Functional Evolution of Benthic Communities in the Rance Basin: Analysis of Biological Traits and Functional Trajectories.

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Highlights:

- Absence of major changes in species dominance and the persistence of a common pool of structuring species;
- Since 1976, the communities in the downstream/median area of the basin have shown a overall functional stability;
- In the upstream area, remarkable instability is observed, explained by a recent marinisation of the area and notable changes in the distribution of superficial sediments;
- Functional diversity and redundancy remain in good condition throughout the different years of the study, suggesting a high level of ecological resilience.

Abstract:

The Community Trajectory Analysis Framework was used in conjunction with conventional methods to analyse, characterize, and represent long-term functional changes in soft sediment communities in the Rance basin (Normano-Breton Gulf) sampled in 1976, 1995, 2010, and 2020, in connection with the operation of the Rance Tidal Power Station (RTPP). The results of this study have shown a functional stability of assemblages in the downstream/median areas of the basin, driven by the absence of major changes in the dominance of species and the persistence of a common pool of structuring species. On the contrary, in the upstream area, the observed instability over time is largely explained by (i) marinisation caused by changes in the tidal prism and (ii) an increase of surficial sediments grain size in the main channel. Despite the changes observed in 2020, the functional diversity index indicates a relative functional stability at the basin scale, suggesting a high level of ecological resilience.

Keyword: Community Trajectory Analysis, functional stability, structuring species, resilience

Introduction

Aquatic ecosystems are under the influence of multiple stressors of natural or anthropogenic origin, which lead to a degradation of ecological quality and compromise the ability to provide goods and services to humans (Costanza et al., 1997; Costanza and Farber, 2002; Worm et al., 2006; Halpern et al., 2008). Monitoring, management and restoration are crucial steps to characterize, minimize or reverse the effects of disturbances on the structure and functioning of ecosystems (Simenstad et al., 2006; Elliott et al., 2007; Borja et al., 2010). To assess the health of an ecosystem, biodiversity indices related to the species richness and taxonomic compositions of a community are generally used (Aarnio et al., 2011). Although very useful, they do not consider interactions with the abiotic components of the system and do not provide information on the functioning of the ecosystem (Bremner et al., 2003). In order to truly understand ecosystem dynamics, it is essential to investigate not only the structure but also the functioning of the biological communities involved (Naeem, 1998; Naeem et al., 2002; Hooper et al., 2005; Weigel et al., 2016; Shojaei et al., 2021). Functional traits-based approach refers to the biological and ecological characteristics of organisms and constitutes a complementary integrative framework for linking changes in biodiversity to their functional consequences (Covich et al., 2004; Hooper et al., 2005; Cardinale et al., 2006; Raffaelli, 2006; Suding et al., 2008; Boyé et al., 2019; Martini et al., 2021). This approach gives a more complete overview of the organisation and evolution of the community (Lausch et al., 2016; Cochrane et al., 2016) and is also successful tool for assessing the health or vulnerability of an ecosystem (Díaz and Cabido, 2001; Bremner, 2005; Fleddum, 2010; Schleuter et al., 2010; Capet et al., 2014).

Functional diversity facets such as functional redundancy is an important component of ecosystem resilience properties (Walker 1992; De Juan et al., 2015). The stability of traits composition indicates that substitutions of functionally similar benthic species can occur commonly and over multiple time scales. This turn over ensures the stability of ecological functioning (Clare et al., 2015; Frid and Caswell, 2015; Naeem, 1998; Shojaei et al., 2021) and increases the ability of a system to absorb various disturbances and reorganize to maintain critical functions while undergoing state changes (Peterson et al., 1998). High functional redundancy between species would allow only minor changes in functionality, even despite considerable variations in taxonomic diversity (Frid and Caswell, 2015; Törnroos et al., 2015; Van der Linden et al., 2016; Weigel et al., 2016; Shojaei et al., 2021). Conversely, low functional redundancy imply that functioning properties are more sensitive to changes in biodiversity (Wong and Dowd, 2015).

The influence of parameters as functional redundancy may be important in maintaining ecosystem resilience (Walker 1992; De Juan et al., 2015). The stability of trait composition indicates that substitutions of functionally similar benthic species can occur commonly and over multiple time scales. This turn over ensures the sustainability of ecological functioning (Clare et al., 2015; Frid and Caswell, 2015; Naeem, 1998; Shojaei et al., 2021) and increases the ability of a system to resist to disturbances (Peterson et al., 1998). High functional redundancy between species would allow only minor changes in functionality, even despite considerable variations in taxonomic diversity (Frid and Caswell, 2015; Törnroos et al., 2015; Van der Linden et al., 2016; Weigel et al., 2016; Shojaei et al., 2021). Conversely, low functional redundancy indicates that functioning is sensitive to changes in biodiversity (Wong and Dowd, 2015).

Different indices of functional diversity are available in the literature (Mason et al., 2005; Mouillot et al., 2005; Petchey and Gaston, 2002; Rao, 1982; Schleuter et al., 2010; Villéger et al., 2008). The functioning of benthic communities was primarily assessed using approaches such as trophic group analysis, relative taxon composition analysis, and integrative indices (Bremner et al., 2003, 2006). These methodologies provide little information on ecological functions and thus provide a reductionist view of functioning as they focus on a single or small number of biological traits (Bremner et al., 2003). Biological Trait Analysis (BTA) is an alternative method of describing ecosystem functioning, that goes beyond traditional approaches (Statzner et al., 1994), through the strong links between traits and ecosystem processes (Díaz and Cabido, 2001). BTA confers advantages over conventional methods (Dolédec et al., 2006; Frid et al., 2008; Neumann and Kröncke, 2011). BTA may use a set of different characteristics (life history, morphological, behavioural) of species present in assemblages (Bremner, 2008) and can be used for management and conservation purposes (Bremner, 2008; Frid et al., 2008).

We used BTA to determine the dominant functional characteristics of the Rance basin after 54 years of operation of a tidal power plant. Commissioning in 1966, the Rance Tidal Power Plant (RTPP) uses the tidal range to create a difference in water height between the open sea and the basin and to produce electricity. This study complements a previous one focused on temporal differences in benthic assemblage structure and ecological trajectories over the last three decades (Brébant et al., submitted-a). During the last decade, the number of species significantly increased, in relation with progression of marine waters, sediment redistribution, habitat heterogeneity increasing and seagrass dynamics. The RTPP operation is responsible of the surficial sedimentary cover by locally slightly increasing the sedimentation rate. The first objective of this study was to assess the functioning of macrobenthic assemblages in the Rance basin in response to hydro-sedimentary modifications. As studying the temporal changes in the functioning of benthic assemblages is indispensable to validate management plan (Veríssimo et al., 2012), the second objective was to identify functional trajectory differences between benthic assemblages during the last three decades by applying the Community Trajectory Analysis framework (De Caceres et al., 2019) to functional dynamics (Sturbois et al., 2021b)

Materials and methods

1. Study site and data set

The study area focuses on the Rance maritime basin, which extends on 22 km² at high tide from the Chatelier lock upstream to the RTPP downstream (Figure 1). This basin is a narrow ria (Evans and Prego, 2003) located on the north coast of Brittany (France). After the RTPP was built in 1966, the salinity front migrated several km upstream. Currently, the Rance basin is divided in two zones: the downstream zone corresponding to marine waters and the upstream zone where evolve the salinity front (Bonnot-Courtois and Lafond, 1991, Figure 1). During the last decade, in response to climatic change, the salinity front has moved upstream allowing the progression of marine species. The Rance basin has become a privileged study site to characterise the impact of such large structure on biological recolonization modalities, sedimentological changes or structure and functioning of benthic assemblages. Surficial sedimentary cover was studied in 1994 (Bonnot-Courtois et al., 1995) and 2020 at the scale of the basin and in 2010 in the upstream. Benthic assemblages were studied by maps in 1971, 1976, 1995 and 2020 at the scale of the basin (Retière, 1979; Desroy, 1998, Brébant et al., submitted–b) and in 2010 in the upstream zone (Brébant et al., submitted-b). Unfortunately, the lack of impact assessment prior to the construction of the RTPP prohibits any comparison with pre-impact data.

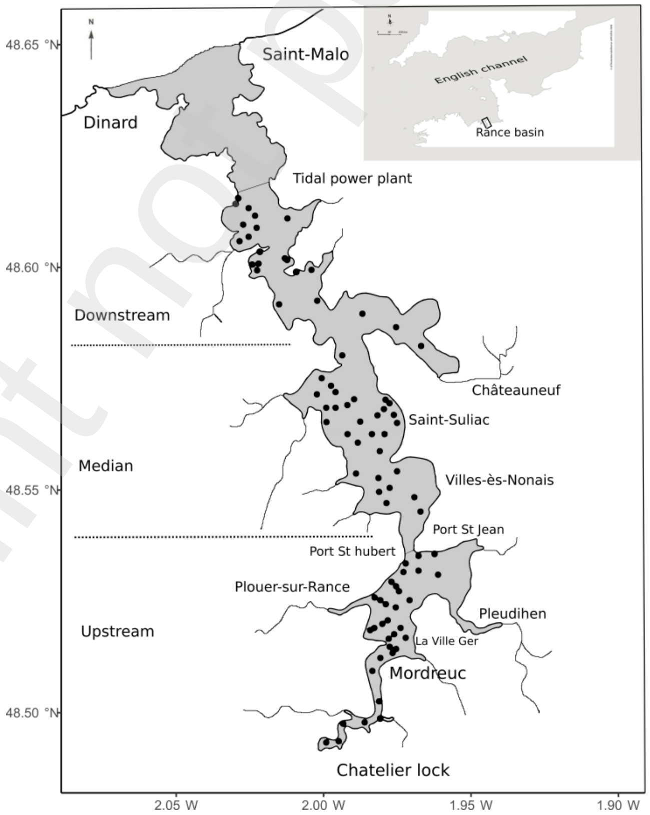


Figure 1: Situation map of the Rance basin and sampling grid (84 stations) common to the different surveys (adapted from Bonnot-Courtois and Lafond, 1991).

2. Sampling and analytical procedures

2.1. Sediment

Granulometric data were collected in 1994, 2010, and 2020. In 1994, 211 samples were collected and analysed through seven granulometric sieves (Bonnot-Courtois et al., 1995). In 2010, 32 stations located in the upstream part of the Rance basin had been sampled. In 2020, sediment has been collected on 99 stations (integrating stations sampled in 2010) distributed in the whole basin Sampling grid performed in 1994 and 2020 were different, but granulometric analysis were conducted with the same protocol. The classification of sedimentary facies distinguishes 12 facies, ranging from gravels to muds, regrouped in this study in 3 categories: mud (<100 µm), sand (100 µm – 2 mm) or gravel (> 2mm)-dominated habitats.

2.2. Fauna

Data collected in 1976, 1995 and 2020 at the scale of the basin (84 common stations) and in 2010 in the upstream zone (32 common stations) were considered (Figure 1). For each survey, two replicates were collected using a Smith McIntyre grab (1976, 1995, 2010) or Day grab (2020), sampling on a unitary surface of 0.1 m^{-2}. The replicates were sieved *in situ* using a 1 mm-mesh sieve and the material was preserved in a 4% buffered formalin solution. Specimens were counted and identified to the lower possible taxonomic level. Taxa found during each year of study were standardized and named in accordance with the World Register of Marine Species (WoRMS Editorial Board, 2023). Abundances were expressed as ind.0.1 m^{-2}.

3. Taxonomic description

In order to assess the different components of α-diversity, the mean numbers of individuals per 0.1m^{-2} (N) and taxa richness (S) were calculated for each survey and station prior to any transformations of the dataset. Values characterising downstream, median, and upstream zones of the Rance basin were compare and statistically tested using analysis of variance (ANOVA).

4. Biological traits

Based on the literature, seven traits were selected and divided into thirty-six modalities of traits to characterise the responses of organisms to the main pressures identified in the study area: sedimentation and eutrophication (Table 1). Selected traits provide a broad view of the functioning of the ecosystem, while limiting redundant information. Traits include (i) feeding mode, linked to resource availability and use; (ii) life history, related to sediment reworking and biogeochemical fluxes at the water-sediment interface; (iii) mobility, linked to movement activities and occupation of the environment; (iv) size, associated to the morphology of taxa; (v) ecological group, related to the tolerance of species to sedimentation or organic enrichment (Degen and Faulwetter, 2019)]; (vi) lifespan, proxy of productivity dynamics (Brey, 1999); (vii) bioturbation, related to the ability of species to rework the sediment (Borja and Tunberg, 2011) and (viii) position of organisms in the sediment, related to habitat use and the potential of disturbance. Each trait was divided into 4-5 modalities to encompass the wide range of macro- and megafaunal characteristics. Affinity of organisms for traits was coded in a fuzzy manner (Chevene et al., 1994) by assigning them a score ranging from 0 (no affinity for a given trait) to 3 (full affinity). Community weighted mean values (CWMs) were calculated to characterise the functional structure (Ricotta and Moretti, 2011). Information was extracted from the primary literature on specific taxa, existing matrices (Robert, 2021; Sturbois et al., 2021a; Clare et al., 2022), expert knowledge and three publicly available databases: polytraits (http://polytraits.lifewatchgreece.eu), the World Register of Marine Species (WoRMS Editorial Board, 2023) and the Biological Trait Information Catalogue (BIOTIC, http://www.marlin.ac.uk/biotic/). When no data were available (5% of taxa), trait modalities were coded 0. For subsequent trait analyses, these taxa took the average profile of all other taxa [*i.e.* they did not contribute to potential models of the given trait (Statzner and Beche, 2010)].

Hierarchical Cluster Analysis (HCA) and Non-Metric Multidimensional Scaling (NMDS) was performed on the biological traits matrix’s to distinguish functional groups between each pair of samples (Legendre and Gallagher, 2001) and applying the Ward's clustering method (Ward, 1963).

