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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.

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 α and β -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 (1/8m²) 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 m²), 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 m². 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 μ m), fine sand (250 to 125 μ m), very
215 fine sand (125 to 63 μ m), and mud (<63 μ m) contents (%).

216

217 **2.5.2 Taxonomic α -diversity**

218 In order to assess the different components of taxonomic α -diversity, the mean
219 number of individuals per m² (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 μ 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⁻² ± 593.83) increased over the study period.
302 Annelids, molluscs and crustaceans dominated the community (Appendix E).
303 *Chaetozone gibber* (133.07 ind.m⁻² ± 94.14), *Varicorbula gibba* (95.87 ind.m⁻² ±
304 187.35), *Aponuphis bilineata* (60.07 ind.m⁻² ± 34.39), *Abra alba* (44.67 ind.m⁻² ±
305 92.79), *Ampelisca sarsi* (44.00 ind.m⁻² ± 128.14), *Notomastus latericeus* (25.67

306 ind.m⁻² ± 26.07), and *Ampelisca brevicornis* (24.93 ind.m⁻² ±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 *Polittapes*
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 ± 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 ± 1.09) than in cluster A (20.35 ± 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 ± 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 ± 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 ± 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 ± 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 β 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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756 **Declaration of Competing Interest**

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**
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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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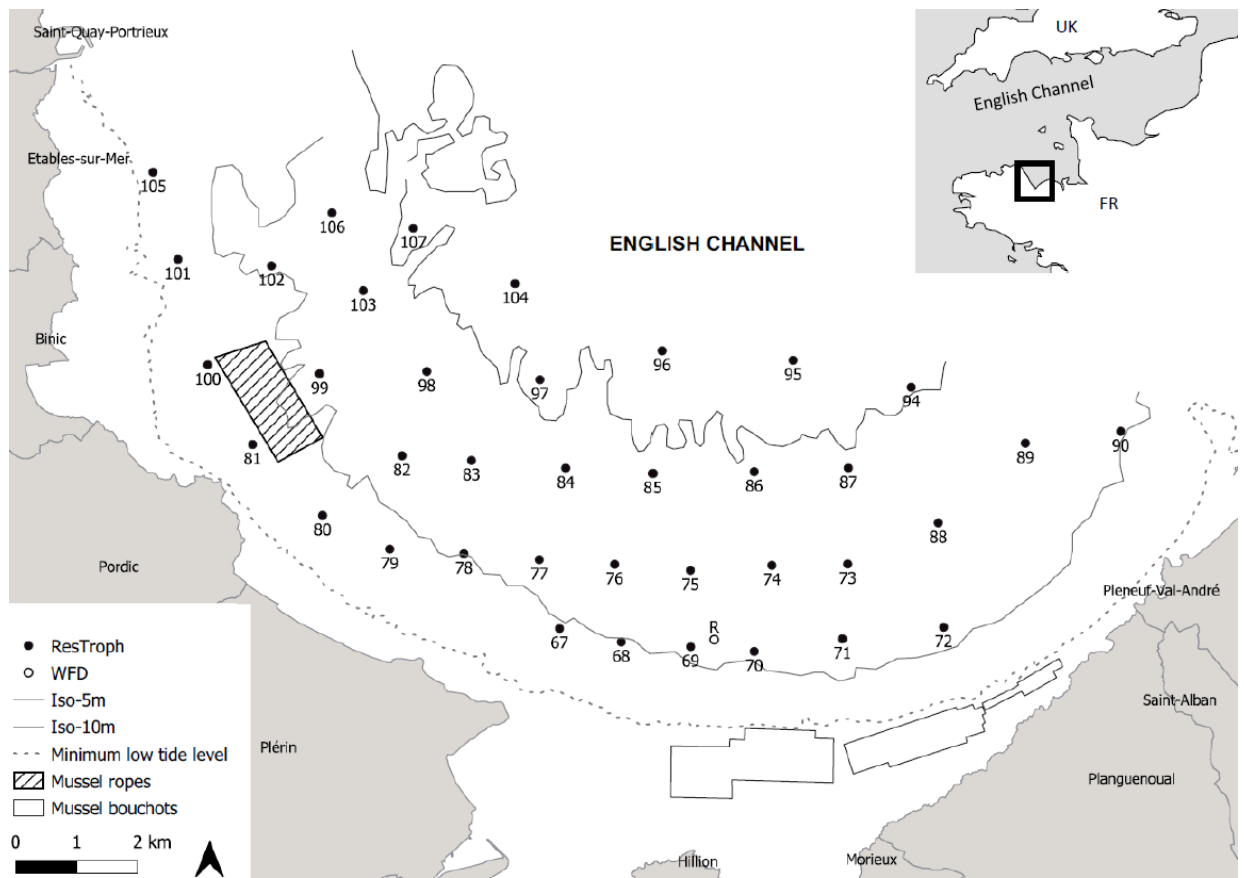
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1107 **FIGURES ET TABLES**



