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

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### 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, tubicolous 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.

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

## 62        **1. Introduction**

63

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

78 The comparison to reference conditions based on pristine or slightly disturbed areas  
79 is recommended by the European WFD to track changes in environmental status,  
80 although it is generally recognized that non-disturbed marine and estuarine habitats  
81 are rare (Borja, Dauer & Grémare, 2012), and that historical data rarely constitute a  
82 pristine state (Callaway, 2016; Bacouillard et al., 2020). In this context, acceptable  
83 levels of disturbances can be used to define reference conditions (Borja, Dauer &  
84 Grémare, 2012). Such approach requires repeated and standardized surveys over  
85 time to 1) track changes with respect to baselines conditions, and 2) provide up-to-  
86 date ecological state to stakeholders involved in the development of management  
87 plans for coastal and marine areas. Benthic macrofauna has been considered as a  
88 relevant descriptor to characterize the biological status of water bodies by the  
89 European WFD (Borja, Muxika & Rodríguez, 2009; Borja, Dauer & Grémare, 2012),

90 as this compartment influences nutrient cycling, represents an important food  
91 resource for higher trophic levels (Snelgrove, 1997; McLusky & Elliott, 2004), and  
92 reacts rapidly to disturbances (Gray, 1997; Claudet & Fraschetti, 2010).

93 Among sublittoral macrobenthic assemblages, very shallow subtidal habitats (0-  
94 15m), accessible for sampling only during high tide, are often excluded from  
95 sampling programmes and remain to a large extent poorly monitored (Desroy et al.,  
96 2002). Very shallow communities are notably characterized by high diversity and  
97 productivity levels (Gray, 1997; Levinton, 2001; Snelgrove, 1999). This knowledge  
98 gap and the scarcity of data constitute a serious impediment for the implementation  
99 of conservation strategies (Ellis, Norkko & Thrush, 2000).

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

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

115 This study, based on a resampling of the stations sampled in 1987 in the bay of  
116 Saint-Brieuc and on the WFD long-term monitoring of the benthic assemblage at one  
117 shallow station, aims to analyse taxonomic and functional trajectories of benthic

118 assemblages in order to: (1) detect patterns of changes over the last 30 years at  
119 different spatial scales using the 38 stations sampled in 1987 and 2019, and (2)  
120 analyse recent dynamics at one station sampled yearly from 2005 to 2019 as part of  
121 the WFD monitoring programme. As single or multiple disturbances differently affect  
122 species composition and structure, temporal changes of the benthic community were  
123 tracked, both with  $\alpha$  and  $\beta$ -diversity metrics (Ellis, Norkko & Thrush, 2000; Cimon &  
124 Cusson, 2018). In accordance with Dornelas et al. (2013), Magurran et al. (2019),  
125 and Yang (2020) recommendations to develop new multivariate metrics devoted to  
126 the study of temporal ecological changes and response to disturbance (Cimon &  
127 Cusson, 2018), we specifically focused on taxonomic and functional spatio-temporal  
128 trajectories coupling classic multivariate analysis with the recent Community  
129 Trajectory Analysis framework (De Cáceres et al., 2019; Sturbois et al., 2021), finally  
130 discussing conservation prospects for such coastal areas.

131

## 132 **2. Material and methods**

### 133 **2.1. Study area**

134 Fieldwork was conducted in the bay of Saint-Brieuc (France, Figure 1). The study  
135 area encloses 11,700 ha of very shallow soft-bottom sediments. The bay is under the  
136 influence of a semi-diurnal megatidal regime. Tidal range varies between 4 m at neap  
137 tides and nearly 13 m during spring tides. Despite bordering the National Nature  
138 Reserve of the bay of Saint-Brieuc and partially belonging to the Natura 2000 “Baie  
139 de Saint-Brieuc-Est” site (FR5300066), the study area is exposed to a number of  
140 anthropogenic pressures including mussel culture, scallop dredging and  
141 eutrophication. Mussels are farmed on bouchots (wooden poles, Figure 1) in the  
142 north-eastern part of the intertidal area, occupying 277 ha and 312 ha in 1987 and  
143 2019, respectively (Sturbois et al., under review) and are also farmed on ropes in the  
144 western part of the study area, around stations 81, 99 and 100. The sea bed is also

145 exposed to long-term scallop dredging activities as the bay of Saint-Brieuc is  
146 characterized by the highest fishing pressure in Brittany (Appendix A-1). Regulation  
147 changes have led, since 2010, to the concentration of dredging, at the beginning of  
148 the fishing season, in areas colonized by the the non-indigenous slipper limpet  
149 *Crepidula fornicata* (Appendix A-2). The bay also suffers from eutrophication  
150 resulting in macroalgae proliferation and cyclic green tides episodes (Charlier et al.,  
151 2007; Gravier, 2012), which notably impact fishes nursery grounds (Le Luherne et  
152 al., 2016, 2017) and influence the dynamics of some intertidal benthic populations of  
153 invertebrates of the intertidal area (Sturbois et al., under review).

## 154 **2.2. Field sampling**

155 Benthic macrofauna was sampled at 38 stations during winter (March) in 1987 and  
156 2019 (ResTroph research programme) following the grid (Figure 1) and the protocol  
157 defined in 1987 by Gros & Hamon (1988). During both surveys, five replicates were  
158 collected at each station with a small Hamon grab (1/8m<sup>2</sup>) for macrobenthos  
159 analyses. The grab contents were gently sieved on board either through 1) a 2 mm  
160 circular mesh sieve (1 replicate) to describe benthic assemblages, or through 2) a 5  
161 mm circular mesh sieve (4 replicates) to specifically analyse bivalve populations. The  
162 retained material was preserved for analysis in 5% buffered formaldehyde. Only the  
163 replicate sieved on a 2 mm mesh was used for the long-term comparison of the  
164 benthic community. Two samples of sediment were collected in one additional grab  
165 using a handcorer, and subsequently analysed for grain size distribution and organic  
166 matter content respectively. All replicates were collected at a maximal distance of 50  
167 m from each station, using DGPS position-fixing. As part of the ecological status  
168 monitoring, one station (R) was additionally sampled yearly (nine replicates,  
169 following national recommendation of the REBENT benthic network as part of the  
170 WFD) in March from 2005 to 2019, with a Smith McIntyre grab (0.1 m<sup>2</sup>), and sieved

171 on 1 mm circular mesh sieve. Data at station R were used to assess the year-to-year  
172 variability of taxonomic and functional diversity at this site.

173

### 174 **2.3. Laboratory analyses**

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

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

183

### 184 **2.4. Traits collection**

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



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

200

## 201 **2.5. Data analysis**

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

208

### 209 **2.5.1 Sedimentary dataset**

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

216

### 217 **2.5.2 Taxonomic $\alpha$ -diversity**

218 In order to assess the different components of taxonomic  $\alpha$ -diversity, the mean  
219 number of individuals per m<sup>2</sup> (N), species richness (S), Shannon-Weaver index (H'),  
220 Simpson index (D) and Pielou's species evenness (J) were calculated for each  
221 station (2 mm circular mesh sieve) prior to any transformations of the dataset.

### 222 **2.5.3 Spatial and temporal taxonomic clustering**

223 Hierarchical Cluster Analyses (HCA) were performed on both taxonomic datasets to  
224 distinguish benthic assemblages (i.e. stations/surveys groups) by using the Hellinger

225 distance between each pair of samples/dates (Legendre & Gallagher, 2001) and by  
226 applying the Ward's clustering method. The indicator value method (Indval) was  
227 performed for characterizing assemblages (Dufrene & Legendre, 1997).

228

#### 229 **2.5.4 Detecting trajectory patterns**

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

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

247 *Inter-annual dynamics.* For the long-term WFD dataset (yearly sampling from 2005 to  
248 2019), Trajectory segments lengths (*i.e.* S1=2005 to 2006, S2=2006 to  
249 2007,...S14=2018 to 2019), Net change, Directionality and Net change ratio were  
250 calculated. Recovering (station returning toward an initial ecological state) and  
251 departing (station for which change increased over time) consecutive trajectory

252 segments were identified by subtracting Net change n-1 by Net change n (Sturbois et  
253 al., 2021).

254

### 255 **2.5.5 Relation between taxonomic structure and environmental and spatial** 256 **variables**

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

268

### 269 **2.5.6 Species changes in bivalve populations**

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

273

## 274 **3. Results**

### 275 **3.1 General description of sediment**

276 Sediments were dominated by sands in 1987 ( $74.33\% \pm 12.85$ , mean  $\pm$  sd) and  
277 2019 ( $78.74\% \pm 12.35$ ) (Appendix C). Fine sands (125-250  $\mu$ m) were the most  
278 represented sedimentary class in both years ( $42.34\% \pm 17.92$  in 1987;  $46.60\% \pm$   
279  $17.99$  in 2019). Mud content significantly decreased in 79 % of stations ( $-11.12\% \pm$

280 6.89; min= -0.79%; max= -31.15%, p-value < 0.001). In contrast, 21% of stations  
281 were characterized by an increase in mud content (+11.53% ± 17.56) especially at  
282 stations 101 (+52.46%), 81 (+16.16%), and 100 (+13.61%). Gravel accounted for  
283 8.43% ± 10.59 in 1987 and 10.23% ± 6.96 in 2019. Mean particle size (356.55µm ±  
284 258.94 vs 421.54µm ± 192.55) slightly and significantly increased (p-value < 0.001)  
285 over the study period.

