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Long-term changes of benthic communities of the Rance maritime basin

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ABSTRACT

The monitoring and quantification of ecological changes following the construction of the Rance Tidal Power Plant (RTPP) have been extensively discussed in the past and provide us with a valuable reservoir of knowledge on restoration ecology. The Community Trajectory Analysis Framework was used in conjunction with conventional methods to analyse, characterize, and represent long-term changes in soft sediments in the Rance basin (Normano-Breton Gulf) sampled in 1976, 1995, 2010 and 2020. A total of 483 species have been identified since 1976 on soft bottoms. At the basin scale, a group of six species were among the most abundant in each study, revealing a strong impact of dominant species on community structuring in the basin. Benthic assemblages continue to structure themselves nearly 50 years after the construction of the RTPP. The taxonomic trajectories of benthic assemblages were studied at both the basin and local scales. Mainly in response to sedimentological changes, ecological trajectories showed temporal variability upstream and downstream. Local variations in species abundances also contributed to differences in composition observed at the assemblage scale. After a slowdown in the colonization of bottoms in the '90s, the number of species experienced a significant increase in 2020, linked to the progression of marine waters, sediment redistribution, the habitat heterogeneity, and the dynamics of seagrass, which have created complex habitat architecture.

1. Introduction

Estuaries are typified by high spatio-temporal variability in physico-chemical, morphological, and hydrological characteristics (Carter and Pritchard, 1988; Ysebaert and Herman, 2002) as well as a mosaic of benthic habitats (Pelletier et al., 2021), including vulnerable habitats (e.g. seagrass meadows). Estuaries are considered among the most productive environments on the planet (Kennish, 2002; McLusky and Elliott, 2004) and offer a large range of ecosystem services (Basset et al., 2013; Yoskowitz and Russell, 2015; Yee et al., 2019). Due to their location at the sea-land interface, they are exposed to a wide variety of anthropogenic sources of disturbances such as coastal urbanisation, general eutrophication, various contaminants, marine aggregate extraction, fishing activities, etc (Wolanski et al., 2001; Thomas et al., 2002; Tönis et al., 2002; Van Der Wal et al., 2002; Lesourd et al., 2003; Hossain et al., 2004; Blott et al., 2006; Wolanski, 2006; Morris and Mitchell, 2013; Pye and Blott, 2014). As for most of marine environments, the increase in sea level and the global warming are also a major threat for estuaries ecosystems (Church et al., 2011; Levitus et al., 2012). A gradient in both the number and the intensity of anthropogenic pressures is generally observed between the upstream and the downstream limits of the estuaries but how pressures interact with each other is still debated. Together, all these pressures could dramatically alter the biotic and abiotic environment of the estuaries over the long-term.

The Rance basin (northern Brittany, France) is characterized by the presence of a tidal power station, built between 1963 and 1966, which can produce energy during both flood and ebb. The Rance tidal power plant (RTPP) remained the largest tidal power plant in the world for 45 years (Pelc and Fujita, 2002) and is currently the second-largest operational tidal power plant (Wang and Wang, 2019). The RTPP has a strong influence on the environmental characteristics of the Rance basin, by reducing the tidal range, by inducing an offset of water mass immobilisation periods, by inducing a 4m increase of the water level (which resulted in a reduction by 70 %–50 % of the intertidal area) and by increasing the current speed (Desroy, 1998). The RTPP now regulates the natural flow of water with, as its main characteristics, a distortion of tidal waves, as also observed by Angeloudis and Falconer (2017) in the Severn estuary and Bristol Channel (UK) and an important stability of

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water levels since the 1990s (Desroy, 1998).

Due to its history, the RTPP provides a wonderful opportunity to investigate the dams-related impacts on the benthic communities. First studies addressing this issue have been performed at the end of the 70's thanks to a qualitative survey (Retière, 1979). This author demonstrated that, after a quasi-total defaunation, a new equilibrium gradually established after the construction of the dam. In 1971, which was five years after the construction, he reported a re-colonization of the seabed by benthic organisms, enabled by the biological permeability of the dam (Retière, 1979; Clavier et al., 1983). Despite the limited number of species observed in 1971 (114), the structuration of benthic organisms into benthic assemblages was already detectable in relation with the seabed nature. Note that a Before-After-Controlled-Impact (BACI) study was impossible to carry out due to the lack of available data before the construction of the RTPP. In 1976, Retière (1979) observed that the benthic ecosystem functioning presented its own variability, independent of the initial stress generated during the construction. Benthic communities of the Rance basin were then revisited in 1995 by Desroy (1998) who found a very similar structure of benthic assemblages between 1976, suggesting that a mature state was reached at the scale of the basin. Nevertheless, local changes were visible for certain assemblage sub-units, in response to siltation in the upstream part of the basin,

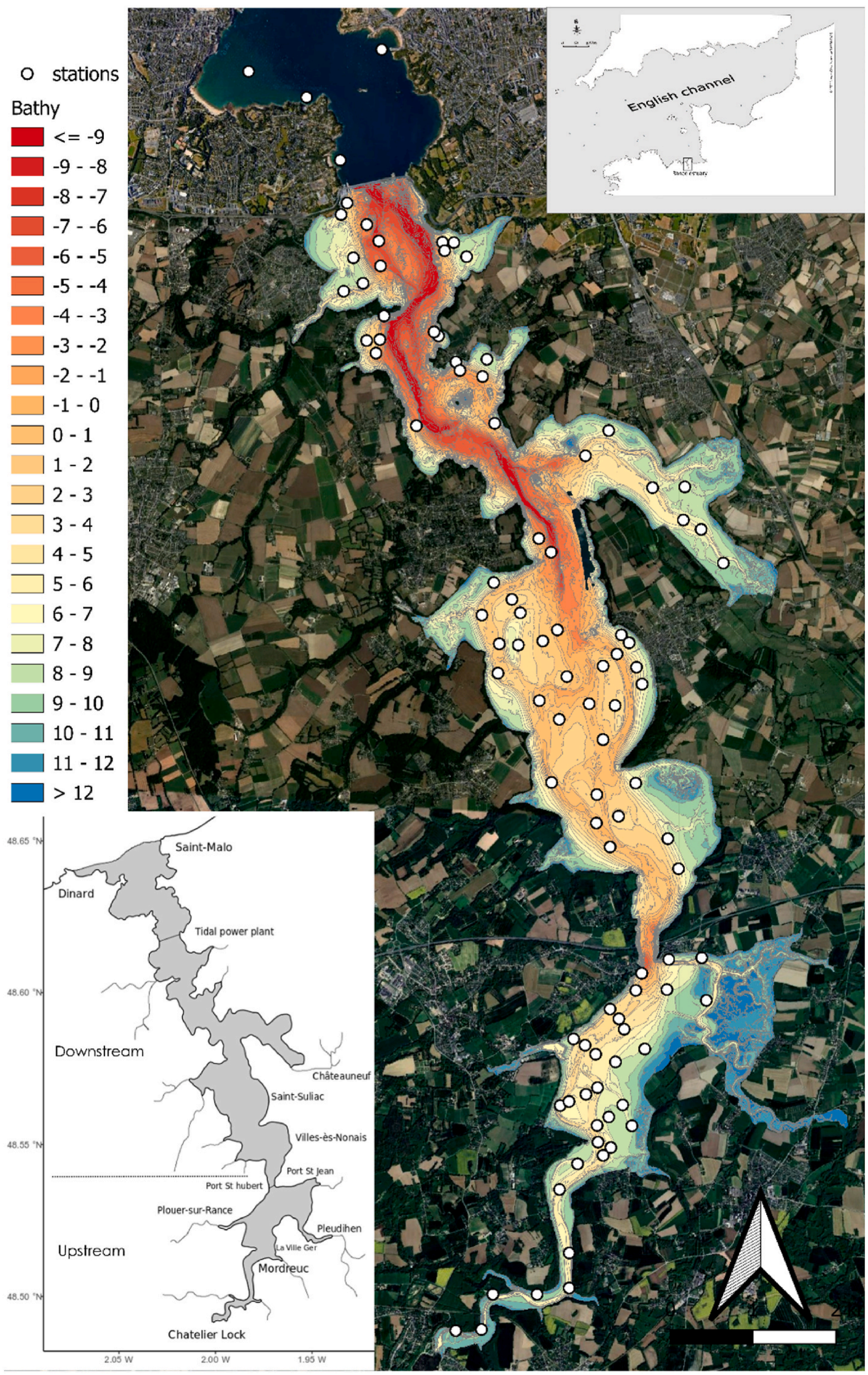

Fig. 1. Bathymetry (m) of the Rance basin during the neap spring tide as well as the location of the sampling stations in 2020.

the adjustment of the water level in the basin and the proliferation of introduced species *Crepidula fornicata* (Desroy and Retière, 2003). This warrants further investigation to determine whether these local changes have persisted in recent years.

