

1 **Mesoscale assemblages of fish and megainvertebrates as evidence of**
2 **benthiscapes on continental shelves.**

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19 **Abstract**

20 Despite the relatively small proportion of ocean surface they represent, continental
21 shelf ecosystems are among the most productive in the world. Located at the interface
22 between terrestrial and marine environments, these habitats are structured by strong

23 environmental forcings, especially on the sea bottom. A clear understanding of the spatial
24 distribution of these habitats, along with knowledge on the composition and functioning of
25 their associated communities, is essential for fisheries management and ecosystem
26 conservation. Here, we used data from yearly EVHOE otter trawl surveys (2008–2020) to
27 characterize the spatial structuration of benthic communities of the entire continental shelf
28 of the Bay of Biscay (France), and to investigate the potential environmental drivers of
29 these patterns. Two separate biological components were studied: epibenthic
30 megainvertebrates and benthic-demersal fish. Clustering analyses identified seven
31 assemblages within each component. We detected a strong correlation between the
32 spatial organization of the different assemblages identified for fish and megainvertebrates,
33 providing evidence for broad-scale spatial structuration of benthic habitats—
34 benthiscapes—in this shelf ecosystem. The most influential environmental variables were
35 identified as bottom temperature, sediment type, and primary production. Patterns in
36 certain structural parameters, such as biomass, revealed possible spatial differences in
37 ecological functioning. For example, we observed a drop in biomass from the coast to the
38 central part of the shelf, followed by an increase in biomass near the edge of the Armorican
39 shelf. These patterns reflect major large-scale processes (river inputs *versus* shelf-break
40 upwelling) structuring the entire Bay of Biscay ecosystem. A comparative analysis
41 revealed that the biological features and functioning observed in this study are shared with
42 other European continental shelves. In addition to improving our knowledge of benthic
43 environments, studies such as this one can promote improvements in ecosystem-based
44 management and marine spatial planning of a fast-changing ecosystem under multiple
45 anthropogenic stresses.

46

47 **Keywords:** Continental shelf, Bay of Biscay, Benthos, Demersal, Environmental
48 forcings, Spatial structure

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49 **1 INTRODUCTION**

50 Continental shelves occupy a small proportion of the total ocean surface (review in Hall,
51 2002) but are among the most productive ecosystems in the world (Costanza et al., 1997).
52 In addition, the ecosystem services they provide are among the most valuable (e.g.,
53 carbon storage, fisheries, biogeochemical cycling) (Costanza et al., 1997; Longhurst et
54 al., 1995; Raffaelli et al., 2003). Within these environments, the benthic domain is of
55 considerable importance: it is responsible for a significant proportion of marine biological
56 production, especially the part exploited by humans (Hall, 2002), it makes an essential
57 contribution to benthic-pelagic coupling, and it represents a major reservoir for terrestrial
58 carbon storage (Zhang et al., 2021). The spatial location of these ecosystems—at the
59 interface between terrestrial and marine environments—places them under strong
60 pressure from natural processes that vary in time and space, and exposes them to
61 extensive anthropogenic influences (Halpern et al., 2008; Worm et al., 2006). These
62 intense and dynamic environmental conditions structure the habitats and ecological
63 niches present and determine how species are brought together and interact with one
64 another (Guimerà et al., 2010).

65 Due to their long (multi-year) lifespans and wide spatial dispersion, assemblages of
66 epibenthic megainvertebrates (i.e., invertebrates larger than 1 cm living on the seabed)
67 and benthic-demersal fish (fish species living on or near the seabed) can provide useful
68 information on the structure of the benthic ecosystem and its response to environmental
69 drivers across large spatial and temporal scales. This approach—investigating the spatial
70 structure of ecosystems through the analysis of various benthic components—has been
71 previously applied to different European shelves (Bremner et al., 2006; Daan et al., 2005;
72 Neumann et al., 2016; Sánchez et al., 2008). While some recent studies have considered

73 epibenthic megainvertebrates and benthic-demersal fish separately (e.g., Reiss et al.,
74 2010; Sánchez et al., 2008), many older studies did not (Colloca et al., 2004; Ellis et al.,
75 2011; Kaiser et al., 2004; Rees et al., 1999), relying instead on the hypothesis that these
76 two communities share common biological traits and could therefore be grouped together.

77
78 Whether grouped together or separately, knowledge on the spatial structuration of these
79 two benthic communities can provide a better understanding of the meso-scale (from 10
80 to 100 km) functioning of shelf ecosystems (Hooper et al., 2005; Shojaei et al., 2021) in
81 the face of local and/or global environmental change. Moreover, this type of work can help
82 to identify ecologically coherent spatial entities which can then be integrated into
83 management efforts (e.g., Bell et al., 2021), with particular benefits for the ecosystem-
84 based management of fisheries (Garcia et al., 2003).

85 Our study focuses on the Bay of Biscay (France) as a representative case study of a North
86 Atlantic temperate continental shelf. This zone features an extensive shelf that stretches
87 far offshore until finally breaking towards the abyssal plain (review in Borja et al., 2019).
88 In its coastal section, it faces numerous anthropogenic pressures (eutrophication,
89 pollution) and is the site of major fishing activity, which targets benthic-demersal species
90 in particular (Druon et al., 2021). Additionally, this area is now of growing interest for the
91 development of technologies for renewable marine energy production (Fofack-Garcia et
92 al., 2023; Taormina et al., 2018).

93 The first overview of benthic communities in the Bay of Biscay and the Celtic Sea is
94 credited to Le Danois (1948); although descriptive and not quantitative, this study provided
95 an initial picture of the overall structure of communities from the shelf to the slope.

96 Macrobenthic communities of the Bay of Biscay were further characterized in the north by
97 Glémarec (1969) and in the south by Lagardère (1973), who both described spatial
98 structuration that was mainly determined by a thermal depth gradient and sedimentary
99 substrate characteristics. A partial revisitation in the north in 2001–2002 revealed notable
100 changes in macrobenthic fauna as the result of strong fishing pressure (Hily et al., 2008).
101 At the scale of the entire bay, work by Souissi et al. (2001) provided a characterization of
102 the main assemblages of benthic-demersal fish. To date, though, there has not been a
103 wide-scale study to generate a standardized picture of the larger benthic communities of
104 the entire Bay of Biscay. In particular, there is a need for the identification of the main
105 patterns and environmental factors that structure communities, especially with respect to
106 a joint analysis of fish and invertebrate fauna.

107 The aim of this study was to assess the spatial structuration of the benthic ecosystem of
108 the continental shelf of the Bay of Biscay, specifically by analyzing communities of
109 epibenthic megainvertebrates and benthic-demersal fish and their relationships with
110 environmental forcings. For this, we made use of the large, homogenous dataset available
111 thanks to the recurrent international bottom trawl survey “EVHOE” (Laffargue et al., 2020).

112 Our work was carried out in two steps:

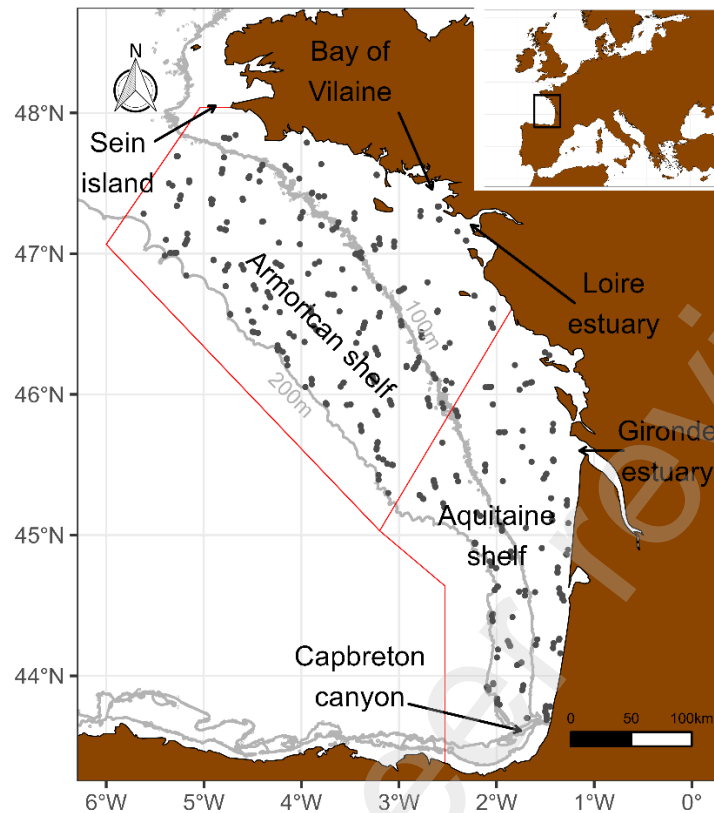
- 113 1. Identify and characterize assemblages of epibenthic megainvertebrates and benthic-
114 demersal fish and their spatial distribution within the study area
- 115 2. Analyze the links between the spatial patterns observed and the environmental forcings
116 that structure the identified assemblages.

117 **2 MATERIALS AND METHODS**

118 **2.1 Study area**

119 This study covers the entire French part of the continental shelf of the Bay of Biscay,
120 extending from the island of Sein to the canyon of Capbreton (Figure 1). The present work
121 considers both coastal and deep circalittoral areas along the margin of the continental
122 shelf, with bathymetry ranging from 16 to 200 m in depth. This continental shelf is
123 composed of a broad northern shelf (Armorican shelf, ~180 km wide) and a narrower
124 southern shelf (Aquitaine shelf, ~90 km wide) (K. Koutsikopoulos & Le Cann, 1996).

125 The shelf is characterized by numerous complex seasonal hydrographic processes:
126 slope-shelf exchanges, northern slope fronts, southern coastal upwellings, and high
127 terrigenous contributions, mainly from the Loire, Vilaine, and Gironde Rivers (Akpınar et
128 al., 2020; Borja et al., 2019; Charria et al., 2013; K. Koutsikopoulos & Le Cann, 1996;
129 Labry et al., 2001; Loyer et al., 2006).



130

131 *Figure 1. Study area: continental shelf of the Bay of Biscay. Gray dots represent*
 132 *sampling points from EVHOE survey used in the analysis. Red frame divides the shelf*
 133 *into the northern Armorian shelf and the southern Aquitaine shelf.*

134

135 **2.2 Biological data**

136 The observations used in this study were recorded as part of the EVHOE (EValuation
 137 Halieutique Ouest de l'Europe) survey undertaken within the framework of IBTS surveys
 138 of European fisheries (ICES, 2017). The EVHOE survey took place each year between
 139 October and December. Samples were collected using an otter trawl with a large vertical
 140 opening (GOV, *Grande Ouverture Verticale*) and a 20-mm mesh size cod-end (Laffargue
 141 et al., 2020). Each haul lasted 30 minutes at a speed of about 4 knots and covered about
 142 0.07 km². The dataset covers the period 2008–2020 (except 2017, which was incomplete
 143 due to cruise damage), with a total of 685 stations sampled.

