

1 **Characterizing spatio-temporal changes in benthic communities: taxonomic and**  
2 **functional trajectories of intertidal assemblages in the bay of Saint-Brieuc**  
3 **(English Channel)**

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13  
14 **Abstract:**

15 Tracking and quantifying ecological changes at large and long-term scales is a  
16 central point for monitoring and conservation issues. The Community Trajectory  
17 Analysis Framework was used in complement with classical methods to analyse and  
18 represent long-term changes in marine habitats at 42 stations in the bay of Saint-  
19 Brieuc (western English Channel), sampled in 1987, 2001 and 2019. The taxonomic  
20 and functional trajectories of intertidal benthic assemblages were studied at local and  
21 assemblage scales. Whatever the perennial contribution of dominant prevalent  
22 species at the site scale, some species were highly variable over time and space,  
23 influencing the structuration of assemblages. Taxonomic changes were not  
24 systematically associated with significant changes in the functional properties at local  
25 and community scale. The consideration of local changes and variations at the  
26 species level explained the differences in composition observed at the scale of  
27 assemblages. Observed changes mainly reflected random population dynamics of  
28 structuring prevalent species in habitat under strong natural pressures, rather than  
29 specific changes of the community. Few species reveal the long-term effect of green

30 tides in some assemblages. Overall, this study confirms the complexity to  
31 disentangle factors of changes in the absence of a monitoring strategy specifically  
32 devoted the measurement of environmental factors and anthropogenic pressures.  
33 The study also highlights the need for the development of benthic monitoring  
34 strategies at multiple spatial and temporal scales.

35

36 **Keywords:** community trajectory analysis, ecological trajectories, benthic  
37 macrofauna, stability, variability, marine protected area

38

### 39 **1. Introduction**

40 Costal ecosystems face severe natural and anthropogenic pressures that affect,  
41 sometimes strongly, both the structure and functioning of benthic communities  
42 (Harris, 2012; Cimon and Cusson, 2018). Although assessment of stability/variability  
43 of benthic communities, often in relation with management considerations, has  
44 received a large attention by scientists, it remains a central point of ecological  
45 research and conservation (Ellis et al., 2000). Studying stability/variability in  
46 ecological systems requires the consideration of disturbances defined as “any  
47 discrete event in time that disrupt ecosystems, community or populations structure”  
48 (Pickett and White, 1985). Ecological theory suggests that small scale disturbance  
49 events at intermediate frequencies may have positive effects on the system at larger  
50 scales whereas disturbance on larger scales are much more likely to reduce  
51 heterogeneity in communities and induce slower recovery rates (Bazzaz, 1983;  
52 Caswell and Cohen, 1991; Connell, 1978; Ellis et al., 2000). Understanding the  
53 effects of environmental changes on natural communities requires to distinguish  
54 natural and anthropogenic variability (Osenberg and Schmitt, 1996; Stewart-Oaten,  
55 1996). However, the lack of reference, non-impacted sites in modern ecosystems,  
56 makes this task a real challenge (Boldina et al., 2014). Temporal surveys assessing  
57 the evolution of benthic communities are therefore essential to establish baselines

58 and detect ecological changes (Desroy et al., 2002; Hardman-Mountford et al., 2005;  
59 Schückel et al., 2015; Veiga et al., 2017).

60 Benthic communities are commonly sampled *via* a network of stations and a  
61 sampling periodicity varying from seasonal to decadal. Such an approach allows  
62 detecting major changes in benthic macrofauna without being able to infer on the  
63 causes of changes (Bacouillard et al., 2020). The simultaneous sampling of several  
64 stations distributed in the area of interest makes possible to investigate temporal  
65 changes occurring at different inter-connected scales: (1) at the scale of a station,  
66 where local processes may drive the composition of communities (sedimentary  
67 changes, local anthropogenic pressures), and (2) at the scale of cluster of stations  
68 with similar composition (hereafter called assemblages), where processes operating  
69 at larger scale may drive the temporal variability (climate, diffuse and chronic  
70 anthropogenic disturbances).

71 Although there is a large consensus that diversity losses threaten ecosystem  
72 functioning, man-induced changes do not systematically impact diversity. Studying  
73 the temporal variability of benthic assemblages through analysis of composition and  
74 structure gains or losses seems consequently limited regarding functional  
75 considerations. For example, substantial changes in species composition and  
76 structure in space and time may not systematically results in proportional  $\alpha$  diversity  
77 (Whittaker, 1972; Dornelas et al., 2014) and trait-based functional changes (McLean  
78 et al., 2019; de Sousa Gomes-Gonçalves et al., 2020). In this context, trait-based  
79 approaches offer a complementary integrative framework to link functional  
80 consequences to biodiversity changes (Suding et al., 2008; Boyé et al., 2019).

81 Studies combining composition, structure and functioning assessments of  
82 assemblages in a multidimensional scale allow the detection of multi-faceted  
83 responses to environmental variability in faunal communities (McLean et al., 2019).

84 The detection of future potential changes in species distribution and assemblage  
85 compositions, which can be helpful for monitoring and conservation issues (Desroy et

86 al., 2002; Schückel et al., 2013; Veiga et al., 2017), requires the establishment of  
87 baseline knowledge. In the English Channel, scientific studies have largely focused  
88 on benthic communities in the main coastal bays and estuaries (Desroy et al., 2002).  
89 In the bay of Saint-Brieuc (western English Channel), where intertidal habitats are  
90 partially protected since 1998 by a National Nature Reserve, the analysis of  
91 diachronic changes of benthic assemblages has not been updated for 20 years (Gros  
92 and Hamon, 2021). Previous studies underlined the close link between benthic  
93 resources and waders which prey on macro-invertebrates (Sturbois et al., 2015;  
94 Ponsoero et al., 2016), highlighting the need to study and conserve benthic habitats.  
95 After two decades, an analysis of benthic assemblages using the same protocols as  
96 those used for the definition of historical baselines was needed to assess temporal  
97 changes of intertidal habitats in this bay representative of coastal areas characterised  
98 by range of impacts due to the complex co-occurrence of management's mosaic and  
99 anthropogenic uses (Ellis et al., 2000). Natural and anthropogenic contexts  
100 (Supplementary material, Appendix A) make the study site suitable to contribute to  
101 the debate about the definition of impact assessment at spatial and temporal scales  
102 and the feasibility of such research. It is also essential to provide up-to-date  
103 knowledge to policy makers and managers about the evolution of the composition,  
104 structure and functioning of benthic assemblages.

105 This study, based on a long-term survey in the intertidal soft-bottom sediments of the  
106 bay of Saint-Brieuc, aims to analyse the taxonomic and functional variability of  
107 benthic communities over the last 30 years at different spatial scales using 42  
108 stations sampled in 1987, 2001 and 2019. The approach specifically focused on the  
109 detection of trajectory patterns by applying the recent Community Trajectory Analysis  
110 Framework (De Cáceres et al., 2019; Sturbois et al., 2021b). Results were discussed  
111 regarding potential environmental and anthropogenic driving factors and some  
112 propositions were made for such long-term study approaches.

113

## 114 2. Material and methods

### 115 2.1. Study area

116 Fieldwork was conducted in the bay of Saint-Brieuc, France (Figure 1). The study  
117 area includes about 2900 ha of tidal flats divided in two coves (Yffiniac and Morieux)  
118 mainly dominated by fine to medium sands. The most sheltered parts are dominated  
119 by salt marshes. The bay is under the influence of a semi-diurnal megatidal regime.  
120 Tidal range varies between 4 m at neap tides and nearly 13 m during spring tide  
121 (Figure 2). Divagation of channels is particularly dynamic, with increasing magnitude  
122 in low levels (Supplementary material, Appendix B). A large part of the bay (1140 ha)  
123 is included in the National Nature Reserve of the bay of Saint-Brieuc, created in 1998  
124 to protect wader populations (Figure 1). The study area undergoes a variety of  
125 anthropogenic pressures (Supplementary material, Appendix A): sediment extraction  
126 conducted until 2004 ( $1000\text{m}^3\cdot\text{y}^{-1}$ , around stations 3 and 5) and muddy sediment  
127 deposits (near station 11) dredged from the Saint-Brieuc harbour since 2004 ( $120$   
128  $000\text{ m}^3\cdot\text{y}^{-1}$ ). The bay also suffers from eutrophication, resulting in strong ephemeral  
129 macroalgae proliferation and cyclic green tides episodes. Professional  
130 (*Cerastoderma edule*) and recreational (*Cerastoderma edule*, *Pecten maximus*,  
131 *Arenicola marina*) fishing activities has been an important activity for many decades,  
132 especially in Yffiniac cove. In the lower level of Morieux cove, mussel farming on  
133 wooden poles, called “bouchots” (Figure 1) has increased over the study period, from  
134 277 ha in 1987 to 386 ha in 2001 and 312 ha in 2019.

135

### 136 2.2. Field sampling

137 Macrofauna was sampled during winter (March) in 1987, 2001 and 2019 at 42  
138 stations, following the sampling grid (Figure 1) and the protocol defined in 1987 by  
139 (Gros and Hamon, 2021). At each site, four replicates were collected for  
140 macrobenthos analysis using a  $1/32\text{m}^2$  hand corer (diameter: 20cm), at a depth of 25  
141 cm. The content of the cores was gently sieved on site through 1-mm square mesh

142 sieve. Retained material was preserved for analysis in 5% buffered formaldehyde.  
143 Density per m<sup>2</sup> of *Arenicola marina*, which is difficult to sample with a handcorer, was  
144 estimated visually by counting worm casts at each station within 10 quadrats of 1 m<sup>2</sup>.  
145 A visual description of the sediment type was recorded and two samples of sediment  
146 were collected from additional cores (diameter 5 cm, depth 5 cm) and subsequently  
147 analysed for grain size distribution, and water and organic matter contents. All  
148 replicates were collected at the four corners of a 1m<sup>2</sup> square, using GPS position-  
149 fixing (GPS Etrex Garmin).

150

### 151 **2.3. Laboratory analysis**

152 Macrofauna was identified to the lowest possible level (usually species level),  
153 counted, and abundances were expressed as densities per 1 m<sup>2</sup>. Taxon were named  
154 following the World Register of Marine Species. For granulometric analysis, sediment  
155 was desalted with freshwater during 48 h before being dried at 60°C for 48 h, sieved  
156 through AFNOR standard sieves (from 40 to 25000µm), and weighed. Water and  
157 organic matter contents were respectively determined after drying (60°C for 48 h)  
158 and combustion of sediment at 550 °C for 4 h (Hedges and Stern, 1984; Salonen,  
159 1979).

160

### 161 **2.4. Traits collection**

162 The functional dataset was composed of six traits divided in 23 categories  
163 (Supplementary material, Appendix C). These traits characterized the morphology  
164 (body size, flexibility, fragility) and behavioural traits [feeding behaviour, living habit,  
165 tolerance, (Degen and Faulwetter, 2019)]. This set of traits is related to the  
166 vulnerability of species to mechanical disturbances (associated to recreational and  
167 professional fishing activity and the circulation of vehicles) and organic enrichment  
168 (tolerance). They were chosen to analyse functional changes in the community, in  
169 relation to the main pressures identified in the study area. Information was retrieved

170 from primary literature on specific taxa, expert knowledge and three publicly available  
171 databases: polytraits (<http://polytraits.lifewatchgreece.eu>), the World Register of  
172 Marine Species (WoRMS Editorial Board, 2020), and Biological Trait Information  
173 Catalogue (BIOTIC, <http://www.marlin.ac.uk/biotic/>). Scores were attributed to  
174 species according to their affinity to each category of traits, using a fuzzy coding from  
175 0 (no affinity) to 3 [high affinity (Chevene et al., 1994)]. Community-weighted trait  
176 values (CWMs) were calculated to characterize the functional structure (Ricotta and  
177 Moretti, 2011).

## 178 **2.5. Data analysis**

179 Data collected in 1987, 2001 and 2019 were analysed to track taxonomic and  
180 functional changes. Analysis of sediments (sub-section 2.5.1) and  $\alpha$ -diversity (2.5.2)  
181 were followed by spatial taxonomic clustering (2.5.3) and taxonomic and functional  
182 trajectory analysis (2.5.4). All the statistical analysis was performed with R 4.0.