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

### 289 **3.2 General description of the macrofauna**

290 Overall, 208 taxa were collected on the 2mm mesh size sieves (with 72 taxa common  
291 to both datasets). Between 1987 and 2019, 57 taxa were lost and 79 taxa gained.  
292 Macrofauna was dominated by annelids, molluscs and crustaceans (Appendix E). In  
293 1987, annelids were the most numerous taxonomic group (9344 ind., 55.73%) ahead  
294 of molluscs (3168 ind., 18.89%) and crustaceans (3080 ind., 18.37%). Molluscs were  
295 the most numerous group in 2019 (6600 ind., 42.26%) ahead of annelids (6080 ind.,  
296 38.93%) and crustaceans (2448 ind., 15.68%). Sipunculids, echinoderms,  
297 platyhelminths and nemerteans contributed less than 5% of the total species richness  
298 and abundance. H', D, J and mean Richness all slightly decreased over time while  
299 total richness increased.

300 A total of 202 taxa were reported over 15 years at the station R. Richness (63.47 ±  
301 11.27) and abundance (928.52 ind.m<sup>-2</sup> ± 593.83) increased over the study period.  
302 Annelids, molluscs and crustaceans dominated the community (Appendix E).  
303 *Chaetozone gibber* (133.07 ind.m<sup>-2</sup> ± 94.14), *Varicorbula gibba* (95.87 ind.m<sup>-2</sup> ±  
304 187.35), *Aponuphis bilineata* (60.07 ind.m<sup>-2</sup> ± 34.39), *Abra alba* (44.67 ind.m<sup>-2</sup> ±  
305 92.79), *Ampelisca sarsi* (44.00 ind.m<sup>-2</sup> ± 128.14), *Notomastus latericeus* (25.67

306 ind.m<sup>-2</sup> ± 26.07), and *Ampelisca brevicornis* (24.93 ind.m<sup>-2</sup> ±30.93) were dominant  
307 over the period studied. Some of them exhibited strong temporal variations,  
308 especially in the second part of the time series between 2012 and 2019 (Figure 2).

309 Changes were observed in the contribution of the main taxonomic groups to total  
310 local abundance between 1987 and 2019 (Figure 3, A and B): the contribution of  
311 molluscs increased in most stations, especially in the southern part of the study area.  
312 This change, also visible in the fauna of the station R occurred around 2015 (Figure  
313 3, C). Before 2015, the abundance of each taxonomic group at station R was similar  
314 to the abundances measured in 1987 at the southern stations of the bay of Saint-  
315 Brieuc (stations 62 to 72).

316

### 317 **3.3 Taxonomic clustering**

#### 318 **3.3.1 Spatial clustering in 1987 and 2019**

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

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

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

### 348 **3.3.1 Temporal clustering from 2005 to 2019**

349 The HCA performed on the station R dataset separated three clusters (Table II).  
350 Cluster I, composed of seven years, was characterized by *Caulleriella alata* and  
351 *Edwardsia claparedii*. Cluster II (4 years) was characterized by *Cirratulidae* spp. and  
352 *Tritia varicosa*. Cluster III, composed of four of the most recent surveys (2015, 2017,  
353 2018, 2019), was typified by *Calyptraea chinensis* and *Spisula elliptica*. *C. gibber*, *A.*  
354 *bilineata* and *Ampelisca* spp. remained in the first five highest-ranking species in  
355 terms of abundance over the entire study period, and *V. gibba* and *A. alba* became  
356 dominant during the more recent surveys. Taxonomic diversity indices were quite

357 stable between clusters except richness and abundance, which increased during  
358 recent observations (cluster III, Table II).

359

### 360 **3.4 Species changes in bivalve populations**

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

366

### 367 **3.5 Detecting trajectory patterns**

#### 368 **3.5.1 Taxonomic trajectories**

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

383 Most stations encountered similar changes in the multivariate space, as indicated by  
384 the similar trajectory directions. Direction (i.e. specific initial and final composition)  
385 and trajectory length seemed mainly responsible for the separation of clusters. The  
386 convergence of most trajectories, especially from clusters A and B, which grouped 87  
387 % of trajectories, illustrate an homogenization over time with respect to the ecological  
388 state described in 1987.

389

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

400

### 401 **3.5.2 Functional trajectories**

402 *Long-term comparison.* Net change was variable spatially ( $7.94 \pm 2.53$ ), ranging from  
403 3.97 (station 87) to 15.24 (station 88). The HCA performed on CTA analysis of  
404 trajectory similarities separated three clusters of functional trajectories (Figure 7, A, B  
405 and C). Trajectory length and direction were mainly responsible for the separation of  
406 clusters. Cluster E grouped 27 stations ( $7.34 \pm 0.36$ ) which highest net change  
407 values were mainly located in the southern part of the study area, and were  
408 characterized by a decrease in the relative contribution of the following categories: 1)  
409 medium size, flexible, fragile; and 2) tubicolous, burrowers and tolerant species.  
410 Simultaneously, the contribution of suspension-feeders, predators and scavengers



411 increased, as well as rigid, robust, and large and small species. Free-living species  
412 became dominant and the contribution of second-order opportunistic species  
413 increased. Cluster F grouped six trajectories characterized by higher net changes  
414 ( $10.59 \pm 1.64$ ). The main functional changes consisted in a decrease of deposit-  
415 feeders, tubicolous, and flexible and fragile species. This group of trajectories was  
416 specifically characterized by an important increase of CWM values of very sensitive  
417 species, and attached species mainly represented by *A. ehippium*. Cluster G  
418 characterized five trajectories ( $7.96 \pm 0.79$ ). In addition to a similar pattern  
419 concerning depositivorous and tubicolous species, these trajectories were specifically  
420 characterized by an increase in the contribution of predator, flexible, fragile, and  
421 burrowing species and a decrease of rigid, suspension-feeders and tolerant species.  
422 At the scale of the whole area including all stations, a similar global pattern was  
423 observed (Figure 8). Compared to 1987, the community was dominated by  
424 suspension-feeders and free-living species in 2019. Even if significant functional  
425 shifts in morphologic traits were observed over time, the fauna remained dominated  
426 by medium size, flexible and fragile species. According to the tolerance to nutrient  
427 enrichment trait, fauna remained dominated by very sensitive and indifferent species.  
428 *Inter-annual dynamics*. Functional net change increased over time (Figure 6, B).  
429 Different categories of traits influenced the functional stability: axis I (41.4%) opposed  
430 organisms filter feeders, living free, rigid and robust to organisms deposit feeders,  
431 living in tubes and highly flexible (Appendix H). The alternation of recovering and  
432 departing dynamics resulted in low directionality (0.387) and net change ratio  
433 (10.04%).

434

### 435 **3.6 Relation between taxonomic structure and environmental and spatial** 436 **variables**

437 According to the VIF analysis, coarse sand and mean particle size were excluded  
438 from the following analysis. The part of the variance explained by sedimentary

439 variables was higher in 1987 ( $R^2_{adj}=0.177$ ;  $F=2.547$ ;  $Pr(>F)=0.001$ ) than in 2019  
440 ( $R^2_{adj}=0.055$ ;  $F=1.420$ ;  $Pr(>F)=0.003$ ). Sedimentary variables characterized by finest  
441 grain size were significantly correlated to the taxonomic structure in 1987: fine sand  
442 ( $R^2_{adj}=0.157$ ), mud ( $R^2_{adj}=0.123$ ), and very fine sand ( $R^2_{adj}=0.059$ ). In 2019, two  
443 sedimentary variables were correlated: mud ( $R^2_{adj}=0.050$ ) and D50 ( $R^2_{adj}=0.032$ ).  
444 A linear spatial structuration was revealed for both years ( $R^2_{adj}=0.089$ ;  $F=2.752$ ;  
445  $Pr(>F)=0.001$  in 1987 vs  $R^2_{adj}=0.100$ ;  $F=2.994$ ;  $Pr(>F)=0.001$  in 2019). In 1987,  
446 sedimentary and spatial variables explained 12% and 5% of the variance,  
447 respectively, while 4% was shared. In 2019, the part of the explained variance  
448 decreased and the contribution of spatial variables was higher (sedimentary: 2%,  
449 spatial: 7%, shared: 3%).

450

## 451 **4. Discussion**

### 452 **4.1 Changes probably occurred recently**

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

457 Among the four taxonomic clusters identified in 2019, two of them, representing 74%  
458 of stations, pointed towards a potential degradation of habitats indicated by 1) the  
459 numerical increase of the opportunistic species *V. gibba*, and 2) the lower species  
460 diversity in one of the two assemblages. This was further confirmed by the analysis  
461 of trajectory similarity, which revealed that 87% of the stations (clusters A and B)  
462 were notably characterized by increases in the density of *V. gibba* from 1987 to 2019.

463 At the scale of the study area, however, decreases of  $\beta$  species diversity remained  
464 very moderate (Appendix E).