Table 1: Traits, modalities and descriptions used for the analysis of biological traits.

Trait	Modalities	Description
Feeding mode	1- Deposit-feeder 2- Suspension-feeder 3- Herbivorous 4- Predator/ Scavengers	1- Feeds on detritus (including algal material) on the sediment surface and within the sediment matrix. 2- Feeds on particulate food resources suspended in the water column. 3- Feeds exclusively on plant material. 4- Actively predates on animals (including small zooplankton) and Feeds on dead animals (carrion).
Living habit	1- Tube-dwelling 2- Burrow-dwelling 3- Free-living 4- Crevice/hole/under stones 5- Epi/endo-biotic 6- Attached to substratum	1- Adults live in a tube, lined with sand, mucus or calcium carbonate. 2- Adults live in a permanent or temporary burrow. 3- No restrictive structure. Able to move freely in and/or on the sediment. 4- Adults are usually cryptic and in coarse/rocky substrate or algal spikes. 5- Adults live on or in another organism. 6- Adults are attached to coarse substrate or rock.
Mobility	1- Sessile 2- Swim 3- Crawl/creep/climb 4- Burrower	1- Adults have little or no mobility. Attached or lives in (semi-) permanent burrow/tube. 2- Adults actively swim in the water column 3- Adults capable of (usually limited) movement along the surface of sediments or rocks. 4- Adults able to move actively in the sediment
Maximun size	1- <1 cm 2- 1-2 cm 3- 2-10 cm 4- >10 cm	The maximum lifespan (years) of the adult stage of the taxon.
Tolerance (AMBI)	1- Sensitive 2- Indifferent 3- Tolerant 4- Second-order opportunist 5- First order opportunistic	1- Species disappear when there is hypertrophy of the environment. 2- Species that are little influenced by an increase in the quantity of organic matter. 3- Naturally present in the mud. Their proliferation is stimulated by an enrichment of the environment, a sign of the imbalance of the system. 4- Small short-cycle species (<1 year) abundant in the reduced sediments of polluted areas. 5- Depositor species, proliferating in reduced sediments
Lifespan	1- <1 year 2- 1-3 years 3- 3-10 years 4- >10 years	The maximum reported lifespan (years) of the adult stage of the taxon.
Bioturbation	1- Diffusive mixing 2- Surface deposition 3- Upward conveyor 4- Downward conveyor 5- None	1- Vertical and horizontal redistribution of sediment/other particles. 2- Deposition of particles on the sediment surface (e.g. pseudofeces). 3- Translocation of particles from the depth to the sediment surface. 4- Subduction of particles from the sediment surface to the depth (e.g. feeding and/or defecation). 5- Does not have bioturbation capacity.
Sediment position	1- Surface 2- Shallow infauna 3- Mid-depth infauna 4- Deep infauna	1- Adults live on or just above the sea floor. 2- Adults live below the surface of the sediment (0 and 5 cm deep). 3- Adults live below the sediment surface (5 and 10 cm deep). 4- Adults live below the surface of the sediment (more than 10 cm deep).

5. Functional diversity

The studied community is composed of S species. Each species i has a number of T traits with standardized values (xi1, xi2, ..., xiT), which are conceived as coordinates in the functional trait space. When plotting all the S species in a multi-trait space, functional diversity is simply the distribution of species and their abundances in this functional space (Villéger et al., 2008). The functional space was defined with a Principal Coordinate Analysis (see the review of Mouillot et al., 2013) and functional diversity was estimated from four univariate indices: functional richness (FRic), functional evenness (FEve), functional divergence (FDiv) [calculated following the method of Villéger et al., (2008)] and functional redundancy (FRed). FRed corresponds to the ratio of Functional Diversity to Shannon-Weaver index [FD/H' (van der Linden et al., 2012)]. FRic ranges from 0 to 1 when the functional richness of the assembly fills the entire possible functional space. FEve determines the distribution among species and their abundances within the functional space. FDiv represents the average distance of species (weighted by their abundances) between the position of each species present at the considered station in the functional space and the center of gravity of that space. FRed values decrease as functional redundancy increases. Functional diversity indicators were calculated using the "FD" package (Laliberté et al., 2014). Maps presenting the distribution of univariate indices of functional diversity were produced using Rstudio software (package Krigiing), according to the kriging interpolation method.

ANOVA were conducted to test differences between indices values across space (three zones) and time (three sampling periods).

6. Detecting trajectory patterns

A PCA was performed on CWMs and analysed with the Community Trajectory Analysis framework (CTA, De Caceres et al., 2019) applied to functional dynamics (Sturbois et al., 2021b).

CTA is based on the geometric properties of ecological trajectories (De Cáceres et al., 2019). Trajectories corresponds to a set of ecosystem states (i.e., coordinates in a multidimensional space) derived from temporal observations that can be analysed and compared using a distance matrix. States are expressed by a vector specifying the site corresponding to each consecutives ecosystem status and a vector specifying the survey (sampling year) corresponding to the sampling of each ecosystem status. A set of distance-based metrics was calculated. The segment length represents the distance between two consecutive surveys. The trajectory path corresponds to the sum of segment lengths belonging to a trajectory. NC provides information about the overall change occurred during the study period. The net change ratio (ratio between the net changes and the trajectory path) indicates the linearity of recovery and/or departure processes relative to the initial status. Consecutive recovery and departure trajectory segments (RDT) were identified by the difference between the net change n-1 and the net change n (Sturbois et al., 2021b). CTA were conducted using the 'ecotraj' package (De Cáceres et al., 2019, Sturbois et al., 2021b).

Hierarchical Cluster Analysis (HCA) was performed on the Directed Segment Path Distance (DSPD) to distinguish clusters of functional trajectories between each pair of samples (Legendre and Gallagher, 2001) and applying the Ward's clustering method (Ward, 1963).

Results

1. Sedimentary characteristics

Although maps of surficial sediment coverage are not comparable because of their different sampling grids, some sedimentary changes occurred over a span of 26 years (see Brébant et al., submitted-b for details).

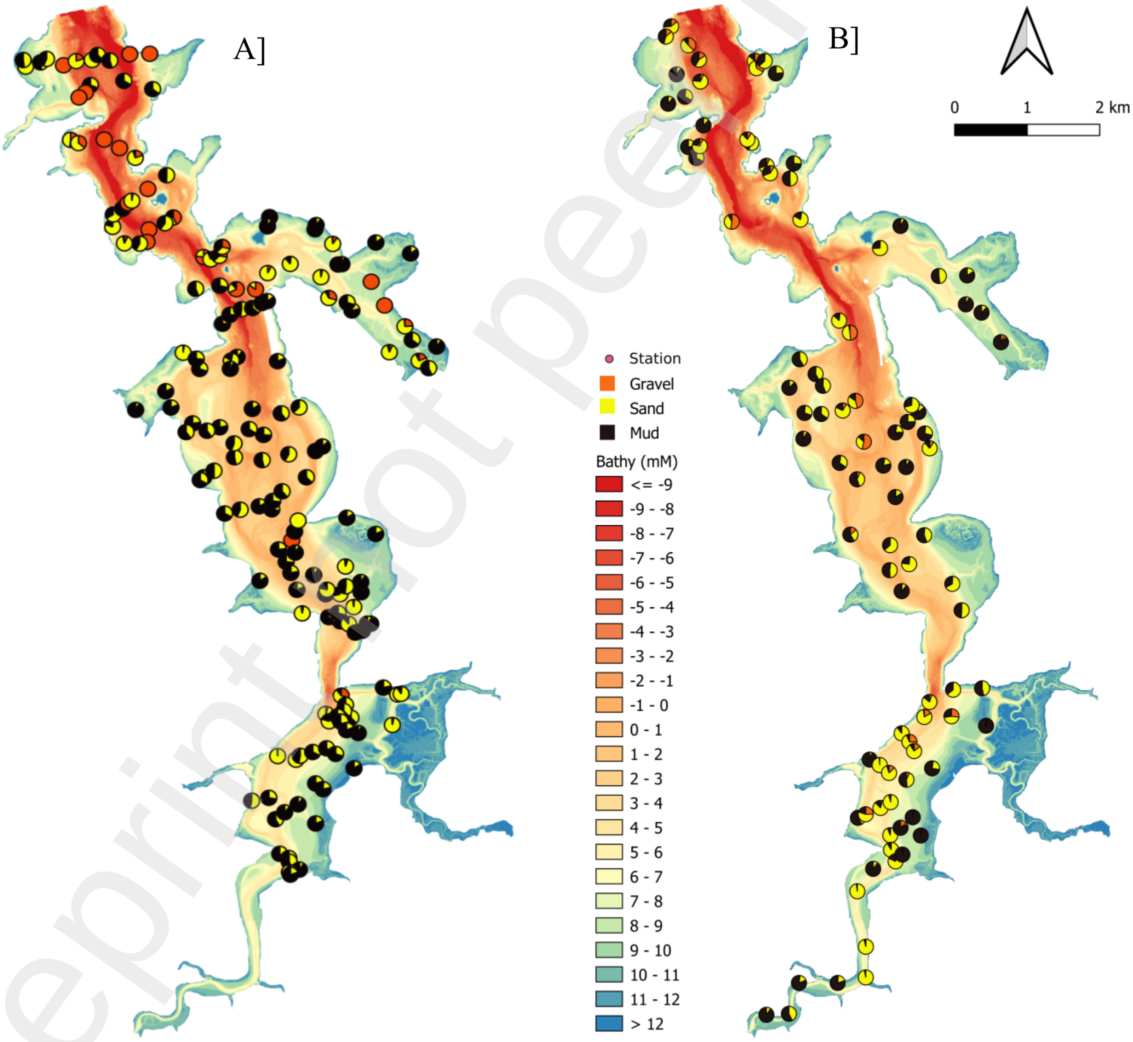


Figure 2: Pie chart representing the sedimentary facies (mud, sand and gravel-dominated sediment) for the year 1994 (A) and 2020 (B). Background colours of the map represent the bathymetry (m: maximum, M: minimum). A common bathymetry recorded in 2018 was used for the two years.

Sediment has been enriched between 1994 and 2020 in fine particles (<100 µm) downstream in lateral coves and upstream, on upper intertidal flats. In the upstream zone, the main channel was clearly delineated in 2020, with predominantly sandy sediment and important proportions of coarse fractions. In contrast, sediments in the channel were richer in fine particles (mud notably). Data could not be statically tested as only 13 stations were comparable between 1994 and 2020.

2. Macrobenthic communities

2.1. General characteristics

At the scale of the 84 stations sampled in the whole basin, 98 taxa were common to the 1976, 1995, and 2020 surveys. On the upstream part, 28 species were common to the three sampling periods.

The number of taxa recorded in the basin has significantly increased between 1976–1995 (respectively 164 and 212) and 2020 (361; p-value < 0.001). In 2020, the number of taxa followed an increasing gradient (not observed in 1976 and 1995) from upstream to downstream zones (Figure 3). Similarly to the species richness, abundance values were significantly higher only in 2020, compared to 1976-1995. Abundance followed a similar gradient of increasing from upstream to downstream (Figure 3). In 1976, the most abundant species were the polychaetes *Euclymene oerstedii*, *Melinna palmata*, and *Chaetozone gibber*. In 1995, they were replaced by oligochaetes and in 2020, by the phoronid *Phoronis psammophila* and the polychaete *Leiochone leiopygos*. For each survey, the number of taxa and abundances were significantly different between zones, values observed in the median and downstream zones being different of values observed in the upstream zone (Figure 3). In 1976, 1995 and 2020, species richness and abundance were not significantly different in median and downstream zones but significantly different in the upstream zone.

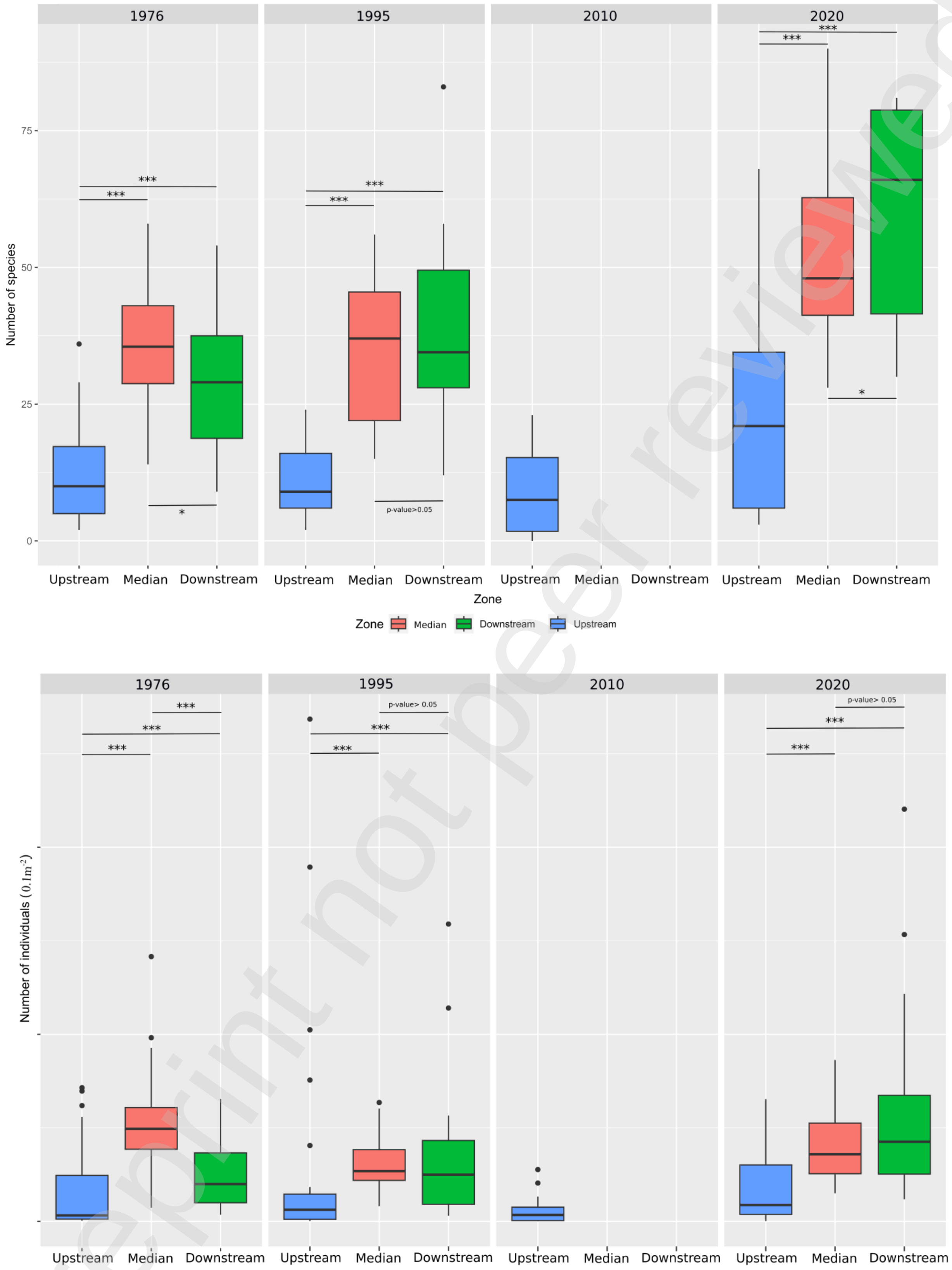


Figure 3: Boxplot representing changes in species richness (A) and abundance (B) between different areas over time. Richness and abundance are expressed over 0.1m^{-2}. Statistical differences have been assessed thanks to pairwise-Wilcoxon tests. ***: *p-value* <0.001; **: *p-value* <0.01; *: *p-value* <0.05.