183

### 184 **2.5.1 Sedimentary dataset**

185 Statistical description of sediments, based on grain-size distributions, was computed  
186 with the R package 'G2Sd' (Fournier et al., 2014). Ten sedimentary parameters were  
187 selected to describe sediment characteristics: water content ( $H_2O$ ), organic matter  
188 content (OMC), arithmetic mean, median ( $d_{50}$ ), gravel ( $> 2mm$ ), coarse sand (1mm  
189 to  $250\mu m$ ), fine sand (250 to  $125\mu m$ ), very fine sand (125 to  $63\mu m$ ), and mud  
190 ( $<63\mu m$ ) contents.

191

### 192 **2.5.2 Taxonomic $\alpha$ -diversity**

193 In order to assess the different components of  $\alpha$ -diversity, the mean number of  
194 individuals per  $m^2$  (N), taxa richness (S), Shannon-Weaver index ( $H'$ ), Simpson index  
195 (D) and Pielou's species evenness (J) were calculated for each station prior to any  
196 transformations of the dataset.

197

198 **2.5.3 Spatial taxonomic clustering**

199 Hierarchical Cluster Analysis (HCA) was performed to distinguish benthic  
200 assemblages (*i.e.* site groups) at each campaign by using the Hellinger distance  
201 between each pair of samples (Legendre and Gallagher, 2001) and by applying the  
202 Ward's clustering method. The indicator value method (Indval) was performed to  
203 characterize assemblages (Dufrene and Legendre, 1997).

204

205 **2.5.4 Detecting trajectory patterns**

206 PCAs were performed on Hellinger transformed data and followed by Community  
207 Trajectory Analysis (CTA). CTA is based on geometrical properties of ecological  
208 trajectories (De Cáceres et al., 2019). The original framework and its new extension  
209 (Sturbois et al., 2021b) were used to study and represent temporal changes at the  
210 station scale taking into account all the dimensions of the multivariate analysis  
211 through trajectories of surveys in the multivariate space. A set of distance-based  
212 metrics were calculated. Segment-length represents, for a station, the distance  
213 between two consecutive surveys. S1 informs about changes between 1987 and  
214 2001, and S2 between 2001 and 2019. The trajectory path represents the sum of  
215 segment length (S1+S2). Net changes were calculated to analyse trajectories  
216 between 1987 and 2019, considering the 1987 data set as an initial state (*i.e.* the first  
217 ecological state of the time series). Net changes informs about the overall change  
218 occurring during the study. The net change ratio represents the ratio between the net  
219 changes and the trajectory path. It informs about the straightness of recovering and  
220 or departing processes with respect to the initial state. Recovering and departing  
221 consecutive trajectory segments (RDT) were identified by subtracting Net change n-1  
222 to Net change n (Sturbois et al., 2021b).

223 De Cáceres et al. (2019) developed a geometrically-based approach to trajectory  
224 resemblance which includes the shape, size, direction and position of trajectories  
225 with respect to the resemblance between all observations (state) belonging to a

226 same trajectory. Dissimilarities between ecological trajectories (1987-2001-2019)  
227 were calculated to test their resemblance (De Cáceres et al., 2019) to underline  
228 potential spatial pattern with HCAs. Indicator value method (Dufrene and Legendre,  
229 1997) was performed on taxonomic trajectory clusters to test differences between  
230 1987, 2001 and 2019. The relative contribution of all categories of functional traits  
231 between 1987, 2001 and 2019 were compared for each functional trajectory clusters  
232 and at the scale of the whole study area.

233

### 234 **3. Results**

#### 235 **3.1 General description of sediment**

236 The sampling area was dominated by fine sediment at the three sampling dates:  
237 (arithmetic means=  $144.4\mu\text{m} \pm 52.5$ ,  $135.9\mu\text{m} \pm 44.9$  and  $159.5\mu\text{m} \pm 70.6$  in 1987,  
238 2001 and 2019, respectively). Sand was the most represented grain size class over  
239 the last three decades:  $97.0\% \pm 1.9$ ,  $98.5\% \pm 4.1$  and  $95.6\% \pm 5.6$ . Mud and gravel  
240 were less represented and respectively ranged between  $1.2\% \pm 4.0$  to  $3\% \pm 5.5$ , and  
241  $0.3\% \pm 0.8$  to  $1.4\% \pm 5.0$ . Overall, surficial sediment of the study area can be  
242 summarized as fine sands organised along a *continuum* of fine to very fine sands  
243 characterised by local variations in mud or gravel contributions.

#### 244 **3.2 General description of the benthos**

245 The number of taxa reported in the intertidal flat was variable across the sampling  
246 period (Table I): 50 in 1987, 53 in 2001 and 85 in 2019. In comparison to 1987, 11  
247 taxa disappeared and 14 taxa appeared in 2001 and 14 taxa disappeared and 46  
248 taxa appeared in 2019. 36 taxa were common to the three datasets and represented  
249  $95.5\% \pm 2.9$  of the total abundance. Polychaetes, crustaceans, and molluscs were  
250 dominant. The number of taxa of these three dominant groups increased over the  
251 study period. Other categories contributed to less than 5% of the taxa richness,  
252 except for echinoderms, which represented 8.26% of the total abundance in 2019.

253 The high total abundance observed in 2001 was due to a strong increase of the  
254 mollusc *Donax vittatus* in the low shore (Figure3), responsible for 51,8% of the total  
255 abundance.

256 In 1987, macrofauna was dominated by molluscs excepted in the low shore, where  
257 annelids were the most numerous group (Figure 3). In 2019, distribution between  
258 taxonomic groups was less contrasted, especially in the low shore, mostly due to an  
259 increase in mollusc abundances. Abundance of crustaceans also increased in most  
260 of the study area and a clear extension of the echinoderms distribution was observed  
261 in the western part of the study area, mostly due to the ophiuroid *Acrocnida*  
262 *spatulispina*.

263 Taxa richness increases from high to low shore whereas abundances follow an  
264 inverse pattern (Table I). Density, taxa richness and diversity (H, D) recorded from  
265 all samples were spatially and temporally variable. Compared to 1987, abundance  
266 ( $815 \text{ ind.m}^{-2} \pm 1617$  vs  $1206 \text{ ind.m}^{-2} \pm 1530$ ), taxa richness ( $10.42 \pm 3.21$  vs  $16.80 \pm$   
267  $6.69$ ) and species diversity slightly increased in 2019.

268

### 269 **3.3 Benthic assemblages**

270 The hierarchical classification separated four clusters in 1987 and 2001 and five  
271 clusters in 2019. Mainly influenced by bathymetry (Figure 2), the distribution and  
272 structuration of assemblages was stable from upper to lower flat, despite the south-  
273 westward extension of assemblage IV, and the apparition of a new assemblage in  
274 2019 (Figure 4).

275 Assemblage I, located in muddy sands on the upper part of the flat, was  
276 characterized *Pygospio elegans* in 1987, and *Peringia ulvae* in 2001 and 2019 (first  
277 rank indval, Table II). *P. ulvae* was dominant in 1987 and 2019, whereas *Corophium*

278 *arenarium* was the most abundant species in 2001. Assemblage II, associated to  
279 very fine to fine sand of the upper mid-flat, was characterized by *Macomangulus*  
280 *tenuis* in 1987 and 2019 and *Urothoe poseidonis* in 2019. *M. tenuis* remained the  
281 most abundant species over time. Assemblage III, associated to very fine to fine  
282 sand of the lower mid-flat, was characterized by *U. poseidonis* in 1987 and *Acrocnida*  
283 *spatulispina* in 2001, and 2019. This assemblage was dominated by *M. tenuis* in  
284 1987, *U. poseidonis* in 2001, and *A. spatulispina* in 2019. Assemblage IV, associated  
285 to sands mainly located in low tide levels, was characterised by *Scoloplos armiger* in  
286 1987, *Donax vittatus* in 2001, and *Magelona mirabilis* in 2019. It was dominated by *P.*  
287 *medusa* in 1987 and *D. vittatus* in 2001 and 2019. A new assemblage was identified  
288 in 2019, in the upper part of the shore, on bare sands associated to major sand  
289 intakes. *Eurydice affinis* characterized this assemblage and *Bathyporeia pilosa* was  
290 the most abundant species. Distribution maps of species used to describe  
291 assemblages (Table II) are detailed in Supplementary material, Appendix D.

### 292 **3.4 Detecting trajectory patterns**

#### 293 **3.4.1 Taxonomic trajectories**

294 The first period was characterized by less change (total S1 lengths = 453.05, mean=  
295  $10.79 \pm 3.46$ ) than the second [total S2 lengths= 582.34, mean=  $13.87 \pm 5.56$  (Figure  
296 5, A)]. Highest net changes occurred in the low shore where eight stations  
297 concentrated 31% of changes (179.24). A positive correlation ( $0.529$ ,  $p=0.0002$ ) was  
298 found between net change and latitude. RDT was positive for 31 stations (71.43%)  
299 and negative for 11 stations, showing an overall departure dynamics from the initial  
300 taxonomic state. Total net change (582.34) represented only 56 % of the total  
301 trajectory path (1035.39). This low net change ratio ( $53.14\% \pm 0.12$ ) indicated  
302 significant direction changes (*i.e.* driving species groups) in the multivariate space  
303 between 1987-2001 and 2001-2019 for departing trajectories, and included  
304 recovering ones.

305 The HCA performed on CTA of trajectory similarities separated four main clusters of  
306 taxonomic trajectories (Figure 5, B and C). Cluster A was composed of 8 stations  
307 from the sheltered part of the bay, and describing the evolution from an assemblage  
308 characterized *P. elegans* in 1987 and *B. pilosa* in 2019 and dominated by *P. ulvae* in  
309 1987 and 2019 and *C. arenarium* in 2001. Cluster B, the most common group (28  
310 stations), was characterised by *M. tenuis* in 1987, *U. poseidonis* in 2001 and *E.*  
311 *dolfusi* in 2019. *M. tenuis* remained the most numerous species over time. Cluster C  
312 (NC=25.06 ± 0.38; TP=35.33 ± 0.83) and D (NC=20.78 ± 1.91; TP=40.65 ± 5.28)  
313 were characterised by longer net changes and trajectory path compared to cluster A  
314 (NC=10.49 ± 0.83; TP=21.20 ± 1.43) and B (NC=12.74 ± 0.81; TP=23.94 ± 1.11), but  
315 represented a limited number of trajectories (14 % of stations). Cluster C grouped 4  
316 stations located in the north-west, characterized by *C. gibber* at the three campaigns  
317 and dominated by *P. medusa* in 1987 and *D. vittatus* in 2001 and 2019. Cluster D  
318 which regrouped only two stations located in the eastern low shore, was  
319 characterised by *Bathyporeia guilliamsoniana* in 1987, *P. medusa* in 2001 and  
320 *Nucula nitidosa* in 2019. *Magelona mirabilis* was the most numerous species in 1987  
321 and 2019 and *D. vittatus* remained dominant in 2001. Distribution maps of species  
322 used to describe taxonomic trajectory clusters (Table III) are detailed in  
323 Supplementary material, Appendix D.

324

### 325 **3.4.2 Functional trajectories**

326 Functional trajectory paths were, for all sites, similar for both periods, revealing  
327 similar level of functional variability between 1987 and 2001 (254.55, 6.06 ± 2.88)  
328 and 2001 and 2019 (223.41, 5.32 ± 2.61). Seven stations concentrated 30 %  
329 (143.67) of the overall trajectory path, illustrating a high functional variability in these  
330 areas over the last 30 years. RDT revealed recovering trajectories for 25 stations (60  
331 %), evenly distributed in the study area (Figure 6, A). The low net change ratio  
332 (46.78% ± 0.11) was influenced by recovering trajectories.

333 The HCA performed on CTA of trajectory similarities separated four main clusters  
334 according to the shape of functional trajectories (Figure 6, B and C).  
335 Cluster E grouped six stations located in sheltered and upper parts of the shore and  
336 characterised by the highest net changes ( $7.50 \pm 1.27$ ) and moderate trajectory path  
337 ( $10.80 \pm 1.09$ ). Cluster E trajectories were mainly defined by an increase in the  
338 contribution of very sensitive, free living and small species (Figure 7). Cluster F,  
339 which concerned only one station, was characterised by the highest trajectory path  
340 ( $27.29$ ) but one of the smallest net change ( $2.63$ ) in relation with an effective  
341 recovering trajectory between 1987-2001 and 2001-2019. Cluster G was the most  
342 common pattern of functional trajectories (30 stations) characterized by moderate net  
343 changes ( $4.66 \pm 0.28$ ) and trajectory path ( $9.53 \pm 0.48$ ). This cluster was  
344 characterised by moderate functional changes, except for an increase in the  
345 contribution of flexible and small size species. Cluster H grouped five stations of the  
346 low shore characterised by high trajectory path ( $19.97 \pm 1.72$ ) and moderate net  
347 changes ( $5.71 \pm 0.94$ ), in relation with recovering trajectories occurring at this sites.  
348 The main functional shift in cluster H concerned a positive shift of suspension-  
349 feeders, free living, medium fragile, and rigid species, notably attributable to strong  
350 variation of *D. vittatus* observed at these stations.

