



Thriving life beneath: Biodiversity and functioning of macrobenthic communities within two human-shaped European estuaries

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1. Introduction

Ecosystems work as dynamic entities through which higher-order ecological functions are realized, leading to a range of beneficial outputs known as ecosystem services (Costanza et al., 1997; Daily, 1997). Estuaries, with their diverse biotic and abiotic conditions, are particularly notable for providing a variety of essential ecosystem services. These include the discharge of nutrient to coastal shelves (Guillaud et al., 2008; Hall et al., 2015), serving as migratory pathways for fish (Hayes and Kocik, 2014), providing stopover sites for birds such as waders and ducks (Wang et al., 2022; Jakubas et al., 2014), and offering sheltered nursery areas for juvenile fish to grow in favorable conditions (Gibson, 1994; McLusky and Elliott, 2004).

Among these services, tidal estuaries often feature highly productive habitats for juvenile fish (Beck et al., 2001). In particular, intertidal mudflats are crucial due to their unique contribution to the ecosystem functioning and energy flow. During high tide, weak currents allow nutrient-rich suspended matter to settle over these habitats. This matter is then exposed to solar energy during low tide, promoting energy incorporation through the photosynthetic activity of microalgae (Boyes and Elliott, 2006; Schelske and Odum, 1962).

Moreover, intertidal mudflats host particular organisms that play diverse functional roles (Dissanayake et al., 2018; Passarelli et al., 2018). For instance, they host heterotrophic consumers, namely the zoobenthos, which convey energy from autotrophic and detritic sources to higher trophic levels (McLusky and Elliott, 2004). This energy input into the estuarine food web partly originates from nutrient and detrital discharge flowing from the catchment into the estuary and thus enhancing benthic production (Rybarczyk and Elkaïm, 2003; Underwood and Kromkamp, 1999). Macrobenthic organisms in estuarine ecosystems, including mudflats, feature a variety of roles by modifying sediment structure through feeding, burrowing, and tube-building

activities (Wong and Dowd, 2021; Warwick and Clarke, 1984). They alter the surrounding topography (e.g., engineering species), and play a key role in serving as food resource for fish and other predators (Passarelli et al., 2018; Saulnier et al., 2020).

Given the critical ecological roles performed by macrobenthic organisms, understanding biodiversity extends beyond mere species counts. It becomes essential to assess how functional diversity—representing the range of roles and processes contributed by different species—affects ecosystem health. Traditional measures of biodiversity based on taxonomy—“who you are”—provide important information but may not fully capture the complexities of ecosystem functioning. Examining biological traits—“what you do”—can offer more insight into the functional attributes of communities. This approach may reveal variations that influence ecosystem processes more significantly than taxonomic diversity alone (Streit and Bellwood, 2023; Belley and Snelgrove, 2017; Ieno et al., 2006). Therefore, evaluating both taxonomic and functional diversity provides a comprehensive assessment of estuarine mudflats under various pressures, offering a detailed view of ecosystem health and functionality. This approach helps identifying critical situations in order to prevent the deterioration of ecosystem functions. This gain of anticipation is essential for developing effective conservation strategies to ensure the long-term sustainability of estuarine ecosystems (Díaz and Cabido, 2001; Cadotte et al., 2011).

Human activities, including industrialization, resource utilization, and urban development, impose significant pressures on estuarine ecosystems, leading to habitat loss, environmental modifications, and organic contamination. Global change, manifested by long-term decreases in river flow rates, exacerbates these threats (Defeo and Elliott, 2021; Cloern and Jassby, 2012). In this study, we aimed to understand the effects of persistent anthropogenic pressures on the abiotic forcing factors and biotic structure of estuarine ecosystems. Specifically, we

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focused on the inter-annual evolution of three components—morphological, hydrological, and biological (macro-benthic)—under continuous anthropogenic pressure. To this end, we conducted a comparative study of the macro-benthic communities of the Loire and the Seine estuaries, which represent two of the largest tidal estuaries in Western Europe. In these two areas, we employed a variety of approaches to examine the potential effects of ongoing anthropogenic pressures on the structure and functioning of estuarine ecosystems. Using multiple indices, we assessed biodiversity by describing the diversity of organisms (α -diversity) and the interactions between them (β -diversity). These analyses were conducted regarding both taxonomic and functional aspects in order to gain extensive information about macro-benthic communities. Finally, we estimated macro-benthic production in order to investigate its variations in space and time, along with its relationship with diversity indices to address the existence of a link between macro-benthic biodiversity and ecosystem functioning.

2. Materials and methods

2.1. Study sites

The Loire and Seine estuaries are macrotidal semi-diurnal estuaries located in the northeast Atlantic, on the French coasts of the Bay of Biscay and the English Channel, respectively (Fig. 1). They are among the largest European estuaries in terms of dimensions and catchment area, and were formed around 10,000 years ago after the Holocene glacial retreat, classifying them as coastal plain estuaries (Weckström et al., 2017). Both of these estuaries have a tidal range of more than 6 m, giving rise to extensive intertidal surfaces that play a pivotal role in these ecosystems. To facilitate comparisons with historical knowledge, we subdivided each estuary into smaller spatial units based on bathymetry, sediment composition, and management considerations.

Information on the position of each unit along the estuarine gradient is provided by the haline sectors indicated, although we acknowledge this approach is imperfect due to the high dynamism of the salinity gradient (Taupp and Wetzel, 2014). Intertidal mudflats were represented by the sites Méan, Bilho, Corsept, Donges (polyhaline), and Pipy (mesohaline) in the Loire estuary, and the Lateral Bank sandy mudflat and the Great Mudflat (polyhaline) in the Seine estuary. The remaining intertidal unit of the Seine, Pennedepie (euhaline), was composed of a sandy beach and sandbars. The subtidal units of the Loire—the Mouth (euhaline), the Middle unit (polyhaline), and the Inner unit (mesohaline) sites—were mainly muddy, whereas the subtidal units of Seine—the Mouth, South Trench, North Trench (euhaline), and Channel (polyhaline)—were heterogeneously characterized by a patchwork of muddy sand and sand. The Loire units included reaches of the mesohaline sector (Pipy, Inner) that lacked a counterpart in the Seine estuary due to the absence of consistent monitoring of the narrow intertidal areas in the mesohaline sector of that estuary. Characterization of the haline sectors in both estuaries was informed by observations and model outputs (Anonymous, 2021; Bacq et al., 2013). Long-term shifts were observed in the salinity gradient of both estuaries, paralleling the loss of estuarine aquatic surfaces (Supplementary Material A).

2.2. Morphological and hydrological components

The quantification of estuarine aquatic surfaces and determination of the historical positions of the salinity gradient were based on an extensive analysis of the literature (Verger, 2009; Anonymous, 2021; Marchand, 1993, 1972; Maquet, 1974; Ferronnière, 1901; Lesourd et al., 2016; Bacq et al., 2013; Delsinne, 2005). One of the main drivers of variability in benthic communities is flow rate, which influences nutrient discharge, larval drift, and seasonal shifts in the salinity gradient. Flow rate time-series data (1942–2023) were retrieved from hydrological stations upstream of the influence of dynamic tides, at Montjean-sur-Loire for the Loire River, and at Poses and Vernon for the Seine River (Anonymous, 2023b). The annual average of daily flow rate measurements was computed from January to June, encompassing the bloom period of photosynthetic organisms that leads to a boost in primary production. This period also coincides with the settlement and growth period of benthic macro-invertebrates, which benefit from the enhanced primary production.

