Aquatic Conservation: Marine and Freshwater Ecosystems
November 2021, Volume 31, Issue 11, Pages 3013-3033
https://doi.org/10.1002/aqc.3704
https://archimer.ifremer.fr/doc/00724/83611/

Using ecological trajectories to track long- term taxonomic and functional changes in benthic shallow soft- bottom communities (Bay of Saint- Brieuc, English Channel)

Sturbois Anthony [1, 2, 3, 5, *], Cormy Gaetan [1, 2], Le Moal Alexandre [1, 2], Schaal Gauthier [3], Broudin Caroline [6], Thiébaut Eric [6], Ponsero Alain [2, 4], Le Mao Patrick [5], Jones Auriane [7], Riera Pascal [6], Gauthier Olivier [3], Desroy Nicolas [5]

[1] Vivarmor Nature, Ploufragan, France
[2] Réserve naturelle nationale de la Baie de Saint-Brieuc, Hillion, France
[3] Laboratoire des Sciences de l'Environnement Marin (LEMAR), UMR 6539 CNRS/UBO/IRD/IFREMER Plouzané ,France
[4] Saint-Brieuc Agglomération Baie d'Armor ,Saint-Brieuc ,France
[5] Laboratoire Environnement et Ressources Bretagne nord, Ifremer Dinard ,France
[6] CNRS, Station Biologique de Roscoff, UMR7144 Sorbonne Université Roscoff Cedex, France
[7] MARBEC, Univ Montpellier, CNRS, Ifremer, IRD Sète, France

* Corresponding author : Anthony Sturbois, email address : anthony.sturbois@espaces-naturels.fr

---

Abstract :

1. Taxonomic and functional trajectories of benthic assemblages were studied in shallow soft-bottom sediments in the bay of Saint-Brieuc (Western English Channel). Changes were assessed at different spatial and temporal scales using a macrobenthic dataset based on 38 stations sampled in 1987 and 2019, coupled with data from one station sampled annually between 2005 and 2019 as part of the European Water Framework Directive monitoring programme.

2. Taxonomic trajectories indicated 1) changes in the structure and distribution of benthic assemblages, 2) an homogenization of the assemblages, and 3) significant functional shifts.

3. Fishing activities and nutrient enrichment are probably strong drivers of the observed changes, as suggested by the higher mortality rate of fragile, flexible, tubiculous and burrowing species, and the increase in the abundance of opportunistic species in the assemblages. Certain populations of macroinvertebrates seem jointly controlled by climate change and by the aforementioned local factors of disturbance.

4. The Community Trajectory Analysis framework appears as a new and interesting method to track ecological changes in marine ecosystems by measuring change with respect to a baseline state, to help define ecological recovery (station returning to the initial ecological state) and departure (station presenting increased changes over time), and to analyse trajectory similarity.

5. According to the degradation of habitat over time, we identify the need for the implementation of knowledge-based conservation strategies, especially within Natura 2000 sites.

Keywords : benthic assemblages, community trajectory analysis, conservation, ecological trajectories, eutrophication, long-term changes, macrofauna, Natura 2000, scallop dredging

1. Introduction

Worldwide, marine ecosystems are suffering severe taxonomic and functional changes in response to cumulative effects of anthropogenic disturbances including overfishing, pollution, global climate change, habitat degradation and introduction of non-indigenous species (Gray, 1997; Claudet & Fraschetti, 2010). Human influences induce both acute and chronic effects over various temporal and spatial scales, and can ultimately lead to broad-scale loss of productive habitats, and alteration of community structure and function (Ellis, Norkko & Thrush, 2000). As a result, 60% of major marine ecosystems worldwide are currently degraded or suffer from unsustainable levels of exploitation, leading to the adoption of conservation policies by many countries (Convention on Biological Diversity, 2010; UNEP, 2011). The European Water Framework Directive (WFD, Directive 2000/60/EC) and the Marine Strategy Framework Directive (European MSFD, Directive 2008/56/EC) require that European Member States implement measures to achieve a good environmental status of their water bodies.

The comparison to reference conditions based on pristine or slightly disturbed areas is recommended by the European WFD to track changes in environmental status, although it is generally recognized that non-disturbed marine and estuarine habitats are rare (Borja, Dauer & Grémare, 2012), and that historical data rarely constitute a pristine state (Callaway, 2016; Bacouillard et al., 2020). In this context, acceptable levels of disturbances can be used to define reference conditions (Borja, Dauer & Grémare, 2012). Such approach requires repeated and standardized surveys over time to 1) track changes with respect to baselines conditions, and 2) provide up-to-date ecological state to stakeholders involved in the development of management plans for coastal and marine areas. Benthic macrofauna has been considered as a relevant descriptor to characterize the biological status of water bodies by the European WFD (Borja, Muxika & Rodríguez, 2009; Borja, Dauer & Grémare, 2012), as this compartment influences nutrient cycling, represents an important food resource for higher trophic levels (Snelgrove, 1997; McLusky & Elliott, 2004), and reacts rapidly to disturbances (Gray, 1997; Claudet & Fraschetti, 2010).

Among sublittoral macrobenthic assemblages, very shallow subtidal habitats (0-15m), accessible for sampling only during high tide, are often excluded from sampling programmes and remain to a large extent poorly monitored (Desroy et al., 2002). Very shallow communities are notably characterized by high diversity and productivity levels (Gray, 1997; Levinton, 2001; Snelgrove, 1999). This knowledge gap and the scarcity of data constitute a serious impediment for the implementation of conservation strategies (Ellis, Norkko & Thrush, 2000).

On the French coast of the English Channel, scientific studies have largely focused on benthic communities of the main coastal bays and estuaries [e.g. Rance estuary, (Desroy & Retière, 2004), bay of Seine (Dauvin & Desroy, 2005; Desroy et al., 2007; Bacouillard et al., 2020) or bay of Mont-Saint-Michel (Trigui, 2009)]. In the bay of Saint-Brieuc (Western English Channel), the ecological state of subtidal communities defined in 1987 by Gros & Hamon (1988) has never been updated, contrasting with the monitoring strategy deployed in the adjacent intertidal area, partially protected since 1998 by a National Nature Reserve primarily devoted to the conservation of birds and, *de facto*, to benthic habitats (Sturbois et al., under review). This shallow subtidal area, belonging to the “Baie de Saint-Brieuc – Est” Natura 2000 site, supports intense fishing activities (dominated by scallop dredging) and mussel rope culture.

Historical data are rare in this very shallow area, and limited to the ecological assessment carried out in 1987 by Gros & Hamon (1988) and to the WFD monitoring conducted at one station from 2005 to 2019.

This study, based on a resampling of the stations sampled in 1987 in the bay of Saint-Brieuc and on the WFD long-term monitoring of the benthic assemblage at one shallow station, aims to analyse taxonomic and functional trajectories of benthic assemblages in order to: (1) detect patterns of changes over the last 30 years at different spatial scales using the 38 stations sampled in 1987 and 2019, and (2) analyse recent dynamics at one station sampled yearly from 2005 to 2019 as part of the WFD monitoring programme. As single or multiple disturbances differently affect species composition and structure, temporal changes of the benthic community were tracked, both with α and β-diversity metrics (Ellis, Norkko & Thrush, 2000; Cimon & Cusson, 2018). In accordance with Dornelas et al. (2013), Magurran et al. (2019), and Yang (2020) recommendations to develop new multivariate metrics devoted to the study of temporal ecological changes and response to disturbance (Cimon & Cusson, 2018), we specifically focused on taxonomic and functional spatio-temporal trajectories coupling classic multivariate analysis with the recent Community Trajectory Analysis framework (De Cáceres et al., 2019; Sturbois et al., 2021), finally discussing conservation prospects for such coastal areas.

2. Material and methods

2.1. Study area

Fieldwork was conducted in the bay of Saint-Brieuc (France, Figure 1). The study area encloses 11,700 ha of very shallow soft-bottom sediments. The bay is under the influence of a semi-diurnal megatidal regime. Tidal range varies between 4 m at neap tides and nearly 13 m during spring tides. Despite bordering the National Nature Reserve of the bay of Saint-Brieuc and partially belonging to the Natura 2000 “Baie de Saint-Brieuc-Est” site (FR5300066), the study area is exposed to a number of anthropogenic pressures including mussel culture, scallop dredging and eutrophication. Mussels are farmed on bouchots (wooden poles, Figure 1) in the north-eastern part of the intertidal area, occupying 277 ha and 312 ha in 1987 and 2019, respectively (Sturbois et al., under review) and are also farmed on ropes in the western part of the study area, around stations 81, 99 and 100. The sea bed is also exposed to long-term scallop dredging activities as the bay of Saint-Brieuc is characterized by the highest fishing pressure in Brittany (Appendix A-1). Regulation changes have led, since 2010, to the concentration of dredging, at the beginning of the fishing season, in areas colonized by the the non-indigenous slipper limpet *Crepidula fornicata* (Appendix A-2). The bay also suffers from eutrophication resulting in macroalgae proliferation and cyclic green tides episodes (Charlier et al., 2007; Gravier, 2012), which notably impact fishes nursery grounds (Le Luherne et al., 2016, 2017) and influence the dynamics of some intertidal benthic populations of invertebrates of the intertidal area (Sturbois et al., under review).

2.2. Field sampling

Benthic macrofauna was sampled at 38 stations during winter (March) in 1987 and 2019 (ResTroph research programme) following the grid (Figure 1) and the protocol defined in 1987 by Gros & Hamon (1988). During both surveys, five replicates were collected at each station with a small Hamon grab (1/8m²) for macrobenthos analyses. The grab contents were gently sieved on board either through 1) a 2 mm circular mesh sieve (1 replicate) to describe benthic assemblages, or through 2) a 5 mm circular mesh sieve (4 replicates) to specifically analyse bivalve populations. The retained material was preserved for analysis in 5% buffered formaldehyde. Only the replicate sieved on a 2 mm mesh was used for the long-term comparison of the benthic community. Two samples of sediment were collected in one additional grab using a handcorer, and subsequently analysed for grain size distribution and organic matter content respectively. All replicates were collected at a maximal distance of 50 m from each station, using DGPS position-fixing. As part of the ecological status monitoring, one station (R) was additionally sampled yearly (nine replicates, following national recommendation of the REBENT benthic network as part of the WFD) in March from 2005 to 2019, with a Smith McIntyre grab (0.1 m²), and sieved on 1 mm circular mesh sieve. Data at station R were used to assess the year-to-year variability of taxonomic and functional diversity at this site.

2.3. Laboratory analyses

Macrofauna was identified to the lowest possible taxonomic level (usually species level), counted, and abundances were standardized to 1 m^2. Taxon names follow the World Register of Marine Species (WoRMS Editorial Board, 2020).

For granulometric analysis, sediment was desalted with fresh water and left to settle for 48 h. Sediment was then dried at 60°C for 48 h and sieved through AFNOR standard sieves, before weighing. Organic matter content was determined after drying (60°C for 48 h) and combustion of sediment at 550 °C for 4 h (Salonen, 1979; Hedges & Stern, 1984).

2.4. Traits collection

The functional dataset was composed of six traits representing a total of 25 categories (Appendix B). These traits characterized the morphology (body size, flexibility, fragility) and behaviour (feeding behaviour, living habit, tolerance to organic enrichment) (Degen & Faulwetter, 2019). This set of traits is related to vulnerability to mechanical disturbance (fishing activities), and to tolerance to organic enrichment (eutrophication) and was chosen to analyse functional changes in benthic fauna, in relation to the main pressures identified in the study area. Information was collected from primary literature on specific taxa, expert knowledge and the databases polytraits (http://polytraits.lifewatchgreece.eu), the World Register of Marine Species (WoRMS Editorial Board, 2020), and Biological Trait Information Catalogue (BIOTIC, http://www.marlin.ac.uk/biotic/). Scores were attributed to species according to their affinity to each category of traits using a fuzzy coding from 0 (no affinity) to 3 (high affinity) (Chevene, Doleadec & Chessel, 1994). Community-weighted trait values

(CWMs) were calculated to characterize the functional community structure for both datasets (Ricotta & Moretti, 2011).

2.5. Data analysis

Long-term (38 stations, 1987 vs 2019) and inter-annual (station R; 2005 to 2019) datasets were analysed to track for taxonomic and functional changes. The study focused specifically on the analysis of ecological trajectories depicted at different temporal scales taking the advantage of both data sets: 32 year long-term comparison vs 15 year long-term series. All statistical analyses were performed with R 4.0 (R Development Core Team, 2020).

2.5.1 Sedimentary dataset

Statistical description of sediments, based on grain-size distributions, was computed with the R package 'G2Sd' (Fournier, Gallon & Paris, 2014). Sediment characteristics and changes were described from ten sedimentary parameters and tested with a Wilcoxon paired-test: organic matter content (OMC), mean and median (d50) particle size, gravel (> 2mm), coarse sand (2mm to 500µm), fine sand (250 to 125 µm), very fine sand (125 to 63µm), and mud (<63µm) contents (%).

2.5.2 Taxonomic α-diversity

In order to assess the different components of taxonomic α-diversity, the mean number of individuals per m² (N), species richness (S), Shannon-Weaver index (H'), Simpson index (D) and Pielou's species evenness (J) were calculated for each station (2 mm circular mesh sieve) prior to any transformations of the dataset.

2.5.3 Spatial and temporal taxonomic clustering

Hierarchical Cluster Analyses (HCA) were performed on both taxonomic datasets to distinguish benthic assemblages (i.e. stations/surveys groups) by using the Hellinger distance between each pair of samples/dates (Legendre & Gallagher, 2001) and by applying the Ward’s clustering method. The indicator value method (Indval) was performed for characterizing assemblages (Dufrene & Legendre, 1997).

2.5.4 Detecting trajectory patterns

On ResTroph and WFD datasets, PCAs were performed on Hellinger-transformed data and followed by Community Trajectory Analysis (CTA). CTA is based on geometrical properties of ecological trajectories (De Cáceres et al., 2019). The original framework and its new extension (Sturbois et al., 2021) were used to study and represent temporal changes at the station scale taking into account all the dimensions of the multivariate analysis through trajectories of surveys in the multivariate space.