351 Despite some local functional shift depending on functional trajectory clusters, and  
352 some slight significant shifts for some categories of traits, the overall functional  
353 properties remained stable over time at the site scale (Figure 8).

354

## 355 **4. Discussion**

### 356 **4.1 Local ecological dynamics influence benthic assemblages**

357 As expected in such coastal environment (McLachlan and Brown, 2006), macrofauna  
358 was dominated by molluscs, polychaetes, and crustaceans, and 95.5% of the total  
359 abundance was due to 36 species common to the three sampling periods. This  
360 revealed a strong stability in the pool of species influencing community abundance and

361 composition. Some gains and losses of occasional and rare species influenced  
362 variations of the relative contribution of taxonomic group to overall richness. Changes  
363 in assemblages mainly involved some of the prevalent species, suggesting a strong  
364 impact of fluctuating population dynamics rather than species replacement in the  
365 community. Different indicators and numerous species were involved in the definition  
366 of assemblages and taxonomic trajectory clusters but the contribution of some species  
367 to these descriptions was constant over time, notably *P.ulvae*, *L. balthica*, *U.*  
368 *poseidonis*, *C. edule*, *M. tenuis*, *C. gibber* and *M. mirabilis*. At the scale of stations,  
369 despite an overall departing taxonomic trend, we observed mainly recovering  
370 functional trajectories.

371 Two main mechanisms are involved in the long-term variability of benthic  
372 assemblages: the dynamics of structuring species and the existence of strong local  
373 variability.

374 1. Coupled with random gain or losses of species (Legendre, 2019), the dynamics of  
375 structuring species results in moderate specific taxonomic changes in the multivariate  
376 structure of assemblages. However, several species can induce strong trends, such  
377 as *D. vittatus*, whose abundance varied from  $13.4 \pm 15$  ind.m<sup>2</sup> (20 stations) in 1987 to  
378  $3107 \pm 6347$  ind.m<sup>2</sup> (16 stations) in 2001 and  $72.8 \pm 101$  ind.m<sup>2</sup> (19 stations) in 2019  
379 or *A. spatulispina* and *Kurtiella bidentata*, whose occurrence and abundance  
380 increased. In assemblage I, the decline in *L. balthica* populations is potentially  
381 attributable to climate change (temperature increase) as suggested by different works  
382 in European regions (Beukema et al., 2009; Genelt-Yanovskiy et al., 2017; Jansen et  
383 al., 2007; Ong et al., 2017; Philippart et al., 2003; Van Colen et al., 2018). The bay of  
384 Saint-Brieuc being located in the southern part of *L. balthica*'s distribution, populations  
385 are likely to be affected by climate warming.

386 2. The stronger local variability is able to induce changes in assemblage definition,  
387 according to the initial state defined in 1987. The identification of a new assemblage  
388 in 2019, in relation to sedimentary variations, and the re-affectation of some stations  
389 to different assemblages illustrate such spatial changes. The distribution of *A.*  
390 *spatulispina* and *K. bidentata* in particular significantly extended in the sampling area  
391 over time.

392 At some stations, local taxonomic variability was of higher magnitude than the within-  
393 assemblages dispersion observed in 1987, which resulted in changes in the affectation  
394 of assemblage over time. Depending on stations, differences between assemblages  
395 were driven by differences in species compositions and/or dynamic of densities (see  
396 differences in table II). Some stations were also located at the border of some  
397 assemblages implying that they can be influenced by one assemblage or another  
398 depending on the year. Because changes in species composition and/or abundance  
399 (maybe favoured by hydrodynamics and/or sediments), some stations move from one  
400 assemblage to another. For instance, the station 15 located at the border of two  
401 assemblages in an area of high tidal channels dynamic was characterised by  
402 successive changes over time: some species were sampled at least at two dates (e.g.  
403 *Cerastoderma edule*, *Sigalion mathildae*, *Macomangulus tenuis* or *Bathyporeia sarsi*)  
404 whereas others rised high abundance at only one date (e.g. *Scolecopsis squamata* in  
405 1987; *Macomangulus tenuis* and *Polycirrus medusa* in 2001; *Bathyporeia elegans*,  
406 *Cumopsis longipes* in 2019).

407 At the opposite, others trajectories buffered local functional changes in some stations  
408 at the assemblage scale, especially in the low part of the shore. Taken separately,  
409 stations were characterized by different functional trajectories, and the concentration  
410 of local recovering trajectories in these assemblages contributed to explain the overall  
411 functional persistence. Macrobenthic communities are often associated to a mosaic of  
412 micro-habitats where natural disturbance events result in the creation of patches  
413 characterized by different recovering stages (Defeo et al., 2009; Ellis et al., 2000).

414 According to Grimm and Wissel (1997), persistence is defined as a stability property  
415 of ecological systems which nevertheless integrate moderate temporal variations. It  
416 differs of the concept of constancy, which describes unchanged systems. Despites  
417 changes observed at the scale of assemblages coupled with fluctuating population  
418 dynamics of structuring species, we assume an overall persistence of the whole  
419 benthic community in the bay of Saint-Brieuc. Such assumptions are in accordance  
420 with Bacouillard et al. (2020), which suggest that local turnover can be very high,  
421 especially in response of hydrologic and sedimentary dynamics (Desroy et al., 2007),  
422 without adversely affecting the long-term persistence of the community.

#### 423 **4.2 Low shore concentrates taxonomic changes**

424 The CTA approach revealed that the taxonomic variability increased following an  
425 inshore-offshore gradient. In the upper flat, sheltered conditions, strong influence of  
426 salinity variations and emersion time limit the number of species and the variability  
427 due to species gain. Inversely, the taxa richness increasing towards the lower flat  
428 contributes to the magnitude of change in low levels. As observed in 2019 for  
429 *Aponuphis bilineata* and *Nucula nitidosa*, the local presence of subtidal species on  
430 the intertidal flat constitutes a source of variation.

431 The northwest part of the bay, characterised by professional and recreational fishing  
432 activities known to impact benthic community properties (Boldina et al., 2014;  
433 Mosbahi et al., 2016), concentrated the highest net changes. Tides associated to  
434 hydrodynamics, particularly strong in our study area, is recognized as a dominant  
435 factor shaping the variability of coastal systems (Monbet, 1992; Wildish, 1977;  
436 Wildish and Kristmanson, 1979). This factor is responsible for surficial sediment  
437 coverage and, consequently, for the dynamics of the distribution of macrofauna as  
438 demonstrated by Fujii (2007) in the Humber estuary (UK), Compton et al. (2013) in  
439 the Wadden sea, or Veiga et al. (2017) on North Portuguese coasts. The influence of  
440 intertidal channels divagation (within a 1420 ha area since 1988, Supplementary

441 material, Appendix A) must also be considered as a driver of sediments  
442 resuspension and habitat resetting, particularly important in the low western shore. In  
443 the eastern part, low net changes associated with high trajectory path and recovering  
444 trajectories could be explained by sand banks displacement from north to south.  
445 Such impact of sediment transport has already been highlighted in different coastal  
446 areas in New Zealand (Thrush et al., 2003), France (Gouleau et al., 2000) or  
447 experimentally in the UK (Whomersley et al., 2010). In this way, we expect any  
448 anthropogenic activity potentially modifying sedimentary parameters (bio deposition,  
449 sediment deposition, beach nourishment, dredging...) to, in turn, modify intensely the  
450 composition, structure and functioning of soft bottom assemblages as suggested by  
451 Veiga et al. (2017).

452 Whomersley et al. (2010) suggested that benthic communities frequently disturbed  
453 by sediment movements or other natural environmental conditions would show  
454 greater resilience against further physical disturbance. Such resilient responses to  
455 disturbance, due to the selection of adapted species, depend on the history of prior  
456 disturbance and on the inherent ecological plasticity exhibited by species (Davic,  
457 2003). In our study, 36 prevalent species contribute to the persistence of the  
458 community over time. Most of these species are adapted to living in mobile  
459 sediments (McLachlan and Brown, 2006) and facing erosion and sedimentation.  
460 They could then persist because of their tolerance to the harshness of the  
461 environment as suggested by Callaway (2016).

462 In many coastal ecosystems, multiple disturbance sources, both natural and  
463 anthropogenic, are often confounded (Whomersley et al., 2010), which makes  
464 difficult the definition of their respective contribution (Harris, 2012). Our study  
465 confirms the complexity to disentangle factors of changes in dynamic areas, where  
466 strong natural variability results in regular community resets (Defeo and McLachlan,  
467 2013), which may overshadow anthropogenic impact. On the opposite, areas  
468 characterized by low hydrodynamics where benthic communities are not naturally

469 adapted to disturbances would therefore be very sensitive to additional physical  
470 disturbance as showed by Jac et al. (2020). In the bay of Saint-Brieuc characterised  
471 by severe natural constrains, further studies coupling experimental and high  
472 frequency field samplings should deal with the respective role of hydrodynamics and  
473 anthropogenic activities in resetting benthic communities (shear stress measurement  
474 in area concerned and not by the circulation of vehicles from mussels farming,  
475 analysis of the benthic macrofauna variability coupled with different gradients of  
476 fishing activities and or local dynamics...).

477

#### 478 **4.3 Functional properties of the community persist over time**

479 The CTA resulted in contrasted taxonomic and functional trajectory patterns (*i.e.* net  
480 changes, departing and recovering trajectory). Clare et al. (2015) showed that density  
481 compensation by redundant taxa buffers ecological functioning changes, but that  
482 functional stability is subjected to aperiodic disruption due to substitutions of dissimilar  
483 taxa or uncompensated population fluctuations. Accordingly, high trajectory paths  
484 observed in the low shore reflected an important functional variability, but recovering  
485 trajectories notably influenced by *D. vittatus* fluctuating population dynamics led to low  
486 net changes. Functional properties persisted over time at the scale of the whole  
487 community. Low sensitivity of traits such as body size, flexibility, fragility to genus and,  
488 in a lesser extent, species changes also contribute to limit the influence of taxonomic  
489 variability on the functional stability. Lower influence of traits relative to feeding  
490 behaviour finally suggested no major changes at the scale of intertidal sedimentary  
491 habitats, in accordance with (Sturbois et al., 2021b) who showed that high sedimentary  
492 variability was limited to few sites.

493 To choose the set of traits in relation to main pressures, we hypothesised that fishing  
494 activities in the lower flat may influence benthic assemblages over time according to  
495 changes in relative values of body size, flexibility, fragility. Low net changes in the

496 lower part of the shore for the widespread functional trajectory cluster G and the  
497 influence of *D. vittatus* in the functional trajectory of cluster H does not support such  
498 a functional response to human pressures.

499 A similar interest was devoted to the tolerance of species to organic matter  
500 enrichment according to the eutrophication process, mainly due to green tides. No  
501 major change was observed at the scale of the whole study area in the contribution  
502 of the different categories of tolerance. In accordance, changes were moderate in the  
503 different functional clusters except in cluster E characterized by an important positive  
504 shift in the contribution of very sensitive species. Despite a slow long-term water  
505 quality improvement trend and a progressive decrease of green tides associated to  
506 local water development and management plan, these events still strongly affect the  
507 study area. Quillien et al. (2015a) discussed the potential influence of *Ulva sp.* mats  
508 on abundance peak of *D. vittatus* (improved recruitments and negative effect on  
509 predators of larvae), which could explain high densities reaching 21 487 ind.m<sup>2</sup> in  
510 2001 and 14685 ind.m<sup>2</sup> in 2011 (unpublished data). Quillien et al. (2015b) also  
511 highlighted large-scale effects of green tides on macrotidal sandy beaches in  
512 Brittany, showing notably that the echinoderm *A. spatulispina* and the mollusc *K.*  
513 *bidentata* were stimulated in soft bottom sediments impacted by green tides, contrary  
514 to the crustaceans *B. elegans* and *Cumopsis spp.*, which were impacted. In our  
515 study, the abundance and occurrence of these four taxa increased over the study  
516 period, revealing a more complex gradient of sensitivity to green tides and/or nutrient  
517 enrichment and the implication of other driving factors. As suggested by Bolam et al.  
518 (2000), Everett (1994), and Raffaelli et al. (1999), generalisations on the effect of  
519 algae mat are not straightforward. In the study area, we believe that the important  
520 green-tides associated to nutrient uptake buffer the influence of nutrient enrichment  
521 on macrofauna.