2.3. Benthic macro-invertebrates

Our analysis of the inter-annual evolution of benthic features was based on data on the abundance and ash-free dry biomass of macro-invertebrates collected in scientific surveys conducted at the end of summer (September or October) between 2000 and 2017 in the Seine estuary (Chouquet, 2014; Brind'Amour, 2021), and irregularly between 2010 and 2021 in the Loire estuary (Barillé, 2011, 2015). Details regarding the spatial and temporal sampling design along with the related statistical imbalances are provided in Supplementary Material B. In each survey, sampling was conducted using grabs (van Veen, Day, Smith-McIntyre) with a standard sampling area of 0.1 m², which are effective for targeting macrofauna. The obtained sediment was screened on a 1-mm-mesh sieve and the residue was fixed in a solution of formaldehyde (4 %) and ambient water. Organisms were identified at the finest taxonomic resolution possible and counted in the laboratory. Each sample was composed of an average of 3 to 5 replicates. For each taxon of the Loire estuary dataset, abundance-to-biomass relationships were calculated based on observational data from several historical surveys; these were then used to compute biomass from raw count data. Abundance and biomass data were expressed per square meter. Taxa were filtered to keep those identified at the species level with the exception of annelids in the genera *Kirkegaardia* (0.5 % of abundance in the Seine) and *Tharyx* (1.4 % of abundance in the Loire) and the class Clitellata (2.2 % of abundance in Loire). Because these taxa represented non-

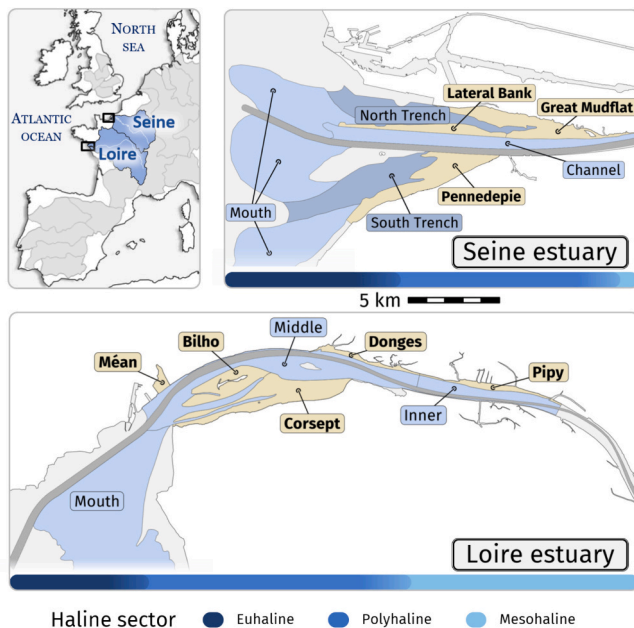


Fig. 1. Geography of the Loire and Seine estuaries. Top-left panel: location of the Loire River and the Seine River catchments (blue areas) and estuaries (black boxes) on the Atlantic coast of Western Europe. Top-right panel: the Seine estuary study area and its division into seven spatial units. Bottom panel: the Loire estuary study area and its division into eight spatial units. The wheat-colored units represent the intertidal area. The dark grey polygon represents the navigation channel, which was not considered in this work. The historical position of the haline sectors is given for guidance in the form of blue gradient bars. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

negligible portions of the total abundance of macrobenthic communities, they were retained and respectively aggregated into *Kirkegaardia* spp., *Tharyx* spp., and *Clitellata* spp.

2.4. Biodiversity assessment

2.4.1. Taxonomic β -diversity

Macrobenthic communities were first analyzed by computing the pairwise dissimilarity between the Loire and Seine samples altogether based on the Hellinger-transformed abundance of taxa per year (Hellinger, 1909; Rao, 1995). By comparing the two estuaries, we aimed to identify the similarities in their macrobenthic communities. A Principal Coordinates Analysis (PCoA) was then used to summarize community gradients in samples from both estuaries in a two-dimensional ordination. A Hierarchical Clustering Analysis (HCA) using Ward's method (Ward, 1963, details in Supplementary Material C) was performed on the matrix of pairwise dissimilarity to identified assemblages of taxa based on both estuaries. The resulting groups were visually represented using t-distribution ellipses at a 50 % confidence level around the respective samples (Friendly et al., 2013).

Secondly, we computed balanced variations (equivalent to replacement) and abundance gradients (equivalent to nestedness) by partitioning a matrix based on the multiple-site abundance-based Ruzička dissimilarity (Ruzička, 1958). This analysis helps to distinguish between changes in species composition due to replacement versus changes due to differences in abundance patterns (Baselga, 2017; Legendre, 2014). These dissimilarity indices were calculated using the function *beta.multi.abund* in the R package *betapart* v1.6 (Baselga et al., 2023). Finally, the function *beta.div* from the R package *adespatial* v0.3–21 (Legendre, 2014; Dray et al., 2023) was used to calculate the local contribution to β -diversity for each sample (LCBD) and each taxon (SCBD). LCBD was employed as a diversity index to identify samples with particularly unique taxonomic assemblages (Supplementary Material C).

2.4.2. Taxonomic α -diversity

The α -diversity of macrobenthic communities was assessed separately in the Loire and the Seine estuaries using Hill numbers, which are effective in capturing diversity even when there is considerable variation in species abundances (Hill, 1973). These values measure the number of effective species and allow for accurate comparisons between samples (Chao and Jost, 2012). Rather than focusing on individual diversity indices (Green and Chapman, 2011; Daly et al., 2018), we examined in here the diversity profiles composed of Hill numbers (qD) calculated using different degrees of sensitivity to species relative abundance, e.g., $q \in [0; 3]$ (Chao and Jost, 2015; Tóthmérész, 1995). An illustrative case would be $q = 0$ at which the Hill number reduces to species richness, without any consideration of abundance. For this, we used the diversity profile estimator proposed by Chao and Jost (2015) as it returns nearly unbiased estimates of true diversity, rather than empirical Hill numbers that may exhibit biases due to under-sampling.

A confidence interval was estimated around diversity profiles by bootstrapping. A site was considered more diverse than another if its profile was entirely above the other and the two confidence intervals did not overlap. Changes in taxonomic biodiversity across space and time were quantified through variance partitioning for richness ($S = OD$) and evenness ($J' = \frac{h^1D}{h^0D}$) using the function *varpart* in the R package *vegan* v2.6–4 (Oksanen et al., 2022).

2.4.3. Functional framework

To enhance our understanding of the functioning of the Loire and Seine estuaries, individuals were also assessed based on their roles in the ecosystem. Specifically, we examined a set of state traits related to production—maximal size, feeding mode, bioturbation activity, and motion capability—which shape interactions between organisms and their biotic compartments. State traits are considered to be valuable for

functional purposes when they relate to a specific process (Streit and Bellwood, 2023; Violle et al., 2007), which in the context of this study is the function of production.

This set of production-related state traits was complemented with measurements of turnover, an empirical rate trait representing the dynamic process through which biomass is generated (Brey, 2012). This quantitative trait was made semi-quantitative by categorization into one of four modalities of turnover. The “slow” modality characterized organisms that were unable to generate the equivalent of their own biomass in a year, and corresponds to rates observed in sub-Antarctic macrobenthic organisms ($0.12\text{--}0.87 \text{ yr}^{-1}$, Brey and Clarke, 1993). The “intermediate” modality corresponded to the rate of biomass generation of macrobenthic organisms in sub-tropical to temperate regions (worldwide median of 2 yr^{-1} , Cusson and Bourget, 2005; Robertson, 1979). Only a few macrobenthic organisms belong to the “fast” and “very fast” modalities, which are more representative of rates observed in the suprabenthos (e.g., copepods ranging from 3 to 31.7 yr^{-1} , Tremblay and Roff, 1983) or meiobenthos (e.g., nematodes ranging from 4 to 69 yr^{-1} , Vranken et al., 1986).

In parallel, multiple response traits related to abiotic forcing factors (living habit, vertical position in the substrate, tolerance to organic matter (OM) enrichment, and haline domain suitability) were investigated to assess potential disruptions in macrobenthic communities due to habitat loss and estuarine hydrological changes (e.g., lowered flow rate).

Altogether, the production-related traits and response traits examined in this study formed a set of 9 traits with a total of 37 modalities (Table 1). Organisms were described at the genus level based on a regional trait collection of marine invertebrates (Clare et al., 2022), and extrapolated to lower taxonomic resolution when necessary. The categorization was completed with information from online databases (tolerance to OM enrichment: Borja et al., 2000; haline domain suitability: WoRMS Editorial Board, 2023). All traits were fuzzy-coded to convey the relative degree of certainty that a given taxon featured a given trait modality. Different organisms that were characterized by the exact same trait modalities were aggregated into functional entities to avoid redundancy of information.

The pairwise dissimilarity between taxa was computed using the Gower distance, implemented through the *gawdis* function in the eponymous R package v0.1–4. This approach enabled us to ensure that all traits contributed equally to the analysis, regardless of the number of modalities (de Bello et al., 2021).

As a first step, an HCA using Ward's method was performed on the dissimilarity matrix to identify functional groups of taxa with similar functional characteristics. This analysis helped uncover patterns in how these taxa interact with their environment or contribute to ecological functions, potentially highlighting partially shared ecological roles or responses to environmental variations. After defining the functional groups, the abundance of each group was calculated per sample by summing the abundances of the taxa within each group. A PCoA was then performed on the Hellinger distances derived from the functional composition of samples from the Loire and Seine estuaries together. This joint analysis allows for a direct comparison between the two estuaries, providing insights into whether the functional structure of communities is similar or distinct between them.