465 Inter-annual dynamics at station R suggests that these changes are very recent  
466 (Figure 3). The lower variability observed at station R from 2005 to 2014 may depict

467 natural dynamics, while recent changes since 2015 seem driven by a strong and  
468 cumulative disturbance regime. The recent shift in the taxonomic multivariate  
469 structure was driven by variations in the abundance of a few dominant species,  
470 among which *V. gibba*, *A. alba*, *C. chinensis* and *S. elliptica*. Interestingly, although  
471 benthic communities were highly variable over the last five years, sediment  
472 properties and organic matter content did not exhibit such variability, suggesting that  
473 the recent pattern in benthic community structure may not be strictly related to habitat  
474 characteristics.

475

#### 476 **4.2 Functional shifts**

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

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

488

489 *Fishing activities.* Trawling and dredging fishing activities are responsible of many  
490 impacts on the seabed, such as the modification of benthic communities and  
491 sedimentary habitats (Newell, Seiderer & Hitchcock, 1998; Ellis, Norkko & Thrush,  
492 2000; Thrush & Dayton, 2002; Eigaard et al., 2017). Watling & Norse (1998)  
493 compared the consequences of disturbance induced on the seabed by mobile fishing  
494 gear to forest clear cutting. Scallop dredging in the Irish Sea has been shown to

495 significantly modify benthic communities and *P. maximus* populations under  
496 experimental and commercial fishing pressure conditions (Bradshaw et al., 2001).  
497 Dredging activities tend to modify the structure of mounds, tubes, and burrows  
498 created by organisms living on the sediment surface, and limit small scale habitat  
499 structure heterogeneity (Thrush & Dayton, 2002). As underlined by Gray et al.  
500 (2006), the homogenization of heterogeneous habitats and the reduction of three-  
501 dimensional structures above and below the sediment-water interface constitute one  
502 of the most damaging effects of fishing activities.

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

519 Overall sedimentary changes may also have contributed to the decrease of deposit-  
520 feeders in the study area, as dredging activities are known to homogenise the  
521 sediment. Mengual et al. (2019, 2016) showed for example an overall erosion of

522 muddy areas in the bay of Biscay in relation with fishing activities, and a coarsening  
523 trend of surface sediments (5cm). Morys, Brüchert & Bradshaw (2021) showed a  
524 significant decrease of surface organic matter content in a recent experimentation  
525 about the impact of bottom trawling on benthic biogeochemistry. Such organic matter  
526 content decrease were observed at station R from 2014 (Appendix D). In our study,  
527 sedimentary parameters partly shaped the taxonomic multivariate structure of the  
528 benthic community, but the amount of explained variance decreased between 1987  
529 and 2019 indicating that sedimentary variables explain only a limited part of the  
530 observed changes.

531

532 *Organic enrichment.* The positive functional shift observed for second-order  
533 opportunistic species, and particularly *V.gibba*, seems to indicate an impact of  
534 organic matter enrichment in accordance with Hrs-Brenko (2006) who suggested that  
535 eutrophication increases the fecundity of *V. gibba*. During our study, small individuals  
536 of *V. gibba* were observed attached with their byssus to drifting *Ulva* sp., suggesting  
537 (1) a potential influence of algal mats offering new attachment substrates for early  
538 recruitment stages and (2) individuals could drift when attached to algal mats, hence  
539 facilitating the colonization of new areas. In the western English Channel,  
540 eutrophication can also extend the spawning season of *Abra alba* (Dauvin & Gentil,  
541 1989) which could be partly responsible for the high abundance of *A. alba* observed  
542 at station R in 2015 and 2017. Local disturbance, predation/competition, and climatic  
543 factors are also known to control *A. alba* populations (Dauvin et al., 1993). The  
544 persistence of the observed changes needs to be confirmed as *A. alba* and *V. gibba*  
545 are known to present high population variations in such soft-bottom communities  
546 (Cabioch, 1968), however, such high inter-annual variability was not observed until  
547 the mid 2010s.

548 Despite the fact the positive shift of second-order species was mainly driven by *V.*  
549 *gibba*, the community was still dominated by species very sensitive to nutrient  
550 enrichment in 2019, some molluscs having increased in abundance and occurrence  
551 (*B. incarnata*, *Laevicardium crassum*, *T. ovata*, *M. donacina*, *N. hanleyi*, *P.*  
552 *maximus*). The diversity of temporal dynamics suggests a complex gradient of  
553 sensitivity to organic matter enrichment and the implication of additional driving  
554 factors. Indeed, (1) discards from scallop dredging could promote opportunistic  
555 species and scavengers leading to increases in their abundances (Depestele et al.,  
556 2019) and (2) by capturing nutrients, green tides are particularly suspected to buffer  
557 the influence of nutrient enrichment on macrofauna as discussed by Ponsero & Le  
558 Mao (2011) and Sturbois et al. (under review) concerning the neighbouring intertidal  
559 area.

560  
561 As in other ecosystems impacted by anthropogenic activities, changes observed in  
562 the bay of Saint-Brieuc result from different pressures acting simultaneously at  
563 different spatio-temporal scales.

564 The selective mortality of fragile, flexible, tubicolous and burrower organisms  
565 suggests the influence of a physical disturbance. As wave regime was stable over  
566 the survey period (SHOM: Supplementary material, Appendix H), dredging activities  
567 appear as the most likely factor of disturbance. The magnitude of fishing influence is  
568 difficult to assess because of the lack of accurate data concerning dredging pressure.  
569 However, changes in fisheries regulations (i.e. fishing ground zonation) in 2010 and  
570 2017, coupled to an increase in the *P. maximus* population, has led to an increase of  
571 scallop dredging activities and inherent mechanical disturbances of the seabed and  
572 associated benthic macrofauna. Nutrient enrichment probably drove the ecological  
573 response of the primary disturbed benthic assemblages by the stimulation of  
574 opportunistic-species, and concomitantly other suspension-feeder species. Climate

575 change occurring at a larger scale, combined with the aforementioned local factors of  
576 disturbance, may also jointly control some other bivalve's populations.

577

### 578 **4.3 Regional scale insights**

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

592 Among other bivalve species, *Moerella donacina* and to a lesser extent *Timoclea*  
593 *ovata* increased in abundance and occurrence. These trends are congruent with  
594 those reported by Gaudin et al. (2018) who tracked changes in response to climate  
595 change in the English Channel. They notably showed, between the 1960s and 2014,  
596 important and moderate increases in occurrence and eastward movements of  
597 populations (i.e. tracking colder conditions) for *M. donacina* and *T.ovata*,  
598 respectively. Climate change (temperature increase) is also suspected to be  
599 responsible for changes in the abundance of *Albra alba* at station R [Dauvin et al.,  
600 1993 ; Thiébaud & Houbin (comm. pers.)], and of *Limecola balthica* in the nearby  
601 intertidal mudflats of the bay of Saint-Brieuc (Sturbois et al., under review).

602 In the past decades, the slipper limpet *Crepidula fornicata* has progressively become  
603 an important component of soft-bottom benthic ecosystems in the English channel  
604 (Blanchard et al., 2001; Blanchard, 2005). Total stock reached an estimated 450000  
605 tons in the bays of Saint-Brieuc and Mont Saint-Michel in the early 2000s (Blanchard  
606 & Hamon, 2006). Current trends are not documented, except in the bay of Brest,  
607 where Blanchet-Aurigny et al. (2012) reported that historical *Crepidula fornicata* beds  
608 are currently mainly made up of dead shells. In our study, a decrease in the mean  
609 density *C. fornicata* was observed ( $40.21 \text{ ind.m}^{-2} \pm 182.42$  in 1987 vs  $21.11 \text{ ind.m}^{-2} \pm$   
610  $48.46$  in 2019), but this overall trend is driven by change observed at a single station  
611 (105), while densities remained stable for the rest of the bay.

612

#### 613 **4.4 What conservation perspectives for such coastal areas?**

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

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



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

633 The massive recruitment of *V. gibba* also characterizes the pioneer stages of benthic  
634 community dynamics following a perturbation (Pranovi, Giovanardi & Franceschini,  
635 1998). Bonvicini-Pagliai & Serpagli (1988) called this species “a time recorder of  
636 environmental stress”. As a dominant suspension-feeder, with rapid juvenile and  
637 adult growth, *V. gibba* plays an important role in the food web by transferring pelagic  
638 production to the benthic compartment (Hrs-Brenko, 2006). Once the disturbance  
639 regime decreases, biotic interactions will progressively regulate *V. gibba* populations  
640 (Olafsson, Peterson & Ambrose, 1994). Knowledge on the level of disturbance  
641 required for the persistence of an abundant *V. gibba* population and its ability to  
642 increase in abundance in the absence of a primary disturbance factor is crucial to  
643 disentangle effects of natural and anthropogenic factors (Australian government,  
644 2008).

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

652 The ecological state defined in 1987 does not constitute a reference state, and even  
653 less a conservation target, as nutrient enrichment and fishing pressures were  
654 probably already well established. CTA could bring new perspectives to the  
655 assessment of the ecological distance between current and reference status (Borja,  
656 Dauer & Grémare, 2012), by measuring net changes with respect to a predefined

657 reference state. Ideally, such ecological baseline should be defined within an  
658 ecological entity, in unaffected areas. In the absence of a local pristine state, or of an  
659 ecological state that could be considered as a conservation target, it should be  
660 possible to include in the analysis data from similar ecosystems located in the same  
661 region to define a reference state in the multivariate space (e.g. a centroid of  
662 samples considered as a potential conservation target, including natural variability).  
663 Net change calculations over time, with respect to the reference status, may allow  
664 the accurate measurement of the restoration process through recovering trajectories.  
665 The definition of conservation targets in multivariate spaces could underline the  
666 degradation level, with respect to historical data, and help local governance adapt  
667 management perspectives.