Long-term comparison. Net changes between 1987 and 2019 were calculated to analyse trajectories considering the 1987 data set as the initial state. Dissimilarities between ecological trajectories were calculated to test their resemblance (De Cáceres et al., 2019) and underline potential spatial patterns in temporal variations with HCAs. 1) For taxonomic trajectories, the Indicator value method (Dufrene & Legendre, 1997) was performed on taxonomic trajectories clusters to test differences between 1987 and 2019. 2) For functional trajectories, the relative contribution of all categories of functional traits between 1987 and 2019 were compared for each functional trajectory cluster and tested at the scale of the whole community (paired samples Student’s permutation tests; p-value < 0.05).

Inter-annual dynamics. For the long-term WFD dataset (yearly sampling from 2005 to 2019), Trajectory segments lengths (*i.e.* S1=2005 to 2006, S2=2006 to 2007,…S14=2018 to 2019), Net change, Directionality and Net change ratio were calculated. Recovering (station returning toward an initial ecological state) and departing (station for which change increased over time) consecutive trajectory segments were identified by subtracting Net change n-1 by Net change n (Sturbois et al., 2021).

2.5.5 Relation between taxonomic structure and environmental and spatial variables

Multi-collinearity in sedimentary variables was detected with the Variable Inflation Factors methods (VIF). Variables characterized by highest VIF were excluded for further analysis. (1) Redundancy analyses (RDA) was performed to determine the part of variance respectively explained by sedimentary variables in the taxonomic Restroph dataset (Blanchet, Legendre & Borcard, 2008). When significant, (2) a forward selection was used to test the significance of each variable. (3) Linear and non-linear multi-scale structures of the spatial model were analysed and a linear spatial model was performed to determine the variance explained by spatial variables (Legendre & Legendre, 2012). (4) A variation partitioning analysis was undertaken to assess the variation explained and shared by sedimentary and spatial variables (Legendre & Legendre, 2012).

2.5.6 Species changes in bivalve populations

The evolution of the abundance (raw data) of the main bivalve species (four replicates sieved on 5 mm circular mesh) was analysed and differences were tested with paired samples Student's permutation tests (p-value < 0.05).

3. Results

3.1 General description of sediment

Sediments were dominated by sands in 1987 (74.33% ± 12.85, mean +/- sd) and 2019 (78.74% ± 12.35) (Appendix C). Fine sands (125-250 µm) were the most represented sedimentary class in both years (42.34% ± 17.92 in 1987; 46.60% ± 17.99 in 2019). Mud content significantly decreased in 79 % of stations (-11.12% ±

6.89; min= -0.79%; max= -31.15%, p-value < 0.001). In contrast, 21% of stations were characterized by an increase in mud content (+11.53% ± 17.56) especially at stations 101 (+52.46%), 81 (+16.16%), and 100 (+13.61%). Gravel accounted for 8.43% ± 10.59 in 1987 and 10.23% ± 6.96 in 2019. Mean particle size (356.55µm ± 258.94 vs 421.54µm ± 192.55) slightly and significantly increased (p-value < 0.001) over the study period.

Sediment properties at station R varied inter-annually (Appendix D): after a first period of high inter-annual variability between 2005 and 2014, sediment granulometry was less variable from 2015 onward.

3.2 General description of the macrofauna

Overall, 208 taxa were collected on the 2mm mesh size sieves (with 72 taxa common to both datasets). Between 1987 and 2019, 57 taxa were lost and 79 taxa gained. Macrofauna was dominated by annelids, molluscs and crustaceans (Appendix E). In 1987, annelids were the most numerous taxonomic group (9344 ind., 55.73%) ahead of molluscs (3168 ind., 18.89%) and crustaceans (3080 ind., 18.37%). Molluscs were the most numerous group in 2019 (6600 ind., 42.26%) ahead of annelids (6080 ind., 38.93%) and crustaceans (2448 ind., 15.68%). Sipunculids, echinoderms, platyhelminths and nemerteans contributed less than 5% of the total species richness and abundance. H', D, J and mean Richness all slightly decreased over time while total richness increased.

A total of 202 taxa were reported over 15 years at the station R. Richness (63.47 ± 11.27) and abundance (928.52 ind.m^{-2} ± 593.83) increased over the study period. Annelids, molluscs and crustaceans dominated the community (Appendix E). *Chaetozone gibber* (133.07 ind.m^{-2} ± 94.14), *Varicorbula gibba* (95.87 ind.m^{-2} ± 187.35), *Aponuphis bilineata* (60.07 ind.m^{-2} ± 34.39), *Abra alba* (44.67 ind.m^{-2} ± 92.79), *Ampelisca sarsi* (44.00 ind.m^{-2} ± 128.14), *Notomastus latericeus* (25.67

ind.m^{-2} ± 26.07), and *Ampelisca brevicornis* (24.93 ind.m^{-2} ±30.93) were dominant over the period studied. Some of them exhibited strong temporal variations, especially in the second part of the time series between 2012 and 2019 (Figure 2).

Changes were observed in the contribution of the main taxonomic groups to total local abundance between 1987 and 2019 (Figure 3, A and B): the contribution of molluscs increased in most stations, especially in the southern part of the study area. This change, also visible in the fauna of the station R occurred around 2015 (Figure 3, C). Before 2015, the abundance of each taxonomic group at station R was similar to the abundances measured in 1987 at the southern stations of the bay of Saint-Brieuc (stations 62 to 72).

3.3 Taxonomic clustering

3.3.1 Spatial clustering in 1987 and 2019

In both campaigns, HCAs separated the stations into four main clusters (i.e. benthic assemblages) (Figure 4). In 1987, according to indicator values (p-value<0.05), the southern assemblage I-87 was characterized by *C. gibber* and *Sigalion mathildae*, species occurring in shallower fine sands (Table I). *C. gibber* and *A. bilineata* were the most abundant species. Assemblage II-87, mainly located in western muddy-sands, was characterized by *A. brevicornis* and *V. gibba* and dominated by *A. brevicornis* and *Euclymene oerstedii*. Assemblage III-87, mainly located in the central part of the study area, occurred in muddy heterogeneous sediment. It was characterized by *Ampharete* spp. and dominated by *Ampharete* spp. and *Crepidula fornicata*. Assemblage IV-87 was located in the north of the study area, characterized by *Nototropis vedlomensis* and *N. latericeus,* and dominated by *N. latericeus* and *Nucula hanleyi*.

In 2019, the southern cluster was the most widespread assemblage (I-19, 19 stations), occurring in fine to muddy sands located between the southern and the central part of the study area. It was characterized by *V. gibba* and *Phyllodoce groenlandica* and dominated by *V. gibba* and *A. tenuicornis*. Assemblage II-19, occurring at nine stations mainly located in the northern-central part, was characterized by *Nephtys hombergii* and dominated by *N. latericeus* and *V. gibba*. Assemblage III-19 (6 stations) was identified in muddy heterogeneous sediments in the north and central parts, and typified by *C. fornicata* and *P. maximus* and dominated by *C. fornicata* and *N. latericeus*. Assemblage IV-19 was characterized and dominated by *Timoclea ovata* and *N. hanleyi* and limited to four north-western stations.

Species diversity was variable among assemblages (Table I). In 2019, the lowest H' values were observed in assemblages I-19 and IV-19. Temporal changes in the distribution of assemblages were concentrated in the southern part of the bay (Figure 4). The overall diversity (H', D, J) decreased in the shallower parts, as a consequence of the increase of *V. gibba*, and shallower bottoms gradually homogenised as showed by the assemblage I-19 distribution (50% of stations).

3.3.1 Temporal clustering from 2005 to 2019

The HCA performed on the station R dataset separated three clusters (Table II). Cluster I, composed of seven years, was characterized by *Caulleriella alata and Edwardsia claparedii.* Cluster II (4 years) was characterized by *Cirratulidae* spp. and *Tritia varicosa*. Cluster III, composed of four of the most recent surveys (2015, 2017, 2018, 2019), was typified by *Calyptraea chinensis* and *Spisula elliptica*. *C. gibber*, *A. bilineata* and *Ampelisca* spp*.* remained in the first five highest-ranking species in terms of abundance over the entire study period, and *V. gibba* and *A. alba* became dominant during the more recent surveys. Taxonomic diversity indices were quite stable between clusters except richness and abundance, which increased during recent observations (cluster III, Table II).

3.4 Species changes in bivalve populations

The abundance (Table III) and distribution (Appendix F) of the main bivalve species changed over time. Significant increases in abundance were detected for *Varicorbula gibba, Anomia ephippium, Bosemprella incarnata, Moerella donacina, Nucula hanleyi, Nucula nitidosa, Timoclea ovata* and *Pecten maximus*. Inversely *Polititapes rhomboides* and to a lesser extent *Fabulina fabula* decreased significantly over time.

3.5 Detecting trajectory patterns

3.5.1 Taxonomic trajectories

Long-term comparison. All sampling stations were characterised by taxonomic changes over time (Figure 5, A). Mean net change (± sd) calculated on the 38 stations was variable spatially (15.5 ± 2.23), ranging from 11.4 (station 74) to 21.5 (station 104). The HCA performed on CTA analysis of trajectory similarities separated four clusters according to the shape of taxonomic trajectories (Figure 5, A, B and C). Cluster A was composed of 20 stations describing the evolution from an assemblage dominated by *Ampharete* spp. and *A. brevicornis* in 1987 to an assemblage dominated by *V. gibba* and *C. fornicata* in 2019. Cluster B grouped 13 stations characterized by *A. bilineata* in 1987 and *V. gibba* in 2019. A shift between the dominant species *A. brevicornis* and *A. bilineata* (1987) to *V. gibba* and *A. tenuicornis* (2019) was observed. Mean net changes (± se) were slightly lower in cluster B (16.59 ± 1.09) than in cluster A (20.35 ± 0.66). The two other clusters characterized a limited number of specific trajectories exhibiting longer trajectory path in the north part of the study area (stations 105 and 106, and 107,104 and 94).

Most stations encountered similar changes in the multivariate space, as indicated by the similar trajectory directions. Direction (i.e. specific initial and final composition) and trajectory length seemed mainly responsible for the separation of clusters. The convergence of most trajectories, especially from clusters A and B, which grouped 87 % of trajectories, illustrate an homogenization over time with respect to the ecological state described in 1987.

Inter-annual dynamics. A first period from 2005 to 2014 was characterized by lower net changes than measured at the end of the time series, indicating a greater stability during this first period as underlined by consecutive departing and recovering patterns. This period was followed by a recent period of higher variability in composition and characterized by higher net change values (Figure 6, A). Even if *C. gibber* and *A. bilineata* remained among the five most dominant species, the trajectory underlined 1) the shift in dominance by different *Ampelisca* spp. Species, and 2) the dominance of *V. gibba* and *A. alba* in recent surveys (Table II). The alternation of recovering and departing dynamics resulted in low directionality (0.359) and low net change ratio (10.11%).

3.5.2 Functional trajectories

Long-term comparison. Net change was variable spatially (7.94 ± 2.53), ranging from 3.97 (station 87) to 15.24 (station 88). The HCA performed on CTA analysis of trajectory similarities separated three clusters of functional trajectories (Figure 7, A, B and C). Trajectory length and direction were mainly responsible for the separation of clusters. Cluster E grouped 27 stations (7.34 ± 0.36) which highest net change values were mainly located in the southern part of the study area, and were characterized by a decrease in the relative contribution of the following categories: 1) medium size, flexible, fragile; and 2) tubiculous, burrowers and tolerant species. Simultaneously, the contribution of suspension-feeders, predators and scavengers increased, as well as rigid, robust, and large and small species. Free-living species became dominant and the contribution of second-order opportunistic species increased. Cluster F grouped six trajectories characterized by higher net changes (10.59 ± 1.64). The main functional changes consisted in a decrease of deposit-feeders, tubiculous, and flexible and fragile species. This group of trajectories was specifically characterized by an important increase of CWM values of very sensitive species, and attached species mainly represented by *A. ephippium*. Cluster G characterized five trajectories (7.96 ± 0.79). In addition to a similar pattern concerning deposivorous and tubiculous species, these trajectories were specifically characterized by an increase in the contribution of predator, flexible, fragile, and burrowing species and a decrease of rigid, suspension-feeders and tolerant species. At the scale of the whole area including all stations, a similar global pattern was observed (Figure 8). Compared to 1987, the community was dominated by suspension-feeders and free-living species in 2019. Even if significant functional shifts in morphologic traits were observed over time, the fauna remained dominated by medium size, flexible and fragile species. According to the tolerance to nutrient enrichment trait, fauna remained dominated by very sensitive and indifferent species.

Inter-annual dynamics. Functional net change increased over time (Figure 6, B). Different categories of traits influenced the functional stability: axis I (41.4%) opposed organisms filter feeders, living free, rigid and robust to organisms deposit feeders, living in tubes and highly flexible (Appendix H). The alternation of recovering and departing dynamics resulted in low directionality (0.387) and net change ratio (10.04%).

3.6 Relation between taxonomic structure and environmental and spatial variables

According to the VIF analysis, coarse sand and mean particle size were excluded from the following analysis. The part of the variance explained by sedimentary variables was higher in 1987 (R^2adj=0.177; F=2.547; Pr(>F)=0.001) than in 2019 (R^2adj=0.055; F=1.420; Pr(>F)=0.003). Sedimentary variables characterized by finest grain size were significantly correlated to the taxonomic structure in 1987: fine sand (R^2adj=0.157), mud (R^2adj=0.123), and very fine sand (R^2adj=0.059). In 2019, two sedimentary variables were correlated: mud (R^2adj=0.050) and D50 (R^2adj=0.032). A linear spatial structuration was revealed for both years (R^2adj=0.089; F=2.752; Pr(>F)=0.001 in 1987 vs R^2adj=0.100; F=2.994; Pr(>F)=0.001 in 2019). In 1987, sedimentary and spatial variables explained 12% and 5% of the variance, respectively, while 4% was shared. In 2019, the part of the explained variance decreased and the contribution of spatial variables was higher (sedimentary: 2%, spatial: 7%, shared: 3%).

4. Discussion

4.1 Changes probably occurred recently

The results highlight the relevance of the Community Trajectory Analysis method to assess long-term changes in the spatial structure of benthic assemblages over the study area, based on the comparison of historical and up-to-date data in multivariate spaces.

Among the four taxonomic clusters identified in 2019, two of them, representing 74% of stations, pointed towards a potential degradation of habitats indicated by 1) the numerical increase of the opportunistic species *V. gibba*, and 2) the lower species diversity in one of the two assemblages. This was further confirmed by the analysis of trajectory similarity, which revealed that 87% of the stations (clusters A and B) were notably characterized by increases in the density of *V. gibba* from 1987 to 2019. At the scale of the study area, however, decreases of β species diversity remained very moderate (Appendix E).