Inter-annual variability in functional composition was evaluated for each unit of the Loire and the Seine separately using a PERMANOVA test with year as the explanatory variable. The PERMANOVA procedure was executed on unit-wise dissimilarity matrices as described above using the function *adonis2* from the R package *vegan* v2.6–4 (Anderson, 2001; Oksanen et al., 2022).

To further investigate functional diversity, we measured various functional diversity indices in macrobenthic communities of the two estuaries combined to ensure comparability. Two parallel functional spaces were constructed using the Gower dissimilarity matrix to distinguish between traits related to production and those associated

Table 1

Summary of the set of biological traits examined, along with their different modalities and relevance to the research topics addressed.

Biological trait	Modalities			Functional relevance
Maximal size	≤ 10 mm	11 – 20 mm	21 – 100 mm	Biomass-specific metabolic rates and ability to produce biological material
	101 – 200 mm	201 – 500 mm	> 500 mm	
Feeding mode	Suspensivore		Deposivore	Type of energy source that fuels organisms' metabolism and growth
	Scavenger		Carnivore	
Turnover	Slow (0 – 1 yr ⁻¹)		Intermediate (1 – 3 yr ⁻¹)	Production modulation Rate at which biomass is generated (empirically computed – Brey 2012)
	Fast (3 – 7 yr ⁻¹)		Very fast (> 7 yr ⁻¹)	
Bioturbation mode	None	Diffusive mixing	Surface deposit	Tuning of detritic resource stock or provision for other organisms to exploit
		Upward conveyor	Downward conveyor	
Motion capability	Burrower	Crawler	Swimmer	Ability to forage resources available at local versus wide-range scales
Living habit	Tube-dwelling		Burrow-dwelling	Habitat loss Necessity for a specific habitat to successfully live in, shelter and feed
	In crevices		Free-living	
Vertical position	Epifauna		Shallow infauna	Requirement of a certain sediment type and granulometry to dig and live in
	Mid-depth infauna		Deep infauna	
Suitable estuarine haline domain	Marine	Brackish	Freshwater	Hydrological change Distribution changes along a shifting salinity gradient (marinization) Variations in discharge and induced ambient pollution (Borja et al. 2000)
Tolerance to organic enrichment	Sensitive	Indifferent		
	Tolerant	Opportunist		

with forcing factors. In both spaces, five dimensions were retained, achieving an optimal balance between the amount of information explained and the magnitude of errors introduced (Maire et al., 2015). Six functional diversity indices were deemed to be ecologically meaningful for our purpose (Supplementary Material D, Schleuter et al., 2010; Mouillot et al., 2013, 2008; Villéger et al., 2010, 2008; Mason et al., 2005). These indices were computed from macrobenthic abundances using the function *alpha.fd.multidim* in the R package *mFD* v1.0–3 (richness, divergence, specialization, and originality, Magneville et al., 2022), the function *FunImbalance* in the R package *adiv* v2.2 (imbalance, Ricotta et al., 2022), and a functional extension of the LCBD (XLCBD, Nakamura et al., 2020).

2.5. Macrobenthic production

Ecosystem functioning was assessed using the production generated by the macrobenthic communities rather than raw biomass, as the former accounts for differences in the production rate, or turnover, while the latter does not (Forster et al., 2006). Macrobenthic production, in J·m⁻¹·yr⁻¹, was estimated as:

$$P = \sum_{i \text{ taxa}} CR \cdot \bar{B}_i \cdot \left[\frac{P}{B} \right]_i \cdot E_i \quad (1)$$

where CR is a seasonal correction ratio (Saulnier et al., 2019), \bar{B}_i is the mean biomass per unit and per year (g·m⁻²), $\left[\frac{P}{B} \right]_i$ is the turnover rate (yr⁻¹) estimated from an empirical model (Brey, 2012; Cusson and Bourget, 2005), and E_i is the energy density (J·g⁻¹) of the i^{th} taxon (Brey et al., 2010).

Turnover rate estimations required information on bathymetry and temperature. To estimate the bathymetry of each sampling site, we used a combination of a digital elevation model of the French coast and local radar/lidar readings for the internal estuarine sectors (Anonymous, 2015). The water temperature of both estuaries was computed using reprocessed ODYSSEA satellite observations of mean sea surface temperature (Anonymous, 2023a). Temperatures were averaged over the

spring and summer (March to September) to cover the production period of the settled macrobenthic communities.

Multiple parameters used throughout the estimation procedure macrobenthic production presented uncertainty. A quantification of the uncertainty accumulated by calculations was computed using the Monte Carlo iterative method, by randomly sampling within the parameters distribution (Tableau et al., 2019; Metropolis and Ulam, 1949).

The macrobenthic production of different spatial units was statistically compared using a Kruskal-Wallis rank-sum test, with an estimation of the effect size η^2 (Kruskal and Wallis, 1952; Tomczak and Tomczak, 2014). We then identified groups of spatial units with similar levels of production through a post hoc Dunn test with a Benjamini-Hochberg correction for multiple comparisons (Dunn, 1964; Benjamini and Hochberg, 1995). The Dunn test is an appropriate follow-up procedure to the Kruskal-Wallis test for groups with unequal numbers of observations (Zar, 2010; Agbangba et al., 2024).

The response of macrobenthic production to variations in diversity indices was explored with generalized additive models (GAM) constructed using a restrictive maximum likelihood (REML) method with a Γ probability distribution and a logarithmic link. Biodiversity indices, both taxonomic (richness (S), evenness (J')), LCBD) and functional (richness, imbalance, divergence, specialization, originality, XLCBD), were individually fitted as predictors in independent GAM models. All models incorporated an interaction term between the tidal level and the diversity index. The generic formula for the GAM was as follows:

$$\log_{10} P \sim \text{Tidallevel} + \text{smooth}(\text{Index}) + \text{smooth}(\text{Index} \times \text{Tidallevel}) \quad (2)$$

where *smooth* indicates the use of a smooth term, and \times represents an interaction term. The individual GAM models were computed using the *gam* function in the R package *mgcv* v1.8–42 (Wood, 2017). Since multiple GAM were performed on data sampled from the same communities, we adjusted the test results for multiple comparisons using the Holm-Bonferroni method (Holm, 1979). Partial effects of individual diversity indices are presented in Supplementary Material E.

Analyses were conducted using R v4.3.2 (R Core Team, 2023) through RStudio IDE v2023.12.1 + 402 (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. Tidal surfaces and hydrology: long-term evolution

Historically, the overall extent of intertidal areas in the Loire was lower than in the Seine, though both had a comparable amount of subtidal areas. Since the 1990s, both of their respective intertidal areas have decreased to become roughly equivalent (Fig. 2). Throughout the 20th century, considerable portions of the estuarine aquatic surfaces were claimed by human activities (28 % in the Loire, 43 % in the Seine). In the Loire, the loss has affected subtidal areas, while in the Seine, it has mainly reduced intertidal surfaces through lateral compression. Beyond the raw loss of surface area, the distribution of the remaining intertidal surfaces has changed significantly in both estuaries, shifting from largely oligo- and mesohaline sectors towards poly- and euhaline dominance. A diachronic map of the Loire and the Seine estuaries is presented in Supplementary Material A.

The average winter-to-spring flow rates over the 1942–2023 period were $592 \text{ m}^3 \cdot \text{s}^{-1}$ and $367 \text{ m}^3 \cdot \text{s}^{-1}$ for the Loire and Seine rivers, respectively, with twice as much variation around the average for the Loire ($1479 \text{ m}^3 \cdot \text{s}^{-1}$) as for the Seine ($739 \text{ m}^3 \cdot \text{s}^{-1}$). The temporal patterns observed in flow rate were comparable between the two estuaries: both reached maximum values in the 1980s and have subsequently exhibited decreasing trends, with lower annual flow rates in recent years that are comparable to those recorded in the 1950s (Fig. 2).

The morphology of both estuaries has likely been approximately unchanged along the sampling periods of the macrobenthic communities (2010 to 2021 in Loire, and 2000 to 2017 in Seine). However, both rivers flow rate displayed a decreasing trend since the late 1990s that

could induce a response of the sampled macrobenthic communities.

3.2. Spatio-temporal patterns of macrobenthic biodiversity

The Loire estuary macrobenthic dataset included 280 samples collected over 5 years of surveys (2010, 2014, 2015, 2020, and 2021). In total, 86 macrobenthic taxa were identified, for an overall abundance (mean \pm standard deviation) of $333 \pm 1046 \text{ individuals} \cdot \text{m}^{-2}$. The Seine estuary macrobenthic dataset included 350 samples collected over 11 years of surveys (earliest 2000, latest 2017). A total of 155 macrobenthic taxa was identified, for an overall abundance (mean \pm standard deviation) of $248 \pm 843 \text{ individuals} \cdot \text{m}^{-2}$.

