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## ► To cite this version:

Adeline Tauran, Julien Dubreuil, Benjamin Guyonnet, Jacques Grall. Impact of fishing gears and fishing intensities on maerl beds: An experimental approach. *Journal of Experimental Marine Biology and Ecology*, 2020, 533, pp.151472. 10.1016/j.jembe.2020.151472 . hal-03311942

**HAL Id: hal-03311942**

**<https://hal.science/hal-03311942>**

Submitted on 17 Oct 2022

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1 *Impact of fishing gears and fishing intensities on maerl beds: an*  
2 *experimental approach*

3

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## 17           **1. INTRODUCTION**

18           Maerl beds are formed by an aggregation of live and dead unattached and non-  
19           geniculated coralline algae, also called rhodoliths, which form highly complex three-  
20           dimensional biogenic habitats (BIOMAERL team, 1999; Foster et al., 2013). Considering  
21           their slow growth rate (~500  $\mu\text{m}/\text{year}$ ), maerl beds are regarded as non-renewable resources  
22           (Bosence and Wilson, 2003), although they can be long-lived when undisturbed. Indeed, some  
23           maerl beds in the Glenan archipelago (France) are estimated to be more than ~8000 years old  
24           (Birkett et al., 1998). The main factors affecting the presence of maerl appear to be light  
25           penetration together with hydrodynamic conditions. The latter must be sufficiently strong to  
26           maintain low turbidity and allow the maerl to photosynthesize while also preventing burial of  
27           the maerl under fine particle sedimentation (Grall, 2003). Maerl beds can be locally structured  
28           in ripple marks from exposure to these strong hydrodynamic conditions, but those from  
29           sheltered areas lack such features (personal observations).

30           These habitats are found worldwide, from the Arctic to the tropics. In Europe, they are  
31           especially present in the Mediterranean Sea and on the North-East Atlantic coast, particularly  
32           in Galicia, Brittany, Ireland, Scotland, and Norway (Foster, 2001). Maerl beds are highly  
33           ecologically important biogenic habitats with a complex three-dimensional structure involved  
34           in numerous ecosystem functions, such as habitat and shelter for many benthic species (some  
35           of them of economic value) and settlement and nursery areas for juveniles (Kamenos et al.,  
36           2004). As a result, maerl beds are considered to be bioengineers and have been viewed as  
37           “biodiversity hotspots” for supporting high faunal and floral biodiversity and serving essential  
38           ecological functions in coastal ecosystems (BIOMAERL team, 1999; Grall et al., 2006; Peña  
39           et al., 2014).

40           Considering their ecological value, maerl beds are under national, European, and  
41           international conservation legislation. At an international level, maerl beds are covered under

42 an “Action Plan for Coralligenous and other Calcareous Bio-Concretion” adopted during the  
43 COP15 from 2008 and as a part of the *Convention for the protection of the Mediterranean Sea*  
44 *against pollution* (UNEP-MAP, 2015). The OSPAR Convention is an agreement signed in  
45 1992 and ratified by 15 European governments aiming, within the OSPAR maritime area, to  
46 deal with the prevention and elimination of pollution, the assessment of the marine  
47 environment quality and the protection and conservation of ecosystems and their biological  
48 diversity (OSPAR Convention, 1998). The OSPAR maritime area covers the North-East  
49 Atlantic and parts of the Arctic ocean between 36°N to the North pole and from 44°W to 51°E  
50 (excluding the Baltic Sea and the area covering 44°W and 42°W to 36°N and 59°N)(Dinter,  
51 2001). In this area, maerl beds are coastal habitats occurring in open or semi-enclosed spaces  
52 at depths ranging from 0 to 51 m (Peña et al., 2014).

53 Maerl extraction was banned in France in 2012, and two of the main maerl-forming  
54 species *Phymatolithon calcareum* (Pallas) W.H.Adey & D.L.McKibbin ex Woelkerling &  
55 L.M.Irvine, 1986 and *Lithothamnion corallioides* (P.Crouan & H.Crouan) P.Crouan &  
56 H.Crouan, 1867 are now included in Annex V of the EC Habitats Directive (Council  
57 Directive 92/43/EEC). Maerl beds occur in half of the Breton Natura 2000 areas (Grall and  
58 Hall-Spencer, 2003) and cover up to 64% of their surface (CRPMEM de Bretagne, 2020). In  
59 addition, the main Breton maerl beds are in these protected areas.

60 Marine ecosystems – and more specifically benthic habitats – are increasingly  
61 threatened by human activities and anthropogenic factors (Glover and Smith, 2003; Halpern et  
62 al., 2007). Maerl beds are no exception because they are highly vulnerable to climate change  
63 and ocean acidification (Amado-Filho et al., 2012), eutrophication (BIOMAERL team, 1999),  
64 aquaculture and fish farms (Hall-Spencer et al., 2006), invasive species (such as the slipper  
65 limpet *Crepidula fornicata*) (Grall and Hall-Spencer, 2003), and the fishery industry.

66           The dredging activities associated with fishing have a well-documented negative  
67 impact on benthic ecosystems (de Groot, 1984; Dayton et al., 1995; Jennings and Kaiser,  
68 1998; Blanchard et al., 2004), including maerl bed habitats. The repercussions of bivalve  
69 dredging on maerl grounds have received considerable attention over the last decade, leading  
70 to a better understanding of the impact of mobile bottom-contacting gears on this fragile and  
71 unique habitat (Barberá et al., 2003, 2017; Kamenos et al., 2003). These studies showed that  
72 the principal effects of bivalve dredging on maerl grounds are burial of live maerl, changes in  
73 maerl structure and complexity, and reduced biodiversity and changes in the benthic  
74 community.

75           Although the results of these and other studies (Cabanellas-Reboredo et al., 2017;  
76 Coquereau et al., 2017) broadly illustrate how dredging affects maerl beds, they did not  
77 evaluate outcomes by intensity of dredging or type of dredge used, which depends on the  
78 targeted species. Here, we focus on the experimental assessment of specific gear types and the  
79 level of pressure applied to the habitat. Our aim was to distinguish how two fishing intensities  
80 and three dredge types (targeting clams, king scallops, and queen scallops) affect the habitat  
81 and macrofauna biodiversity of the maerl beds. For this work, we used an experimental  
82 Before – After – Control – Impact (BACI) design (Stewart-Oaten et al., 1986), which has  
83 been commonly applied for benthic community impact assessments of anthropogenic  
84 disturbances, including dredging (Currie and Parry, 1996; Guerra-García et al., 2003; Clarke  
85 et al., 2014). This design involves simultaneous sampling of two groups of stations (“control”  
86 and “impacted”) multiple times before and after an experimentally induced disturbance.

87           Based on current evidence, we tested the following hypotheses: (1) that dredging  
88 would lead to biodiversity loss that varies with pressure level and/or gear type; (2) that fishing  
89 pressure and gear type would affect habitat structure through reduced maerl complexity and

90 vitality; and (3) that dredging intensity would variably affect the one-year temporal evolution  
91 of this habitat, depending on the pressure levels.

92 This work was called for by the fishing industry as part of the DECIDER program  
93 (*Diagnostic of gear/habitat interaction: the dredge/maerl example*) and strongly supported by  
94 managers. Permission was granted by the *Armorique Regional Natural Park (Parc naturel*  
95 *régional d'Armorique, PNRA)*, which took part in the decision making regarding the location  
96 of the study area, which was within the Natura 2000 zone of the Bay of Brest.

97

## 98 2. METHODS

### 99 2.1. Study site

100 The Bay of Brest is a 180 km<sup>2</sup> semi-enclosed area located in Brittany, Western France.  
101 The bay is connected to the Atlantic Ocean and the Iroise Sea by a narrow strait (~2.5 km)  
102 and is under the influence of freshwater run-off from two main rivers (the Aulne and Elorn)  
103 draining a 2800 km<sup>2</sup> watershed (Le Pape and Menesguen, 1997). Approximately half of the  
104 surface of the bay is <5 m deep (Monbet and Bassoullet, 1989), which makes it a rather  
105 shallow bay. Maerl beds cover >30% of the bottom of the bay (Martin et al., 2005) and  
106 consist mainly of *Lithothamnion corallioides* and *Phymatolithon calcareum*.

107 The fishery industry in the Bay of Brest mainly focuses on three species: king scallops  
108 (*Pecten maximus*, Linnaeus 1758), queen scallops (*Mimachlamys varia*, Linnaeus 1758), and  
109 clams (*Venus verrucosa*, Linnaeus 1758). In recent years, 10–30 tonnes of queen scallops,  
110 150–300 tonnes of king scallops, and 100–150 tonnes of clams were fished in the bay all  
111 habitats considered (unpublished data from the Fishery Committee of Finistère (*Comités des*  
112 *Pêches du Finistère*)). The fishing fleet exploiting these species consists of about 35 fishing  
113 vessels of 11 m or less in length, with engines with a maximum power of 150 kW. Fishing  
114 occurs every year from October to March. For this study, we focused on a 0.164km<sup>2</sup> (~4000

115 m<sup>2</sup>) area in the eastern part of the bay, selected for the presence of an unfished homogeneous  
116 maerl bed.