Based on an extension of the Community Trajectory Analysis (CTA; De Cáceres et al., 2019; Sturbois et al., 2021a), as well as the re-sampling of the 99 stations in 2020 in the Rance basin, the present study provides data from 84 stations common to the different surveys (i) an update information about the distribution of benthic communities within the Rance basin and (ii) a finer insight about spatio-temporal changes that occurred during the 54 years of commissioning of the RTPP.

2. Material and methods

2.1. Study area

The Rance basin (Brittany, France) is located on the southwestern coast of the English Channel (Fig. 1). The basin is a narrow, steep-sided ria (*sensu* Evans and Prego, 2003) which can be divided into two distinctive parts on either side of the Chatelier lock, one marine/-brackish and the other fresh (not investigated in this study).

The brackish/marine part extends over 22 km^2 downstream of the lock, up to the tidal plant. The maximum depth occurs in the channel, from the dam to the latitude of Chateauneuf (13.50m during the neap spring tide). From Chateauneuf to Port St Hubert, depth decreases to 1–3m below the spring tide level. Nevertheless, a depression of 8–9m in depth exists between Port St Hubert and Port St Jean. On average, the depth is lower in the upstream part of the Rance basin compared to the downstream part. Coves hosting large intertidal mudflats are mostly found on the eastern banks as well as in the southernmost part of the basin.

There are longitudinal and transverse granulometric gradients in the Rance basin. From the central channel towards the banks, the gravel forming the channel bottom gradually gives way to coarse sands, followed by the finer sands becoming silted in the lateral coves. From downstream to upstream, sediments become finer in a succession of coarse and medium sands, finer sands that become silted.

2.2. Data collection

Quantitative data on macrobenthic taxa from the 1976 (130 stations), 1995 [140 stations (see Desroy and Retière, 2003) for details] and 2010 surveys (54 stations located only in the upstream part of the basin, unpublished data) have been gathered and compiled from existing database.

In 2020, 99 stations (95 inside the basin and 4 outside) were resampled (Fig. 1). Among them, 84 stations were common with historical surveys carried out in 1976 and 1995 (see Desroy and Retière, 2003 for details) and 32 stations were common with the survey conducted in 2010, in the upstream area. With the exception of the grabs, which remain similar in depth penetration and sampling surface, the sampling protocol remained unchanged between the four periods: two replicates per station were sampled in spring, with a 0.1 m^2 Smith MacIntyre (1976, 1995, 2010) and day grab (2020). Samples were gently sieved on board through a 1 mm circular mesh and were fixed with a 4–5 % buffered formaldehyde solution before further processing. In the laboratory, samples were washed, and benthic organisms were sorted from the sedimentary matrix, identified to the lowest taxonomic levels as possible (usually species level) and counted.

One additional sample was collected for each of the 99 stations in order to assess the sedimentary characteristics. Once again, the protocol was similar to that of historical sedimentological studies, performed in 1994 (Bonnot-Courtois et al., 1995) and 2010 [unpublished data (no sediment sample in 1976)]. Grain size analyses were performed using a standardized AFNOR set of sieves. The sediment retained on each sieve was weighed with a 1 mg accuracy. The seabed nature at each station has been defined by combining the Folk and Ward (1957) classification with information about the presence of biogenic elements (e.g. shell debris) from photographs taken *in situ*.

2.3. Data analysis

Species names were harmonised by matching taxa within the World Register of Marine Species dataset (WoRMS Editorial Board, 2023) to avoid biases due to taxonomic evolution. When species have been split into two or more sister species or in case of doubtful species, the taxonomic sufficiency principle was applied and taxa were considered at the genus level.

After Hellinger's transformation of the dataset (as recommended by Legendre and Gallagher, 2001), benthic assemblages were identified using an Ascending Hierarchical Classification (AHC) with the Euclidean distance and the Ward's method of clustering (Ward Jr, 1963). Indicator species (defined as species present in a given assemblage and absent from the others) for each group were identified using the Indicator value (IndVal) method proposed by Dufrêne and Legendre (1997) and calculated as the product of the relative frequency and relative average abundance in clusters. The IndVal index measures the association between a species and each site group and then looks for the group corresponding to the highest association value. The statistical significance of this relationship was tested using a permutation test (999 random permutations). Each assemblage was also characterized by calculating the mean (±standard-deviation) number of individuals per station but also according to the mean species richness (S), Shannon-Weaver index (H′), Simpson index (D) and Pielou's evenness (J) per station. Differences between assemblages in the values of univariate descriptors were tested using Analysis of Variance tests (ANOVAs). In case of significant differences (p-value$<$0.05), the Tukey's post-hoc test was performed to identify between which pair of assemblages the differences occurred. Two-way ANOVA tests were also performed with year and zone (downstream *vs* upstream) as explanatory factors to assess spatio-temporal variation in univariate descriptors.

Community trajectories Analysis (CTA) was performed to study and represent the temporal changes by considering all dimensions in the multivariate space. A set of six univariate indicators was calculated in order to summarize the temporal changes in the species composition of each sampling station, between 1976, 1995, 2010 (for upstream stations only) and 2020. The length of the segments represents the distance between two consecutive surveys. In the present study, S1 provides information about changes that occurred between 1976 and 1995, and S2 between 1995 and 2020. The trajectory path (TP) was calculated as the sum of the segment lengths (S1 + S2). The net change (NC) was calculated between 1976 and 2020, considering the 1976 data set as an initial state. NC indicates the overall change that occurred during the study. Recovering and departing consecutive trajectory segments (RDT) were identified by subtracting NC_{n-1} from NC_n (Sturbois et al., 2021a). The RDT take positive values in case of recovery patterns and negative values for departing patterns.

Groups of ecological trajectories considering the entire period of time (1976–2020) were identified. To address this issue, Directed Segment Path Dissimilarity (De Cáceres et al., 2019) have been computed with results from the CTA as input data. Once calculated, the dissimilarities were used to perform an AHC (with the Ward's aggregation method; Ward Jr, 1963). Trajectory groups were characterized based on their mean (± standard deviation) values of TP, NC and RDT values and inter-groups differences were assessed using ANOVA tests and Tukey's post-hoc analyses. The zone (upstream *vs* downstream) was also used as explanatory variable in these analyses. Finally, species responsible for the differences between successive surveys were identified, independently for each trajectory group, via Simper tests (Clarke, 1993).

Statistical analyses were performed using R statistical software (R core team, 2023). The CTA was run using the "ecotraj" package (De

Cáceres et al., 2019; Sturbois et al., 2021a) whereas the "labdsv" (Roberts and Roberts, 2016) and the "vegan" (Oksanen et al., 2019) packages were used to perform the IndVal and the Simper test.

3. Results

3.1. General characteristics of the macrobenthic fauna

All surveys considered, 483 taxa were recorded within the Rance basin. Annelids represented 72 % of the organisms collected during successive surveys. Among them, *Melinna palmata* (20 % of the catches), *Chaetozone* sp. (12 %), *Euclymene oerstedii* (8 %), *Leiochone leiopygos* (6 %) and *Ampharete baltica* (5 %) were prevalent. To a lesser extent, macrobenthic organisms were consisted of molluscs (10 % of the catches) such as *Peringia ulvae* (3 %) and *Abra alba* (2 %), and crustaceans including *Ampelisca tenuicornis* (5 %).

A total of 122 species were common between 1976 and 1995 datasets, of 111 between 1976 and 2020 datasets, and of 145 between 1995 and 2020 datasets. In the upstream area, 28 taxa were common across all datasets (1976, 1995, 2010 and 2020). The number of rare species (present in less than 5 % of stations) recorded at the basin scale has increased over time from, 60 % of species in 1976 to 68 % in 1995 and 73 % in 2020.

3.2. Characteristics of benthic assemblages

The AHC, drawn from the whole dataset, revealed 7 assemblages of species, distributed roughly according to both an upstream/downstream and depth gradient (Fig. 1; Fig. 2). The key characteristics of each assemblage, including the indicator species, are concisely summarized in Table 1.