144 Whenever possible, sampled organisms were sorted to the lowest possible taxonomic
145 level on board, with verification in the laboratory for some specimens, if necessary.
146 Species names were assigned as per the World Register of Marine Species (WoRMS,
147 2022).

148 Only epibenthic megainvertebrates and benthic-demersal fish were retained for these
149 analyses. “Megainvertebrates” refers here to organisms with a size greater than 1
150 centimeter that can live on or in the substrate and that need to move on the substrate to
151 perform a vital and/or reproductive function. This excluded from the analysis large
152 swimming cephalopods (e.g., *Loligo sp.*, *Illex sp.*) and gelatinous taxa. Colonial organisms
153 (from the groups Bryozoa, Hydrozoa, and Ascidiacea) were uncountable on-board, and
154 thus were also removed from the analyses. The epibenthic megainvertebrates component
155 will be further referred to as “benthos”.

156 As we were particularly interested in benthic-demersal fish, we excluded species whose
157 lifecycles and activities are mainly related to pelagos. The benthic-demersal ichthyofauna
158 component will be further referred to as “fish”.

159 **2.3 Environmental variables and data**

160 We selected a total of seven major environmental variables that are assumed to have a
161 structuring effect on benthic communities.

162 The coupled hydrodynamic-ecosystem 3D model NEMO-NEMOVAR-ERSEM was used
163 to obtain data for a large number of environmental variables at each haul station (EU-
164 Copernicus, 2020b, 2020a). Those variables were: chlorophyll concentration, mixed layer
165 depth, nitrate concentration, dissolved oxygen concentration, pH, phytoplanktonic carbon,
166 phosphate concentration, primary production, salinity, and temperature. Monthly

167 averaged environmental data were gridded with a resolution of $0.111^\circ \times 0.067^\circ$ (cells of
168 about 7 km of horizontal and vertical resolution). Considering the distribution of stations
169 and the distance sampled per haul (about 3.5 km), we judged that this resolution was
170 appropriate for the spatial scale of the study. With the exception of primary production, we
171 selected the surface and near-bottom values for each of these variables. For net primary
172 production, we considered the maximum value in the water column for each station and
173 each month. Data were integrated over the three years preceding each sampling event,
174 since the life expectancy for the majority of taxa considered here is expected to be at least
175 three years. For each available environmental variable and each year of the dataset, we
176 calculated the minimum, maximum, standard deviation, and mean values. The values
177 assigned to each station were then averaged over the three years prior to the observation
178 date. In this way, we obtained an initial set of 72 environmental variables and derived
179 calculations for each sampling station.

180 To complete the set of environmental variables, additional data were selected regarding
181 bottom current and substrate. Bottom stress, which represents the velocity of the water
182 movements experienced by benthic organisms due to currents and waves, has been
183 found to be an important variable structuring the diversity of benthic communities (Reiss
184 et al., 2010). Here, this was quantified as the 90th percentile of the kinetic energy at 1 m
185 from the seabed, with a horizontal resolution of $1/36^\circ$ (about 3 km). Since the NEMO-
186 NEMOVAR-ERSEM model does not include wave components, we obtained data on the
187 kinetic energy due to currents from the MANGA500 model, available on the EMODnet
188 platform (Accensi & Maisondieu, 2015), and data on the kinetic energy due to waves from
189 the WAVEMATCH III model (Caillaud et al., 2016). Data were averaged between 2010
190 and 2015. We assumed that there were no strong temporal variations in these two

191 variables (energy due to currents and energy due to waves). These two types of energy
192 were summed into a single quantitative “bottom energy” variable.

193 We performed a preliminary analysis to avoid over-correlation among variables. From the
194 initial set of variables, we selected six quantitative descriptors corresponding to key
195 ecological processes:

- 196 • **Standard deviation of surface salinity** ('sd_Sal'), assumed to reflect the
197 proximity to river plumes with variable seasonal inputs.
- 198 • **Standard deviation of bottom seafloor temperature** ('sd_Temp'), reflecting the
199 climatic gradation of the benthic domain (infralittoral, coastal circalittoral, and deep
200 circalittoral) (Chassé & Glémarec, 1976).
- 201 • **Bottom dissolved oxygen minimum** ('min_Oxy'), reflecting the input at the
202 air/water interface and the use by living organisms (respiration, bacterial organic
203 mineralization).
- 204 • **Kinetic energy at the seabed** ('q90_Energy'). This variable has a direct influence,
205 through the physical pressure exerted, on the ability of a species to colonize or live
206 in a given habitat, as well as an indirect influence on the trophic capacity of an area
207 through organic matter resuspension and export for example.
- 208 • **Average depth of the mixed layer** ('avg_MLD'). This variable was assumed to
209 increase close to frontal zones, where strong mixing occurs that is thought to
210 support primary production.
- 211 • **Maximum net primary production in the water column** ('max_NetPP'),
212 averaged over the year. This highlighted areas with high net primary production
213 rates, notably below the water surface in offshore areas.

214 Calculation of these six quantitative descriptors is summarized in Appendix Table A.1.
215 To this subset of environmental descriptors, we added a qualitative variable representing
216 substrate type, following the categories defined by the French Marine Hydrographic and
217 Oceanographic Service (SHOM, 2021): mud, silt, fine sand, sand, gravel, and rock.
218 Substrate categories were viewed as indicative of overall environmental conditions, with
219 low current and high deposition rates in muddy areas, and strong hydrological conditions
220 in coarser areas.
221 This set of seven descriptors (six quantitative and one qualitative) was found to strongly
222 reflect the variability in the original data (Gower's dissimilarity, Spearman's correlation:
223 85.6%, Mantel permutation test significance: p -value < 0.001).

224 **2.4 Biological data analysis**

225 Each analysis was conducted separately on benthos and fish. Analyses were
226 performed using the *vegan*, *stats*, and *cluster* packages in R 4.3.1 software (Oksanen et
227 al., 2022; R core team, 2023). Only species with an occurrence equal to or greater than
228 5% were retained, and abundance matrices were double square-root transformed to avoid
229 the distorting effect of heavily abundant species. Bray-Curtis dissimilarity matrices were
230 generated for each biological component (fish or benthos), and the dissimilarity matrices
231 were used to conduct ascendant hierarchical clustering using Ward linkage to aggregate
232 hauls into several clusters, the number of which was determined using visual and inertia
233 criteria (Borcard et al., 2018b). Clusters that were faunistically distinct from others were
234 denoted "assemblages". The significance of the clustering pattern was assessed through
235 an analysis of similarity using the "ANOSIM" function of the *vegan* package.

236 Spatial overlap between benthos and fish assemblages was first assessed visually and
237 then quantified using a Spearman's correlation between the two dissimilarity matrices.
238 This correlation was tested with a Mantel permutation test.

239 Each cluster was taxonomically characterized using the IndVal method from the labdsv
240 package. Indices reflecting structural parameters—biomass ($kg.km^{-2}$), abundance
241 (thousands of individuals per km^2) ($10^3 ind.km^{-2}$), and Shannon diversity—were used to
242 identify spatial patterns in both benthos and fish clusters. Calculations of observed
243 taxonomic richness (per haul) and Pielou's evenness are available in the Appendix
244 (Tables A.2 and A.3). Pairwise Wilcoxon tests were performed to assess differences
245 between clusters with respect to the structural indices. We also compared the overall
246 distribution of the structural parameters of each assemblage per station by performing
247 Pearson correlations between invertebrates and fish for each parameter (biomass,
248 abundance, and diversity). In order to balance the weight of the different assemblages
249 depending on the number of stations represented, we calculated median correlations
250 based on 1000 random selections of 26 stations per cluster. For this analysis, we only
251 kept the stations (444 stations out of a total of 685) with a similar cluster attribution for the
252 two biological components.

253 We performed distance-based redundancy analyses (db-RDAs) on Bray-Curtis
254 dissimilarity matrices to explicitly explore the relationships between species distributions
255 and environmental variables (Borcard et al., 2018a). Variance partitioning was performed
256 to assess the importance of each environmental variable in determining the structure of
257 benthic assemblages. By combining the results of the variance partitioning with canonical
258 ordination, we were able to identify relationships among the identified assemblages as
259 well as relationships between the assemblages and environmental variables.

260 **3 RESULTS**

261 **3.1 Spatial organization of the clusters**

262 In total, 141 fish and 342 benthos taxa were recorded during the sampling period. Of these,
263 47 fish and 77 benthos taxa were considered to be non-rare species (occurrence > 5%)
264 and were retained for the hierarchical clustering. This procedure identified seven clusters
265 within each of the two communities (corresponding dendrograms are in Appendix Figures
266 A.3 and A.4). For both fish and benthos, clustering patterns were spatially coherent
267 (Figure 2) and significant (ANOSIM, $R = 0.555$ ($p\text{-value} < 0.001$) and 0.542 ($p\text{-value} <$
268 0.001) for benthos and fish, respectively).

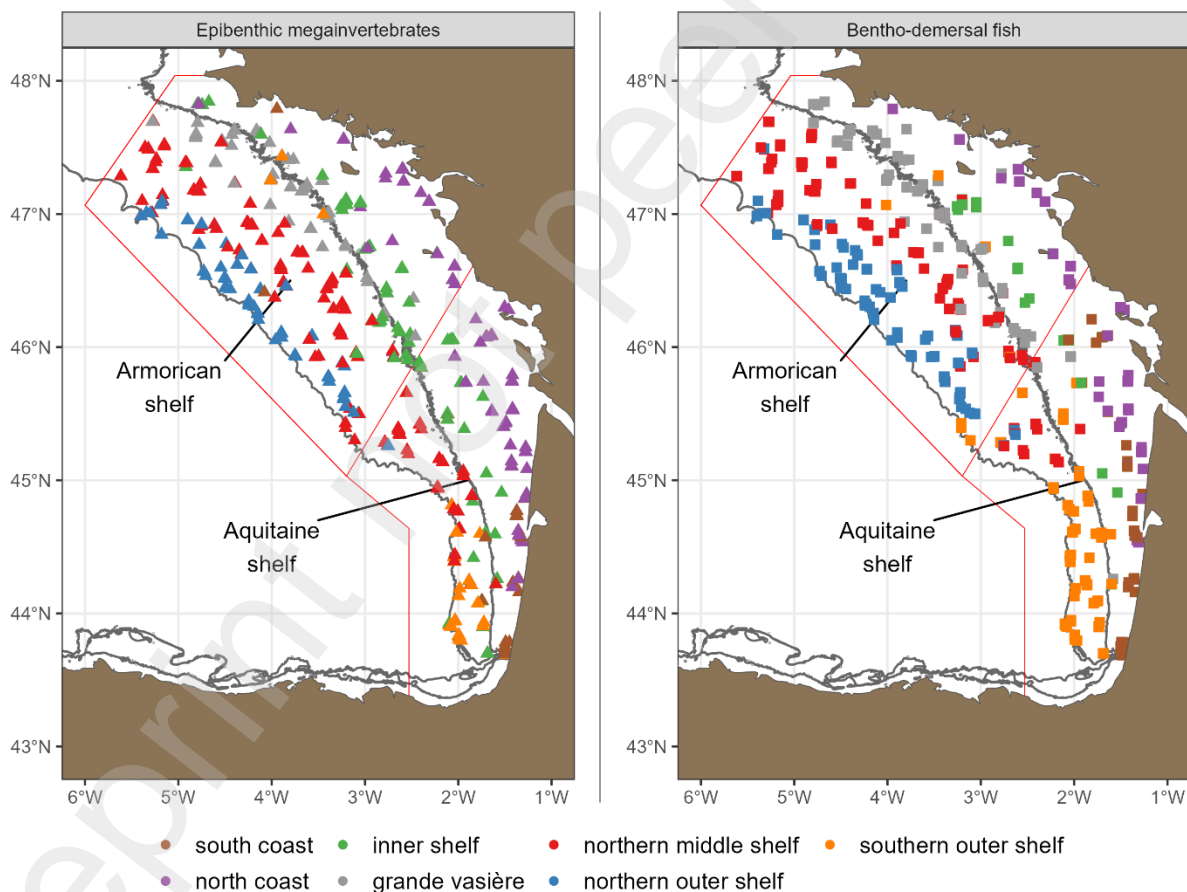


Figure 2. Clustering of megainvertebrates and benthic-demersal fish. Each color represents one cluster. Triangular points represent invertebrate samples; square points represent fish.