Compared to previous surveys, Shannon index (Table 2) was also significantly different only in 2020 (*p-value* < 0.001). Over time, values of Shannon index are not significantly different in median and downstream zones but significantly different in the upstream zone (*p-value* <0.001). Values of Simpson and Pielou index (Table 2) are not significantly different at the scale of the basin.

Table 2: Mean values per station of Shannon (H'), Simpson (D) and Pielou index (J), and of species richness (S) for the different zones in 1976, 1995, 2010, and 2020. Standard deviations are indicated in italics.

	Upstream				Median			Downstream		
	1976	1995	2010	2020	1976	1995	2020	1976	1995	2020
H'	**1.53** ± *0.57*	**1.49** ± *0.57*	**1.18** ± *0.86*	**1.80** ± *0.76*	**2.04** ± *0.52*	**2.20** ± *0.49*	**2.50** ± *0.44*	**2.08** ± *0.59*	**2.36** ± *0.68*	**2.62** ± *0.81*
D	**0.68** ± *0.17*	**0.66** ± *0.18*	**0.57** ± *0.33*	**0.70** ± *0.18*	**0.75** ± *0.15*	**0.80** ± *0.12*	**0.83** ± *0.08*	**0.77** ± *0.16*	**0.81** ± *0.17*	**0.84** ± *0.17*
J	**0.68** ± *0.14*	**0.68** ± *0.18*	**0.53** ± *0.33*	**0.67** ± *0.15*	**0.58** ± *0.11*	**0.63** ± *0.10*	**0.64** ± *0.08*	**0.63** ± *0.14*	**0.66** ± *0.15*	**0.64** ± *0.14*
S	**12** ± *14*	**11** ± *11*	**9** ± *7*	**24** ± *21*	**35** ± *13*	**35** ± *13*	**52** ± *18*	**29** ± *14*	**38** ± *18*	**62** ± *26*

2.2. Functional properties

At the basin scale, the overall functional properties remained stable over time between 1976, 1995 and 2020 (Figure 4). Deposit feeders were largely dominant, representing up to 60% of the trophic group, whatever the year considered. Fauna was mainly composed of tubicolous organisms, so sessile, and burrowers, living in the few first cm of sediment, with a short lifespan (1-3 y) and tolerant to organic enrichment. Over time, some light changes can be observed: among bioturbators, the contribution of organisms inducing surface deposition decreased to the benefit of upward conveyor species. The ratio of small organisms decreased over time to the benefit of medium size organisms. Contribution of sensitive species (group I) tended to increase at the expense of indifferent species (group II). Finally, tubicolous and free-living organisms decreased, and burrowers increased.

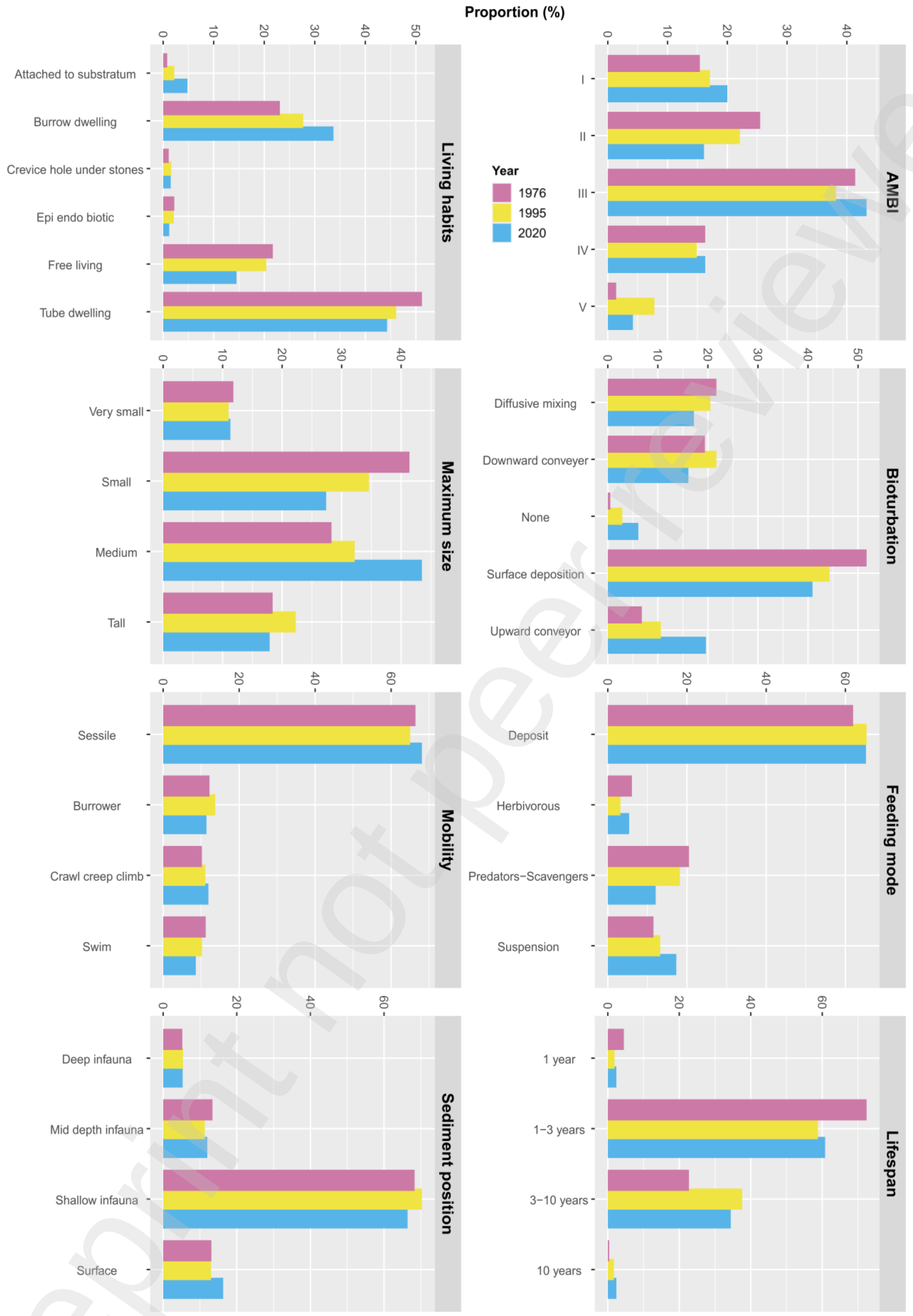


Figure 4 : Profiles of functional traits (including the 36 modalities) at the scale of the whole basin in1976, 1995 and 2020.

At the scale of the upstream area, which exhibit the most variable environmental conditions, some modality contributions changed between 2010 and 2020: contribution of medium size, long-lived (3-10 y) organisms and organisms inducing surface deposition increased and contribution of tube dwellers decreased (supplementary material, annex 1). However, these changes are in the variability range observed since 1976 and did not modify the main contributions pattern of functional traits which were comparable to those observed at the scale of the basin.

2.3. Functional diversity

Various univariate indices of functional diversity were calculated for each station in 1976, 1995 and 2020 at the scale of the basin and represented, using kriging, to determine trends in species trait diversity within the ecosystems (Figure 5A, B and C).

Functional richness (FRic) exhibits similar distribution patterns in 1976 and 2020, with hight values in the downstream and median parts and in the channel of the upstream area (*p-value* > 0.05). In 1995, values observed in the upstream area were lower. As a consequence, FRic values are significantly different between 1976 and 1995 (F: 5.42, *p-value* <0.001) and between 1995 and 2020 (F: 12.36, *p-value* <0.001). Functionnal eveness (FEve) values were higher to 0.4 and regularly distributed in the whole basin in 1976 and 1995. Values, which were not significantly different between 1976 and 1995, became significantly different in 2020 (F: 3.21, *p-value* < 0.001). In 2020, regarding the abundance of species, FEve strongly decreased in 2020 in the whole basin, at the exception of some stations located upstream. Functional divergence (FDiv) follows the same pattern, with non significant differences between 1976 and 1995, which became significant in 2020 (F: 4.55, *p-value* <0.05). High in 1976 and 1995, values of FDiv decreased in 2020, notably on the periphery of the basin. Values of functionnal redundancy (FRed) are low at the scale of the basin (except in the most upstream part), whatever the year considered, which means that functional redundancy is high. Values remained non significantly different between 1976 and 1995 and became significantly different in 2020 (F: 3.90, *p-value*<0.001).

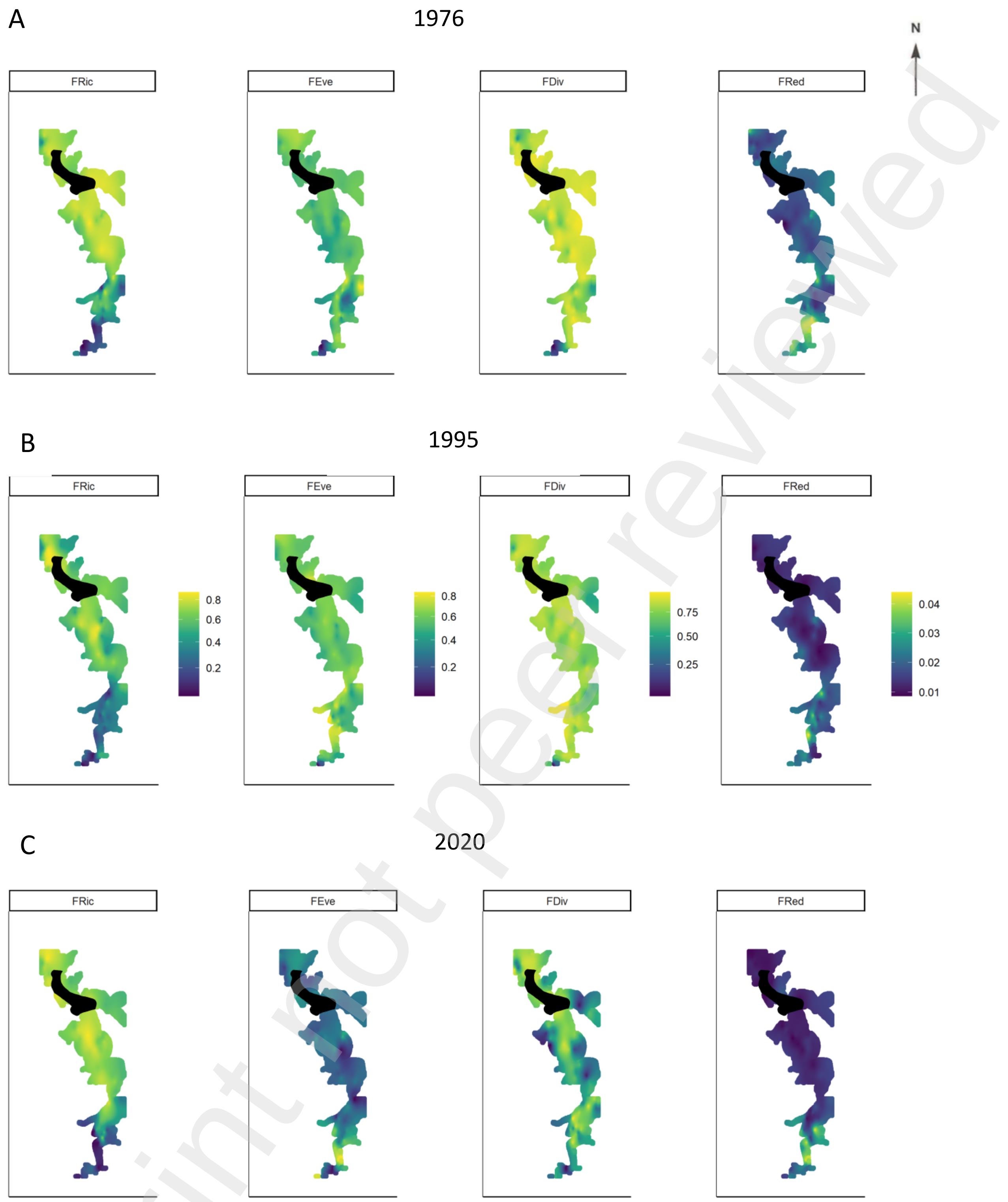


Figure 5: Spatial distribution FRic, FEve, FDiv and FRed in 1976, 1995 and 2020. The highest values are coloured in yellow. The black area represents the portion of the basin without station, and therefore without data.