117

## 118 2.2. *Experimental dredging*

119 Eight 25×200m zones (three controls and five impacted) were delimited to test the  
120 impact of (1) three different dredges commonly used for bivalve dredging in the Bay of Brest  
121 and (2) different fishing intensities on the maerl habitat (Figure 1). Features of the dredges  
122 were as follows: (1) a clam dredge (CD), 70 to 90 kg, 1.5 m wide, 40 teeth of 11 cm each; (2)  
123 a queen scallop dredge (QSD), 120 kg, 1.8 m wide, with a blade; and (3) a king scallop  
124 dredge (KSD), 190 kg, 1.8 m wide, 18 teeth of 10 cm each every 9 cm (Figure 2). Penetration  
125 into the substratum was estimated for each gear based on diver observation, as follows: ~5 cm  
126 for the KSD, ~10 cm for the QSD, and ~15 cm for the CD (clams are difficult to access).  
127 Pressure levels were measured as the number of dredge tows performed on the zone during  
128 the experimental dredging session, i.e., 0, 10, or 30 dredge tows. These levels of pressure can  
129 be expressed as the number of times a zone was totally dredged by considering the width of  
130 the zones and of each gear. With these factors, the zone would be totally dredged 0.6 times for  
131 the CD\_10 treatment, 0.72 times for the QSD\_10 and KSD\_10 treatments, 1.8 times for the  
132 CD\_30 treatment, and 2.16 times for the QSD\_30 treatment. Each of the three dredges was  
133 tested with two levels of pressure, except for the KSD, which was tested only for the  
134 moderate pressure level because of funding limitations. The decision was made to conserve a  
135 third replicate of control instead of dedicating a zone to a KSD\_30 treatment for three  
136 reasons: (1) to allow for maximum spatial variability in the control areas; (2) of the three  
137 fisheries being compared, the king scallop fishery is not the main fishery on maerl beds; and  
138 (3) king scallops have large epibenthic shells that can be easily captured without a significant  
139 application of pressure.

140           The experimental pressures selected for this study are not equivalent to the most  
141 extreme fishing intensities recorded (~60 dredge tows) (Bernard et al., 2019; Pantalos, 2015)  
142 but still offer a good representation of the situation in the Bay of Brest. Indeed, fishing  
143 intensities recorded in 50 m<sup>2</sup> cells on a nearby maerl bed for the 2015–2016 fishing season  
144 showed a maximum of one cell being totally dredge 2.15 times in the span of 6 months  
145 (unpublished data from the *IMPECAPE* program). Reproducing these levels of fishing  
146 intensity would require recapitulating a ~60 dredge tows using a 1.8m wide dredge on a 50m<sup>2</sup>  
147 cell. In comparison, the highest level of pressure selected in this study (30 dredge tows using  
148 a 1.8m wide dredge) would correspond to a 50 m<sup>2</sup> cell being totally dredged 1.08 times.

149

### 150 *2.3. Sampling protocol*

151           Samples were collected on four occasions from April 2016 to April 2017. The study  
152 area was monitored for a year according to the BACI approach: session 1 was sampled on  
153 April 15, 2016 (T<sub>0</sub>), just before dredging; session 2 on April 27, 2016 (T<sub>0</sub> + 1 week); session 3  
154 on May 25, 2016 (T<sub>0</sub> + 1 month), and session 4 on April 6, 2017 (T<sub>0</sub> + 12 months).

155           In this study, 24 stations (3 stations randomly located for each of the 8 zones with 3  
156 replicates per station) were sampled each session with a Smith grab (0.1 m<sup>2</sup>) to study the  
157 macrofauna population (Figure 3). For each station, three replicates were sampled a few  
158 meters apart, but their position is not displayed in Figure 3 for clarity and readability  
159 purposes. In addition, 15 normalized 0.1 m<sup>2</sup> quadrats (1.5 m<sup>2</sup> total) were randomly selected  
160 and photographed in each zone and for each session (480 quadrats total) by professional scuba  
161 divers for investigation of how dredging affected habitat (Figure 4).

162

### 163 *2.4. Characterization of the benthic community and the maerl habitat*

164           Regarding the macrofauna community, each replicate was rinsed thoroughly in the  
165 laboratory using a 1mm mesh sieve to eliminate the formaldehyde used for preservation. All  
166 samples were sorted and the organisms isolated in 70% alcohol until identification at the  
167 lowest taxonomic level possible using a binocular and/or a microscope.

168           The quadrats were analyzed using geographic information system (GIS) software  
169 (ArcGis 10.3). Using a grid in which each cell was 0.33 cm<sup>2</sup>, the surface occupied by maerl  
170 (live, dead, and broken), algae, sediment (mud), fauna, or “other” (eggs, dead shell) was  
171 digitally measured (for more details, see TBM Environnement, (2017)). All visible complex  
172 aggregations of pink/purple maerl were characterized as living maerl, pink/purple small maerl  
173 fragments on sediment (mud) or other maerl fragments were characterized as broken maerl,  
174 and all white/orange maerl fragments were characterized as dead maerl.

175

## 176 *2.5. Statistical analysis*

177           The effects of experimental dredging on the species richness and density of individuals  
178 were tested using R<sup>®</sup> software (R Core Team, 2019). One-way analyses of variance  
179 (ANOVAs) were performed when the ANOVA assumptions (normality of residuals and  
180 homogeneity of variance) were verified. Otherwise, non-parametric Kruskal–Wallis tests were  
181 used. When a significant effect was identified ( $p < 0.05$ ), Tukey’s post-hoc test (ANOVA) or  
182 the post-hoc Nemenyi test (Kruskal–Wallis) were used to characterize the differences. In  
183 addition, two-sample Wilcoxon Mann–Whitney tests were used on arcsine-transformed  
184 percentages of cover from the quadrats data. To assess the impact of dredging on the  
185 macrofauna population spatially (among the different zones) and temporally (among the  
186 different sessions), we performed non-metric multidimensional scaling (nMDS) on the non-  
187 standardized, log-transformed mean abundance data, using the Bray–Curtis similarity (Clarke,  
188 1993). For comparing the observed species richness to the real diversity calculated by the

189 estimator, we computed the nonparametric diversity estimator Jackknife 2<sup>nd</sup> order (Jack2;  
190 1000 randomizations) using *EstimateS* version 9 (Colwell, 2013) for each dredge and pressure  
191 level tested and each session. Jack2 is reported to yield the best results for different benthic  
192 communities and as such to be the most suitable non-parametric diversity estimator when  
193 dealing with marine habitats (Canning-Clode et al., 2008). In addition, the number of  
194 singleton and unique species were computed using the same software. The computation of  
195 Jack2 and of the number of singletons allowed us to consider transient and highly dispersed  
196 species that in situ measurements do not encompass. These species have an important role in  
197 the functional richness of a habitat (Boyé et al., 2019) and also rely on maerl beds, so their  
198 inclusion was expected to yield a better estimation of the actual diversity of the study area.

199         To distinguish the initial impact ( $t = 0$ ) of the three dredges on the benthic community  
200 and the rate of habitat recovery following such perturbations, we applied a previously  
201 described method (Sciberras et al., 2018). We used the unadjusted log response ratio ( $\ln(\text{RR})$ )  
202 because the different intensities of fishing were of interest. As specified, we used a weighted  
203 linear mixed-effects model with the *rma.uni* function in the *metaphor* R package  
204 (Viechtbauer, 2010) with a restricted maximum-likelihood estimator. Model selection was  
205 guided by small sample–corrected Akaike information criterion (AICc) because our sample  
206 size was small. The different models tested are listed in the supplementary material.

207         Replicate samples were used as replicates for all analyses except for the nMDS  
208 analysis, in which stations were used as replicates (as the mean of the samples) for the  
209 purposes of clarity. In the present study, the level of replication was different between the  
210 controls and the impacted zones. For this reason, we considered each control as an  
211 independent zone for the analysis and figures to illustrate the variability that can exist among  
212 unaffected zones from the same area.

213

## 214 3. RESULTS

### 215 3.1. Impact of experimental dredging on the habitat

216 To investigate the impact of dredging on habitat structure, 15 photographs of quadrats,  
217 per zone and per session (480 photographs total) were digitally analyzed using GIS (Figure 5).  
218 The results showed that during session 1, the live maerl was predominant in all zones and  
219 covered around 90% of the quadrats. Dead maerl, fauna, and mud in small percentages  
220 covered the remaining 10%. During session 2, mud covered around 20% of the surface at  
221 CD\_10 and KSD\_10 and >50% at CD\_30, QSD\_10, and QSD\_30. The percentage of mud  
222 cover significantly increased in all zones compared to CTRL1 ( $p \leq 0.02$ ), in all zones ( $p \leq$   
223  $0.01$ ) except CD\_10 compared to CTRL2 ( $p = 0.08$ ), and in all zones ( $p \leq 0.01$ ) except for  
224 KSD\_10 compared to CTRL3 ( $p = 0.16$ ) and CD\_10 compared to CTRL3 ( $p = 0.62$ ). The  
225 percentage of mud cover did not differ significantly between KSD\_10 and the other dredged  
226 zones ( $p > 0.05$ ) or among CD\_30, QSD\_10, and QSD\_30 ( $p > 0.05$ ). However, the  
227 percentage of mud cover significantly differed between CD\_10 and CD\_30 ( $p = 0.01$ ), CD\_10  
228 and QSD\_10 ( $p = 0.007$ ), and CD\_10 and QSD\_30 ( $p = 0.02$ ). In addition, the results showed  
229 a greater presence of broken maerl in the dredged zones (5%–15%) compared with very small  
230 percentages in the three controls (<1%).