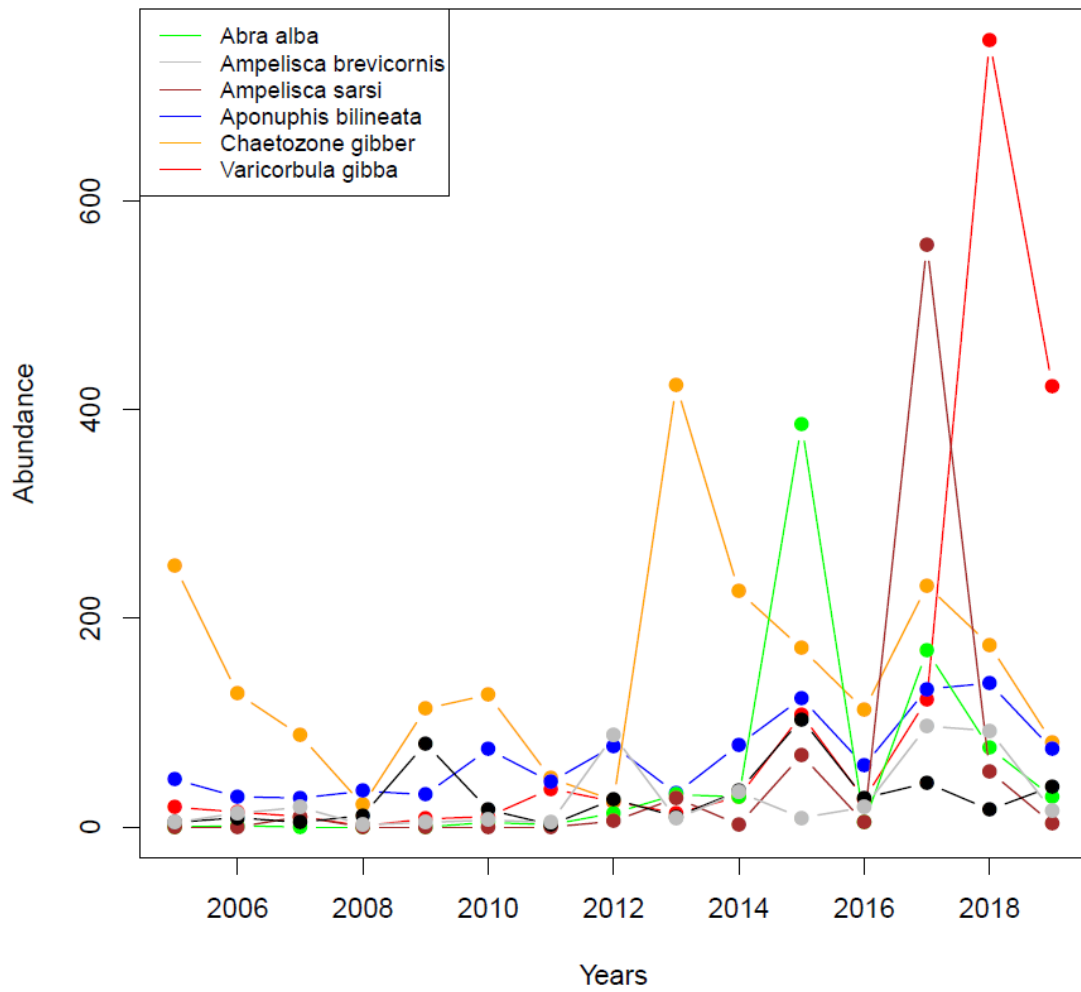
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1109 Figure 1: Location of the study area and sampling strategy. Black dots corresponds to the 38
 1110 stations of the ResTroph research program sampled in 1987 and 2019 and white one (station
 1111 R) to the Water Framework Directive (WFD) monitoring 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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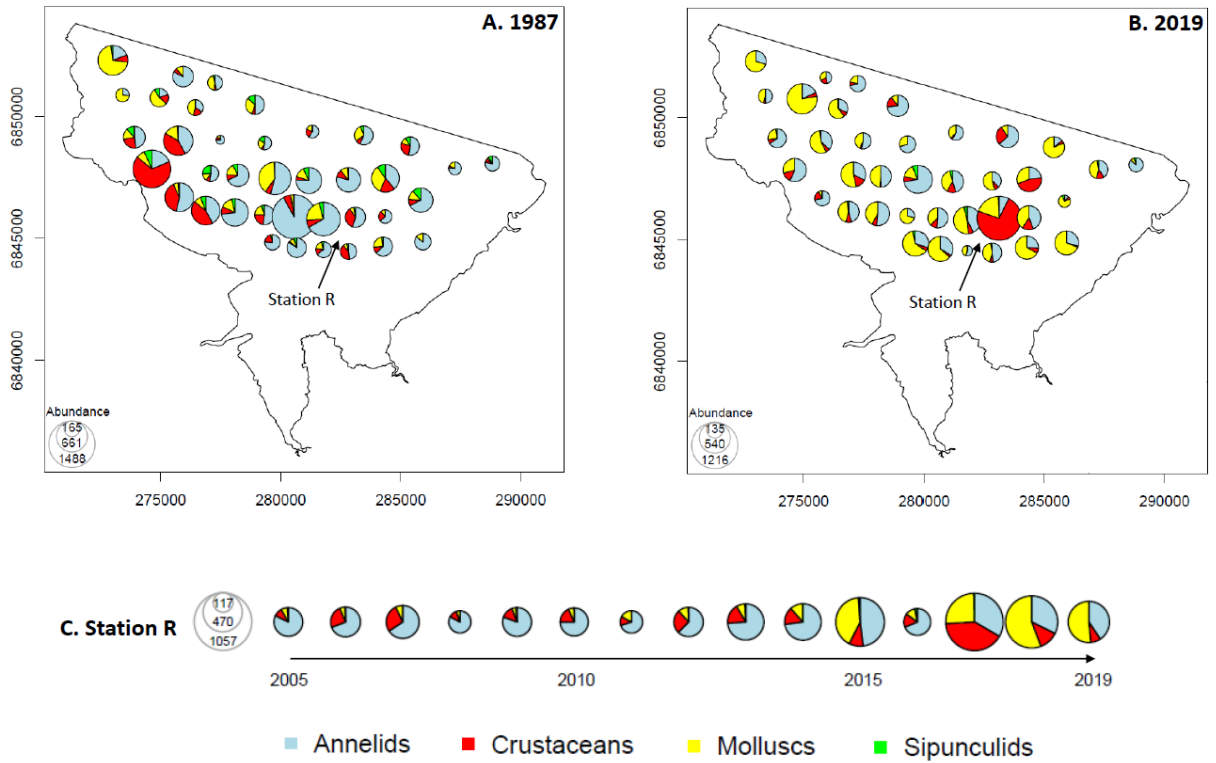
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1118 Figure 2: Abundance (ind.m²) of dominant species sampled at the station R