2.4. Inter-annual variability

HCA and n-MDS were conducted on the entire dataset (1976, 1995, 2010, and 2020), revealing the presence of 7 functional groups (Figure 6E), which were mapped for each sampling date (Figure 6A to D). The stress value for HCA was below 0.2. Two clusters (2 and 3) dominate at the basin scale.

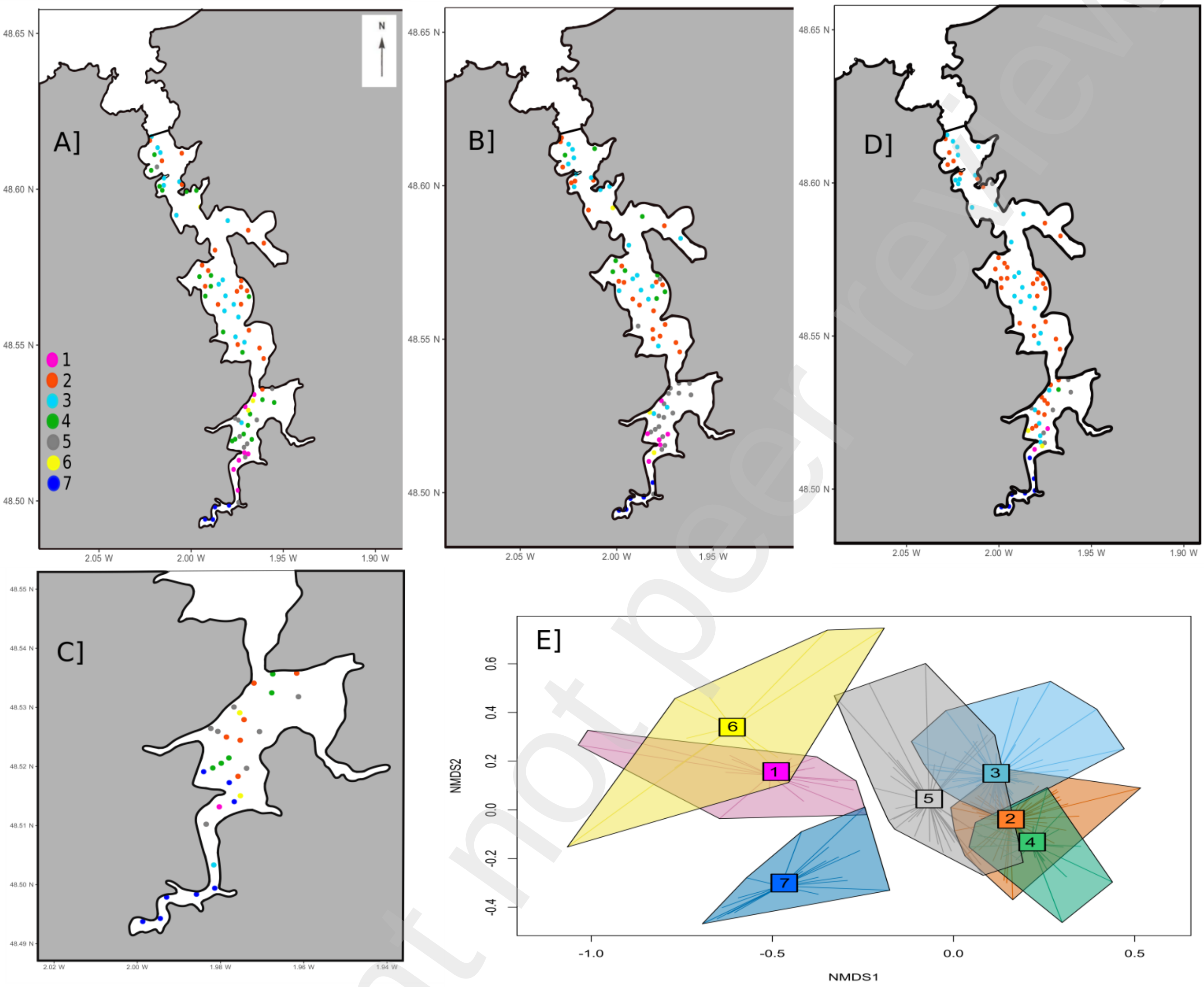


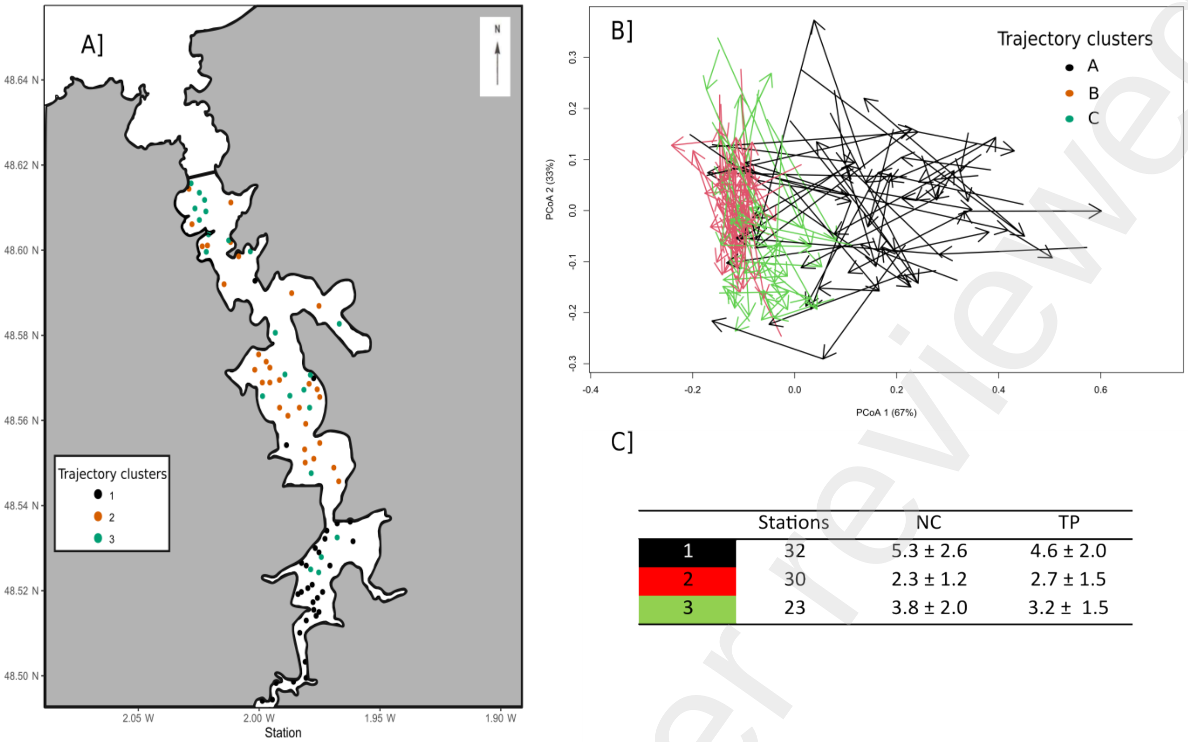
Figure 6: Distribution of functional assemblages in the Rance basin in 1976 (A), 1995 (B), 2010 (C) and 2020 (D). (E): non-metric multidimensional positioning based on HAC, each polygon representing an functionnal assemblage.

Functional asssemblages seemed to be separated in two groups in the multidimensional space (Figure 8E). The first, comprising clusters 1 (17 stations), 6 (10 stations) and 7 (24 stations) grouped upstream stations (at the exception of one station of group 6 located downstream in 1976 and 1995). The number of stations of each group and their location in the basin was stable over time. Cluster 1 was dominated by carnivores and scavengers species (>60%) indifferent to organic matter rate and inducing diffusive mixing. Clusters 6 and 7 were mainly composed of deposit feeders,carnivores and scavengers tolerant to organic enrichment and moving in or on the sediment. The second group, composed of clusters 2 (87 stations), 3 (65 stations), 4 (36 stations) and 5 (43 stations), grouped mainly downstream stations and and locally some upstream stations. Contribution and distribution of each cluster changed over the study period (Figure 6A to D). In 1976 and 1995, cluster 2 was distributed on muddy fine sands in the downstream and median areas. In 2010, it extended upstream and became the dominant cluster in this zone in 2020. For each sampling date, stations of cluster 3 were located in the downstream and median areas, in or near the main channel. In 2020, this cluster was present in the upstream zone. Unlike 1976 and 1995, in 2020, downstream and median areas host only clusters 2 and 3. Distribution of cluster 4 decreased over time, from 1976 where it was present on intertidal mudfltats throughout the basin to 2020 where it was present in only one station. Cluster 5 was located upstream at each sampling date. Clusters 2, 3, 4 and 5 were mainly composed of deposit feeders (>60%), sessile organisms dwelling in tubes or burrows, generating surface deposition (pseudofeces). Species included in clusters 4 and 5 are more tolerant to organic matter enrichment than species of clusters 2 and 3.

To summarise, downstream and median parts exhibited relative stable functional assemblages. Changes observed resulted in a reduction of the number of assemblages until they only host clusters 2 and 3 in 2020. Upstream area is characterise by permanent change of functional assemblages dominance (cluster 4 and 5 in 1976, cluster 5 in 1995, mosaic of cluster in 200 and cluster 2 in 2020).

2.5. Functional trajectories

Functional trajectories of the 84 stations sampled in 1976, 1995 and 2020 were separated in 3 clusters of trajectories (Figure 7A and B). Cluster A regroups 32 stations quasi-exclusively located in the upstream zone. Stations of this group exhibits longest TP and NC value is high (NC: 5.3 ± 2.6 and TP: 4.6 ± 2, Figure 7C), which indicate important functional changes over time. Cluster B is composed of 30 stations, mainly distributed in the median part. TP are tight and NC value is the lowest (NC: 2.3 ± 1.2 and TP: 2.7 ± 1.5). Such low values indicate a high degree of stability of functional trait in the median part of the basin. Cluster C was composed of 23 stations located all along the basin and characterised by intermediate values of TP and NC (NC: 3.8 ± 2.0 and TP: 3.2 ± 1.5).



C]

	Stations	NC	TP
1	32	5.3 ± 2.6	4.6 ± 2.0
2	30	2.3 ± 1.2	2.7 ± 1.5
3	23	3.8 ± 2.0	3.2 ± 1.5

Figure 7: A - Location of functional trajectory clusters calculated from 1976, 1995 and 2020 datasets. B - Trajectory diagram (ecological states of each station have been linked to represent trajectories). C – Summary of trajectory metrics. Taxonomic trajectories are coloured according to trajectory clusters and described using measures based on mean distance ± sd (NC: net change, TP: trajectory path).

Functional trajectory maps were represented in downstream (Figure 8A) and upstream (Figure 8B) areas. Of the 84 stations in the basin, one half presents departing trajectories (42 stations) and the other half, recovering trajectories (42 stations). Thus, from a global point of view, no dynamic deviation from the initial functional state is observed in the basin, however, locally, some trends can be detected, notably in the upstream area. In this area, stations exhibiting departing trajectories are globally located in the main channel (with differences in magnitude of changes, stations located in the most upstream arm presenting lowest TP and NC values). Stations showing recovering trajectories are globally located on intertidal flats and are characterised by TP and NC values of the same order of magnitude. Their sediment is characterised by high rates of fine particles (mud).

In the median and downstream areas, no general trend can be observed. Recovering patterns seems however to be mainly distributed in and around the main channel.