231 During session 3, macroalgae covered from 28% to 76% of the surface in dredged  
232 zones and more than 80% in the three control zones. The surface area covered by algae was  
233 significantly higher in the three controls than the dredged zones ( $p \leq 0.05$ ), except for the  
234 comparison between KSD\_10 and CTRL3 ( $p = 0.26$ ), but this coverage did not differ  
235 significantly among CD\_10, CD\_30, QSD\_10, and QSD\_30 ( $p > 0.05$ ). Mud still covered an  
236 important portion of the surface during session 3 in CD\_10, CD\_30, and QSD\_30 (20%–  
237 33%). CD\_10 and CD\_30 significantly differed from KSD\_10 (both  $p = 0.02$ ) and QSD\_30 ( $p$   
238  $= 0.001$  and  $p = 0.003$ , respectively), and CD\_10 also differed from QSD\_10 ( $p = 0.02$ ).

239 Results from session 4 showed that living maerl predominantly covered the surface  
240 (from 60% to 95% of the surface) and mud and dead maerl were present in variable  
241 proportions, especially in CD\_30 (dead maerl = 26%). Mud was significantly more abundant  
242 in CD\_30 ( $p = 0.02$ ) and QSD\_30 ( $p = 0.03$ ) than in at least one of the three control zones and  
243 in CD\_30 compared to QSD\_30 ( $p = 0.004$ ). In addition, the results showed a significant loss  
244 in the cover of live maerl at CD\_30 and QSD\_30 between sessions 1 and 4 ( $p = 0.03$  and  $p =$   
245  $0.02$ , respectively).

246 The results shown in Figure 5B may seem redundant with those already described, but  
247 they attest to the important variability observed among photoquadrats taken in the same zone,  
248 during the same session. Their position in relation to the dredge track influenced the  
249 proportion of mud, maerl, and algae observed, factors that are important to consider when  
250 using photoquadrats. Indeed, the cover of live maerl appeared to be extremely variable among  
251 the 15 analyzed quadrats, except in the three controls and in CD\_10 and KSD\_10 during  
252 session 3, where the variability was rather small. In contrast, the surface covered by dead  
253 maerl appear to be similar between quadrats during sessions 1 and 2 but tended to increase  
254 during session 3. There was an important heterogeneity in all zones in the surface covered by  
255 mud during session 2 (except for the three controls). This high variability was still present  
256 during session 3 in CD\_10 and CD\_30 only. Finally, the surface covered by algae during  
257 session 3 appeared extremely variable among quadrats in all zones, except for the three  
258 controls and KSD\_10.

259

### 260 *3.2. Impact of the experimental dredging on the benthic community*

261 To investigate the impact of dredging on the benthic community, we performed  
262 several analyses, using an important dataset produced from 288 grab samples, with 238  
263 identified species and 101446 individuals counted (see supplementary material), including the

264 three target species in this study. Based on the general model ( $\ln(RR) \sim \log_2(t+1)$ ), dredging  
 265 (all gears and pressure combined) led to a significant reduction in benthic community  
 266 abundance at  $t = 0$  (mean response: -67%; 95% confidence interval [CI]: -73% to -53%;  $R^2 =$   
 267 42%) and species richness (mean response: -30%; 95% CI: -40% to -18%;  $R^2 = 10\%$ ).  
 268 Predicted recovery rates were estimated at ~8 years for benthic community abundance and  
 269 >100 years for species richness.

270 Based on AICc values, the optimal model (that with the lowest AICc value) for both  
 271 abundance and species richness was  $\ln(RR) \sim \text{gear} + \log_2(t+1)$ . The reduction in benthic  
 272 abundance was the most important for QSD (-70%; 95% CI: -81% to -52%), followed by CD  
 273 (-65%; -73% to -54%) and KSD (-58%; -74% to -32%). Time to recovery was estimated at  
 274 ~16 years for QSD, ~6 years for CD, and ~1.5 years for KSD. Regarding species richness, the  
 275 reduction was steepest for QSD (-35%; -49% to -15%), followed by KSD (-27%; -45% to -  
 276 4%) and CD (-26%; -36% to -12%). Time to recovery was estimated at ~17 years for CD, ~34  
 277 years for KSD, and ~900 years for QSD.

278 Figure 6 shows the significant effects of both gear characteristics and pressure levels  
 279 during the course of a year on species richness and density of individuals. No significant  
 280 differences were found regarding the species richness and density of individuals among the  
 281 three control zones for sessions 1 to 4. Species richness (Figure 6A) also did not differ  
 282 significantly between experimental zones during session 1 (ANOVA;  $p = 0.89$ ), whereas we  
 283 found a significant effect of dredging from sessions 2 to 4 (ANOVA; sessions 2 and 3:  $p <$   
 284  $0.001$ ; session 4:  $p < 0.002$ ). A significant decrease in species richness was visible during  
 285 session 2 compared to one or more controls at CD\_30 ( $p_{\text{CD}_30\text{-CTRL1}} < 0.001$ ;  $p_{\text{CD}_30\text{-CTRL2}} =$   
 286  $0.052$ ;  $p_{\text{CD}_30\text{-CTRL3}} = 0.02$ ), QSD\_10 ( $p_{\text{QSD}_10\text{-CTRL1}} = 0.029$ ), and QSD\_30 ( $p_{\text{QSD}_30\text{-CTRL1}} <$   
 287  $0.001$ ;  $p_{\text{QSD}_30\text{-CTRL2}} = 0.02$ ;  $p_{\text{QSD}_30\text{-CTRL3}} = 0.01$ ). During session 3, three zones experienced a  
 288 significant decrease in species richness compared to the three control zones (CD\_30,  $p < 0.05$ ;

289 QSD\_10,  $p < 0.01$ ; QSD\_30,  $p < 0.002$ ), but CD\_10 ( $p > 0.1$ ) and KSD\_10 ( $p > 0.1$ ) did not.

290 A significant reduction in species richness was still detectable during session 4 at CD\_30 ( $p$

291 CD\_30-CTRL1 = 0.0085), KSD\_10 ( $p_{\text{KSD}_10\text{-CTRL1}} = 0.004$ ;  $p_{\text{KSD}_10\text{-CTRL3}} = 0.04$ ), and QSD\_30 ( $p$

292 QSD\_30-CTRL1 = 0.001;  $p_{\text{QSD}_30\text{-CTRL3}} = 0.02$ ).

293 The density of individuals (Figure 6B) did not differ significantly among zones during

294 session 1 (ANOVA;  $p = 0.55$ ), but a significant effect of dredging was detectable from

295 sessions 2 to 4 (session 2 ANOVA,  $p < 0.001$ ; session 3 ANOVA,  $p < 0.001$ ; session 4

296 Kruskal–Wallis test,  $p = 0.0006$ ). During session 2, all zones underwent a significant decrease

297 in density of individuals compared to at least one of the three controls. The densities of

298 individuals at CTRL1 and CTRL3 were significantly higher than in almost all impacted zones

299 ( $p$  at least  $< 0.05$  for CTRL1 and all  $p \leq 0.002$  for CTRL3), with the exception of CTRL3

300 compared with CD\_10 ( $p = 0.18$ ). The density of individuals in CTRL2 differed significantly

301 from CD\_30 only ( $p = 0.04$ ). During session 3, almost all zones showed a significant decrease

302 in density of individuals (all  $p \leq 0.03$ ) compared with the three control zones; the exception

303 was CD\_10, which differed only from CTRL2 and CTRL3. During session 4, QSD\_30 still

304 had a lower density of individuals than CTRL1 ( $p = 0.003$ ), CTRL3 ( $p = 0.0015$ ), and

305 QSD\_10 ( $p = 0.009$ ).

306 Figure 7 shows the results from the computation of the nonparametric estimator Jack2

307 and the measure of the number of singletons and unique species for each session and each

308 zone. The estimated and observed species richness findings are shown in Figure 7A. The

309 results for each session show that the estimated species richness was always higher than the

310 observed diversity. During session 1, there was no particular pattern, and both the estimated

311 and observed species richness appeared to be similar among zones. During session 2, all of

312 the dredged zones showed a decrease in both estimated and observed species richness.

313 CTRL3 had similar results between sessions 1 and 2, whereas CTRL1 and CTRL2 had lower

314 levels of diversity between these two sessions. During session 3, almost all zones had a  
315 decrease in species richness, with the exception of CD\_30, where both the estimated and  
316 observed species richness increased. A clear pattern was visible for the observed species  
317 richness during session 3 among the three groups: (1) CTRL3 and CD\_30, (2) CTRL1,  
318 CTRL2, KSD\_10, and CD\_10, and (3) QSD\_10 and QSD\_30 had the lowest diversity.  
319 During session 4, the results were similar to those for session 1 but with a lower diversity.  
320 QSD\_10 and QSD\_30, which had the poorest diversity in session 3, showed an increase in  
321 diversity in session 4.

