho and Ria de Aveiro had the lowest (26 and 27 species, respectively). The GAM model explained 35.1% of the variance in species richness and demonstrated significant differences in fish species richness in space (among the nine study estuaries) and time (at annual and monthly scales), and these differences were influenced by abiotic factors such as salinity and temperature. Species richness decreased with higher latitudes and varied yearly, showing a downward trend post-2002. Monthly variations showed increases in February–March and September–October. Higher species richness correlated with salinity levels between 25 and 37 and temperatures between 14 and 25 °C. Possible scenarios of future variations caused by the effects of climate change on the significant factors are also discussed. These GAMs could be useful as a preliminary tool to prepare long-term conservation plans for national legislation.

1. Introduction

Estuaries are transitional systems between freshwater and marine environments and are among some of the most biologically productive areas on Earth (Costanza et al., 1997; Beck et al., 2001; Kennish, 2002). They have been considered essential habitats for fish stocks, since they act as nursery areas for many fish species (Beck et al., 2001; Able, 2005; Elliott et al., 2007; Franco et al., 2008; Hughes et al., 2015). Estuaries are also highly variable environments: strong geomorphological and hydrological variations may occur within and between systems, namely in terms of their total area, depth, sediment type, mouth width and subtidal and intertidal areas; but also, regarding the marked influence of marine and fluvial environments, with factors such as salinity or turbidity varying at different spatial and temporal scales (Jenkins et al., 2010; Lauchlan and Nagelkerken, 2020).

Despite the high biological productivity and ecosystem services they provide, estuaries are amongst the most threatened and altered aquatic systems. Worldwide, numerous anthropogenic actions related with land

* Corresponding author.
E-mail address: reisbrandao98@gmail.com (P. Brandão).

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reclamation, drainage of wastewater, industrial and agricultural activities, shipping and dredging, hydropower, reservoir building, invasive species, fisheries and aquaculture affect the health, functions, activities and services of these ecosystems, contributing to habitat degradation and inducing changes in the structure and dynamics of biotic communities (Kennish, 2002; Lotze et al., 2006; Worm et al., 2006; Freeman et al., 2019; O'Brien et al., 2019; Viana et al., 2021). Moreover, climate change and occurrence of extreme weather events may also accentuate these systems' vulnerability (Elsdon et al., 2009; Vivier et al., 2010; Dolbeth et al., 2011). The impacts of climate change, which are expected to increase (IPCC et al., 2021), are further altering estuarine systems by amplifying variations of environmental variables and intensifying the effects of anthropogenic actions (Attrill and Power, 2002; Baptista et al., 2010, 2015; Chessman, 2013; Gillanders et al., 2022; Whitfield et al., 2022).

For these ecosystems, it has been shown that the effects of natural pressures are similar to the effects of anthropogenic actions on the present fauna and flora, which is known as *Estuarine Quality Paradox* (Elliott and Quintino, 2007). To distinguish between these two effects, it is necessary either to fully quantify and explain natural variation and stress and subtract it from anthropogenic impacts or, alternatively, to have an adequate set of methods that can detect anthropogenic stress, but in the same context as natural stress.

The use of statistical regression models as predictive tools has been increasing in estuarine ecology projects. These tools have been playing an important role in estuarine communities' assessment, being used to model fish-habitat relationships in estuaries (França et al., 2012a; Vasconcelos et al., 2013), develop distribution models of economically and ecologically important species (James et al., 2018; França and Cabral, 2019), modeling invasive species dynamics (Gago et al., 2016), and assess global patterns and predictions of species richness (Pasquaud et al., 2015; Vasconcelos et al., 2015; Duque et al., 2020).

The Portuguese marine coast represents a latitudinal transition zone between warm-temperate and cold-temperate regions (Briggs, 1974). Consequently, this geographic area presents a unique ecological context, where several fish species, with different biogeographic affinities, are found in sympatry, with southern and northern limits of their distribution overlapping and potentially changing due to environmental alterations. Previous studies using statistical regression models concluded that species richness and abundance of fishes along the Portuguese coast were influenced by environmental variables such as temperature, salinity, depth, percentage of mud in the sediment, presence of seagrass, importance of intertidal areas, relative distance from the estuary mouth, macrozoobenthos densities and latitude (França et al., 2011, 2012a; França and Cabral, 2015, 2016; Vasconcelos et al., 2015). Although important for their contribution to understand the variation patterns of estuarine fish assemblages, these studies rely on episodic sampling events, limited in time and space. Most of these models' quality depend on the biological information they are based on, with their reliability and prediction errors related to a wide variety of factors and methodological aspects including limitations imposed by survey design and sampling. Furthermore, the lack of estuarine long-term data impairs the thorough understanding of the relationship between fish assemblages and environmental variables, limiting conclusions and potential predictions on it.

Efforts have been made to overcome these problems and, in this context, the Portuguese Coastal Monitoring Network (CoastNet) Research Infrastructure (RI) was created, to improve the understanding of the national coastal ecosystems functioning, through the development of a remote coastal monitoring system, working autonomous and continuously. Moreover, this RI also contains a historical data section which includes data collected by research projects over the last three decades (1986–2010). Although fragmented, these data are of great importance and utility to promote the development of new and widely applicable tools to analyze, assess and provide insight into long-term trends in dynamic and functional responses of estuarine assemblages, especially in fish communities. Long-term data are crucial and adequate for assessing changes related to climate variations or persistent human pressures. Based on Biguino et al. (2023), the ideal data set (if it is possible to quantify) should cover more than 30 years and be as extensive (temporally and spatially) as possible, to permit robust climatological analyses. However, this type of data is rare, leaving the need to explore and use fragmented series as a way of assessing these factors.

The present study aims to assess trends in fish assemblages in nine estuarine systems along the Portuguese coast, based on historical databases provided by the CoastNet RI and collected over the past three decades. This will explore the use of long-term spatial and temporal data to understand the patterns in species richness variation in estuaries. In addition, it will show that the acquisition of accurate, intensive and long-term data is crucial to effectively manage these ecosystems, which contrasts with the most frequently used data for coastal ecological assessments, which include temporal and spatial limits often imposed by short-term scientific projects.