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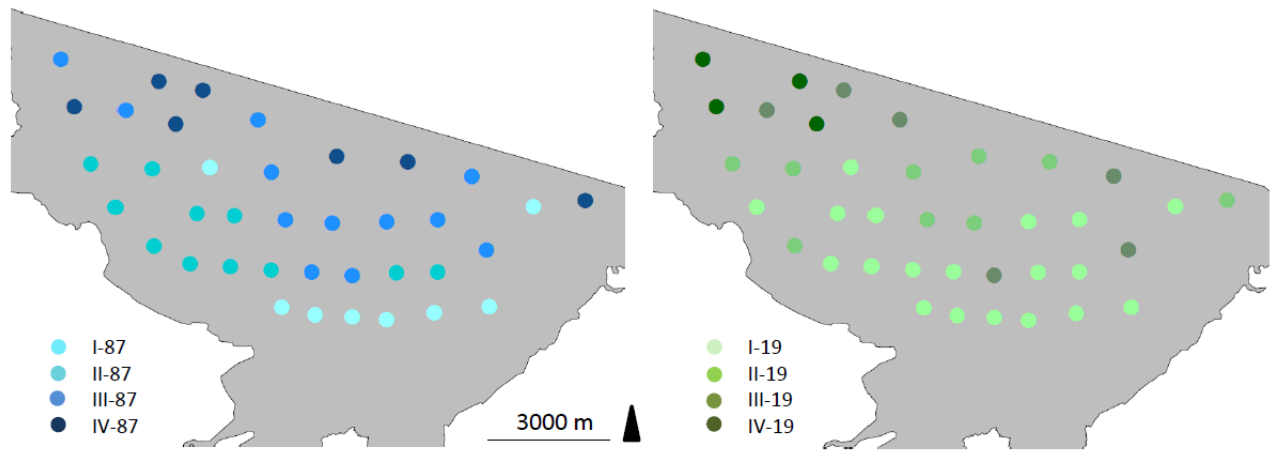