Inter-annual dynamics at station R suggests that these changes are very recent (Figure 3). The lower variability observed at station R from 2005 to 2014 may depict natural dynamics, while recent changes since 2015 seem driven by a strong and cumulative disturbance regime. The recent shift in the taxonomic multivariate structure was driven by variations in the abundance of a few dominant species, among which *V. gibba*, *A. alba, C. chinensis* and *S. elliptica*. Interestingly, although benthic communities were highly variable over the last five years, sediment properties and organic matter content did not exhibit such variability, suggesting that the recent pattern in benthic community structure may not be strictly related to habitat characteristics.

4.2 Functional shifts

Ecological processes shaping energy flows in ecosystems are induced by a complex feedback system reflecting species adaption to their environment, while the environment is, in turn, constantly modified by biological activities (Levins & Lewontin, 1985; Díaz & Cabido, 2001; Pacheco et al., 2011).

Trait-based approaches have been widely used to characterize functional shifts, in response to different natural or human disturbance context (Thrush & Dayton, 2002; van Denderen et al., 2015; Bolam et al., 2017). The use of biological traits is expected to provide a good view of functional shifts over space and time (Pacheco et al., 2011). In our study, traits were chosen to assess the potential impacts of 1) fishing activities (size, flexibility, fragility, habitats, feeding habits) and 2) organic matter enrichment (tolerance, feeding habits).

Fishing activities. Trawling and dredging fishing activities are responsible of many impacts on the seabed, such as the modification of benthic communities and sedimentary habitats (Newell, Seiderer & Hitchcock, 1998; Ellis, Norkko & Thrush, 2000; Thrush & Dayton, 2002; Eigaard et al., 2017). Watling & Norse (1998) compared the consequences of disturbance induced on the seabed by mobile fishing gear to forest clear cutting. Scallop dredging in the Irish Sea has been shown to significantly modify benthic communities and *P. maximus* populations under experimental and commercial fishing pressure conditions (Bradshaw et al., 2001). Dredging activities tend to modify the structure of mounds, tubes, and burrows created by organisms living on the sediment surface, and limit small scale habitat structure heterogeneity (Thrush & Dayton, 2002). As underlined by Gray et al. (2006), the homogenization of heterogeneous habitats and the reduction of three-dimensional structures above and below the sediment-water interface constitute one of the most damaging effects of fishing activities.

In our study, current functional shifts within assemblages led to a relative dominance of robust, rigid and free living species which suggests selective mortality processes of fragile, flexible, and sedentary species due to fishing pressure and human disturbances (Constantino et al., 2009; Duplisea et al., 2002; Jennings et al., 2001; Kaiser et al., 2006; Pedersen et al., 2009). Despite concentrating the highest scallop dredging pressure in Brittany (Appendix A-1), no accurate spatio-temporal assessment of fishing pressure is available for the bay of Saint-Brieuc. The existence of a potential impact of fishing activities on macrobenthos may seem at odds with the increase of suspension-feeder abundances over time in the study area. Van Denderen et al. (2015) studied benthic functional response to fishing activities according to natural disturbance regimes. They showed that fishing impacts are smaller or absent in areas exposed to high natural disturbance, leading to the hypothesis that, depending on local hydrodynamics, natural and fishing disturbances may affect benthic communities in similar ways. The local wave regime has been broadly stable over the last 30 years (SHOM, Appendix H) ruling out a strong influence of hydrodynamics on the observed patterns.

Overall sedimentary changes may also have contributed to the decrease of deposit-feeders in the study area, as dredging activities are known to homogenise the sediment. Mengual et al. (2019, 2016) showed for example an overall erosion of muddy areas in the bay of Biscay in relation with fishing activities, and a coarsening trend of surface sediments (5cm). Morys, Brüchert & Bradshaw (2021) showed a significant decrease of surface organic matter content in a recent experimentation about the impact of bottom trawling on benthic biogeochemistry. Such organic matter content decrease were observed at station R from 2014 (Appendix D). In our study, sedimentary parameters partly shaped the taxonomic multivariate structure of the benthic community, but the amount of explained variance decreased between 1987 and 2019 indicating that sedimentary variables explain only a limited part of the observed changes.

Organic enrichment. The positive functional shift observed for second-order opportunistic species, and particularly *V.gibba,* seems to indicate an impact of organic matter enrichment in accordance with Hrs-Brenko (2006) who suggested that eutrophication increases the fecundity of *V. gibba*. During our study, small individuals of *V. gibba* were observed attached with their byssus to drifting *Ulva* sp., suggesting (1) a potential influence of algal mats offering new attachment substrates for early recruitment stages and (2) individuals could drift when attached to algal mats, hence facilitating the colonization of new areas. In the western English Channel, eutrophication can also extend the spawning season of *Abra alba* (Dauvin & Gentil, 1989) which could be partly responsible for the high abundance of *A. alba* observed at station R in 2015 and 2017. Local disturbance, predation/competition, and climatic factors are also known to control *A. alba* populations (Dauvin et al., 1993). The persistence of the observed changes needs to be confirmed as *A. alba* and *V. gibba* are known to present high population variations in such soft-bottom communities (Cabioch, 1968), however, such high inter-annual variability was not observed until the mid 2010s.

Despite the fact the positive shift of second-order species was mainly driven by *V. gibba*, the community was still dominated by species very sensitive to nutrient enrichment in 2019, some molluscs having increased in abundance and occurrence (*B. incarnata*, *Laevicardium crassum*, *T. ovata*, *M. donacina*, *N. hanleyi, P. maximus*). The diversity of temporal dynamics suggests a complex gradient of sensitivity to organic matter enrichment and the implication of additional driving factors. Indeed, (1) discards from scallop dredging could promote opportunistic species and scavengers leading to increases in their abundances (Depestele et al., 2019) and (2) by capturing nutrients, green tides are particularly suspected to buffer the influence of nutrient enrichment on macrofauna as discussed by Ponsero & Le Mao (2011) and Sturbois et al. (under review) concerning the neighbouring intertidal area.

As in other ecosystems impacted by anthropogenic activities, changes observed in the bay of Saint-Brieuc result from different pressures acting simultaneously at different spatio-temporal scales.

The selective mortality of fragile, flexible, tubiculous and burrower organisms suggests the influence of a physical disturbance. As wave regime was stable over the survey period (SHOM: Supplementary material, Appendix H), dredging activities appear as the most likely factor of disturbance. The magnitude of fishing influence is difficult to assess because of the lack of accurate data concerning dredging pressure. However, changes in fisheries regulations (i.e. fishing ground zonation) in 2010 and 2017, coupled to an increase in the *P. maximus* population, has led to an increase of scallop dredging activities and inherent mechanical disturbances of the seabed and associated benthic macrofauna. Nutrient enrichment probably drove the ecological response of the primary disturbed benthic assemblages by the stimulation of opportunistic-species, and concomitantly other suspension-feeder species. Climate change occurring at a larger scale, combined with the aforementioned local factors of disturbance, may also jointly control some other bivalve's populations.

4.3 Regional scale insights

Recent fishing ground assessments have shown an important increase in the populations of *P. maximus* from the English channel, and particularly in the Normano-Breton gulf where landings have increased from 1200 tons in 1989 to an average of 7000 tons since the early 2000s (Foucher et al., 2015; Foucher, 2017; Le Mao et al., 2019). Over the last ten years, *P. maximus* densities across all age classes have increased in the lowest levels of the intertidal area (pers. obs.) suggesting a similar scenario in shallow bottoms between the low water mark and a depth of 5 m. The management of *P. maximus* populations by fishermen in collaboration with scientists, as well as climate change, have favoured this stock increase (Shephard et al., 2010). Fishing activities in the bay, associated to recruitment fluctuations, may be involved in the drastic decline of other bivalve populations, such as *Polititapes rhomboides,* which was commercially harvested in the Bay until recently (Huet & Pitel, 2006).

Among other bivalve species, *Moerella donacina* and to a lesser extent *Timoclea ovata* increased in abundance and occurrence. These trends are congruent with those reported by Gaudin et al. (2018) who tracked changes in response to climate change in the English Channel. They notably showed, between the 1960s and 2014, important and moderate increases in occurrence and eastward movements of populations (i.e. tracking colder conditions) for *M. donacina* and *T.ovata,* respectively. Climate change (temperature increase) is also suspected to be responsible for changes in the abundance of *Albra alba* at station R [Dauvin *et al.*, 1993 ; Thiébaut & Houbin (comm. pers.)], and of *Limecola balthica* in the nearby intertidal mudflats of the bay of Saint-Brieuc (Sturbois et al., under review).

In the past decades, the slipper limpet *Crepidula fornicata* has progressively become an important component of soft-bottom benthic ecosystems in the English channel (Blanchard et al., 2001; Blanchard, 2005). Total stock reached an estimated 450000 tons in the bays of Saint-Brieuc and Mont Saint-Michel in the early 2000s (Blanchard & Hamon, 2006). Current trends are not documented, except in the bay of Brest, where Blanchet-Aurigny et al. (2012) reported that historical *Crepidula fornicata* beds are currently mainly made up of dead shells. In our study, a decrease in the mean density *C. fornicata* was observed (40.21 ind.m^{-2} ± 182.42 in 1987 vs 21.11 ind.m^{-2} ± 48.46 in 2019), but this overall trend is driven by change observed at a single station (105), while densities remained stable for the rest of the bay.

4.4 What conservation perspectives for such coastal areas?

Among the different species sampled in this study, *V. gibba* experienced the strongest increase in abundance, especially in the southern part of the study area. *V. gibba* is considered as an indicator of environmental instability whose strong increase across Europe has been largely associated to disturbances (Hrs-Brenko, 2006), particularly pollution and sedimentary instability (Pearson & Rosenberg, 1978; Salen-Picard, 1981; FAO & UNEP, 1985; Pranovi, Da Ponte & Torricelli, 2007). Unstable conditions have been reported to promote *V. gibba* populations (Rosenberg, 1977; Pranovi, Giovanardi & Franceschini, 1998). Cabioch (1968) already noted an alternation between *V. gibba* and *A. alba* abundance peaks in the Western English channel, similar to what we observed at station R.

High larval settlement of *V. gibba* is known to frequently appear after catastrophic events (Hrs-Brenko, 2006). This species, which grows rapidly (Jensen, 1990), shows strong survival capacity to different abiotic (resistant to pollution, turbidity, hypoxia, and sedimentation) and biotic stressors. In Australia, where this species is invasive, dramatic rises in abundance can have negative effects on the growth rate of *Pecten fumatus* juveniles, a commercial species, as demonstrated experimentally by Talman

& Keough (2001). The bay of Saint-Brieuc, which suffers from eutrophication (but without hypoxic episodes) and supports intensive scallop dredging activities, appears to be a favourable area for the proliferation of this species.

The massive recruitment of *V. gibba* also characterizes the pioneer stages of benthic community dynamics following a perturbation (Pranovi, Giovanardi & Franceschini, 1998). Bonvicini-Pagliai & Serpagli (1988) called this species “a time recorder of environmental stress”. As a dominant suspension-feeder, with rapid juvenile and adult growth, *V. gibba* plays an important role in the food web by transfering pelagic production to the benthic compartment (Hrs-Brenko, 2006). Once the disturbance regime decreases, biotic interactions will progressively regulate *V. gibba* populations (Olafsson, Peterson & Ambrose, 1994). Knowledge on the level of disturbance required for the persistence of an abundant *V. gibba* population and its ability to increase in abundance in the absence of a primary disturbance factor is crucial to disentangle effects of natural and anthropogenic factors (Australian government, 2008).

When developing management plans for marine areas and benthic resources, stakeholders must consider that benthic communities have the capacity to adapt to a predictable and moderate level of anthropogenic disturbance. However, there is a threshold beyond which populations, even composed of ‘resistant’ species, will collapse and cause the impoverishment of communities, with loss of major ecological functions and inevitable negative feedbacks, even on target species (Pranovi, Giovanardi & Franceschini, 1998).

The ecological state defined in 1987 does not constitute a reference state, and even less a conservation target, as nutrient enrichment and fishing pressures were probably already well established. CTA could bring new perspectives to the assessment of the ecological distance between current and reference status (Borja, Dauer & Grémare, 2012), by measuring net changes with respect to a predefined reference state. Ideally, such ecological baseline should be defined within an ecological entity, in unaffected areas. In the absence of a local pristine state, or of an ecological state that could be considered as a conservation target, it should be possible to include in the analysis data from similar ecosystems located in the same region to define a reference state in the multivariate space (e.g. a centroid of samples considered as a potential conservation target, including natural variability). Net change calculations over time, with respect to the reference status, may allow the accurate measurement of the restoration process through recovering trajectories. The definition of conservation targets in multivariate spaces could underline the degradation level, with respect to historical data, and help local governance adapt management perspectives.

Activities with potentially conflicting goals are concentrated in the “Baie de Saint-Brieuc-Est” Natura 2000 site with fishing on the one hand and benthic habitat conservation on the other. The assessment of fishing impacts on Natura 2000 sites require high-resolution spatial environmental data, including distribution of natural habitats and species, as well as fine-scale data on the distribution of ongoing fishing activities that overlap with high-value conservation zones (Pedersen et al., 2009; AFB et al., 2019; Lusenius, H. et al., 2019). In this context, this study (1) underlines the value of historical data, even if they do not constitute a pristine state and the limitations in their use as conservation targets, (2) provides up-to-date information about the distribution of benthic assemblages and associated species, and (3) confirms the necessity of measuring the fishing pressure to correctly interpret changes in marine ecosystems attributable to human activities. In our study, the use of the station R data set was essential to the better understanding of long-term changes observed between only two sampling dates (1987 vs 2019). It confirms that the coupling of different spatial and temporal scales in any sampling strategy [few stations with high frequency sampling (Hewitt, Ellis & Thrush, 2016) *vs* low frequency larger sampling networks (Kröncke et al., 2011)] helps to track changes between long-term sampling networks as suggested by Bacouillard et al. (2020) and Callaway (2016) and that the development of such monitoring strategy is important for the future.