#### 522 **4.4 The crucial need of data at multiple spatial and temporal scales**

523 The CTA applied to marine communities offers new trajectory metrics and tools (De  
524 Cáceres et al., 2019; Sturbois et al., 2021b), useful to the accurate quantification and  
525 description of changes as suggested by Cimon and Cusson (2018), which claimed  
526 for the development of new metrics to document effects on community dynamics.

527 The potential and the interest of such framework focused on the analysis of  
528 ecological dynamics increases significantly with the size of the time series.

529 There is virtually no appropriate benchmark data describing natural standards and  
530 alterations of most environmental systems concerned by impacts accumulation (Ellis  
531 et al., 2000). Like many estuarine and coastal areas, the bay of Saint-Brieuc has  
532 been exposed to strong human influence over the last decades. The ecological state  
533 identified in 1987 and considered as the initial state in this study, was defined under  
534 a pressure context already well established (notably nutrient enrichment, macroalgae  
535 proliferation, mussel farming, fishing activities). The absence of a pristine reference  
536 state constitutes a strong limitation in the analysis of long-term trends (Hardman-  
537 Mountford et al., 2005; Rubal et al., 2014; Veiga et al., 2017). Furthermore, our study  
538 suffers from the absence of long-term measurements of environmental factors and  
539 anthropogenic pressures, especially to disentangle natural vs anthropogenic  
540 changes.

541 Our results illustrate the value of historical data for marine and coastal management,  
542 as well as the importance of maintaining consistent protocols, as underlined by  
543 Callaway (2016). Overall, the complementary methods and scales used to analyse the  
544 data set contributed to the research frameworks focused on the definition of changes  
545 and impact assessments at spatial and temporal scales in marine ecosystems.

546 However, it pointed the limitations of sampling strategies that only imply long-term  
547 networks. The patterns of changes described were based only on three sampling  
548 occasions, which limits the understanding of processes occurring between each  
549 surveys, and potentially overshadowing important intermediate changes (e.g.  
550 occasional dominance by very large numbers from very few species as observed for

551 *D. vittatus*). As suggested by Bacouillard et al. (2020), the coupling of different spatial  
552 and temporal scales in sampling strategy [few stations with high frequency sampling  
553 (Hewitt et al., 2016) vs low frequency larger sampling networks (Kröncke et al., 2011)]  
554 could help to track changes between long-term networks. Bacouillard et al. (2020)  
555 propose in the bay of Seine 60 stations sampled every five years to assess long-term  
556 changes in the beta diversity (i.e. assemblages distributions) and five stations sampled  
557 at least once a year to analyse the heterogeneity in the responses of local community  
558 to multiple stressors. Sturbois et al. (2021a) have also demonstrated such interests of  
559 coupling different spatial and temporal scales by the use of two complementary data  
560 sets (38 stations in 1987 and 2019, and one station from 2005 to 2019). In this study,  
561 the 15 years time series suggested that changes observed in a subtidal benthic  
562 community over the last 30 years occurred probably from 2015. It claims for the local  
563 development of an ambitious monitoring strategy in the intertidal area based on the 42  
564 stations network sampled every 10 years coupled with at least one station sampled  
565 once a year in each assemblage.

566 An overarching question in conservation biology is the assessment of marine  
567 protected area effect on marine habitats (Appolloni et al., 2017; Bevilacqua et al.,  
568 2006; Day et al., 2012; Klein et al., 2015; Thompson et al., 2012). In this study, it was  
569 not possible to assess accurately any conservation effect of the National Nature  
570 Reserve as 1) species and assemblages remained locally very contrasted between  
571 unprotected and protected areas and 2) such assessment ideally requires a global  
572 network of protected and unprotected areas.

573 However, this study provides an up-to-date assessment to policy makers and  
574 managers about the evolution of the composition, structure and functioning of benthic  
575 assemblages. This knowledge will integrate future governance rounds, in a multi-  
576 scale approach involving policy makers and stakeholders, and will make marine  
577 habitats, a central part of the conservation process (Greathead et al., 2020), which  
578 aim notably to extend the current natural reserve perimeter. Such approaches should

579 not only focus on aggregating local present day practices, but also on exploring  
580 future visions and potential scenarios (Pereira L., 2021).

581

## 582 **5. Conclusion**

583 The CTA framework brings new quantitative and qualitative insights to characterize  
584 and illustrate changes in marine habitats. The consideration of both local changes  
585 and variations at population levels helps to explain the differences observed at the  
586 scale of assemblages. Observed changes mainly reflected random population  
587 dynamics of structuring prevalent species in habitat under strong natural constraints,  
588 rather than strong specific changes of the community. Few species may underline  
589 the long-term effect of green tides in some assemblages. This study also claims for  
590 ambitious monitoring strategy in order to integrate multiple spatial and temporal  
591 scales, and efficient measurements of environmental and anthropogenic driven  
592 factors.

## 593 **Acknowledgments**

594 We thank the three anonymous reviewers of previous versions of this manuscript for  
595 their constructive comments. We acknowledge all people involved in field sampling  
596 and analysis with a special mention for Alexandre Le Moal and Charles Veillard,  
597 which significantly contribute to laboratory analysis.

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 605 Occidentale.

606 **Supplementary material:**

607 **Appendix A:** Time line of sampling dates with respect to main anthropogenic uses,  
 608 pressures and conservation and protection regulations

609 **Appendix B:** Channel intertidal divagation in last the thirty years.

610 **Appendix C:** Categories of functional traits

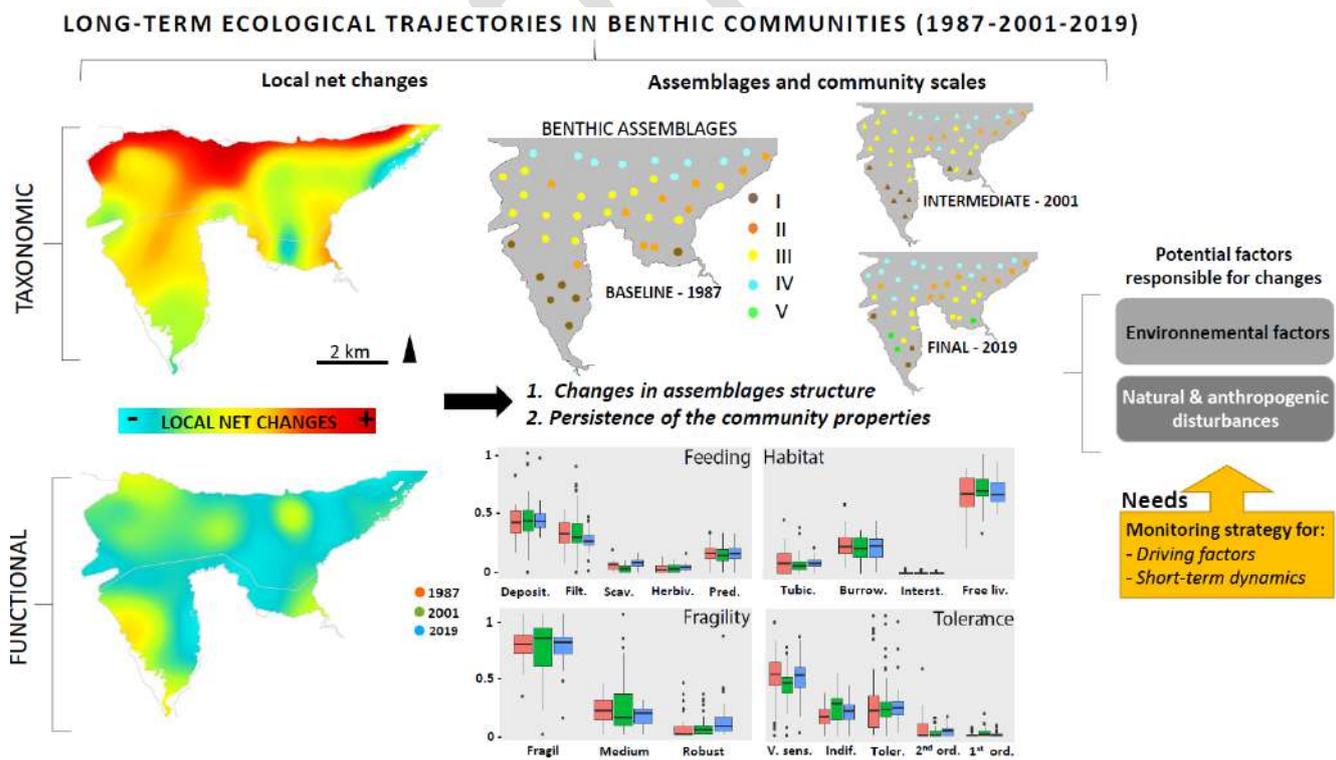
611 **Appendix D:** Distribution and abundance of species used to describes assemblages  
 612 and taxonomic trajectory clusters

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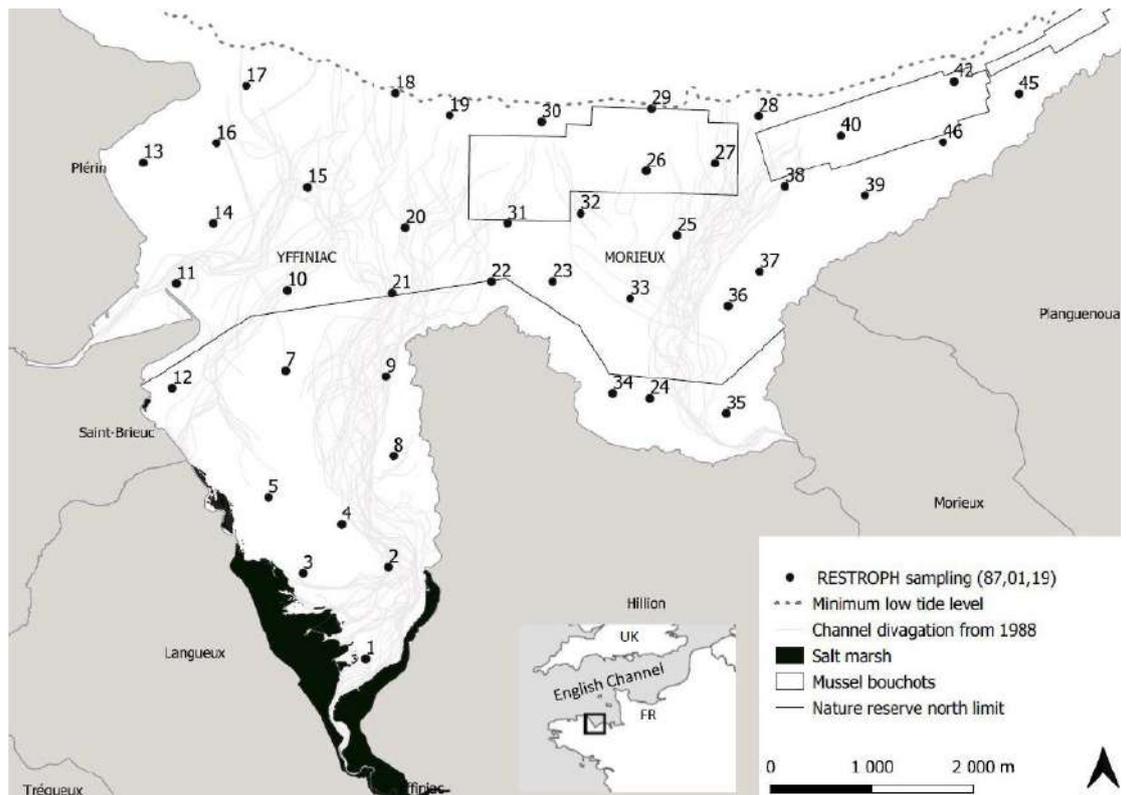
616 **Graphical abstract**