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1123 Figure 3: Distribution maps of main taxonomic group with mean total abundance (m^2) classes
 1124 superimposed given as the sum for 1987 and 2019. Colours represents each group: Annelids
 1125 errant (blue), Annelids sedentary (light blue), Crustaceans (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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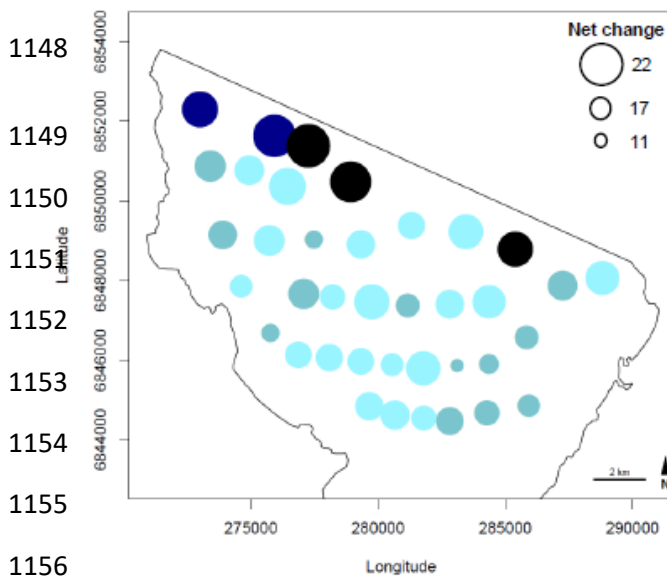
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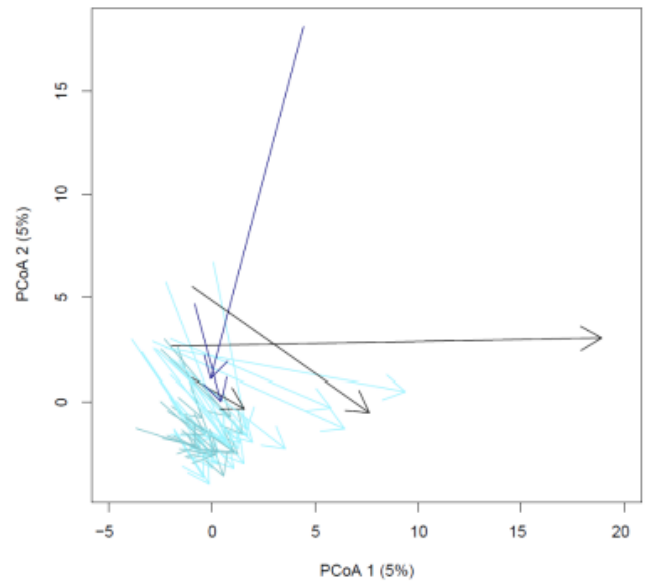
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A. Local taxonomic trajectories