3.2.1. Taxonomic assemblages of the macrobenthos

The analysis of the β -diversity of macrobenthos from the Loire and Seine combined revealed that diversity patterns were almost exclusively explained (99.9 %) by balanced variation, i.e., the replacement of taxa along gradients. The ordination analysis exhibited a U-shaped distribution of spatial units along the estuarine gradient, with the euhaline units (e.g., the Mouth of Loire and Seine) represented in the top-left corner of the factorial plane, the polyhaline units (e.g., Donges in Loire and the Great Mudflat in Seine) on the right, and the mesohaline units (e.g., the Inner subtidal unit in Loire) in the bottom-left corner (Fig. 3). Overall, the Loire units were distributed throughout the entire U-shaped estuarine gradient while the Seine did not contain any units in the mesohaline sector. The classification procedure isolated five assemblages of taxa, with four of them being mostly specific to one of the two estuaries (Fig. 3 A, details in Supplementary Material C). The two assemblages specific to the Loire were a polyhaline assemblage characterized by high densities of *Heteromastus filiformis* and *Scrobicularia plana* (the Middle subtidal unit, and Méan, Bilho, and Corsept mudflats)

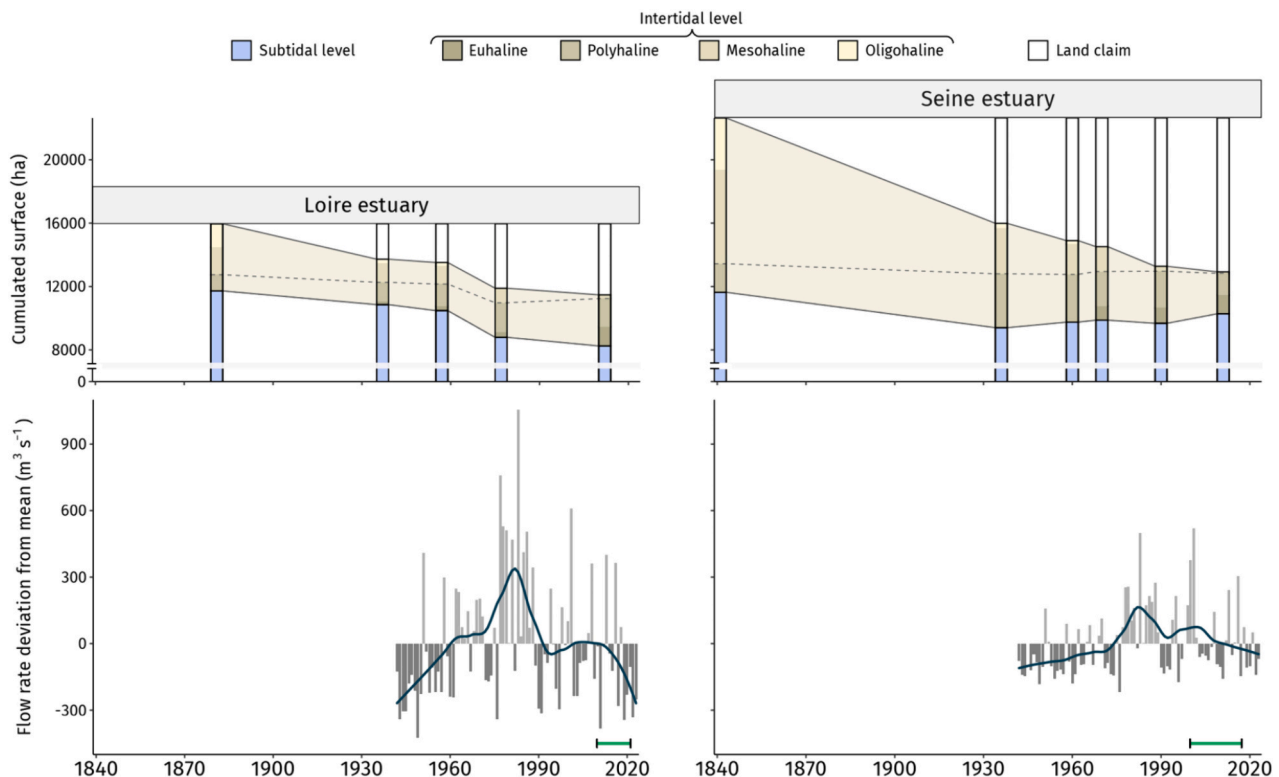


Fig. 2. Top panels: distribution of estuarine surfaces among different tidal levels, with details on the haline sector for intertidal areas. The dashed line highlights the boundary separating the polyhaline sector from the mesohaline sector. Note that the ordinate axis is cropped at the bottom of the plot. Bottom panels: deviations in April-to-August flow rate from the 1942–2023 average. A smooth spline is superimposed to help visualize trends. The green horizontal lines near the abscissa axis indicate the temporal coverage of the macrobenthic datasets of each estuary. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

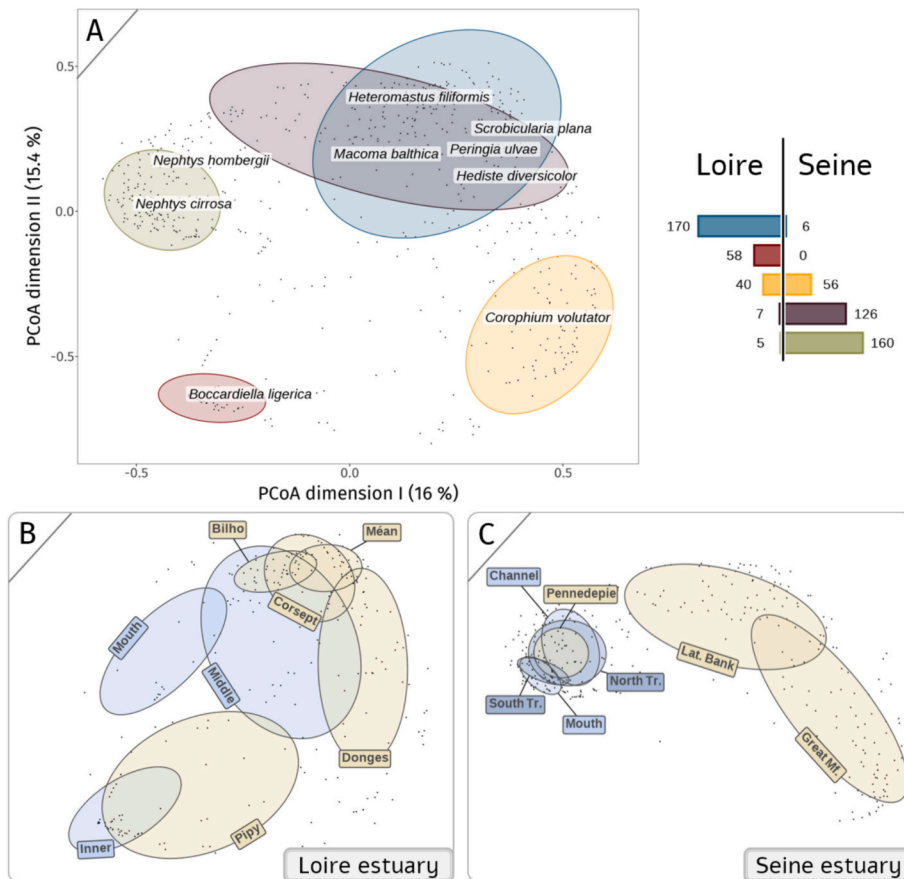


Fig. 3. Ordination of macrobenthos samples based on their abundance, with the first factorial plane presented (31.3 % of variability explained in total). Top panel: classification of samples into five assemblages, represented by ellipses (A). Taxa with the largest contributions to β -diversity (SCBD) are displayed at their weighted average position along the axes. To the right, the histogram indicates the number of samples belonging to each assemblage per estuary. Bottom panels: position of Loire (B) and Seine (C) units grouped in the form of ellipses on the same factorial plane of ordination.

and a mesohaline assemblage dominated by *Boccardiella ligERICA* located over the Pipy mudflat and the Inner subtidal unit (Fig. 3 B). The fifth assemblage, however, was shared between both estuaries—specifically, it was associated with Donges (Loire) and the Great Mudflat (Seine)—and characterized by high densities of *Corophium volutator*. Within the Seine estuary, there was a clear division between a sandy euhaline assemblage characterized by *Nephtys* spp. (overlapping all subtidal units and Pennedepie beach) and a muddy assemblage dominated by *Macoma balthica* and *Hediste diversicolor* that was found over the Lateral Bank and the Great Mudflat (Fig. 3 C); the latter was separated from the Loire polyhaline assemblage along the third ordination axis (not shown in the figure).

