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Evolution of benthodemersal fish communities in a changing European estuary at fine and broad temporal scales

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1. Introduction

As locations where two distinct bodies of water naturally mix, estuaries are characterized by a variable environment with numerous abiotic gradients at multiple temporal scales (McLusky, 1993). The preponderant salinity gradient is invariably found across estuarine ecosystems worldwide; salinity typically increases from catchment fresh water to oceanic salt water but can fluctuate significantly depending on river discharge and tides (Telesh and Khlebovich, 2010). The suspended-matter gradient peaks in a zone of maximum turbidity that is enriched in organic matter (Mitchell, 2013; McLusky and Elliott, 2004), in which heat-catalyzed biochemical processes involving bacterial mineralization deplete concentrations of dissolved oxygen (DO) in water and induce hypoxic conditions (Riemann et al., 2016). Estuarine organisms—from microalgae to fish predators—are distributed according to their tolerance along these abiotic gradients, with each species occurring in the range of environmental conditions it can withstand (Kinne, 1964). Within these ranges, species have evolved physiological adaptations, such as mucus exudation, or behavioral adaptations through, e.g., a risk avoidance strategy (Ordóñez-Grande et al., 2021; Eby and Crowder, 2002). The need for such adaptations naturally restrains the quantity of taxa present within the estuarine range compared to neighboring ocean and river ecosystems (Whitfield et al., 2012).

As emphasized by Potter et al. (2010), estuaries are very diverse entities that are difficult to describe using a single definition. Like most Atlantic estuaries, contemporary European estuaries are classified as coastal plains (Fairbridge, 1980) that formed during the Holocene as the sea level rose after the end of the last glacial period, drowning European river valleys (Durand et al., 2016). They are highly exposed to numerous human-induced pressures originating from endogenous sources (Halpern et al., 2015; Lotze et al., 2006) such as the high levels of heavy metals and organic contamination reported in the Gironde and Seine estuaries (Courrat et al., 2009), which contribute to the degradation of habitats and water quality.

Furthermore, these ecosystems are also currently subjected to exogenous anthropogenic pressures stemming from global change. As a result of the intensification of human activities since the middle of the 20th century, planetary-scale environmental modifications are rapidly inducing imbalances in climatic and marine systems worldwide (Stips et al., 2015; Occhipinti-Ambrogi, 2007). Disruptions linked with global change have been documented for multiple abiotic variables on European estuaries, representing a potential threat to the integrity of estuarine ecosystems (Robins et al., 2016). At a regional scale, the changes that are most likely to occur in the estuaries of western Europe are, in order (Intergovernmental Panel on Climate Change, 2022): an increase in sea surface temperature and the intensity of marine heatwaves (Costoya et al., 2015; Oliver et al., 2021); a decrease in rainfall, resulting in reduced river discharge, extended residence times for turbidity maximum zones, and the formation of dead zones from hypoxic conditions (Jalón-Rojas et al., 2017; Schneider et al., 2013; Altieri and Gedan, 2015); and sea level rise and salinity intrusion in the upper reaches of estuaries (Rodrigues et al., 2019). Compared to other regions of the world, European estuarine communities are mainly shaped by rainfall and river discharge (Leal Filho et al., 2022). The local consequences of these regional changes are expected to impair estuarine ecosystem health, functioning, and services (Barbier et al., 2011) and increase the possibility of dead zones spreading across estuarine ecosystems (Díaz and Rosenberg, 2008).

One way of assessing the health of an ecosystem is by examining its biodiversity, a concept that comprises not only the diversity of biological entities (i.e., living organisms) in an area, but also the interactions between them (UNEP, 1992). Although intangible, biodiversity is an inherent feature of ecosystems that affects numerous underlying processes (e.g., overyielding or portfolio effect) related to ecosystem stability and performance (Stachowicz et al., 2007). By studying biodiversity at different scales, it is possible to investigate the influence of anthropogenic pressures on ecosystem functioning and services, determine causality, and assess the ability of ecological assemblages to

cope with global and local disturbances (Boero, 2010; Costanza and Mageau, 1999).

In natural conditions, estuarine ecosystems support fish communities in a number of ways, across a wide spectrum of life cycle stages and habitat uses. Changes in these assemblages may thus serve as important indicators of the health and functioning of these ecosystems (Elliott et al., 2007; Potter et al., 2015). Moreover, anthropogenic pressures in these habitats may negatively affect the conservation status of fish species (Pasquaud et al., 2015). For example, of the 24 fish species in the northeast Atlantic for which ICES provides advice, 22 are affected by human influences in coastal and estuarine habitats during at least one of their life stages (Brown et al., 2018). Previous research has documented some of the ways in which fish assemblages can be altered as a result of environmental changes. For example, salinity intrusion modifies fish communities in favor of marine species (Costa et al., 2007), while increases in water temperature affect the regional pool of fish species by shifting their biogeographic ranges northward (Martinho et al., 2010; Fossheim et al., 2015).

In this field, several questions remain equivocal: at the scale of decades, how sizeable are the modifications in the estuarine biotope? To what extent has fish biodiversity changed in these changing conditions? How have fish communities responded to the abiotic changes identified?

The aim of this work was to analyze spatial and temporal variability in estuarine fish communities in the changing environment of a representative large European estuary, that of the Loire River (France). To this end, the temporal changes were first described in four abiotic variables (flow rate, temperature, salinity and DO) over the course of four decades. In parallel, using data on benthodemersal fish collected in three non-consecutive annual cycles (intra-annual scale) and over four decades (inter-annual scale), spatio-temporal patterns were investigated in estuarine fish biodiversity (α and β components) in parallel with how fish community composition has shifted in response to abiotic change, using data on environmentally sensitive fish taxa.

2. Materials and methods

2.1. The case of the loire estuary

The Loire estuary is comparable to other large estuaries of western Europe (e.g., Elbe or Tagus) with regard to catchment area or river length. It is located on the French Atlantic coast ($47°25'00''$ N) at the interface of the emerged land of western Europe and the Bay of Biscay continental shelf. It is characterized by a semidiurnal macrotidal regime and is considered highly turbid; indeed, a turbidity maximum zone is nearly always present, with suspended matter concentrations peaking at 1 kg m^{-3} and extending over 20–50 km (Gallenne, 1974). Regional climatic disruptions have resulted in local modifications such as an upstream shift in both dynamic tide and salinity intrusion (Migniot and Le Hir, 1994; GIP Loire Estuaire, 2014). The selected study area covered the downstream reaches of the Loire estuary from a turbid meso-to oligohaline site to a clear-water euhaline site (Fig. 1).

2.2. Environmental parameters

The choice was made to analyze river flow rate and temperature, two factors that reflect regionally driven abiotic parameters, along with salinity/conductivity and DO, which represent the associated local pressures upon communities. Conductivity measures were converted to salinity using conversion formulas presented by Aminot and Kérouel (2004) and were used to complete the salinity observations obtained by the GIP Loire Estuaire (2023) (Practical Salinity Scale). DO was converted to an indicator of biochemical stress by counting the number of days in a year during which hypoxic conditions occurred; hypoxia was defined based on a threshold of 5 mg l^{-1}, under which several fish species begin to experience adverse effects such as growth lag (Bozorg-Haddad et al., 2021).