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 |

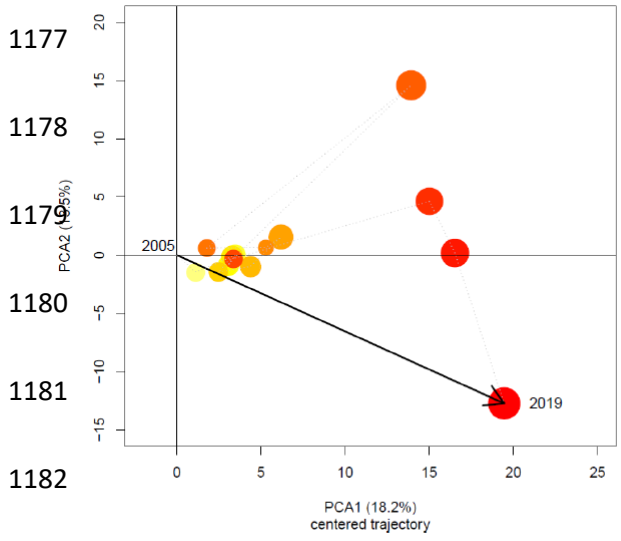
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1168 Figure 5: Taxonomic trajectories. A.: Maps of local trajectories. Size of circles corresponds to
 1169 net change between 1987 and 2019 and colours to cluster of trajectories determined by HCA
 1170 on CTA trajectory similarity analysis. All the 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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A. TAXONOMIC



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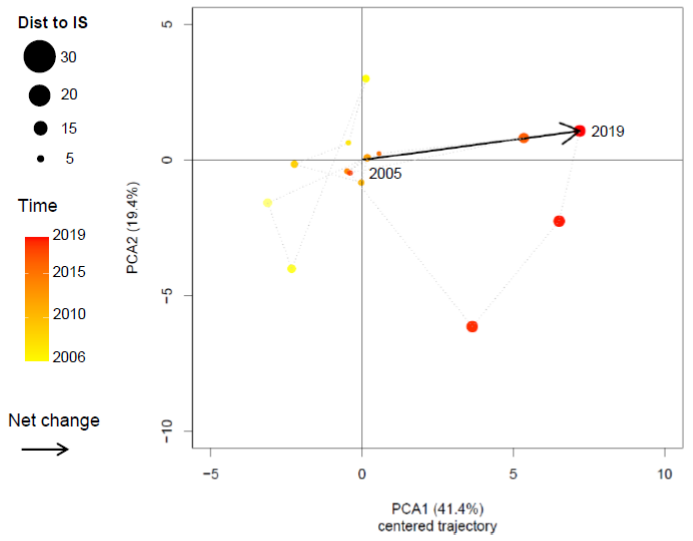
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B. FUNCTIONAL