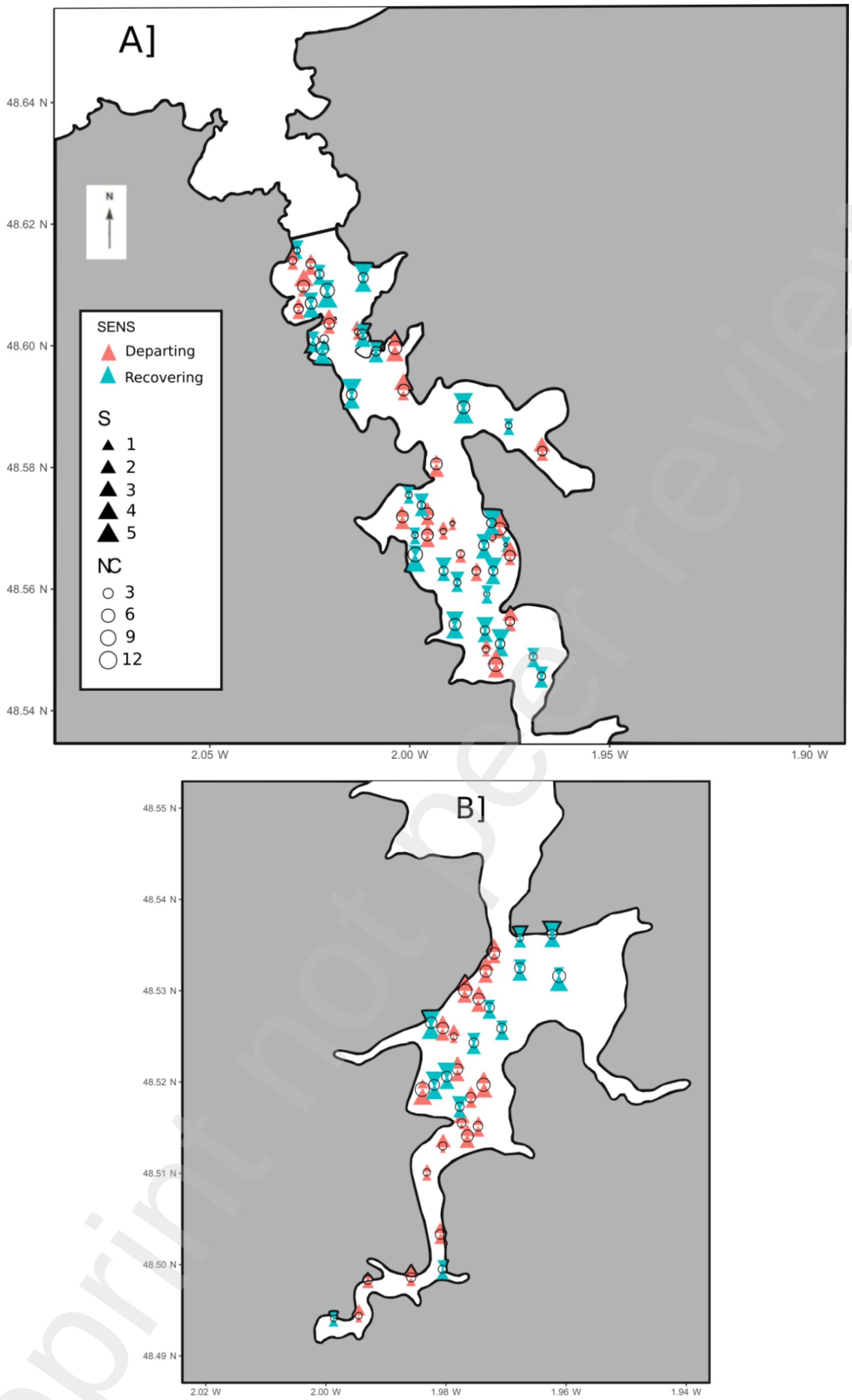


Figure 8: Trajectory maps (A – downstream area, B – upstream area). Net changes between 1976 and 2020 are represented by central black circles. Lower triangles represent the trajectory segment S1 (1976-1995) and the upper ones, the trajectory segment S2 (1995-2020). Size of symbols corresponds to the lengths and colours of triangles indicate pattern followed (recovering or departing).

Discussion

Human activities have caused significant alteration of estuarine ecosystems worldwide, reducing their species richness, diversity, and productivity (Lotze et al., 2006). Overexploitation, habitat destruction, and pollution have disrupted the natural balances of species and interactions within estuarine species, leading to an increase in local extinctions of species and invasions by non-indigenous species (Loreau et al., 2001; Hooper et al., 2005; Lotze et al., 2006; Worm et al., 2006). With the construction of the RTPP at its mouth, the Rance estuary does not escape this rule. After the disturbance caused by the construction of the RTTP (1963-1966), benthic assemblages progressively recolonised bottoms and exhibited, after about 10 years, structures comparable to those of undisturbed assemblages (Retière, 1979). In 1995, around 30 years after the commisioning of the RTPP, benthic assemblages appeared stable and mature and approaching their climacic status (Desroy, 1998). Species richness and abundances increases observed in 2020 raise question about previous observations. New community distributions have been observed, with marine species establishing their presence on sediments historically under influence of brackish waters (Brébant et al., submitted-b). Such marine species transgression must be monitored as it is established that species range expansions first occur at a small scale before spreading to larger scales (Wilson et al., 2005).

The intertidal communities of the Rance share similarities with other similar systems in terms of species composition and abundance, for example, long-lived bivalves, epibenthic gastropods, amphipods, burrowing polychaetes, and tube builders (McLusky and Elliott, 2004).

Classically, the assessment of ecological status of benthic assemblages were based on taxonomy (Mouillot et al., 2006; Elliott and Quintino, 2007). However, measures based on biological characteristics, often considered as better indicators of ecosystem functions and processes, are now also carried out, (Díaz et al., 2007; Griffin et al., 2009; Gagic et al., 2015). The originality of estuarine environments is the high variability of presssures (natural and anthropogenic), to which benthic invertebrates will respond (van der Linden et al., 2012). Such variabilities have significant repercussions on functional balance and dynamics, and shape the functioning of estuarine ecosystems (Hooper et al., 2005; Lotze et al., 2006; Worm et al., 2006). At the scale of the basin, values of FEve and FDiv were lower in 2020. Lower values of FDiv suggest a lower degree of niche differentiation and more intense resource competition (Mason et al., 2005; Dolbeth et al., 2013). On the contrary, the Functional redundancy increased in 2020. Functional redundancy is an important property for ecosystem stability (Díaz and Cabido, 2001), since redundant taxa mitigate changes ecological functioning (Clare et al., 2015). Biggs et al., (2020) demonstrated, in a meta-analysis, a positive average correlation between functional redundancy and ecological stability/resilience. These scientists hypothesised that functional redundancy promotes ecological resilience and stability, as the function of ecosystems in communities composed of more redundant species (those that perform similar functions) should be less affected by the loss of individual species. Results of this study corroborates this affirmation.

1. Importance of dominant species

The functioning of the RTPP, associated to the narrow morphology of the basin create intense hydrodynamics in the Rance basin. Although less strong than previous the comissioning of the RTPP, hydrodynamics is responsible for sediment distribution and resuspension, directly impacting the distribution of benthic macrofauna (Fujii, 2007; Compton et al., 2013; Veiga et al., 2017). Downstream, the surficial sediment coverage of the main channel remained stable since 1994. Upstream, in contrast, the channel was silted in 1994 and sandy in 2020. Such changes influence the structure and the functioning of benthic assemblages and their resilience level (Whomersley et al., 2010). This resilience is attributed to species selection and their inherent ecological plasticity (Davic, 2003).

A total of 98 taxa were common to fauna sampled in 1976, 1995 and 2020, representing 76% of abundances (Brébant et al., submitted-a). In the upstream area, 28 taxa were common to 1976, 1995, 2010 and 2020 datasets. Most of these species are able to support high level of sedimentary disturbances (erosion or deposition). Species with high abundances, as the polychaetes *Ampharete baltica*, *Leiochone leiopygos* or *Melinna palmata*, as species with long life cycles (as the polychaetes *Euclymene oerstedii*, *M. palmata* or *Nepthys hombergii*) contribute to the persistance of assemblages over time. The production by large, long-lived species might be more sustainable, potentially fueling a richer trophic chain (Emmerson, 2012) and contributing to improved ecosystem functioning through other functions such as nutrient dynamics resulting from increased bioturbation (Queirós et al., 2013). Despite this stable consortium, the selectivity induced by environmental constraints inevitably reflects in the composition of species traits.

2. Trends of functional properties

Functional diversity informs about environmental factors and types of disturbances that shape the diversity of functional traits within assemblages and their distribution in space and time (Gerisch et al., 2012; Bremner et al., 2006). The gains or losses of species can have more significantly implications for certain ecosystems than for others (Isbell et al., 2018) and can affect the functional diversity of assemblages in various ways (Cadotte et al., 2011). In the Rance basin, despite some local functional changes in functional assemblages and trait modalities, functional characteristics remained stable over time at the scale of the whole study area. The increase in species richness between 1995 and 2020 did not questionned the respective patterns of contributions of the different modalities of functional traits. Gains of species or stability seems sufficient to compensate losses of species. This pattern is confirmed by analysis of departing - recovery trajectories. At the scale of the basin, departing and recovery trajectories seemed balanced, but locally, patterns were different between upstream and median/downstream parts.

2.1. Functional stability of downstream and median areas

Despite an increase in the number of species between 1995 and 2020 (Brébant et al., submitted-b), the year 2020 is individualised since downstream and middle areas became functionally homogeneous (assemblages belonging to two clusters). Stations previoulsy assignated to different functional assemblages than cluster 2 and 3 defined by the HAC no longer exist in 2020. FRic values increased from 1995 to 2020, suggesting richer assemblages in 2020. This result are consistent with the good to very good ecological status calculated by Brébant et al. (submitted-b) for soft-bottom assemblages. The lower FDiv values and higher redundancy characterising this area in 2020 indicate assemblages with a lower relative abundance of species exhibiting extreme/unique functional trait modalities (Gerisch et al., 2012).

No pattern of distribution can be identified, departing and recovering trajectories being associated to stations located in the periphery or in the center of the basin. These areas, hosting a stable consortium of species (98 species common in 1976, 1995 and 2020, mostly long-lived), exhibited a relative functional stability. Functional diversity indices further support these observations. As functional stability can be subject to aperiodic disturbances caused by different taxon substitutions or uncompensated population fluctuations (Clare et al., 2015), the strong functional redundancy observed from year to year in the basin (Figure 5) suggests that density compensation by redundant taxa mitigates changes in ecological functioning (Naeem, 1998). Persistence, defined by Grimm and Wissel (1997) as a property of ecological systems that incorporates moderate temporal variations, seems to characterise the species dynamics observed in the Rance basin, which results in an overall persistence in the respective contribution of traits modalities within the system. Assemblages of these areas are dominated by sessile (>80% of species) detritivores (>60%), primarily consisting of tube-dwelling organisms (*e.g.* the amphipod *Ampelisca tenuicornis* or the polychaetes *Euclymene oerstedii*, *Melinna palmata*…). The high contribution of tubicolous organisms in subtidal assemblages can be a consequence of the absence of professionnal fishing activities in the basin. The high functional stability illustrate the fact that the sediment variability has been confined to specific stations in the downstream or middle zone over time, without disrupting the dominance of fine sediment habitats. The high local contribution of burrowers on intertidal flats or sandbanks, as the Manilla clam *Ruditapes philippinarum*, in fauna may be responsible for erosion processes, as already reported for several species of bivalves (Dairain et al., 2020) and local changes in functional trajectories. Similar findings were observed in intertidal habitats of the Bay of Saint-Brieuc (Sturbois et al., 2021a). Intertidal mudflats being more exposed to predation by birds (Dolbeth et al., 2015), the strategy of deep burial in sediment and the ability to feed in suspension seem highly advantageous to cope with potentially higher predation pressure.

Local changes often observed on intertidal mudflats can also be due to the proliferation of opportunistic green macroalgae, general phenomenon observed in many coastal and estuarine habitats in the northwest of france (Ménesguen, 2003; Charlier et al., 2006), may strongly impact benthic assemblage composition (Quillien et al., 2018) and functional properties. Their proliferation illustrates the high level of nitrates concentrations in the basin (Ménesguen and Piriou, 1995). Although pressure exerced by *Enteromorpha* mats may be one of the causes of benthic fauna changes over time, the generalisation of their effects is not straightforward (Bolam et al., 2000; Everett, 1994; Raffaelli et al., 2000).

2.2. Upstream area concentrates functional changes

In the upstream area, departing patterns concerned assemblages located in the main channel, up to the Chatelier lock and recovering patterns, assemblages located on the intertidal mudflats. Theses trends were supported by significant trajectory segments and substantial trajectories, suggesting a functional instability. Highly variable environmental conditions, particularly hydrological, characterises the upstream area (Desroy and Retière, 2003). As underlined by Defeo and Mclachan (2013), such a natural variability may lead to a strong control, up to a reset, of community composition. Assemblages are characterised by small detritivorous species, tolerant to organic matter increase. These species exhibit traits of opportunistic species, as defined by van der Linden et al., (2012). Their life cycle are short, their productivity and ability to (re-)colonise the environment, high as already observed by Dolbeth et al*.,* (2015) in the Mondego estuary. These traits are highly advantageous in unpredictable environments subject to a source of disturbance, such as tidal fluctuations, providing additional but ephemeral food resources *e.g*., freshwater inputs (Borja et al., 2000). As reported by Mouchet et al. (2010), functional composition of assemblages are consistent with low values of FDiv and FRic on intertidal mudflat areas. This strategy is reflected in large populations of small-sized individuals, indicating higher production. In the channel leading to the Chatelier lock, the instability of the sediment is such that sessile species cannot settle. High concentrations of suspended sediments in the water column can also disrupt suspension-feeding species (Schönberg, 2016; Pineda et al., 2017), affecting their energy, health, and reproductive fitness (Bell et al., 2015; Pineda et al., 2016; Schönberg, 2016; Stubler et al., 2015; Tompkins-MacDonald and Leys, 2008; Pineda et al., 2017).

In the upstream area, the tidal prism have evolved since the 1990s, leading to a new distribution of surficial sediments, with the reappearance of coarser sediment in the main channel, and the intrusion of marine species in 2020 in this area historically bathed by brackish waters (Brébant et al., submitted-b). Congruently, benthic assemblages located upstream exhibited strong functional changes in 2020 in the main channel up to the Chatelier lock, with departing trajectory patterns and high NC values. From a structural and functional points of view, downstream assemblages have extended upstream. As a consequence, the increase in the contribution of some traits characteristics of marine species was observable in 2020.

3. Implications for environmental management and monitoring

The first ecological state in the data series is 1976, so we do not have an initial state before the construction of the RTPP in this study. However, the value of this historical data for basin management remains essential, just as the importance of maintaining consistent protocols, as emphasized by Callaway (2016) for the management of marine and coastal environments.

As suggested by various authors (Hewitt et al., 2016; Bacouillard et al., 2020; Sturbois et al., 2021a), coupling different spatial and temporal scales in the sampling strategy could help track changes between long-term networks. Particularly in the upstream part of the Rance basin, which is unpredictable and subject to numerous disturbances and functional instability. A smaller number of stations sampled two or three times per decade could allow us to better understand the mechanisms at play in this area, as well as the factors that disrupt these habitats.