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618

619 **Figures:**



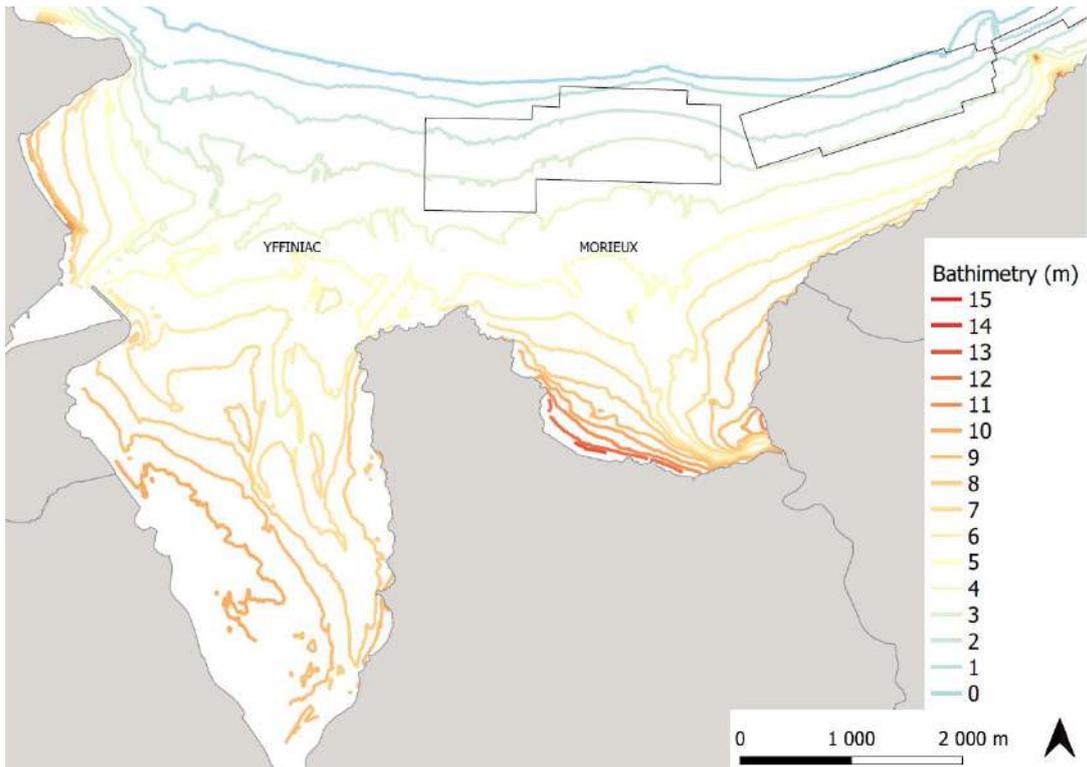
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621 Figure 1: Location of the study area and sampling strategy. Black dots corresponds to  
 622 the 42 stations sampled in 1987, 2001 and 2019. The North limit of the Nature reserve  
 623 is indicated by a black line and mussel bouchots by polygons.

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628 Figure 2: Bathymetry of the study area. Isolines are coloured according to altitude from  
629 the top (red) to the low tide level (blue). Mussel bouchots are represented by  
630 polygones.

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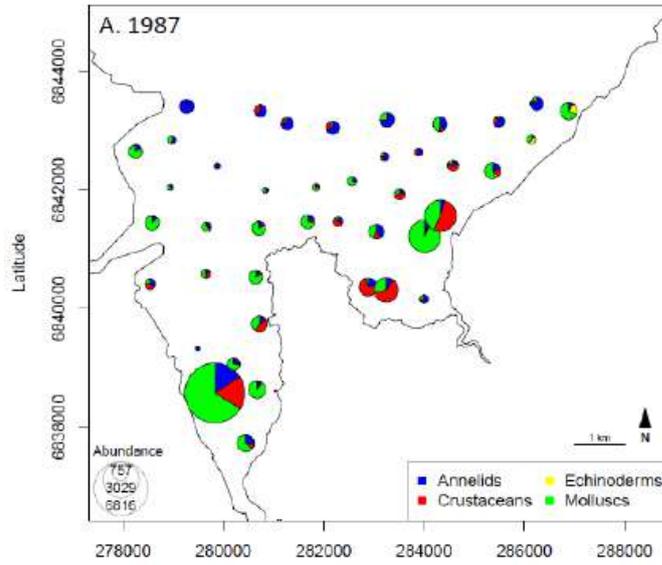
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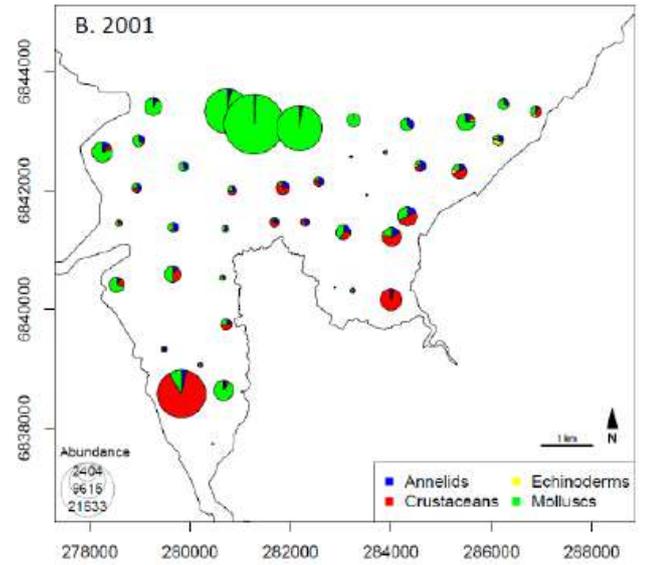
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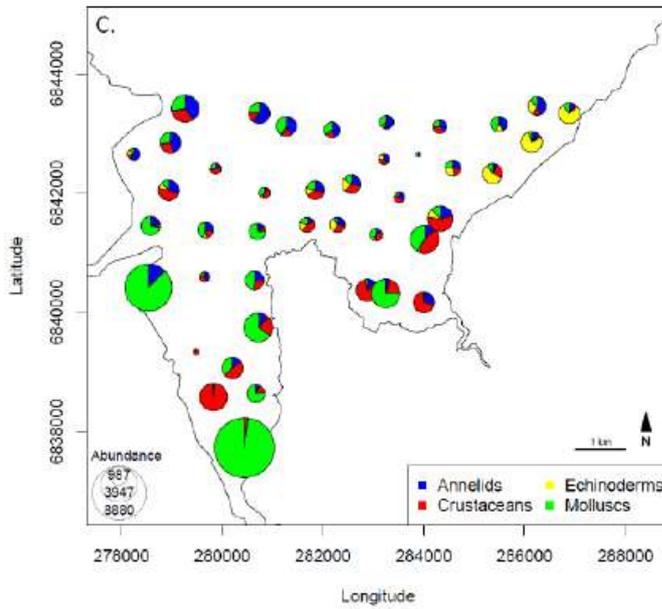
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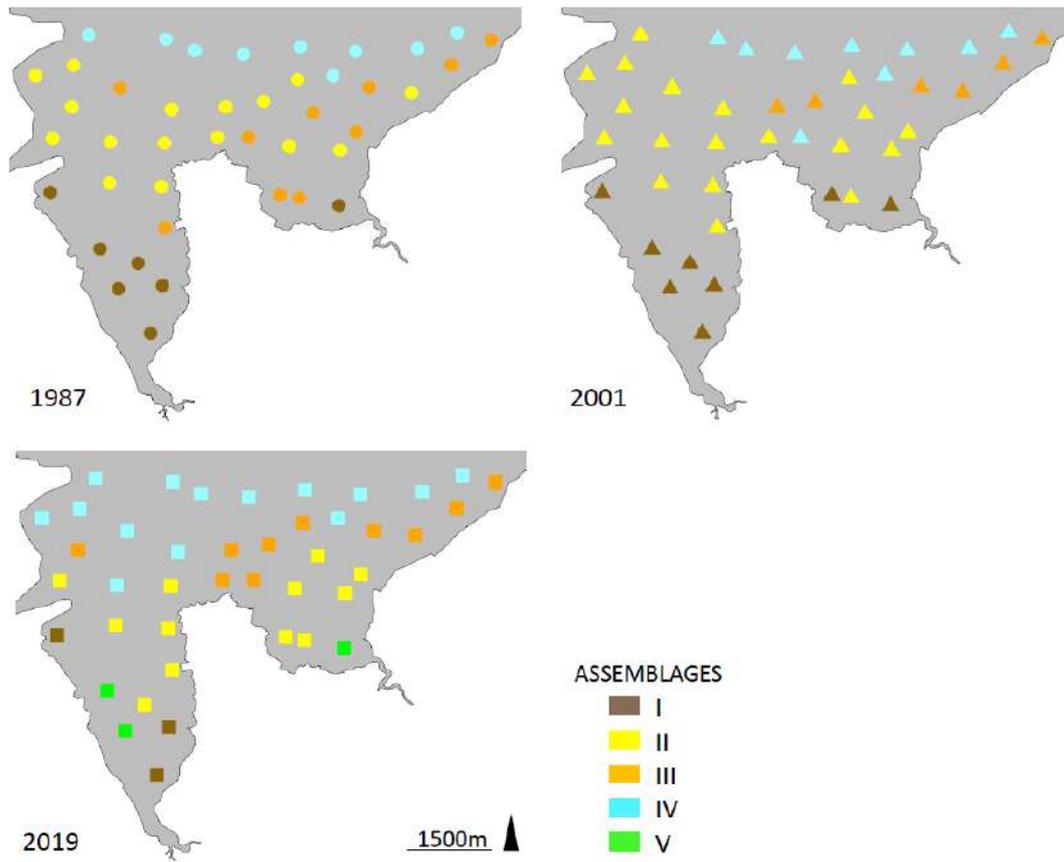
656 Figure 3: Variations in relative abundance of the main numerous taxonomic group  
 657 between 1987 (A), 2001 (B) and 2019 (C). Size of pies corresponds to total abundance  
 658 and sections to taxonomic group contributions.

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664 Figure 4: Spatial distribution of benthic assemblages identified with Hierarchical  
 665 Cluster Analysis performed on 42 stations in 1987, 2001 and 2019.

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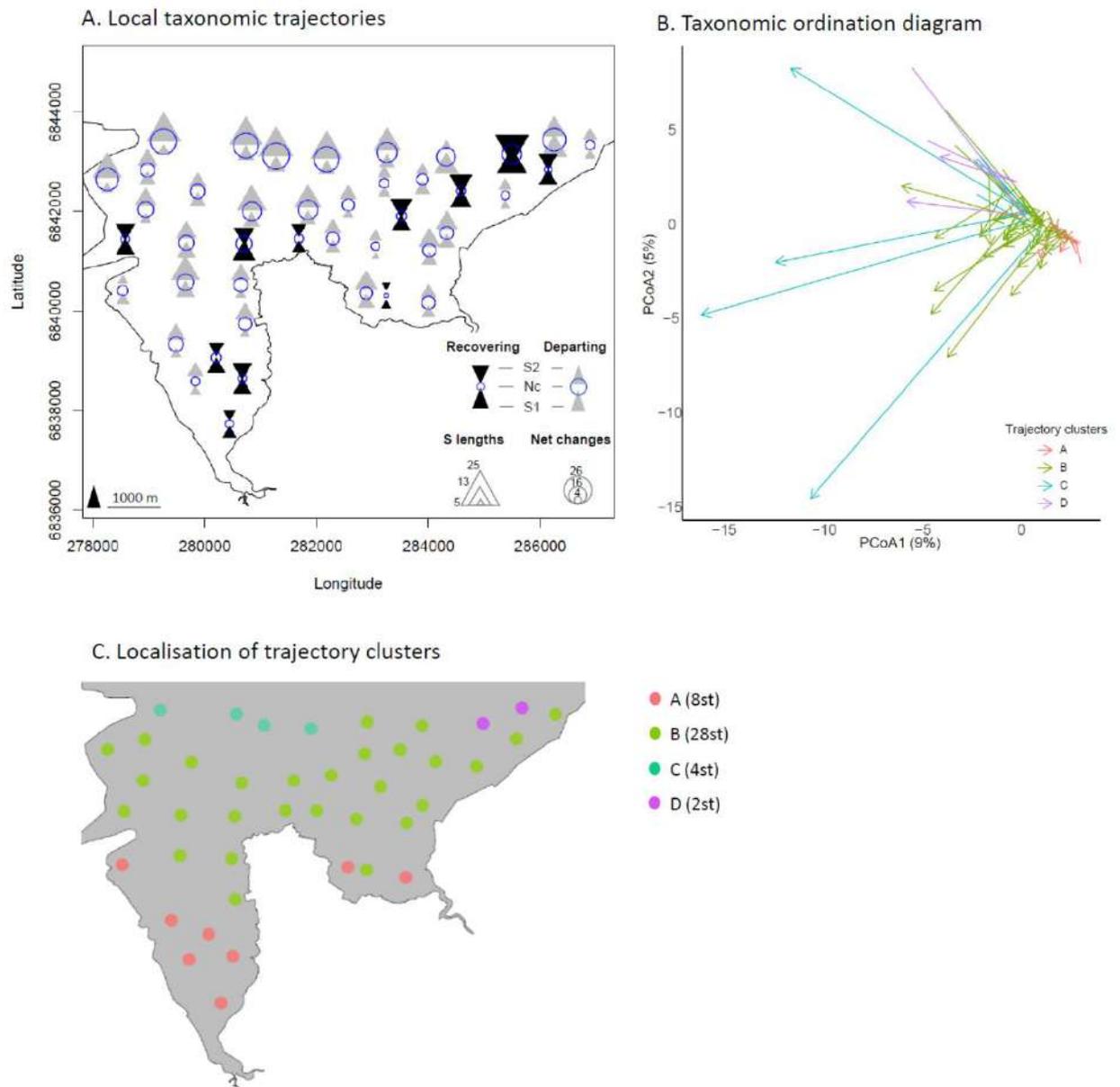
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678 Figure 5: Taxonomic trajectories. A.: Maps of local trajectories. Distance based  
 679 metrics are represented with circular and triangle symbols. Net changes are  
 680 represented with blue circles between 1987 and 2019. Bottom triangles represent the  
 681 trajectory segment S1 (1987 to 2001) and top ones S2 (2001 to 2019). Size of  
 682 symbols corresponds to lengths. For triangles, colors are used to distinguish  
 683 recovering (black) from departing trajectories (grey). B: Trajectory ordination  
 684 diagram. The three ecological state of each station were connected with arrows in  
 685 order to represent the whole trajectory path. Each trajectory path was coloured  
 686 according to taxonomic trajectory clusters defined with Hierarchical Cluster Analysis  
 687 based on CTA trajectory similarity analysis. Despite trajectory distance-based metrics  
 688 and dissimilarity were calculated considering all of the dimensions of the PCA, the  
 689 first two dimensions show only 14% of the total variation, which may potentially hide  
 690 some patterns. C.: Localisation of trajectory clusters within the study area.