2. Materials and methods

2.1. Study area

The geographical area under study is comprised between 36°57′ N and 42°9′ N and between 6°12′ W and 9°30′ W. Nine estuaries (Minho, Douro, Ria de Aveiro, Mondego, Tejo, Sado, Mira, Ria Formosa and Guadiana) along the Portuguese coast were considered in this study (Fig. 1). Each ecological system differs considerably in terms of hydrogeomorphological characteristics (Table 1). The Tejo and the Sado estuaries are the larger systems, while Mira estuary, with its channel-like shape, is the smallest, covering an area of 5 km^2. Ria de Aveiro and Ria Formosa are shallow coastal lagoon systems with large intertidal areas. Mean depth varies between 1 and 6 m, which indicates that shallow areas predominate in all estuaries. River flow differs markedly: the Minho, Douro and Tejo have mean flow values higher than 300 m^3s^{-1}, contrasting with low freshwater flow estuaries such as the Mira and Ria Formosa. The most impacted estuarine system is Tejo which is also affected by a wide range of anthropogenic pressures due to its location, along the capital city, Lisbon (Vasconcelos et al., 2007a). This city has more than 2.5 million people in its surrounding and overexploited areas, which represents approximately 27.7% of the total national population, and nearly 18,000 industries (Santos et al., 2017). On the contrary, Mira estuary is the least affected by human activities, where the main impacts are caused by the resource exploitation component (Vasconcelos et al., 2007a). Estuaries in the north of Portugal are characterized by being narrower and in the southern estuaries, rivers have irregular discharges characterized by long periods of low flow.

2.2. Historical data access

The datasets used in this study were obtained from the historical data section in the CoastNet RI geoportal (http://geoportal.coastnet.pt/). This section has a compilation of data collected by fifteen research projects. To avoid dealing with different sampling methodology constrains, data were obtained from projects using the same sampling gear: a beam trawl (approximately, 2 m wide beam, tickler chain, net with 5 mm mesh in the cod end). In all these projects, several environmental variables were measured in each tow using a multiparameter probe (YSI or WTW): salinity, dissolved oxygen (% and mg L^{-1}), chlorophyll *a* (μg L^{-1}), temperature (°C), conductivity (mS cm^{-1}), pH, total dissolved solids (mg L^{-1}), and total suspended solids (mg L^{-1}). Transparency (cm) was recorded with the Secchi disk. Sediment was collected using a van Veen grab (0.05 m^2) for the quantification of organic matter and sediment type. Depth (m) was also registered. A GPS signal was used to record geographic coordinates at the beginning and end of each tow and were towed at a constant speed (of approximately 0.8 m s^{-1}).

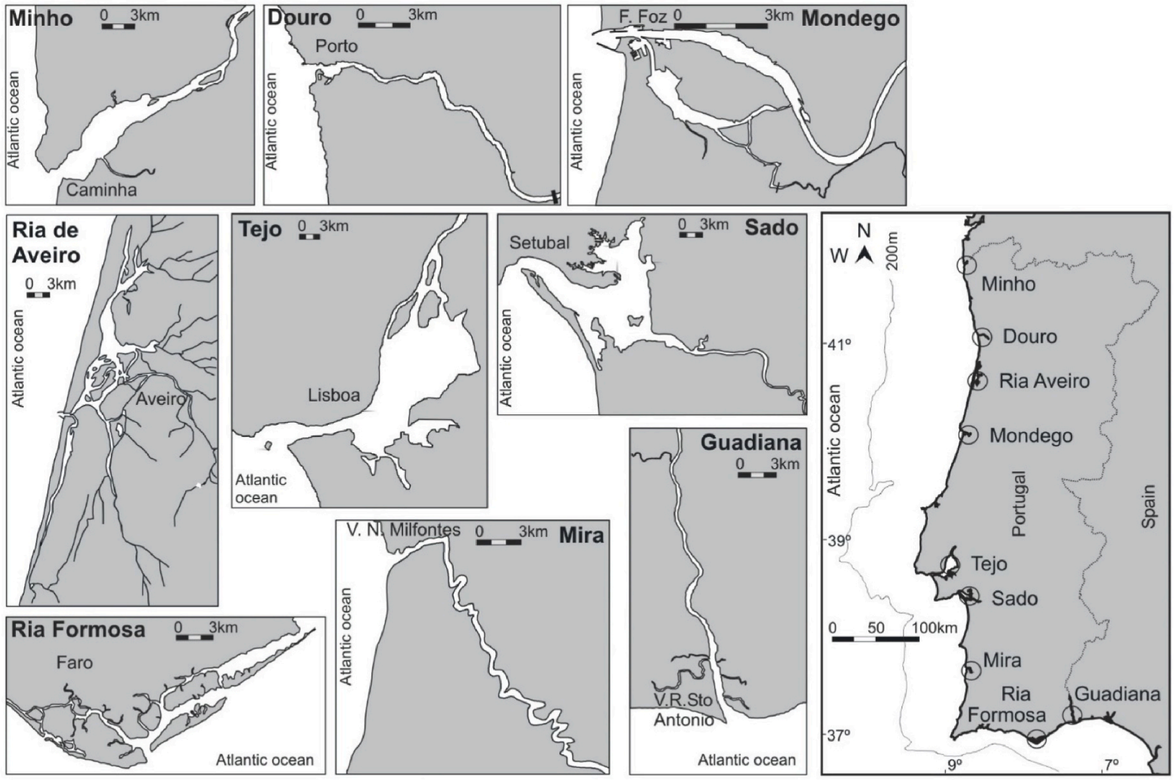

Fig. 1. Map of the Portuguese coast with the sampled estuarine systems.

Table 1
Main geomorphologic and hydrologic characteristics in the nine estuarine systems along the Portuguese coast (adapted from Vasconcelos et al., 2007b).

Estuaries	Estuarine Total area (km^2)	Mean river flow (m^3s^{-1})	Mean depth (m)	Volume (10^6 m^3)	Latitude (°N)	Intertidal area (% of total estuarine area)
Minho	023	300	3	0070	41.9	09
Douro	010	450	4	0059	41.1	11
Ria de Aveiro	074	040	2	0084	40.6	87
Mondego	010	079	2	0022	40.1	64
Tejo	320	300	5	1900	38.7	40
Sado	180	040	6	0500	38.5	44
Mira	005	003	4	0027	37.7	42
Ria Formosa	091	002	1	0092	37.0	81
Guadiana	020	080	3	0100	37.2	24

2.3. Database construction

Based on the compilation of historical data, two datasets were organized and compiled, with available and non-continuous data from the last three decades for the nine estuaries under study on the Portuguese coast. To provide insights into long-term trends in estuarine fish communities, namely in terms of fish species richness variation, dataset A was created, with a temporal scale ranging from 1978 to 2013. Dataset A contained the species captured at each tow. To access the relationship between the variation associated to these communities and the environmental variables measured, dataset B was compiled, with a temporal scale comprised between 1991 and 2010. Dataset B contained the values of environmental variables measured, for each tow performed.