This study clearly suffers from the lack of knowledge concerning fishing pressure and potential control areas free of fishing impacts. Unfortunately, there is no area free of dredging activity in the study site or in peripheral areas. Alternatives to characterize the impact of fishing activities in the study area could consist in studying the response of benthic communities to a gradient of fishing pressures as proposed by van Denderen et al. (2015), or within an experimental area closed to commercial fishing as tested by Bradshaw et al. (2001). Further work is needed to 1) quantify fishing efforts in the shallow area (via abrasion maps) as such accurate information is lacking, and 2) design a strategy based on the comparison between dredged and un-dredged areas.

Overall, access to highly resolved information about fishing activities is paramount to help understand changes in benthic communities and distinguish the impact of fishing activities and other driving factors (nutrient enrichment, sediment instability, climate change) on benthic communities. Up-to-date documented reports on ecological changes and conservation status must be shared with stakeholders to effectively inform public debates (Eastwood et al., 2007; Pedersen et al., 2009). Consultation processes should involve policy makers, members of fishing institutions, fishermen, environmental organizations, and managers of Marine Protected Areas (MPAs) when present. This step should ideally lead to the implementation of fishery management measures to reduce threats, and achieve conservation objectives (Pedersen et al., 2009; AFB et al., 2019; Lusenius, H. et al., 2019).

Although progress in expanding the coverage of MPAs has been made, the application of management tools has not yet been implemented in most of these areas (Torriente et al., 2019). Conservation of the marine environment is effectively a relatively new phenomenon and is currently playing ‘catch-up’ with its terrestrial counterpart where protected areas have been established for many decades (Morris et al., 2014). Despite the need for a worldwide improvement in the designation and management processes of marine areas, it has already been demonstrated that local human impacts on the marine environment could be effectively reduced within networks of Natura 2000 and Marine protected Areas (Fraschetti et al., 2018; Zupan et al., 2018). Management plans are recommended for Natura 2000 sites but are not mandatory under the Habitats Directive. Nevertheless, they appear to be an appropriate solution to reflect transparent conservation objectives (European Commission, 2011). Despite their complexity, fishing regulations implemented through a consultation process and management scheme have been shown to represent win-win scenarios between economic and conservation goals in different marine protected areas around the world (N2K group, 2018). In the bay of Saint-Brieuc, the implementation of such win-win scenarios enabled the long-term management of *P. maximus* population with benefits for the fishermen, and more modestly, promoted Cockle fishing grounds (Ponsero, Dabouineau & Allain, 2009). Similar trends were reported in the Irish sea by Bradshaw et al. (2001), who showed positive effects of commercial fishing area closures on *P. maximus* (and indirectly on fishermen) and on benthic communities which became more diverse.

Faced with our results, which clearly underlined a degradation of soft-bottom macrobenthos, the ball is in stakeholder's court to integrate this new knowledge in governance processes and impulse an ambitious conservation strategy. The existence of a national nature reserve, strongly involved in the study, constitute a breeding ground for such an approach.

Acknowledgements

We thank anonymous reviewers of previous versions of this manuscript for their constructive comments. We sincerely thank the crew of the R/V“Thalia” which participated in the oceanographic cruise RESTRO 19. We acknowledge all people involved in the laboratory analyses with a special mention to Charles Veilllard, which made a significant contribution to the laboratory analyses. This work was carried out as part A. Sturbois’ PhD thesis at the Université de Bretagne Occidentale. It was funded by Agence de l’Eau Loire-Bretagne (grant number 180212501), the Région Bretagne (OSIRIS FEA621219CR0530023), the Europe for the European maritime and fisheries fund (grant number FEAMP 621-B) and the Ministère de la Transition Ecologique et Solidaire (grant number EJ N°2102930123) who fund the ResTroph Baie de Saint-Brieuc research program. The long-term monitoring program at Station R is part of the REBENT program, coordinated by Sandrine Derrien (MNHN) and of the WFD monitoring program, coordinated by Ifremer. It was funded by Agence de l'Eau Loire Bretagne, the Région Bretagne and the Ministère de la Transition Ecologique et Solidaire. We thank Heloise Michaud and Léo SeyFried from the SHOM for providing information about the regime of waves.

Declaration of Competing Interest

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

Credit authorship contribution statement

Anthony Sturbois: Conceptualization, Methodology, Validation, Formal analysis, Data curation, Writing - original draft, Visualization, Project administration, Funding acquisition, Investigation (Restro 19). **Gaëtan Cormy:** Writing - review & editing, Investigation (Restro 19). **Alexandre Le Moal:** Writing - review & editing, Investigation (Restro 19). **Gauthier Schaal:** Writing - review & editing, Investigation (Restro 19), Supervision. **Caroline Broudin:** Writing - review & editing, Investigation (WFD). **Eric Thiébault:** Writing - review & editing, Investigation (WFD). **Alain Ponsero:** Writing - review & editing, Visualization, Investigation (Restro 19). **Patrick Le Mao:** Writing - review & editing, Investigation (Restro 19). **Auriane Jones:** Writing - review & editing. **Pascal Riera:** Writing - review & editing. **Olivier Gauthier:** Methodology, Writing - review & editing, Validation. **Nicolas Desroy:** Methodology, Writing - review & editing, Investigation (Restro 19), Supervision, Validation.

References

AFB, MNHN, MAA & MTES. (2019). *Habitats benthiques et activités de pêche professionnelle dans les sites Natura 2000: Méthodologie d'évaluation des risques de porter atteinte aux objectifs de conservation des sites.*

Australian government. (2008). *National Control Plan. European or basket shell clam Varicorbula gibba*.

Bacouillard, L., Baux, N., Dauvin, J.-C., Desroy, N., Geiger, K.J., Gentil, F., et al. (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(2), 105062. https://doi.org/10.1016/j.marenvres.2020.105062

Blanchard, M. (2005). *Dynamique de la population de crépidule (Crepidula fornicata) en Baie du Mont Saint-Michel.* IFREMER.

Blanchard, M. & Hamon, D. (2006). *Bilan du suivi de l'exploitation industrielle de la crépidule en Bretagne Nord (baies de Saint-Brieuc et du Mont Saint-Michel) 2002–2005.* IFREMER.

Blanchard, M., Blanchet, A., Gaffet, J.D. & Hamon, D. (2001). *Dynamique de population de la crépidule (Crepidula fornicata) en baie de Saint-Brieuc (Manche-Ouest)*. IFREMER.

Blanchet, F.G., Legendre, P. & Borcard, D. (2008). Forward selection for explanatory variables. *Ecology*, 89(9), 2623–2632. https://doi.org/10.1890/07-0986.1

Blanchet-Aurigny, A., Dubois, S., Hily, C., Rochette, S., Le Goaster, E. & Guillou, M. (2012). Multi-decadal changes in two co-occurring ophiuroid populations. *Marine Ecology Progress Series*, 460, 79–90. https://doi.org/10.3354/meps09784

Bolam, S.G., Garcia, C., Eggleton, J., Kenny, A.J., Buhl-Mortensen, L., Gonzalez-Mirelis, G., et al. (2017). Differences in biological traits composition of benthic assemblages between unimpacted habitats. *Marine Environmental Research*, 126, 1–13. https://doi.org/10.1016/j.marenvres.2017.01.004

Bonvicini-Pagliai, A.M. & Serpagli, F. (1988). *Corbula gibba (Olivi) as a time recorder of environmental stress. A first contribution.* Rapp. Comm. int. Mer Médit., Report number: 31(2):17.

Borja, Á., Dauer, D.M. & Grémare, A. (2012). The importance of setting targets and reference conditions in assessing marine ecosystem quality. *Ecological Indicators*, 12(1), 1–7. https://doi.org/10.1016/j.ecolind.2011.06.018

Borja, A., Muxika, I. & Rodríguez, J.G. (2009). Paradigmatic responses of marine benthic communities to different anthropogenic pressures, using M-AMBI, within the European Water Framework Directive. *Marine ecology*, 30(2), 214–227.

Bradshaw, C., Veale, L.O., Hill, A.S. & Brand, A.R. (2001). The effect of scallop dredging on Irish Sea benthos: Experiments using a closed area. *Hydrobiologia*, 465(1/3), 129–138. https://doi.org/10.1023/A:1014573731609

Cabioch, L. (1968). *Contribution à la connaissance des peuplements benthiques de la Manche occidentale*. Station biologique de Roscoff.

Callaway, R. (2016). Historical Data Reveal 30-Year Persistence of Benthic Fauna Associations in Heaviy Modified Waterbody. *Frontiers in Marine Science*, 3, 1-13. https://doi.org/10.3389/fmars.2016.00141

Charlier, R.H., Morand, P., Finkl, C.W. & Thys, A. (2007). Green Tides on the Brittany Coasts. *Environmental Research, Engineering and Management*, 3(41), 52–59.

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

Cimon, S. & Cusson, M. (2018). Impact of multiple disturbances and stress on the temporal trajectories and resilience of benthic intertidal communities. *Ecosphere*, 9(10), e02467. https://doi.org/10.1002/ecs2.2467

Claudet, J. & Fraschetti, S. (2010). Human-driven impacts on marine habitats: A regional meta-analysis in the Mediterranean Sea. *Biological Conservation*, 143(9), 2195–2206. https://doi.org/10.1016/j.biocon.2010.06.004

Constantino, R., Gaspar, M.B., Tata-Regala, J., Carvalho, S., Cúrdia, J., Drago, T., et al. (2009). Clam dredging effects and subsequent recovery of benthic communities at different depth ranges. *Marine Environmental Research*, 67(2), 89–99. https://doi.org/10.1016/j.marenvres.2008.12.001

Convention on Biological Diversity. (2010). *Aichi Biodiversity Targets. Tenth meeting of the conference of the parties - COP10*.

Dauvin, J.-C. & Desroy, N. (2005). The food web in the lower part of the Seine estuary: a synthesis of existing knowledge. *Hydrobiologia*, 540(1–3), 13–27. https://doi.org/10.1007/s10750-004-7101-3

Dauvin, J.-C. & Gentil, F. (1989). Long-term changes in populations of subtidal bivalves (*Abra alba* and *A. prismatica*) from the Bay of Morlaix (Western English Channel). *Marine Biology*, 103(1), 63–73. https://doi.org/10.1007/BF00391065

Dauvin, J.-C., Dewarumez, J.-M., Elkaim, B., Bernardo, D., Fromentin, J.-M. & Ibanez, F. (1993). Cinétique de *Abra alba* (mollusque bivalve) de 1977 à 1991 en Manche-Mer du Nord, relation avec les facteurs climatiques. *Oceanologica Acta*, 16(4), 413–422.

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

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

van Denderen, P., Bolam, S., Hiddink, J., Jennings, S., Kenny, A., Rijnsdorp, A., et al. (2015). Similar effects of bottom trawling and natural disturbance on composition and function of benthic communities across habitats. *Marine Ecology Progress Series*, 541, 31–43. https://doi.org/10.3354/meps11550

Depestele, J., Feekings, J., Reid, D.G., Cook, R., Gascuel, D., Girardin, R., et al. (2019). *The Impact of Fisheries Discards on Scavengers in the Sea*. In: , Uhlmann SS, Ulrich C, & , Kennelly SJ (eds). *The European Landing Obligation*. Springer International Publishing, 129–162.

Desroy, N. & Retière, C. (2004). Using benthos as a tool for coastal management: The impact of the tidal power station on benthic communities of the Rance basin. *Aquatic Ecosystem Health & Management*, 7(1), 59–72. https://doi.org/10.1080/14634980490281263

Desroy, N., Janson, A.-L., Denis, L., Charrier, G., Lesourd, S. & Dauvin, J.-C. (2007). The intra-annual variability of soft-bottom macrobenthos abundance patterns in the North Channel of the Seine estuary. *Hydrobiologia*, 588(1), 173–188. https://doi.org/10.1007/s10750-007-0661-2

Desroy, N., Warembourg, C., Dewarumez, J.M. & Dauvin, J.C. (2002). Macrobenthic resources of the shallow soft-bottom sediments in the eastern English Channel and southern North Sea. *ICES Journal of Marine Science*, 60(1), 120–131. https://doi.org/10.1006/jmsc.2002.1333

Díaz, S. & Cabido, M. (2001). Vive la différence: plant functional diversity matters to ecosystem processes. *Trends in Ecology & Evolution*, 16(11), 646–655. https://doi.org/10.1016/S0169-5347(01)02283-2

Dornelas, M., Magurran, A.E., Buckland, S.T., Chao, A., Chazdon, R.L., Colwell, R.K., et al. (2013). Quantifying temporal change in biodiversity: challenges and opportunities. *Proceedings of the Royal Society B: Biological Sciences*, 280(1750), 20121931. https://doi.org/10.1098/rspb.2012.1931

Dufrene, M. & Legendre, P. (1997). Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological monographs*, 67(3), 345–366.

Duplisea, D.E., Jennings, S., Randall, K. & Dinmore, T.A. (2002). A size-based model of the impacts of bottom trawling on benthic community structure. *Canadian Journal of Fisheries and Aquatic Sciences*, 59(11), 1785–1795.

Eastwood, P.D., Mills, C.M., Aldridge, J.N., Houghton, C.A. & Rogers, S.I. (2007). Human activities in UK offshore waters: an assessment of direct, physical pressure on the seabed. *ICES Journal of Marine Science*, 64(3), 453–463. https://doi.org/10.1093/icesjms/fsm001

Eigaard, O.R., Bastardie, F., Hintzen, N.T., Buhl-Mortensen, L., Buhl-Mortensen, P., Catarino, R., et al. (2017). The footprint of bottom trawling in European waters: distribution, intensity, and seabed integrity. M Kaiser, *ICES Journal of Marine Science*, 74(3), 847–865. https://doi.org/10.1093/icesjms/fsw194

Ellis, J.I., Norkko, A. & Thrush, S.F. (2000). Broad-scale disturbance of intertidal and shallow sublittoral soft-sediment habitats; effects on the benthic macrofauna. *Journal of Aquatic Ecosystem Stress and Recovery*, 7, 57–74. https://doi.org/10.1023/A:1009923530894

European Commission. (2011). *Guidelines on the implementation of the Birds and Habitats Directives in estuaries and coastal zones with particular attention to port development and dredging.*

FAO & UNEP. (1985). *Meeting on the Effects of Pollution on Marine Ecosystems.* Blanes, Spain.