In the Rance basin, sediment removal experiments (Autonomous Robot "Nessie") and dredging activities have accelerated in recent years with the aim of maintaining secondary channels, reducing sedimentation in certain inlets, and improving water circulation. The potential environmental consequences of maintenance dredging are multifaceted. On one hand, morphological changes and variations in the nature of the surface sediment are likely to alter benthic habitats (Marmin et al., 2014). On the other hand, the turbidity conditions of the environment can be affected, either indirectly depending on changes in hydro-morpho-sedimentary functioning, or directly in the dredged area in the case of the release of fine particles during dredging operations (Duclos, 2012), inevitably leading to direct effects on the morphology of the study area and indirect repercussions on the overall ecological functioning and productivity of the basin (Rhoads et al., 1978).

These sediment extractions have already been carried out both upstream and downstream in the basin, with inherent consequences in each zone. Mainly located on the left bank of the downstream area, these operations could disrupt the positive dynamics of seagrass beds observed in recent years. Seagrass beds do not tolerate rapid and prolonged changes in water turbidity well (Auby et al., 2011). Upstream, in a context of lower sediment availability, the upstream part of the estuary would be more sensitive to rising waters and climatic events such as storms due to greater depths, which facilitate the propagation of marine energy upstream, as already suggested in the Seine estuary (Lemoine, 2021).

In the context of sustainable preservation of the integrity and functioning of the Rance basin, there was a real need to assess the functional characteristics of the inherent species and their responses to all these pressures in order to establish appropriate monitoring and management tools. For the future, management of biodiversity must integrate, towards relevant spatial and temporal scales, the implications for functional diversity (Jarzyna and Jetz, 2018).

Conclusion

Results of this study have shown a functional stability of assemblages in the downstream/median areas of the basin, driven by the absence of major changes in the dominance of species and the persistence of a common pool of structuring species. On the opposite, in the upstreamarea, instability observed over time is largely explained by (i) a marinisation caused by changes in the tidal prism and (ii) increase in the granulometry of surficial sediments in the main channel. Despite a slight decrease in the values of some functional diversity indices in 2020, the respective contribution of each modalities of traits remained stable at the scale of the basin. It suggests a high level of ecological resilience drived by the pool of structuring prevalent species and the associated functionnal redundance. Further investigation dealing with secondary production and its transfert in the trophic food web could complement these ecological findings, functional diversity being positively linked to benthic secondary production (Dolbeth et al., 2015).

References

Aarnio, K., Mattila, J., Törnroos, A., & Bonsdorff, E., 2011. Zoobenthos as an environmental quality element: the ecological significance of sampling design and functional traits. Marine Ecology, 32, pp. 58-71. https://doi.org/10.1111/j.1439-0485.2010.00417.x.

Auby, I., Bost, C. A., Budzinski, H., Dalloyau, S., Desternes, A., Belles, A., Trut, G., Plus, M., Pere, C., Couzzi, L., Feigne, C., & Steinmetz, J., 2011. Régression des herbiers de zostères dans le Bassin d'Arcachon: état des lieux et recherche des causes. RST/ODE/LER/AR/11.007. https://archimer.ifremer.fr/doc/00054/16507/.

Bacouillard, L., Baux, N., Dauvin, J. C., Desroy, N., Geiger, K. J., Gentil, F., & Thiébaut, É., 2020. Long-term spatio-temporal changes of the muddy fine sand benthic community of the Bay of Seine (eastern English Channel). Marine Environmental Research, 161, 105062. https://doi.org/10.1016/j.marenvres.2020.105062.

Bell, J. J., McGrath, E., Biggerstaff, A., Bates, T., Bennett, H., Marlow, J., & Shaffer, M., 2015. Sediment impacts on marine sponges. Marine pollution bulletin, 94(1-2), pp 5-13. https://doi.org/10.1016/j.marpolbul.2015.03.030.

Biggs, C. R., Yeager, L. A., Bolser, D. G., Bonsell, C., Dichiera, A. M., Hou, Z., Keyser. S. K., Khursigara, A. J., Lu, K., Muth, A. f., Negrete, J. B., & Erisman, B. E., 2020. Does functional redundancy affect ecological stability and resilience? A review and meta-analysis. Ecosphere, 11(7), e03184. https://doi.org/10.1002/ecs2.3184.

Bolam, S. G., Fernandes, T. F., Read, P., and Raffaelli, D., 2000. Effects of macroalgal mats on intertidal sandflats: an experimental study. Journal of Experimental Marine Biology and Ecology, 249(1), pp 123-137. https://doi.org/10.1016/S0022-0981(00)00185-4.

Bonnot-Courtois, C., Caline, B., Le Vot, M., Malassingne, O., and Ousset, O., 1995. A new sedimentological map of the Rance estuary (Brittany, France). IAS 16th Reg. Meet. Sedimentology, 5ème Congrès Français de Sédimentologie, ASF; Publication ASF Paris, pp 22, 24.

Bonnot-Courtois C., Lafond L.R., 1991 – Caractérisation et comportement des vases dans l'estuaire de la Rance. Rapport EDF/Lab. De Géomorphologie EPHE. 107p.

Borja, A., Elliott, M., Carstensen, J., Heiskanen, A. S., & van de Bund, W., 2010. Marine management–towards an integrated implementation of the European Marine Strategy Framework and the Water Framework Directives. Marine pollution bulletin, 60(12), pp 2175-2186. https://doi.org/10.1016/j.marpolbul.2010.09.026.

Borja, A., Franco, J., & Pérez, V., 2000. A marine biotic index to establish the ecological quality of soft-bottom benthos within European estuarine and coastal environments. Marine pollution bulletin, 40(12), 1100-1114. https://doi.org/10.1016/S0025-326X(00)00061-8.

Borja, A., and Tunberg, B. G., 2011. Assessing benthic health in stressed subtropical estuaries, eastern Florida, USA using AMBI and M-AMBI. Ecological indicators, 11(2), 295-303. https://doi.org/10.1016/j.ecolind.2010.05.007.

Boyé, A., Thiébaut, É., Grall, J., Legendre, P., Broudin, C., Houbin, C., Le Garrec, V., Maguer, M., Droual, G., & Gauthier, O., 2019. Trait-based approach to monitoring marine benthic data along

500 km of coastline. Diversity and Distributions, 25(12), pp 1879-1896. https://doi.org/10.1111/ddi.12987.

Brébant, T., Sturbois, A., Robert. A. E., and Desroy. N., Submitted-a. Long-term changes of benthic communities of the Rance maritime basin. Preprint, not peer reviewed.

Brébant, T., Robert. A. E., Andres. S., Monnier. B., Desroy. N., Submitted-b. Spatial distribution of biosedimentary units in the Rance basin after 54 years of functioning of a tidal power plant. Preprint, not peer reviewed.

Bremner, J., 2005. Assessing ecological functioning in marine benthic communities (Doctoral dissertation, Newcastle University).

Bremner, J., 2008. Species' traits and ecological functioning in marine conservation and management. Journal of Experimental Marine Biology and Ecology, 366(1-2), pp 37-47. https://doi.org/10.1016/j.jembe.2008.07.007.

Bremner, J., Rogers, S. I., and Frid, C. L. J., 2003. Assessing functional diversity in marine benthic ecosystems: a comparison of approaches. Marine Ecology Progress Series, 254, 11-25. DOI : https://doi.org/10.3354/meps254011.

Bremner, J., Rogers, S. I., and Frid, C. L. J., 2006. Methods for describing ecological functioning of marine benthic assemblages using biological traits analysis (BTA). Ecological Indicators, 6(3), pp 609-622. https://doi.org/10.1016/j.ecolind.2005.08.026.

Brey, T., 1999. Growth performance and mortality in aquatic macrobenthic invertebrates. In Advances in Marine Biology (Vol. 35), pp. 153-223. Academic Press. https://doi.org/10013/epic.11058.d001.

Cadotte, M. W., Carscadden, K., & Mirotchnick, N., 2011. Beyond species: functional diversity and the maintenance of ecological processes and services. Journal of applied ecology, 48(5), pp 1079-1087. https://doi.org/10.1111/j.1365-2664.2011.02048.x.

Callaway, R., 2016. Historical data reveal 30-year persistence of benthic fauna associations in heavily modified waterbody. Frontiers in Marine Science, 3, pp 141. https://doi.org/10.3389/fmars.2016.00141.

Capet, A., Drion, R., & Grégoire, M., 2014. Effect of the long-term variability of hypoxia in the Black Sea northwestern shelf on macrobenthos functional composition. In EGU General Assembly Conference Abstracts. pp 160).

Cardinale, B. J., Srivastava, D. S., Emmett Duffy, J., Wright, J. P., Downing, A. L., Sankaran, M., & Jouseau, C., 2006. Effects of biodiversity on the functioning of trophic groups and ecosystems. Nature, 443(7114), pp 989-992. https://doi.org/10.1038/nature05202.

Charlier, R. H., Morand, P., Finkl, C. W., and Thys, A., 2006. Green tides on the Brittany coasts. In 2006 IEEE US/EU Baltic International Symposium. pp. 1-13. IEEE. https://doi.org/10.1109/BALTIC.2006.7266128.

Chevene, F., Doleadec, S., & Chessel, D., 1994. A fuzzy coding approach for the analysis of long-term ecological data. Freshwater biology, 31(3), pp 295-309. https://doi.org/10.1111/j.1365-2427.1994.tb01742.x.

Clare, D. S., Culhane, F., & Robinson, L. A., 2022. Secondary production increases with species richness but decreases with species evenness of benthic invertebrates. Oikos, 2022(4), pp 629. https://doi.org/10.1111/oik.08629.

Clare, D. S., Robinson, L. A., & Frid, C. L. J., 2015. Community variability and ecological functioning: 40 years of change in the North Sea benthos. Marine environmental research, 107, pp 24-34. https://doi.org/10.1016/j.marenvres.2015.03.012.

Cochrane, A., Hoyle, G. L., Yates, C. J., Neeman, T., & Nicotra, A. B., 2016. Variation in plant functional traits across and within four species of Western Australian Banksia (Proteaceae) along a natural climate gradient. Austral Ecology, 41(8), pp 886-896. https://doi.org/10.1111/aec.12381.

Compton, T. J., Holthuijsen, S., Koolhaas, A., Dekinga, A., ten Horn, J., Smith, J., & Piersma, T., 2013. Distinctly variable mudscapes: distribution gradients of intertidal macrofauna across the Dutch Wadden Sea. Journal of Sea Research, 82, pp 103-116. https://doi.org/10.1016/j.seares.2013.02.002.

Costanza, R. & Farber, S., 2002. Introduction to the special issue on the dynamics and value of ecosystem services: integrating economic and ecological perspectives, Ecological Economics, vol 41, pp 367–373. https://doi.org/10.1016/S0921-8009(02)00087-3.

Costanza, R., d'Arge, R., De Groot, R., Farber, S., Grasso, M., Hannon, B., & Van Den Belt, M., 1997. The value of the world's ecosystem services and natural capital. nature, 387(6630), pp 253-260. https://doi.org/10.1038/387253a0.

Covich, A. P., Austen, M. C., Bärlocher, F., Chauvet, E., Cardinale, B. J., Biles, C. L., Inchausti, P., Dangles, O., Solan, M., Gessner, M. O., Statzner, B., & Moss, B., 2004. The role of biodiversity in the functioning of freshwater and marine benthic ecosystems. BioScience, 54(8), pp 767-775. https://doi.org/10.1641/0006-3568(2004)054[0767:TROBIT]2.0.CO;2.

Dairain, A., Maire, O., Meynard, G., Richard, A., Rodolfo-Damiano, T., & Orvain, F., 2020. Sediment stability: can we disentangle the effect of bioturbating species on sediment erodibility from their impact on sediment roughness?. Marine Environmental Research, pp 162, 105147. https://doi.org/10.1016/j.marenvres.2020.105147.

Davic, R. D., 2003. Linking keystone species and functional groups: a new operational definition of the keystone species concept. Conservation Ecology, 7(1). https://hdl.handle.net/10535/2966.

De Cáceres, M., Coll, L., Legendre, P., Allen, R. B., Wiser, S. K., Fortin, M. J., & Hubbell, S., 2019. Trajectory analysis in community ecology. Ecological Monographs, 89(2), e01350. https://doi.org/10.1002/ecm.1350.

Defeo, O., & McLachlan, A., 2013. Global patterns in sandy beach macrofauna: Species richness, abundance, biomass and body size. Geomorphology, 199, pp 106-114. https://doi.org/10.1016/j.geomorph.2013.04.013.

Degen, R., & Faulwetter, S., 2019. The Arctic Traits Database–a repository of Arctic benthic invertebrate traits. Earth System Science Data, 11(1), pp 301-322. https://doi.org/10.5194/essd-11-301-2019.

De Jong, G. D., & Hoback, W. W., 2006. Effect of investigator disturbance in experimental forensic entomology: succession and community composition. Medical and Veterinary Entomology, 20(2), pp 248-258. https://doi.org/10.1111/j.1365-2915.2006.00618.x.

De Juan, S., Hewitt, J., Thrush, S., & Freeman, D., 2015. Standardising the assessment of Functional Integrity in benthic ecosystems. Journal of Sea Research, 98, pp 33-41. https://doi.org/10.1016/j.seares.2014.06.001.

Desroy, N., 1998. Les peuplements benthiques de substrats meubles du bassin maritime de la Rance: évolution de la biodiversité et effets de l'activité prédatrice de *Nephtys hombergii* (annelide polychète) sur le recrutement (Doctoral dissertation, Rennes 1).

Desroy, N., & Retière, C., 2003. The influence of structure and dynamics of infaunal predator populations on predatory activity: the example of *Nephtys hombergii*. Estuarine, Coastal and Shelf Science, 58(3), pp 445-453. https://doi.org/10.1016/S0272-7714(03)00110-0.