In addition, each species was classified according to its climatic affinity, which could be: lower (species whose geographical distribution is further south from the native area (Northern Europe)); core (species whose geographical distribution is on the Portuguese coast) and upper range (species whose distribution is further north from the native area (tropical and north African species)). This classification was done by consulting the distribution range of each fish species in Fishbase (Froese and Pauly, 2024).

2.4. Data analysis

Data from dataset A, organized by year and estuarine system were used to assess fish species richness (i.e., number of species), which involves counting or listing species without considering the number of individuals, thus giving equal weight to all of them. To evaluate species richness independently of the sampling effort, a resampling procedure was implemented. A fixed number of tows was selected, based on the estuary where the least number of tows were made, Minho estuary. Following this, 30 tows were chosen randomly without replacement from each estuary and the mean species richness was calculated. This process was permuted 1000 times. An exploratory analysis was performed to produce a list of sampled species and to develop species accumulation curves per estuary, using the original data over timeline. No estuary was discarded in order to meet the main objectives of the scope of the work (Larger spatial and temporal area).

For the analysis of the dataset B, a filtering of the environmental variables was conducted to obtain a final version of it comprising the largest possible temporal and spatial scales, meaning that only the environmental variables measured for all the projects considered were used.

The final data matrix is represented by 1380 tows and 7 variables that include: latitude, estuary, year, month, depth, temperature, and salinity; and the response variable: species richness (total number of species). In terms of data standardization, it was possible to compare the data from the various projects despite having different numbers of tows. Tow was considered as the sampling unit used in data analyses.

For the modeling approach, the spatiotemporal variation in species richness explained by the abiotic variables was explored using a generalized additive model (GAM). GAMs were used because traditional statistical regression methods are not adequate when variables have non-linear relationships, as is expected for most biological contexts. They allowed estimating response curves with a non-parametric smoothing function (Wood and Augustin, 2002) and are known to be effective predictive instruments within the study area (França and Cabral, 2016, 2019). A Poisson distribution, a discrete probability distribution, often used to express the probability of a given number of events occurring in a fixed interval of time or space (Haight, 1967), with a link log function was used to model fish species richness. To avoid overfitting a maximum of five degrees of freedom for the smooth terms were considered when fitting the models. For the month variable a cyclic cubic regression spline was chosen to enforce that the values estimated in January and December are consistent, reflecting the 12-month annual cycle. To check for multicollinearity and redundancy of variables, following Fielding and Haworth (1995), a Spearman correlation analysis was conducted. No variables presented a high correlation coefficient ($r > 0.8$). The best model was obtained by using different variable combinations and was selected using Akaike information criterion (AIC), with the most parsimonious models presenting the smallest AIC (goodness-of-fit measure) and having the highest percentage in deviance explained. The final model for interpretation was fitted only with the significant variables since the AIC values between the two models (with and without significant variables) showed no major differences. A statistical significance level of 0.05 was considered in all test procedures. Statistical analyses were performed within the R Studio Software environment (Version 1.1.463) (Posit team, 2022) using the "mgcv" (Wood, 2011), the "ggplot2" (Wickham, 2016) and the "tidyverse" packages (Wickham et al., 2019).

3. Results

3.1. Species richness

A total of 142 species belonging to 45 families were identified in the data compiled from the 15 scientific projects for the nine estuaries under study (see Table S1 supplementary material). *Anguilla anguilla*, *Pomatoschistus microps*, *Pomatoschistus minutus*, and *Syngnathus acus* were found in all the estuaries, while *Atherina presbyter*, *Chelon auratus*, *Chelon ramada*, *Dicentrarchus labrax*, *Engraulis encrasicolus*, *Gobius niger*, *Sardina pilchardus*, and *Symphodus bailloni* were the species that appeared in most of the sampling years.

Overall, the Tejo, Mira and Sado estuaries had the highest number of species sampled: 92, 72, and 64 respectively, and the Minho and Ria de Aveiro estuaries had the lowest number of species sampled, 26 and 27 respectively (Fig. 2). Considering the data obtained by the resampling procedure, and thus estimates of species richness for an equivalent sampling effort, results indicate that the estuaries with the highest average species richness are the Ria Formosa, the Sado and the Tejo, respectively. On the other hand, the Minho and the Ria de Aveiro have the lowest average specific richness values (Fig. 3).

In terms of overall species richness sampled per year with all estuaries combined, 2001 and 2006 were the years with the most species sampled (66 species sampled in each year) followed by 1995 totaling 62 species sampled. The least represented year was 2010, with only 12 species sampled. This was also with the lowest number of tows conducted.

Since the data used were collected from distinct projects with different objectives, the experimental design and the number of tows per project was also different. Species accumulation curves over time performed with the original data allow to understand and analyze the variation in the number of species caught in relation to the number of tows per estuary (Fig. 4).