322         Regarding the number of singletons (Figure 7B), there was no evident pattern in  
323 session 1. CTRL3 had the highest number of singletons during session 2, followed by CTRL2  
324 and KSD\_10. CD\_30 had an important increase in singletons during session 3, whereas the  
325 three controls and KSD\_10 had a decrease. During session 4, QSD\_10 and QSD\_30 had an  
326 important increase in number of singletons, but the other zones remained stable.

327         The findings regarding the number of uniques in the samples (Figure 7C) were similar.  
328 There is no particular pattern during session 1. CTRL3 had an increase in the number of  
329 unique species during session 2 whereas CTRL1, CTRL2, and KSD\_10 showed stable results.  
330 The other zones showed decreasing curves during session 2, and CD\_30 had a larger number  
331 of unique species than the other zones during session 3.

332

### 333 *3.3. Temporal evolution of the habitat after the experimental dredging*

334         The results of the nMDS performed on the log-transformed mean abundance data (stress  
335 = 0.13) are shown in Figure 8. The different zones during session 1 are gathered on the  
336 ordination plot. For sessions 2 and 3, there was differentiation among zones, with the  
337 appearance of a pressure gradient effect in increasing order as follows: control zones (CTRL  
338 1, CTRL2, CTRL3), zones affected by 10 dredge tows (CD\_10, KSD\_10, QSD\_10), and

339 zones affected by 30 dredge tows (CD\_30, QSD\_30). In session 4, the position of the zones  
340 on the ordination plot still showed a clear separation from session 1. However, in the plot, the  
341 zones appear to be more closely gathered than during sessions 2 and 3, although the pressure  
342 gradient is still visible. In addition, the position of the objects on the ordination plot shows a  
343 different trajectory over time depending on the pressure levels, as indicated in the upper right  
344 corner of Figure 8.

345

#### 346 **4. DISCUSSION**

347         The objectives of this study were to use an experimental BACI approach to  
348 characterize the effects on maerl habitat and benthic community structure of two fishing  
349 intensities and three dredge types commonly used in the Bay of Brest for bivalve fisheries.

350

##### 351 *4.1. The BACI design*

352         The BACI design is one of many possible approaches to assessing environmental  
353 impact (Underwood, 1991). Underwood described how to implement a robust BACI sampling  
354 design to detect environmental changes, recommending the use of several control sites. In this  
355 way, our experimental design is consistent with Underwood's recommendations: we  
356 established three control sites, one in the middle of the study area and one each at the north  
357 and south extremities, thus allowing for consideration of spatial variability at the study site. In  
358 addition, we sampled these three control areas at each session to obtain temporal and spatial  
359 data from unaffected sites, as recommended by Green (1979). One could argue that sampling  
360 only one area per treatment (per fishing gear and intensity) was insufficient (Figure 1);  
361 however, we found clear differences in the temporal evolution of each zone (Figure 8), mostly  
362 based on fishing effort, which suggests that these results are valid even if replicate zones  
363 would have strengthened them.

364

## 365 4.2. Impact of dredging on the maerl habitat

366 We have illustrated the variability of the immediate impact of dredging on maerl beds,  
367 using an analysis of 288 grab samples and 480 *in situ* photographs of quadrats, sampled over a  
368 year from eight zones affected by three dredges and two fishing intensities. The consequences  
369 of dredging were visible starting from session 2 (one week after dredging) through the  
370 presence of broken maerl, an increase in mud-covered surface, and the loss of diversity  
371 (Figures 5–7). Broken maerl is visually distinguishable from unbroken maerl because the  
372 three-dimensional structure of the former is far less complex. The mechanical action of  
373 bottom-contacting gears (which are very destructive to such fragile habitats) fragment the  
374 maerl thalli into smaller pieces. Depending on the perturbation intensity, broken maerl can  
375 range from rectilinear to small round pieces with a heterogeneity similar to gravel (Kamenos  
376 et al., 2003), leading to reduced habitat complexity (Hall-Spencer et al., 2003; Bernard et al.,  
377 2019). Hall-Spencer and Moore (2000) reported that one immediate impact of dredging is  
378 increased suspended matter in the water column, reducing light availability and thus maerl  
379 photosynthesis. When these fine particles settle, they cover the maerl bed, fill its interstices,  
380 and limit light availability, thus reducing *Lithothamnion sp.* productivity by up to 70% (Riul  
381 et al., 2008). Our current observations are consistent with these previous findings, given that  
382 the significant differences between the control and dredged zones clearly link the surface  
383 covered by mud to dredging activities, with mud covering over 50% of the quadrats surface in  
384 the most damaged stations. We note, however, the quite high variability at each zone among  
385 the 15 photographed quadrats (Figure 5B), which precluded our using Kruskal–Wallis tests to  
386 evaluate the impact of dredging, despite previous observations (Figure 5A). Indeed,  
387 depending on the location of the quadrats regarding the dredge track, variable proportions of  
388 maerl (live, broken, or dead), mud, and algae could be observed (see Figure 4).

389 Severe impacts of dredging were recorded in terms of macrofauna diversity, with a  
390 significant decline in density and species richness observed during sessions 2 and 3 (Figures 6  
391 and 7). These results were expected because similar outcomes have already been reported  
392 previously. Kaiser and Spencer (1996) concluded that trawling was responsible for the  
393 disappearance of 50% of the species richness in their samples, a value slightly higher than our  
394 estimated reduction of 37% after dredging, but our results still confirm the severity of the  
395 impact. In addition, Bordehore et al. (2003) compared two maerl beds with different trawling  
396 histories in the Iberian Peninsula (one preserved from all dredging activities and one dredged  
397 for 25 years) and concluded that macrofauna species richness, biomass, and density of  
398 individuals at the control site were significantly higher than at the impacted site. This  
399 substantial body of evidence thus illustrates the impact of dredging on habitat structure  
400 through ecological diversity declines and suggests consequences for ecosystem functioning  
401 related to the nursery role of maerl beds for fishes and bivalves (Kamenos et al., 2004), effects  
402 on nutrient cycling (Martin et al., 2007; López-Acosta et al., 2018), and benthic primary  
403 production (Martin et al., 2005).

404 Our observations from session 3 may not be totally representative of the actual impact  
405 one month after dredging because of the seasonal development of macroalgae covering the  
406 maerl bed in abundance. This seasonal phenomenon is well known in this zone of the bay and  
407 appears to be linked to eutrophic conditions (personal observation). However, some  
408 interesting results emerged related to the percentages of surface covered by algae during  
409 session 3, which tended to decrease when the pressure level increased (Figure 5). The algae  
410 visible during season 3 were principally epiphytic macroalgae. Given these results, we  
411 hypothesize that the removal of maerl and the amount of surface covered by mud because of  
412 dredging prevented the algae from settling in a fixation spot, limiting their development. This  
413 effect would not only highlight the negative indirect impact of dredging on macroalgae but

414 also indicate an alteration in natural ecosystem functioning and the natural dynamics of  
415 species that were not even present when dredging occurred.

416         After a year, the impacts of experimental dredging were still visible in the diversity  
417 parameters from the grab samples, suggesting the long-lasting nature of these effects, as  
418 previously reported (Hall-Spencer and Moore, 2000), but they were not discernible on the  
419 quadrats. These authors noted no signs of recuperation in a previously unfished Scottish maerl  
420 bed, even 4 years after experimental dredging that had triggered a 70% decrease in the  
421 number of live thalli in core samples after 5 months. These results are more consistent with  
422 the literature than those from our study regarding the live maerl surface, especially  
423 considering the extremely slow growth rate of maerl-forming species, and indicate problems  
424 in our selected methodology. We do note that the previous study involved a thin (and thus  
425 vulnerable) layer of maerl, whereas the thickness of the maerl bed in our study area was  
426 estimated at ~5 m on muddy substratum (Berthois and Guilcher, 1959); thus, the thickness of  
427 the layer of live maerl can be expected to be important. In addition, external factors, such as  
428 storms, water currents, or wave actions, can be responsible for maerl movements (Harris et  
429 al., 1996). Session 3 occurred in May 2016 and session 4 in April 2017, and we cannot  
430 exclude potential live maerl movements from adjacent areas that might have led to  
431 overestimation of the live maerl surface one year after dredging. Considering the existing  
432 literature and the *in situ* observations (Figure 4), these movements appear to be the most  
433 logical explanation for these findings.