Foucher, E. (2017). *Evaluation annuelle du stock de coquilles Saint-Jacques (Pecten maximus) de la baie de Seine : résultats de la campagne COMOR 2017.*

Foucher, E., Blanchard, M., Cugier, P., Desroy, N., Dreanno, C., Fauchot, J., et al. (2015). *Ecosystem interactions and anthropogenic impacts on King scallop (Pectenmaximus) populations in the English Channel.*

Fournier, J., Gallon, R.K. & Paris, R. (2014). G2Sd: a new package for the statistical analysis of unconsolidated sediments. *Géomorphologie: relief, processus, environnement*, 1, 73–78.

Fraschetti, S., Pipitone, C., Mazaris, A.D., Rilov, G., Badalamenti, F., Bevilacqua, S., et al. (2018). Light and Shade in Marine Conservation Across European and Contiguous Seas. *Frontiers in Marine Science*, 5, 420. https://doi.org/10.3389/fmars.2018.00420

Gaudin, F., Desroy, N., Dubois, S.F., Broudin, C., Cabioch, L., Fournier, J., et al. (2018). Marine sublittoral benthos fails to track temperature in response to climate change in a biogeographical transition zone. *Ices Journal Of Marine Science* , 75(6), 1894-1907 . https://doi.org/10.1093/icesjms/fsy095

Gravier, D. (2012). Monitoring of green tides on the Brittany coasts (France). *Primary Producers of the Sea*, Bio 458, 9.

Gray, J.S. (1997). Marine biodiversity: patterns, threats and conservation needs. *Biodiversity and Conservation*, (6), 153–175.

Gray, J.S., Dayton, P., Thrush, S. & Kaiser, M.J. (2006). On effects of trawling, benthos and sampling design. *Marine Pollution Bulletin*, 52(8), 840–843. https://doi.org/10.1016/j.marpolbul.2006.07.003

Gros, P. & Hamon, D. (1988). *Typologie biosédimentaire de la Baie de Saint-Brieuc (Manche ouest) et estimation de la biomasse des catégories trophiques macrozoobenthiques.* IFREMER.

Hedges, J.I. & Stern, J.H. (1984). Carbon and nitrogen determinations of carbonate-containing solids [In sediments, sediment trap materials and plankton]. *Limnology and Oceanography*, 29(3), 657–663.

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), 2665–2675. https://doi.org/10.1111/gcb.13176

Hrs-Brenko, M. (2006). The basket shell, *Corbula gibba* Olivi, 1792 (Bivalve Mollusks) as a species resistant to environmental disturbances: A review. *Acta Adriatica*, 47(1), 49-64.

Huet, J. & Pitel, M. (2006). *Evaluation du stock de palourdes roses Paphia rhomboïdes en baie de St Brieuc*. IFREMER.

Jennings, S., Pinnegar, J.K., Polunin, N.V.C. & Warr, K.J. (2001). Impacts of trawling disturbance on the trophic structure of benthic invertebrate communities. *Marine Ecology Progress Series*, 213, 127–142.

Jensen, J.N. (1990). Increased abundance and growth of the suspension-feeding bivalve *Corbula gibba* in a shallow part of the eutrophic Limfjord, Denmark. *Netherlands Journal of Sea Research*, 27(1), 101–108. https://doi.org/10.1016/0077-7579(90)90038-I

Kaiser, M., Clarke, K., Hinz, H., Austen, M., Somerfield, P. & Karakassis, I. (2006). Global analysis of response and recovery of benthic biota to fishing. *Marine Ecology Progress Series*, 311, 1–14. https://doi.org/10.3354/meps311001

Kröncke, I., Reiss, H., Eggleton, J.D., Aldridge, J., Bergman, M.J.N., Cochrane, S., et al. (2011). Changes in North Sea macrofauna communities and species distribution between 1986 and 2000. *Estuarine, Coastal and Shelf Science*, 94(1), 1–15. https://doi.org/10.1016/j.ecss.2011.04.008

Le Luherne, E., Le Pape, O., Murillo, L., Randon, M., Lebot, C. & Réveillac, E. (2017). Influence of Green Tides in Coastal Nursery Grounds on the Habitat Selection and Individual Performance of Juvenile Fish. *HM Patterson, Ed. Plos One*, 12(1), e0170110. https://doi.org/10.1371/journal.pone.0170110

Le Luherne, E., Réveillac, E., Ponsero, A., Sturbois, A., Ballu, S., Perdriau, M., et al. (2016). Fish community responses to green tides in shallow estuarine and coastal areas. *Estuarine, Coastal and Shelf Science*, (175), 79–92.

Le Mao, P., Godet, L., Fournier, J., Desroy, N., Gentil, F., Thiébaut, E., et al. (2019). *Atlas de la faune marine invertébrée du golfe Normano-Breton. Volume 6. Espèces d'intérêt particulier*. Editions de la Station biologique de Roscoff.

Legendre, P. & Gallagher, E.D. (2001). Ecologically meaningful transformations for ordination of species data. *Oecologia*, 129(2), 271–280.

Levins, R. & Lewontin, R. (1985). *The Dialectical Biologist.* Aakar Books

Levinton, J.S. (2001). *Marine biology: function, biodiversity, ecology*. Oxford:University Press Oxford.

Lusenius, H., Nylén, T., Kuris, M., Karvinen, V. & Vikström, S. (2019). *Marine Natura 2000 areas and Maritime Spatial Planning*. Plan4Blue report.

Magurran, A.E., Dornelas, M., Moyes, F. & Henderson, P.A. (2019). Temporal β diversity—A macroecological perspective. *D Storch, Ed. Global Ecology and Biogeography*, 28(12), 1949–1960. https://doi.org/10.1111/geb.13026

McLusky, D.S. & Elliott, M. (2004). The estuarine ecosystem: ecology, threats, and management. Oxford: University Press Oxford (UK).

Mengual, B., Cayocca, F., Le Hir, P., Draye, R., Laffargue, P., Vincent, B., et al. (2016). Influence of bottom trawling on sediment resuspension in the 'Grande-Vasière' area (Bay of Biscay, France). *Ocean Dynamics*, 66(9), 1181–1207. https://doi.org/10.1007/s10236-016-0974-7

Mengual, B., Le Hir, P., Cayocca, F. & Garlan, T. (2019). Bottom trawling contribution to the spatio-temporal variability of sediment fluxes on the continental shelf of the Bay of Biscay (France). *Marine Geology*, 414, 77–91. https://doi.org/10.1016/j.margeo.2019.05.009

Morris, R.K.A., Bennett, T., Blyth-Skyrme, R., Barham, P.J. & Ball, A. (2014). Managing Natura 2000 in the marine environment – An evaluation of the effectiveness of ‘management schemes’ in England. *Ocean & Coastal Management*, 87, 40–51. https://doi.org/10.1016/j.ocecoaman.2013.10.017

Morys, C., Brüchert, V. & Bradshaw, C. (2021). Impacts of bottom trawling on benthic biogeochemistry: an experimental field study. *Marine Environmental Research*, 105384. https://doi.org/10.1016/j.marenvres.2021.105384

N2K group. (2018). *Review of fisheries management measures in Natura 2000 sites.*

Newell, R., Seiderer, L. & Hitchcock, D. (1998). The impact of dredging works in coastal waters: a review of the sensitivity to disturbance and subsequent recovery of biological resources on the sea bed. *Oceanography and marine biology*, 36, 127–178.

Olafsson, E.B., Peterson, W.G. & Ambrose, Jr. (1994). Does recruitment limitation structure populations and communities of macro-in-vertebrates in marine soft sediments?: the relative significance of pre and post-settlement processes. *Oceanography and Marine Biology*, 32, 65–109.

Pacheco, A.S., González, M.T., Bremner, J., Oliva, M., Heilmayer, O., Laudien, J., et al. (2011). Functional diversity of marine macrobenthic communities from sublittoral soft-sediment habitats off northern Chile. *Helgoland Marine Research*, 65(3), 413–424. https://doi.org/10.1007/s10152-010-0238-8

Pearson, T.H. & Rosenberg, R. (1978). Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Oceanography and Marine Biology: Annual Review*, 16, 229–311.

Pedersen, S.A., Fock, H., Krause, J., Pusch, C., Sell, A.L., Böttcher, U., et al. (2009). Natura 2000 sites and fisheries in German offshore waters. *ICES Journal of Marine Science*, 66(1), 155–169. https://doi.org/10.1093/icesjms/fsn193

Ponsero, A. & Le Mao, P. (2011). Consommation de la macro-faune invertébrée benthique par les oiseaux d’eau en baie de Saint-Brieuc. *Revue d’Ecologie*, 66, 383–397.

Ponsero, A., Dabouineau, L. & Allain, J. (2009). Modelling of the Cockle (*Cerastoderma edule* L.) fishing grounds in a purpose of sustainable management of traditional harvesting. *Fisheries Science*, 75(4), 839–850.

Pranovi, F., Da Ponte, F. & Torricelli, P. (2007). Application of biotic indices and relationship with structural and functional features of macrobenthic community in the lagoon of Venice: an example over a long time series of data. *Marine Pollution Bulletin*, 54(10), 1607–1618.

Pranovi, F., Giovanardi, O. & Franceschini, G. (1998). Recolonization dynamics in areas disturbed by bottom fishing gears. In: , Baden S, , Phil L, , Rosenberg R, , Strömberg J-O, , Svane I, & , Tiselius P (eds). *Recruitment, Colonization and Physical-Chemical Forcing in Marine Biological Systems*. Springer Netherlands: Dordrecht, 125–135.

R Development Core Team. (2020). *A language and environment for statistical computing*. http://www.R-project.org/.

Ricotta, C. & Moretti, M. (2011). CWM and Rao’s quadratic diversity: a unified framework for functional ecology. *Oecologia*, 167(1), 181–188. https://doi.org/10.1007/s00442-011-1965-5

Rosenberg, R. (1977). Benthic macrofaunal dynamics, production, and dispersion in an oxygen-deficient estuary of west Sweden. *Journal of Experimental Marine Biology and Ecology*, 26(2), 107–133. https://doi.org/10.1016/0022-0981(77)90102-2

Salen-Picard, C. (1981). Évolution d’un peuplement de Vase Terrigène Côtière soumis à des rejets de dragages dans le golfe de Fos. *Téthys*, (10), 83–88.

Salonen, K. (1979). A versatile method for the rapid and accurate determination of carbon by high temperature combustion1. *Limnology and Oceanography*, 24(1), 177–183. https://doi.org/10.4319/lo.1979.24.1.0177

Shephard, S., Beukers-Stewart, B., Hiddink, J.G., Brand, A.R. & Kaiser, M.J. (2010). Strengthening recruitment of exploited scallops *Pecten maximus* with ocean warming. *Marine Biology*, 157(1), 91–97. https://doi.org/10.1007/s00227-009-1298-7

Snelgrove, P.V.R. (1997). The importance of marine sediment biodiversity in ecosystem processes. *Ambio*, 26(8), 578–583.

Snelgrove, P.V.R. (1999). Getting to the Bottom of Marine Biodiversity: Sedimentary Habitats. BioScience, 49(2), 129. https://doi.org/10.2307/1313538

Sturbois, A., Cormy, G., Schaal, G., Gauthier, O., Ponsero, A., Le Mao, P., et al. (under review). Quantifying spatio-temporal changes in benthic communities: taxonomic and functional trajectories of intertidal assemblages in the bay of Saint-Brieuc.

Sturbois, A., De Cáceres, M., Sánchez-Pinillos, M., Schaal, G., Gauthier, O., Le Mao, P., et al. (2021). Extending Community Trajectory Analysis: new metrics and representation. *Ecological Modelling*, 440, 109400. https://doi.org/10.1016/j.ecolmodel.2020.109400

Talman, S. & Keough, M. (2001). Impact of an exotic clam, Corbula gibba, on the commercial scallop Pecten fumatus in Port Phillip Bay, south-east Australia: evidence of resource-restricted growth in a subtidal environment. *Marine Ecology Progress Series*, 221, 135–143. https://doi.org/10.3354/meps221135

Thrush, S.F. & Dayton, P.K. (2002). Disturbance to marine benthic habitats by trawling and dredging: implications for marine biodiversity. *Annual Review of Ecology and Systematics*, 33, 449–473.

Torriente, A., González-Irusta, J.M., Aguilar, R., Fernández-Salas, L.M., Punzón, A. & Serrano, A. (2019). Benthic habitat modelling and mapping as a conservation tool for marine protected areas: A seamount in the western Mediterranean. Aquatic Conservation: *Marine and Freshwater Ecosystems*, 29(5), 732–750. https://doi.org/10.1002/aqc.3075

Trigui, R.J. (2009). I*nfluence des facteurs environnementaux et anthropiques sur la structure et le fonctionnement des peuplements benthiques du Golfe Normano-Breton.* Museum National d'Histoire Naturelle.

UNEP. (2011). *Towards a green economy: Pathways to sustainable development and poverty eradication (a synthesis for policy makers)*.