Assemblage 1 was found only in 2020. It was mainly located in the upstream part of the basin, on muddy fine sands and was characterized by 29 indicator species. The dominant species included *Leiochone leiopygos* (160 ± 250 ind.0.1 m^{-2}), *Melinna palmata* (115 ± 112 ind.0.1 m^{-2}), *Phoronis psammophila* (103 ± 267 ind.0.1 m^{-2}), *Euclymene oerstedii* (87 ± 93 ind.0.1 m^{-2}) and *Ampelisca tenuicornis* (77 ± 99 ind.0.1 m^{-2}). Assemblage I was the second assemblage in terms of species richness (50 ± 15 species.0.1 m^{-2}), Shannon's diversity (2.45 ± 0.44), Simpson diversity (0.82 ± 0.08) and exhibited high values of Pielou's

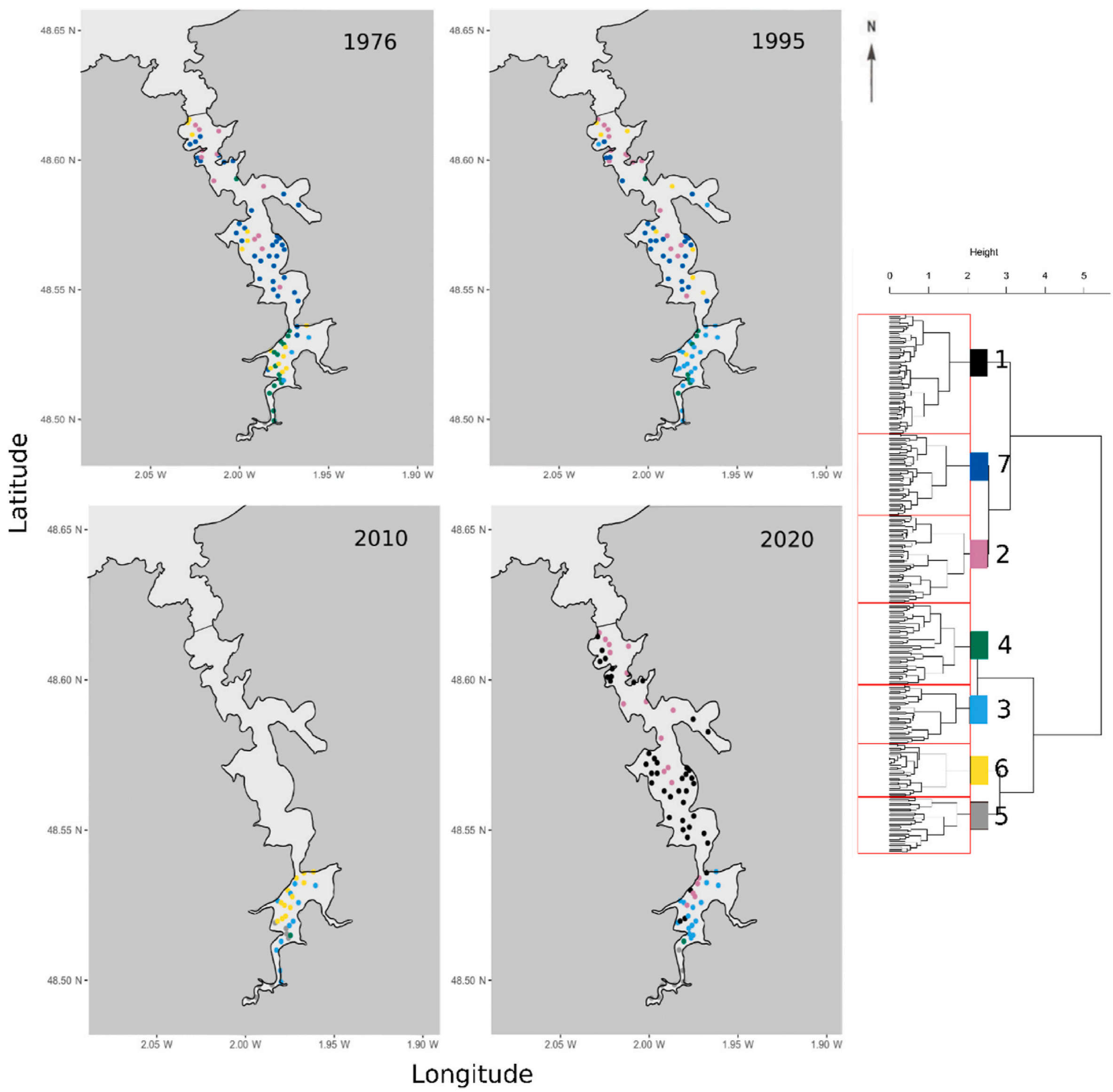

Fig. 2. Spatial distribution of benthic assemblages identified with Hierarchical Cluster Analysis performed on 84 stations common to 1976, 1995 and 2020 datasets and 32 stations (2010 dataset).

Table 1
Characteristic of the seven macrobenthic assemblage found within the Rance basin, whatever the year. Mean ± standard-deviation of the species richness (S), Shannon's diversity (H), Simpson's diversity and Pielou's evenness are indicated. The five main indicator species, as defined thanks to the IndVal index, as well as the five dominant species in term of number of individual are provided.

Assemblage	Total abundance (ind.0.1m$^{-2)}$	S	H'	D	J	Number of indicator species	Main indicator species	Dominant species
1	966 ± 811	50 ± 15	2.45 ± 0.44	0.82 ± 0.08	0.63 ± 0.09	29	*Leiochone leiopygos, Nucula hanleyi, Paucibranchia bellii, Phoronis psammophila, Aponuphis ornata*	*Leiochone leiopygos, Melinna palmata, Phoronis psmamophila, Euclymene oerstedii, Ampelisca tenuicornis*
2	669 ± 354	55 ± 17	2.7 ± 0.41	0.86 ± 0.07	0.68 ± 0.09	37	*Caulleriella alata, Pista cristata, Acromegalomma veiculosum, Syllis* sp., *Calyptraea chinensis*	*Chaetozone* sp., *Mediomastus fragilis, Caulleriella alata, Melinna palmata, Cirriformia tentaculata*
3	576 ± 1043	17 ± 9	1.71 ± 0.55	0.70 ± 0.17	0.67 ± 0.18	5	*Peringia ulvae, Abra tenuis, Cerastoderma edule, Manayunkia aesturina, Gammarus duebeni*	Oligochaeta, *Peringia ulvae, Ampharete baltica, Abra tenuis, Heteromastus filiformis*
4	42 ± 47	9 ± 4	1.66 ± 0.40	0.73 ± 0.13	0.79 ± 0.13	5	*Nephtys cirrosa, Goniada emerita, Saccocirrus papillocercus, Pontocrates norvegicus, Armandia polyophtalma*	*Abludomelita gladiosa, Abludomelita obtusata, Abra alba, Abra tenuis, Acanthochitona fascicularis*
5	75 ± 72	8 ± 5	1.42 ± 0.50	0.64 ± 0.14	0.72 ± 0.12	2	*Cyathura carinata, Idotea chelipes*	*Hediste diversicolor, Cyathura carinata, Abra tenuis, Scrobicularia plana, Melinna palmata*
6	439 ± 596	16 ± 10	1.53 ± 0.54	0.65 ± 0.18	0.65 ± 0.17	0	No indicator species	*Pygospio elegans, Ampharete baltica, Melinna palmata, Chaetozone* sp., *Nephtys hombergii*
7	789 ± 416	34 ± 11	2.0 ± 0.3	0.78 ± 0.09	0.61 ± 0.07	9	*Nucula nitidosa, Ampelisca brevicornis, Aora typica, Cerianthus lloydi, Pandora albida*	*Melinna palmata, Chaetozone* sp., *Euclymene oerstedii, Ampelisca tenuicornis, Nephtys hombergii*

evenness (0.63 ± 0.09). It was also the assemblage with the highest mean abundance (966 ± 811 ind.0.1 m^{-2}).

Assemblage 2 was located in areas of high hydrodynamic (channels and constriction zones) with coarse sands, sometimes silted. It was characterized by 37 indicator species. The five principal dominant species in term of density were *Chaetozone* sp. (126 ± 135 ind.0.1 m^{-2}), *Mediomastus fragilis* (68 ± 138 ind.0.1 m^{-2}), *Caulleriella alata* (51 ± 51 ind.0.1 m^{-2}), *Melinna palmata* (26 ± 33 ind.0.1 m^{-2}) and *Cirriformia tentaculata* (26 ± 95 ind.0.1 m^{-2}). Assemblage 2 recorded the highest values of species richness (55 ± 17), Shannon's diversity (2.7 ± 0.41) and Simpson's diversity (0.86 ± 0.07). It also showed high values of mean abundance (669 ± 354 ind.0.1 m^{-2}) and Pielou's evenness (0.68 ± 0.09).

Assemblage 3 occurs in muddy fine sands exposed to desalination and/or exondation. It was mostly present upstream and characterized by 5 indicator species. Assemblage 3 was also typified by high densities of oligochaeta (179 ± 545 ind.0.1 m^{-2}). To a lesser extent, it was also dominated by *Peringia ulvae* (92 ± 346 ind.0.1 m^{-2}), *Ampharete baltica* (39 ± 89 ind.0.1 m^{-2}), *Abra tenuis* (31 ± 72 ind.0.1 m^{-2}) and *Heteromastus filiformis* (23 ± 72 ind.0.1 m^{-2}). This assemblage showed relatively high values of diversity (total abundance = 576 ± 1043 ind.0.1 m^{-2}; S = 17 ± 9; H = 1.71 ± 0.55; D = 0.70 ± 0.17 and J = 0.67 ± 0.18).