Dı́az, S., & Cabido, M., 2001. Vive la différence: plant functional diversity matters to ecosystem processes. Trends in ecology and evolution, 16(11), pp 646-655. https://doi.org/10.1016/S0169-5347(01)02283-2.

Díaz, S., Lavorel, S., Chapin, F. S., Tecco, P. A., Gurvich, D. E., & Grigulis, K., 2007. Functional diversity at the crossroads between ecosystem functioning and environmental filters. Terrestrial ecosystems in a changing world, 81-91. https://doi.org/10.1007/978-3-540-32730-1_7.

Dolbeth, M., Cardoso, P., Grilo, T., Raffaelli, D., & Pardal, M. Â., 2013. Drivers of estuarine benthic species distribution patterns following a restoration of a seagrass bed: a functional trait analyses. Marine pollution bulletin, 72(1), pp 47-54. https://doi.org/10.1016/j.marpolbul.2013.05.001.

Dolbeth, M., Dolédec, S., & Pardal, M. Â., 2015. Relationship between functional diversity and benthic secondary production in a disturbed estuary. Marine Ecology Progress Series, 539, 33-46. https://doi.org/10.3354/meps11473.

Dolédec, S., Phillips, N., Scarsbrook, M., Riley, R. H., & Townsend, C. R., 2006. Comparison of structural and functional approaches to determining landuse effects on grassland stream invertebrate communities. Journal of the North American Benthological Society, 25(1), pp 44-60. https://doi.org/10.1899/0887-3593(2006)25[44:COSAFA]2.0.CO;2.

Duclos, P. A., 2012. Impacts morpho-sédimentaires de l'extraction de granulats marins-application au bassin oriental de la manche (Doctoral dissertation, Université de Rouen).

Elliott, M., Burdon, D., Hemingway, K. L., & Apitz, S. E., 2007. Estuarine, coastal and marine ecosystem restoration: confusing management and science–a revision of concepts. Estuarine, Coastal and Shelf Science, 74(3), pp 349-366. https://doi.org/10.1016/j.ecss.2007.05.034.

Elliott, M., & Quintino, V., 2007. The estuarine quality paradox, environmental homeostasis and the difficulty of detecting anthropogenic stress in naturally stressed areas. Marine pollution bulletin, 54(6), pp 640-645. https://doi.org/10.1016/j.marpolbul.2007.02.003.

Emmerson, M. C., 2012. The importance of body size, abundance, and food-web structure for ecosystem functioning. Marine biodiversity and ecosystem functioning: frameworks, methodologies, and integration. Oxford University Press, Oxford, pp 85-100. https://doi.org/10.1093/acprof:oso/9780199642250.003.0007.

Evans, G., & Prego, R., 2003. Rias, estuaries and incised valleys: is a ria an estuary?. Marine geology, 196(3-4), pp 171-175. https://doi.org/10.1016/S0025-3227(03)00048-3.

Everett, R. A., 1994. Macroalgae in marine soft-sediment communities: effects on benthic faunal assemblages. Journal of Experimental Marine Biology and Ecology, 175(2), pp 253-274. https://doi.org/10.1016/0022-0981(94)90030-2.

Fleddum, A. L., 2010. Effects of human disturbance on biological traits and structure of macrobenthic communities. Hong Kong: Kowloon, City University of Hong Kong, PhD Thesis.

Frid, C. L. J., & Caswell, B. A., 2015. Is long-term ecological functioning stable: The case of the marine benthos?. Journal of Sea Research, 98, pp 15-23. https://doi.org/10.1016/j.seares.2014.08.003.

Frid, C. L. J., Paramor, O. A. L., Brockington, S., & Bremner, J., 2008. Incorporating ecological functioning into the designation and management of marine protected areas. Hydrobiologia. pp. 69-79. Springer Netherlands. https://doi.org/10.1007/s10750-008-9343-y.

Fujii, T., 2007. Spatial patterns of benthic macrofauna in relation to environmental variables in an intertidal habitat in the Humber estuary, UK: Developing a tool for estuarine shoreline management. Estuarine, Coastal and Shelf Science, 75(1-2), pp 101-119. https://doi.org/10.1016/j.ecss.2007.02.027.

Gagic, V., Bartomeus, I., Jonsson, T., Taylor, A., Winqvist, C., Fischer, C., Slade, E. M., Steffan-Dewenter, I., Emmerson, M., Potts, S. G., Tscharnthe, T., Weisser, W., & Bommarco, R., 2015. Functional identity and diversity of animals predict ecosystem functioning better than species-based indices. Proceedings of the Royal Society B: Biological Sciences, 282(1801), 20142620. https://doi.org/10.1098/rspb.2014.2620.

Gerisch, M., Agostinelli, V., Henle, K., & Dziock, F., 2012. More species, but all do the same: contrasting effects of flood disturbance on ground beetle functional and species diversity. Oikos, 121(4), pp 508-515. https://doi.org/10.1111/j.1600-0706.2011.19749.x.

Griffin, J. N., Méndez, V., Johnson, A. F., Jenkins, S. R., & Foggo, A., 2009. Functional diversity predicts overyielding effect of species combination on primary productivity. Oikos, 118(1), pp 37-44. https://doi.org/10.1111/j.1600-0706.2008.16960.x.

Grimm, V., and Wissel, C., 1997. Babel, or the ecological stability discussions: an inventory and analysis of terminology and a guide for avoiding confusion. Oecologia, 109, pp 323-334. https://doi.org/10.1007/s004420050090.

Halpern, B. S., Walbridge, S., Selkoe, K. A., Kappel, C. V., Micheli, F., d'Agrosa, C., Bruno, J. F., Casey, K. S., Ebert, C., Fox, H. E., Fujita, R., Heinemann, D., Lenihan, H. S., Madin, E. M. P., Perry, M. T., Selig, E. R., Spalding, M., Steneck, R., & Watson, R., 2008. A global map of human impact on marine ecosystems. Science, 319(5865), pp 948-952. https://doi.org/10.1126/science.1149345.

Hewitt, J. E., Ellis, J. I., & Thrush, S. F., 2016. Multiple stressors, nonlinear effects and the implications of climate change impacts on marine coastal ecosystems. Global change biology, 22(8), pp 2665-2675. https://doi.org/10.1111/gcb.13176.

Hooper, D. U., Chapin, F. S., Ewel, J. J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J. H., Lodge, D. M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A. J., Vandermeer, J., Wardle, D. A., & Wardle, D. A., 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecological monographs, 75(1), pp 3-35. https://doi.org/10.1890/04-0922.

Isbell, F., Cowles, J., Dee, L. E., Loreau, M., Reich, P. B., Gonzalez, A., Hector, A., & Schmid, B., 2018. Quantifying effects of biodiversity on ecosystem functioning across times and places. Ecology Letters, 21(6), pp 763-778. https://doi.org/10.1111/ele.12928.

Jarzyna, M. A., & Jetz, W., 2018. Taxonomic and functional diversity change is scale dependent. Nature Communications, 9(1), pp 2565. https://doi.org/10.1038/s41467-018-04889-z.

Kröncke, I., Reiss, H., and Dippner, J. W., 2013. Effects of cold winters and regime shifts on macrofauna communities in shallow coastal regions. Estuarine, Coastal and Shelf Science, 119, pp 79-90. https://doi.org/10.1016/j.ecss.2012.12.024.

Laliberté, E., Legendre, P., Shipley, B., and Laliberté, M. E., 2014. Measuring functional diversity from multiple traits, and other tools for functional ecology. R Package FD.

Lausch, A., Bannehr, L., Beckmann, M., Boehm, C., Feilhauer, H., Hacker, J. M., Heurich, M., Jung, A., Klenke, R., Neumann, C., Pause, M., Rocchini, D., Schaepman, M. E., Scmidtlein, S., Schulz, K., Selsam, P., Settele, J., Skidmore, A. K., & Cord, A. F., 2016. Linking Earth Observation and taxonomic, structural and functional biodiversity: Local to ecosystem perspectives. Ecological Indicators, 70, pp 317-339. https://doi.org/10.1016/j.ecolind.2016.06.022.

Legendre, P., & Gallagher, E. D., 2001. Ecologically meaningful transformations for ordination of species data. Oecologia, 129, pp 271-280. https://doi.org/10.1007/s004420100716.

Lemoine, J. P., 2021. Dynamique morpho-sédimentaire de l'estuaire de la Seine: rôle des dragages d'entretien (Doctoral dissertation, Université de Bretagne occidentale-Brest).

Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J. P., Hector, A., Hooper, D. U., Huston, M. A., Raffaelli, D., Schmid, D., Tilman, D., & Wardle, D. A., 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. Science, 294(5543), pp 804-808. https://doi.org/10.1126/science.1064088.

Lotze, H. K., Lenihan, H. S., Bourque, B. J., Bradbury, R. H., Cooke, R. G., Kay, M. C., & Jackson, J. B., 2006. Depletion, degradation, and recovery potential of estuaries and coastal seas. Science, 312(5781), 1806-1809. https://doi.org/10.1126/science.1128035.

Marmin, S., Dauvin, J. C., & Lesueur, P., 2014. Collaborative approach for the management of harbour-dredged sediment in the Bay of Seine (France). Ocean & coastal management, 102, pp 328-339. https://doi.org/10.1016/j.ocecoaman.2014.10.012.

Martini, S., Larras, F., Boyé, A., Faure, E., Aberle, N., Archambault, P., Bacouillard, L., Beisner, B. E., Bittner, L., Castella, e., Danger, M., Gauthier, O., Karp-Boss, L., Lombard, F., Maps, F., Stemmann L., Thiébaut E., Usseglio-Polatera, P., Vogt, M., Laviale, M., & Ayata, S. D., 2021. Functional trait-based approaches as a common framework for aquatic ecologists. Limnology and Oceanography, 66(3), pp 965-994. https://doi.org/10.1002/lno.11655.

Mason, N. W., Mouillot, D., Lee, W. G., & Wilson, J. B., 2005. Functional richness, functional evenness and functional divergence: the primary components of functional diversity. Oikos, 111(1), pp 112-118. https://doi.org/10.1111/j.0030-1299.2005.13886.x.

McLenaghan, N. A., Tyler, A. C., Mahl, U. H., Howarth, R. W., & Marino, R. M., 2011. Benthic macroinvertebrate functional diversity regulates nutrient and algal dynamics in a shallow estuary. Marine Ecology Progress Series, 426, pp 171-184. https://doi.org/10.3354/meps09029.

McLusky, D.S., Elliott, M., 2004. The estuarine ecosystem: ecology, threats and management. OUP Oxford. https://doi.org/10.1093/acprof:oso/9780198525080.001.0001.

Ménesguen, A., 2003. Les marées vertes en Bretagne, la responsabilité du nitrate. https://archimer.ifremer.fr/doc/00000/143/.

Ménesguen, A., and Piriou, J. Y., 1995. Nitrogen loadings and macroalgal (*Ulva sp.*) mass accumulation in Brittany (France). Ophelia, 42(1), 227-237. https://doi.org/10.1080/00785326.1995.10431506

Mouchet, M. A., Villéger, S., Mason, N. W., & Mouillot, D., 2010. Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. Functional Ecology, 24(4), 867-876. https://doi.org/10.1111/j.1365-2435.2010.01695.x.

Mouillot, D., Graham, N. A., Villéger, S., Mason, N. W., & Bellwood, D. R., 2013. A functional approach reveals community responses to disturbances. Trends in ecology and evolution, 28(3), pp 167-177. https://doi.org/10.1016/j.tree.2012.10.004.

Mouillot, D., Mason, W. N., Dumay, O., & Wilson, J. B., 2005. Functional regularity: a neglected aspect of functional diversity. Oecologia, 142, pp 353-359. https://doi.org/10.1007/s00442-004-1744-7.

Mouillot, D., Spatharis, S., Reizopoulou, S., Laugier, T., Sabetta, L., Basset, A., & Chi, T., 2006. Alternatives to taxonomic-based approaches to assess changes in transitional water communities. Aquatic Conservation: Marine and Freshwater Ecosystems, 16(5), pp 469-482. https://doi.org/10.1002/aqc.769.

Naeem, S., 1998. Species redundancy and ecosystem reliability. Conservation biology, 12(1), pp 39-45. https://doi.org/10.1111/j.1523-1739.1998.96379.x.

Naeem, S., Loreau, M., & Inchausti, P., 2002. Biodiversity and ecosystem functioning: the emergence of a synthetic ecological framework. Biodiversity and ecosystem functioning: synthesis and perspectives, 3-11. https://doi.org/10.1111/j.1061-2971.2004.120401.x.

Neumann, H., & Kröncke, I., 2011. The effect of temperature variability on ecological functioning of epifauna in the German Bight. Marine Ecology, 32, pp 49-57. https://doi.org/10.1111/j.1439-0485.2010.00420.x.

Ottersen, G., Planque, B., Belgrano, A., Post, E., Reid, P. C., & Stenseth, N. C., 2001. Ecological effects of the North Atlantic oscillation. Oecologia, 128, pp 1-14. https://doi.org/10.1007/s004420100655.

Petchey, O. L., & Gaston, K. J., 2002. Functional diversity (FD), species richness and community composition. Ecology letters, 5(3), pp 402-411. https://doi.org/10.1046/j.1461-0248.2002.00339.x.

Peterson, G., Allen, C. R., & Holling, C. S., 1998. Ecological resilience, biodiversity, and scale. Ecosystems, 1, pp 6-18. https://doi.org/10.1007/s100219900002.

Pineda, M. C., Duckworth, A., & Webster, N., 2016. Appearance matters: sedimentation effects on different sponge morphologies. Journal of the Marine Biological Association of the United Kingdom, 96(2), pp 481-492. https://doi.org/10.1017/S0025315414001787.

Pineda, M. C., Strehlow, B., Sternel, M., Duckworth, A., Jones, R., and Webster, N. S., 2017. Effects of suspended sediments on the sponge holobiont with implications for dredging management. Scientific reports, 7(1), 4925. https://doi.org/10.1038/s41598-017-05241-z.