3.2.2. Taxonomic diversity profiles

The diversity profiles revealed comparable levels of α -diversity along the gradient of the order q (abscissa), representing the sensitivity to species relative abundance between the two estuaries and across spatial units. We did not detect any significant temporal variability in richness or evenness (i.e., effect of year: p -values >0.05). Higher diversity levels were observed in the Mouth of both estuaries and lower levels in the mesohaline units of the Loire (Fig. 4). This observation reflected a trend of decreasing diversity from ocean to river, which was supported by the fact that the spatial units were found to explain a significant part of the variance detected in richness (S) and evenness (J') (respective variance partitioning, 45.11 % and 33.74 % in the Loire, and 39.38 % and 16.35 % in the Seine).

3.2.3. Functional groups and indices

Using a clustering procedure, taxa were classified into five functional groups based on similarities in their biological traits (Table 2). The functional groups were related to ecologically meaningful assemblages of species based on the main trait modalities that led to their identification. Hence, we characterized tube- and burrow-dweller depositors (**DwelDep**), suspensivores that are sensitive to an enrichment in organic matter (**SenSusp**), marine carnivores (**MarCar**), organisms adapted to brackish waters (**BrachHet**), and productive shallow endobenthic organisms (**ShaProd**).

The PERMANOVA procedure conducted per spatial unit revealed that none of the units featured significant temporal variations in the abundance of the different functional groups. Because of this, all of the results presented thereafter are temporally averaged in order to highlight the spatial distribution of functional diversity within the estuaries of the Loire and the Seine.

Similar to our analysis of taxonomic diversity, the PCoA on the functional dissimilarity of samples returned a U-shaped gradient that reflected the succession of haline sectors, from mesohaline (bottom) to polyhaline (top-left) and euhaline (top-right) (Fig. 5). The spatial units demonstrated functional replacement along the first axis of the ordination: going from the euhaline units to the polyhaline sector in both estuaries, the dominant **DwelDep**, **SenSusp**, and **MarCar** groups appear to be substituted by the **BrachHet** group. The mesohaline units of the Loire were further distinguished by the dominance of the **ShaProd** group.

With respect to production modulation traits (Fig. 6), spatial units featured relatively high divergence (median of 86 %) and specialization

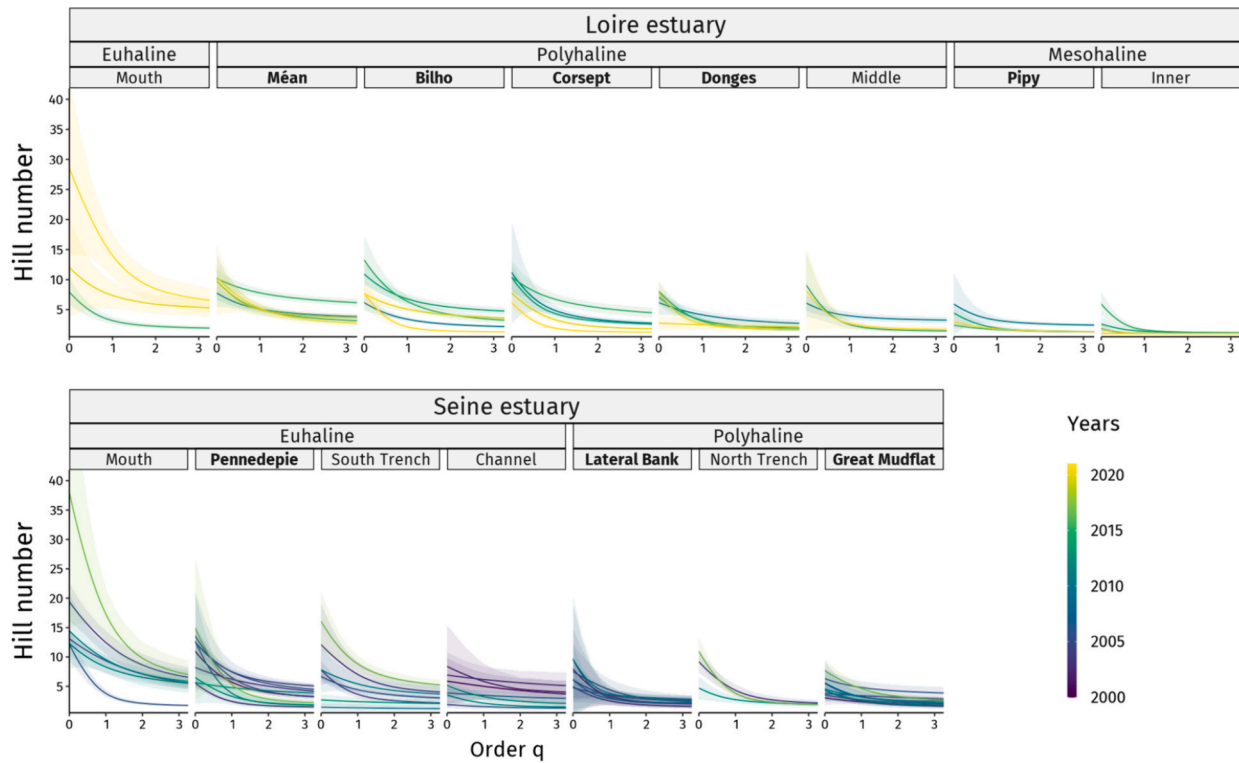


Fig. 4. Diversity profiles of an average macrobenthos sample per spatial unit and per year. The order q tunes the degree of sensitivity to species relative abundance along the abscissa axes. The ribbon around each profile corresponds to its confidence interval computed by a bootstrap procedure. Units are presented from ocean (left) to river (right); samples from the Loire estuary cover a longer spatial gradient including the mesohaline sector. Names of intertidal units are written in bold.

Table 2

Summary of the five functional groups identified by a hierarchical clustering analysis of macrobenthos abundance. The name of each group is derived from an abbreviation of its dominant modalities.

	Functional group	Dominant modalities	Major taxa
Organisms belonging to the...	DwelDep	Deposivore – burrower Dweller – shallow endobenthic	<i>Heteromastus filiformis</i> <i>Owenia fusiformis</i> <i>Lagis koreni</i>
...tend to be...	SenSusp	Suspensivore – burrower Sensitive [†] – endobenthic	<i>Donax vittatus</i> <i>Mya arenaria</i> <i>Spisula solida</i>
	MarCar	Carnivore – crawler Marine – free-living – indifferent [†]	<i>Tritia reticulata</i> Phyllodocida Ophiuridae
	ShaProd	Productive – small Shallow endobenthic – tube-dweller	<i>Boccardiella ligERICA</i> <i>Ampelisca brevicornis</i> Gammaridae
	BracHet	Heterogeneous regarding all traits Brackish – tolerant [†]	<i>Hediste diversicolor</i> <i>Scrobicularia plana</i> <i>Corophium volutator</i>

[†]Adjectives relative to an organic matter enrichment.

(75 %), low XLCBD (25 %) and richness (22 %), and intermediate levels of imbalance and originality (respectively, 54 % and 55 %). Donges featured the highest degree of originality of all spatial units (both Loire and Seine), whereas Pipy and Inner (Loire) displayed the lowest degree of specialization. Among the other perceptible differences noted, values of functional indices seemed to decrease from ocean to river in the Loire, with the exception of XLCBD, which remained steady. In the Seine, only richness displayed a similar pattern, being the highest in the Mouth and lower in the Lateral Bank and the Great Mudflat. The other indices did not show any marked variation between units.

Regarding the abiotic forcing traits, high divergence (72 %) and

specialization (65 %) were also observed, along with moderate originality (31 %) and low XLCBD (23 %). All spatial units were characterized by intermediate levels of imbalance and richness (respectively, 41 % and 40 %). Specialization was on average higher in the Loire than in the Seine. Functional richness followed a decreasing trend from ocean to river in both estuaries, and the upstream units of both the Loire (Pipy, Inner) and the Seine (Lateral Bank, Great Mudflat) featured relatively higher specialization, with the latter also presenting a lower degree of imbalance.