Assemblage 4 was also found in the upstream area, where muddy to clean fine sands were subjected to desalination. The five dominant species in term of density were *Abludomelita gladiosa* (6 ± 7 ind.0.1 m^{-2}), *Abludomelita obtusata* (5 ± 25 ind.0.1 m^{-2}), *Abra alba* (5 ± 12 ind.0.1 m^{-2}), *Abra tenuis* (3 ± 7 ind.0.1 m^{-2}) *and Acanthochitona fascicularis* (3 ± 3 ind.0.1 m^{-2}). This assemblage displayed a very low species richness (9 ± 4 species.0.1 m^{-2}) but relatively high values of Shannon's diversity (1.66 ± 0.40), Simpson's diversity (0.73 ± 0.13) and Pielou's eveness (0.79 ± 0.13).

Assemblage 5 was found on subtidal muds subjected to desalination. It was mainly observed in a narrow channel presents just downstream of the Chatelier lock. It was characterised by 2 indicator species only. It was numerically dominated by *Hediste diversicolor* (20 ± 30 ind.0.1 m^{-2}), *Cyathura carinata* (7 ± 21 ind.0.1 m^{-2}), *Abra tenuis* (6 ± 29 ind.0.1 m^{-2}), *Scrobicularia plana* (6 ± 12 ind.0.1 m^{-2}) and *Melinna palmata* (5 ± 16 ind.0.1 m^{-2}). This assemblage exhibited an oligospecific fauna with the lowest values of species richness (8 ± 5), Shannon's diversity (1.42 ± 0.50), Simpson's diversity (0.64 ± 0.14) recorded in the present study. Total abundance (75 ± 72 ind.0.1 m^{-2}) and Pielou's evenness were also low (0.72 ± 0.12).

Assemblage 6 was present with muddy fine sands in some downstream coves and the upstream area. There was no indicator species for this assemblage. The five dominant species in term of density were the polychaetes *Pygospio elegans* (123 ± 436 ind.0.1 m^{-2}), *Ampharete baltica* (84 ± 166 ind.0.1 m^{-2}), *Melinna palmata* (83 ± 160 ind.0.1 m^{-2}), *Chaetozone* sp. (38 ± 89 ind.0.1 m^{-2}) *and Nephtys hombergii* (22 ± 33 ind.0.1 m^{-2}). This assemblage was also typified by low values of biodiversity, with a species richness of 16 ± 10 species.0.1 m^{-2}, a Shannon's diversity of 1.53 ± 0.54, a Simpson's diversity equivalent to 0.65 ± 0.18 and a Pielou's evenness equal to 0.65 ± 0.17. It displayed intermediate values of total abundance with 439 ± 596 ind.0.1 m^{-2}.

Assemblage 7 was recorded in intertidal muddy fine sands. It was characterized by 9 indicator species. The most abundant species were *Melinna palmata* (282 ± 176 ind.0.1 m^{-2}), *Chaetozone* sp. (97 ± 104 ind.0.1 m^{-2}), *Euclymene oerstedii* (93 ± 73 ind.0.1 m^{-2}), *Ampelisca tenuicornis* (56 ± 85 ind.0.1 m^{-2}) and *Nephtys hombergii* (49 ± 21 ind.0.1 m^{-2}). This assemblage showed intermediate values of biodiversity (S = 34 ± 11; H = 2.0 ± 0.3; D = 0.78 ± 0.09 and J = 0.61 ± 0.07) but high values of abundance with 789 ± 416 ind.0.1 m^{-2}.

3.3. Spatio-temporal variations

3.3.1. Spatio-temporal variations of univariate descriptors

The Anova revealed significant variations of the univariate descriptors in relation to the zone (not shown). This marginal effect was characterized by higher values in the downstream part of the basin than in the upstream part (see Fig. 3 for species richness). Significant inter-

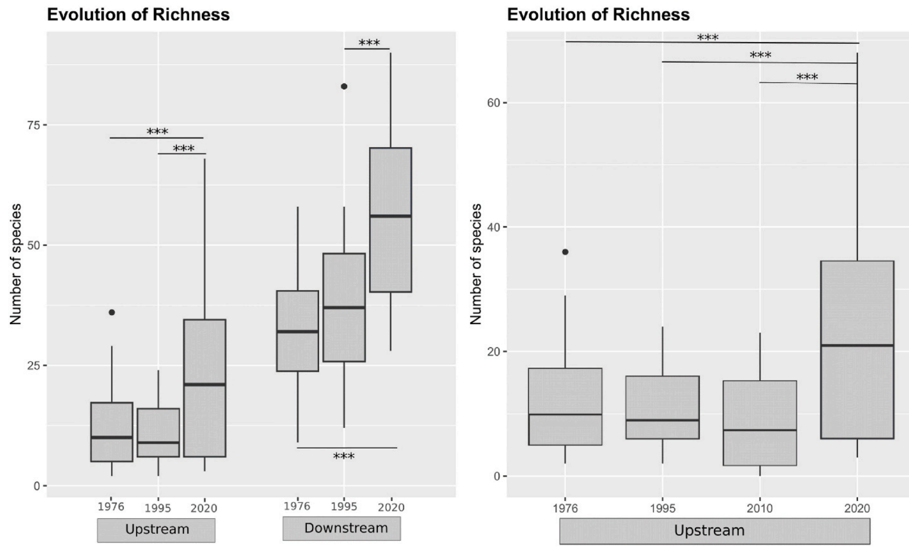

Fig. 3. Variation of species richness in relation with the zone (upstream vs downstream part of the basin) and the year. A focus on the upstream part of the basin is provided by the rich panel, including the sampling performed in 2010. Stars denote the p-value of Tukey's HSD post-hoc performed after an Anova: ***: p-value <0.001; **: p-value <0.01; *: p-value <0.05.

annual variations have also been observed for the species richness (p-value<0.001), Shannon's diversity (p-value<0.001) and Simpson's diversity (p-value<0.01) whereas total abundance and Pielou's evenness remained relatively stable over time. Indeed, these descriptors have shown a continuous increase within the basin over the years. Mean species richness increased from 24.9 ± 14.6 species.0.1 m^{-2} in 1976, to 26.6 ± 17.3 species.0.1 m^{-2} in 1995 and showed a sharp increase in 2020 with 43.8 ± 24.2 species.0.1 m^{-2}. Shannon diversity showed a similar pattern, passing from 1.86 ± 0.57 to 1.97 ± 0.63 between 1976 and 1995 and reached 2.27 ± 0.69 in 2020. Simpson diversity increased from 0.73 ± 0.16 to 0.75 ± 0.16 and 0.79 ± 0.15 between these three periods. The total abundance remained relatively constant between 1976 (624.56 ± 560.85 ind.0.1 m^{-2}) and 1995 (598.73 ± 828.83 ind.0.1 m^{-2}) but increased in 2020 (5.91 ± 693.7 ind.0.1 m^{-2}) although this effect was not statistically significant.

Temporal variations were not the same between the upstream and the downstream part of the basin, as revealed by a significant interaction between the factors year and zone in the Anova for all the indicators except for the total abundance. When looking at the ratio of univariate descriptor values between 2020 and 1995, almost all stations showed a substantial increase in biodiversity. Stations located in the channel of the upper part of the basin, as well as certain stations located in downstream coves, experienced the highest increase in biodiversity (see Fig. 4 for the species richness).

In the upstream area, the comparison of the 32 stations sampled between the different surveys revealed a recent significant increase in species richness (Fig. 3) in 2020 (Anova, p-value<0.001). Indeed, while the number of species remained around 15 species per 0.1 m^2 in 1976, 1995, and 2010, it reached 25 ± 19 species per 0.1 m^2 in 2020.

3.3.2. Spatio-temporal variations in the species composition

The distribution of macrobenthic assemblages remained relatively stable between 1976, 1995 and 2010 at the scale of the basin (Fig. 2). Nevertheless, some local variations deserve to be highlighted. Indeed, the assemblage 1 was found only in 2020, encompassing most of the downstream stations and two upstream stations. It replaced the assemblages 6 and 7 found in 1976 and 1995 at some stations. The assemblage 2 exhibited a strong extension of its surface. In particular, it spread toward the upstream channel where it was absent in previous years. Conversely, the spatial extent of the assemblage 4 decreased over time: whereas it included about half of the upstream stations in 1976, it was only represented by one station in 2010 and 2020. Assemblage 6 was not recorded in 2020 whereas the assemblage 7 was present throughout the whole basin in 1976 and was restricted to some stations located downstream of Port-Saint-Jean constriction in 1995 and 2010. This assemblage disappeared in 2020.

Four groups of ecological trajectories have been identified from the Community Trajectory Analysis (Fig. 5). As seen in Table 2, these groups differed in their values of NC (Anova, p-value<0.01) and TP (p-value<0.001) but displayed similar RDT values (p-value>0.05).