Tejo, Mira and Sado estuaries had the highest number of tows (1131, 388, and 161, respectively), and on the opposite end, the Minho estuary had the lowest number of tows (34). Species accumulation curves seem to present an initial plateau (between 30 and 50 tows approximately)

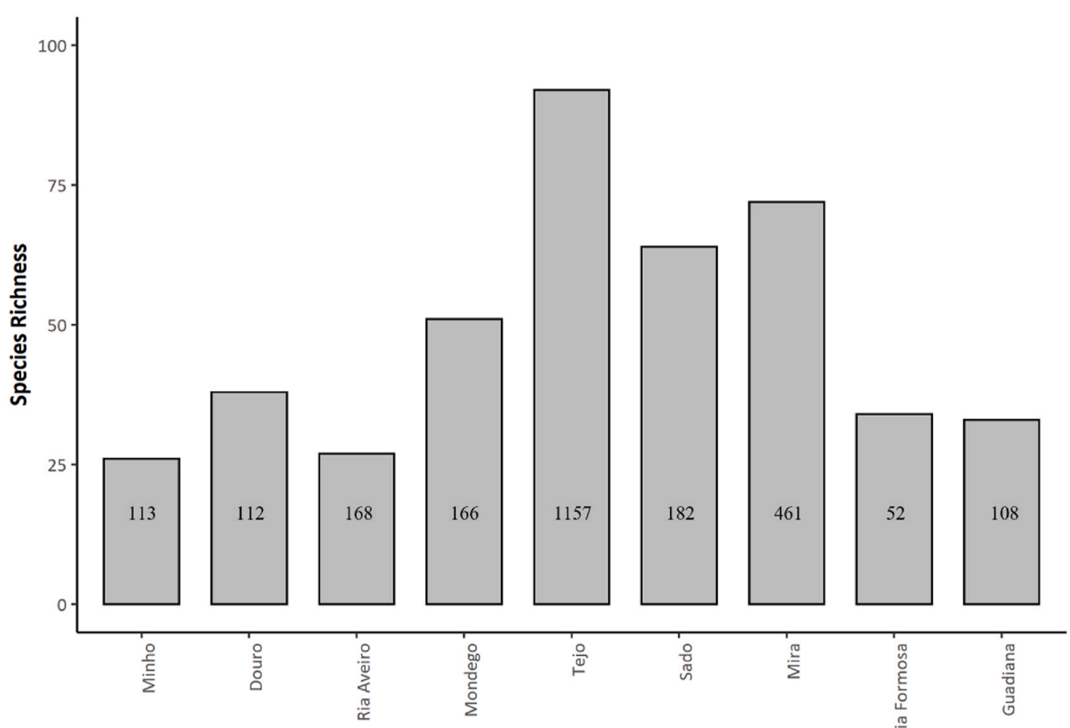

Fig. 2. Fish species richness (pooled over time) in the nine estuaries under study. In each bar the number represents the number of tows performed.

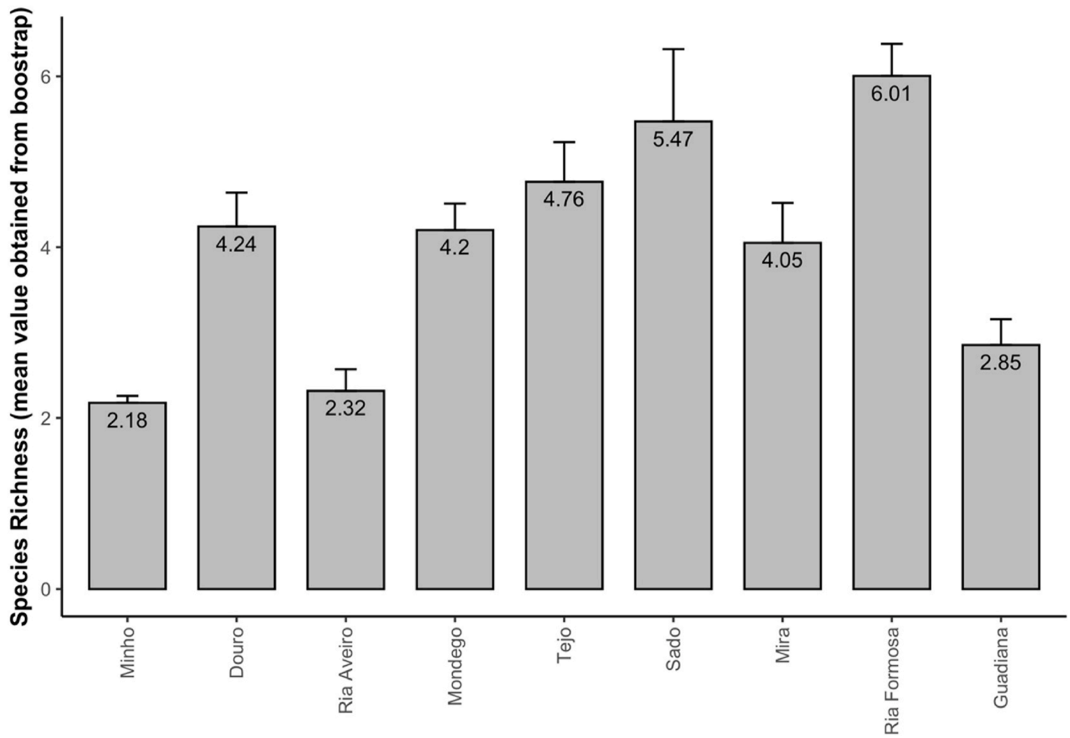

Fig. 3. Mean values of fish species richness (pooled over time) in the nine estuaries using bootstrap data, with the error bar representing the standard deviation.