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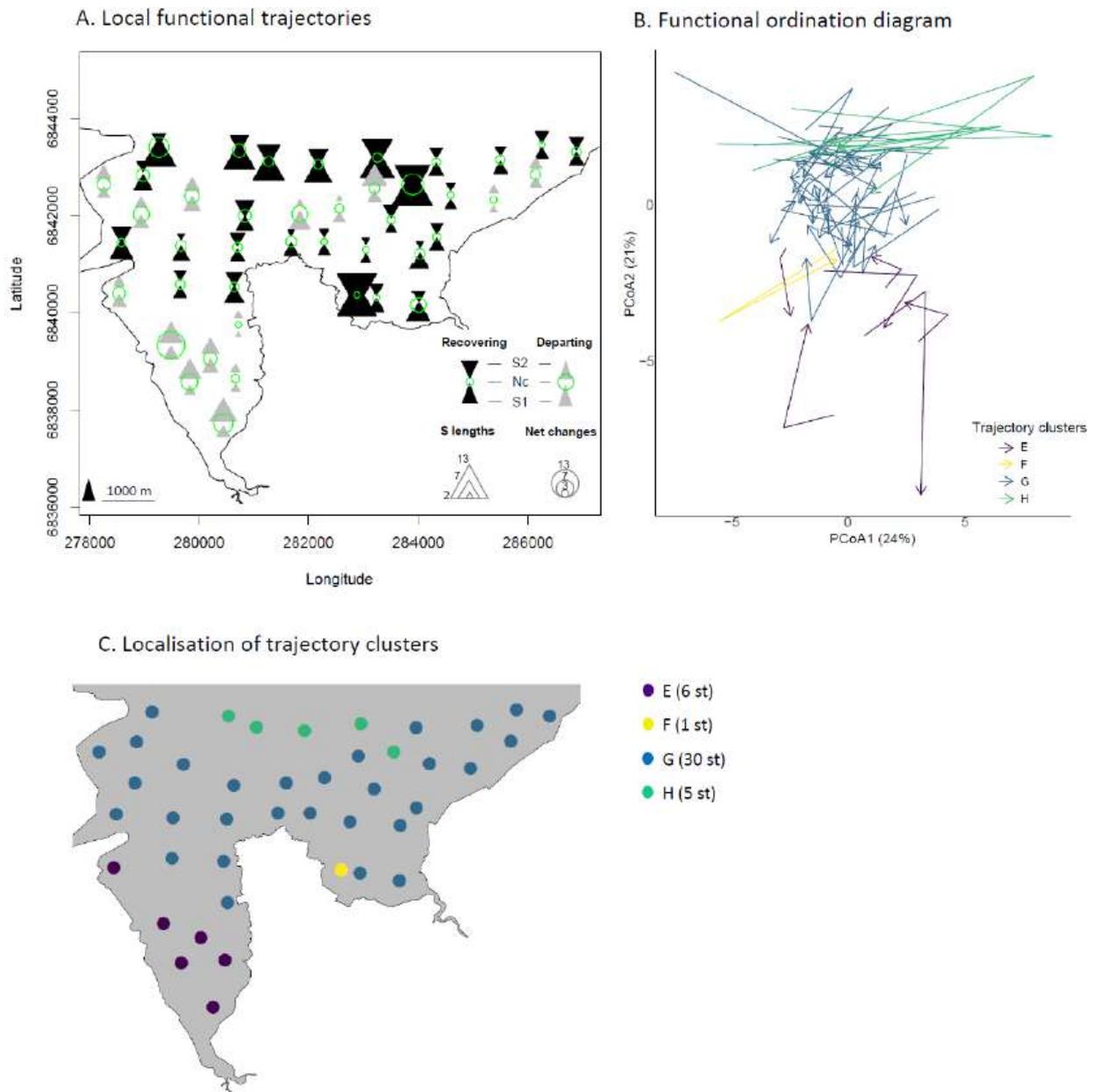
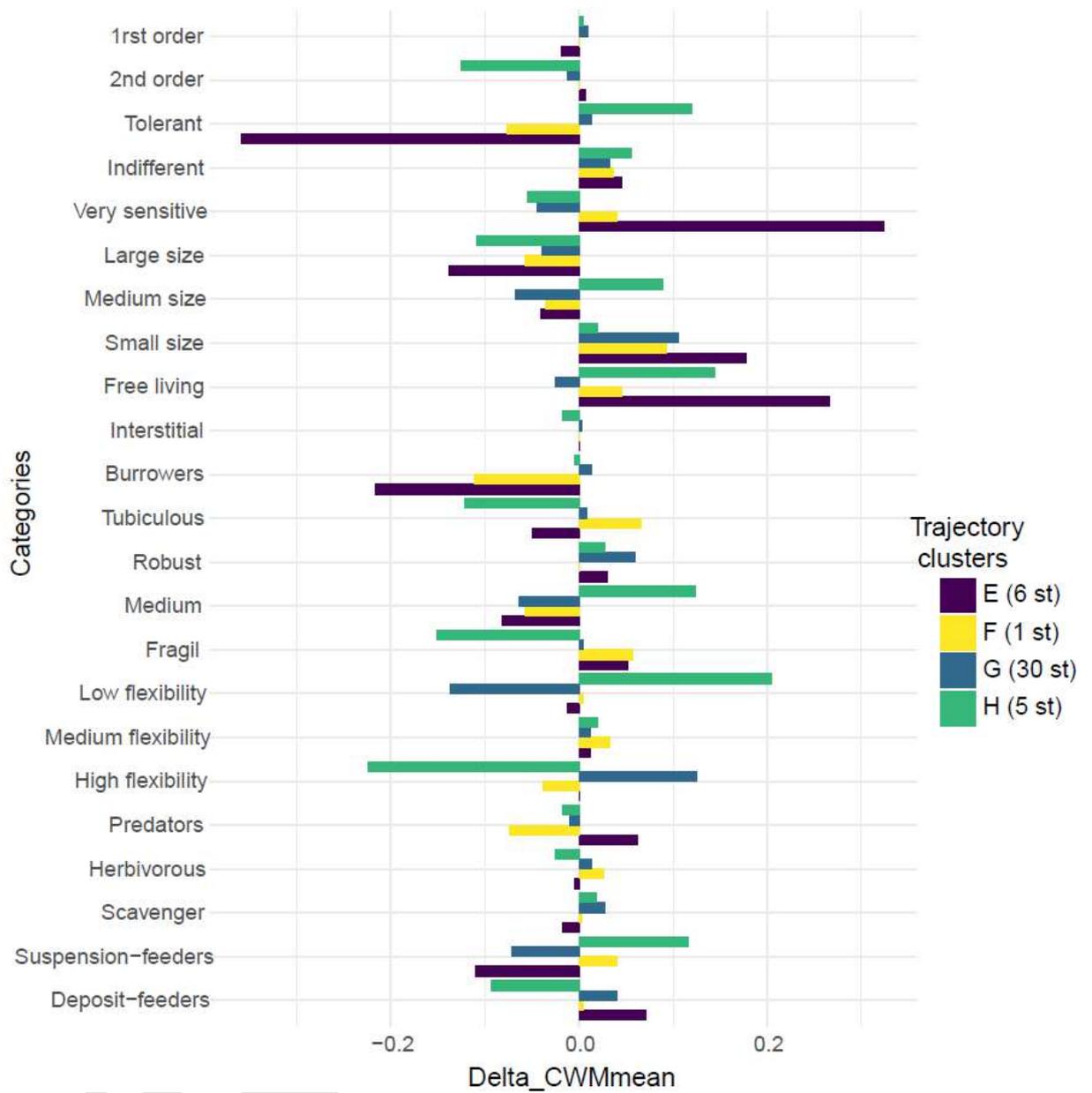


Figure 6: Functional trajectories. A.: Maps of local trajectories. Distance based metrics are represented with circular and triangle symbols. Net changes are represented with green circles between 1987 and 2019. Bottom triangles represent the trajectory segment S1 (1987 to 2001) and top ones S2 (2001 to 2019). Size of symbols corresponds to lengths. For triangles, colors are used to distinguish recovering (black) from departing trajectories (grey). B: Trajectory ordination diagram. The three ecological state of each station were connected with arrows in order to represent the whole trajectory path. Each trajectory path was coloured according to functional trajectory clusters defined with Hierarchical Cluster Analysis based on CTA trajectory similarity analysis. C.: Localisation of trajectory clusters within the study area.



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729 Figure 7: Barplots of Community-weighted trait values (CWM) values shift for each  
 730 categories of traits (mean 2019 – mean 1987). Bars are coloured according to  
 731 functional trajectory clusters.