Queirós, A. M., Birchenough, S. N., Bremner, J., Godbold, J. A., Parker, R. E., Romero-Ramirez, A., Reiss, H., Solan, M., Somerfield, P. J., Van Colen, C., Van Hoey, G., Widdicombe, S., & Widdicombe, S., 2013. A bioturbation classification of European marine infaunal invertebrates. Ecology and evolution, 3(11), pp 3958-3985. https://doi.org/10.1002/ece3.769.

Quillien, N., Nordström, M. C., Le Bris, H., Bonsdorff, E., & Grall, J., 2018. Green tides on inter-and subtidal sandy shores: differential impacts on infauna and flatfish. Journal of the Marine Biological Association of the United Kingdom, 98(4), pp 699-712. https://doi.org/10.1017/S0025315416002010.

Raffaelli, D., 2000. Interactions between macro-algal mats and invertebrates in the Ythan estuary, Aberdeenshire, Scotland. Helgoland Marine Research, 54, pp 71-79. https://doi.org/10.1007/s101520050004.

Raffaelli, D., 2006. Biodiversity and ecosystem functioning: issues of scale and trophic complexity. Marine Ecology Progress Series, 311, pp 285-294. https://doi.org/10.3354/meps311285.

Rao, C. R., 1982. Diversity and dissimilarity coefficients: a unified approach. Theoretical population biology, 21(1), pp 24-43. https://doi.org/10.1016/0040-5809(82)90004-1.

Reiss, H., Meybohm, K., & Kröncke, I., 2006. Cold winter effects on benthic macrofauna communities in near-and offshore regions of the North Sea. Helgoland Marine Research, 60(3), pp 224-238. https://doi.org/10.1007/s10152-006-0038-3.

Retière, C., 1979. Contribution à la connaissance des peuplements benthiques du golfe Normano-Breton (Doctoral dissertation, Université de Caen, France).

Rhoads, D. C., McCall, P. L., & Yingst, J. Y., 1978. Disturbance and Production on the Estuarine Seafloor: Dredge-spoil disposal in estuaries such as Long Island Sound can be managed in ways that enhance productivity rather than diminish it. American Scientist, 66(5), pp 577-586.

Ricotta, C., & Moretti, M., 2011. CWM and Rao's quadratic diversity: a unified framework for functional ecology. Oecologia, 167, pp 181-188. https://doi.org/10.1007/s00442-011-1965-5.

Robert, A. E., Quillien, N., Bacha, M., Caulle, C., Nexer, M., Parent, B., Garlan, T., & Desroy, N., 2021. Sediment migrations drive the dynamic of macrobenthic ecosystems in subtidal sandy bedforms. Marine Pollution Bulletin, 171, 112695. https://doi.org/10.1016/j.marpolbul.2021.112695.

Schleuter, D., Daufresne, M., Massol, F., & Argillier, C., 2010. A user's guide to functional diversity indices. Ecological monographs, 80(3), pp 469-484. https://doi.org/10.1890/08-2225.1.

Schönberg, C. H. L., 2016. Effects of dredging on filter feeder communities, with a focus on sponges. Report of Theme, 127.

Shojaei, M. G., Gutow, L., Dannheim, J., Schröder, A., and Brey, T., 2021. Long-term changes in ecological functioning of temperate shelf sea benthic communities. Estuarine, Coastal and Shelf Science, 249, 107097. https://doi.org/10.1016/j.ecss.2020.107097.

Simenstad, C., Reed, D., & Ford, M., 2006. When is restoration not?: Incorporating landscape-scale processes to restore self-sustaining ecosystems in coastal wetland restoration. Ecological Engineering, 26(1), pp 27-39. https://doi.org/10.1016/j.ecoleng.2005.09.007.

Statzner, B., & Beche, L. A., 2010. Can biological invertebrate traits resolve effects of multiple stressors on running water ecosystems?. Freshwater Biology, 55, pp 80-119. https://doi.org/10.1111/j.1365-2427.2009.02369.x.

Statzner, B., Resh, V. H., & Roux, A. L., 1994. The synthesis of long-term ecological research in the context of concurrently developed ecological theory: design of a research strategy for the Upper Rhône River and its floodplain. Freshwater biology, 31(3), pp 253-263. https://doi.org/10.1111/j.1365-2427.1994.tb01739.x.

Stubler, A. D., Duckworth, A. R., & Peterson, B. J., 2015. The effects of coastal development on sponge abundance, diversity, and community composition on Jamaican coral reefs. Marine pollution bulletin, 96(1-2), pp 261-270. https://doi.org/10.1016/j.marpolbul.2015.05.014.

Sturbois, A., De Cáceres, M., Sánchez-Pinillos, M., Schaal, G., Gauthier, O., Le Mao, P., Ponsero, A., & Desroy, N., 2021-b. Extending community trajectory analysis: New metrics and representation. Ecological Modelling, 440, 109400. https://doi.org/10.1016/j.ecolmodel.2020.109400.

Sturbois, A., Cormy, G., Schaal, G., Gauthier, O., Ponsero, A., Le Mao, P., Riera, P., & Desroy, N., 2021-a. Characterizing spatio-temporal changes in benthic communities: Taxonomic and functional trajectories of intertidal assemblages in the bay of Saint-Brieuc (English Channel). Estuarine, Coastal and Shelf Science, 262, 107603. https://doi.org/10.1016/j.ecss.2021.107603.

Suding, K. N., Lavorel, S., Chapin Iii, F. S., Cornelissen, J. H., Diaz, S., Garnier, E., Goldberg, D., Hooper, D. U., Jackson, S. S., & Navas, M. L., 2008. Scaling environmental change through the community-level: A trait-based response-and-effect framework for plants. Global Change Biology, 14(5), pp 1125-1140. https://doi.org/10.1111/j.1365-2486.2008.01557.x.

Tompkins-MacDonald, G. J., & Leys, S. P., 2008. Glass sponges arrest pumping in response to sediment: implications for the physiology of the hexactinellid conduction system. Marine Biology, 154, pp 973-984. https://doi.org/10.1007/s00227-008-0987-y.

Törnroos, A., Bonsdorff, E., Bremner, J., Blomqvist, M., Josefson, A. B., Garcia, C., & Warzocha, J., 2015. Marine benthic ecological functioning over decreasing taxonomic richness. Journal of Sea Research, 98, pp 49-56. https://doi.org/10.1016/j.seares.2014.04.010.

van der Linden, P., Marchini, A., Dolbeth, M., Patrício, J., Veríssimo, H., & Marques, J. C., 2016. The performance of trait-based indices in an estuarine environment. Ecological Indicators, 61, 378-389. https://doi.org/10.1016/j.ecolind.2015.09.039.

van der Linden, P., Patrício, J., Marchini, A., Cid, N., Neto, J. M., & Marques, J. C., 2012. A biological trait approach to assess the functional composition of subtidal benthic communities in an estuarine ecosystem. Ecological Indicators, 20, pp 121-133. https://doi.org/10.1016/j.ecolind.2012.02.004.

Veiga, P., Redondo, W., Sousa-Pinto, I., & Rubal, M., 2017. Relationship between structure of macrobenthic assemblages and environmental variables in shallow sublittoral soft bottoms. Marine Environmental Research, 129, pp 396-407. https://doi.org/10.1016/j.marenvres.2017.07.002.

Veríssimo, H., Bremner, J., Garcia, C., Patrício, J., van der Linden, P., & Marques, J. C., 2012. Assessment of the subtidal macrobenthic community functioning of a temperate estuary following environmental restoration. Ecological Indicators, 23, pp 312-322. https://doi.org/10.1016/j.ecolind.2012.04.020.

Villéger, S., Mason, N. W., & Mouillot, D., 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. Ecology, 89(8), pp 2290-2301. https://doi.org/10.1890/07-1206.1.

Walker, B. H., 1992. Biodiversity and ecological redundancy. Conservation biology, 6(1), pp 18-23. https://www.jstor.org/stable/2385847.

Ward Jr, J.H., 1963. Hierarchical grouping to optimize an objective function. Journal of the American statistical association 58, 236–244. Whittaker, R. H., 1972. Evolution and measurement of species diversity. Taxon, 21(2-3), pp 213-251. https://doi.org/10.1080/01621459.1963.10500845.

Weigel, B., Blenckner, T., & Bonsdorff, E., 2016. Maintained functional diversity in benthic communities in spite of diverging functional identities. Oikos, 125(10), pp 1421-1433. https://doi.org/10.1111/oik.02894.

Whomersley, P., Huxham, M., Bolam, S., Schratzberger, M., Augley, J., & Ridland, D., 2010. Response of intertidal macrofauna to multiple disturbance types and intensities–an experimental approach. Marine environmental research, 69(5), pp 297-308. https://doi.org/10.1016/j.marenvres.2009.12.001.

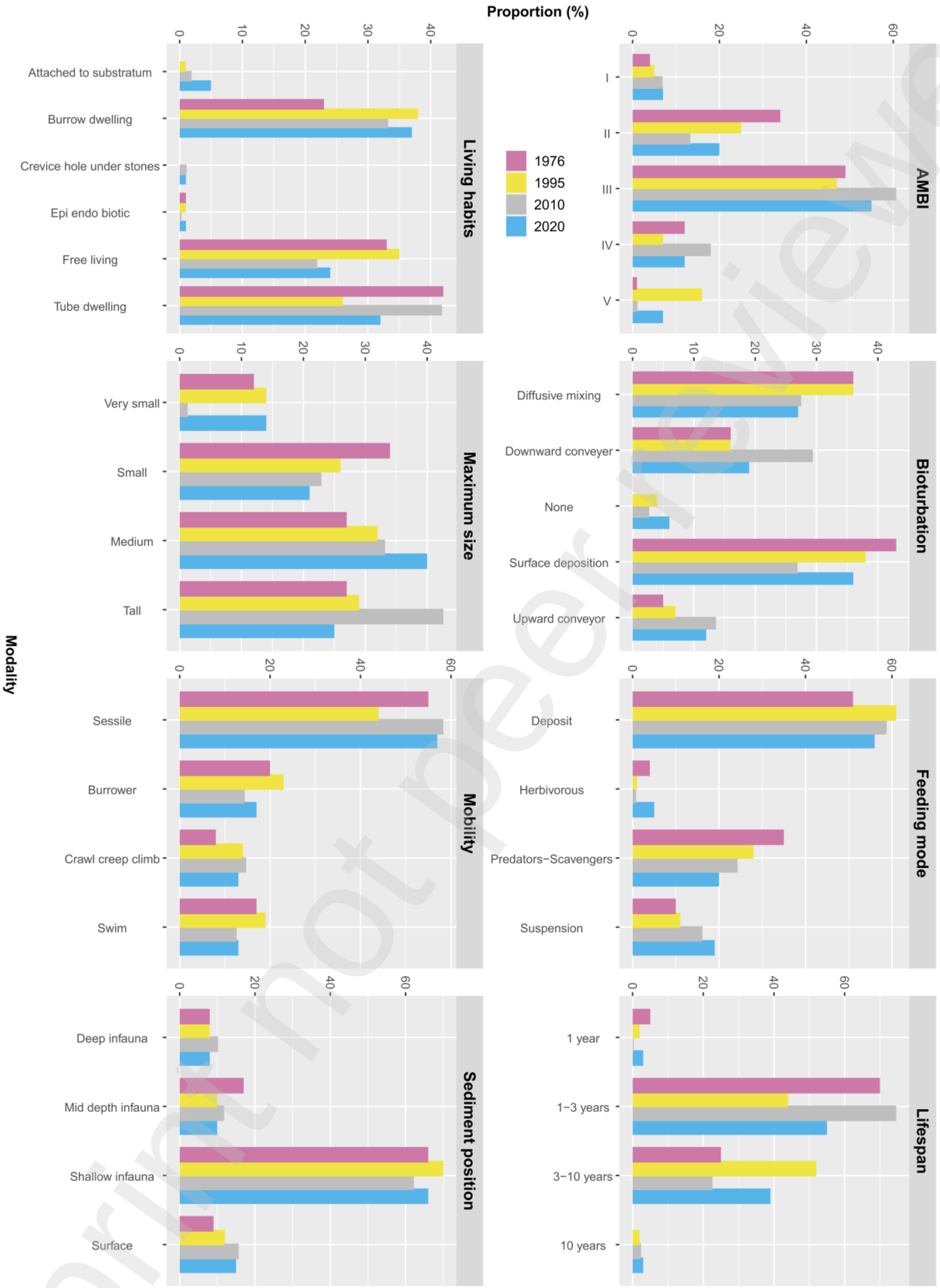
Wilson, R. J., Gutiérrez, D., Gutiérrez, J., Martínez, D., Agudo, R., & Monserrat, V. J., 2005. Changes to the elevational limits and extent of species ranges associated with climate change. Ecology letters, 8(11), pp 1138-1146. https://doi.org/10.1111/j.1461-0248.2005.00824.x.

Wong, M. C., & Dowd, M., 2015. Patterns in taxonomic and functional diversity of macrobenthic invertebrates across seagrass habitats: a case study in Atlantic Canada. Estuaries and Coasts, 38, pp 2323-2336. https://www.jstor.org/stable/45277402.

Worm, B., Barbier, E. B., Beaumont, N., Duffy, J. E., Folke, C., Halpern, B. S., & Watson, R., 2006. Impacts of biodiversity loss on ocean ecosystem services. science, 314(5800), pp 787-790. https://doi.org/10.1126/science.113229.

WoRMS Editorial Board, 2023. World Register of Marine Species.

Supplementary material



Annex 1: Profiles of functional traits (including the 36 modalities) at the scale of the uptream part in 1976, 1995 ,2010 and 2020.