Daily flow-rate data for the Loire River were obtained from a hydrological station located at Montjean-sur-Loire, upstream of the influence of dynamic tides (EauFrance, 2023). The river flow was separated into two components: a flood state, estimated as the annual 95th percentile, and the low-flow state, estimated as the annual 5th percentile. Quantitative data on water salinity/conductivity, temperature, and DO were retrieved from monitoring stations at Le Pellerin and Paimbœuf, part of the measurement networks SYMEL (1985–2000) and later SYVEL (2007–2020) (GIP Loire Estuaire, 2023). Abundant time-series data were available from Le Pellerin station, enabling us to analyze long-term evolution in abiotic conditions (Table 1); instead, data from Paimbœuf were used to characterize spatial variability in abiotic conditions within the study area (Fig. 1). For all of these *in situ* data, the time steps varied between 10 min and 24 h. Each variable was averaged at a
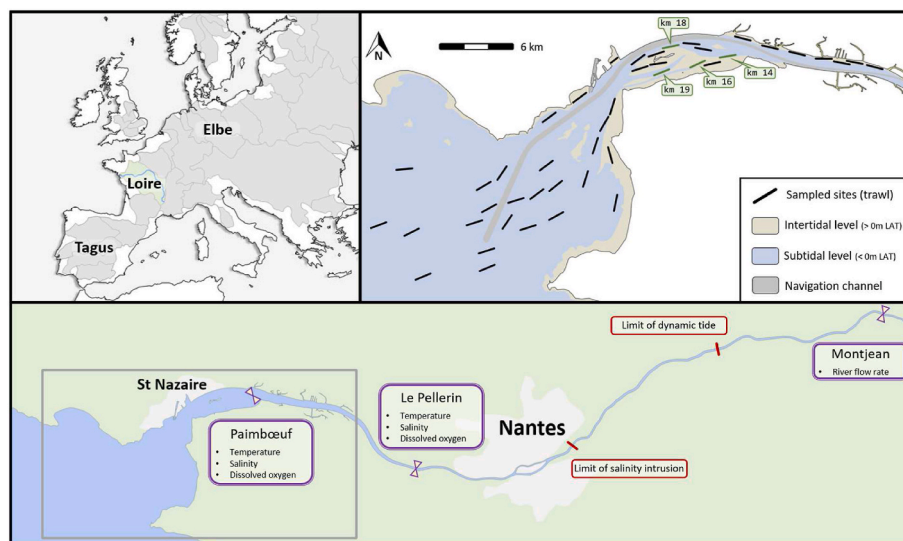

Fig. 1. Geography of the Loire estuary. Above on left: location of the Loire catchment relative to other large European catchments (e.g., Tagus and Elbe). Above on right: Loire estuary study area with locations of inter-annual beam trawl sampling sites. Labeled sites (green) were sampled monthly in 1982, 2011, and 2019. LAT: Lowest Astronomical Tide (reference tidal level). Below: Loire river lower reaches, along with locations of environmental monitoring stations (purple) and upper limits of tidal effects (red). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 1
Time series of environmental and biological datasets. The benthodemersal fish time series includes both the inter-annual and intra-annual scales, the latter being represented by the character "M" standing for Monthly.

daily scale to form a common baseline prior to any other calculation (e. g., annual percentiles or monthly averages).

For the purpose of visualization, locally estimated scatterplot smoothing (LoESS) regressions were fitted, with the associated 95% confidence intervals, as a function of the evolution of abiotic parameters using the R base package *stats* (Cleveland and Devlin, 1988). When appropriate, a Mann-Kendall test for monotonic trends was computed at the confidence level of 95% to test for significant trends in environmental time series (Mann, 1945; Kendall, 1975).

2.3. Benthodemersal fish

The evolution of benthodemersal fish communities was investigated at two overlapping temporal scales. The first examined their intra-annual variability using monthly fish abundance data from three annual cycles (1982, 2011, and 2019). The second investigated inter-annual variability based on fish abundance data collected irregularly by 29 scientific surveys that were conducted at the end of summer between 1980 and 2021 (Table 1). In each survey, sampling was conducted using a beam trawl with an opening of 2.7 m × 0.5 m without a tickler chain and a 20-mm stretched mesh net in the cod-end. Each haul lasted ca. 15 min at 2.8 kt for an average trawled surface area of 0.35 ha. Raw abundance data were standardized by the corresponding trawled surface. Individuals were identified at the species level with the exception of fish in the genus *Pomatoschistus*, which were aggregated into *Pomatoschistus* spp. due to the difficulty of distinguishing between *P. minutus* and *P. microps* at the juvenile stage.

2.3.1. Intra-annual dataset

The intra-annual dataset included three year-round monitoring surveys (annual cycles from October to the next October) designated by the year in which they concluded: 1982, 2011, and 2019. These surveys shared four sites identified after their location on the estuarine gradient (kilometer milestones 14, 16, 18, and 19). The sampling design in 1982 was slightly different from the other years, with no samples collected in May and September. As a consequence, analyses that required homogeneity in the statistical treatment of samples were conducted using a comparable subset of samples from 2011 to 2019.

2.3.2. Inter-annual dataset

Inter-annual surveys were carried out irregularly over varying spatial extents and sites between kilometer 2 (upstream of the estuarine spatial gradient) and 44 (downstream) in late summer (September or October) in 26 years between 1980 and 2021. Data were thus selected to maximize spatial comparisons among years. This was done by representing the estuarine gradient as a linear transect along which unique sampling sites were assigned per year.

2.3.3. Biodiversity assessment

Biodiversity was quantified using measurements of α-diversity, which captures the complexity of a community (Thukral, 2017), and β-diversity, which describes community heterogeneity (Tuomisto, 2010). The latter was assessed based on the dissimilarity of samples in terms of their taxonomic composition (Legendre and De Cáceres, 2013; Whittaker, 1972). Diversity indices were then compared using multivariate methods to provide insights on the evolution of the taxonomic composition of assemblages.

2.3.3.1. Diversity indices.
To quantify α-diversity, the taxonomic richness S and Pielou evenness J' were computed, with $J' = \frac{H'}{ln(S)}$ in which H' is Shannon entropy (Hill, 1973). Taxonomic richness equals the number of taxa present in a sample, while evenness quantifies homogeneity in the relative abundance of different taxa.

For β-diversity, multiple-site abundance-based Ružička dissimilarity was broken down into two components: balanced-variation (equivalent to replacement) and abundance-gradients (equivalent to nestedness). Balanced-variation describes the distribution of taxa along gradients whereas abundance-gradients reflect non-random processes of taxa loss (Baselga, 2017; Legendre and Gauthier, 2014). The dissimilarity parameters were computed using the function *beta.multi.abund* in the R package *betapart* v1.6 (Baselga et al., 2023).

2.3.3.2. Taxonomic composition.
The β-diversity was assessed using measurements of pairwise dissimilarity between samples based on the taxonomic composition of their fish communities. Specifically, the Hellinger distance (Hellinger, 1909; Rao, 1995) between assemblages was calculated as recommended by Legendre and De Cáceres (2013). Spatial and temporal variability in pairwise dissimilarity values among samples was then analyzed using principal coordinates analysis (PCoA). The spread of sample groups in the first ordination plane was quantified and compared using t-distribution ellipses at the confidence level of 50% (Friendly et al., 2013).