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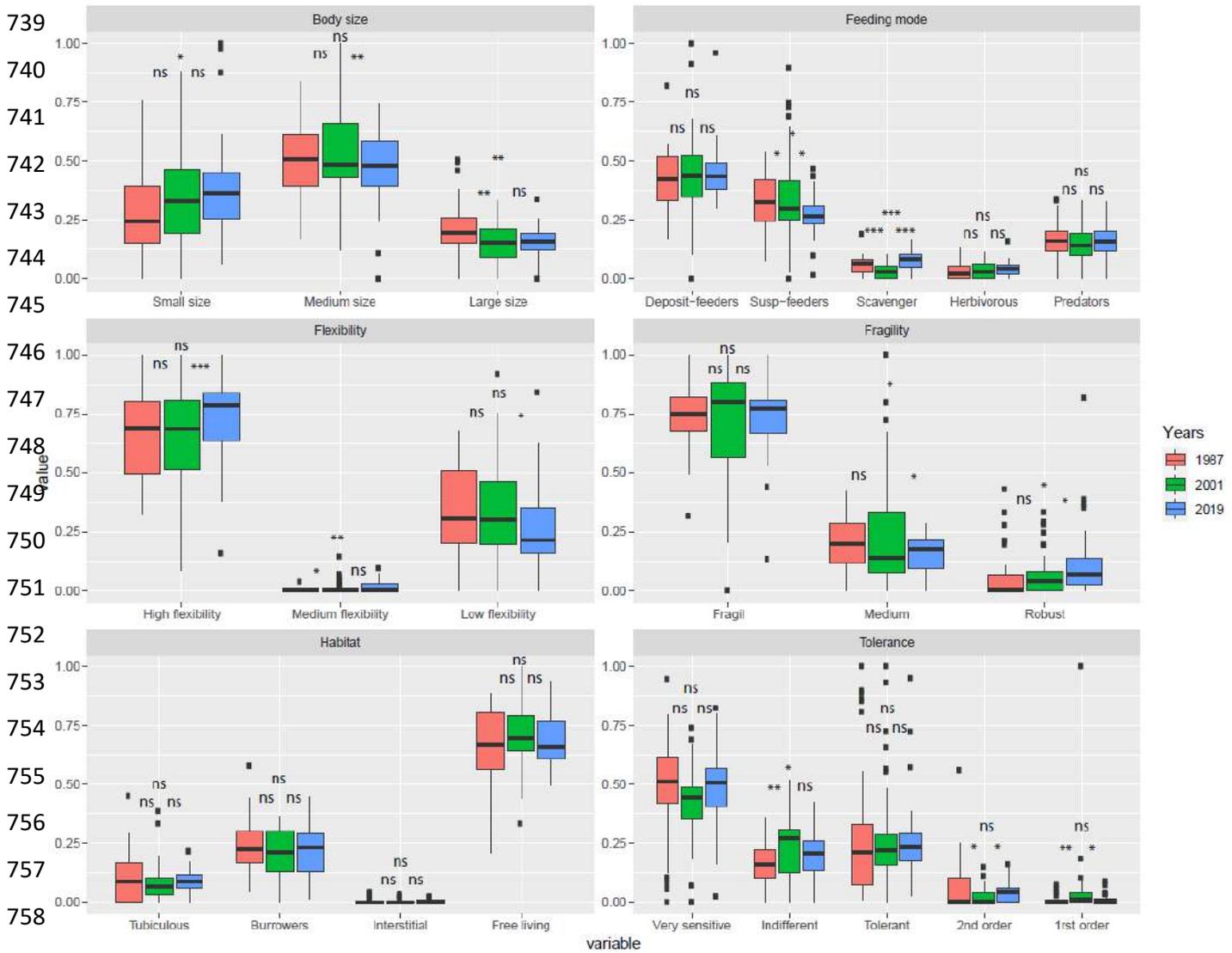
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759 Figure 8: Box plots of Community-weighted trait values (CWM) traits values in levels  
 760 of respective categories according to year (1987: red; 2001: green; 2019: blue). Box  
 761 plot indicates the median (line in the box), the first and third quartiles (hinges) and  
 762 extreme data points (black points). Significance of student permutation paired tests  
 763 are indicated for each category traits (ns: non significant; \*: pval<0.05; \*\*: pval<0.01;  
 764 \*\*\* pval:<0.001).

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770 **Tables:**

771 Table I: General description of macrofauna

|                      | 1987            | 2001           | 2019           | All years |
|----------------------|-----------------|----------------|----------------|-----------|
| Total Richness       | 50              | 53             | 85             | 133       |
| Mean Richness        | 10.4 (sd=3.21)  | 10.8 (sd=5.23) | 16.8 (sd=6.69) |           |
| N Annelids           | 26              | 23             | 32             | 54        |
| N Crustaceans        | 13              | 19             | 35             | 45        |
| N Echinoderms        | 1               | 2              | 1              | 2         |
| N Molluscs           | 9               | 9              | 15             | 24        |
| N Nemertea           | 0               | 0              | 1              | 1         |
| N Plathelminthe      | 0               | 0              | 1              | 1         |
| N Sipuncles          | 1               | 0              | 0              | 1         |
| N Constant species   | 7               | 4              | 12             |           |
| N Common species     | 5               | 13             | 12             |           |
| N Occasional species | 13              | 11             | 11             |           |
| N Rare species       | 25              | 25             | 50             |           |
| Total abundance      | 34222           | 95991          | 50639          |           |
| Mean abundance       | 815 (sd=1617)   | 2286 (sd=4496) | 1206 (sd=1530) |           |
| Shannon (H)          | 1.62(sd=0.46)   | 1.46 (sd=0.76) | 1.98 (sd=0.70) |           |
| Simpson (D)          | 0.696(sd=0.153) | 0.61 (sd=0.29) | 0.74 (sd=0.21) |           |
| Pielou (J)           | 0.704(sd=0.153) | 0.65 (sd=0.29) | 0.71 (sd=0.21) |           |

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784 Table II: Characteristics of assemblages identified with the Hierarchical Cluster  
 785 Analysis in 1987, 2001 and 2019: Assemblages (Ass), number of station (N st), Taxa  
 786 richness (S), Mean density per m<sup>2</sup> (M Dens), Shannon-Weaver Index (H), Simpson  
 787 Index (D) and Pielou's evenness (J) ( $\pm$  = standard error). Distribution of species  
 788 used to describe assemblages are detailed in Supplementary material, Appendix D.  
 789

| Ass. | Indicator species             | Indval | p      | Most numerous species         | Mean.m <sup>2</sup> $\pm$ se | N st | S          | Abund         | H          | D          | J          |
|------|-------------------------------|--------|--------|-------------------------------|------------------------------|------|------------|---------------|------------|------------|------------|
| 790  | <i>Pygospio elegans</i>       | 0.857  | 0.0001 | <i>Peringia ulvae</i>         | 1076.57 $\pm$ 958.91         | 7    | 8.29       | 1864.14       | 1.44       | 0.67       | 0.71       |
| 791  | <i>Hediste diversicolor</i>   | 0.714  | 0.0001 | <i>Pygospio elegans</i>       | 260.57 $\pm$ 223.57          |      | $\pm$ 0.96 | $\pm$ 1410.00 | $\pm$ 0.15 | $\pm$ 0.05 | $\pm$ 0.07 |
| 792  | <i>Peringia ulvae</i>         | 0.714  | 0.0001 | <i>Corophium arenarium</i>    | 194.29 $\pm$ 182.40          |      |            |               |            |            |            |
|      | <i>Limecola balthica</i>      | 0.696  | 0.0001 | <i>Limecola balthica</i>      | 148.57 $\pm$ 58.63           |      |            |               |            |            |            |
|      | <i>Arenicola marina</i>       | 0.612  | 0.0003 | <i>Bathyporeia pilosa</i>     | 98.29 $\pm$ 77.83            |      |            |               |            |            |            |
| 793  | <i>Macomangulus tenuis</i>    | 0.595  | 0.0001 | <i>Macomangulus tenuis</i>    | 344.75 $\pm$ 152.13          | 16   | 9.63       | 537.56        | 1.45       | 0.63       | 0.65       |
| 794  | <i>Cerastoderma edule</i>     | 0.498  | 0.0026 | <i>Cerastoderma edule</i>     | 59.94 $\pm$ 20.50            |      | $\pm$ 0.60 | $\pm$ 172.02  | $\pm$ 0.12 | $\pm$ 0.05 | $\pm$ 0.04 |
|      |                               |        |        | <i>Nephtys hombergii</i>      | 25.50 $\pm$ 8.42             |      |            |               |            |            |            |
|      |                               |        |        | <i>Urothoe poseidonis</i>     | 19.50 $\pm$ 6.89             |      |            |               |            |            |            |
|      |                               |        |        | <i>Bathyporeia sarsi</i>      | 12.00 $\pm$ 3.72             |      |            |               |            |            |            |
| 795  | <i>Urothoe poseidonis</i>     | 0.502  | 0.0007 | <i>Macomangulus tenuis</i>    | 238.4 $\pm$ 118.43           | 10   | 10.00      | 837.90        | 1.61       | 0.73       | 0.71       |
| 796  | <i>Acrocnida spatulispina</i> | 0.486  | 0.0021 | <i>Bathyporeia sarsi</i>      | 225.6 $\pm$ 101.72           |      | $\pm$ 0.70 | $\pm$ 265.84  | $\pm$ 0.09 | $\pm$ 0.02 | $\pm$ 0.03 |
| 797  |                               |        |        | <i>Urothoe poseidonis</i>     | 163.2 $\pm$ 61.37            |      |            |               |            |            |            |
|      |                               |        |        | <i>Acrocnida spatulispina</i> | 36.8 $\pm$ 19.93             |      |            |               |            |            |            |
|      |                               |        |        | <i>Nephtys hombergii</i>      | 35.2 $\pm$ 12.97             |      |            |               |            |            |            |
| 798  | <i>Scoloplos armiger</i>      | 0.947  | 0.0001 | <i>Polycirrus medusa</i>      | 92.556 $\pm$ 32.18           | 9    | 14.00      | 465.89        | 2.07       | 0.81       | 0.79       |
| 799  | <i>Chaetozone gibber</i>      | 0.889  | 0.0001 | <i>Magelona mirabilis</i>     | 71.333 $\pm$ 21.28           |      | $\pm$ 1.13 | $\pm$ 45.52   | $\pm$ 0.13 | $\pm$ 0.03 | $\pm$ 0.03 |
| 800  | <i>Polycirrus medusa</i>      | 0.763  | 0.0001 | <i>Chaetozone gibber</i>      | 53.333 $\pm$ 17.44           |      |            |               |            |            |            |
|      | <i>Magelona filiformis</i>    | 0.667  | 0.0001 | <i>Fabulina fabula</i>        | 41.778 $\pm$ 25.11           |      |            |               |            |            |            |
|      | <i>Magelona mirabilis</i>     | 0.613  | 0.0002 | <i>Bathyporeia sarsi</i>      | 34.667 $\pm$ 16.71           |      |            |               |            |            |            |
| 801  | <i>Peringia ulvae</i>         | 0.713  | 0.0002 | <i>Corophium arenarium</i>    | 1371.33 $\pm$ 1371.33        | 9    | 6.89       | 2630.33       | 1.10       | 0.53       | 0.58       |
| 802  | <i>Cerastoderma edule</i>     | 0.390  | 0.0179 | <i>Peringia ulvae</i>         | 405.56 $\pm$ 179.62          |      | $\pm$ 1.33 | $\pm$ 1487.69 | $\pm$ 0.23 | $\pm$ 0.10 | $\pm$ 0.12 |
|      | <i>Eurydice affinis</i>       | 0.351  | 0.0184 | <i>Bathyporeia sarsi</i>      | 297.78 $\pm$ 297.78          |      |            |               |            |            |            |
|      | <i>Pygospio elegans</i>       | 0.344  | 0.0287 | <i>Cerastoderma edule</i>     | 180.44 $\pm$ 100.01          |      |            |               |            |            |            |
|      |                               |        |        | <i>Macomangulus tenuis</i>    | 128.89 $\pm$ 88.14           |      |            |               |            |            |            |
| 803  | <i>Macomangulus tenuis</i>    | 0.544  | 0.0001 | <i>Macomangulus tenuis</i>    | 382.07 $\pm$ 116.231         | 15   | 9.73       | 874.20        | 1.54       | 0.69       | 0.74       |
| 804  | <i>Lekanesphaera levii</i>    | 0.333  | 0.0142 | <i>Urothoe poseidonis</i>     | 112.67 $\pm$ 51.27           |      | $\pm$ 1.19 | $\pm$ 206.65  | $\pm$ 0.11 | $\pm$ 0.04 | $\pm$ 0.05 |
|      | <i>Bathyporeia tenuipes</i>   | 0.283  | 0.0335 | <i>Cumosopsis fagei</i>       | 72.87 $\pm$ 42.31            |      |            |               |            |            |            |
|      |                               |        |        | <i>Spiophanes bombyx</i>      | 57.73 $\pm$ 17.96            |      |            |               |            |            |            |
|      |                               |        |        | <i>Nephtys hombergii</i>      | 45.00 $\pm$ 11.32            |      |            |               |            |            |            |
| 805  | <i>Acrocnida spatulispina</i> | 0.870  | 0.0001 | <i>Urothoe poseidonis</i>     | 122.70 $\pm$ 30.46           | 10   | 15.40      | 740.10        | 2.33       | 0.87       | 0.86       |
| 806  | <i>Eocuma dollfusi</i>        | 0.692  | 0.0001 | <i>Macomangulus tenuis</i>    | 94.60 $\pm$ 26.62            |      | $\pm$ 0.75 | $\pm$ 96.79   | $\pm$ 0.06 | $\pm$ 0.01 | $\pm$ 0.02 |
|      | <i>Sigalion mathildae</i>     | 0.622  | 0.0001 | <i>Acrocnida spatulispina</i> | 74.40 $\pm$ 27.36            |      |            |               |            |            |            |
|      | <i>Urothoe poseidonis</i>     | 0.581  | 0.0001 | <i>Eocuma dollfusi</i>        | 56.20 $\pm$ 22.26            |      |            |               |            |            |            |
|      | <i>Malmgrenia arenicolae</i>  | 0.524  | 0.0008 | <i>Cumosopsis fagei</i>       | 37.20 $\pm$ 10.64            |      |            |               |            |            |            |
| 807  | <i>Donax vittatus</i>         | 0.863  | 0.0001 | <i>Donax vittatus</i>         | 6175.63 $\pm$ 2846.18        | 8    | 11.38      | 6475.50       | 0.61       | 0.25       | 0.30       |
| 808  |                               |        |        | <i>Magelona mirabilis</i>     | 52.25 $\pm$ 24.80            |      | $\pm$ 2.24 | $\pm$ 2880.00 | $\pm$ 0.19 | $\pm$ 0.09 | $\pm$ 0.08 |
|      |                               |        |        | <i>Macomangulus tenuis</i>    | 31.00 $\pm$ 12.14            |      |            |               |            |            |            |
|      |                               |        |        | <i>Sigalion mathildae</i>     | 22.50 $\pm$ 6.75             |      |            |               |            |            |            |
|      |                               |        |        | <i>Polycirrus medusa</i>      | 19.75 $\pm$ 13.64            |      |            |               |            |            |            |
| 809  | <i>Peringia ulvae</i>         | 0.955  | 0.0001 | <i>Peringia ulvae</i>         | 4437.33 $\pm$ 2503.19        | 3    | 11.67      | 5128.80       | 0.98       | 0.41       | 0.39       |
| 810  | <i>Limecola balthica</i>      | 0.877  | 0.0010 | <i>Macomangulus tenuis</i>    | 181.33 $\pm$ 90.78           |      | $\pm$ 3.53 | $\pm$ 2396.89 | $\pm$ 0.50 | $\pm$ 0.22 | $\pm$ 0.19 |
|      |                               |        |        | <i>Pygospio elegans</i>       | 157.33 $\pm$ 157.33          |      |            |               |            |            |            |
|      |                               |        |        | <i>Cerastoderma edule</i>     | 88.00 $\pm$ 84.03            |      |            |               |            |            |            |
|      |                               |        |        | <i>Corophium arenarium</i>    | 72.00 $\pm$ 46.88            |      |            |               |            |            |            |
| 811  | <i>Urothoe poseidonis</i>     | 0.510  | 0.0004 | <i>Macomangulus tenuis</i>    | 410.667 $\pm$ 137.42         | 12   | 14.67      | 1135.00       | 1.80       | 0.72       | 0.67       |
| 812  | <i>Macomangulus tenuis</i>    | 0.451  | 0.0019 | <i>Urothoe poseidonis</i>     | 194.000 $\pm$ 73.74          |      | $\pm$ 0.82 | $\pm$ 198.53  | $\pm$ 0.13 | $\pm$ 0.04 | $\pm$ 0.04 |
|      | <i>Cerastoderma edule</i>     | 0.451  | 0.0287 | <i>Bathyporeia sarsi</i>      | 144.667 $\pm$ 79.88          |      |            |               |            |            |            |
|      |                               |        |        | <i>Cerastoderma edule</i>     | 94.000 $\pm$ 27.35           |      |            |               |            |            |            |
|      |                               |        |        | <i>Spio martinensis</i>       | 44.667 $\pm$ 17.04           |      |            |               |            |            |            |
| 813  | <i>Acrocnida spatulispina</i> | 0.629  | 0.0001 | <i>Acrocnida spatulispina</i> | 324.80 $\pm$ 307.86          | 10   | 18.30      | 825.04        | 2.07       | 0.76       | 0.71       |
|      | <i>Kurtiella bidentata</i>    | 0.62   | 0.0001 | <i>Kurtiella bidentata</i>    | 66.40 $\pm$ 33.742           |      | $\pm$ 1.69 | $\pm$ 86.42   | $\pm$ 0.20 | $\pm$ 0.06 | $\pm$ 0.06 |
| 814  | <i>Malmgrenia marphysae</i>   | 0.617  | 0.0079 | <i>Bathyporeia elegans</i>    | 49.60 $\pm$ 52.092           |      |            |               |            |            |            |
|      | <i>Polycirrus medusa</i>      | 0.497  | 0.0007 | <i>Polycirrus medusa</i>      | 48.00 $\pm$ 38.088           |      |            |               |            |            |            |
|      | <i>Bathyporeia elegans</i>    | 0.496  | 0.0125 | <i>Cumosopsis longipes</i>    | 45.60 $\pm$ 68.201           |      |            |               |            |            |            |
| 815  | <i>Magelona mirabilis</i>     | 0.595  | 0.0001 | <i>Donax vittatus</i>         | 81.71 $\pm$ 31.58            | 14   | 20.50      | 730.37        | 2.49       | 0.88       | 0.85       |
|      | <i>Donax vittatus</i>         | 0.505  | 0.0109 | <i>Magelona mirabilis</i>     | 68.00 $\pm$ 15.68            |      | $\pm$ 2.00 | $\pm$ 128.38  | $\pm$ 0.12 | $\pm$ 0.01 | $\pm$ 0.02 |
|      | <i>Aponuphis bilineata</i>    | 0.500  | 0.005  | <i>Acrocnida spatulispina</i> | 46.28 $\pm$ 15.89            |      |            |               |            |            |            |
|      | <i>Scoloplos armiger</i>      | 0.486  | 0.0271 | <i>Pseudocuma longicorne</i>  | 45.71 $\pm$ 34.59            |      |            |               |            |            |            |
|      |                               |        |        | <i>Polycirrus medusa</i>      | 43.42 $\pm$ 16.49            |      |            |               |            |            |            |
| 816  | <i>Eurydice affinis</i>       | 1.000  | 0.0004 | <i>Bathyporeia pilosa</i>     | 818.67 $\pm$ 500.23          | 3    | 7.33       | 1053.10       | 0.98       | 0.47       | 0.54       |
|      | <i>Eurydice pulchra</i>       | 0.905  | 0.0004 | <i>Scolecopsis squamata</i>   | 85.33 $\pm$ 85.33            |      | $\pm$ 2.03 | $\pm$ 540.33  | $\pm$ 0.28 | $\pm$ 0.15 | $\pm$ 0.17 |
|      | <i>Bathyporeia pilosa</i>     | 0.714  | 0.0003 | <i>Eurydice pulchra</i>       | 64.00 $\pm$ 25.72            |      |            |               |            |            |            |
|      |                               |        |        | <i>Nemertea</i>               | 18.67 $\pm$ 14.85            |      |            |               |            |            |            |
|      |                               |        |        | <i>Eurydice affinis</i>       | 10.67 $\pm$ 2.67             |      |            |               |            |            |            |