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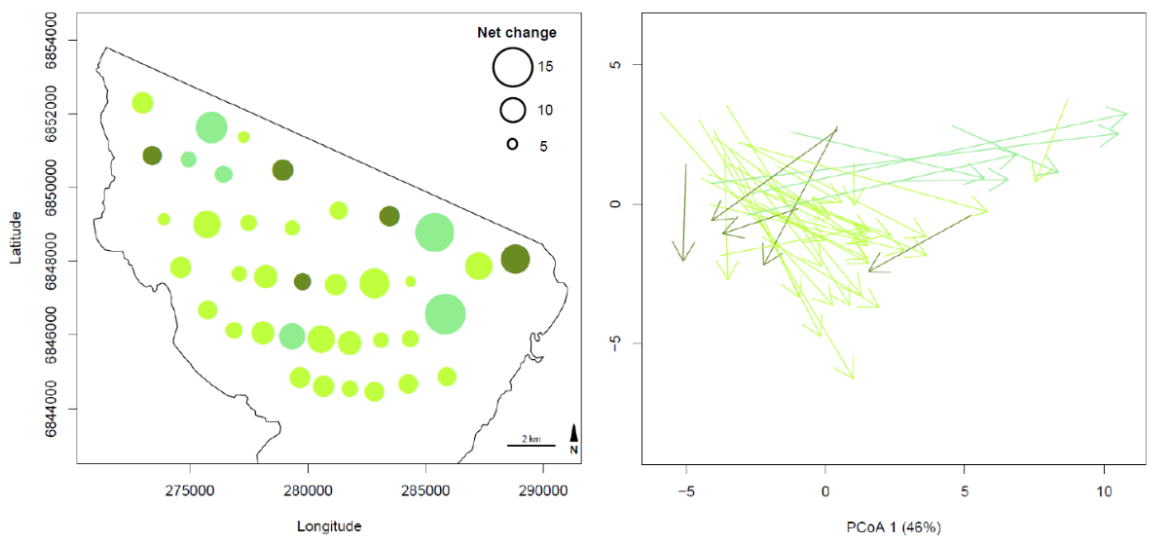
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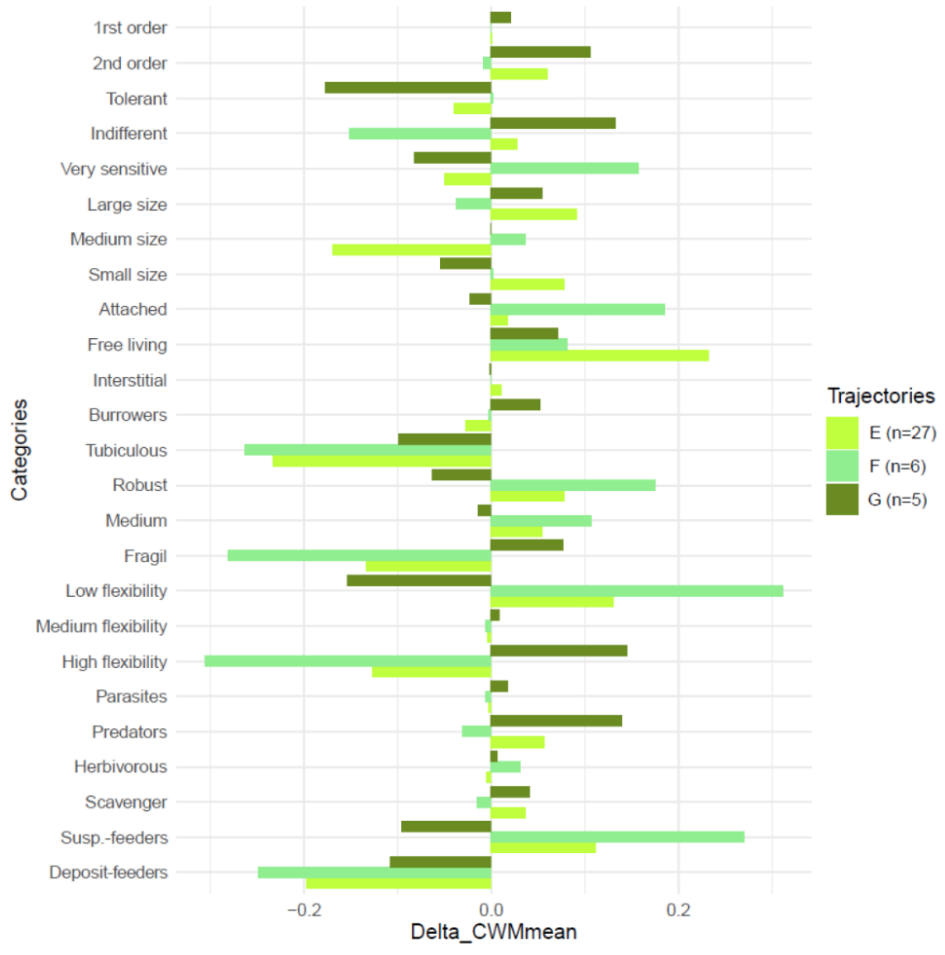
Figure 6: Trajectory of the station R between 2005 and 2019. The origin of the ordination diagram represents the initial state characterized in 2005 after trajectory centering. Only two dimensions are shown. Points corresponds to intermediate ecological states (size= length of each state to initial state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