434         According to the literature, sand habitats require ~100 days to recover from a single  
435 dredging event, meaning that these habitats can withstand three fishing events per year before  
436 being in a “permanent(ly) altered state” (Collie et al., 2000). Considering our observations,  
437 the fragility and low resilience of maerl beds, and the results of Hall-Spencer and Moore  
438 (2000), it seems that maerl beds could reach a “permanently altered state” more rapidly than

439 sand habitats. Indeed, the estimated time needed to recover from the dredging session was ~8  
440 years for abundance and >100 years for species richness. Even though this latter value seems  
441 to be overestimated, it still highlights the low resilience of maerl beds. Commercially fished  
442 maerl beds in the Bay of Brest are dredged every 6 months, as the fishing season runs from  
443 October to March each year. Traces of our single dredging event were still visible after a year,  
444 meaning that the maerl beds had not returned to their initial state by the time a new fishing  
445 period began, suggesting that dredging commonly occurs on an already altered habitat. As a  
446 result, recovery of long-term dredged maerl beds seems very unlikely.

447

#### 448 *4.3. The importance of the gear characteristics and pressure level*

449 Although numerous studies based on the impact of dredging on maerl beds already  
450 exist, the objective of the present work was to characterize precisely the repercussions of  
451 different fishing gears and pressure levels on this particular habitat. We observed differences  
452 in the immediate impact of the three dredges and two pressure levels tested. For example,  
453 there was a significant difference in the percentage of mud during session 2 with use of the  
454 CD 10 or 30 times but no difference with use of the QSD. Moreover, the percentages covered  
455 by algae during session 3 differed between two groups of zones, the first one consisting of the  
456 three controls and KSD\_10 and the second consisting of the remaining dredged zones  
457 (CD\_10, CD\_30, QSD\_10, and QSD\_30). Significantly less surface was covered by algae in  
458 the second group, suggesting that dredge features, along with the pressure level, may  
459 negatively affect algae development, as hypothesized previously.

460 The most damaged zones in terms of the macrofauna diversity appeared to be CD\_30  
461 and QSD\_30, which showed significantly lower levels of diversity compared with one or  
462 more of the controls during session 4 (Figure 6). The absence of significant differences in  
463 species richness in CD\_10 and QSD\_10 compared with controls can be attributed to the

464 important number of singletons and unique species present in the samples, biasing the results  
465 and inducing an overestimation of the total number of species.

466         After a year, none of the zones had returned to their initial state (Figure 8).  
467 Observations prior to dredging (session 1) illustrated the natural variability of the maerl bed,  
468 whereas the different positions occupied by the three controls during session 1 and session 4  
469 are indicative of the natural evolution of the undisturbed habitat. A clear gradient primarily  
470 attributed to fishing intensity appeared in session 2 and was still visible a year after the  
471 experimental dredging (Figure 8). The dredged zones showed different trajectories depending  
472 on fishing intensity, but as noted, none had returned to their original state after a year,  
473 suggesting that fishing intensity affects the temporal evolution of maerl beds and that  
474 dredging has a lasting impact on the habitat. These results, coupled with those depicted in  
475 Figure 6, are consistent with the findings of Hiddink et al. (2006), who modeled recovery  
476 rates of biomass and production as a function of dredging intensity. In their study, for a single  
477 dredging event, recovery times in terms of macrofauna diversity were measured in years to  
478 reach initial biomass (1–41 years) and production (1–12 years) levels of the pristine maerl  
479 bed, suggesting that trawling intensity affects the long-term evolution of the habitat. Thus, the  
480 observed fishing intensity–based gradient we observed at one year after our single  
481 experimental dredging event is not unexpected.

482         Our results also echo those of Kaiser et al. (2000), who studied the effects of chronic  
483 fishing disturbances on benthic community structure in gravel and coarse sand sediments and  
484 reported that repeated dredging led to significant changes. In their study, the removal of large  
485 organisms led to a population dominated by smaller and more resilient organisms after such  
486 physical disturbances. They concluded that if a habitat is altered to such an extent that it  
487 significantly differs from its original state, it might become unsuitable for species relying on it  
488 for their development, including commercial species, leading to decreased exploitable stocks.

489 Overall, our findings indicate that the QSD was the most destructive gear among the  
490 three dredges tested because we observed no significant difference between the effects of a  
491 pressure level of 10 or 30 with this gear. Conversely, the clam dredge may be less destructive  
492 if used with a moderate intensity because we observed clear differences between CD\_10 and  
493 CD\_30 regarding the percentages of surface covered by mud, species richness, and density of  
494 individuals. The KSD used for 10 tows appeared to be the least damaging of the five  
495 combinations of dredges and fishing intensity we tested, as the habitat seemed to recover  
496 more rapidly than with the other two dredges (~1.5 years to reach the same level of abundance  
497 as before dredging compared to ~6 years for CD and ~16 years for QSD). However, we  
498 cannot conclude that the KSD did not affect the habitat because the results clearly show a  
499 significant reduction in the density of individuals compared to controls and an increase in  
500 mud surface one week after dredging. In addition, the estimated depletion of species richness  
501 was similar between KSD and CD, whereas the estimated time to recovery was longer for  
502 KSD (~34 years) than for CD (~17 years), highlighting a severe impact on the benthic  
503 community. Indeed, a relatively moderate pressure in a short time period can still be  
504 responsible for significant long-term impacts, especially on repetitively dredged beds, as  
505 highlighted in the Bay of Brest with the *IMPECAPE* research project (Bernard et al., 2019). If  
506 the fishing activity recurs, the KSD would be responsible for the same habitat alteration as the  
507 other two dredges we tested.

508 These findings are in agreement with previous work by Thrush and Dayton (2002),  
509 who reported that the physical impact of a fishing gear on a habitat depends on the gear's  
510 characteristics (e.g., mass) and the way it is used (e.g., the degree of contact with the sea-  
511 bottom, speed). In addition, MacDonald et al. (1996) reported that the severity of these effects  
512 will depend on the type of gear and how deeply it penetrates the sediment, the latter of which  
513 is directly linked to the gear's characteristics. Moreover, the differences between the QSD and

514 the KSD are interesting considering that scallop dredges are more destructive than otter or  
515 beam trawling (Foden et al., 2010). Our result implies that differences can exist between gears  
516 in the same category, depending on the targeted species. In comparison with the hydraulic  
517 dredge, which is currently considered one of the most destructive gears in bivalve fisheries,  
518 our results showed similarities with those of Hauton et al. (2003) (reduced live maerl cover,  
519 burial of maerl under fine particles, presence of broken maerl). Those authors estimated the  
520 penetration depth of their hydraulic dredge to  $\pm 10$  cm, which was similar to the penetration  
521 depth estimated for the QSD in our study ( $\sim 10$  cm). A reduction by  $\sim 67\%$  of the live maerl  
522 cover on photoquadrats after dredging with the hydraulic dredge compared to an average  
523 decrease of  $\sim 35\%$  in our study (by  $\sim 57\%$  with the QSD,  $\sim 27\%$  with CD\_10,  $\sim 61\%$  with  
524 CD\_30, and  $\sim 11\%$  with the KSD) suggests that hydraulic dredges are more destructive than  
525 the three dredges we tested.

526

#### 527 *4.4. Limitations and the possible improvements*

528 Experimental assessments of anthropogenic impacts such as dredging are commonly  
529 used because they allow researchers to work on data closely related to a disturbance and  
530 control factors such as intensity, time period, and gear employed (Lokkeborg, 2005). In this  
531 paper, the experimental design we chose was intended to allow for the comparison of impacts  
532 on the maerl habitat resulting from different dredges and pressure levels. The study zone was  
533 not ideally located because it was subject to a seasonal phenomenon of eutrophication,  
534 introducing a bias in the results. In addition, the eight zones delimited for this study were (1)  
535 located on a previously unfished maerl bed and (2) relatively small. As a result, the  
536 experimental observations do not entirely reflect the reality of a repeatedly dredged bed or  
537 large-scale and long-term effects of such disturbances on the habitat (Lokkeborg, 2005). As a  
538 matter of fact, a recent study based on a nearby maerl bed subject to annual commercial

539 dredging for bivalves showed far more severe consequences than those we report here  
540 (Bernard et al., 2019). Those authors differentiated three levels of pressure (control, moderate,  
541 and high) based on the intensity of dredging over the past 5 years, for which they studied  
542 different proxies of the maerl condition. The vitality of the maerl appeared to be strongly  
543 affected by dredging and tended toward zero at the most severely dredged stations. Their  
544 results, based on a maerl bed dredged for over 5 years, indicate the long-term effect of  
545 dredging on maerl vitality in a way that the present approach was not designed to highlight. In  
546 addition, they recorded a modification of the vertical structure of the maerl bed resulting from  
547 the fragmentation and compaction of the maerl thalli and the filling of interstices by fine  
548 particles. All of these consequences of dredging led to the destruction of suitable ecological  
549 niches for the benthic macro- and megafauna and to the deterioration of the habitat, thus  
550 diminishing its role in ecosystem functioning.

551         As we have described, however, the present experimental design followed the  
552 recommendations of Underwood (1991) and Green (1979), and thus presents reliable results  
553 regarding the immediate impact of dredging based on fishing intensity and gear features. A  
554 potential improvement in the design would be to include replicates for each impacted zone to  
555 consolidate the present observations. The estimation of time to recovery could also be  
556 improved because the estimates seemed to be surprisingly long (>100 years for abundance,  
557 ~900 years for species richness). It would also be of interest to apply this method in future  
558 assessment along with *in situ* data on fishing pressure and different fishing histories because  
559 the impact of dredging is greater on previously unfished maerl beds. However, we found it  
560 useful to distinguish the initial impact of the dredges tested and to classify their impact on the  
561 maerl benthic community.