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

685 long-term sampling networks as suggested by Bacouillard et al. (2020) and Callaway  
686 (2016) and that the development of such monitoring strategy is important for the  
687 future.

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

698 Overall, access to highly resolved information about fishing activities is paramount to  
699 help understand changes in benthic communities and distinguish the impact of  
700 fishing activities and other driving factors (nutrient enrichment, sediment instability,  
701 climate change) on benthic communities. Up-to-date documented reports on  
702 ecological changes and conservation status must be shared with stakeholders to  
703 effectively inform public debates (Eastwood et al., 2007; Pedersen et al., 2009).

704 Consultation processes should involve policy makers, members of fishing institutions,  
705 fishermen, environmental organizations, and managers of Marine Protected Areas  
706 (MPAs) when present. This step should ideally lead to the implementation of fishery  
707 management measures to reduce threats, and achieve conservation objectives  
708 (Pedersen et al., 2009; AFB et al., 2019; Lusenius, H. et al., 2019).

709 Although progress in expanding the coverage of MPAs has been made, the  
710 application of management tools has not yet been implemented in most of these  
711 areas (Torriente et al., 2019). Conservation of the marine environment is effectively a  
712 relatively new phenomenon and is currently playing 'catch-up' with its terrestrial

713 counterpart where protected areas have been established for many decades (Morris  
714 et al., 2014). Despite the need for a worldwide improvement in the designation and  
715 management processes of marine areas, it has already been demonstrated that local  
716 human impacts on the marine environment could be effectively reduced within  
717 networks of Natura 2000 and Marine protected Areas (Fraschetti et al., 2018; Zupan  
718 et al., 2018). Management plans are recommended for Natura 2000 sites but are not  
719 mandatory under the Habitats Directive. Nevertheless, they appear to be an  
720 appropriate solution to reflect transparent conservation objectives (European  
721 Commission, 2011). Despite their complexity, fishing regulations implemented  
722 through a consultation process and management scheme have been shown to  
723 represent win-win scenarios between economic and conservation goals in different  
724 marine protected areas around the world (N2K group, 2018). In the bay of Saint-  
725 Brieuc, the implementation of such win-win scenarios enabled the long-term  
726 management of *P. maximus* population with benefits for the fishermen, and more  
727 modestly, promoted Cockle fishing grounds (Ponsero, Dabouineau & Allain, 2009).  
728 Similar trends were reported in the Irish sea by Bradshaw et al. (2001), who showed  
729 positive effects of commercial fishing area closures on *P. maximus* (and indirectly on  
730 fishermen) and on benthic communities which became more diverse.

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

736

737

738

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757 The authors declare that they have no known competing financial interests or  
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763

764 **Credit authorship contribution statement**

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

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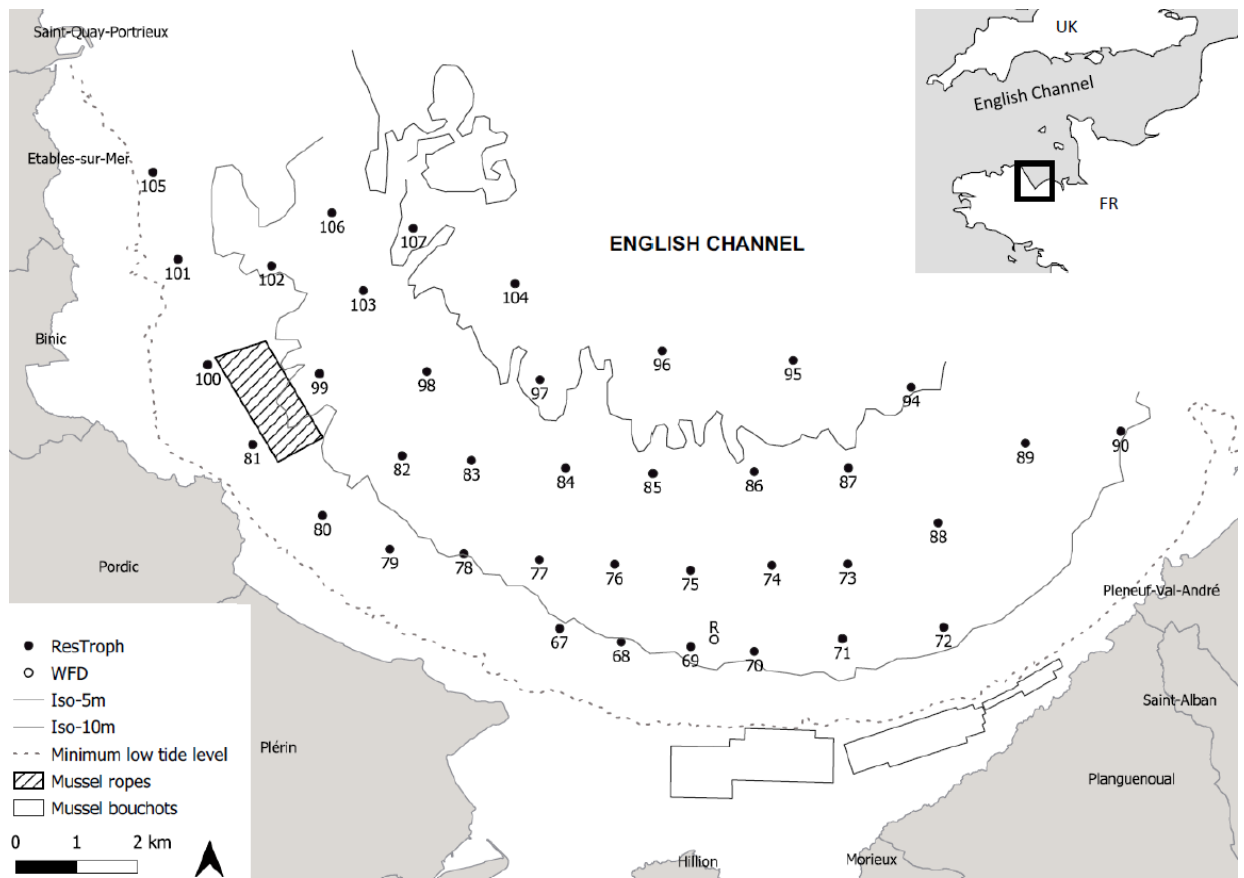
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1107 **FIGURES ET TABLES**



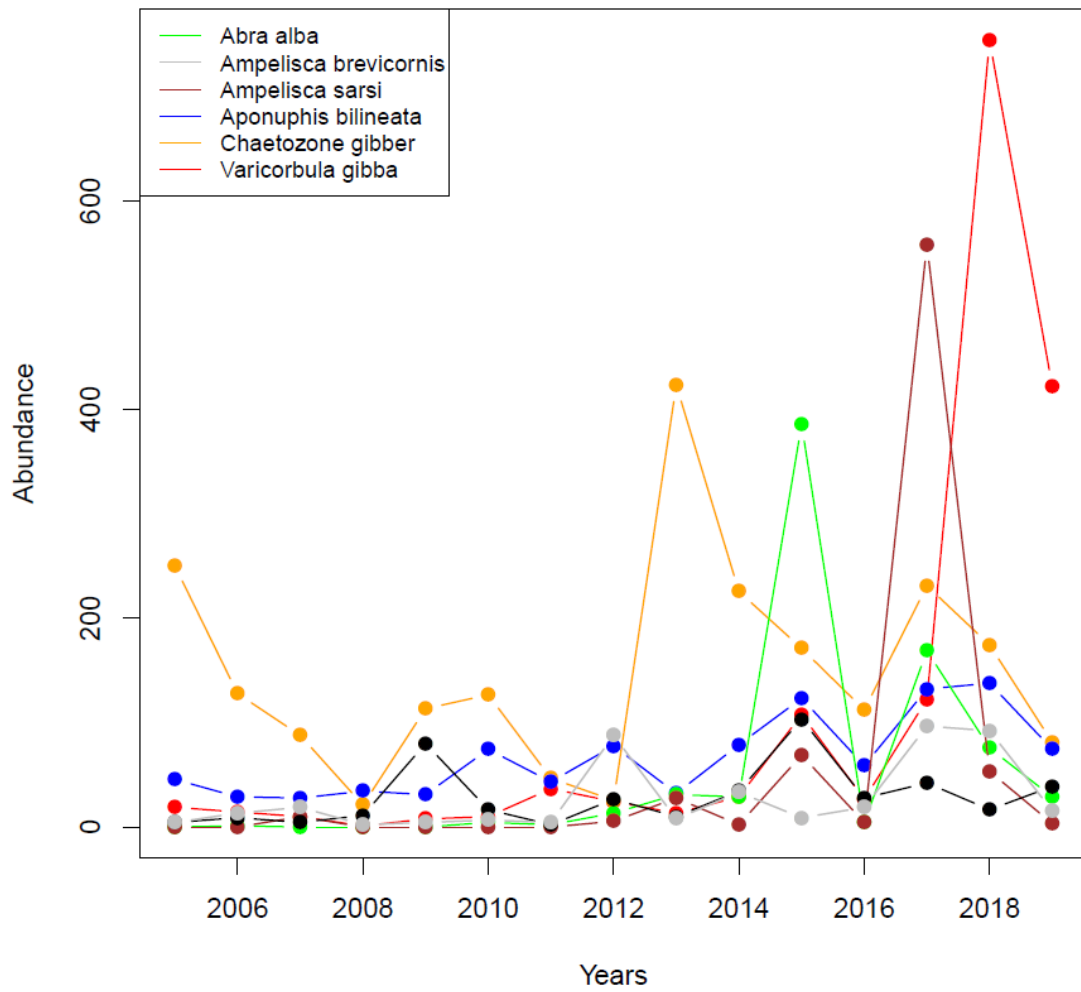
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1109 Figure 1: Location of the study area and sampling strategy. Black dots corresponds to the 38  
 1110 stations of the ResTroph research program sampled in 1987 and 2019 and white one (station  
 1111 R) to the Water Framework Directive (WFD) monitoring program conducted from 2005 to  
 1112 2019. Water depth is represented by dotted (0 m) and continuous lines (5 and 10 m) and  
 1113 mussel bouchots and ropes by polygons.