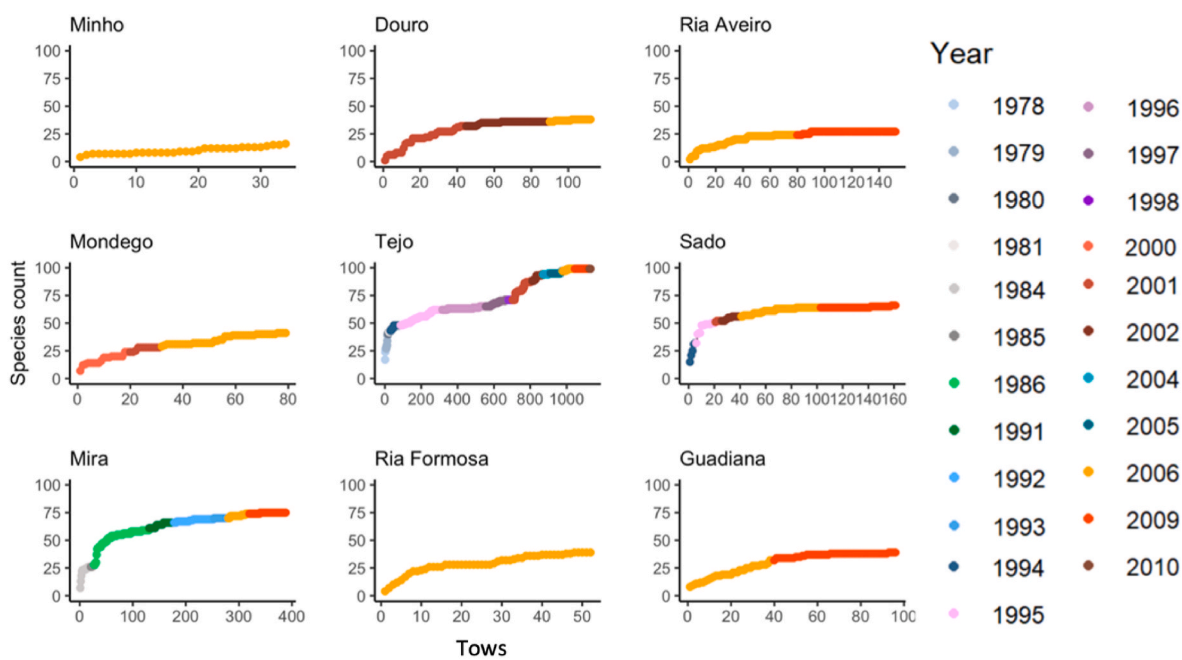

Fig. 4. Species accumulation curves for each sampled estuary performed with the original data, addressed with a chronological scale (annual variation represented by colors). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

where the number of sampled species remains fairly similar as the number of tows increases. In the Minho estuary this pattern is naturally lacking given the low number of tows performed. On the other hand, looking at the chronological scale, the estuaries that were more sampled, with a higher number of tows (Tejo, Mira and Sado) tend to have other episodes of increase in the number of new sampled species associated with a respective plateau in later years starting around 2000 (Fig. 4).

In terms of climate affinity, the results show an increase throughout the years, in species presenting their core distribution along the Portuguese coast (Core Range), while there are fluctuations in the number of species classified as Lower and Upper Range. In the period from 2000 to 2013, there was an increase in the number of species for all climate affinity groups (Fig. 5).

3.2. Relationships between species richness and environmental variables

In addition to the differences in geomorphologic features of the sampled estuaries, environmental variables such as depth, temperature

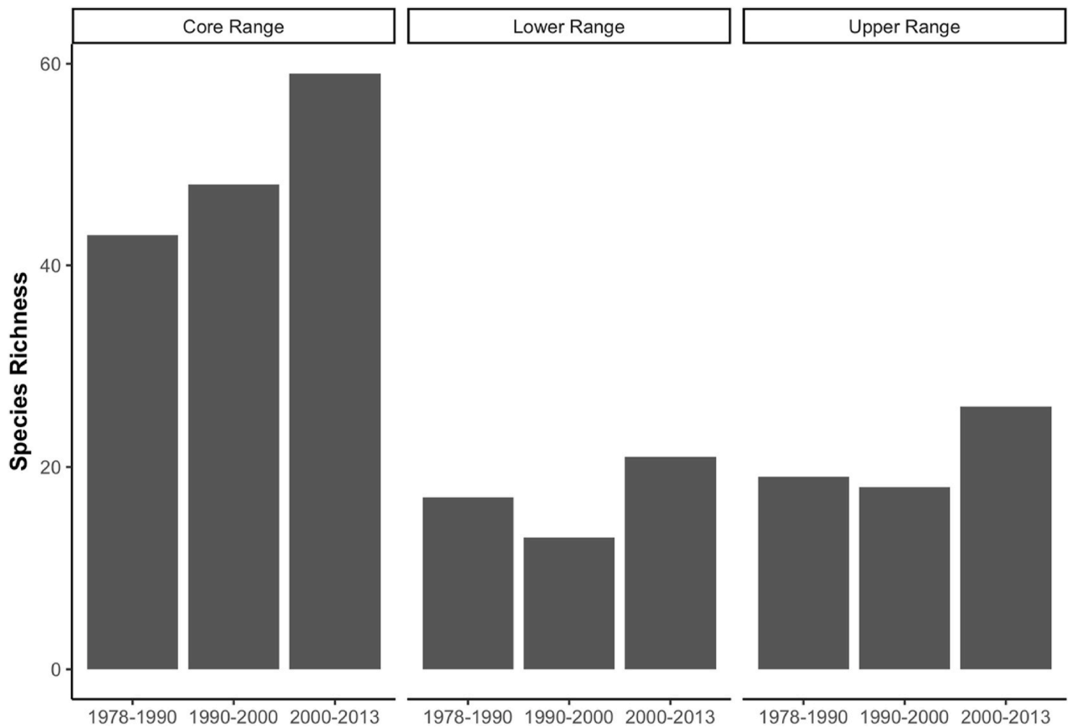

Fig. 5. Variation in specific richness for each climate affinity group pooled over time.

and salinity also presented relevant variation across estuaries (see Table S2 in supplementary material) as well as in years (see Table S3 in supplementary material).

Results of the GAM exploring for factors influencing the variation of species richness among the nine estuaries and the thirty sampled years are reported in Table 2. The model explained 35.1% of the total deviance for fish species richness variation in estuaries along the Portuguese coast. The variables that contributed significantly to explain this variation were: estuary; latitude; year and month, and environmental variables: salinity and temperature ($p < 0.05$).

The effect that each statistically significant variable has on the species richness is represented in Fig. 6. There is a marked separation of data by estuaries, corresponding to the orientation of the Portuguese estuaries, due to their strong latitudinal separation, with a decrease in fish species number from low to high latitudes (Fig. 6a).

The analysis of the influence of the variable year on the fish species variation showed that, between 1991 and 2002, the species richness remained stable in each year with slight changes, and that after 2002, there has a downward trend in species richness (Fig. 6b).

The monthly variation in species richness showed two main increases: the first between February and March and the second between September and October (Fig. 6c). A more tenuous increase can also be observed in July.

Fish species richness increases slightly with higher salinity values (Fig. 6d). A higher concentration of data was registered when salinity values range between 25 and 37, with most of these data largely comprised by samples from 2006 to 2009 (see Fig. S1 in supplementary materials).

Highest values of species richness were registered for temperatures between 14 and 25 °C (Fig. 6e). Similar to salinity, this range also includes more data, corresponding to the values obtained for 2006 and 2009. Although presenting some variability, in general, the highest temperature values were consistently recorded in 2006 (see Fig. S2 in supplementary materials).