Watling, L. & Norse, E.A. (1998). Disturbance of the Seabed by Mobile Fishing Gear: A Comparison to Forest Clearcutting. *Conservation Biology*, 12(6), 1180–1197. https://doi.org/10.1046/j.1523-1739.1998.0120061180.x

WoRMS Editorial Board. (2020). *World Register of Marine Species*. http://www.marinespecies.org

Yang, L.H. (2020). Toward a more temporally explicit framework for community ecology. *Ecological Research*, 35(3), 445–462. https://doi.org/10.1111/1440-1703.12099

Zupan, M., Bulleri, F., Evans, J., Fraschetti, S., Guidetti, P., Garcia-Rubies, A., et al. (2018). How good is your marine protected area at curbing threats? *Biological Conservation*, 221, 237–245. https://doi.org/10.1016/j.biocon.2018.03.013

FIGURES ET TABLES

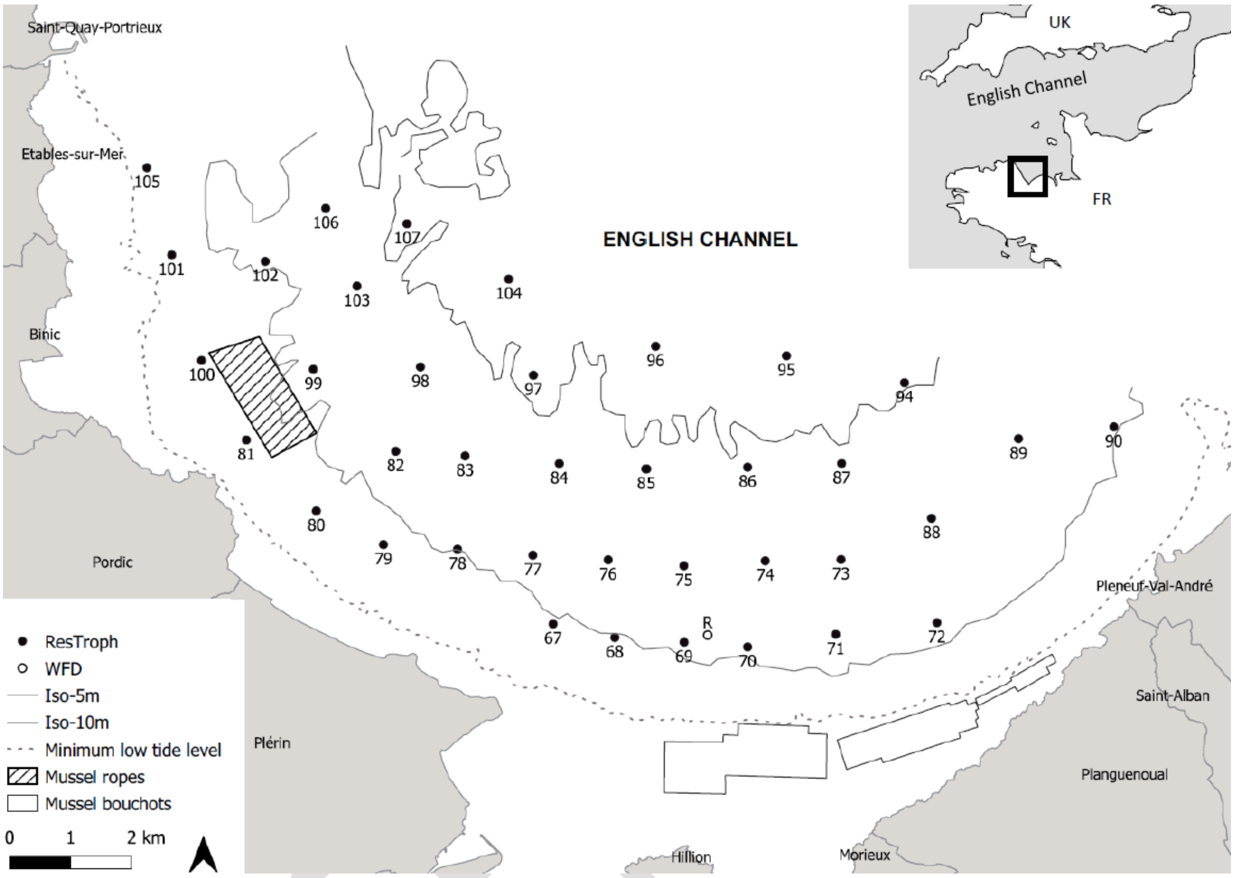


Figure 1: Location of the study area and sampling strategy. Black dots corresponds to the 38 stations of the ResTroph research program sampled in 1987 and 2019 and white one (station R) to the Water Framework Directive (WFD) monitoring program conducted from 2005 to 2019. Water depth is represented by dotted (0 m) and continuous lines (5 and 10 m) and mussel bouchots and ropes by polygons.

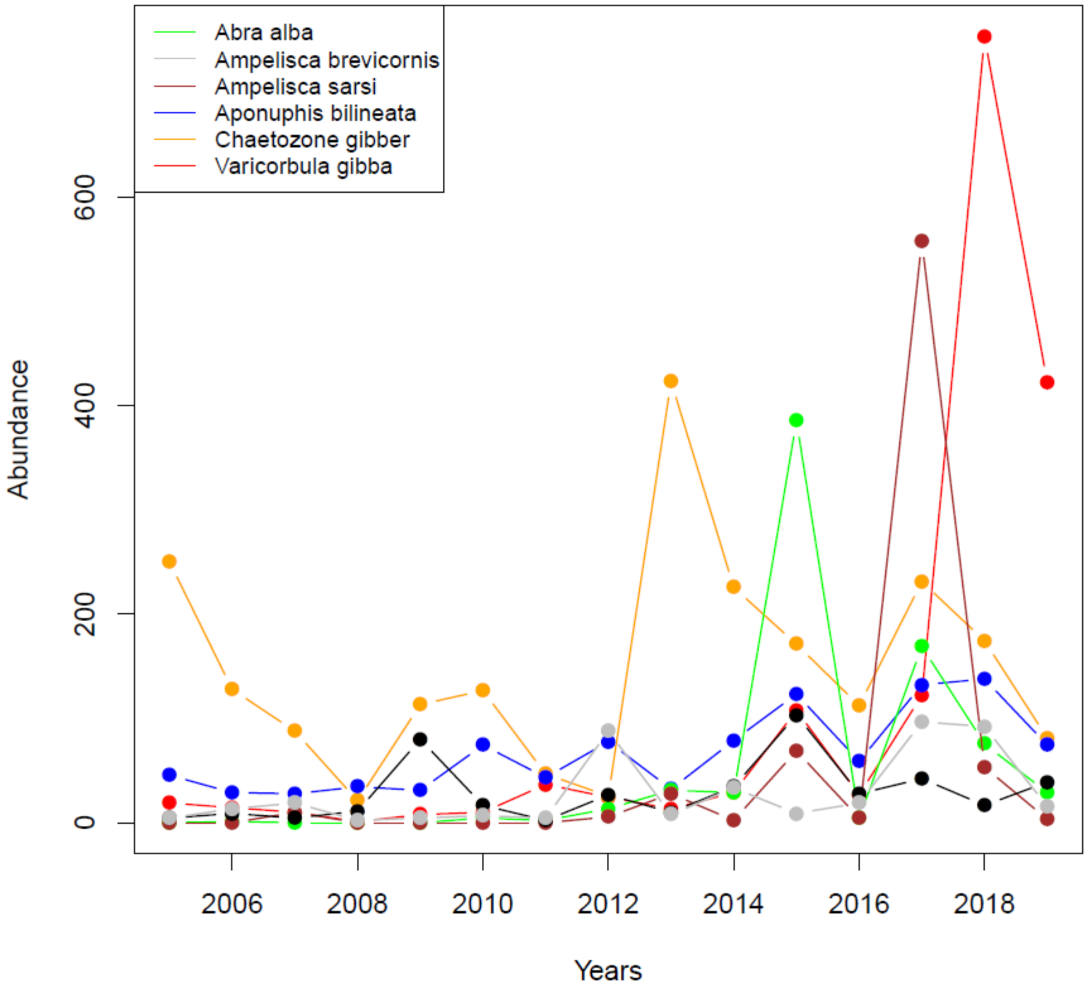


Figure 2: Abondance (ind.m^2) of dominant species sampled at the station R

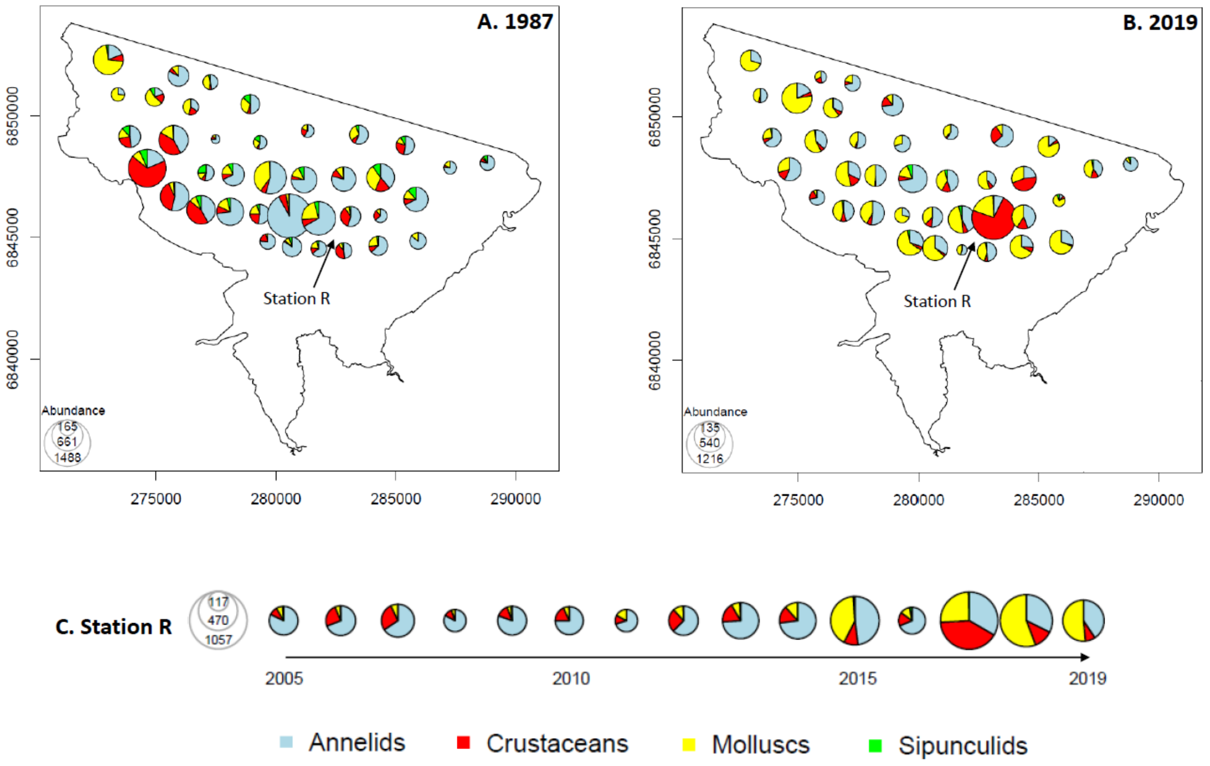


Figure 3: Distribution maps of main taxonomic group with mean total abundance (m²) classes superimposed given as the sum for 1987 and 2019. Colours represents each group: Annelids errant (blue), Annelids sedentary (light blue), Crustaceans (red), Molluscs (yellow) and Sipunculids (green). Pies section corresponds to relative abundance of each taxonomic group. A. and B. represent 1987 and 2019 ResTroph surveys and C. represents surveys conducted from 2005 to 2019 at station R.

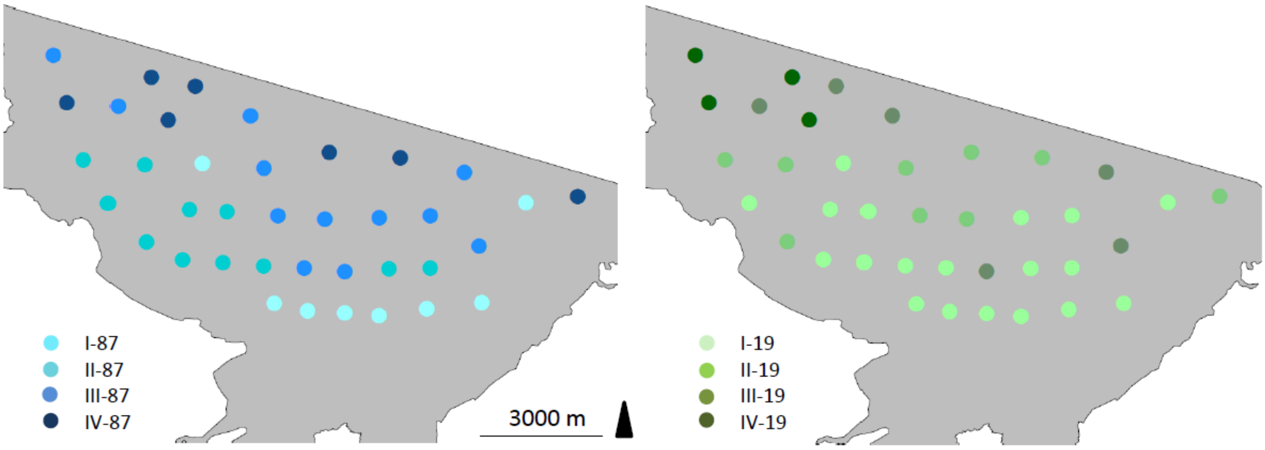
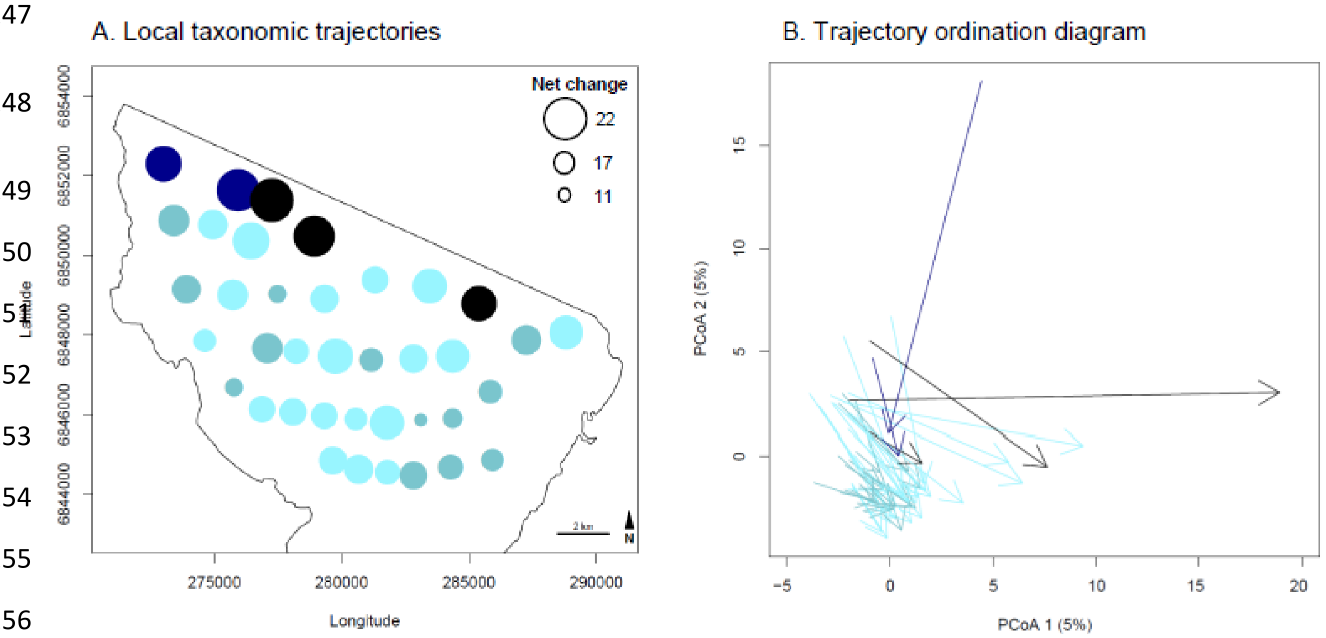
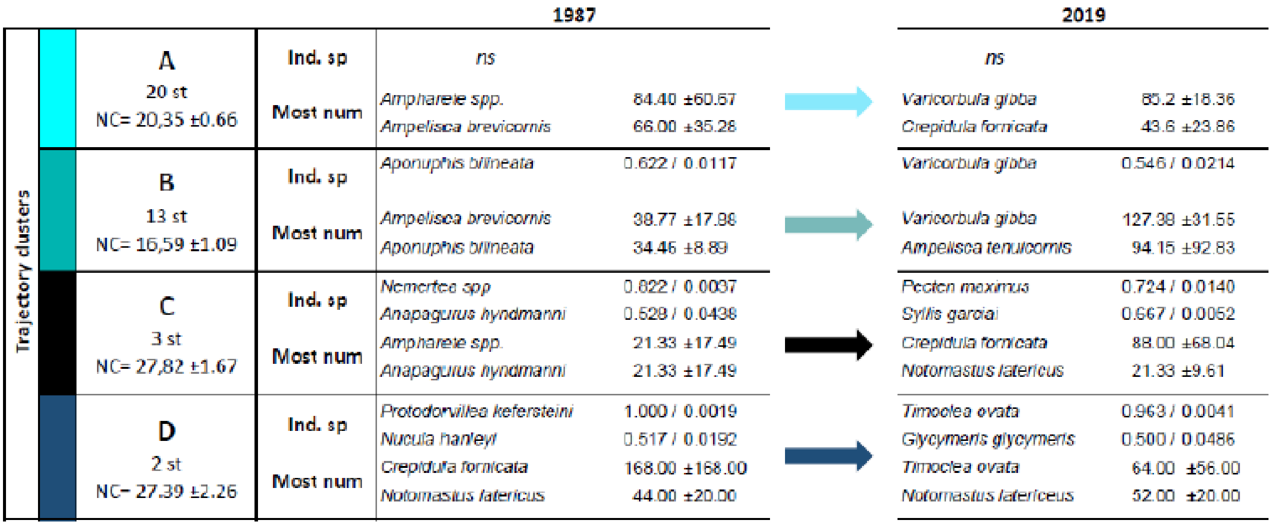