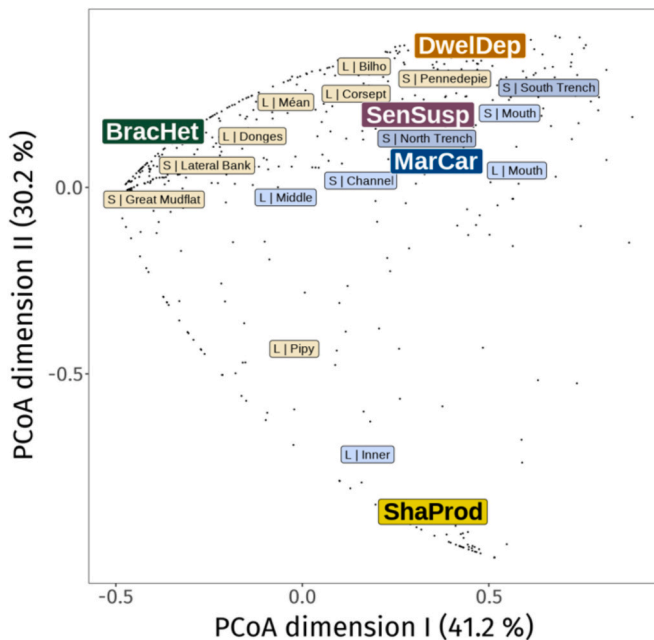


Fig. 5. Ordination of macrobenthos samples based on the composition of their functional groups, with the first two factorial axes presented. Functional groups are displayed at their weighted average position along both axes. The unit labels (L = Loire, S = Seine) are positioned at the barycenter of the coordinates of their respective samples.

3.3. Macrobenthic production and its relationship with community biodiversity

The estimated annual production of macrobenthic communities varied in magnitude among spatial units but was associated with substantial uncertainty (Fig. 7). A Kruskal-Wallis test confirmed the existence of large and significant differences in the average production of units ($\chi^2 = 52.7$, p -value < 0.001 , $df = 14$, $\eta^2 = 0.42$). Subsequent comparisons highlighted units with high levels of production (Méan, Bilho, Corsept, the Mouth (Seine), Pennedepie, the Lateral Bank, and the Great Mudflat) and those with low production (Middle, Inner, Dongses, Pipy, South Trench, North Trench, and Channel). However, these differences were significant only between the high production of the Mouth of the Seine and the low production of the Inner unit, Pipy (Loire), South Trench and Channel (Seine). Intertidal units in both estuaries generally exhibited high production, with the exception of Dongses, Pipy, and Pennedepie, with the last displaying consistently low production since 2009. At the subtidal level, the Seine Mouth featured comparable production levels to those observed at the intertidal level.

An analysis of the relationship between annual production and a set of biodiversity-related explanatory variables revealed a statistically significant positive effect of functional richness. This effect was observed for both types of traits in both estuaries (Table 3). In the Loire, annual production also demonstrated positive responses to functional specialization regarding production modulation, and to functional divergence regarding forcing factors. The other biodiversity indices had no significant explanatory power regarding annual production in either estuary.

4. Discussion

4.1. The fate of intertidal habitats in anthropized estuaries

Over the past century, the Seine estuary has experienced a substantial loss of intertidal areas. In the same time, the Loire estuary has undergone changes in the distribution of these areas, some of which have

diminished (e.g., Méan) while others have expanded (e.g., Corsept). Both estuaries have suffered a significant reduction in mesohaline intertidal surfaces due to anthropogenic activities (Benyoucef et al., 2014; Cuvilliez et al., 2009), such as the development of major harbors, which has led to extensive morphological alterations to accommodate large ships. This is a common trend in other estuaries globally, such as the Santos estuary in Brazil and the Thames estuary in the UK (Reid et al., 2022; Rossington and Spearman, 2009). Upstream mesohaline sectors of the Loire and Seine have experienced sediment filling from dredging, raising intertidal surfaces and narrowing the stream, and ultimately resulting in the downstream concentration of intertidal areas. Moreover, reduced lateral friction and channel deepening have modified the estuarine salinity gradient by enabling the intrusion of salt water farther upstream. The impact of heavy engineering in the Loire estuary between 1950 and 1980 can be seen in the observed tidal range, which increased by approximately +1 m downstream and up to +4 m upstream (Anonymous, 2022, 2013). This phenomenon has also been seen in the Seine and in other estuaries like the Hudson (USA) and the Modaomen (China) (Bacq et al., 2013; Hoagland et al., 2020; Cai et al., 2012). Haline intrusion is further exacerbated by ongoing global change, which is increasing sea levels and reducing river flow rates in temperate regions (Leal et al., 2022; Musseau et al., 2018; Rilo et al., 2013). The recent decline in the flow rates of the Loire and the Seine rivers, though still comparable to the 1950s levels, appears to be driven at least in part by a multi-decade alternating pattern possibly influenced by atmospheric teleconnections, particularly the Atlantic Multidecadal Oscillation. This hydroclimatic cycle induces low-frequency variations in the flow rates of Western European rivers and in Atlantic coast sea levels, and may potentially be obscuring long-term trends associated with global change (Boé and Habets, 2014; Ezer et al., 2016). However, it is anticipated to contribute to short-term increases in water temperature anomalies in synergy with human-induced warming (Garcia-Soto and Pingree, 2012).

4.2. Anthropogenic pressures and potential effects on macrobenthic communities

The macrobenthic assemblages in both the Loire and the Seine estuaries largely conform to the typical patterns observed in European estuaries (Wolff and de Wolf, 1977), with certain exceptions. The relative dominance of *Scrobicularia plana* over *Macoma balthica* in the Loire, and the opposite pattern in the Seine, likely reflects their respective latitudinal positions. Overall, the Loire assemblages demonstrate similarities with the Iberian peninsula estuaries, particularly the Tagus (França et al., 2009; Borja et al., 2004), while the Seine aligns more closely with boreal estuaries like the Ythan (Chambers and Milne, 1975). In more challenging environmental conditions, weaker competition allows certain r-strategists, such as *Corophium volutator* and *Boccardiella ligERICA*, to thrive and form dense colonies. This phenomenon has been observed in other estuaries, such as the Scheldt, where these taxa are typical of the mesohaline sector (Ysebaert et al., 2003; Watkin, 1941). In the Loire and the Seine, *C. volutator* is mainly found in mudflats at the boundary between the polyhaline and the mesohaline sectors (Dongses, Great Mudflat), while *B. ligERICA* dominates the macrobenthic assemblage of the Pipy mesohaline mudflat in the Loire. Despite some similarities in their benthic assemblages, the Loire and the Seine both share comparable functional groups of taxa, indicating a degree of functional convergence between two of the most important temperate estuaries in Western Europe.

Human activities, such as sediment dredging, have documented impacts on estuarine communities, notably by disrupting water stratification and biocenosis (Barletta et al., 2016). For example, power plants can generate heated water plumes at their cooling system outlets, leading to disturbances in local communities (Ingleton and McMinn, 2012; Hoffmeyer et al., 2005). Such disturbances have the potential to influence species like *Alitta succinea*, a predatory Nereididae, whose increased presence could lead to changes in community structure