2.3.3.3. Intra-annual scale.
Spatial and temporal variations in monthly-surveyed fish communities were investigated using Community Trajectory Analysis (De Cáceres et al., 2019). Site-specific ecological trajectories were constructed by sequentially linking month-ordered samples defined by their rank in the trajectory (i, $i + 1$, …) with directed segments (s_i), forming a year-round continuum in the ordination space Ω.

Segment speed (S) was computed along ecological trajectories to provide information on the month-to-month variation in taxonomic composition. Segment speed is the length (L) of a segment—i.e., the

distance separating the segment's endpoints in the first plane of ordi-nation—divided by the time interval between the two corresponding samples. The net change ratio (NCR), a synthetic metric comparing the dissimilarity between the beginning and end of an ecological trajectory to the sum of the length of its segments, was also computed. NCR reflects the consistency of the gradients that drive the trajectory path through time (Sturbois et al., 2021).

Overlaps between ellipses were used to assess the overall dissimilarity between the year-round taxonomic composition of different annual cycles. Differences in the distribution of segment speeds between annual cycles were investigated by pairing monthly samples from different monitoring surveys and using a Wilcoxon signed-rank test (Wilcoxon, 1945).

2.3.3.4. Inter-annual scale. To ensure the consistency of outputs, Community Trajectory Analysis requires a continuous sampling timeline, which precluded its use at the inter-annual scale. Instead, a classification procedure that used Ward's method (hierarchical clustering analysis, HCA) was employed on the samples' pairwise Hellinger distance matrix (Ward, 1963). This method was coupled with an ordination to identify clusters of samples that were similar in terms of fish taxonomic composition from 1980 to 2021 along the estuarine spatial gradient and to pinpoint patterns of modification in space and/or time.

The Dufrêne-Legendre index (IndVal) was computed for each taxon as the product of its relative frequency and relative average abundance in each cluster formed by the HCA (Dufrêne and Legendre, 1997; De Cáceres et al., 2010), using the function *multipatt* in the R package *indicspecies* v1.7.12 (De Cáceres and Legendre, 2009). A taxon with a significant IndVal for a given cluster was considered to be an indicator taxon, meaning that it was highly represented in that cluster's samples (fidelity) and rare in other clusters (specificity).

To highlight spatial and/or temporal changes in fish communities, variability in biodiversity indices and taxonomic composition was partitioned over space (estuarine gradient) and time (years, months) using the function *varpart* in the R package *vegan* v2.6.4 (Oksanen et al., 2022). Variability in univariate diversity indices was partitioned using partial linear regressions (Whittingham et al., 2006; Sokal and Rohlf, 1995) while the partitioning of multivariate taxonomic composition was conducted using partial distance-based redundancy analysis (McArdle and Anderson, 2001; Legendre and Legendre, 1998). Tests for the significance of conditional effects were based on adjusted coefficients of determination (i.e., adjusted R^2) at a significance threshold of 0.05.

2.3.3.5. The response of taxa to abiotic variations. At the fine spatial scale investigated in this study, the lack of environmental data prevented from direct comparisons between abiotic conditions and fish diversity indices. In order to investigate how fish communities responded to environmental modifications, an indirect comparison was set using the tolerance range of fish taxa to salinity and DO. Tolerance range values were retrieved from a meta-analysis of fish environmental niches conducted on estuarine and coastal nurseries of the Bay of Biscay (Supplementary Material A). These were used to assign fish taxa to ecological valency groups using a classification procedure based on three tolerance range categories (wide: eury-, medium: meso-, narrow: steno-) for both salinity (-haline) and DO (-oxybiontic). The response of fish communities to long-term warming trends was also explored by analyzing their boreal, Atlantic, or Lusitanian biogeographic origin of distribution (Engelhard et al., 2011; Yang, 1982), and, for each category, the evolution of its spatially averaged relative abundance in time was studied.

Analyses were conducted using R v4.2.3 (R Core Team, 2023) through RStudio IDE v2023.03.0 + 386 (Posit team, 2023). The main data manipulation and visualization functions were sourced from the core R packages of *tidyverse* v2.0.0 (Wickham et al., 2019).

3. Results

3.1. Long-term trends in abiotic parameters

Over the last 40 years, the flood flow rate of the Loire River has decreased by nearly 1300 m^3 s^{-1} (Mann-Kendall test: $\tau = -0.231$, p-value = 0.035), corresponding to approx. -15% per decade relative to the 1980–2020 average. This same trend was also visible in low-flow rates, although restricted to the most recent decade (Mann-Kendall test: $\tau = -0.159$, p-value = 0.147). Maximal salinity and median temperature have increased by approx. 1 PSU and 2 °C, respectively, over the last 25 years (respective Mann-Kendall tests: $\tau = 0.422$ and 0.436, p-values = 0.107 and 0.044), whereas the frequency of hypoxic events decreased from 1995 until the early 2000s but then increased by 40 days from that point to 2021 (Fig. 2).

However, these long-term environmental trends were not visible at finer temporal scales, which were instead characterized by extreme variability. Seasonal patterns remained nearly unchanged over the period of time observed, highlighting the intensity of monthly environmental variability in this estuarine ecosystem. The three annual cycles studied featured strikingly different environmental conditions, with exceptionally high floods in 1982 but consistently low river flow rates in 2011 and 2019. Salinity and temperature were comparable among the three annual cycles, but oxygenation was lower in 1982, with hypoxic conditions occurring more frequently during summer (Supplementary Material B).

3.2. Evolution of fish communities over three non-consecutive annual cycles (intra-annual scale)

The analyzed dataset included 148 samples collected from four sites located in the middle estuary (Fig. 1) over the course of 11 months in 1982 and 13 months in 2011 and 2019. A total of 25 fish taxa were identified, with an overall fish abundance (mean ± standard deviation) of 50 ± 110 individuals per ha.

In the monthly dataset, fish α-diversity was generally low, with a median richness of 5 taxa and median evenness of 0.71. No significant spatial variation was detected in taxonomic richness, likely due to the limited size of the area in which monthly samples were collected (Supplementary Material E). However, significant variability was found in sample richness between different sampling years (13.15%, p-value <0.001) and months (10.11%, p-value = 0.004), which might be explained by, respectively, lower overall richness in 1982 compared to 2011 and 2019, and by low spring and summer richness compared to that found in October or November. Analyses of Pielou's evenness detected no significant variation attributable to sampling location or month, but did reveal variation in evenness among sampling years (6.47%, p-value = 0.006), most likely due to globally higher values in 2011 (Fig. 3). Patterns of β-diversity were dominated by the influence of balanced-variation (96.3% in 1982, 98.8% in 2011, and 98.4% in 2019), highlighting the importance of fish succession along the estuarine spatial gradient.