Figure 4: Spatial distribution of benthic assemblages identified with Hierarchical Cluster Analysis of the ResTroph data set (38 stations) in 1987 and 2019.



C. Characterization of initial and final ecological states of trajectory clusters



Trajectory clusters		1987			2019	
A 20 st NC= 20,35 ±0.66	**Ind. sp**	*ns*		→	*ns*	
	Most num	*Ampharete spp.*	84.40 ±60.57		*Varicorbula gibba*	85.2 ±18.36
		Ampelisca brevicornis	66.00 ±35.28		*Crepidula fornicata*	43.6 ±23.86
B 13 st NC= 16,59 ±1.09	**Ind. sp**	*Aponuphis bilineata*	0.622 / 0.0117	→	*Varicorbula gibba*	0.546 / 0.0214
	Most num	*Ampelisca brevicornis*	38.77 ±17.88		*Varicorbula gibba*	127.38 ±31.55
		Aponuphis bilineata	34.46 ±8.89		*Ampelisca tenuicornis*	94.15 ±92.83
C 3 st NC= 27,82 ±1.67	**Ind. sp**	*Nemertea spp*	0.822 / 0.0037	→	*Pecten maximus*	0.724 / 0.0140
		Anapagurus hyndmanni	0.528 / 0.0438		*Syllis garciai*	0.667 / 0.0052
	Most num	*Ampharete spp.*	21.33 ±17.49		*Crepidula fornicata*	88.00 ±68.04
		Anapagurus hyndmanni	21.33 ±17.49		*Notomastus latericus*	21.33 ±9.61
D 2 st NC= 27.39 ±2.26	**Ind. sp**	*Protodorvillea kefersteini*	1.000 / 0.0019	→	*Timoclea ovata*	0.963 / 0.0041
		Nucula hanleyi	0.517 / 0.0192		*Glycymeris glycymeris*	0.500 / 0.0486
	Most num	*Crepidula fornicata*	168.00 ±168.00		*Timoclea ovata*	64.00 ±56.00
		Notomastus latericus	44.00 ±20.00		*Notomastus latericeus*	52.00 ±20.00

Figure 5: Taxonomic trajectories. A.: Maps of local trajectories. Size of circles corresponds to net change between 1987 and 2019 and colours to cluster of trajectories determined by HCA on CTA trajectory similarity analysis. All the dimensions of the multivariate space were considered in net change calculation and analysis of trajectory similarities. B.: Trajectory ordination diagrams. Only two dimensions are show. C.: Characteristics of initial and final taxonomic ecological states of trajectory clusters. Taxonomic trajectory are coloured according to trajectory clusters (blue gradient).

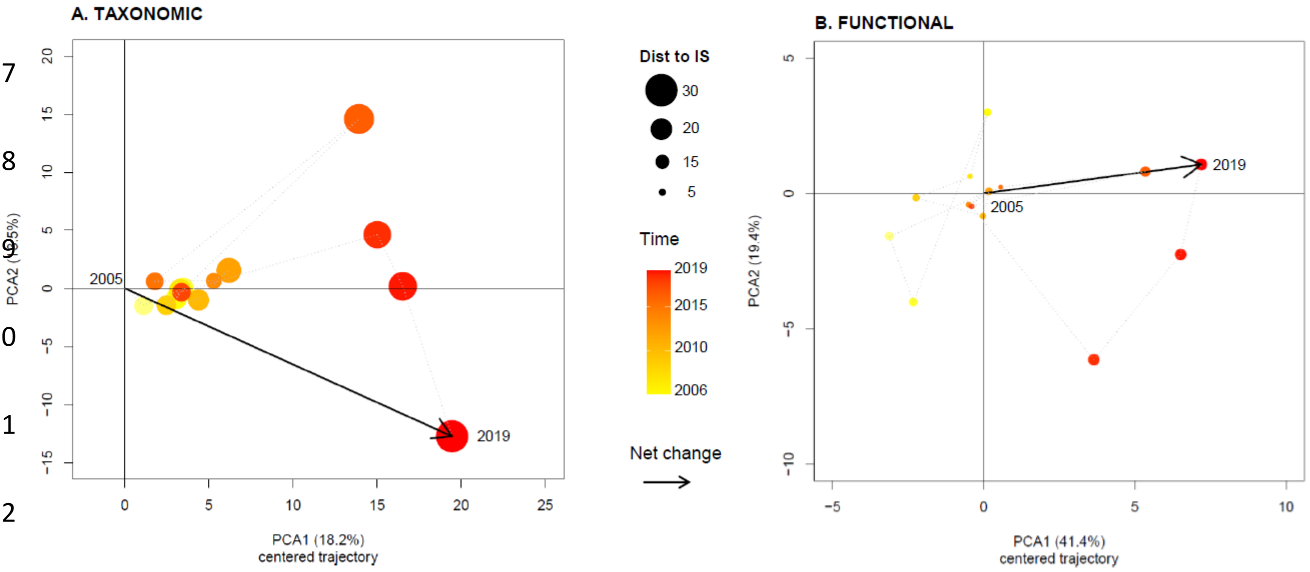
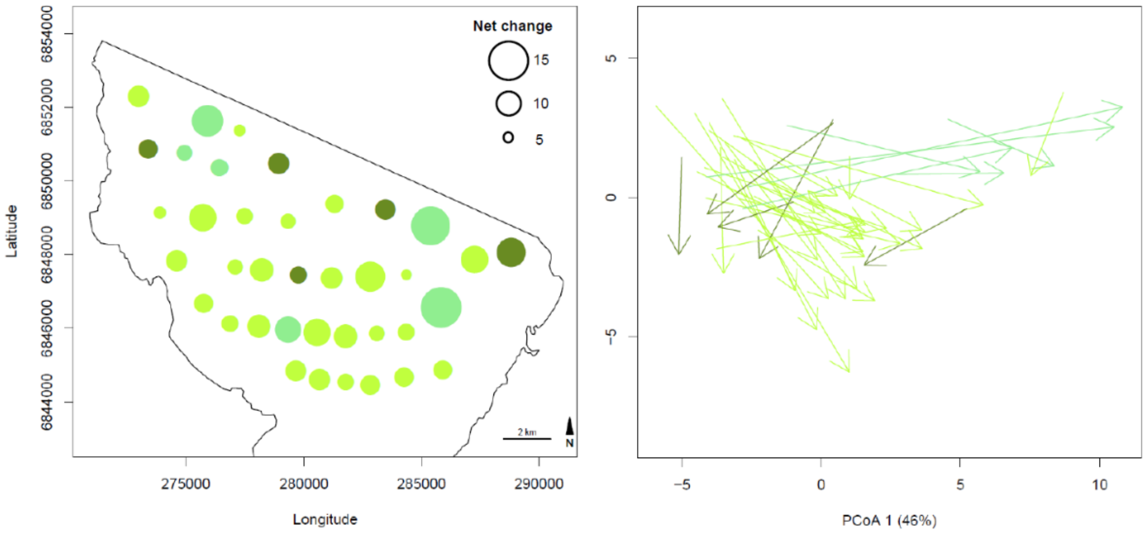
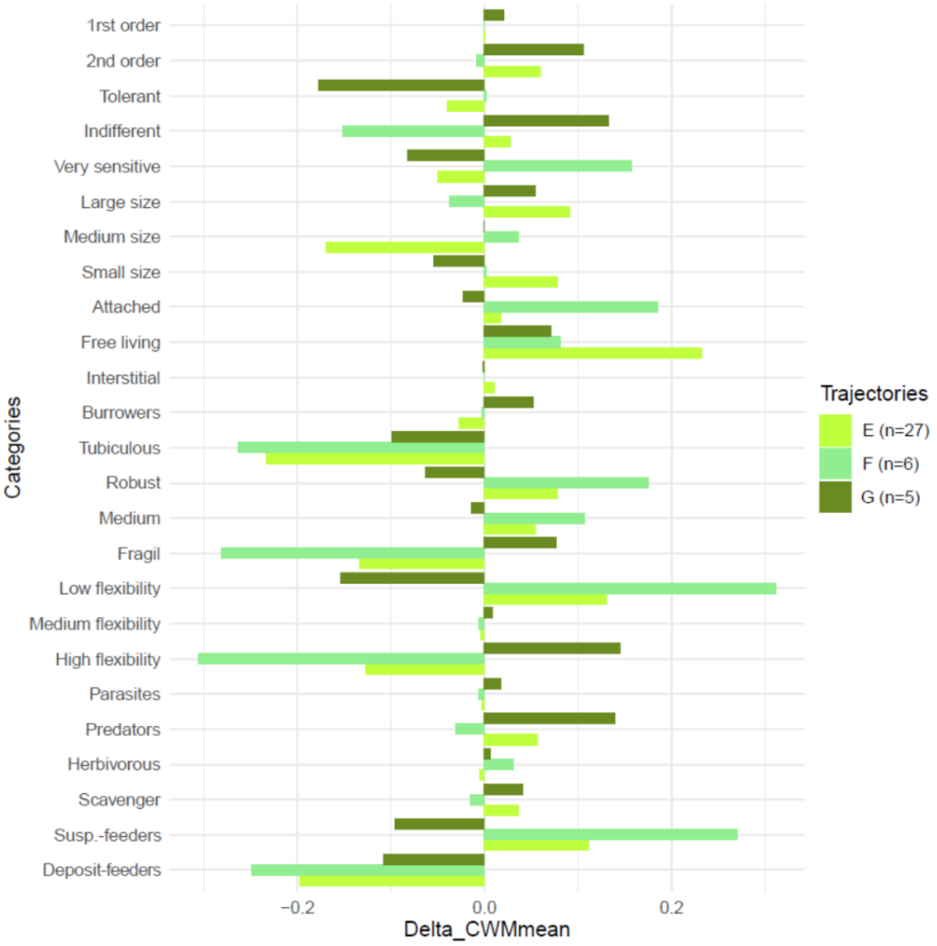


Figure 6: Trajectory of the station R between 2005 and 2019. The origin of the ordination diagram represents the initial state characterized in 2005 after trajectory centering. Only two dimensions are shown. Points corresponds to intermediate ecological states (size= length of each state to initial state considering all PCA components) and are coloured according to time (yellow (2005) to red (2019)). Lines represents segments between transitional state. The black arrow represents the net change between 2005 and 2019.



A. Local functional trajectories B. Trajectory ordination diagram



C. Differences in mean CWM values of categories of traits within functional trajectory cluster

Figure 7: Functional trajectories. A.: Maps of local trajectories. Size of circles corresponds to net change between 1987 and 2019 and colours to cluster of trajectories determined by HCA

on CTA trajectory similarity analysis. All the dimensions of the multivariate space were considered in net change calculation and analysis of trajectory similarities. B.: Trajectory ordination diagrams. Only two dimensions are show. Taxonomic trajectory are coloured according to trajectory clusters (green gradient). Characteristics of initial and final functional ecological states of trajectory clusters are detailed in table IV. C.: Barplots of CWM values shift for each categories of traits (mean 2019 – mean 1987). Bars are coloured according to functional trajectory clusters.