Table 2
Final generalized additive model (GAM) built for all estuaries, considering as response variable fish species richness. Combination of significant predictor variable, percentage of deviance explained [Dev. Expl. (%)] and estimated degrees of freedom (Edf) for the smoothing parameters are shown.

Type	Family	Model	Dev. Expl. (%)	Edf
GAM	Poisson	Estuary	35.1	
		s(Year)		4.036
		s(Month)		5.078
		s(Lat)		2.810
		s(Temperature)		2.297
		s(Salinity)		2.383

4. Discussion

The present study has compiled several datasets, collected from different research projects, creating a spatially extensive and long-term dataset for which a combined analysis has been carried out. In this way, it became possible to assess the abiotic factors influencing the most fish species richness, highlighting in more detail their main variation patterns. This wide-ranging spatial and temporal approach was applied for the first time, at a Portuguese national level.

The results obtained by the exploratory analysis were in line with what has been previously described as the species recorded in all estuaries and appearing in most sampling years (*P. microps*, *P. minutus*) coincide with the species most frequently sampled in Portuguese estuaries (Baptista et al., 2010; Guerreiro et al., 2021). In the present study, the Portuguese estuaries showed differences in species richness at the spatial level. These estuaries show strong differences in their geomorphological and hydrological characteristics, which has been previously shown to be related with their specific estuarine fish assemblage's composition (França et al., 2012a, 2012b; França and Cabral, 2016; Baptista et al., 2021). The higher species richness values recorded in the Tejo and Sado estuaries are probably related to their large estuarine area. In fact, many studies in Europe underlined a positive influence of estuarine area on fish species number (Nicolas et al., 2010; Henriques et al., 2016; Connor et al., 2019). On the other hand, the Mira estuary, with the smaller total area, presents comparatively high values of species richness. The low values of river flow for this system may also play

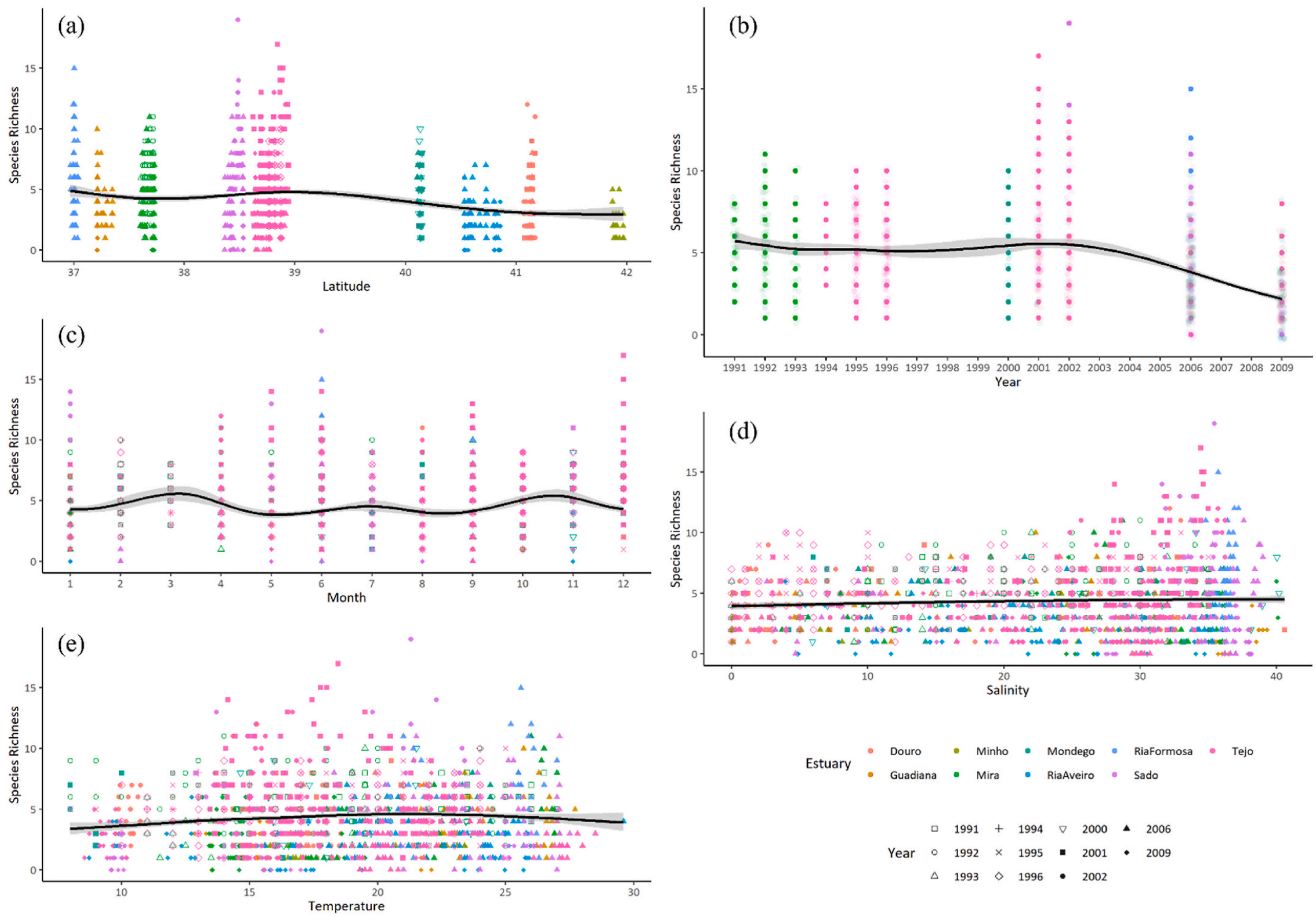

Fig. 6. Effect of each significant variable [(a) – Latitude; (b) – Year; (c) – Month; (d) – Salinity; (e) – Temperature] on fish species richness by the curve in black that refers to the model of each variable (gray shading represents the envelope of the 95% confidence level). The shape and color scale of the data represent the temporal and spatial scale respectively. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

an important role, allowing for greater variety of marine species to enter the estuary. Accordingly, França et al. (2011) showed that river flow influences fish species richness variation at a larger scale along the Portuguese coast, with the number of species decreasing as river flow increases. Nevertheless, it is probably the combined effect of several geomorphological and hydrological variables, with some having more influence than others, that make these three estuaries the most highly represented in terms of number of fish species.