Fish communities were more variable in time—either between annual cycles (18.45%, p-value <0.001) or months (13.69%, p-value <0.001)—than in space (2.48%, p-value <0.01). Therefore, the four site-specific ecological trajectories were averaged in order to focus on the yearly and monthly variations. Site-specific trajectories can be found in Supplementary Material C, while the spatially averaged ones are presented in Fig. 4 for each year of study. Overall, the ecological trajectory in 1982 was distinct from the paths followed in 2011 and 2019; there was minimal overlap between the ellipses for 1982 and 2011 (<1%) and no overlap between 1982 and 2019. Instead, the ellipses for 2011 and 2019 overlapped over approximately 50% of their respective areas, suggesting a high degree of similarity in their fish community composition. The distinctiveness of the path followed by the fish assemblages in 1982 might be explained by variations in the abundance of
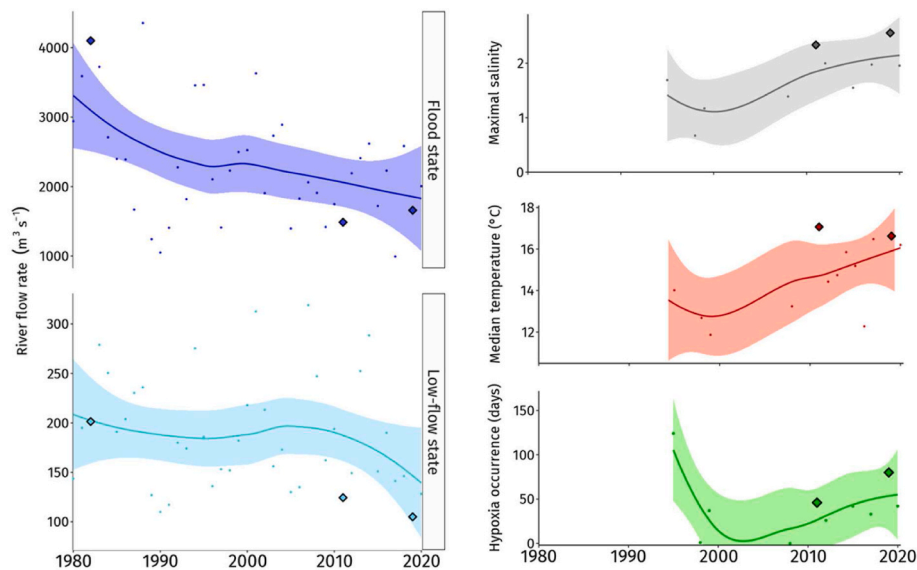
Fig. 2. Inter-annual variability in river flow rate at Montjean-sur-Loire hydrologic station (1980–2020) and salinity, temperature, and DO at Le Pellerin environmental monitoring station (1995–2020) with LoESS regression curves and 95% confidence interval ribbons. River flow rate was divided into flood state (95th percentile annually) and low-flow state (5th percentile annually). Salinity, temperature, and DO are represented as, respectively, annual 90th percentile salinity, annual median water temperature, and number of days featuring a DO 90th percentile under the threshold for hypoxic conditions (5 mg l^{-1}). Diamond-shaped points indicate datapoints from the years of the intra-annual surveys (1982, 2011, and 2019).
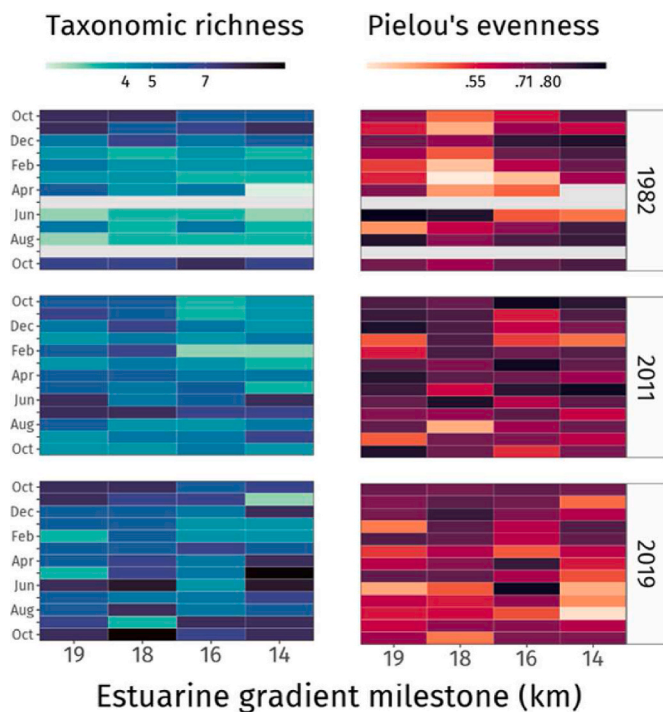
Fig. 3. Intra-annual α-diversity of estuarine fish communities across space and time (years and months). In the legend, the numbers below the gradient bars indicate the quartile cut-offs for each distribution.

a few specific species (*Platichthys flesus*, *Osmerus eperlanus*, and *Solea solea*). The trajectory seemed to alternate between two 'stable' states (characterized by low segment speeds) separated by transition periods in winter and the beginning of summer (January → February and June → July/August, respectively). The spring stable state, which was dominated by *P. flesus*, seemed to represent the most distinctive part of the 1982 monthly succession. Instead, the more-recent trajectories displayed more chaotic paths that were influenced by several other taxa

(*Pomatoschistus* spp., *Aphia minuta*, *Merlangius merlangus* in 2011 and *Pomatoschistus* spp., *Dicentrarchus labrax*, *Trisopterus luscus* in 2019), preventing the identification of any potential seasonality in the monthly successions.

The 1982 trajectory also differed in having a significantly lower mean segment speed and a higher NCR (0.182) compared to the values observed in 2011 and 2019 (0.144 and 0.051). The combination of both higher speeds and lower NCRs in 2011 and 2019 indicated that the gradients structuring the communities were of an unstable nature and that the fish assemblages often experienced dramatic swings from month to month.

The annual cycles were invariably dominated by euryoecious Lusitanian taxa. Meso- to stenoecious fish taxa were rarely found in the monthly samples, with the exception of *Chelon labrosus* (stenoxybiontic), which was caught at the beginning of the 1982 annual cycle. Atlantic taxa, represented by *Anguilla anguilla*, formed a small but steady fraction of the monthly fish assemblages. Boreal fish, predominantly *O. eperlanus* and *Ciliata mustela*, were mostly caught from November to February but with decreasing frequency from year to year, with an average frequency of 16.2% in 1982, 8.5% in 2011, and 2.3% in 2019 (Fig. 5).

3.3. Evolution of fish communities over four decades (inter-annual scale)

The analyzed dataset included 280 samples collected over 26 years (earliest 1980, latest 2021). A total of 46 fish taxa were caught, for an overall fish abundance (mean ± standard deviation) of 50 ± 190 individuals per ha.

At the inter-annual scale, the α-diversity of fish communities was consistently low, with a median richness of 6 taxa. Moreover, the low inter-quartile range (3 taxa) indicated a low degree of spatio-temporal variability (Fig. 6). No significant temporal variations were detected, and only a small spatial signal was found (Supplementary Material E). In terms of β-diversity, these fish communities were widely dominated (99.3%) by the influence of balanced-variation.