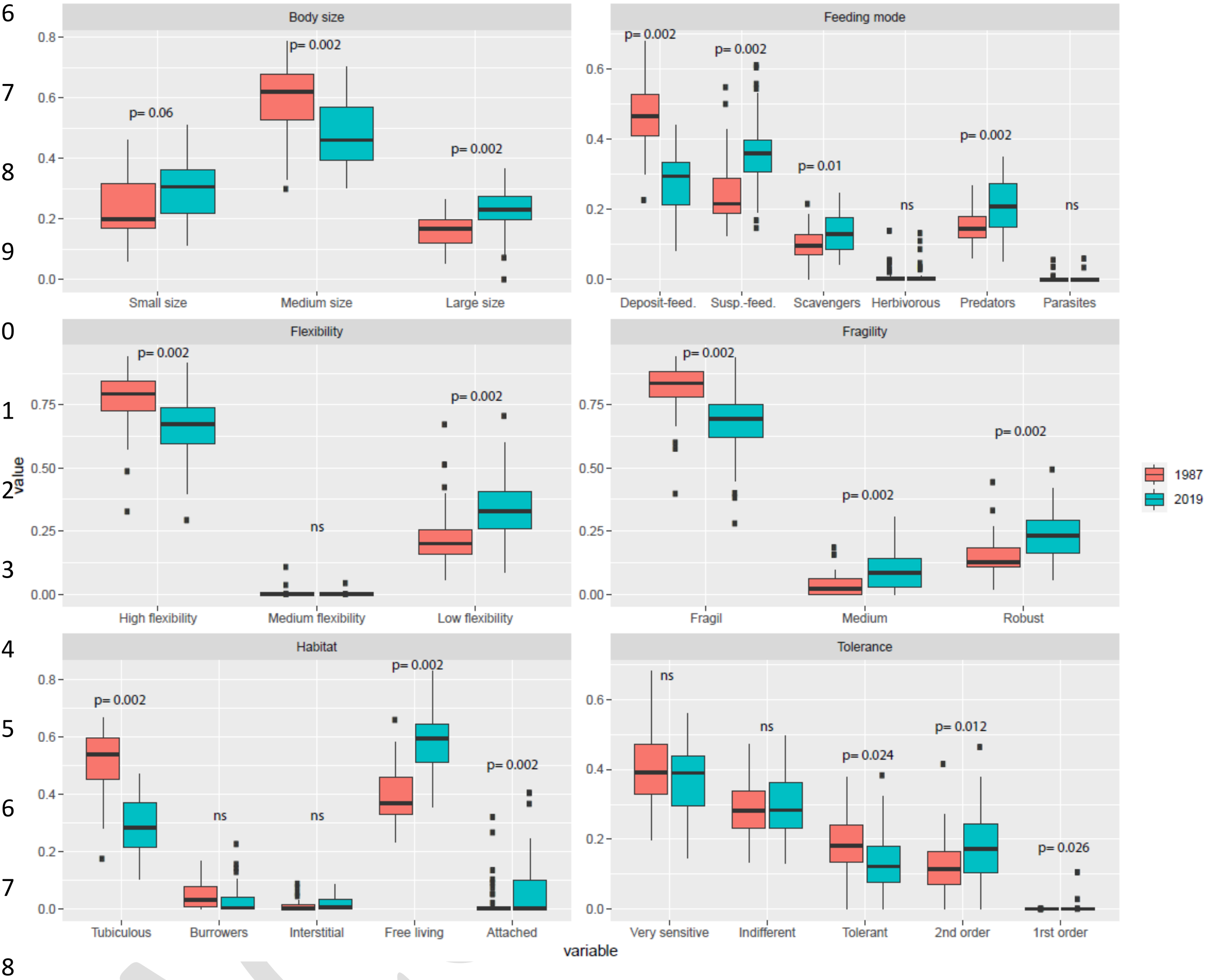


Figure 8: Box plots of CWM traits values in levels of respective categories according to year (1987: red; 2019: green). Box plot indicates the median (line in the box), the first and third quartiles (hinges) and extreme data points (black points). Significance of student permutation paired tests are indicated for each category traits.

Table I: Characteristics of assemblages identified with the Hierarchical Cluster Analysis in 1987 and 2019: number of station (N st), Specific richness (S), Mean density per m² (Abund), Shannon-Weaver Index (H), Simpson Index (D) and Pielou's evenness (J) (± standard error). Assemblages are characterised by indicative and dominant species.

Assemblages		Indicator species	indval	p	Most numerous species	Mean.m² ± se	N st	S	Abund	H	D	J
1987	**I-87**	***Chaetozone gibber***	**0.555**	**0.0006**	***Chaetozone gibber***	**42.00 ±12.98**	8	12.25	219	2.18	0.85	0.88
		Sigalion mathildae	**0.547**	**0.0007**	***Aponuphis bilineata***	**35.00 ±11.60**		± 1.05	± 28.20	± 0.07	± 0.01	± 0.02
		Magelona filiformis	0.500	0.0016	*Ampelisca brevicornis*	21.00 ±6.22						
		Spiophanes bombyx	0.487	0.0032	*Spiophanes bombyx*	18.00 ±6.18						
		Aponuphis bilineata	0.442	0.0067	*Sigalion mathildae*	11.00 ±3.00						
	II-87	***Ampelisca brevicornis***	**0.536**	**0.0004**	***Ampelisca brevicornis***	**145.45 ±59.49**	11	21.09	535.27	2.53	0.87	0.84
		Varicorbula gibba	**0.470**	**0.0013**	***Euclymene oerstedii***	**37.09 ±14.56**		± 1.79	± 88.98	± 0.01	± 0.02	± 0.03
		Ampelisca tenuicornis	0.431	0.0073	*Ampelisca tenuicornis*	37.09 ±11.63						
		Euclymene oerstedii	0.415	0.0143	*Notomastus latericeus*	36.36 ±7.50						
		Nephtys hombergii	0.368	0.0362	*Aponuphis bilineata*	31.27 ±6.95						
	III-87	***Ampharete spp.***	**0.554**	**0.0005**	***Ampharete spp.***	**150.67 ±98.61**	12	24.92	629.33	2.60	0.85	0.82
		Golfingia (Golfingia) elongata	**0.532**	**0.0004**	***Crepidula fornicata***	**71.33 ±34.54**		± 1.96	± 115.25	± 0.16	± 0.04	± 0.04
		Crepidula fornicata	0.443	0.0055	*Notomastus latericeus*	37.33 ±9.96						
		Polycirrus medusa	0.438	0.0051	*Polycirrus medusa*	32.00 ±9.08						
		Sthenelais boa	0.419	0.0085	*Golfingia (Golfingia) elongata*	21.33 ±4.33						
	IV-87	***Nototropis vedlomensis***	**0.384**	**0.0031**	***Notomastus latericeus***	**21.71 ±7.75**	7	15.43	225.14	2.43	0.87	0.90
		Notomastus latericeus	**0.357**	**0.0273**	***Nucula hanleyi***	**14.86 ±13.57**		± 2.08	± 29.90	± 0.17	± 0.03	± 0.03
		Hilbigneris gracilis	0.351	0.0387	*Hilbigneris gracilis*	12.57 ±5.20						
		Glycera capitata	0.286	0.0296	*Polycirrus medusa*	9.14 ±9.14						
		Protomystides bidentata	0.286	0.0293	*Fabulina fabula*	9.14 ±4.43						
2019	**I-19**	***Varicorbula gibba***	**0.612**	**0.0001**	***Varicorbula gibba***	**160.84 ±19.63**	19	16.53	466.11	2.08	0.77	0.76
		Phyllodoce groenlandica	**0.368**	**0.0310**	***Ampelisca tenuicornis***	**64.42 ±63.54**		± 1.04	± 74.66	± 0.09	± 0.02	± 0.03
					Glycinde nordmanni	20.63 ±4.07						
					Streblosoma bairdi	17.26 ±4.63						
					Aponuphis bilineata	16.42 ±6.69						
	II-19	***Nephtys hombergii***	**0.483**	**0.0004**	***Notomastus latericeus***	**29.33 ±7.06**	9	18.78	352.00	2.60	0.90	0.90
					Varicorbula gibba	**27.56 ±10.16**		± 2.14	± 56.04	± 0.10	± 0.01	± 0.01
					Nephtys hombergii	25.78 ±5.62						
					Anomia ephippium	18.67 ±10.67						
					Pista cristata	17.78 ±6.77						
	III-19	***Crepidula fornicata***	**0.728**	**0.0004**	***Crepidula fornicata***	**160.00 ±66.58**	6	18.83	430.67	2.29	0.80	0.80
		Pecten maximus	**0.446**	**0.0239**	***Notomastus latericeus***	**21.33 ±7.35**		± 2.68	± 103.08	± 0.21	± 0.05	± 0.06
		Syllis garciai	0.333	0.0313	*Aponuphis bilineata*	16.00 ±10.93						
		Amphipholis squamata	0.333	0.0304	*Nephtys hombergii*	10.67 ±5.72						
		Aequipecten opercularis	0.333	0.0290	*Anomia ephippium*	10.67 ±9.16						
	IV-19	***Nucula hanleyi***	**0.611**	**0.0024**	***Timoclea ovata***	**34.00 ±28.73**	4	10.50	252.00	1.97	0.81	0.85
		Timoclea ovata	**0.596**	**0.0031**	***Nucula hanleyi***	**30.00 ±11.94**		± 1.32	± 62.18	± 0.08	± 0.01	± 0.03
		Glycera alba	0.481	0.0069	*Crepidula fornicata*	30.00 ±30.00						
					Notomastus latericeus	26.00 ±17.09						
					Polititapes rhomboides	18.00 ±18.00						

Table II: Characteristics of cluster of surveys identified with the Hierarchical Cluster Analysis performed on the WFD data set (2005 to 2015): number of station (N st), Specific richness (S), Mean density per m² (Abund), Shannon-Weaver Index (H), Simpson Index (D) and Pielou's evenness (J) (± standard error). Assemblages are characterised by indicative and dominant species.

Assemblages	Indicator species	indval	p	Most numerous species	Mean.m² ± se	N sv	S	Abund	H	D	J
R-I	***Caulleriella alata***	**0.643**	**0.0003**	***Chaetozone gibber***	**170.95 ± 52.62**	7	62.57	647.30	3.10	0.89	0.75
	Edwardsia claparedii	**0.576**	**0.0259**	***Aponuphis bilineata***	**52.54 ± 7.52**		± 3.62	± 82.30	± 0.12	± 0.03	± 0.03
	Magelona filiformis	0.563	0.0009	*Notomastus latericeus*	26.51 ± 10.09						
	Scoloplos armiger	0.530	0.0023	*Ampelisca brevicornis*	23.02 ± 11.53						
	Apseudpsis latreillii	0.471	0.0263	*Varicorbula gibba*	22.38 ± 3.70						
R-II	***Cirratulidae spp.***	**0.758**	**0.0039**	***Chaetozone gibber***	**90.83 ± 25.03**	4	53.00	576.67	3.03	0.92	0.77
	Tritia varicosa	**0.750**	**0.0194**	***Cirratulidae spp.***	**74.72 ± 24.46**		± 3.34	± 88.18	± 0.07	± 0.01	± 0.01
	Ampelisca spinimana	0.725	0.0001	*Ampelisca tenuicornis*	50.00 ± 16.22						
	Nephtys hombergii	0.645	0.0269	*Aponuphis bilineata*	41.39 ± 11.12						
	Ampelisca tenuicornis	0.590	0.0002	*Chaetozone zetlandica*	29.72 ± 7.39						
R-III	***Calyptraea chinensis***	**1**	**0.0022**	***Varicorbula gibba***	**351.39 ± 152.33**	4	75.50	1772.50	2.92	0.87	0.67
	Spisula elliptica	**0.925**	**0.0010**	***Ampelisca sarsi***	**170.83 ± 129.74**		± 2.40	± 234.74	± 0.11	± 0.02	± 0.02
	Ampelisca spinipes	0.860	0.0035	*Abra alba*	164.72 ± 31.00						
	Thyasira fexuosa	0.790	0.0016	*Chaetozone gibber*	164.44 ± 14.47						
	Amphictene auricoma	0.750	0.0150	*Aponuphis bilineata*	116.94 ± 19.90						

Table III: Main bivalves species identified in the four replicates sieved on 5mm circular mesh size at the 38 Restroph stations in 1987 and 2001 (N: total abundance, sd: standard deviation). The significance of trends was tested with a student permutation paired-test (ns: no trend ; - : decrease ; +: increase). Distribution maps are detailed in appendix F.

Species	**1987**		**2019**		**Trend**	**p_val t perm. paired test**	
	N	**Mean±sd**	**N**	**Mean±sd**			
Acanthocardia echinata	14	0.37 ± 1.02	2	0.05 ± 0.32	.	0.162	ns
Anomia ephippium	24	0.63 ± 1.68	194	5.11 ± 7.71	+	0.002	***
Arcopagia crassa	8	0.21 ± 1.30	10	0.26 ± 1.62	.	0.954	ns
Bosemprella incarnata	16	0.42 ± 1.24	142	3.74 ± 6.10	+	0.002	***
Varicorbula gibba	380	10.00 ± 13.91	3564	93.79 ± 101.08	+	0.002	***
Fabulina fabula	38	1.00 ± 3.15	2	0.05 ± 0.32	-	0.046	*
Glycymeris glycymeris	4	0.11 ± 0.45	54	1.42 ± 5.95	.	0.362	ns
Laevicardium crassum	6	0.16 ± 0.55	46	1.21 ± 1.71	+	0.004	**
Moerella donacina	4	0.11 ± 0.45	112	2.95 ± 4.18	+	0.002	***
Nucula hanleyi	4	0.11 ± 0.45	166	4.37 ± 9.36	+	0.002	***
Nucula nitidosa	2	0.05 ± 0.32	166	4.37 ± 6.47	+	0.002	***
Pandora albida	10	0.26 ± 0.83	18	0.47 ± 1.18	.	0.456	ns
Parvicardium scabrum	0	0.00 ± 0.00	22	0.58 ± 1.39	+	0.010	*
Pecten maximus	0	0.00 ± 0.00	56	1.47 ± 2.17	+	0.002	***
Polititapes rhomboides	226	5.95 ± 9.01	48	1.26 ± 4.89	-	0.002	***
Spisula elliptica	6	0.16 ± 0.55	6	0.16 ± 0.72	.	1.000	ns
Timoclea ovata	10	0.26 ± 0.83	176	4.63 ± 17.47	+	0.006	**

Additional Files

Appendix A: Dredging rules and fishing effort

Appendix B: Categories of functional traits

Appendix C: Map of the sediment properties in the 38 ResTroph stations between 1987 and 2019

Appendix D: Evolution of sediment properties at station R from 2005 to 2019

Appendix E: General description of the benthic macrofauna according to sampling campaigns

Appendix F: Map of the distribution and abundance of the main bivalve species

Appendix G: Station R functional factor map

Appendix H: Evolution of the wave regime over the last 30 years close to station R (SHOM)