Group 1 was composed of 19 stations mainly located at the edge of the channel upstream and downstream. This group had the highest NC (13.58 ± 6.48; Table 2) and the second longest average TP (15.81 ± 6.26). Negative RDT values denoted a departing pattern of the species composition in these stations between 1976 and 2020. Changes in species composition were mostly due to a decrease in the abundance of *Melinna palmata*, *Ampharete baltica*, and *Pista cristata* between 1976 and 1995 (Table 3) and to an increase in the abundance of *Cirriformia tentaculata* and *Heteromastus filiformis.* The main differences between 1995 and 2020 related to an increase in the abundance of *Mediomastus fragilis*, *Caulleriella alata*, *Phoronis psammophila*, *Scalibregma celticum* and *Aphelochaeta marioni.*

Group 2 was composed of 15 stations, which regrouped intertidal stations located all along the basin in mudflats. This group had the longest average trajectory path (18.94 ± 6.14) and the second highest NC values (13.42 ± 6.31). Changes were mostly due to a decrease in the abundance of *Melinna palmata, Pygospio elegans, Chaetozone* sp., and *Nephtys hombergii* between 1976 and 1995, whereas the abundance of oligochaeta increased. The latter considerably declined between 1995 and 2020 and were replaced by *Leiochone leiopygos*, *Ampelisca tenuicornis*, *Phoronis psammophila* and *Abra alba* whose abundance increased.

Group 3 comprised 30 stations located exclusively in the downstream basin, specifically in its southernmost region. This group had intermediate lowest values of NC (13.19 ± 6.34) and TP (12.2 ± 6.2). A recovery pattern occurred for almost all the stations as regards negative RDT values. Changes in species composition were mainly due to a decrease in the abundance of *Melinna palmata*, *Chaetozone* sp., *Nephtys hombergii* and *Lanice conchilega* between 1976 and 1995. Conversely, the abundance of *Galathowenia oculata* increased during this interval but declined in 2020. Conversely, the abundance of *Leiochone leiopygos*, *Ampelisca tenuicornis*, *Phoronis psammophila* and *Abra alba* also increased

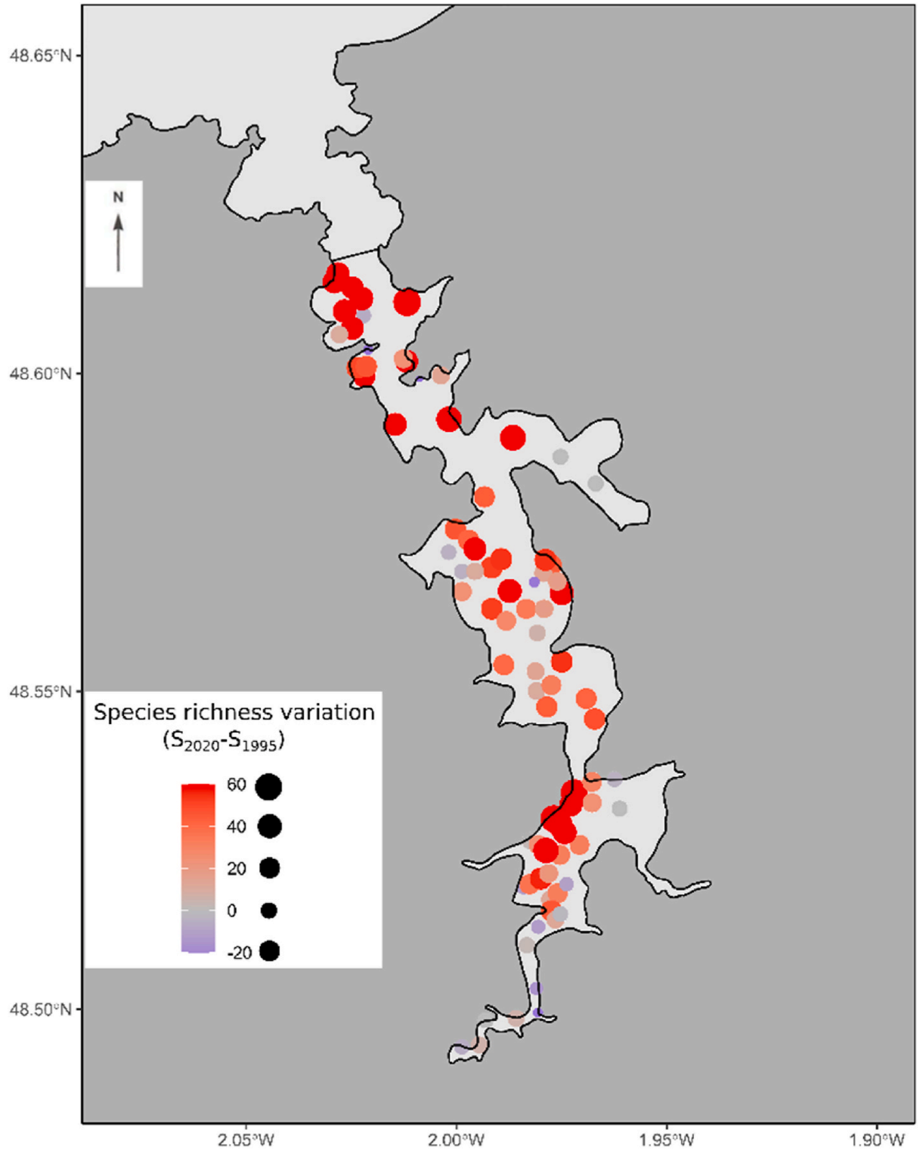

Fig. 4. Difference of species richness between the 1995 and 2020 surveys at each sampling station.

between 1995 and 2020.

Group 4 included 20 stations distributed in the upstream area, on subtidal mudflats subjected to desalination. This group was the most stable, as revealed by the lowest values of NC (12.25 ± 6.3), TP (9.75 ± 724) and RDT (0.29 ± 2.81). Changes were mostly due to an increase in the abundance of *Cerastoderma edule*, *Jassa falcata*, *Mysida* sp., *Cereus pedunculatus* and *Manayunkia aestuarina* between 1976 and 1995. Some species considerably declined between 1995 and 2020: the oligochaeta, *Peringia ulvae*, *Cerastoderma edule* and *Jassa falcata.* A slight increase in the abundance of *Ruditapes philippinarum* was observed between 1995 and 2020.

The zone (upstream *vs* downstream) had a significant effect on the RDT, whatever the group of trajectories (Anova, p-value$<$0.05). Stations showing a 'recovering' trajectory were mainly located close to the channel in the downstream area, on sandy coarse sediments, and on the intertidal mudflats in the upstream area (Fig. 6). Conversely, 'departing' patterns were mainly located on the intertidal mudflats downstream and in the main channel upstream (see Fig. 7).

3.4. Changes in the sedimentary characteristics in the upstream area

A comparison of surficial sediment composition between 2010 and 2020 reveals (i) an increase in the proportion of sand and gravel in and around the main channel and (ii) a higher proportion of silt on lateral mudflats (Fig. 6). The boundary between sandy and muddy sedimentary types is clearer in 2020 than in 2010.

4. Discussion

The construction of the RTPP significantly modified the local hydrodynamics, the sediment transport, the water quality, the benthic assemblages and ultimately the ecosystem functioning (Desroy, 1998; Kirby and Retière, 2009; Xia et al., 2010; Cornett et al., 2013). Studies on the resilience of the benthic ecosystem are often limited to the few years following an initial disturbance event (e.g. in marine aggregates extraction sites: Foden et al., 2009), making it less meaningful to investigate ecological successions, as only the early recovery is considered. Thanks to a unique dataset based on the resampling of historical stations, the present study offers a rare opportunity to assess how the benthic ecosystem of an estuary recovered 54 years after an initial