Clustering analysis differentiated five clusters of samples (Fig. 7, details in Supplementary Material D). The first ordination gradient, representing 27% of the variability, discriminated samples based on their location, with upstream samples characterized by strongly negative coordinates and external samples by positive ones. Similarly,
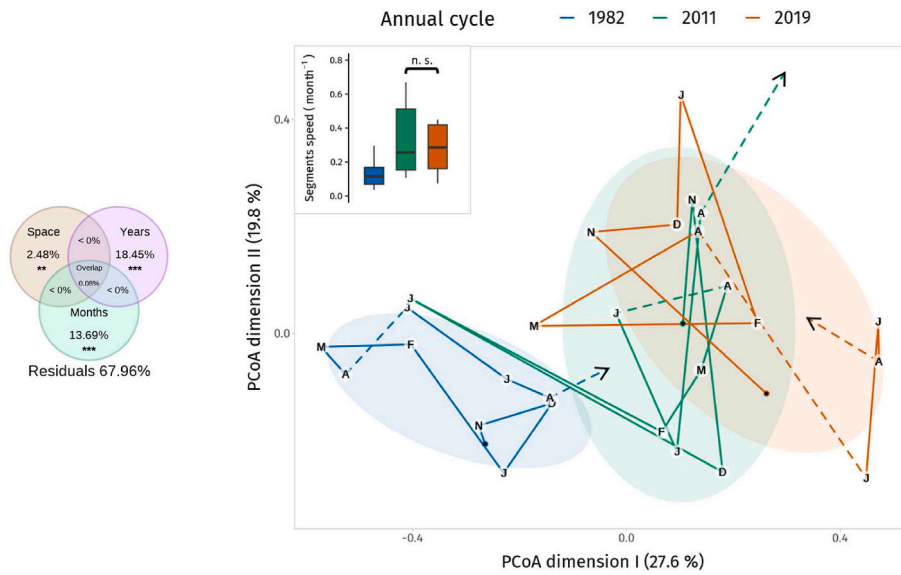
Fig. 4. Partitioning of the variance in fish community composition (Venn diagram) and spatially averaged ecological trajectories for annual cycles (October-to-October) in 1982, 2011, and 2019, encompassed by data ellipses. Dashed segments indicate that the two linked samples are separated by more than one month in time (May and September samples were missing in 1982 and excluded in 2011 and 2019 for the purpose of trajectory analysis). The subplot in the top-left corner presents the distribution of segment speeds per annual cycle, with significantly slower speeds in 1982 (Wilcoxon signed-rank test).
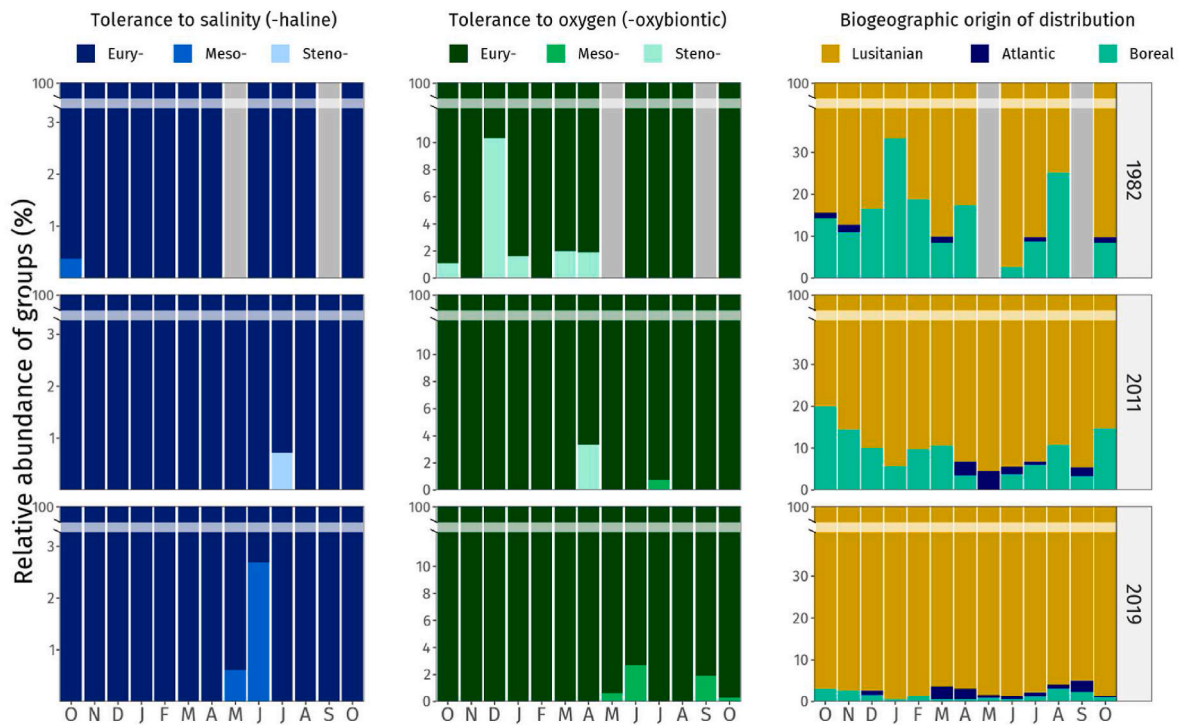
Fig. 5. Relative frequency in the monthly samples of different types of fish, grouped by ecological valency (salinity and oxygen) and biogeographic origin. Gray bars indicate missing data as the months of May and September were not sampled in 1982. The ordinate axes were cropped to focus on the area of the plots featuring variations among months.

variance partitioning highlighted a strong spatial component to variability in the composition of taxonomic assemblages (19.08%, p-value <0.001) but only slight temporal variability (3.37%, p-value <0.001). The strength of the spatial gradient likely reflected the distance and relative distinctiveness of samples in the outer reaches of the estuary from those associated with the internal section. Instead, the temporal variability was probably the result of the appearance of *Callionymus lyra* in one external cluster in 1997 and later years, as well as the upstream intrusion (by approx. 15 km) of external clusters over the analyzed time

window, replacing previously existing clusters. This was paralleled by the receding distribution of *A. anguilla* during this time (Fig. 7, Supplementary Material F).