562

563 *4.5. Implication for fishing activity management on maerl beds*

564           Because we did find differences in impacts among the QSD, KSD, and CD, we suggest  
565 that these parameters be considered when dealing with management measures, both for maerl  
566 conservation and for fishing regulation. To preserve habitat richness and complexity, the  
567 priority should be on areas with intermediate levels of alteration because the most severely  
568 altered beds are not expected to recover from such intense and repeated pressures. Thus, it  
569 appears that non-destructive activities such as hand-collecting bivalves by diving should be  
570 favored when aiming to ameliorate maerl bed exploitation.

571           The conservation of maerl beds through the creation of protected areas would, in the  
572 long run, allow for a higher rate of recruitment and the development of a more diverse  
573 community of species (including species targeted by bivalve fisheries) in terms of genetics  
574 and age range, making them more resistant to natural environmental changes (Roberts et al.,  
575 2005). Ultimately, this conservation would allow for higher stock levels of targeted species  
576 with mature organisms that could potentially (re)colonize less vulnerable adjacent habitats  
577 through spawning. The fisheries would benefit with this version of “insurance” against stock  
578 collapse by the creation of new fishable grounds (Hall-Spencer et al., 2003).

579

## 580 **5. CONCLUSION**

581           Our aim with this study was to add new information about the impact of dredging on  
582 maerl bed by characterizing this impact in terms of different dredges and dredging intensities  
583 using a BACI approach. Overall, the impacts recorded were consistent with the literature (loss  
584 of diversity, increased mud cover, destruction of maerl thalli). We could differentiate the  
585 immediate and one-year impacts of three different dredges and two levels of pressure. In this  
586 context, the high-pressure level appeared to be the main factor affecting maerl habitat,  
587 whereas under low fishing intensity, the extent of damage depended on the type of gear used.  
588 Impacts were still visible after one year whereas fishing occurs every 6 months in the Bay of

589 Brest, raising questions about the recovery capacities of this habitat under repetitive dredging  
590 activity. This issue is particularly important considering the severity of the impacts  
591 highlighted in a field study (non-experimental) in an adjacent maerl bed. This questions the  
592 advantages and drawbacks of the experimental approach *versus* real-life observations and  
593 their reliability in assisting in the development of fishing policies related to the maerl habitat.  
594

### 595 **Funding**

596 This work was supported by the Association du Grand Littoral Atlantique (AGLIA)  
597 and funded by France Filière Pêche, Région Bretagne, Région Pays de la Loire, and Région  
598 Nouvelle Aquitaine as part of the *DECIDER* program (*Diagnostic of gear/habitat interaction:  
599 the dredge/maerl example*).

600

### 601 **Acknowledgments**

602 The authors are grateful to two anonymous referees for their valuable comments and  
603 corrections on this manuscript. The authors wish to thank the crew of the fishing boat *CORTO*  
604 and Marion Maguer for their work during sampling, Erwan Amice and Thierry Le Bec for  
605 diving and providing photographs, and Olivier Gauthier for help with statistical analysis.

606

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791 **FIGURE CAPTIONS**

792

793 Figure 1: Location of the study area (A) in France and (B) in the eastern part of the Bay of  
794 Brest (Brittany, France) and (C) position of the eight zones delimited inside of the study area.  
795 Each zone was either left unaffected (control) or tested with different gears (clam dredge  
796 (CD), king scallop dredge (KSD), or queen scallop dredge (QSD)) and/or different fishing  
797 effort (i.e., number of dredge tows = 0, 10, or 30). The figure was created using QGIS 3.8.0  
798 software (QGIS Development Team, <http://qgis.osgeo.org>).

799

800 Figure 2: Photographs of the three gears used in this study: (A) the king scallop dredge  
801 (KSD), (B) the queen scallop dredge (QSD), and (C) the clam dredge (CD). Image credit:  
802 Fishery Committee of Finistère (*Comités des Pêches du Finistère*).

803

804 Figure 3: Location of the 24 stations (three stations randomly placed for each of the eight  
805 zones) sampled during the four sessions using a Smith grab (0.1 m<sup>2</sup>). For each station, three  
806 replicates were sampled a few meters apart (not displayed). The figure was created using  
807 QGIS 3.8.0 software (QGIS Development Team <http://qgis.osgeo.org>).

808

809 Figure 4: Variability of the maerl bed structure one month after experimental dredging. (A–C)  
810 Control zone. (B–D) Dredged zone. Image credit: Erwan Amice, CNRS - Laboratoire des  
811 sciences de l'Environnement MARin (LEMAR).

812

813 Figure 5: (A) Percentages of cover of maerl (live, dead, and broken), algae, sediment (mud),  
814 fauna, or “other” (eggs, dead shells) and (B) variability of the percentages of cover of the  
815 quadrats for each zone and for the four sessions. Percentages of cover were obtained by  
816 digital analysis of the quadrats.

817

818 Figure 6: Boxplot of (A) the species richness and (B) the density of individuals for the eight  
819 zones and for each session in the Bay of Brest. The horizontal line in the box represents the  
820 median, the box indicates the interquartile range, and the black dots indicate outliers.  
821 ANOVA or Kruskal–Wallis results are indicated ( $p$ ), and different letters indicate significant  
822 differences.