273 The north coast cluster was mostly located in shallow depths (median depth of 32 m for
274 benthos and 26 m for fish) and close to estuarine areas (Loire, Vilaine, and Gironde) on
275 the Armorican shelf and the northern part of the Aquitaine shelf (Figure 2). The south
276 coast cluster was found mainly in shallow waters in the southern portion of the Aquitaine
277 shelf at a median depth of 32 and 35 m for benthos and fish, respectively. Moving offshore,
278 the shallow north coast cluster was followed by the inner shelf cluster (median depth of
279 89 and 64 m for benthos and fish, respectively) and then by a cluster associated with the
280 Grande Vasière (median depth of 102 and 100 m, respectively, for benthos and fish), a
281 well-characterized muddy area that hosted distinct assemblages of both fish and benthos.
282 Further offshore, the southern outer shelf, located on the Aquitaine shelf, was also
283 characterized by unique assemblages of both benthos and fish (median depth of 146 and
284 127 m, respectively), as were the northern middle shelf (respective median depths of 128
285 and 123 m) and the northern outer shelf (respective median depths of 146 and 143 m).
286 The southern portion of the Aquitaine shelf appeared to be predominantly structured into
287 two clusters: the south coast and the southern outer shelf.

288 It was evident from this analysis that there are strong spatial convergences between the
289 benthos and fish communities. Indeed, in a comparison of the fish and benthos
290 components (Bray-Curtis dissimilarity matrices), we detected a significant overall
291 Spearman correlation of 68% (Mantel statistic R: 0.6763, $p < 0.001$, 10000 permutations).

292 **3.2 Description of the assemblages**

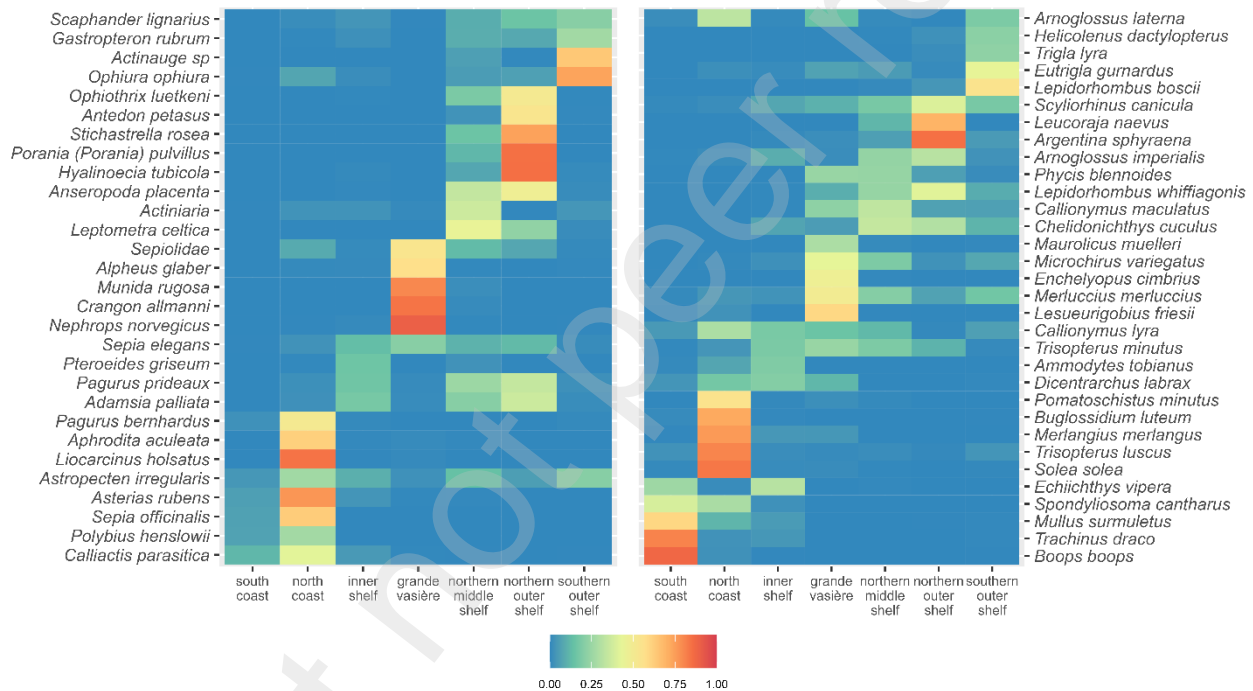
293 The main groups of benthos were Malacostraca (93 taxa), Gastropoda (45 taxa), Bivalvia
294 (37 taxa), Polychaeta (30 taxa), Anthozoa (26 taxa), Asteroidea (19 taxa), Echinoidea (17
295 taxa), Ophiuroidea (16 taxa), Cephalopoda (10 taxa), Holothuroidea (10 taxa), and
296 Ascidiacea (9 taxa).

297 We used an indicator species analysis (IndVal) to identify the most representative species
298 within each cluster (Figure 3). The north coast cluster was represented by coastal species
299 such as the hermit crab *Pagurus bernhardus*, the crab *Liocarcinus holsatus*, and the
300 polychaete *Aphrodita aculeata*. Although the south coast cluster shared many species
301 with the north coast, but was less faunistically typed with the sea anemone *Calliactis*
302 *parasitica* and the crab *Polybius henslowii* as the most characteristic species. Species in
303 the inner shelf cluster were less indicative than those of the other clusters; here, the
304 highest indicator values were assigned to the pennatulid *Pteroeides griseum*, the sea
305 anemone *Adamsia palliata* associated with the hermit crab *Pagurus prideaux*, but these
306 species were all also observed in several other clusters. The Grande Vasière cluster
307 appeared to be highly characterized by the presence of Norway lobster
308 (*Nephrops norvegicus*), the shrimp *Crangon allmanni*, and the squat lobster
309 *Munida rugosa*. Instead, the northern middle shelf was mostly defined by the deep-water
310 crinoid *Leptometra celtica*, and the northern outer shelf by the starfish *Porania* (*Porania*)
311 *pulvillus* and the polychaete *Hyalinoecia tubicola* (Figure 3). Finally, the southern outer
312 shelf cluster was characterized by the brittlestar *Ophiura ophiura* and the anemone
313 *Actinauge sp.*, even those these taxa were also shared with other clusters.

314 With respect to fish, the taxa represented were mainly Gadiformes (22 taxa), Perciformes
315 (20 taxa), Pleuronectiformes (18 taxa), Sparidae (12 taxa), Gobiiformes (11 taxa),
316 Rajiformes (8 taxa), Labridae (7 taxa), and Syngnathiformes (7 taxa).

317 Several species were identified in multiple clusters: the dogfish *Scyliorhinus canicula*, the
318 European hake (*Merluccius merluccius*), the red gurnard (*Chelidonichtys cuculus*), and
319 the thickback sole (*Microchirus variegatus*). The coastal, Grande Vasière, and outer shelf
320 clusters appeared to be more faunistically defined than the northern middle shelf or inner

321 shelf clusters, with more-characteristic species: the bogue (*Boops boops*), greater weever
 322 fish (*Trachinus draco*), and the striped red mullet (*Mullus surmuletus*) for the southern
 323 coast; the whiting (*Merlangius merlangus*) and the common sole (*Solea solea*) for the
 324 northern coast; the goby *Lesueurigobius friesii* for the Grande Vasière; the lesser silver
 325 smelt (*Argentina sphyraena*) and the ray *Leucoraja naevus* for the northern outer shelf;
 326 and the megrim *Lepidorhombus boscii* and two gurnards, *Eutrigla gurnardus* and
 327 *Trigla lyra*, for the southern outer shelf.



328
 329 **Figure 3. The five most indicative taxa of each of the seven clusters, as determined from**
 330 **indicator values (IndVal analysis). The warmer the color of the cell, the higher the**
 331 **indicator value (blue = low; red = high).**

332
 333 For both benthos and fish, the north coast clusters had on average the highest biomass
 334 and abundance (Figure 4, summarized values given in Appendix Tables A.2 and A.3) over
 335 the study period (2008–2020). Within this cluster, benthos had an average biomass of

336 249.75 kg/km² and an average abundance of 20.29 10³ ind.km⁻², and fish had an
337 average of 1302.27 kg/km² of biomass and an abundance of 20.27 10³ ind.km⁻².