As the estuarine spatial gradient was sampled irregularly through time, the focus was placed upon two sections (upstream and downstream) that were characterized by more regular sampling and comparisons of the relative frequency of different fish valency groups were performed. Consistently, the broad majority of fish species were members of the most tolerant category of euryoecious Lusitanian taxa. Meso-
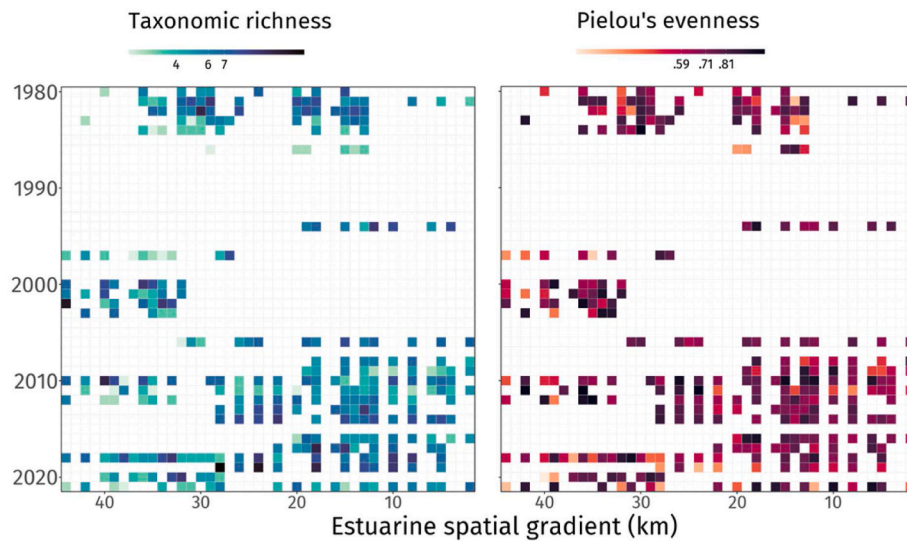
Fig. 6. α-diversity of inter-annual fish surveys across space (kilometers) and time (years). Legend bars indicate the quartile cut-offs of each distribution.
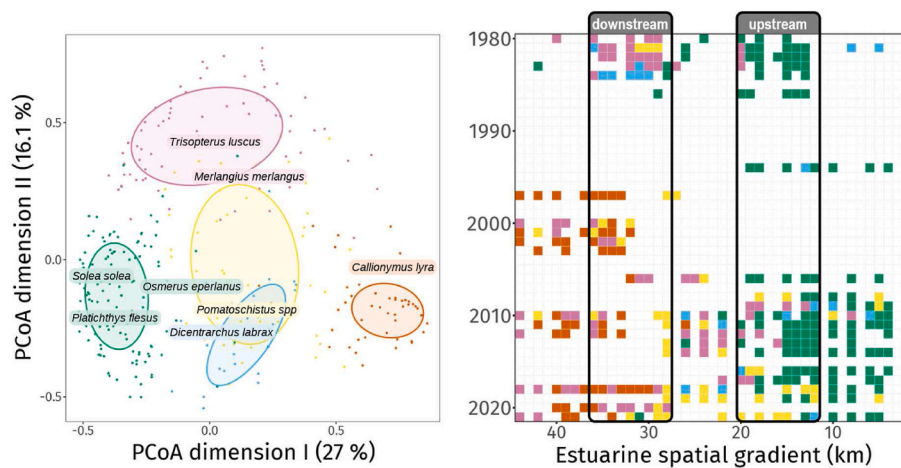
Fig. 7. Classification of inter-annual samples. Left panel: biplot displaying sample clusters with associated data ellipses and weighted average positioning of indicator taxa (significant in IndVal analyses). Right panel: projection of clusters on a grid representing space (kilometers) and time (years). Black frames highlight down- and upstream sections on which subsequent fish valency analyses were conducted.

to stenohaline taxa and their oxybiontic counterparts were seldom present in the upstream section. Meso-to stenohaline fish were also rarely found in the downstream section, with the exception of *Eutrigla gurnardus* in 1980–81 and *Scophthalmus maximus* in 1984, with the latter representing the only occurrences of non-euryhaline fish after 2000 (<2% in 2002, 2010, and 2018). In parallel, a decline in the relative abundance of meso- to stenoxybiontic fish taxa was noted through time, mostly *Dicologlossa cuneata* (Fig. 8). In terms of biogeographic origin, fish communities in both sections of the estuary were dominated by Lusitanian fish (e.g., *Pomatoschistus* spp., *S. solea*, or *D. labrax*). The relative abundance of boreal fish, mainly *O. eperlanus*, has decreased in the downstream section since at least 1997, but populations upstream appear instead to have fluctuated, with an average proportion of approx. 7%.

4. Discussion

4.1. Evolution of estuarine environmental conditions in the context of global change

Over the 40 years analyzed here, the Loire estuary exhibited increasing temperatures (approx. 0.5 °C per decade) and decreasing flood flow rates (−15% per decade relative to the 1980–2020 average), reflecting the expected consequences of global change on European estuaries (Costoya et al., 2015; Schneider et al., 2013). Warming in the waters of the Loire estuary seems to be of greater magnitude than in northern European estuaries such as the Elbe, where an increase of approx. 0.13 °C per decade has been predicted (Hein et al., 2016). It is also stronger than patterns in southern Europe, as exemplified by the Gironde (France) and Tagus estuaries, for which trends of approx. 0.30 °C and 0.16 °C per decade, respectively, were observed prior to 2000 (Pasquaud et al., 2012; Lima et al., 2007). These warming trends are expected to decrease in magnitude during the current decade through the influence of atmospheric teleconnections, in particular the Atlantic Multidecadal Oscillation, a mode of natural climate variability that is predicted to decrease water temperature anomalies along the Atlantic coast of western Europe before increasing them in synergy with human-induced warming (Garcia-Soto and Pingree, 2012). The reduction in flood flow rate that was observed for the Loire contrasts with data from the Elbe, where no such trend was observable prior to 2000 (Bartl et al., 2009), but is similar to reports from the Tagus and Seine (France), for which flood river discharge has decreased since the beginning of the
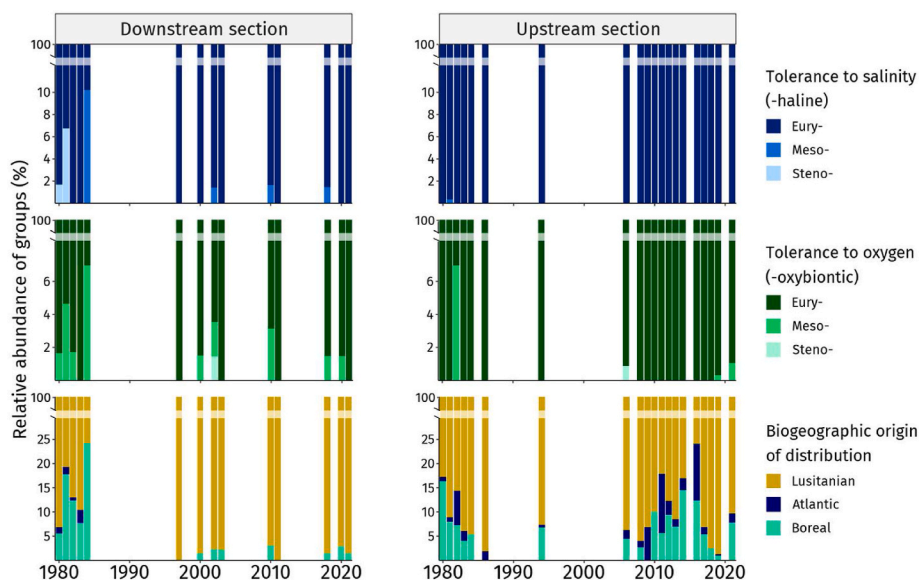
Fig. 8. Inter-annual evolution in the proportion of different fish taxa, grouped by tolerance groups (salinity and oxygen) and biogeographic origin. The ordinate axes were cropped to focus on the area of the plots featuring variations in groups.