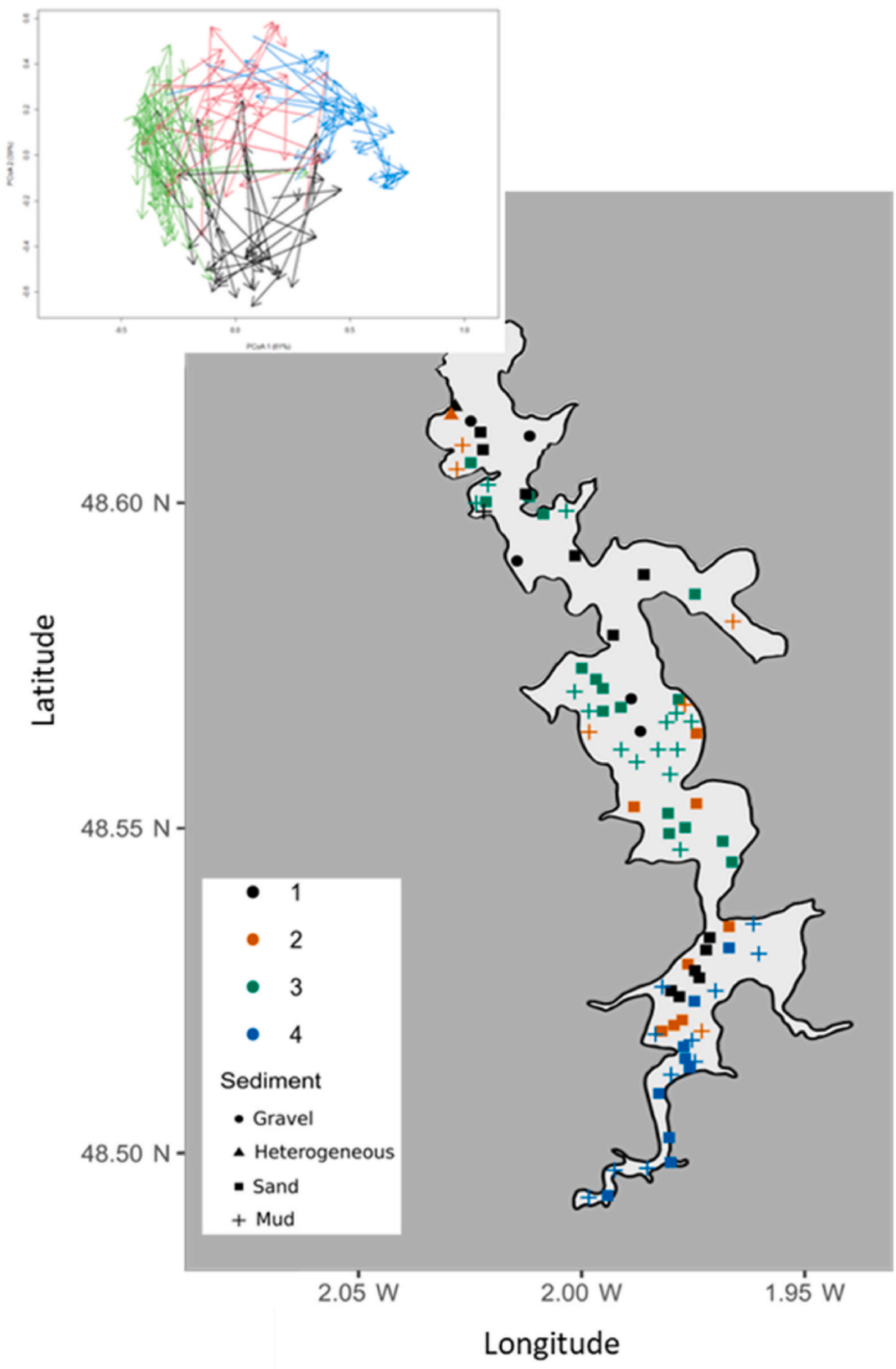

Fig. 5. Map of the trajectory groups defined by applying an Ascending Hierarchical Classification (Euclidean distance, Ward aggregation method) on results from results of a Community Trajectory Analysis (segment lengths, angles and direction) taking into account the 1976, 1995 and 2020 datasets.

defaunation event.

4.1. The Rance basin early reached a new equilibrium

Results revealed that benthic communities remained stable over the successive surveys, both from a univariate perspective (e.g., species richness, Shannon's diversity) and a multivariate one. At the basin scale, a pool of 98 species, representing three-quarters of the macrobenthic abundance, was observed in each survey. Similar observations were made when sampling the upstream area in 2010 (Trigui et al., 2011). These results support the conclusion drawn by Desroy (1998), arguing that the benthic ecosystem of the Rance basin rapidly reached a new state of equilibrium after the construction of the dam at the early 1970's. In 1995, this author considered that the recolonization of soft sediments was almost complete because the species cumulative curve tended to an asymptote. Equilibrium may have been enhanced by the prohibition of towed gears in the Rance. The dominance of tubicolous species, such as *Melinna palmata, Ampelisca tenuicornis* and *Euclymene oerstedii*, reflects the lack of major physical sources of disruption to which these organisms are very sensitive (see Tuck et al., 1998 for *Melinna palmata;* Bremner et al., 2003; Tillin et al., 2006).

Despite the apparent stability in the long term, spatio-temporal

Table 2
Characteristics of each trajectory groups with NC: net change, TP: trajectory path and RDT: recovering and departing consecutive trajectory segments. The mean distance±standard deviations of values are represented.

Group of trajectories	1	2	3	4
Number of stations	19	15	30	20
NC	13.58 ± 6.48	13.42 ± 6.31	13.19 ± 6.34	12.25 ± 6.30
TP	15.81 ± 6.26	18.94 ± 6.14	12.2 ± 6.2	9.75 ± 7.24
RDT	−1.78 ± 3.67	0.15 ± 5.41	−2.84 ± 4.20	0.29 ± 2.81

variations occurred at a local scale, showing departing patterns. They were due to species with lower abundance and were no longer related to the initial disturbance (Desroy, 1998) but rather to a dual gradient of sedimentary characteristics (sometimes increased by the presence of invading species) and salinity (see below). By crossing the various information provided by the present study, four trajectory areas can be identified within the Rance basin (see the graphical abstract).

4.2. Ecological trajectories reflect the sedimentary dynamic

A comparative study of surficial sediment cover between 1994 and 2020 highlighted the reduction in predominantly muddy sedimentary facies in favor of predominantly sandy facies (unpub. data). Upstream, we observed departing patterns due to erosion of the central channel bed, which in 2020 contained medium to coarse sands, medium to fine sands, or fine sands with varying degrees of mud, instead of muds in 1994. The upper part of intertidal mudflats, however, has been enriched with particles <100 μm. Downstream, the proportions of mud and silt decreased between 1994 and 2020, and sediments in lateral coves have also been enriched with fine particles (<100 μm).

These changes led to recovering patterns in benthic assemblages, mainly affecting subtidal stations in the main downstream channel and intertidal stations in the upstream area. Conversely, departing patterns were mainly observed in downstream intertidal stations and upstream subtidal stations. Benthic assemblages have since evolved differently between the upstream and downstream areas of the basin. Since no major changes have occurred in the operation of the RTPP, these changes in surficial sediment cover may be attributed to the reduction of marine inputs (but no data exist to confirm this hypothesis), sediment redistribution, hydrological changes—particularly the decrease in freshwater inflow to the upstream basin—as well as biological interactions.

4.3. The presence of *Crepidula fornicata* influences assemblages located around the main channel in the downstream area

Melinna palmata rapidly spread across the Rance basin just after the construction of the dam (Retière, 1979). More generally, this species has been spreading within the eastern channel and in the southern North Sea since the 1990s. It has exhibited high abundances in the channel of the Seine estuary since the 2000s (Dauvin et al., 2007). In the present study, we found a decline of *M. palmata* as well as of *Ampharete baltica,* between 1976 and 1995 in the downstream part of the Rance basin. This result is not consistent with the expansion of *M. palmata* at a regional scale, but one possible explanation for this pattern lies in the proliferation of *Crepidula fornicata*, which invaded the downstream part of the Rance basin in the late 1980s (Desroy, 1998). As an engineer species, *C. fornicata* is known to alter environmental characteristics and subsequently modify the structure of benthic communities (de Montaudouin and Sauriau, 1999; Gutiérrez et al., 2003; S Sandrini-Neto and da Cunha Lana, 2014). Accumulated shells on the seabed increase the micro-scale heterogeneity of the habitat and create a hard substrate for sessile species (Barnes et al., 1973). The presence of *Crepidula fornicata* can also reduce hydrodynamics in the boundary layer and favor the deposition of muddy particles. The secretion of faeces and pseudofaeces increases the organic matter content at the bottom. Although generally favoured by nutrient enrichment (Hiscock et al., 2005), *M. palmata* may have been negatively affected by the colonization of *C. fornicata*, for instance due to competition for space. Populations of *A. baltica*, mainly found in fine

Table 3
Distribution of the five species contributing the most to differences between two groups (1976/1995 and 1995/2020) per trajectory cluster. Including the species names (Species), the average abundance of species in each of the two groups, and the species' contribution to differences between the two groups (contribution).

	1976 → 1995				1995 → 2020			
	Species	Ab 1976	Ab 1995	Contribution	Species	Ab 1995	Ab 2020	Contribution
1	*Melinna palmata*	46.89	28.21	0.20	*Mediomastus fragilis*	1.31	154.42	0.28
	Ampharete baltica	38.68	16.63	0.25	*Caulleriella alata*	24.47	79.84	0.36
	Cirriformia tentaculata	2.21	30.36	0.34	*Phoronis psammophila*	1.26	36.94	0.45
	Pista cristata	18	1.52	0.41	*Scalibregma celticum*	3.31	27	0.54
	Heteromastus filiformis	7.16	17.36	0.47	*Aphelochaeta marioni*	5.52	20.26	0.58
2	*Melinna palmata*	172.26	59.33	0.20	*Leiochone leiopygos*	52.66	97.06	0.22
	Pygospio elegans	236.26	21.06	0.34	*Ampelisca tenuicornis*	0.53	46	0.37
	Chaetozone sp.	97.26	62.86	0.47	Oligochaeta	83.13	14.93	0.43
	Nephtys hombergii	39.33	39.20	0.64	*Phoronis psammophila*	0.33	70.33	0.60
	Oligochaeta	0	83.13	0.70	*Abra alba*	0.13	42.66	0.68
3	*Melinna palmata*	334.53	201.16	0.24	*Leiochone leiopygos*	2.46	173.83	0.24
	Chaetozone sp.	163.76	56.13	0.36	*Ampelisca tenuicornis*	39.63	87.13	0.33
	Galathowenia oculata	0	34.90	0.57	*Phoronis psammophila*	21.83	112.46	0.55
	Nephtys hombergii	53.33	31.60	0.64	*Galathowenia oculata*	34.90	5.80	0.58
	Lanice conchilega	19.93	0.83	0.68	*Abra alba*	1.20	45.23	0.62
4	*Cerastoderma edule*	0.1	10.20	0.89	Oligochaeta	369.75	36.35	0.20
	Jassa falcata	0	1.50	0.93	*Peringia ulvae*	198.65	20.20	0.35
	Mysida sp.	0	1	0.95	*Ruditapes philippinarum*	0	9.80	0.84
	Cereus pedunculatus	0.1	2.55	0.98	*Cerastoderma edule*	10.20	0.30	0.89
	Manayunkia aestuarina	0	2.05	0.99	*Jassa falcata*	1.50	0	0.95