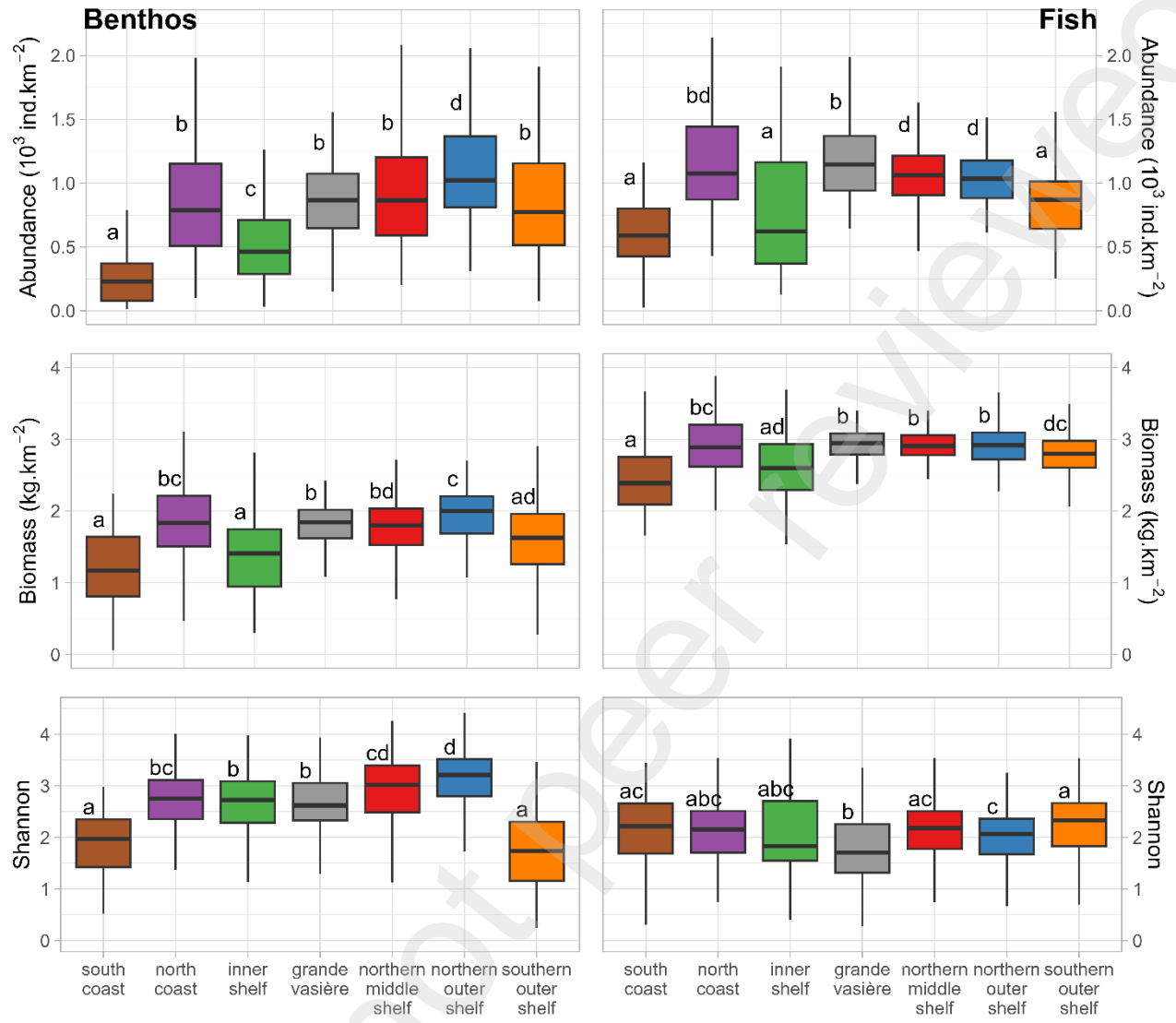
338 When considering the distribution of biomass from the coast to offshore areas, we
339 detected an increase in benthos biomass from the inner shelf to the northern outer shelf
340 cluster (47.06 kg/km² to 132.56 kg/km², respectively) (Figure 4). A similar pattern was
341 observed for abundance (ranges from 4.18 10³ ind.km⁻² to 17.41 10³ ind.km⁻²), with a
342 peak on the northern middle shelf (20.68 10³ ind.km⁻², Figure 4). The northern coastal,
343 middle, and outer shelf clusters of benthos had significantly higher biomass than the
344 others (pairwise Wilcoxon test). High values for biomass in the northern middle shelf
345 cluster were mainly due to the presence of *Leptometra celtica* and the octopus *Eledone*
346 *cirrrosa*, while biomass patterns in the northern outer shelf appeared to be strongly
347 influenced by the crab *Cancer pagurus* and the holothurian *Parastichopus regalis*.
348 Regarding diversity, values of Shannon's index were constant on the shelf and
349 significantly higher close to the shelf edge (northern outer shelf). Benthos diversity was
350 significantly higher in the northern clusters than in the southern clusters (south coast and
351 southern outer shelf).

352 For fish, the same global patterns in biomass and abundance were observed, but with
353 peak abundance occurring in the Grande Vasière cluster. On the inner shelf, average fish
354 biomass and abundance were 693.75 kg/km² and 11.17 10³ ind.km⁻², respectively.
355 These values increased in the direction of the northern outer shelf cluster, with the highest
356 values found for the Grande Vasière cluster (962.49 kg/km² and 22.86 10³ ind.km⁻²,
357 respectively). This cluster, along with the north coast cluster, had significantly higher fish
358 abundance than the others. The main species responsible for the high abundances and
359 biomass observed in these areas were the pouting (*Trisopterus luscus*) for the north coast

360 and the hake (*Merluccius merluccius*) for the Grande Vasière. Values of Shannon diversity
361 and Pielou's evenness were more stable across the shelf for fish than for benthos (Figure
362 4, and Appendix Tables A.2 and A.3), and larger-scale diversity patterns from coast-to-
363 offshore were less clear. However, we did observe that the Grande Vasière was home to
364 a significantly less diverse assemblage of fish than the outer shelf clusters.

365 For both benthos and fish, biomass and abundance were always significantly higher in
366 the Grande Vasière cluster than in the inner shelf cluster. However, the benthos in the
367 northern outer shelf cluster had significantly higher biomass and abundance than those in
368 the Grande Vasière cluster (Figure 4). Among all the clusters, patterns of biomass and
369 abundance were 56% and 60% correlated, respectively, between benthos and fish
370 communities.

371

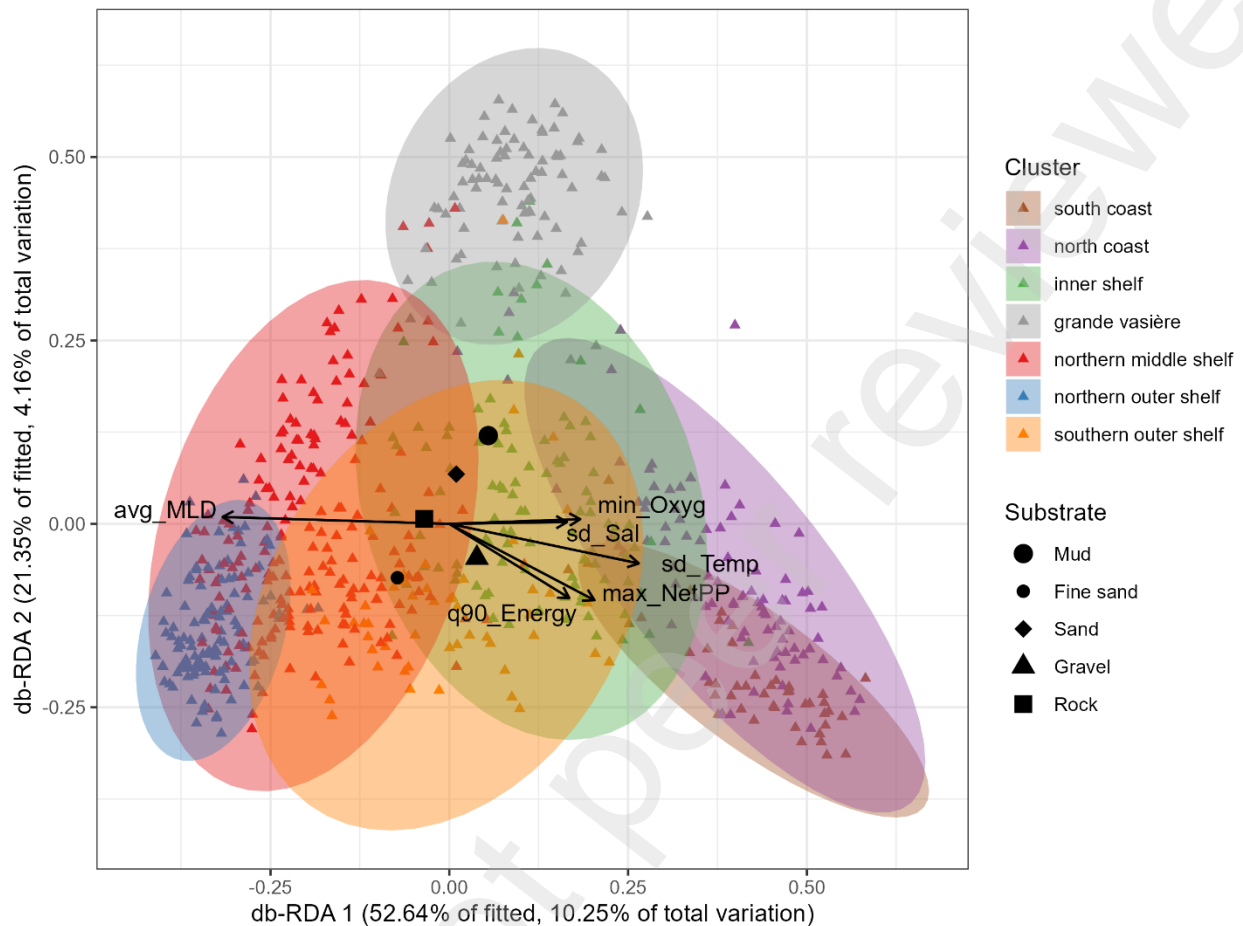


372

373 *Figure 4. Distribution of structural indices for each spatial cluster of benthos (left) and*
 374 *fish (right). Biomass (in kg.km^{-2}) and abundance (in thousands of individuals. km^{-2}) are*
 375 *log-transformed. Within each panel, boxplots with the same letters were not significantly*
 376 *different following a pairwise Wilcoxon test. For visual convenience, outliers are*
 377 *removed from the figure.*

378 **3.3 Role played by environmental forcings**

379 **3.3.1 Influence of environmental forcings on benthos**



380
381 *Figure 5. Distance-based redundancy analysis for benthos abundance at EVHOE*
382 *sampled stations. Ellipses represent the 95% confidence interval. Together with*
383 *substrate type, six environmental drivers were considered: annual average mixed layer*
384 *depth (avg_MLD), annual minimum dissolved oxygen at the seafloor (min_Oxyg), annual*
385 *standard deviation of sea surface salinity (sd_Sal), annual standard deviation of the*
386 *temperature at the seafloor (sd_Temp), annual maximum net primary production in the*
387 *water column (max_NetPP), and 90th percentile of average bottom kinetic energy*
388 *(q90_Energy).*

389
390 With respect to the benthos abundance data, the distance-based redundancy analysis
391 (db-RDA) explained 19.47% of the total variance. The first two axes of the analysis
392 explained 73.99% of the fitted variation and 14.41% of the total variation in benthos
393 clusters (Figure 5). The results highlighted a coast-to-offshore gradient, with a higher

394 range in seafloor temperature and net primary production in coastal areas. The southern
395 coast cluster had higher bottom energy than the north coast cluster, where bottom energy
396 was more variable. The Grande Vasière cluster, which featured the muddiest conditions
397 in the entire area, stood out from the others along axis 2. The inner shelf and southern
398 outer shelf were associated with the widest ellipses, which was likely a function of their
399 lower faunistic specificity (see above) and greater environmental variability. The inner
400 shelf cluster seemed to represent a transitional zone between the coastal and offshore
401 clusters, and did not appear to feature any clearly discriminating environmental
402 characteristics of its own. Offshore areas of the northern shelf were mainly characterized
403 by fine sand with a deep mixed layer, and low variation in bottom temperature. Finally, the
404 substrate of the northern middle shelf cluster was coarser than that of the northern outer
405 shelf.