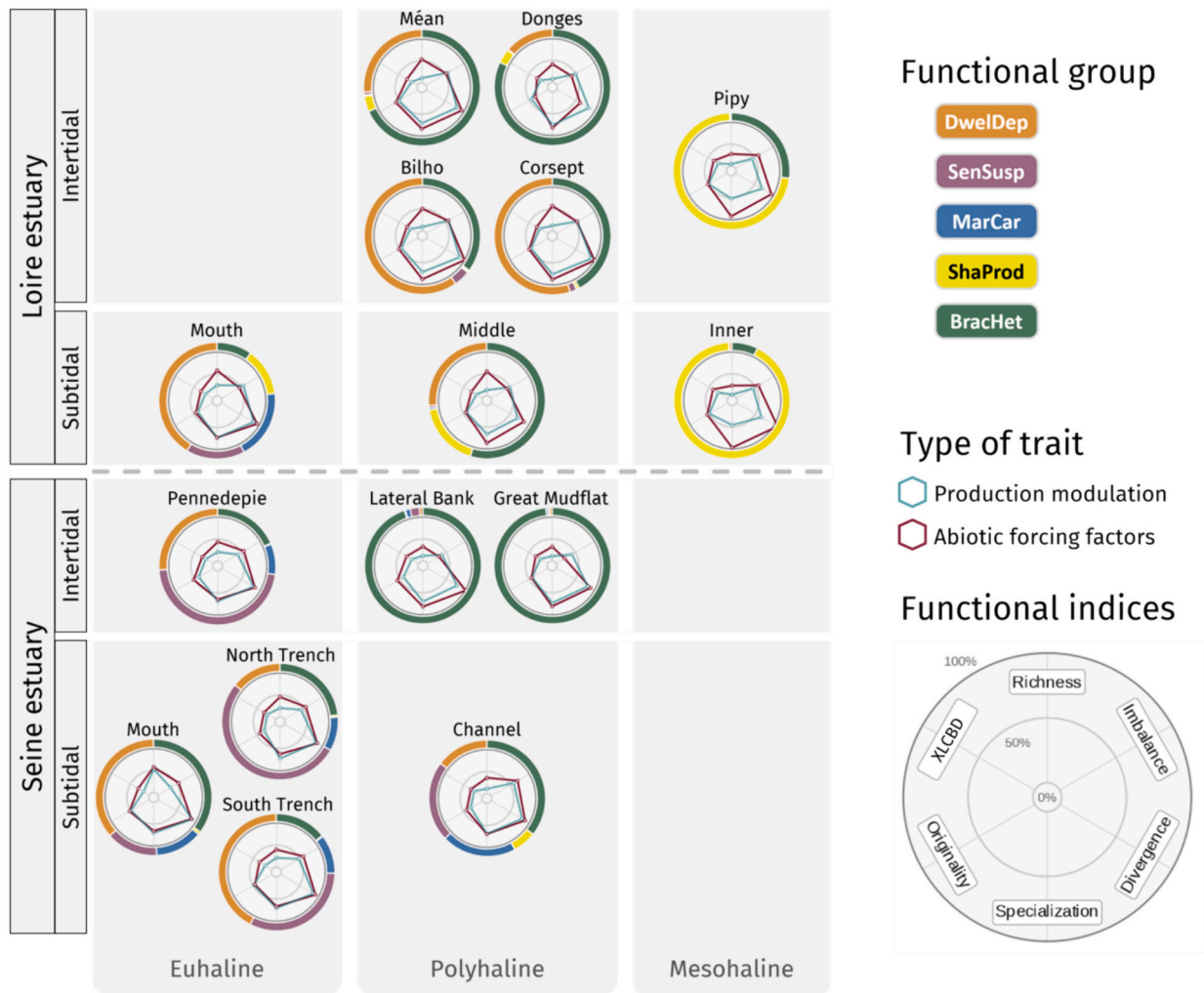


Fig. 6. Radar charts of the functional indices calculated for macrobenthos samples (temporally averaged) from sampling units in the Loire estuary (top) and the Seine estuary (bottom), presented for each type of trait. The surrounding colored rings represent the averaged relative distribution of functional assemblages within each spatial unit. Units are presented from the ocean (left) to the river (right) and reflect the shorter spatial gradient covered in the Seine estuary.

through top-down effects (Hardege et al., 1990). In the Loire estuary, the thermal plume from a coal-fired power plant can lead to strong variations in water temperature alongside daily salinity fluctuations particularly affecting the Pipy mudflat. These conditions may be associated with the distinct macrobenthic assemblage observed, including the high abundance of *B. ligerica*, a spionid known for its adaptability to highly variable environments and possibly benefiting from reduced interspecific competition in this context (Taupp and Wetzel, 2014; Hartmann-Schroder, 1996).

Anthropogenic modifications, such as channelization, can also shift salinity gradients upstream over extended periods, leading to the compression of mesohaline mudflats. This compression can reduce the number and size of colonies of small-sized opportunists, potentially allowing polyhaline assemblages to expand across intertidal mudflats. This pattern aligns with the process of estuarine marinization (Lécuyer et al., 2024; Le Guen et al., 2019; Chaalali et al., 2013). In the Loire estuary, comparisons with historical descriptions of benthic communities indicate the intrusion of polyhaline populations, such as the extension of *S. plana* populations upstream to the Donges mudflat, beyond their previously recorded location around Bilho (Marchand, 1972). Habitat compression could also affect important food sources for benthic macro-invertebrates, like microphytobenthos, which appears to have higher biomass in the mesohaline sector (Benyoucef et al., 2014).

4.3. Functional diversity and macrobenthic production

In the marine realm, several studies have suggested that biodiversity may enhance the production of communities and exert a stabilizing effect on biomass, contributing to the sustained delivery of ecosystem services over time (Cardinale et al., 2013; Stachowicz et al., 2007; Schindler et al., 2010). The analysis of the α -diversity of macrobenthos from the Loire and Seine estuaries indicated generally low but consistent levels of taxonomic diversity across spatial units over the studied periods. This suggests that, despite the long-standing anthropogenic pressures on these habitats, there is relative constancy in their community structure within the limited timespan examined. The functional composition (β -diversity) observed over the different units of both the Loire and the Seine estuaries did not exhibit significant yearly variations. This pattern may be influenced by environmental filtering, where only species capable to tolerate the constraining conditions of the estuarine environment persist. This selection pressure could lead to the observed constancy in functional composition over the studied time periods.

The macrobenthic communities of the Loire and Seine estuaries only filled a limited portion of the overall functional pool within the time frames examined. This limitation becomes even more conspicuous upstream, where the richness of these communities is consistently low. Characterized by only a few taxa, they present a high degree of

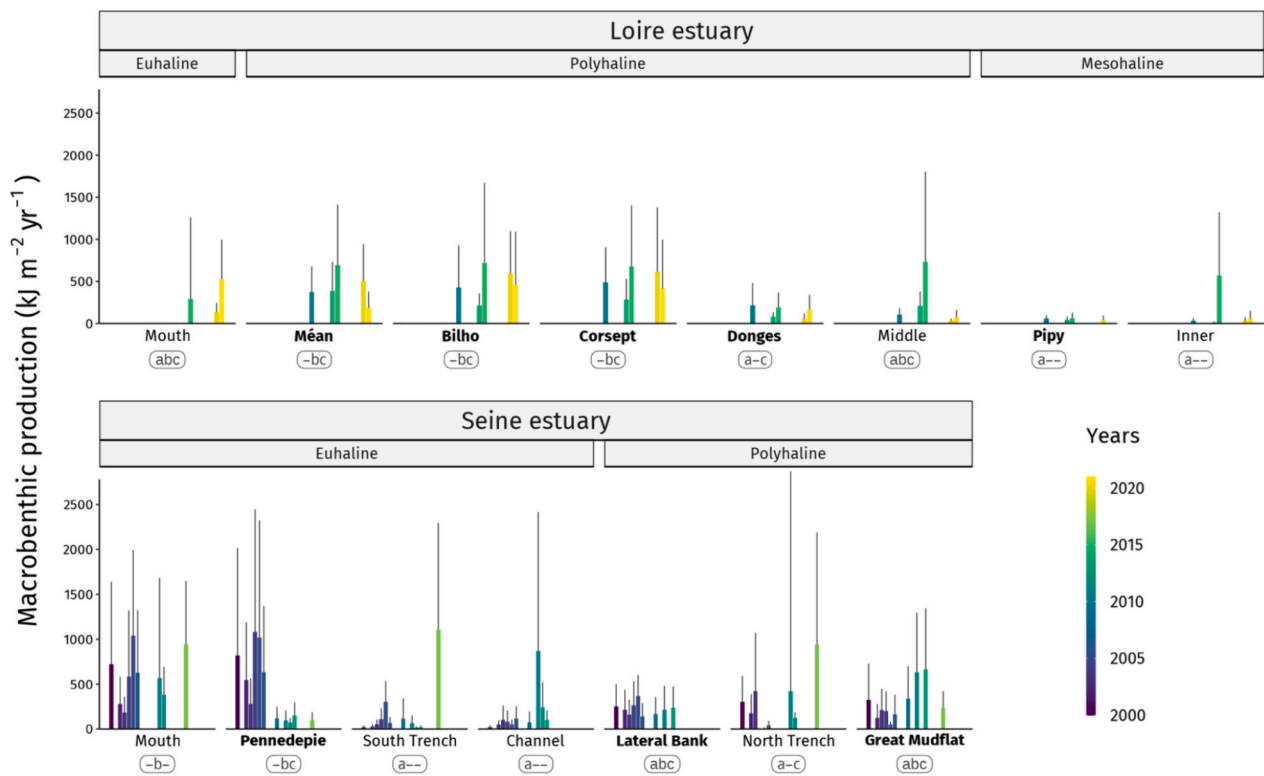


Fig. 7. Bar chart depicting the estimated annual production of macrobenthic communities. The uncertainty range (black line, one-sided) was obtained using the Monte Carlo sampling method. The framed characters under the abscissa axis represent the grouping of units obtained by post hoc comparisons (Dunn test). Spatial units are ordered from ocean (left) to river (right) for each estuary. Intertidal units are written in bold.

specialization and divergence due to their reliance on extreme traits, with respect to both production modulation and abiotic forcing factors. These observations highlight the vulnerability of macrobenthic communities to environmental disturbances in both estuaries within the time frame of a few decades. Such disturbances frequently take the form of habitat loss and hydrological changes, and pose a potential threat to the resilience of the ecosystem.