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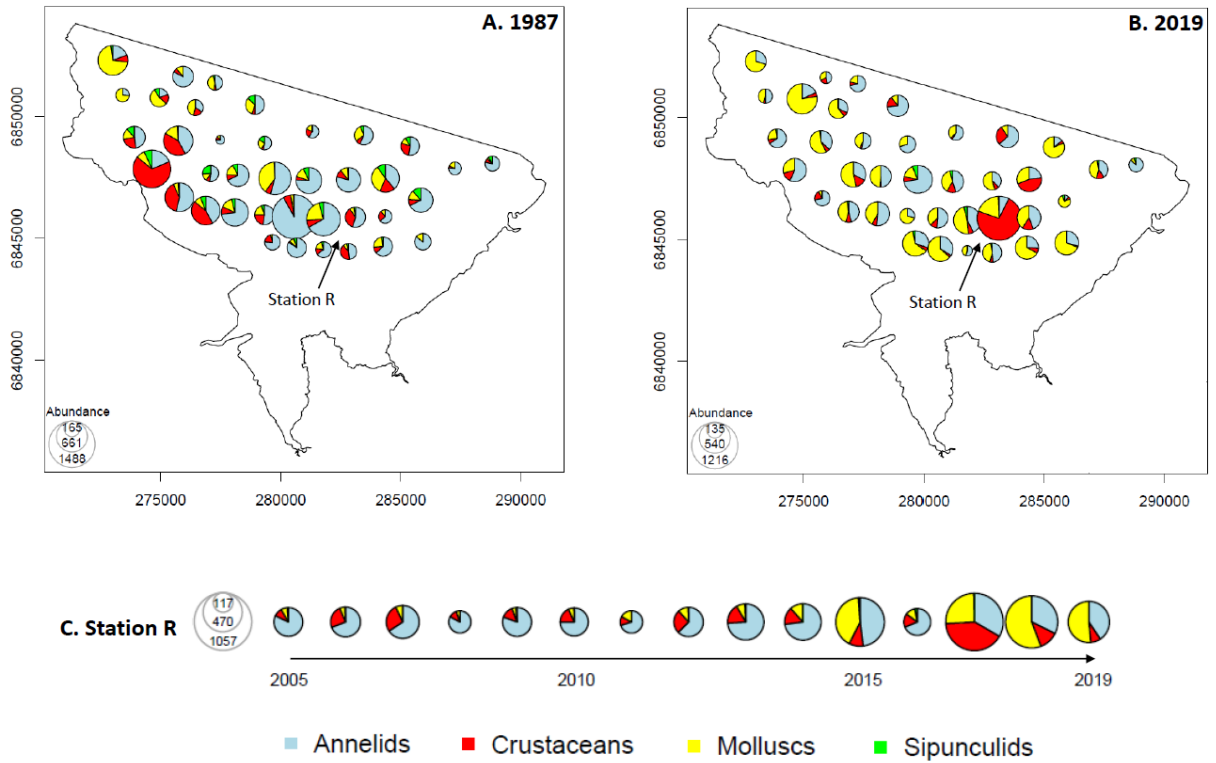
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1118 Figure 2: Abundance (ind.m<sup>2</sup>) of dominant species sampled at the station R

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1123 Figure 3: Distribution maps of main taxonomic group with mean total abundance ( $m^2$ ) classes

1124 superimposed given as the sum for 1987 and 2019. Colours represents each group: Annelids

1125 errant (blue), Annelids sedentary (light blue), Crustaceans (red), Molluscs (yellow) and

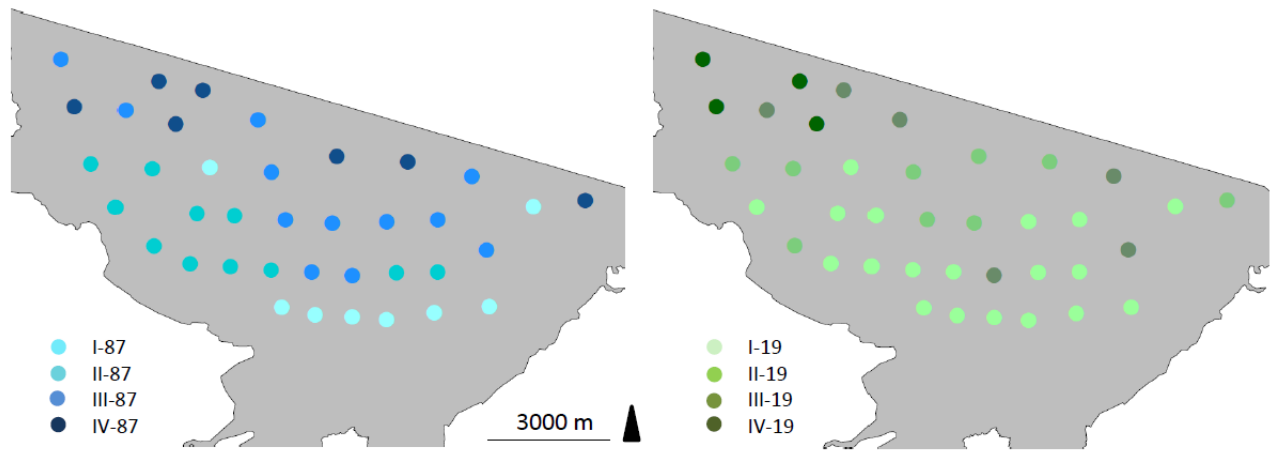
1126 Sipunculids (green). Pies section corresponds to relative abundance of each taxonomic

1127 group. A. and B. represent 1987 and 2019 ResTroph surveys and C. represents surveys

1128 conducted from 2005 to 2019 at station R.

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1132 Figure 4: Spatial distribution of benthic assemblages identified with Hierarchical Cluster

1133 Analysis of the ResTroph data set (38 stations) in 1987 and 2019.

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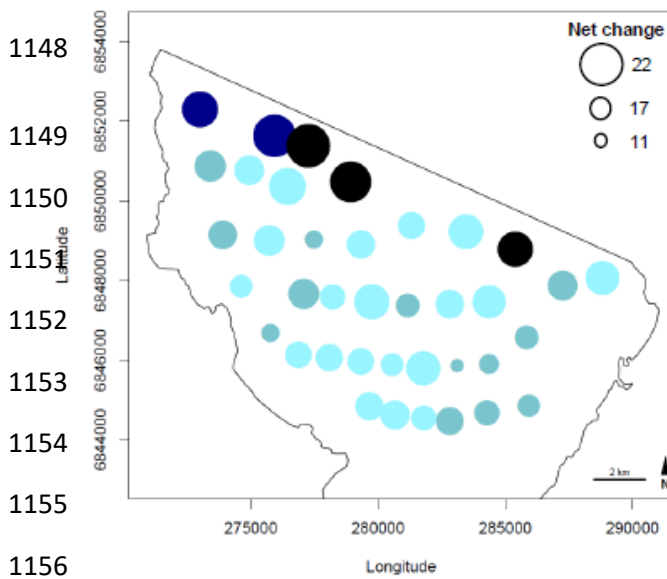
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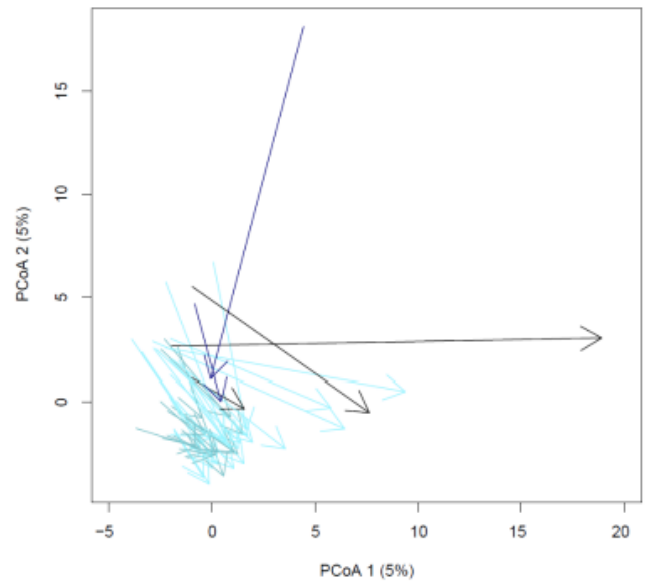
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A. Local taxonomic trajectories