406 Variance partitioning revealed that the seven environmental descriptors explained 18% of
407 the total variability (Appendix Figure A.5). The most influential factors were, in order:
408 mixed layer depth (average), substrate type, seafloor temperature (standard deviation),
409 maximum net primary production (average), and bottom energy (90th percentile). The
410 mixed layer was deeper, on average, for the northern middle and outer shelves than
411 southern ones, and for inner shelf clusters compared to coastal ones. Coastal clusters
412 were also distinguished from the others based on differences in seafloor bottom
413 temperature (standard deviation), maximum net primary production (average), and bottom
414 energy. Surface salinity (standard deviation) was higher only for the northern coast cluster,
415 reflecting the terrigenous influence in that location.

416 **3.3.2 Influences of environmental forcings on fish**



417
 418 *Figure 6. Distance-based redundancy analysis for fish abundance at EVHOE sampled*
 419 *stations. Ellipses represent the 95% confidence intervals. In addition to substrate type,*
 420 *six environmental drivers were considered: annual average mixed layer depth*
 421 *(avg_MLD), annual minimum dissolved oxygen at the seafloor (min_Oxyg), annual*
 422 *standard deviation of sea surface salinity (sd_Sal), annual standard deviation of the*
 423 *temperature at the seafloor (sd_Temp), annual maximum net primary production in the*
 424 *water column (max_NetPP), and 90th percentile of average bottom kinetic energy*
 425 *(q90_Energy).*

426
 427 For the fish abundance dataset, the redundancy analysis constrained 26.55% of the total
 428 variance. The first two axes explained 78% of the fitted variation and 20.7% of the total
 429 variance (Figure 6). Overall, redundancy analysis was able to explain more of the variation
 430 in fish distributions (26.55%) than it was for benthos (19.47%). As for benthos, the first
 431 axis corresponded to a bathymetric gradient. The north coast cluster was associated with
 432 an increasing range (standard deviation) of salinity, while the south coast cluster was

433 linked with stronger bottom energy. Instead, both coastal clusters were associated with
434 stronger net primary production. However, the overall separation of the coastal clusters
435 from the other assemblages was less clear for benthos than for fish. As observed for
436 benthos, the inner shelf cluster seemed to represent a transitional state between the
437 coastal and offshore clusters. Likewise, the northern middle shelf cluster (characterized
438 by a coarse substrate) was located in an intermediate position between the Grande
439 Vasière, the northern outer shelf, and the southern outer shelf (Figures 5 and 6). Variance
440 partitioning revealed that the seven variables explained 25% of the total variability
441 (Appendix Figure A.6). The forcings influencing fish clusters were mixed layer depth
442 (average), seafloor temperature (standard deviation), and maximum net primary
443 production (average). Compared to benthos communities, fish were less influenced by
444 substrate but more influenced by surface salinity variation (standard deviation).

445 To sum up, the coastal clusters corresponded to areas with a higher range of seafloor
446 temperatures and higher primary production. The south coast cluster was located in a
447 sandier and more energetic area than the north coast cluster. The cluster associated with
448 the Grande Vasière was in a muddy area with low bottom energy. The inner shelf
449 represented a transitional zone between the coastal and offshore areas, while the
450 northern middle shelf bridged the gap between the Grande Vasière and the northern outer
451 shelf.

452 With respect to substrate, that of the northern middle shelf was coarser than that of the
453 Grande Vasière and the northern outer shelf. The north and south outer shelf clusters
454 were distinguished from each other by substrate and mixed layer depth, which were finer
455 and deeper, respectively, for the northern shelf.

456 **4 DISCUSSION**

457 **4.1 Definition of assemblages as a tool for understanding the structure and** 458 **functioning of continental shelf ecosystems**

459 There is a pressing need for improved characterizations of the spatial structure and
460 functioning of marine environments (Pittman et al., 2021), especially in the context of
461 marine ecosystem quality assessment and management (Lavialle et al., 2023). The
462 present work—a meso-scale (10–100 km) study of the spatial distribution of epibenthic
463 megainvertebrates and benthic-demersal fish on a continental shelf—represents an
464 important step forward in this regard. In particular, it provides complementary perspectives
465 to the previously published EUNIS typology of the Bay of Biscay, which was mainly based
466 on macrofauna features (Bajjouk et al., 2015).

467 Our study identified seven clusters of epibenthic megainvertebrates and benthic-demersal
468 fish that were biologically coherent and spatially well-delineated and, thus, represented
469 distinct assemblages distributed within the larger study site. A limited number of
470 environmental forcings (e.g., hydrological features, estuarine influence, sediment type)
471 were identified as the main factors responsible for structuring the identified patterns within
472 each biological community (benthos or fish). Despite the biological differences between
473 benthic-demersal fish and epibenthic invertebrates, we found a high degree of similarity in
474 the spatial distribution of the different assemblages within the two communities
475 (correlation 68%), which exhibited similar coast-to-offshore patterns.

476 Any attempt to understand the ecosystem functioning of continental shelves based on the
477 definition of biological assemblages is likely to be influenced by the choice of methodology.
478 The spatial structures resulting from a given analysis can be highly dependent on the
479 sampling strategy and the nature of the data recorded (e.g., sampling gear, spatial

480 resolution, sampling period). In this case, the equipment used was more appropriate for
481 sampling benthic-demersal fish than benthic invertebrates. Because the sampling gear
482 poorly penetrates the soft bottom, only larger epibenthic organisms can be properly
483 sampled. In addition, although our study relies on data from several years (2008–2020),
484 sampling was conducted in only a single month of the year (October). However, the
485 absence of any clear seasonal fluctuation in epifaunal megabenthic communities in
486 comparable environments (e.g., Hinz et al., 2004) gave us confidence that the overall
487 structure described in our study was very likely stable over an annual scale. Moreover,
488 we checked that each of the identified clusters remained distinct from the others over the
489 12 years of our study, and detected no strong inter-annual variations in the observed
490 spatial distributions. This hypothesis was also supported by a recent report that spatial
491 patterns were stable and strongly dominant compared to temporal variations in shaping
492 the beta-diversity of benthic-demersal fish in the Bay of Biscay and the Celtic Sea (Eme
493 et al., 2022).

494

495 **4.2. Spatial distribution of assemblages and environmental drivers on the** 496 **continental shelf of the Bay of Biscay**

497 The spatial structures identified here followed a pattern of coast-to-offshore succession,
498 and were marked by a clear difference between the Armorican shelf in the north and the
499 Aquitaine shelf in the south.

500 The northern coast assemblages are situated in a shallow circalittoral area (around 30 m
501 deep) and are influenced by river (Loire and Gironde) plumes, as evident from their higher
502 variability in surface salinity in the canonical ordination. Communities of both fish and

503 invertebrates featured species that are characteristic of coastal muddy areas, such as the
504 crab *Liocarcinus holsatus* and the flatfish *Solea solea* (C. Koutsikopoulos et al., 1989).
505 With respect to coastal fish, the main indicator species observed in our study (e.g.,
506 *Pomatoschistus minutus* and *Merlangius merlangus*) were the same as those described
507 by Souissi et al. (2001). River plumes are a major structuring factor of the Bay of Biscay
508 as they are significant drivers of primary production (Lunven et al., 2005), leading to high
509 species abundance, biomass, and secondary production in coastal areas (Guillaud et al.,
510 2008; Saulnier et al., 2019). Along the northern coast of the Bay of Biscay, this terrestrial
511 influence is also retrieved in coastal macrofaunal assemblages (Dutertre et al., 2013).
512 Another explanation for the greater taxonomic diversity (Stein et al., 2014) observed in
513 this area could be the high number and variety of small-scale habitats utilized by
514 epibenthic communities (Vasquez et al., 2015).

515 Southern coastal assemblages are also located in shallow circalittoral areas (around 30
516 m deep). They do not benefit from the influence of plumes but are subjected to high-
517 velocity bottom currents, which is reflected in the mud-free nature of the substrate. Thus,
518 both currents and substrate type were found to have a significant structuring effect on the
519 fish and benthos assemblages in this region; as an example, the fish community was
520 characterized by the presence of species such as the lesser weever fish (*Echiichthys*
521 *vipera*), which is known to burrow in clear-sandy substrate (Wheeler, 1969). Similar
522 benthodemersal fish species were identified by Souissi et al. (2001) within this area in
523 October 1990. Such “sandy habitat” was observed by Lagardère (1973) and Monbet (1972)
524 for macrobenthos communities along the Aquitaine shelf, which were also structured
525 along a bathymetric gradient. Compared to the northern coast, the abundance and
526 biomass of both fish and benthos were 10 times lower in the south, possibly the result of

527 a lower nutrient supply due to a weaker river influence. To our knowledge, our study
528 represents the first large-scale study on epibenthic megainvertebrates (with the exception
529 of decapods) along the coast of the Bay of Biscay, and sheds new light on the benthic
530 communities of this area.

531 Further offshore, in the central part of the continental shelf, the inner shelf assemblages
532 appeared to represent a transitional zone between shallow and deeper areas. This area
533 was characterized by a high degree of environmental variability, which likely promoted the
534 development of assemblages composed of habitat generalists rather than specialists.

535 The north central area of the shelf—the Grande Vasière—hosted a unique assemblage of
536 benthos, which appeared to be associated with the characteristic muddy substrate of this
537 zone. Instead, the fish community of this area was less distinctive, probably reflecting the
538 fact that these assemblages are less dependent on substrate type (Appendix Figures A.5
539 and A.6). Among the species observed here were typical burrowers such as the
540 crustacean decapod *N. norvegicus* or the goby *L. friesii* (Ellis et al., 2013). The high
541 amounts of benthos and fish biomass we found were expected, as this area is of great
542 importance to the fishing industry; it benefits from high spring bloom production (Guillaud
543 et al., 2008) and high quantities of detrital matter (Le Loc'h et al., 2008).

544 Offshore on the Armorican shelf, the northern middle shelf hosted assemblages of fish
545 and benthos that were less well defined faunistically and environmentally than their
546 neighbors, and can therefore be viewed as transitional between the Grande Vasière and
547 the deeper areas near the shelf edge. Glémarec (1969) described this area as a barrier
548 with coarser substrate that limits the offshore extent of the Grande Vasière. As in the
549 present study, he identified sandy communities with high densities of *Leptometra celtica*

550 as observed also in our study, marking a transition between the “Grande Vasière” muds
551 and bathyal muds further offshore.