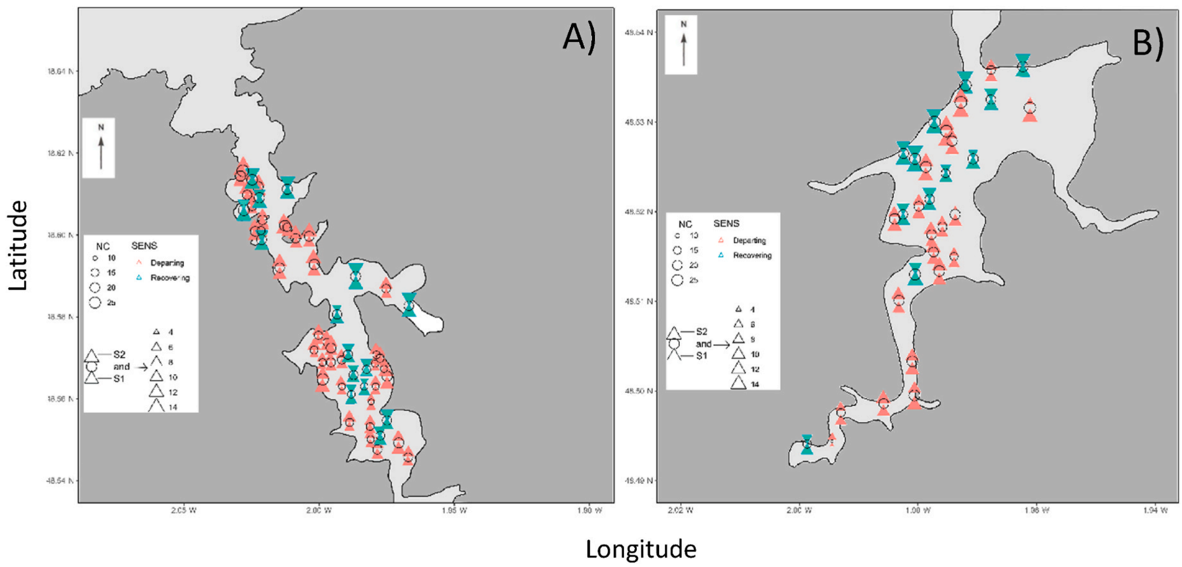

Fig. 6. Trajectory maps in the downstream part of the Rance basin (A) and in the upstream part (B). Net changes between 1976 and 2020 are represented by black circles. The lower triangles represent the trajectory segment S1 (1976–1995) and the upper ones S2 (1995–2020). The size of the symbols corresponds to the lengths whereas their orientation shows the departing (the triangle points up to the top) or recovering (the triangle points down) pattern of the trajectory segments. The colours of the triangles indicate the type of trajectory of the station (recovery or departing). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

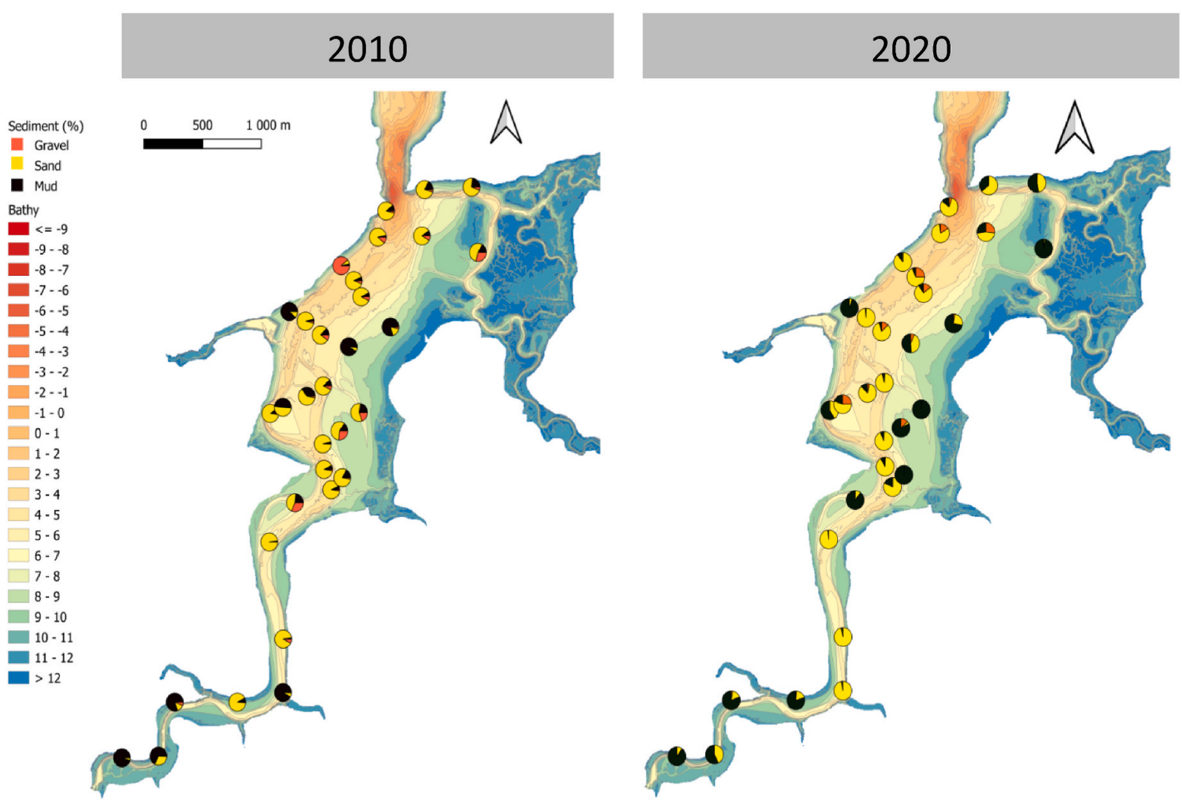

Fig. 7. Pie chart representing the recent variations of sedimentary characteristics in the upstream area of the Rance basin.

sandy bottoms and sensitive to organic matter enrichment in the sediment (Zettler et al., 2013), may also have been strongly affected by the proliferation of *C. fornicata*.

Since the early 2000s, *C. fornicata* has progressively declined in the Rance and other bays, such as the Bay of Brest (Blanchet-Aurigny, 2012; Androuin et al., 2020), without clear explanation, leaving beds of empty shells, more or less fragmented. The associated fine particle deposits could then be progressively eroded. This new habitat could favor the strong increase in abundance of species as *Mediomastus fragilis* and *Aphelochaeta marioni* between 1995 and 2020. During the present study, the presence of several individuals of *M. fragilis* was noted within shell debris (until 10–20 individuals per shell), indicating that dead shells constitute a microhabitat for *M. fragilis*. These two species are often associated with *C. fornicata* and form a particular biotope on “variable salinity mixed sediment", as described by Readman and Rayment (2016) in several station along the southern coasts of the UK. The central channel in the downstream part thus remains under the influence of *C. fornicata.*

4.4. The redistribution of sediment drives assemblage changes in the downstream area

Bonnot-Courtois (2002) conducted a study that revealed changes in the seabed composition, particularly a redistribution of fine sediments in the southern part of the downstream Rance basin: the finest sediment fraction was removed from subtidal areas and redeposited in intertidal mudflats. These changes were directly reflected in the species composition, as evidenced by a decline of *M. palmata,* a species associated with muddy sediments (Cabioch, 1968; Retière, 1979), between 1976 and 1995 in the southern part of the Rance basin's downstream area. Conversely, *Leiochone leiopygos, Ampelisca tenuicornis* and *Phoronis psammophila*, species that prefer muddy fine sand (Dauvin, 2023; La Rivière et al., 2022) or fine to coarse sands (Emig, 2006) with a moderate muddy fraction (Emig, 2009), proliferated between 1995 and 2020.