With respect to production modulation, our analysis revealed moderate to high levels of functional redundancy across estuarine units, with the exception of the polyhaline mudflats of the Loire, specifically Méan, Bilho, and Corsept. In this situation, the loss of certain taxa and their associated traits has the potential to induce cascading effects on other organisms that are dependent on their ecological functions (Keyes et al., 2021). For example, the bioturbation activity of the polychaete *Hediste diversicolor* plays a pivotal role in nutrient generation through bio-irrigation and the enhancement of microbial denitrification (Morelle et al., 2021; Ieno et al., 2006). Likewise, the amphipod *C. volutator*, an engineer species with important bioturbating activity, is crucial in inhibiting the settlement of salt-marsh pioneering plants, thereby preventing sediment stabilization by root systems. Colonies of *C. volutator* are periodically formed through active swimming of juvenile individuals, disseminating over mudflats (Lawrie and Raffaelli, 1998). In doing so, *C. volutator* contributes to the long-term resilience of intertidal mudflats (Hughes and Gerdol, 1997). These ecological changes may have repercussions on the microphytobenthos, which make significant contributions to essential ecosystem services in estuarine mudflats, including primary production or nutrient cycling (Hope et al., 2020).

Despite low levels of macrobenthic biodiversity, estuarine ecosystems often feature high levels of production (Boyes and Elliott, 2006; Schelske and Odum, 1962; Sobczak et al., 2005). In our study, the highest production levels in the Loire and Seine estuaries were observed over the polyhaline intertidal mudflats. In contrast, the Donges and Pipy mudflats exhibited lower production over the time period examined,

comparable to that observed in most subtidal units. Our analysis of the relationship between production and various diversity indices revealed that functional richness, whether associated with production modulation or abiotic forcing factors, helps to enhance production in both the Loire and Seine estuaries. In the Loire, we also identified a positive relationship between functional divergence and production, suggesting that the latter is enhanced by lowered competition. Overall, richness—a major component of diversity—does exhibit a significant relationship with the function of production. In the Mondego estuary, functional diversity had a large effect on the benthic secondary production (Dolbeth et al., 2015). However, we found only limited evidence of significant relationships with the other components of diversity examined in either of the Loire and the Seine estuaries.

4.4. Consequences for several estuarine functions

Substantial portions of the Loire and Seine estuaries have been lost over the last century, mainly in the intertidal surfaces of the mesohaline sector. As a result, it is likely that this area has experienced a drop in overall macrobenthic production, with potential repercussions for energy transfer to macro-invertebrate predators through the food web.

Estuarine habitats are frequently used by various species as feeding areas, and this activity is dependent on macrobenthic production. Migrating shorebirds utilize estuarine salt-marshes and reefs as stopover sites, while juvenile fish rely on the sheltered waters of estuaries as nursery grounds (Butler et al., 2001; Beck et al., 2001). Shorebirds predominantly access the emerged portions of intertidal mudflats, whereas juvenile fish are limited to feeding on the macrobenthos that are small enough to be preyed upon. The production of the fraction of organisms that is accessible may therefore be significantly lower than that of the macrobenthos as a whole (Tableau et al., 2015). Moreover, the exposure time of intertidal mudflats is directly proportional to their elevation. This particular parameter has been identified as a negative

Table 3

Summary of the generalized additive model (Γ distribution, logarithmic link, restrictive maximum likelihood method) investigating the response of estimated annual macrobenthic production to variations in the biodiversity indices of macrobenthic communities. The p -values were adjusted using the Holm-Bonferroni method. An arrow depicts the global direction of the trend for the significant relationships (i.e. adjusted p -value <0.05 , in bold).

Estuary	Smooth term	Dev. expl.	Effective df	F statistic	p-value adjusted	Trend		
Loire	Taxonomic diversity	Richness	63.60	2.24	8.06	0.013	↗	
		Evenness	28.21	1.00	5.50	0.260	–	
		LCBD	68.77	1.00	1.34	1.000	–	
	Functional diversity	Production modulation	Richness	67.16	1.99	8.13	0.013	↗
			Imbalance	19.51	1.00	1.54	1.000	–
			Divergence	42.13	1.00	3.78	0.558	–
			Specialization	59.86	2.01	12.37	< 0.001	↗
			Originality	35.80	1.00	1.67	1.000	–
		Abiotic forcing factors	XLCBD	42.23	1.00	0.60	1.000	–
			Richness	74.50	2.36	23.52	< 0.001	↗
			Imbalance	40.14	1.00	2.03	1.000	–
			Divergence	52.11	2.74	6.17	0.022	↗
			Specialization	31.55	2.31	2.19	1.000	–
	Seine	Taxonomic diversity	Richness	38.93	1.00	3.72	0.627	–
			Evenness	23.28	1.00	0.14	1.000	–
LCBD			45.19	1.01	0.90	1.000	–	
Functional diversity		Production modulation	Richness	60.72	1.30	16.70	< 0.001	↗
			Imbalance	58.01	1.00	9.03	0.052	–
			Divergence	12.12	1.00	3.15	0.738	–
			Specialization	7.84	1.84	0.77	1.000	–
			Originality	22.14	1.00	0.29	1.000	–
		Abiotic forcing factors	XLCBD	12.76	1.00	4.51	0.468	–
			Richness	51.96	1.00	10.44	0.028	↗
			Imbalance	19.43	1.00	0.08	1.000	–
			Divergence	10.99	1.00	0.61	1.000	–
			Specialization	11.34	1.00	3.81	0.627	–
		Originality	14.80	1.00	0.42	1.000	–	
		XLCBD	26.23	2.27	1.79	1.000	–	

driver of the size of macrobenthic organisms, with the higher intertidal level featuring smaller species (e.g., *C. volutator* or *B. ligerica*) or young individuals such as *S. plana* juveniles (Wanink and Zwarts, 1993; França et al., 2009). The higher intertidal level thus aligns with the requirements of both shorebirds and juvenile fish, which feed alternately during low and high tide. The loss of such habitats in the Loire and Seine over the last century has likely impaired the carrying capacity of estuaries with regard to their trophic role for these animals (Wang et al., 2022; Stamp et al., 2022).

4.5. Concluding remarks

European large estuaries, such as that of the Loire and the Seine, have been reshaped over decades to facilitate the navigation of ships and to develop major harbors. Anthropogenic activities had consequences on the estuarine environment, such as the reduction of aquatic habitat surfaces or variations in hydrology. This context of long-standing anthropogenic pressures might disturb communities in a way that could induce the loss of some species featuring essential roles in the ecosystem. In this context, we hereby addressed the recent structure and functioning of the macrobenthic communities as seen through biodiversity, in relation with their function of production. Over the last few decades, a certain constancy of macrobenthic functional diversity was observed, suggesting that the highly variable estuarine environment selected tolerant species. Functional richness was found to have a significant effect on macrobenthic production, pointing at the importance of this component of biodiversity for the function of production. High levels of macrobenthic production were detected over polyhaline mudflats that were also subjected to functional weaknesses, such as low degrees of functional redundancy. The current context of increasing

anthropogenic pressures through, e.g., climate change, highlights the need to identify such situations through the consistent monitoring of the estuarine ecosystem. Observational data is indeed crucial to gain insight into communities' response to anthropogenic pressures in order to anticipate potential disturbances on the estuarine ecosystem functioning in the future.

4.6. Study limits and recommendations for long-term ecological surveys

Our understanding of the impact of anthropogenic pressures on the estuarine ecosystem is hampered by a lack of comparability between past (20th century) and more-recent surveys, due to the use of different sampling gears (the dredges Charcot-Picard and Rallier du Baty). This problem could be mitigated through the partial implementation of inter-calibrated field experiments. Additionally, there is a lack of consistent and regular time-series data on a variety of environmental and biological factors at a fine spatial resolution (Biguino et al., 2023). To address these gaps, stakeholders must actively engage in establishing and maintaining continuous environmental monitoring stations across the estuarine spatial gradient (Schmidt et al., 2019). Furthermore, it is essential to support the implementation of recurring annual sampling surveys as it is the case in the Seine estuary, but not in the Loire estuary. These surveys should be strategically designed with a focus on multiple monitoring sites, using a replicated sampling approach to enhance the statistical robustness of future comprehensive analyses and to provide insights for effective management strategies (Prosser, 2010). This revised sampling scheme should explicitly consider the elevation gradient along intertidal mudflats, a factor that strongly influences the distribution of macrobenthic communities and plays a pivotal role in the trophic relationships in estuarine ecosystems, spanning from

microphytobenthos to bird and fish predators (Heip et al., 1995; Wanink and Zwarts, 1993).

CRedit authorship contribution statement

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

Declaration of competing interest

None.

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.seares.2024.102545>.

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