552 The northern outer shelf assemblages are located in the deep circalittoral area (around
553 145 m deep) and are characterized by a deep mixed layer. This layer is caused by the
554 presence of a frontal zone (K. Koutsikopoulos & Le Cann, 1996) where the interaction of
555 barotropic tide with the slope results in surface-water mixing (Simpson & Sharples, 2012).
556 This promotes the upwelling of cold, nutrient-rich waters from great depths and thus feeds
557 strong primary production (Sharples et al., 2009). The influence of this frontal structure
558 was previously observed in a study of zooplanktonic secondary production on the northern
559 shelf of the Bay of Biscay (Vandromme et al., 2014). In the context of our study, this
560 phenomenon would be more likely to affect the structural parameters (biomass,
561 abundance, and diversity) of invertebrate communities, and to a lesser extent those of the
562 benthic-demersal ichthyofauna. Indeed, here we found that, compared to the assemblages
563 further from edge, the outer shelf boasted significantly higher invertebrate biomass,
564 confirming previous observations by Le Loc’h (2004). This suggests that the unique
565 hydrodynamic processes in this area are a major driver structuring the shelf-edge
566 ecosystem from plankton to benthos.

567 Despite their proximity to the shelf break, the southern outer shelf assemblages differ from
568 the northern ones and do not benefit from the upwelling observed on the Armorican shelf
569 break (Koutsikopoulos and Le Cann, 1996). They are located in a deep circalittoral area
570 (around 135 m deep) and are less faunistically distinct than communities on the northern
571 outer shelf. Prior to our study, the only types of epibenthic megainvertebrates that had
572 been described in this area were the decapod crustaceans (Lagardère, 1973). Here, we
573 observed that the widespread brittle-star *Ophiura ophiura*, known to have no sediment

574 preference (Boos et al., 2010), was the most indicative species. For fish, the species with
575 the highest indicator value was the flatfish *Lepidorhombus boscii*, which was also
576 proposed to be indicative (as a 'secondary species') in this area 20 years earlier (Souissi
577 et al., 2001). No major determining environmental drivers were identified for either the fish
578 or benthos communities.

579 **4.3 Spatial structuration of meso-scale benthic ecosystems across European** 580 **continental shelves**

581 The main benthic features identified in our study can be found in other areas of the North
582 Atlantic European continental shelf system, and reflect certain common characteristics of
583 benthic ecosystem functioning. Although assemblages may differ in terms of faunal
584 composition, similar key species are found in comparable habitats in all European areas.
585 The convergence of spatial structures between the various ecosystem components—
586 mega- and macroinvertebrates and benthic-demersal fish—has also been widely reported,
587 and seems to originate from the effects of common driving factors.

588 Shallow coastal assemblages similar to the north coast assemblages of our study are
589 observed in the Celtic Sea, the English Channel, and the North Sea, which all feature
590 indicator species similar to those found in the shallower area of our study site, such as the
591 crustaceans *Pagurus bernhardus* and *Liocarcinus holsatus* (Ellis et al., 2013; Hinz et al.,
592 2004; Reiss et al., 2010) and the fish *Solea solea*, *Trisopterus luscus*, and *Merlangius*
593 *merlangus* (Vaz et al., 2007) or *Buglossidium luteum* (Reiss et al., 2010). The presence
594 and abundance of these species reflect terrigenous influences, specifically related to the
595 proximity of estuaries (Ruiz-Castillo et al., 2019; Vaz et al., 2007).

596 Along the Welsh coastline (Kaiser et al., 2004) or in the south of the North Sea (Ellis et
597 al., 2011), surveys have identified fish species with affinity for sandy substrate, such as
598 *Echiichthys vipera* (Reiss et al., 2010) which here was detected as an indicator species of
599 the south coast assemblage in the Bay of Biscay. As in the present study, assemblages
600 with this species on the Welsh coastline were also located in areas with high tidal
601 amplitude (Horrillo-Caraballo et al., 2021) and therefore high bottom energy.

602 Further offshore, previous studies of other European shelves have identified assemblages
603 that appear to be similar to the transitional ones we identified between shallow and deeper
604 areas of the Bay of Biscay. For example, Ellis et al. (2013) described a wide mid-shelf
605 invertebrate assemblage in the Celtic Sea featuring the polychaete *Hyalinoecia tubicola*
606 and the crab *Liocarcinus holsatus*. In the same area, Mérillet et al. (2019) reported a broad
607 mid-shelf fish assemblage with widespread species like *Trisopterus minutus*. These
608 widespread assemblages do not seem to be shaped by any clearly identified physical
609 processes and, given their faunistic composition, can be thought of instead as transitional
610 groups.

611 Assemblages typical of muddy areas corresponding to the Grande Vasière of our study
612 site also appear to be common along European shelves, for example in the North Sea
613 close to the English coast (Rees et al., 1999) and in the Celtic Sea offshore of the Bristol
614 Channel (Ellis et al., 2013; Rees et al., 1999). These mud-associated fauna seem to be
615 located in areas where strong primary production occurs in spring blooms (González-Gil
616 et al., 2022; Seguro et al., 2019).

617 Likewise, the outer shelf assemblages found in our study also have their equivalents on
618 other European shelves. Species that were found here to be representative of northern
619 outer shelf assemblages in the Bay of Biscay (e.g., *Lepidorhombus whiffiagonis*, *Ophiotrix*

620 *luetkeni*, or *Argentina sp.*) are commonly found along shelf edges in other European areas
621 like the Celtic Sea (Ellis et al., 2013; Mérillet et al., 2019). These areas are all under the
622 influence of shelf-break upwellings which are known to enhance local biological
623 production (Kossack et al., 2023). This influence can also extend to the more internal
624 assemblages of the continental shelf, for example through high densities of crinoids such
625 as *Leptometra sp.*, as found in deep areas of the Mediterranean shelf (Colloca et al., 2004).

626 **4.4 From spatial assemblages to “benthiscapes”: towards ecological** 627 **modeling and ecosystem-based management**

628 The correspondence of spatial distributions among different components of benthic
629 communities is a common feature of continental shelves. For example, in the Celtic Sea
630 similar spatial patterns were noted for assemblages of epifaunal invertebrates and fish
631 (Ellis et al., 2013; Mérillet et al., 2019). Farther to the north, the benthic communities of
632 the North Sea shelf were found to be structured into mesoscale assemblages comparable,
633 to some extent, to those in the Bay of Biscay, with a strong correlation between
634 communities of epifaunal invertebrates and demersal fish as well as infauna (Reiss et al.,
635 2010). Beyond the European shelves of the North Atlantic, close similarities in mesoscale
636 community structure have also been reported for demersal fish and epibenthic
637 invertebrates in the Mediterranean Sea, in the Gulf of Lions (Gaertner et al., 1999) and
638 along the Italian shelf break (Colloca et al., 2004). Even in regions with stronger
639 environmental gradients, such as the Barents Sea, communities of benthic invertebrates
640 and fish were strongly associated with each other, and co-varied with depth and the
641 ice/temperature gradient (Johannesen et al., 2017). This high degree of spatial similarity
642 between epifaunal invertebrates and fish does not necessarily imply direct interactions
643 (e.g., trophic linkages) between these ecological components. Instead, it may be the result

644 of the strong convergence of intense environmental drivers at the scale of continental
645 shelves that shape and structure different biological communities in similar ways.

646 The strong convergence of the spatial distributions of megainvertebrates and benthic
647 demersal fish in the Bay of Biscay provides evidence for the existence of different benthic
648 habitats characterized by different substrates and hydrological processes, as well as
649 shelf-scale environmental gradients (coast-to-offshore and south-to-north). We propose
650 defining these benthic habitats as “benthiscapes”. In our study, these habitats appear to
651 be consistent with the “hydrological landscapes” described by Planque et al. (2004), which
652 appear to structure both the benthic and the pelagic systems. In the pelagic domain, the
653 main factors shaping the spatial structure of biological communities are the influences of
654 freshwater, water column stratification, and bottom temperature (Petitgas et al., 2018),
655 similar to many of the processes highlighted in the present work. These commonalities
656 strengthen the “meta-ecosystem” vision of the continental shelf proposed by Petitgas et
657 al. (2018). The benthic system is also known to be strongly connected to water column
658 processes (Piepenburg et al., 1997), and the biological components of benthic
659 ecosystems are fundamental to the transfer of matter from the water column to sediments
660 (Zhang et al. 2021). These components are in turn fundamentally shaped by the physical
661 structure of continental shelves, particularly in terms of nutrient sources. Previous work
662 by Ruzicka et al. (2018) defined a few of the major physical processes structuring various
663 shelf ecosystems from the inner to the mid- and outer shelf. Similarly, the benthiscapes
664 identified in our study reflect spatially determined alterations in ecosystem functioning that
665 go beyond simple taxonomy-based structures. Here, these structural patterns have been
666 described very briefly in terms of differences in ecological parameters such as biomass
667 gradients. The spatial variability we observed raises the question of differences in trophic

668 functioning between the different benthiscapes, which is all the more important given the
669 correlations we observed (mostly with respect to abundance and biomass) between
670 communities of invertebrates and fish. Such patterns suggest that ecological functioning
671 varies spatially in the same way for both benthos and fish; further investigation of this
672 issue will improve our understanding of organic matter fluxes at the scale of the continental
673 shelf.

674 One application of the concept of benthiscapes—benthic habitats characterized by unique
675 ecological assemblages, distinct functions, and potentially differing responses to natural
676 and anthropogenic pressures—could be in the development and improvement of
677 strategies for ecosystem-based management. The definition of spatially coherent benthic
678 entities, based on this study and others, could assist in efforts to monitor seafloor
679 biodiversity and understand and manage anthropogenic perturbation at the scale of
680 continental shelves (e.g., Lauria et al., 2020). In this context, the benthiscapes described
681 in our study could therefore be considered as one of the fundamental structures to develop
682 tools for spatial planning. However, our knowledge of seafloor ecosystem functioning in
683 the Bay of Biscay remains incomplete (Galparsoro et al., 2014), and further studies are
684 needed to fill the gaps on the different biological communities of this area. The need is
685 especially pressing given the significance of the natural resources of the Bay of Biscay
686 (e.g., sand extraction, offshore wind farms, fishing for benthic and demersal species),
687 which are already heavily utilized and likely to be increasingly important in the future
688 (Boussarie et al., 2023; Lavialle et al., 2023).

689 **4 CONCLUSION**

690 This study investigated the overall spatial structure of ecological communities on the
691 continental shelf of the Bay of Biscay through the identification and characterization of
692 assemblages of epibenthic megainvertebrates and benthic-demersal fish. These
693 assemblages were faunistically similar to communities described on other European
694 continental shelves. The spatial delineation of biological communities into distinct
695 assemblages was highly similar between fish and invertebrates, suggesting that the
696 continental shelf ecosystem is made up of different spatial habitats that are predominantly
697 structured by environmental drivers such as bottom temperature, sediment type, bottom
698 energy, and primary production. Here, we propose the term “benthiscapes” for such
699 habitats.

700 The benthiscapes characterized in this study differed from each other with respect to
701 multiple structural parameters, particularly biomass, which was highest at the coast and
702 close to the continental slope. This suggests that the trophic functioning of this ecosystem
703 is dependent not only on terrestrial inputs from major rivers but also on the influence of
704 offshore upwelling.

705 The concept of benthiscapes could be particularly useful for applications in the areas of
706 ecosystem-based management and marine spatial planning. Further characterization of
707 these spatially distinct meso-scale entities could lead to an improved understanding of
708 continental shelf ecosystems and the essential ecosystem functions they provide.