823

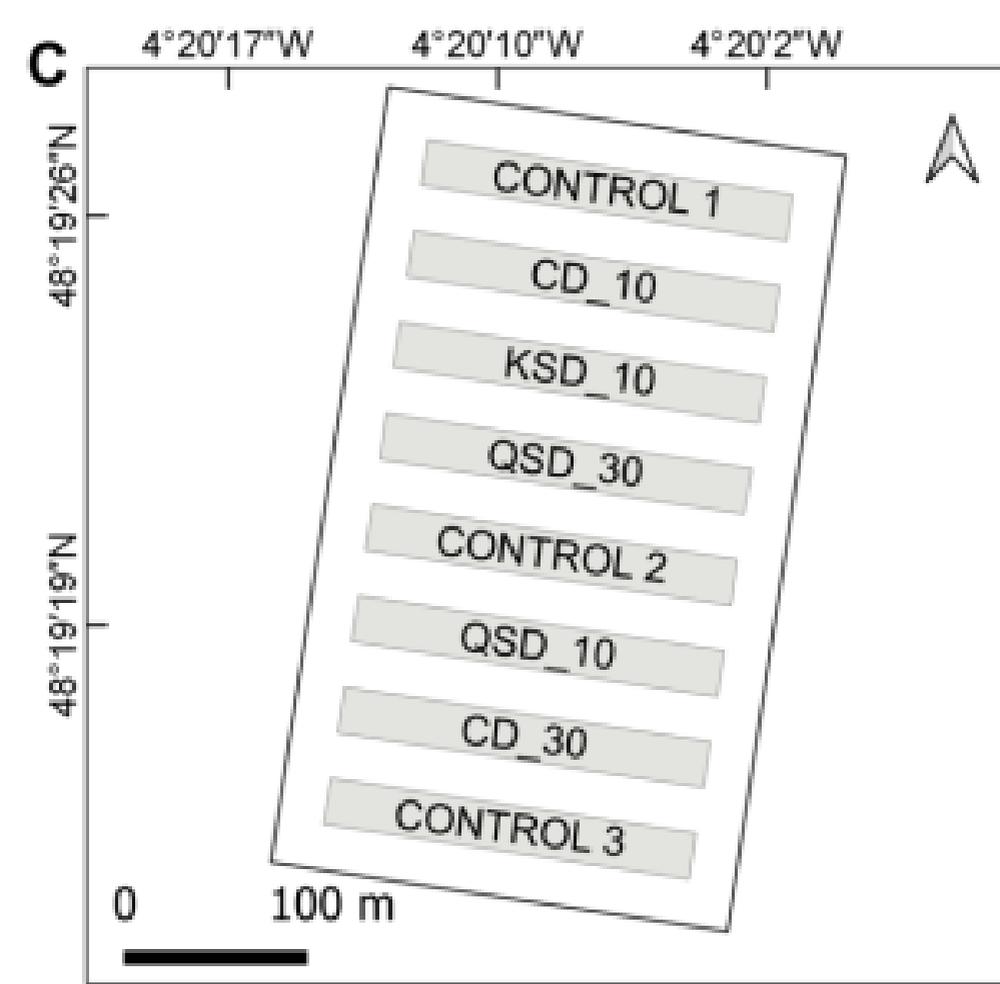
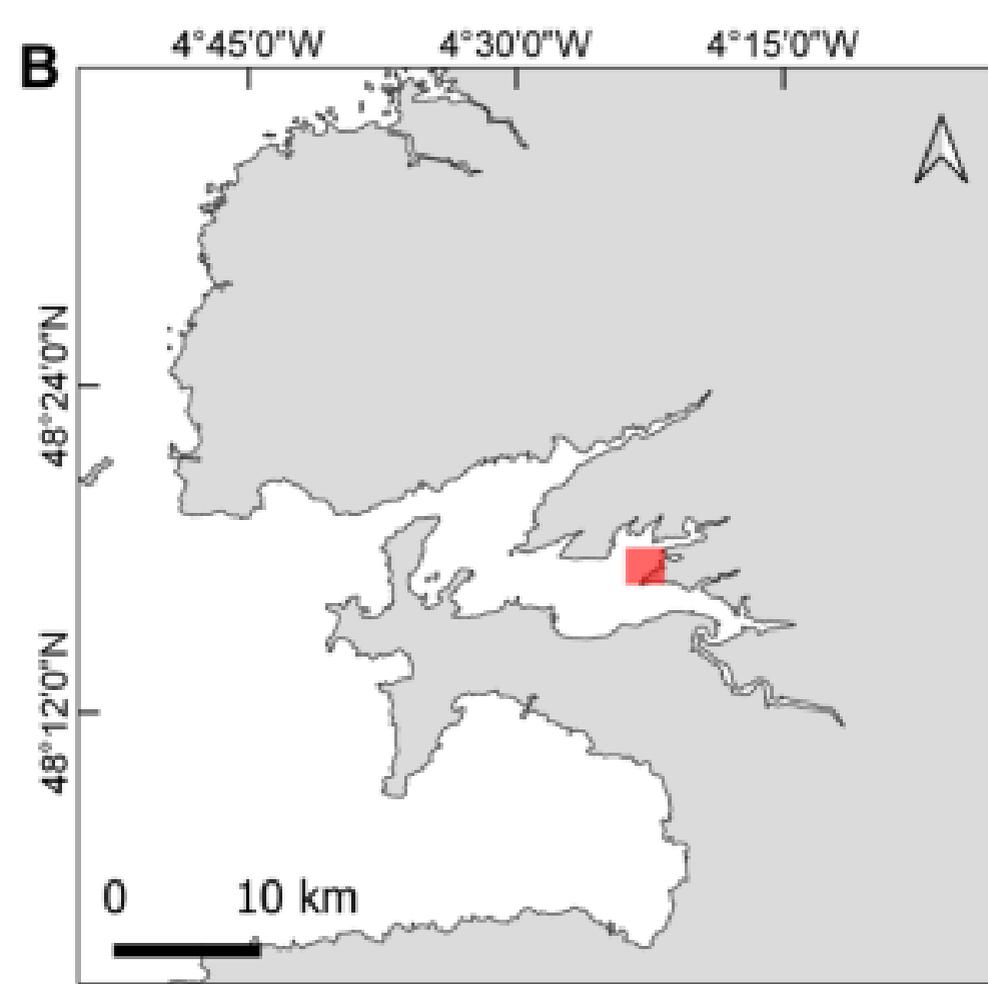
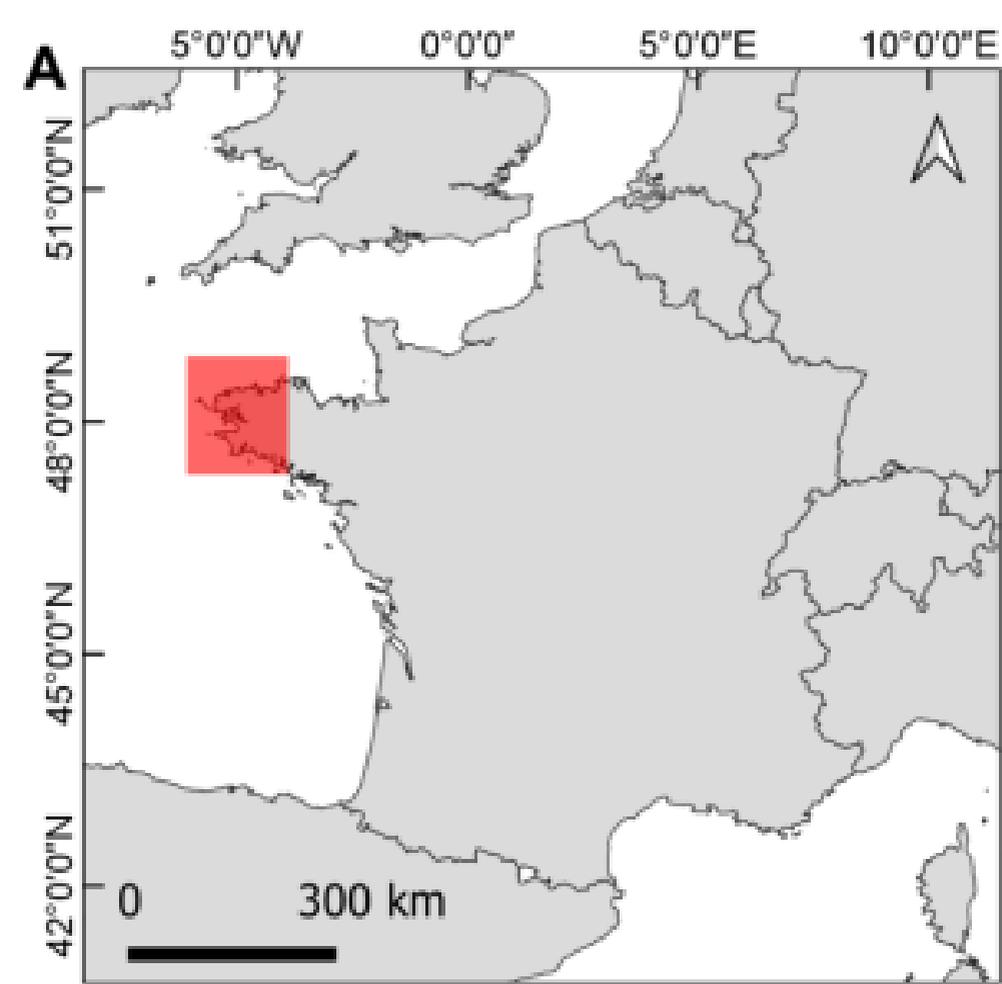
824 Figure 7: (A) Species richness observed (dashed lines) and estimated by Jack2 (solid lines);  
825 (B) number of singleton and (C) unique species measured for each zone and for each session.

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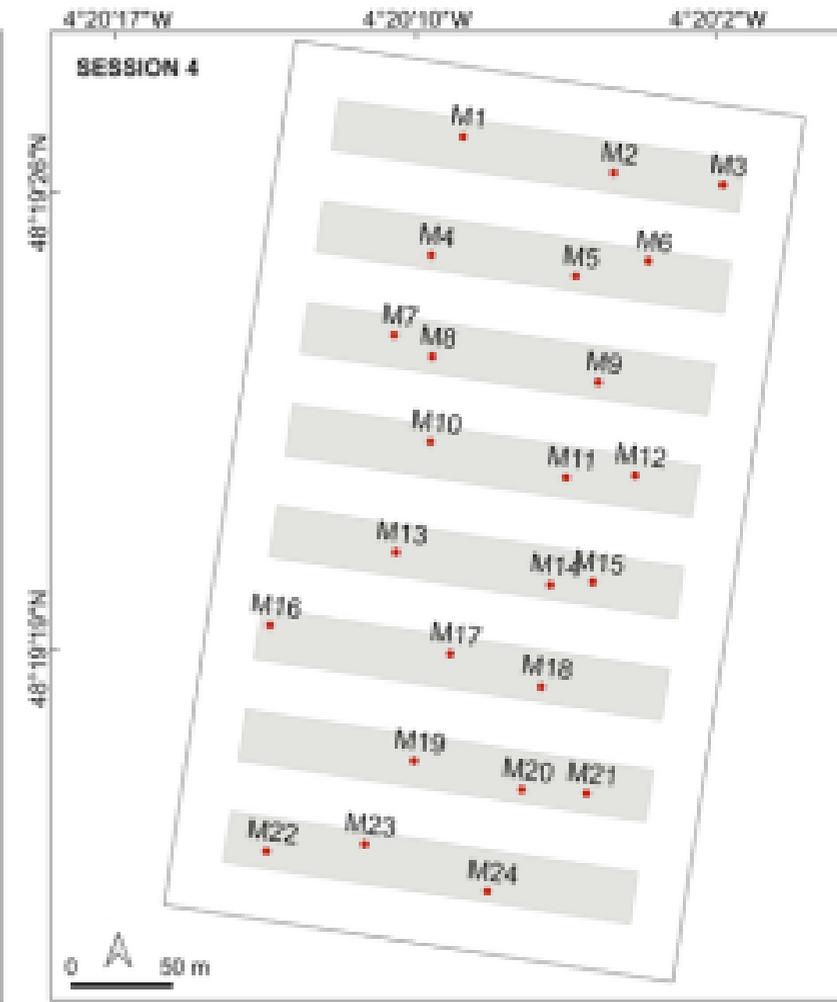
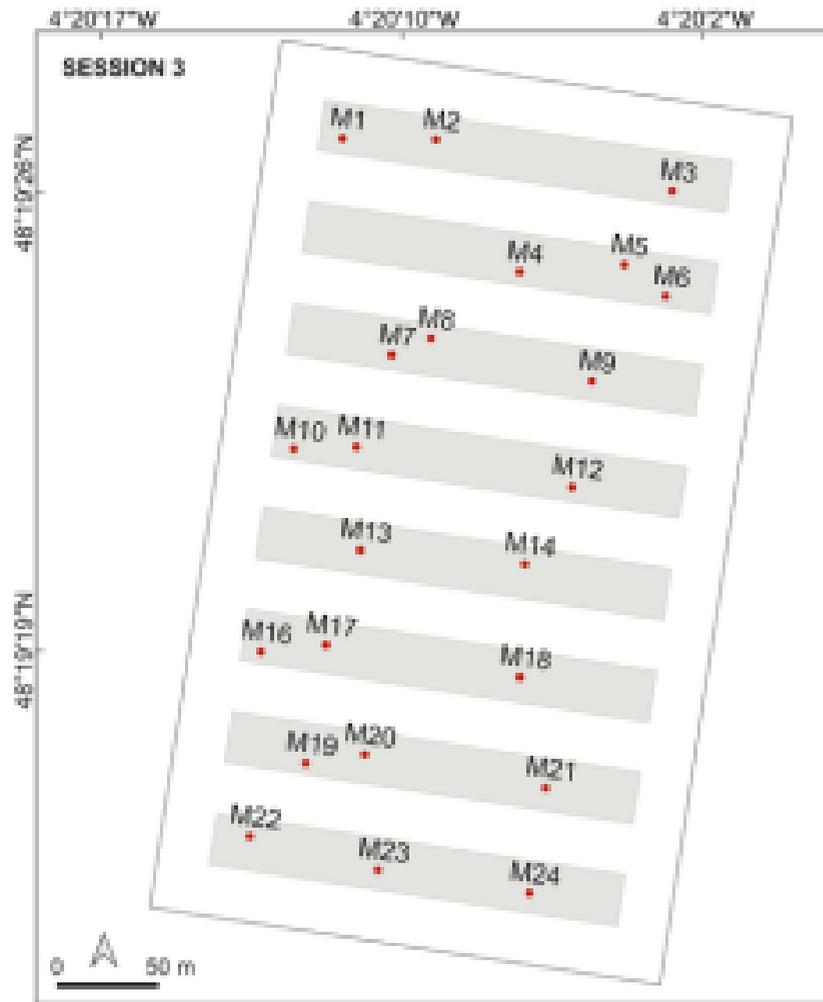
827 Figure 8: Non-metric multidimensional scaling ordination for the eight zones and for the four  
828 sessions based on log-transformed abundance data using the Bray–Curtis similarity. Each  
829 session is represented by a different color (S1: red; S2: green; S3: blue; S4: yellow), and each  
830 fishing effort is indicated by a different symbol (circle: 10 dredge tows; square: 30 dredge  
831 tows; triangle: control). The schema in the upper right corner of the plot indicates the  
832 trajectory of the objects depending on the fishing effort over time.