21st century (Neves, 2010; Dauvin and Pezy, 2013). In the Mondego estuary (Portugal), reduced precipitation—and thus river discharge—was found to induce displacement of the salinity gradient upstream during drought events (Leal Filho et al., 2022). In the Loire, an increase over time was identified in the maximal salinity at a given point, suggesting a similar upstream shift in the overall salinity gradient. Another expected consequence of this warming trend is enhanced depletion of dissolved oxygen through bacterial oxidation of the organic matter contained in the turbidity maximum zone, which is more likely to persist within the estuary due to decreased flushing forces from reduced river discharge, as observed in the Gironde estuary (Bendtsen and Hansen, 2013; Jalón-Rojas et al., 2016). Indeed, our data revealed that hypoxic events in the Loire estuary have been increasing in frequency since the beginning of the 21st century.

4.2. Structural modifications in benthodemersal fish communities

Modifications to the abiotic conditions in estuaries have been found to increase pressure on biological communities through shifts in tolerance range and climatic niches (Shields et al., 2019; Breitburg, 2002; Lauchlan and Nagelkerken, 2020). Global change can also bring about physiological and phenological modifications of the species present in these areas (Erickson et al., 2021; Kimball et al., 2020; Visser et al., 2021). It is possible that the environmental changes observed in our study might lead to alterations in the distribution and seasonality of certain sensitive species, especially during summer in which conditions can become particularly stressful (low water flow and warm temperatures leading to salinity intrusion and hypoxic events).

Compared to other regions, the taxonomic richness (α-diversity) of fish communities in western European estuaries is expected to be low. Indeed, in an examination of 75 estuaries in this region, Vasconcelos et al. (2015) found that 67 contained fewer than 30 fish species, compared to approx. 80 fish species in tropical estuaries in Africa or Brazil (Nicolas, 2010; Gerson Araújo et al., 2018; Albaret et al., 2004). Among large estuaries in western Europe, the Loire is one of the most species-rich, along with the Sado (Portugal), Seine, Gironde, and Thames (Great Britain); the Thames is the richest, with 45 fish species (Nicolas, 2010). In the Loire estuary, although taxonomic richness was relatively low, α-diversity seemed to remain stable over the 40-year window examined here. One exception was observed at the intra-annual scale, with summertime richness in 1982 being low

compared to the more-recent periods (2011 and 2019). This might be the result of strong hypoxic conditions in this period of time, potentially due to massive volumes of sediment resuspension caused by different dredging practices toward the end of the 20th century. Although species-poor, the relative constancy of these species assemblages raises the question of their vulnerability to global change. The ecological vulnerability of a community reflects its sensitivity to stressful conditions (e.g., global change and its associated pressures) along with its capacity to adapt to such stress (Adger, 2006). Because they have evolved in a highly variable environment, estuarine communities are expected to have a strong capacity for adaptation (Elliott and Quintino, 2007; Margalef, 1981). One way to assess a community's stability is by examining the constancy (i.e., invariability in time) of its α-diversity (Van Meerbeek et al., 2021). The relationship linking biodiversity to stability and its components (e.g., resistance and resilience) has long been debated and remains controversial today (Donohue et al., 2016; Ives and Carpenter, 2007; McCann, 2000; Pennekamp et al., 2018; Pimm, 1984). However, generally speaking, a highly diverse ecosystem should be less vulnerable than a poorly diverse one, which is more likely to experience strong variations (Thibaut and Connolly, 2013). In the Loire estuary, the presumed high adaptive capacity and observed relative constancy of fish communities may be exerting a protective effect against population collapse due to limited α-diversity. In other European estuaries, evidence of a capacity to adapt to global change was found for communities of benthic invertebrates, but these findings were not necessarily replicated in coastal seagrass habitats (Crespo et al., 2017; Chust et al., 2013). Compared to other regions, however, European estuaries are dominated by more-vulnerable and less-resilient fish species (Vasconcelos et al., 2017; Lazzari et al., 1999), a difference that might have arisen naturally but has likely been widened by past and current anthropogenic pressures. Further investigations are required to monitor for cues of a potential tipping point and to inform predictions of how long these conditions might last in the face of persistent stress exposure (Dakos et al., 2019).

On an intra-annual scale, heterogeneity was observed in the dynamics of fish communities in the Loire estuary, with more recent years characterized by a succession of complex monthly assemblages (2011 and 2019) unlike the cyclic seasonal patterns observed in the past (1982). The abrupt winter and summer transition periods observed in 1982 are comparable to those reported more recently (2004–2008) from the Gironde estuary (Selleslagh et al., 2012). The seasonal summer shift

in the Gironde was attributed to an annual transfer from a pelagic phase to a benthodemersal phase. In our study, the intricate monthly dynamics in recent years might be explained by the slightly higher evenness of fish communities compared to the past (especially in 2011 and to a lesser extent in 2019; Fig. 3), which blurs the seasonal signal of species succession. In 1982, the fish community was dominated by three species (*Platichthys flesus*, *Osmerus eperlanus*, and *Solea solea*) and variations in their abundance dictated the modifications to the overall assemblage. Instead, in the more-recent years, the assemblages contained several additional major taxa (e.g., in 2011 *Aphia minuta* and *Merlangius merlangus* and in 2019 *Pomatoschistus* spp. and *Dicentrarchus labrax*). This expansion in the number of dominant species in the monthly data, along with an increase in species evenness, provides additional clues regarding the fish communities' gain in stability. Moreover, it suggests that the ecosystem of the Loire estuary has diversified with respect to its ecological niches, allowing a greater number of taxa to thrive. Another possibility is that environmental conditions have shifted over time in a way that reduces the differentiation between seasons (e.g., warmer and longer summers, drier winters), contributing to the recent decline in seasonality in the fish community.

4.3. Communities response to long-term abiotic trends

The species composition of benthodemersal fish communities was mostly structured spatially along the estuarine gradient. In estuarine ecosystems, salinity is considered to be the main ecological driver of species distributions (Whitfield et al., 2012; McLusky and Elliott, 2004). Our results are consistent with this, with a clear distinction between coastal fish clusters in the external section of the Loire estuary and those found in internal brackish water. Moreover, communities were mostly structured through taxon replacement, likely in the form of spatial turnover along the salinity gradient. In addition to this spatial structure, a temporal pattern of intrusion by external communities was also detected towards the inner reaches of the estuary. The major species associated with this intrusion pattern was *Callionymus lyra*, a benthodemersal fish distributed along coastal waters as reported, e.g., in the Tagus estuary (Prista et al., 2003). The opposite pattern was observed for *Anguilla anguilla*, for which identifications have been confined to the internal reaches of the Loire estuary since 1984. These temporal shifts could be evidence of marinization (Albaret and Ecoutin, 1991; David et al., 2007), which is characterized by the gradual penetration of salty seawater further upstream. Global change contributes to the marinization of estuarine ecosystems through sea level rise and lower rainfall, which weaken the resistance of river discharge to tidal forces (Khojasteh et al., 2021; Langston et al., 2020; Veldkornet and Rajkaran, 2019). Marinization might threaten previously established populations adapted to variable estuarine conditions, for example by disrupting salinity-driven processes such as larval colonization and juvenile distribution of *S. solea* across nursery grounds (Marchand, 1993). Moreover, habitat characteristics such as substrate sediment composition are unlikely to undergo a comparable shift, and the consequent spatial mismatch between salinity range and sediment composition may jeopardize the availability of suitable habitats (Parker and Boyer, 2019). Warming-induced marinization could alter the distribution of a wide range of factors that shape estuarine ecosystems, including communities at the base of the food web, potentially leading to trophic cascades (Chaalali et al., 2013; Chevillot et al., 2019). Multiple symptoms of estuarine marinization have already been reported in European estuaries where less precipitation and more frequent droughts are expected, such as the Gironde and the Tagus (Pasquaud et al., 2012; Rodrigues et al., 2019).