817 Table III: Characteristics of ecological states of trajectory clusters in 1987, 2001 and  
 818 2019. Taxonomic trajectory are coloured according to trajectory clusters and  
 819 described with distance-based metrics mean  $\pm$  se (NC: net change, TP: Trajectory  
 820 path). Distribution of species used to describe taxonomic trajectory clusters (Ind.sp.:  
 821 Indicative species, 1st. Num.: two first numerous species) are detailed in  
 822 Supplementary material, Appendix D.

|      | A<br>8 st<br>NC= 10.49 $\pm$ 0.83<br>TP= 21.20 $\pm$ 1.43 |                            |                       |  | B<br>28 st<br>NC= 12.74 $\pm$ 0.81<br>TP= 23.94 $\pm$ 1.11 |                    |  |                              | C<br>4 st<br>NC= 25.06 $\pm$ 0.38<br>TP= 35.33 $\pm$ 0.83 |  |                                    |                     | D<br>2st<br>NC= 20.78 $\pm$ 1.91<br>TP= 40.65 $\pm$ 5.28 |  |  |  |
|------|---|----------------------------|-----------------------|--|--|--------------------|--|------------------------------|---|--|------------------------------------|---------------------|--|--|--|--|
| 1987 | Ind. sp.  | <i>Pygospio elegans</i>    | 0.750 / 0.0116        |  | <i>Macromangulus tenuis</i>                                | 0.748 / 0.0001     |  | <i>Chaetozone gibber</i>     | 0.701 / 0.0159  |  | <i>Bathyporeia guilliamsoniana</i> | 1.000 / 0.0011      |  |  |  |  |
|      | 1st. Num.   | <i>Arenicola marina</i>    | 0.734 / 0.0018        |  | <i>Macromangulus tenuis</i>                                | 283.00 $\pm$ 96.53 |  | <i>Polycirrus medusa</i>     | 120.25 $\pm$ 68.67  |  | <i>Pontocrates altamarinus</i>     | 1.000 / 0.0014      |  |  |  |  |
|      |   | <i>Peringia ulvae</i>      | 942.00 $\pm$ 841.27   |  | <i>Bathyporeia sarsi</i>                                   | 77.71 $\pm$ 38.74  |  | <i>Magelona mirabilis</i>    | 88.00 $\pm$ 43.57   |  | <i>Magelona mirabilis</i>          | 84.00 $\pm$ 52.00   |  |  |  |  |
|      |   | <i>Pygospio elegans</i>    | 228.00 $\pm$ 196.34   |  |  |                    |  |                              |   |  | <i>Magelona filiformis</i>         | 56.00 $\pm$ 16.00   |  |  |  |  |
| 2001 | Ind. sp.  | <i>Peringia ulvae</i>      | 0.673 / 0.0206        |  | <i>Urothoe poseidonis</i>                                  | 0.561 / 0.0075     |  | <i>Chaetozone gibber</i>     | 0.669 / 0.0185  |  | <i>Polycirrus medusa</i>           | 0.622 / 0.0292      |  |  |  |  |
|      | 1st. Num.   | <i>Eurydice affinis</i>    | 0.444 / 0.0367        |  | <i>Macromangulus tenuis</i>                                | 0.514 / 0.0035     |  | <i>Notomastus latericeus</i> | 0.500 / 0.0084  |  | <i>Holothuria spp.</i>             | 0.500 / 0.0454      |  |  |  |  |
|      |   | <i>Corophium arenarium</i> | 1542.75 $\pm$ 1542.75 |  | <i>Macromangulus tenuis</i>                                | 209.14 $\pm$ 48.04 |  | <i>Donax vittatus</i>        | 11424.75 $\pm$ 4404.48                                    |  | <i>Donax vittatus</i>              | 985.50 $\pm$ 478.50 |  |  |  |  |
|      |   | <i>Peringia ulvae</i>      | 336.63 $\pm$ 188.07   |  | <i>Urothoe poseidonis</i>                                  | 106.18 $\pm$ 29.61 |  | <i>Macromangulus tenuis</i>  | 467.25 $\pm$ 407.51                                       |  | <i>Bathyporeia sarsi</i>           | 50.50 $\pm$ 50.50   |  |  |  |  |
| 2019 | Ind. sp.  | <i>Bathyporeia pilosa</i>  | 0.719 / 0.0047        |  | <i>Eocuma dolifusi</i>                                     | 0.571 / 0.0396     |  | <i>Chaetozone gibber</i>     | 1 / 0.0001  |  | <i>Nucula nitidosa</i>             | 0.670 / 0.0081      |  |  |  |  |
|      | 1st. Num.   | <i>Corophium arenarium</i> | 0.625 / 0.0132        |  | <i>Macromangulus tenuis</i>                                | 176.00 $\pm$ 68.66 |  | <i>Nemeritis spp.</i>        | 0.723 / 0.0009  |  | <i>Aponuphis bilineata</i>         | 0.623 / 0.0229      |  |  |  |  |
|      |   | <i>Peringia ulvae</i>      | 1667.00 $\pm$ 1152.91 |  | <i>Acrocnida spatulispina</i>                              | 133.44 $\pm$ 43.81 |  | <i>Donax vittatus</i>        | 194.00 $\pm$ 83.03  |  | <i>Magelona mirabilis</i>          | 176.00 $\pm$ 16.00  |  |  |  |  |
|      |   | <i>Bathyporeia pilosa</i>  | 332.00 $\pm$ 217.43   |  |  |                    |  | <i>Pseudocuma longicorne</i> | 136.00 $\pm$ 118.07                                       |  | <i>Acrocnida spatulispina</i>      | 168.00 $\pm$ 64.00  |  |  |  |  |

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