709

710

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716

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1027

1028 **5. APPENDIX**

1029

1030 Table A.1: Summary of environmental variables analyzed

Variable name	Method of calculation	Time period averaged	Position in the water	References
Bottom energy	90th percentile	2010-2015	1 m from the seabed	(Accensi & Maisondieu, 2015; Caillaud et al., 2016)
Mixed layer depth	Mean	year-2; year- 1; year of sample	Surface of the water column	(EU-Copernicus, 2020b)
Dissolved oxygen	Minimum	year-2; year- 1; year of sample	Near-seafloor value	(EU-Copernicus, 2020a)
Net primary production	Mean	year-2; year- 1; year of sample	Depth where monthly maximum value was reached	(EU-Copernicus, 2020a)
Salinity	Standard deviation	year-2; year- 1; year of sample	Surface of water column	(EU-Copernicus, 2020b)
Seafloor temperature	Standard deviation	year-2; year- 1; year of sample	Seafloor	(EU-Copernicus, 2020b)

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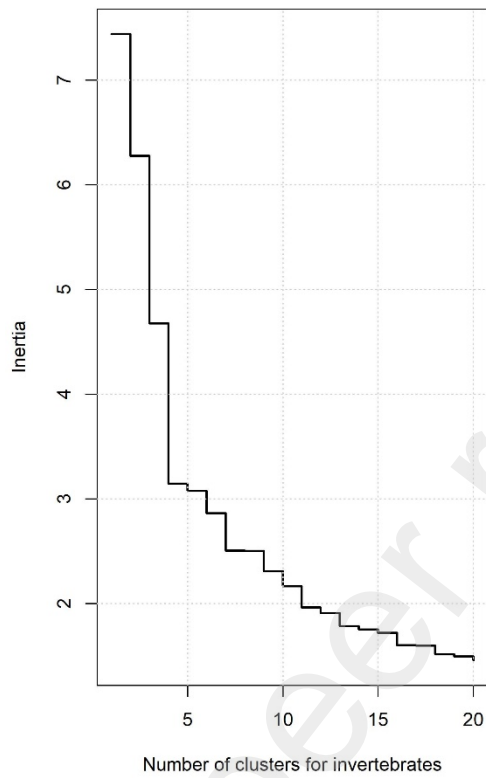
1041 Table A.2: Summary of structural indices for epibenthic megainvertebrate communities
 1042 (average (standard-deviation))

Index	South coast	North coast	Inner shelf	Grande Vasière	Northern middle shelf	Northern outer shelf	Southern outer shelf
Shannon's diversity	1.86 (0.8)	2.69 (0.6)	2.66 (0.65)	2.64 (0.54)	2.8 (0.91)	3.08 (0.67)	1.76 (0.85)
Pielou's evenness	0.72 (0.18)	0.64 (0.14)	0.7 (0.17)	0.62 (0.13)	0.61 (0.2)	0.65 (0.14)	0.46 (0.23)
Taxonomic richness	7.5 (3.71)	20.26 (8.21)	15.64 (6.47)	20.09 (4.86)	24.83 (6.5)	27.8 (5.73)	16.71 (7.11)
Abundance (ind.10³.km⁻²)	1.87 (4.45)	20.29 (52.5)	4.23 (5.9)	8.3 (7.11)	19.18 (41.64)	20.28 (34.49)	18.31 (34.04)
Biomass (kg.km⁻²)	54.36 (173.55)	249.75 (555.39)	43.81 (74.95)	78.15 (51.36)	91.75 (119.64)	132.14 (132.46)	96.82 (157.1)

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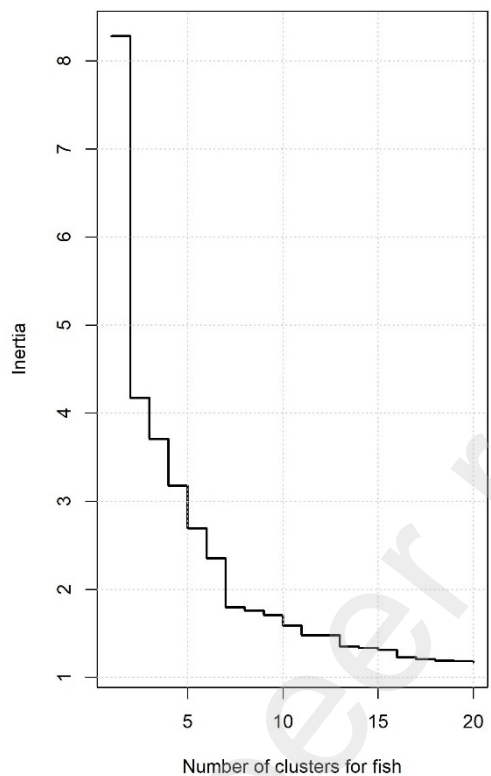
1044 Table A.3: Summary of structural indices for epi-bentho-demersal fish communities
 1045 (average (standard-deviation))

Index	South coast	North coast	Inner shelf	Grande Vasière	Northern middle shelf	Northern outer shelf	Southern outer shelf
Shannon's diversity	2.12 (0.67)	2.09 (0.61)	1.95 (0.84)	1.79 (0.69)	2.13 (0.6)	2.02 (0.54)	2.2 (0.66)
Pielou's evenness	0.6 (0.17)	0.5 (0.14)	0.52 (0.21)	0.43 (0.15)	0.51 (0.14)	0.52 (0.13)	0.56 (0.16)
Taxonomic richness	12.42 (4.41)	19.07 (4.6)	14.44 (4.8)	18.24 (3.67)	18.15 (2.99)	15.16 (3.14)	15.53 (3.53)
Abundance (ind.10³.km⁻²)	4.91 (5.88)	20.27 (23.28)	11.17 (16.91)	22.86 (29.76)	13.1 (9.68)	22.6 (136.18)	7.84 (6.58)
Biomass (kg.km⁻²)	480.1 (728.79)	1302.27 (1391.75)	693.75 (914.57)	962.49 (554.5)	945.35 (564.44)	1039.93 (832.23)	760.45 (555.91)



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Figure A.1: Dendrogram inertia for epibenthic megainvertebrates



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Figure A.2: Dendrogram inertia for benthodemersal fish

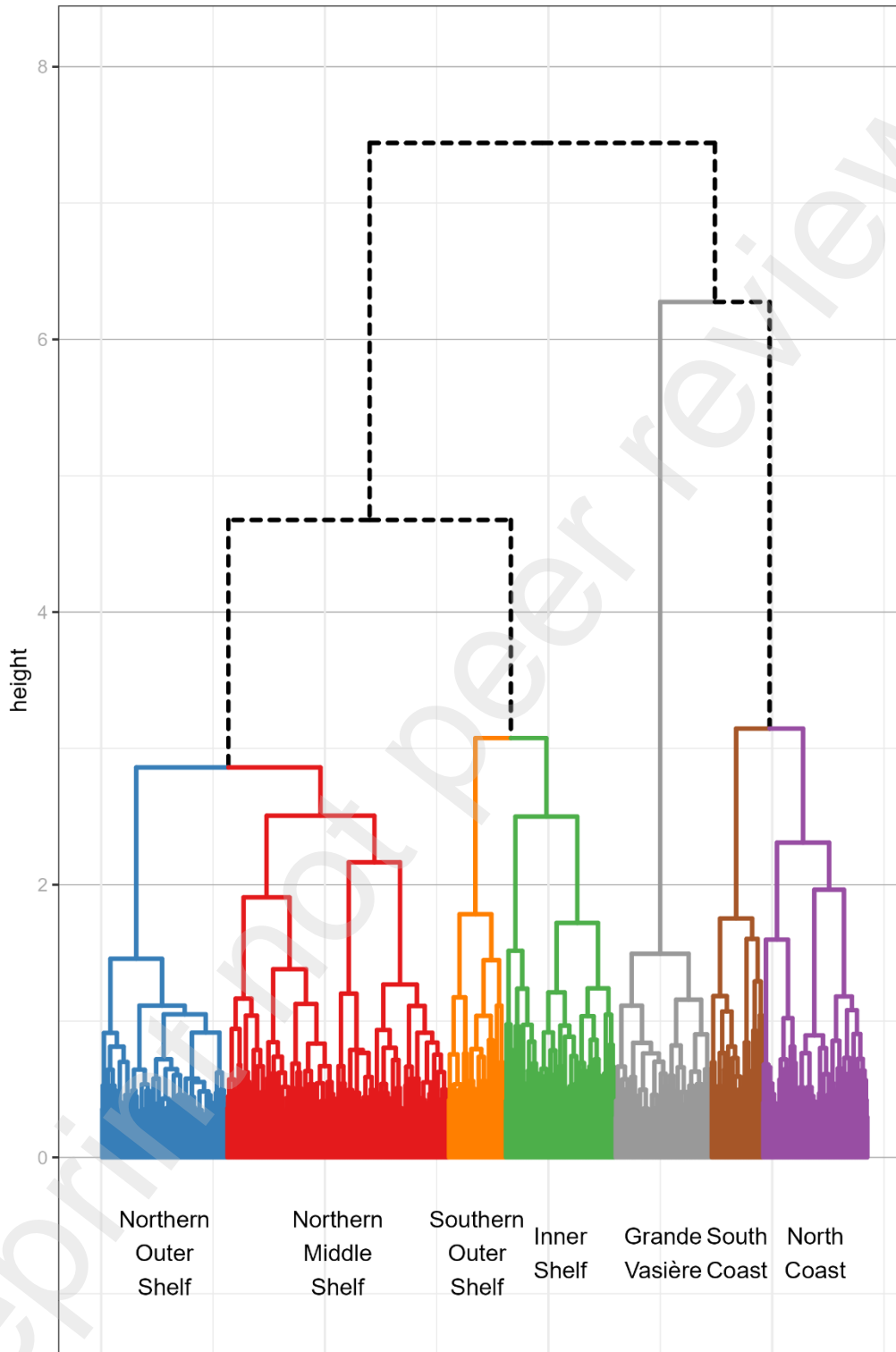
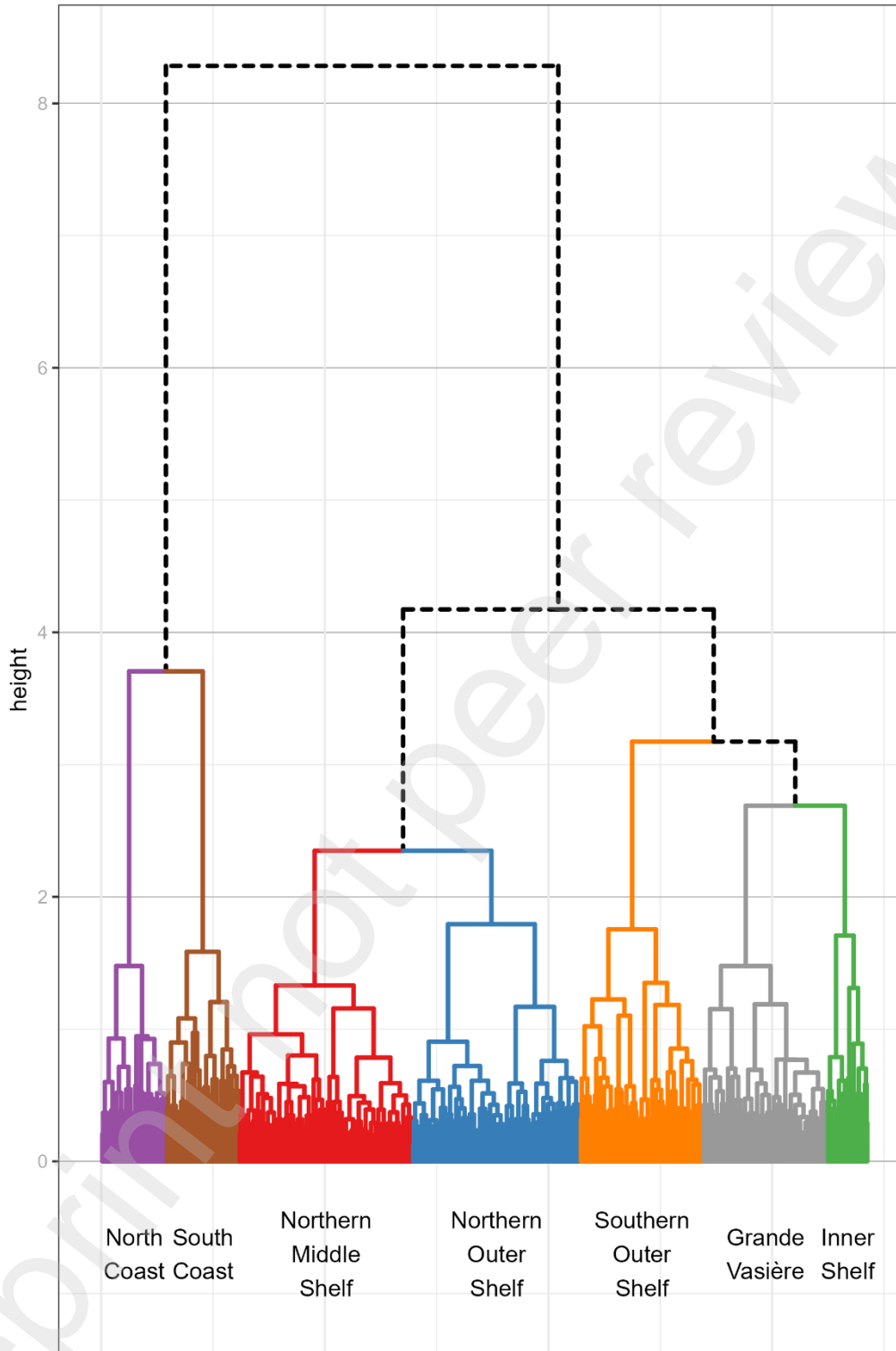