Despite results being consistent with what has already been described, the total number of fish species sampled needs also to be carefully analyzed. The most represented estuaries were those with the highest number of samples, subject to a higher number of scientific projects. Although there is a different number of tows per estuary, it was necessary to understand if there was in fact a minimum number in all of them, to reach a fairly constant number of species, so that the results obtained can be effectively comparable. The species accumulation curves built with that purpose indicated that a first plateau in terms of number of species was reached in all estuaries, excluding Minho, between 30 and 50 tows. This, alongside the resampling results, allows for a reasonable comparison of the species richness values between estuaries. Therefore, it is possible to assume that Tejo and Sado estuaries are not only the most sampled systems but also those presenting higher species richness. Minho estuary presented the lowest species richness, but only a single year (2006) was analyzed. Conversely, the low species richness values for Ria de Aveiro seem to be supported by the total number of tows, indicating that this estuary has sufficient data to be compared with the others. The obtained results agree with Pombo et al. (2002), where data from two different periods were compared for this system. A decrease in species richness over time was obtained, mainly due to large-scale anthropogenic factors, namely the substantial development of industries and the increasing population in the watershed, in addition to overfishing, climatic changes and dredging.

The high mean species richness value for the Ria Formosa system may be associated with the fact that it is a lagoonal system with minimal freshwater influence (smallest input of river flow), meaning that salinity levels are much higher. Consequently, there will be a greater number of marine species. These high species richness values have also been demonstrated for this estuary by França et al. (2009, 2011). The richness of fish species is extremely variable depending on the particularities of each estuary, from its geomorphology to its dynamics, and each case must be analyzed in particular, taking all these aspects into account.

The range for the first plateau obtained by the species accumulation curve is consistent with the normal average number of species sampled in estuaries at the national and global levels (Vasconcelos et al., 2015). Furthermore, the species accumulation curves for the estuaries with the highest number of tows, Tejo, Mira and Sado, tend to have other episodes of increase in the number of new species sampled associated with a respective plateau immediately after. Anthropogenic impacts are a strong and persistent pressure among these estuaries, which are strongly related to alteration and destruction of estuarine habitats, leading to changes in estuarine fish communities, with possible fish species replacement (Vasconcelos et al., 2007a). Additionally, Tejo and Sado estuaries are characterized by having a very high port activity which increases the possibilities of entrance of invasive species (Murray et al., 2014). On the other hand, in the 2000s, efforts were made to control and improve water quality according to the Water Framework Directive (WFD) (INAG, 2006), and an important step was the implementation of wastewater treatment stations to fulfill its objectives (Directive 91/271/EEC). This improvement of water quality in the transition zones, mainly in these three estuaries, may have triggered and allowed the entry of new species or the re-entry of estuarine species, which may be also associated with an increase in the abundance of available food (Azeda et al., 2013). In turn, the effect of climate change may also be one of the factors for these episodes, since the distribution of the species has been undergoing a possible shift towards north, which means that species that had their range predominantly represented in southern Portugal might be covering other areas and starting to appear in further northern estuaries (Cabral et al., 2001).

A GAM model was implemented to assess the spatiotemporal variation in species richness explained by the abiotic variables. The results obtained are in line with other models elaborated at the national level (França et al., 2011, 2012b; França and Cabral, 2015, 2016; Vasconcelos et al., 2015). The percentage of explained variance was 35.1%, which is lower than the values obtained for similar models in previous studies (Vasconcelos et al., 2015; França and Cabral, 2016; Nodo et al., 2017; James et al., 2016; Connor et al., 2019; Lima et al., 2019; Duque et al., 2020). This may be related with the use of the present database, which, although presents large temporal and spatial scales, lacks data from some years when estuaries were not sampled. Moreover, crucial estuarine geomorphological characteristics, along with important environmental variables, were not considered for some estuaries, which preclude their use in the analysis. Additionally, part of the variation in species richness is certainly a consequence of biotic interactions, governed by the inter- and intraspecies relationships, which, at this scale of study, would be difficult to identify and to incorporate. On the other hand, analysis at a more local scale incorporates additional descriptors related to proximate and stochastic processes (Austin, 2007). The distribution of fish species in estuarine environments and their use of specific areas have been shown to result from the responses of individuals to multiple environmental variables. These variables can be dynamic (e.g. salinity, water temperature, food availability) or relatively stable (e.g. sediment type, presence of seagrass).

Latitude was a significant factor in explaining the variation of species richness along estuaries of the Portuguese coast. Despite a relatively small coast at a Continental scale, the obtained general tendency is for species richness to increase towards lower latitudes, which is in accordance with the overall latitudinal gradient of species richness previously described (Chown and Gaston, 2000). This species richness variation has been verified in several studies for marine, estuarine and freshwater fishes (França et al., 2011; Vasconcelos et al., 2015; Connor et al., 2019; Baptista et al., 2021).

The estuary was also a significant variable in explaining fish species richness variation, according to the model. This variable represents the systems' geomorphology, due to the differentiating estuarine characteristics (Table 1), indicating that these may be influencing the specific richness (França and Cabral, 2016; Connor et al., 2019).

Year and month were key temporal variables explaining species richness variation in the final model. The year, which has rarely been used in similar models, hints toward two periods: 1991–2002, with consistent mean values of species richness, and 2002–2009, showing a clear decrease in these values. The first period presented a more consistent temporal and spatial scales, dominated by the Mira, Tejo and Sado estuaries, had more consecutive yearly samples and less variability in species numbers. In contrast, 2006, with the most comprehensive spatial scale sampling, confirmed a decline in species richness, continuing in subsequent years. Ecological and climatic factors have likely contributed to this decline, including severe droughts, higher temperatures and low precipitation values occurring in 2006 and 2009 (IPMA, 2021). Thus, this trend found in the model should warn for possible further decreases in estuarine fish species, with climate change expected to worsen over the next few years.Month was also important in explaining species richness variation patterns, with seasonal fluctuations in the number of species found, representing an increase in species number in spring, summer and autumn (Spring - April, May, June; Summer - July, August, September; Autumn - October, November, December). Accordingly, previous studies have already described similar seasonal patterns in fish species richness, which could be mainly related with the entry of species that use the estuary during a part of their life cycle, namely seasonal marine migratory and juvenile marine species (Pombo et al., 2007; França et al., 2009). On the Portuguese coast, several species have developed strategies such as timing their spawning events and migrating to estuarine areas, by aligning their life cycles with optimal conditions to increase the survival and recruitment of offspring (Martinho et al., 2007, 2009; Tanner et al., 2017; Arevalo et al., 2023). Thus, the detected increases may be mainly related with the entry of species in the estuaries since the ones identified in this work as the best represented at the level of estuaries and years sampled are mainly marine visiting/migrating and diadromous species: *Solea solea*, *Solea senegalensis*, and *D. labrax* which use the estuaries as nursery areas during the warmer months (spring and summer seasons) (Martinho et al., 2020), while species such as *S. pilchardus* opportunistically enter the estuaries during the colder seasons (França et al., 2009; Guerreiro et al., 2021) and, on the other hand, diadromous migrating species, such as *C. auratus*, *C. ramada* and *A. anguilla*, enter the estuaries in spring (Almeida et al., 2018; Guerreiro et al., 2021).