A second type of response to global change was observed in the form of a decrease in the proportion of boreal fish species, mainly during winter, which is reminiscent of the deborealization/tropicalization reported in estuaries of southern and central Europe as a consequence of warming (Nicolas et al., 2011; Martinho et al., 2010). For instance,

certain boreal species, such as *O. eperlanus*, have become rarer in the Tagus and Loire estuaries, while the subtropical fish *Argyrosomus regius* has increased in abundance in the Tagus estuary. *A. regius* has also been reported in the Gironde estuary, but has not yet been detected in the Loire (Cabral et al., 2001; Nicolas, 2010). Similarly, the northern flatfish *Limanda limanda* has been absent from Loire estuary records since 1984; it was found to have definitively departed from the neighboring Vilaine estuary (France) in 1996, but is still currently present in the Seine estuary. Conversely, the southern fish *Dicologlossa cuneata* has increased in abundance in the Vilaine estuary but has not yet been recorded in the Seine (Désaunay et al., 2006; Cariou et al., 2021). These shifts in species abundance stand in contrast to those in northern European estuaries such as the Elbe, where *P. flesus* has increased in abundance and boreal species such as *O. eperlanus* can represent more than 95% of estuarine benthodemersal fish (Eick and Thiel, 2014; Thiel et al., 2003).

Finally, a degradation in water oxygenation was observed that was associated with more frequent hypoxic events. The main driver of the recent increase in oxygen-depleted zones is considered to be human-induced discharge of nutrients and organic matter into enclosed estuarine waters (Díaz and Rosenberg, 1995). Global change is expected to exacerbate this by promoting the persistence and spread of hypoxic zones (Díaz and Rosenberg, 2008). In western Europe, large estuaries are often highly turbid and thus more susceptible to hypoxia (Schmidt et al., 2019). This situation could lead to consequences at the individual level in the form of altered behavior, reduced growth rate, and mortality (Bozorg-Haddad et al., 2021). It is even possible that the spatial extent and frequency of hypoxic events could negate the benefits of these areas for fish populations, e.g., favorable nursery habitats (Breitburg, 2002). At the community level, hypoxia-induced emigration and mortality reduce fish diversity and alter trophic relations through, e.g., disruption of antipredation behaviors (Rahel and Nutzman, 1994; Domenici et al., 2007). Typically, individual fish respond to diel hypoxia through short-term behavioral adjustments and physiological plasticity (Kramer, 1987; Crispo and Chapman, 2010). In response to lower oxygen levels, respiratory rate is increased to enhance gas exchange and the oxygen-depleted area is avoided through active swimming (Breitburg, 2002; Eby and Crowder, 2002). Such behavioral responses increase energy consumption at the expense of numerous somatic activities including growth (Dalla Via et al., 1994). At the same time, phenotypic plasticity can enable rapid physiological acclimation, including modifications to blood cells and solute composition (Jensen et al., 1993). Together, these responses may potentially ward off the type of long-term community variability that is associated with thermal stress (cf. deborealization phenomenon) (Collins et al., 2016). Metabolic plasticity was demonstrated to play an important role in the adaptiveness of local estuarine fish (*P. flesus*) populations to rising temperature and hypoxia in several European estuaries along the Atlantic coast (Pédron et al., 2017). The plasticity of the aerobic metabolism partly explains the large tolerance of estuarine fish taxa to dissolved oxygen concentrations (Reemeyer and Rees, 2020). Given this, it is unsurprising, and indeed expected, in this study that the degradation of oxygenation conditions did not lead to marked response in fish populations except for a variation in the proportions of the mesoxybiontic flatfish *D. cuneata*, whose abundance was higher in the 2000s synchronously with less-frequent hypoxic events (Fig. 2, Supplementary Material F).

4.4. Study limits and recommendations for long-term ecological survey

In this study, the 1980s were considered to be a past ecological state for the purpose of long-term comparison, but the Loire estuary has been subjected to anthropogenic modifications and transformations for well over a century. This work thus suffers from a shifting baselines quandary (Little et al., 2017). Indeed, the observed modifications in fish communities did not represent the entire context of anthropogenic pressures and could not be compared to a more pristine ecological state, as the conditions in the 1980s were also shaped by both endogenous and

exogenous (e.g., global change) pressures.

The data analyzed here from the inter-annual surveys were collected in late September or October, and thus did not reflect the most stressful conditions of the year. In this respect, summer sampling would have been more useful, as it might have captured the response of communities to warm, oxygen-poor waters and a stronger upstream shift in the salinity gradient. In addition, this sampling scheme was ill-suited for analyzing fish communities' responses to deteriorating oxygenation conditions because such events are often short-lived (an hour to a few days), which diminishes the odds of sampling communities that are experiencing hypoxia. Furthermore, these events mainly occur in the turbidity maximum zone, which extends from just within the upper boundary of the spatial area examined here to a few kilometers upstream.

Overall, the observed abiotic patterns in the Loire estuary are consistent with the expected regional consequences of global change in European estuaries, namely, water warming and reduced river discharge. The relatively constant species richness detected in bentho-demersal fish communities suggests the persistence of a form of stability in spite of ongoing long-term environmental trends. However, certain shifts in the composition of species assemblages were highlighted that could reflect processes of marinization along with a northward shift in fish populations.

Although global change is taking place worldwide, only its local consequences can be managed (Lonsdale et al., 2022). Our understanding of these consequences for estuarine ecosystems is currently hindered by a lack of consistent and regular time-series data on the environmental and biological aspects involved (Biguino et al., 2023), and this is particularly true for the Loire. Concerned stakeholders must endeavor to create and maintain continuous environmental monitoring stations across the estuarine spatial gradient (Schmidt et al., 2019) as well as to support the implementation of recurring annual sampling campaigns. Such campaigns should focus on multiple monitoring sites using a replicated sampling design to improve the statistical strength of future comprehensive analyses and inform management strategies (Prosser, 2010).

CRediT authorship contribution statement

Romain Lécuyer: Writing – original draft, Visualization, Software, Methodology, Formal analysis, Data curation, Conceptualization. **Anne-Laure Barillé:** Conceptualization, Funding acquisition, Methodology, Resources. **Hervé Le Bris:** Conceptualization, Funding acquisition, Methodology, Writing – review & editing. **Anik Brind'Amour:** Conceptualization, Funding acquisition, Methodology, Resources, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The authors do not have permission to share data.

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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.2024.108738.

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