4.5. Sedimentary and salinity gradients prevail in the upstream part

Benthic communities in the upstream part are strongly related to salinity gradients (Desroy, 1998). A first retreat of the salinity front was observed after the creation of the RTPP, as the dam modified the hydrological conditions (Retière, 1979; Lang, 1986). The localisation of the salinity front remained stable for more than 45 years. A model developed by Rtimi et al. (2022) based in data collected from six stations spanning the downstream to the upstream parts of the Rance basin between 2019 and 2020, suggests a new retreat of the salinity front upstream. According to this model, the salinity front is now located at the outlet of the Chatelier channel (excluding seasonal variations). The increase in salinity (or the phenomenon marinisation) explains the modifications of benthic communities observed in the upstream area. Marinisation has been observed in major European estuaries, from Portugal to the Netherlands. In the Gironde estuary, for example, anchovies are now moving further upstream (Sautour et al., 2020). In the lower part of the Seine estuary, monitoring of the suprabenthic compartment from the mid-1990s to the late 2010s has shown a marinisation of the system, meaning the penetration of marine species into the estuary, linked to the salinization of this downstream area due to climate change and the decrease in the flow of the Seine (Pezy et al., 2017).

Other factors, such as variations of the sediment coverage, might be involved in observed changes. A significant rainfall deficit at the beginning of the 90' induced the silting up of intertidal stations located upstream (Bonnot-Courtois, 2002) and the adaptation of benthic assemblages. Similarly, in response to recurrent dry years, some stations located in the southernmost part of the Rance basin, close to the Chatelier lock, had a higher proportion of mud in 2020 compared to 2010.

Consequently, benthic assemblages located in the upstream part of the Rance basin depend of a dual gradient of salinity and mud content and two-sub areas can be distinguished:

- in the main channel, the increase in the abundance of *M. fragilis*, *Leiochone leiopygos* and *Phoronis psammophila*, reflected the increase of salinity and the prevalence of sandy sediments.
- in the intertidal mudflats and in the southernmost part, close to the Chatelier lock, assemblages were relatively stable between 1976 and 1995 and mostly typified by a slight increase in the abundance of *Cerastoderma edule.* This species, along with *Peringia ulvae* and oligochaetes, have been progressively replaced by the non-indigenous mollusc *Ruditapes philippinarum* introduced in 1996 and has shown a decline of abundance, probably in response to the increase of salinity in the upstream part of the Rance basin. *R. philippinarum* became a structuring species at the beginning of the 2000's with densities reaching up to 800 ind.m^{-2} (Oualibouch, 2003). *Ruditapes philippinarum* forms dense mats stabilising the sediments, increasing inorganic carbon and ammonium sediment release and regenerating nutrients that support microphytobenthic production, particularly high on intertidal mudflats (Migné et al., 2018). *R. philippinarum* increases the spatial heterogeneity, which in turn, enhances the local biodiversity and influences the species composition (Dannheim and Rumohr, 2012).

4.6. An unexpected increase of biodiversity in 2020

Surprisingly, species richness, Shannon's diversity index, and Simpson's diversity index sharply increased in 2020 compared to previous surveys. There is a lack of inter-annual sampling from a sufficient number of stations to identify the period when changes occurred. In the bay of Saint-Brieuc, the coupling between annual sampling at a single station and long-term interval surveys (1987 and 2019) facilitates the dating of changes observed in benthic assemblages (Sturbois et al., 2021b). The changes are due to both regional and local factors.

On a larger scale, such as the English Channel, marine invertebrates and benthic organisms, in particular, exhibit significant diversity changes over time in two ways: shifts in distribution areas related to climate change and enrichment due to deliberate or unintentional introductions of non-indigenous species, resulting in an increase in the number of species rather than a decline in biodiversity (Dauvin, 2023). Biodiversity changes show an increase in warm-temperate species and, conversely, a decrease in the occurrence of boreal species, with a general movement of benthic species from the English Channel towards the North Sea (Rombouts et al., 2012). Several species described as "Mediterranean-Lusitanian" in the Normano-Breton Gulf Atlas (Le Mao et al., 2019) appeared in the faunistic list collected in 2020 (*Eulalia clavigera, Protula* sp.*, Priosnospio* sp.*, Scolelepis* sp.*, Leptochiton scabridus, Tragula fenestrata, Gammarus insensibilis, Leucothoe procera, Synchelidium maculatum*).

Stations showing the highest improvements in biodiversity were mostly located upstream, in the main channel, and in most of the stations located downstream, for which spatial patterns are difficult to distinguish. Several local factors can explain these sharp increases in biodiversity. Firstly, the general increase of salinity occurred recently (after 2010) in the upstream area is responsible for the colonization by marine species and the increase of biodiversity, as already observed by Remane (1934) and Palmer et al. (2016) in the Baltic Sea. Secondly, the increase in the proportion of coarse elements, mainly biogenic (*R. philippinarum* shells), in the upstream area led to more heterogeneous sediments and contribute to the increase in biodiversity. Mixed sediments, including biogenic components such as barnacle debris, clams, and scallops, are often associated with higher diversity than bare sediments (Ellingsen, 2002; Hewitt et al., 2005; Zajac et al., 2013; Boyé, 2018). The combination of increased salinity and greater sediment heterogeneity may be responsible for the observed recovery trajectory in the upstream area.

An increase in biodiversity was also observed on mudflats. These sheltered areas host, for some of them, engineer species such as *Zostera marina* and *Z. noltei*, which create microhabitats, induce heterogeneity, and favor the development of other organisms (Lawton and Jones, 1995; Watt and Scrosati, 2013). Before the construction of the RTPP, eelgrass beds were present in many of the coves in the downstream part of the Rance basin (Fischer-Piette, 1929; Hamel, 1928; Bugnon, 1929). They disappeared during the construction phase and after 1966 due to changes in currents and the acceleration of fine sedimentation in coves. At the beginning of the 21st century, eelgrass species (*Zostera* sp.) experienced a strong recolonization dynamic on the French coasts. In 2020, eelgrass beds covered approximately 140 ha in the Rance basin (unpub. data). he development of eelgrass on sediments previously bare may be responsible for the increase in biodiversity and the departure pattern observed in colonized areas. In 2020, during sampling, about 20 species associated with eelgrass habitats were collected, including the mollusc *Loripes orbiculatus*, the crustaceans *Gastrosaccus pectinatus, Iphinoe trispinosa, Eualus* sp.*, Praunus flexuosus* and the polychaete *Stylarioides moniliferus*.

Downstream, empty shells of *C. fornicata* increased the heterogeneity and topographic complexity of soft bottom sediments (Gutiérrez et al., 2003), and enhanced local species diversity (Barnes et al., 1973; de Montaudouin et Sauriau, 1999; de Montaudouin and Accolla, 2017). Other studies have reported species richness increase in the presence of slipper limpets (dead and/or living) compared to bare substrates (Barnes et al., 1973; de Montaudouin and Sauriau, 1999; Reynaud, 2013; Androuin et al., 2020). Some species only recording during the 2020 sampling are known to be associated with heterogeneous habitats containing shell debris: the crustacean *Leucothoe procera* (White, 2011), the polychaetes *Micronephtys* sp. (Dnestrovskaya and Jirkov, 2019), *Mysta picta* (Le Mao et al., 2019), *Pherusa plumosa* (Blanchard and Hamon, 2006), *Ebalia tumefacta* (Le Mao et al., 2019), as well as several epibiont species (Blanchard, 2005) such as chitons, anemones, and spirorbes.

To complement these results, functional diversity of benthic assemblages will be studied [biological trait analysis (Bremner et al., 2003)]. A CTA approach on the trait matrix of different years will help to determine the capacity of the ecosystem to maintain or recover key processes and functions in response to disturbance. The differential sensitivities of assemblage and functional structure to stressors may highlight the need for a combined analysis of both structures to gain a comprehensive understanding of the long-term dynamics of the Rance benthic ecosystem.

5. Conclusion

Benthic assemblages in the Rance basin continue to structure themselves more than 50 years after the construction of the RTPP. A comparison of the results collected in 1976, 1995, 2010 (only in the upstream area), and 2020 shows that, after a period of slowdown in the colonization of the seafloor, the number of species has increased significantly, related to the increased influence of marine waters, greater habitat heterogeneity, and the redistribution of fine sediments in the basin. A total of 483 species have been recorded on soft-bottoms. Based on the sampling of 84 common stations in 1976, 1995, and 2020, 98 species were common, representing 76 % of the total abundance. Dominant species, due to their stability, play a key role in structuring the community. Recovery patterns mainly affected subtidal stations located in the main channel downstream and intertidal stations in the upstream area. Departing patterns mainly relate to intertidal stations downstream and subtidal stations upstream. Changes are explained by both regional (global warming) and local (sediment redistribution, retreat of the salinity front, and biological interactions) factors.

CRediT authorship contribution statement

T. Brébant: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **A. Sturbois:** Validation, Methodology. **A.E. Robert:** Writing – review & editing, Supervision, Investigation. **N. Desroy:** Writing – review & editing, Validation, Supervision, Methodology, Investigation, Funding acquisition, Conceptualization.

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Declaration of competing interest

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Data availability

The authors do not have permission to share data.

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