B. Trajectory ordination diagram



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

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Trajectory clusters	1987				2019	
	Ind. sp	Most num	Ind. sp	Most num	Ind. sp	Most num
A 20 st NC= 20,35 ±0.66	<i>ns</i>		<i>ns</i>		<i>ns</i>	
			<i>Ampharete spp.</i>	84.40 ±60.57	<i>Varicorbula globa</i>	80.2 ±18.36
B 13 st NC= 16,59 ±1.09	<i>Aponuphis bilineata</i>	0.622 / 0.0117	<i>Ampelisca brevicornis</i>	38.77 ±17.96	<i>Crepidula fornicata</i>	43.6 ±23.86
			<i>Aponuphis bilineata</i>	34.46 ±8.89	<i>Varicorbula globa</i>	0.546 / 0.0214
C 3 st NC= 27,82 ±1.67	<i>Nemertea spp.</i>	0.822 / 0.0037	<i>Ampharete spp.</i>	21.33 ±17.49	<i>Pecten maximus</i>	0.724 / 0.0140
			<i>Anapagurus hyndmanni</i>	21.33 ±17.49	<i>Syllis garciai</i>	0.667 / 0.0052
D 2 st NC= 27.39 ±2.26	<i>Protodorvillea kefersteini</i>	1.000 / 0.0019	<i>Crepidula fornicata</i>	168.00 ±168.00	<i>Notomastus latericus</i>	21.33 ±9.61
			<i>Nucula hanleyi</i>	0.517 / 0.0192	<i>Timoolea ovata</i>	0.963 / 0.0041
			<i>Notomastus latericus</i>	44.00 ±20.00	<i>Glycymeris glycymeris</i>	0.500 / 0.0486
					<i>Timoolea ovata</i>	64.00 ±56.00
					<i>Notomastus latericus</i>	52.00 ±20.00

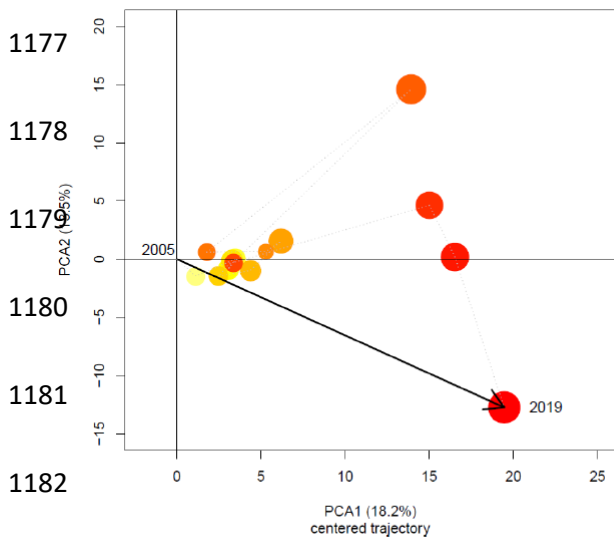
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1168 Figure 5: Taxonomic trajectories. A.: Maps of local trajectories. Size of circles corresponds to  
 1169 net change between 1987 and 2019 and colours to cluster of trajectories determined by HCA  
 1170 on CTA trajectory similarity analysis. All the dimensions of the multivariate space were  
 1171 considered in net change calculation and analysis of trajectory similarities. B.: Trajectory  
 1172 ordination diagrams. Only two dimensions are show. C.: Characteristics of initial and final  
 1173 taxonomic ecological states of trajectory clusters. Taxonomic trajectory are coloured  
 1174 according to trajectory clusters (blue gradient).

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1177 **A. TAXONOMIC**



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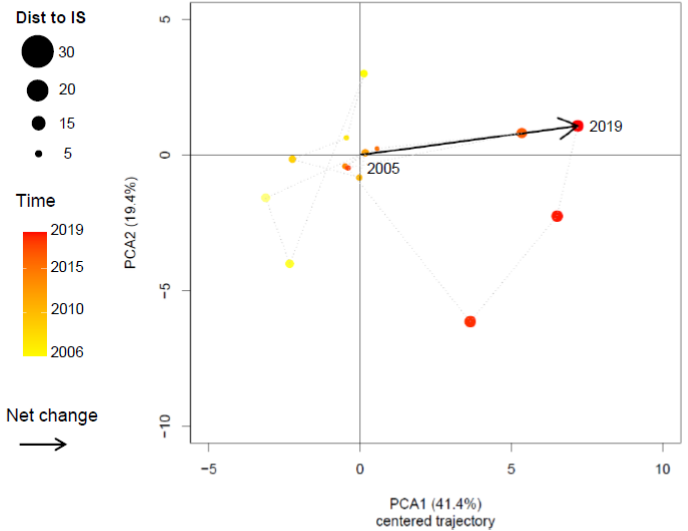
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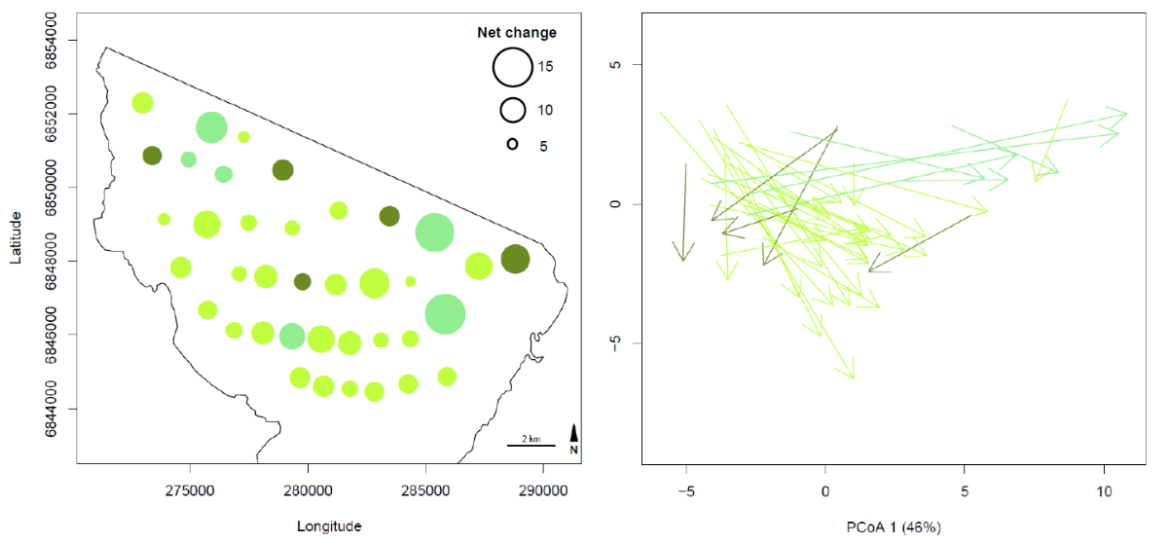
**B. FUNCTIONAL**



1184 Figure 6: Trajectory of the station R between 2005 and 2019. The origin of the ordination  
1185 diagram represents the initial state characterized in 2005 after trajectory centering. Only two  
1186 dimensions are shown. Points corresponds to intermediate ecological states (size= length of  
1187 each state to initial state considering all PCA components) and are coloured according to time  
1188 (yellow (2005) to red (2019)). Lines represents segments between transitional state. The  
1189 black arrow represents the net change between 2005 and 2019.