Salinity and temperature, which were also significant variables in explaining species richness variation, had a similar unimodal relationship, even with tenuous effects. These abiotic factors have a seasonality effect, which implies that estuarine fish communities develop behavioral/physiological strategies to withstand these factors, leading to changes in community structures over time (Blaber and Barletta, 2016; Teodósio et al., 2016; Able et al., 2017).

For the salinity gradient, the results indicated that higher concentrations are associated with higher numbers of species. This effect plays an important role in structuring estuarine fish assemblages (Barletta et al., 2005; Sosa-López et al., 2006; Tanner et al., 2012; Lima et al., 2019) as different species present differential tolerance to it (França et al., 2011). It is important to mention that this variable is strongly influenced by the river input, where estuaries with higher river flow have lower salinity levels, leading to lower species richness, which is in line with the results of the exploratory analysis of this study. On the other hand, the results indicated that recent years (2006 and 2009) were associated with higher salinity values, which may be related with the negative anomalies in precipitation, leading to lower freshwater inflow to the estuaries, compared to the other years (IPMA, 2021).

For temperature, the optimal range for the greatest number of species observed in this study is within normal limits with the usual temperature values described for estuarine species (Attrill and Power, 2004). Most migratory species that use estuaries prefer higher temperatures for spawning, being associated with higher productivity and food availability for early stages (Machado et al., 2017). Temperature is a lethal factor when physiological limits are exceeded (Eaton et al., 1995), but in the global pattern, estuarine species richness increases with an increase in mean water temperature (Vasconcelos et al., 2015). This is one of the main factors related to the latitudinal gradient. From another perspective, the most recent years under study (2006 and 2009) were considered drier years, registering higher temperature values (IPMA, 2021).

Climate change impacts will directly and indirectly affect the statistically significant variables of the model considered for inference, and in turn will alter and impact estuarine fish communities. Moreover, higher temperatures and lower precipitation rates are expected to occur more frequently, enabling accentuated variations in the hydrogeomorphology of the estuaries and thus in their temperature and salinity gradients (Monteiro et al., 2021). For Europe, the effects of climate change are often expressed as heavy precipitation, droughts, and heat waves, which are likely to increase even more in the following years (IPCC et al., 2013). In Portugal, an increase of subtropical species has been observed during the last decade (Baptista et al., 2015) and in the present study this increase was also observed, with the species classified as Upper Range increasing and represented by species such as *S. senegalensis*, *Argyrosomus regius*, *Arnoglossus laterna*, and *Buglossidium luteum* (Prista, 2013). This change seems to support the evidence of tropicalization of the fish community studied, as a result of the gradual increase in temperature, which is advocated in the results, where the recent years recorded higher temperatures. In another perspective, there was also an increase in species that are normally more widely distributed towards the north of Portugal (Lower Range). These southward shifts distribution can be related to local hydrographic conditions (e.g., upwelling) (Brander et al., 2003; Bañón et al., 2024), or local environmental variations (e.g., temperature, precipitation patterns) (Fisher et al., 2008; Pinsky et al., 2013). On the other hand, primarily as a result of rising water and air temperatures as a result of climate change, species composition is changing in estuarine areas around the world. Studies documented the northward migration of fish species in European estuaries, indicating that warmer waters are causing species to move to colder regions. Similar patterns are observed in Japanese estuarine environments, where rising water temperatures lead to changes in the distribution of fish fauna in tidal rivers. These changes are consistent across global regions, underlining the impact of climate-induced temperature changes on estuarine ecosystems and highlighting the need for adaptive management strategies to conserve these vital habitats (Nicolas et al., 2011; Howell and Auster, 2012; James et al., 2016; Itsukushima, 2023). Still, it is very difficult to predict the effects of climate change on marine fish biodiversity (Rubenstein et al., 2023), and in particular on the structure of estuarine communities due to the complexity and adaptability of their interrelationships with the environment.

It would be of great global interest to foster cooperation and interconnection across the various research groups focusing their research on estuarine ecosystems. Platforms such as CoastNet RI are crucial to increase the quantity and quality of data, thus improving the methodologies used in projects. This should, in turn, allow for more precise quantitative explanations of the effect of potential future changes, anthropogenic or naturally induced, and ultimately improve the ability to comprehensively assess the dynamics of coastal aquatic systems. The model built in the present study could also be used as a predictive tool and as an instrument to generate knowledge to be included in national directives. This knowledge is also extremely important for conservation decision-making by creating goals and/or objectives in terms of factors that influence water quality and assessing the effects of climate change, in order to maintain estuarine ecosystems as healthy as possible.

CRediT authorship contribution statement

P. Brandão: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **L.M. da Costa:** Writing – review & editing, Methodology, Investigation, Data curation. **J.L. Costa:** Writing – review & editing, Project administration, Funding acquisition. **H.N. Cabral:** Writing – review & editing, Methodology, Funding acquisition, Conceptualization. **T.A. Marques:** Writing – review & editing, Supervision, Methodology, Formal analysis, Conceptualization. **S. França:** Writing – review & editing, Supervision, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Susana Franca reports financial support was provided by Foundation for Science and Technology. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2024.109048.

Data availability

Publicly available datasets were analyzed in this study. These data can be found at the “Historical data” section, from the CoastNet Research Infrastructure geoportal (http://geoportal.coastnet.pt)

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