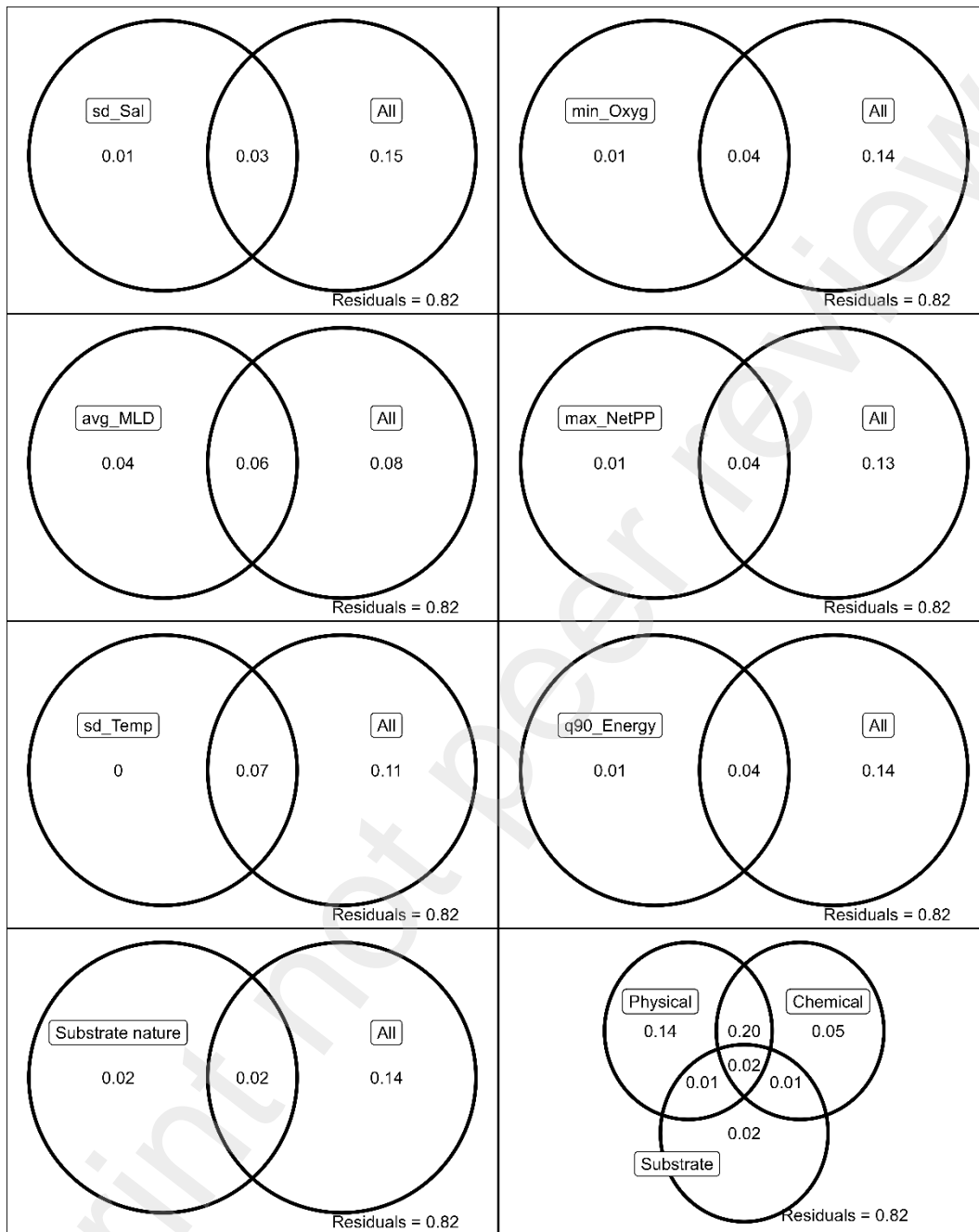
Figure A.3: Clustering dendrogram for epibenthic megainvertebrates



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Figure A.4: Clustering dendrogram for benthic-demersal fish



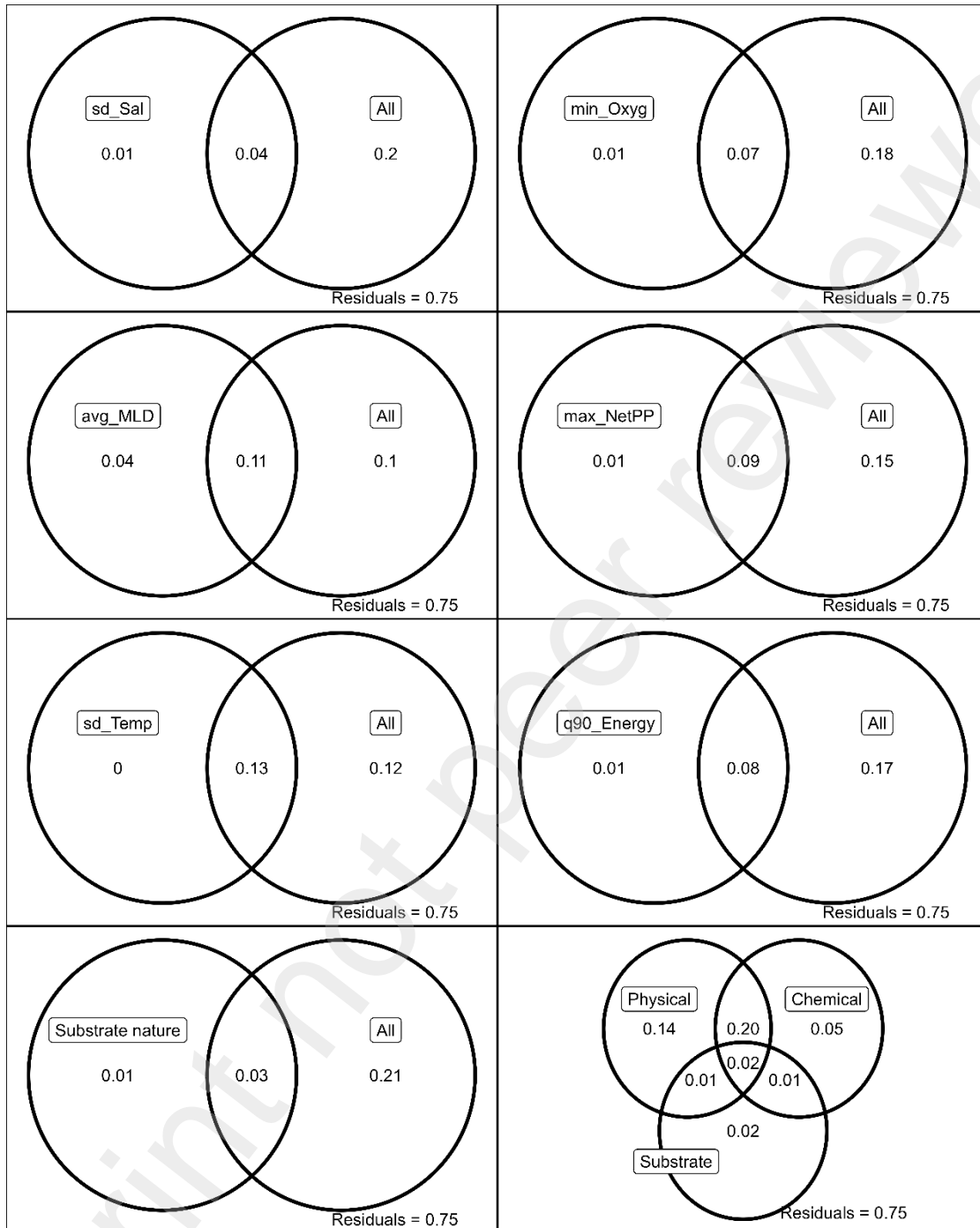
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Figure A.5: Variance partitioning of the effect of each force in shaping benthos communities. Physical forces are temperature, current, and mixed layer depth; chemical forces are oxygen, salinity, and net primary production.



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Figure A.6: Variance partitioning of the effect of each force in shaping fish community structure. Physical forces are temperature, current, and mixed layer depth; chemical forces are oxygen, salinity, and net primary production.