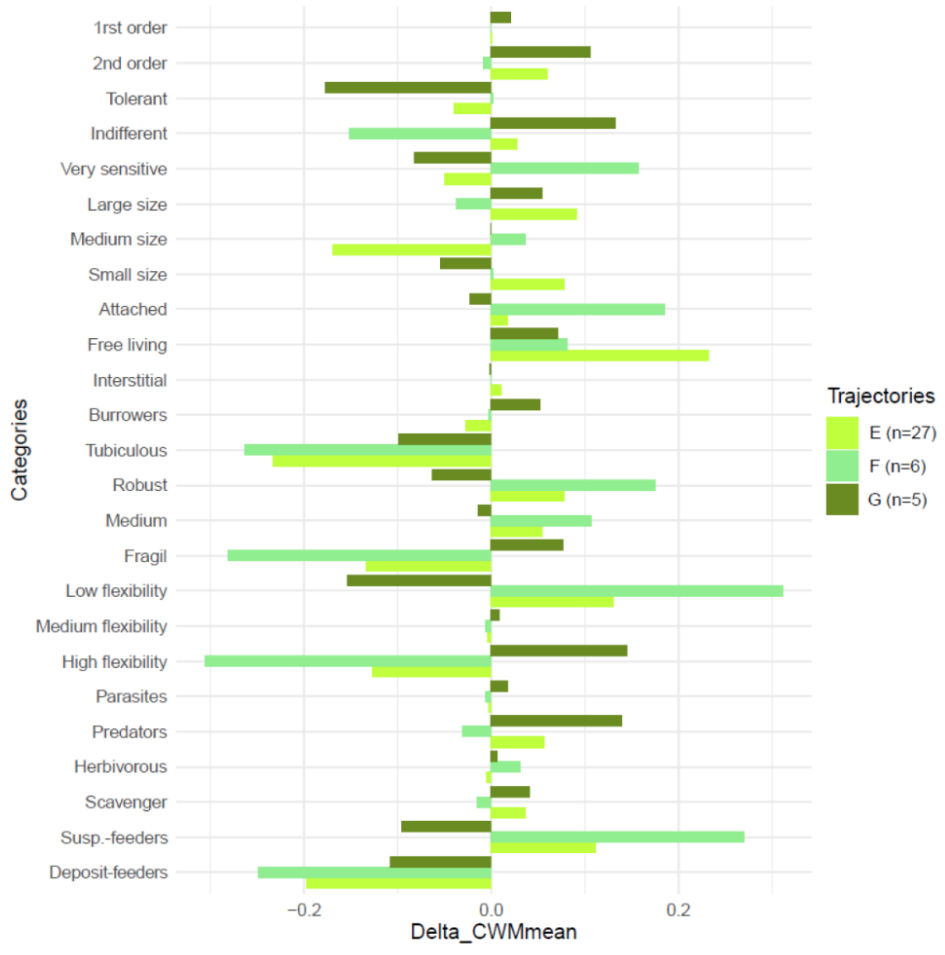


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A. Local functional trajectories      B. Trajectory ordination diagram

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

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1230 Figure 7: Functional trajectories. A.: Maps of local trajectories. Size of circles corresponds to  
1231 net change between 1987 and 2019 and colours to cluster of trajectories determined by HCA

1232 on CTA trajectory similarity analysis. All the dimensions of the multivariate space were  
1233 considered in net change calculation and analysis of trajectory similarities. B.: Trajectory  
1234 ordination diagrams. Only two dimensions are show. Taxonomic trajectory are coloured  
1235 according to trajectory clusters (green gradient). Characteristics of initial and final functional  
1236 ecological states of trajectory clusters are detailed in table IV. C.: Barplots of CWM values  
1237 shift for each categories of traits (mean 2019 – mean 1987). Bars are coloured according to  
1238 functional trajectory clusters.

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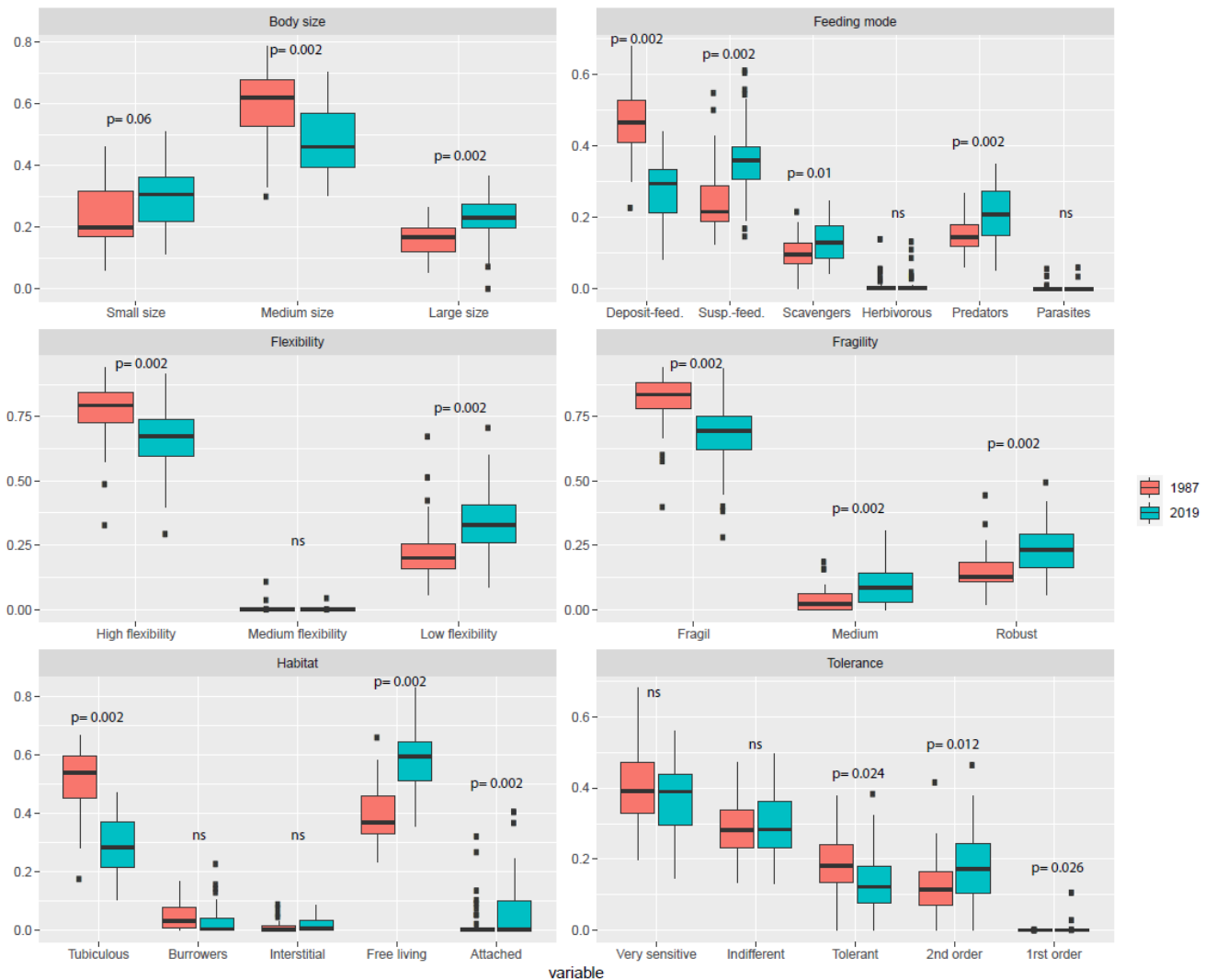
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1269 Figure 8: Box plots of CWM traits values in levels of respective categories according to year

1270 (1987: red; 2019: green). Box plot indicates the median (line in the box), the first and third

1271 quartiles (hinges) and extreme data points (black points). Significance of student permutation

1272 paired tests are indicated for each category traits.

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1278 Table I: Characteristics of assemblages identified with the Hierarchical Cluster Analysis in  
 1279 1987 and 2019: number of station (N st), Specific richness (S), Mean density per m<sup>2</sup> (Abund),  
 1280 Shannon-Weaver Index (H), Simpson Index (D) and Pielou's evenness (J) ( $\pm$  standard error).  
 1281 Assemblages are characterised by indicative and dominant species.