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

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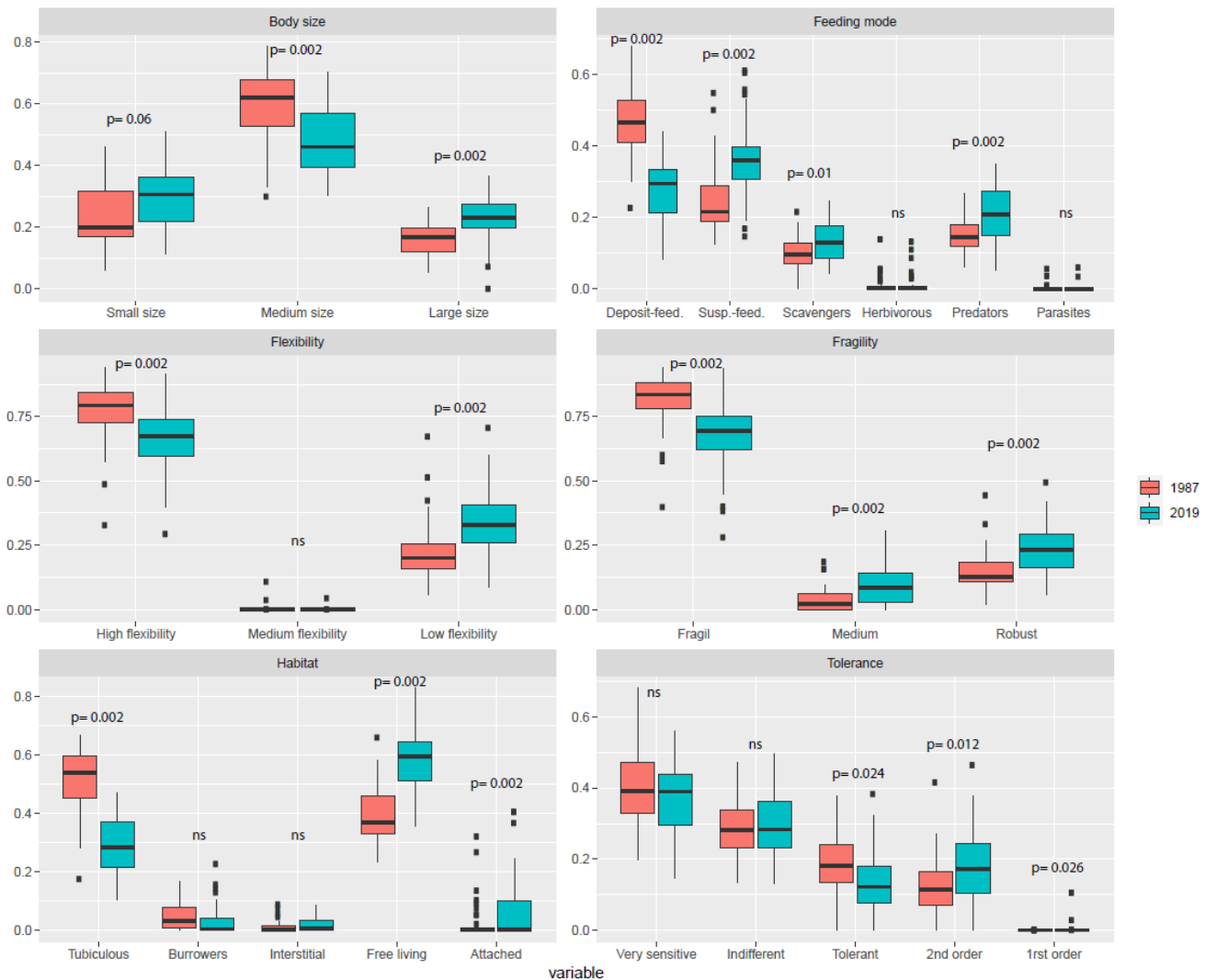
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1269 Figure 8: Box plots of CWM traits values in levels of respective categories according to year

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 m² (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 ² \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 | | | | | | |
| | II-87 | <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 | | | | | | |
| | | <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 |
| | III-87 | <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 | | | | | | |
| | IV-87 | <i>Nephtys hombergii</i> | 0.368 | 0.0362 | <i>Aponuphis bilineata</i> | 31.27 \pm 6.95 | | | | | | |
| | | <i>Ampharete spp.</i> | 0.554 | 0.0005 | <i>Ampharete spp.</i> | 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-19 | <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 | | | | | | | |
| II-19 | <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 | | | | | | | |
| III-19 | <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>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 | |
| IV-19 | <i>Phyllodoce groenlandica</i> | 0.368 | 0.0310 | <i>Ampelisca tenuicornis</i> | 64.42 \pm 63.54 | | | | | | | |
| | <i>Nephtys hombergii</i> | 0.483 | 0.0004 | <i>Glycide nordmanni</i> | 20.63 \pm 4.07 | | | | | | | |
| | <i>Notomastus latericeus</i> | 0.483 | 0.0004 | <i>Streblosoma bairdi</i> | 17.26 \pm 4.63 | 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-19 | <i>Varicorbula gibba</i> | 0.728 | 0.0004 | <i>Aponuphis bilineata</i> | 16.42 \pm 6.69 | | | | | | | |
| | <i>Phyllodoce groenlandica</i> | 0.446 | 0.0239 | <i>Notomastus latericeus</i> | 29.33 \pm 7.06 | | | | | | | |
| | <i>Nephtys hombergii</i> | 0.333 | 0.0313 | <i>Varicorbula gibba</i> | 27.56 \pm 10.16 | 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 | |
| II-19 | <i>Chaetozone gibber</i> | 0.446 | 0.0239 | <i>Nephtys hombergii</i> | 25.78 \pm 5.62 | | | | | | | |
| | <i>Sigalion mathildae</i> | 0.333 | 0.0304 | <i>Anomia ephippium</i> | 18.67 \pm 10.67 | | | | | | | |
| | <i>Amphipholis squamata</i> | 0.333 | 0.0290 | <i>Pista cristata</i> | 17.78 \pm 6.77 | | | | | | | |
| III-19 | <i>Aequipecten opercularis</i> | 0.333 | 0.0290 | <i>Notomastus latericeus</i> | 160.00 \pm 66.58 | | | | | | | |
| | <i>Nucula hanleyi</i> | 0.611 | 0.0024 | <i>Crepidula fornicata</i> | 21.33 \pm 7.35 | | | | | | | |
| | <i>Timoclea ovata</i> | 0.596 | 0.0031 | <i>Notomastus latericeus</i> | 16.00 \pm 10.93 | | | | | | | |
| IV-19 | <i>Glycera alba</i> | 0.481 | 0.0069 | <i>Aponuphis bilineata</i> | 10.67 \pm 5.72 | | | | | | | |
| | <i>Timoclea ovata</i> | 0.481 | 0.0069 | <i>Nephtys hombergii</i> | 10.67 \pm 5.72 | | | | | | | |
| | <i>Glycera alba</i> | 0.481 | 0.0069 | <i>Anomia ephippium</i> | 10.67 \pm 5.72 | | | | | | | |
| V-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 | | | | | | | |
| VI-19 | <i>Nucula hanleyi</i> | 0.611 | 0.0024 | <i>Notomastus latericeus</i> | 26.00 \pm 17.09 | | | | | | | |
| | <i>Timoclea ovata</i> | 0.596 | 0.0031 | <i>Polittapes rhomboides</i> | 18.00 \pm 18.00 | | | | | | | |
| | <i>Glycera alba</i> | 0.481 | 0.0069 | | | | | | | | | |

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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 m² (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 ² \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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