Assemblages	Indicator species	indval	p	Most numerous species	Mean.m <sup>2</sup> $\pm$ se	N st	S	Abund	H	D	J	
1987	I-87	<i>Chaetozone gibber</i>	0.555	0.0006	<i>Chaetozone gibber</i>	42.00 $\pm$ 12.98	8	12.25 $\pm$ 1.05	219 $\pm$ 28.20	2.18 $\pm$ 0.07	0.85 $\pm$ 0.01	0.88 $\pm$ 0.02
		<i>Sigalion mathildae</i>	0.547	0.0007	<i>Aponuphis bilineata</i>	35.00 $\pm$ 11.60						
		<i>Magelona filiformis</i>	0.500	0.0016	<i>Ampelisca brevicornis</i>	21.00 $\pm$ 6.22						
		<i>Spiophanes bombyx</i>	0.487	0.0032	<i>Spiophanes bombyx</i>	18.00 $\pm$ 6.18						
		<i>Aponuphis bilineata</i>	0.442	0.0067	<i>Sigalion mathildae</i>	11.00 $\pm$ 3.00						
	II-87	<i>Ampelisca brevicornis</i>	0.536	0.0004	<i>Ampelisca brevicornis</i>	145.45 $\pm$ 59.49	11	21.09 $\pm$ 1.79	535.27 $\pm$ 88.98	2.53 $\pm$ 0.01	0.87 $\pm$ 0.02	0.84 $\pm$ 0.03
		<i>Varicorbula gibba</i>	0.470	0.0013	<i>Euclymene oerstedii</i>	37.09 $\pm$ 14.56						
		<i>Ampelisca tenuicornis</i>	0.431	0.0073	<i>Ampelisca tenuicornis</i>	37.09 $\pm$ 11.63						
		<i>Euclymene oerstedii</i>	0.415	0.0143	<i>Notomastus latericeus</i>	36.36 $\pm$ 7.50						
		<i>Nephtys hombergii</i>	0.368	0.0362	<i>Aponuphis bilineata</i>	31.27 $\pm$ 6.95						
III-87	<i>Ampharete</i> spp.	0.554	0.0005	<i>Ampharete</i> spp.	150.67 $\pm$ 98.81	12	24.92 $\pm$ 1.96	629.33 $\pm$ 115.25	2.60 $\pm$ 0.16	0.85 $\pm$ 0.04	0.82 $\pm$ 0.04	
	<i>Golfingia (Golfingia) elongata</i>	0.532	0.0004	<i>Crepidula fornicata</i>	71.33 $\pm$ 34.54							
	<i>Crepidula fornicata</i>	0.443	0.0055	<i>Notomastus latericeus</i>	37.33 $\pm$ 9.96							
	<i>Polycirrus medusa</i>	0.438	0.0051	<i>Polycirrus medusa</i>	32.00 $\pm$ 9.08							
	<i>Sthenelais boa</i>	0.419	0.0085	<i>Golfingia (Golfingia) elongata</i>	21.33 $\pm$ 4.33							
IV-87	<i>Nototropis vedfomensis</i>	0.384	0.0031	<i>Notomastus latericeus</i>	21.71 $\pm$ 7.75	7	15.43 $\pm$ 2.08	225.14 $\pm$ 29.90	2.43 $\pm$ 0.17	0.87 $\pm$ 0.03	0.90 $\pm$ 0.03	
	<i>Notomastus latericeus</i>	0.357	0.0273	<i>Nucula hanleyi</i>	14.86 $\pm$ 13.57							
	<i>Hilignernis gracilis</i>	0.351	0.0387	<i>Hilignernis gracilis</i>	12.57 $\pm$ 5.20							
	<i>Glycera capitata</i>	0.286	0.0296	<i>Polycirrus medusa</i>	9.14 $\pm$ 9.14							
	<i>Protomyxides bidentata</i>	0.286	0.0293	<i>Fabulina fabula</i>	9.14 $\pm$ 4.43							
I-19	<i>Varicorbula gibba</i>	0.612	0.0001	<i>Varicorbula gibba</i>	160.84 $\pm$ 19.63	19	16.53 $\pm$ 1.04	466.11 $\pm$ 74.66	2.08 $\pm$ 0.09	0.77 $\pm$ 0.02	0.76 $\pm$ 0.03	
	<i>Phyllodoce groenlandica</i>	0.368	0.0310	<i>Ampelisca tenuicornis</i>	64.42 $\pm$ 63.54							
				<i>Glycinde nordmanni</i>	20.63 $\pm$ 4.07							
				<i>Streblosoma bairdi</i>	17.26 $\pm$ 4.63							
				<i>Aponuphis bilineata</i>	16.42 $\pm$ 6.69							
II-19	<i>Nephtys hombergii</i>	0.483	0.0004	<i>Notomastus latericeus</i>	29.33 $\pm$ 7.06	9	18.78 $\pm$ 2.14	352.00 $\pm$ 56.04	2.60 $\pm$ 0.10	0.90 $\pm$ 0.01	0.90 $\pm$ 0.01	
				<i>Varicorbula gibba</i>	27.56 $\pm$ 10.16							
				<i>Nephtys hombergii</i>	25.78 $\pm$ 5.62							
				<i>Anomia ephippium</i>	18.67 $\pm$ 10.67							
				<i>Pista cristata</i>	17.78 $\pm$ 6.77							
III-19	<i>Crepidula fornicata</i>	0.728	0.0004	<i>Crepidula fornicata</i>	160.00 $\pm$ 66.58	6	18.83 $\pm$ 2.68	430.67 $\pm$ 103.08	2.29 $\pm$ 0.21	0.80 $\pm$ 0.05	0.80 $\pm$ 0.06	
	<i>Pecten maximus</i>	0.446	0.0239	<i>Notomastus latericeus</i>	21.33 $\pm$ 7.35							
	<i>Syllis garciai</i>	0.333	0.0313	<i>Aponuphis bilineata</i>	16.00 $\pm$ 10.93							
	<i>Amphipholis squamata</i>	0.333	0.0304	<i>Nephtys hombergii</i>	10.67 $\pm$ 5.72							
	<i>Aequipecten opercularis</i>	0.333	0.0290	<i>Anomia ephippium</i>	10.67 $\pm$ 9.16							
IV-19	<i>Nucula hanleyi</i>	0.611	0.0024	<i>Timoclea ovata</i>	34.00 $\pm$ 28.73	4	10.50 $\pm$ 1.32	252.00 $\pm$ 62.18	1.97 $\pm$ 0.08	0.81 $\pm$ 0.01	0.85 $\pm$ 0.03	
	<i>Timoclea ovata</i>	0.596	0.0031	<i>Nucula hanleyi</i>	30.00 $\pm$ 11.94							
	<i>Glycera alba</i>	0.481	0.0069	<i>Crepidula fornicata</i>	30.00 $\pm$ 30.00							
			<i>Notomastus latericeus</i>	26.00 $\pm$ 17.09								
			<i>Polittapes rhomboides</i>	18.00 $\pm$ 18.00								

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1283 Table II: Characteristics of cluster of surveys identified with the Hierarchical Cluster Analysis  
 1284 performed on the WFD data set (2005 to 2015): number of station (N st), Specific richness  
 1285 (S), Mean density per m<sup>2</sup> (Abund), Shannon-Weaver Index (H), Simpson Index (D) and  
 1286 Pielou's evenness (J) ( $\pm$  standard error). Assemblages are characterised by indicative and  
 1287 dominant species.

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Assemblages	Indicator species	indval	p	Most numerous species	Mean.m <sup>2</sup> $\pm$ se	N sv	S	Abund	H	D	J
1289 R-I	<i>Cauleriella alata</i>	0.643	0.0003	<i>Chaetozone gibber</i>	170.95 $\pm$ 52.62	7	62.57	647.30	3.10	0.89	0.75
	<i>Edwardsia claparedii</i>	0.576	0.0259	<i>Aponuphis bilineata</i>	52.54 $\pm$ 7.52		$\pm$ 3.62	$\pm$ 82.30	$\pm$ 0.12	$\pm$ 0.03	$\pm$ 0.03
	<i>Magelona filiformis</i>	0.563	0.0009	<i>Notomastus latericeus</i>	26.51 $\pm$ 10.09						
	<i>Scoloplos armiger</i>	0.530	0.0023	<i>Ampelisca brevicornis</i>	23.02 $\pm$ 11.53						
1290	<i>Apseudopsis latreillii</i>	0.471	0.0263	<i>Varicorbula gibba</i>	22.38 $\pm$ 3.70						
1291 R-II	<i>Cirratulidae spp.</i>	0.758	0.0039	<i>Chaetozone gibber</i>	90.83 $\pm$ 25.03	4	53.00	576.67	3.03	0.92	0.77
	<i>Tritia varicosa</i>	0.750	0.0194	<i>Cirratulidae spp.</i>	74.72 $\pm$ 24.46		$\pm$ 3.34	$\pm$ 88.18	$\pm$ 0.07	$\pm$ 0.01	$\pm$ 0.01
	<i>Ampelisca spinimana</i>	0.725	0.0001	<i>Ampelisca tenuicornis</i>	50.00 $\pm$ 16.22						
	<i>Nephtys hombergii</i>	0.645	0.0269	<i>Aponuphis bilineata</i>	41.39 $\pm$ 11.12						
1292	<i>Ampelisca tenuicornis</i>	0.590	0.0002	<i>Chaetozone zettlandica</i>	29.72 $\pm$ 7.39						
1293 R-III	<i>Calyptraea chinensis</i>	1	0.0022	<i>Varicorbula gibba</i>	351.39 $\pm$ 152.33	4	75.50	1772.50	2.92	0.87	0.67
	<i>Spisula elliptica</i>	0.925	0.0010	<i>Ampelisca sarsi</i>	170.83 $\pm$ 129.74		$\pm$ 2.40	$\pm$ 234.74	$\pm$ 0.11	$\pm$ 0.02	$\pm$ 0.02
	<i>Ampelisca spinipes</i>	0.860	0.0035	<i>Abra alba</i>	164.72 $\pm$ 31.00						
	<i>Thyasira flexuosa</i>	0.790	0.0016	<i>Chaetozone gibber</i>	164.44 $\pm$ 14.47						
1294	<i>Amphictene auricoma</i>	0.750	0.0150	<i>Aponuphis bilineata</i>	116.94 $\pm$ 19.90						

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1311 Table III: Main bivalves species identified in the four replicates sieved on 5mm circular mesh  
 1312 size at the 38 Restroph stations in 1987 and 2001 (N: total abundance, sd: standard  
 1313 deviation). The significance of trends was tested with a student permutation paired-test (ns:  
 1314 no trend ; - : decrease ; +: increase). Distribution maps are detailed in appendix F.

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

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1328 **Additional Files**

1329 **Appendix A:** Dredging rules and fishing effort

1330 **Appendix B:** Categories of functional traits

1331 **Appendix C:** Map of the sediment properties in the 38 ResTroph stations between  
1332 1987 and 2019

1333 **Appendix D:** Evolution of sediment properties at station R from 2005 to 2019

1334 **Appendix E:** General description of the benthic macrofauna according to sampling  
1335 campaigns

1336 **Appendix F:** Map of the distribution and abundance of the main bivalve species

1337 **Appendix G:** Station R functional factor map

1338 **Appendix H:** Evolution of the wave regime over the last 30 years close to station R  
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