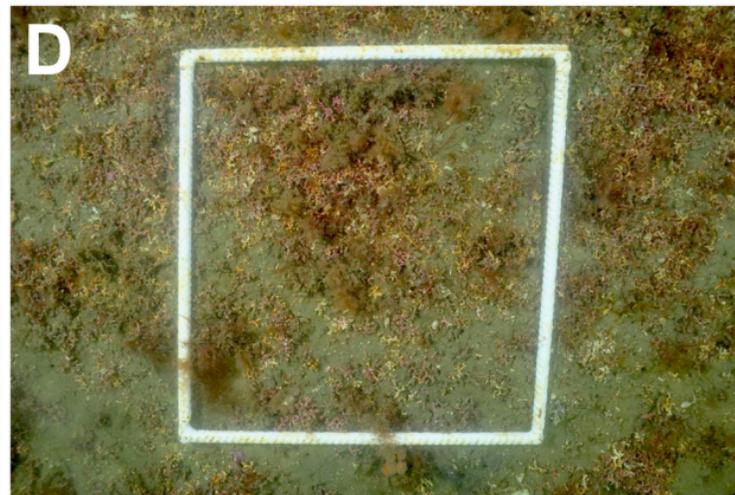
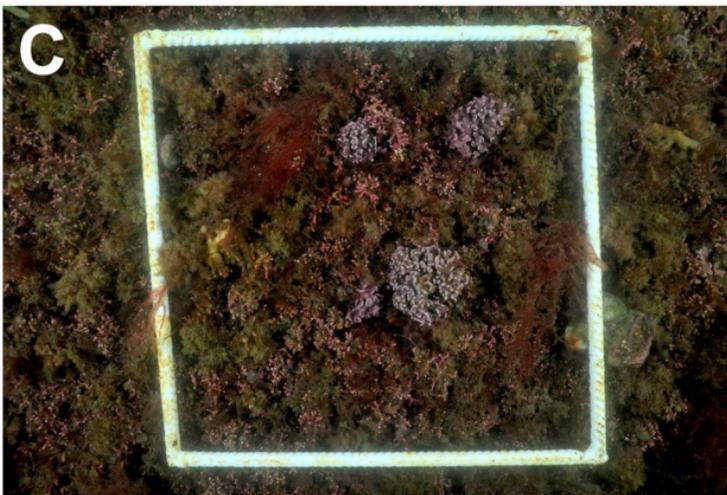
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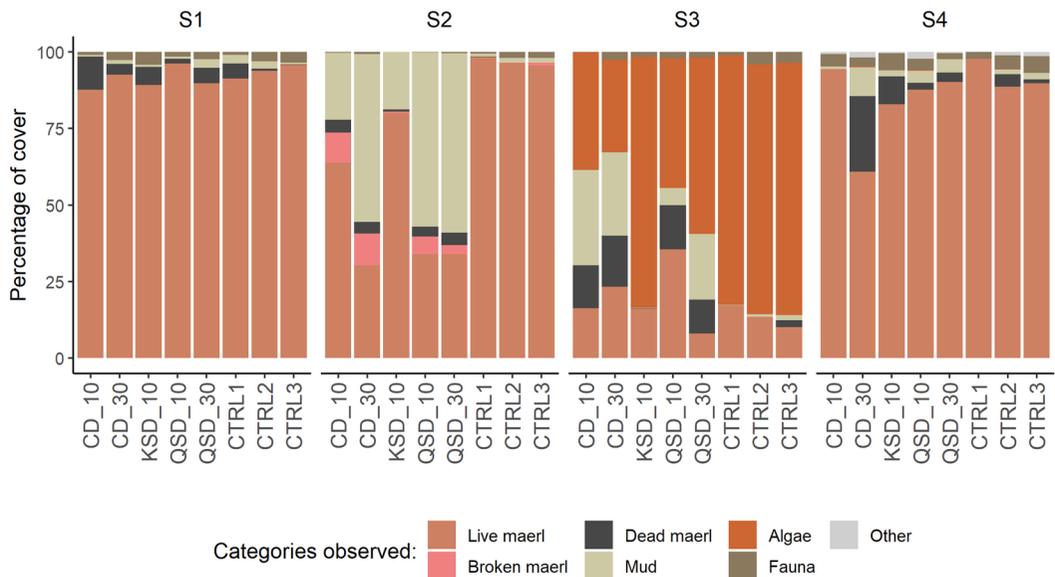
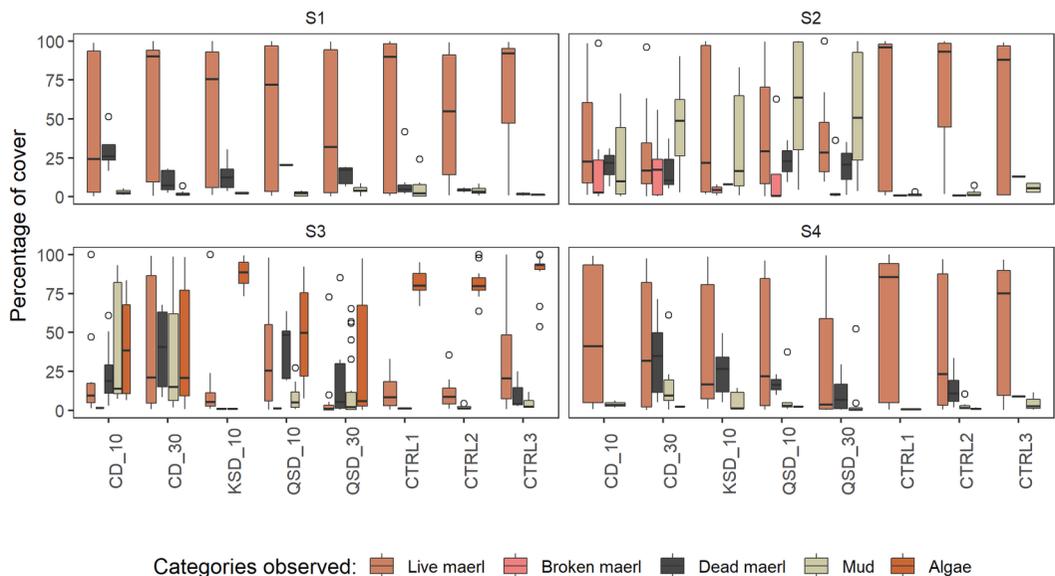
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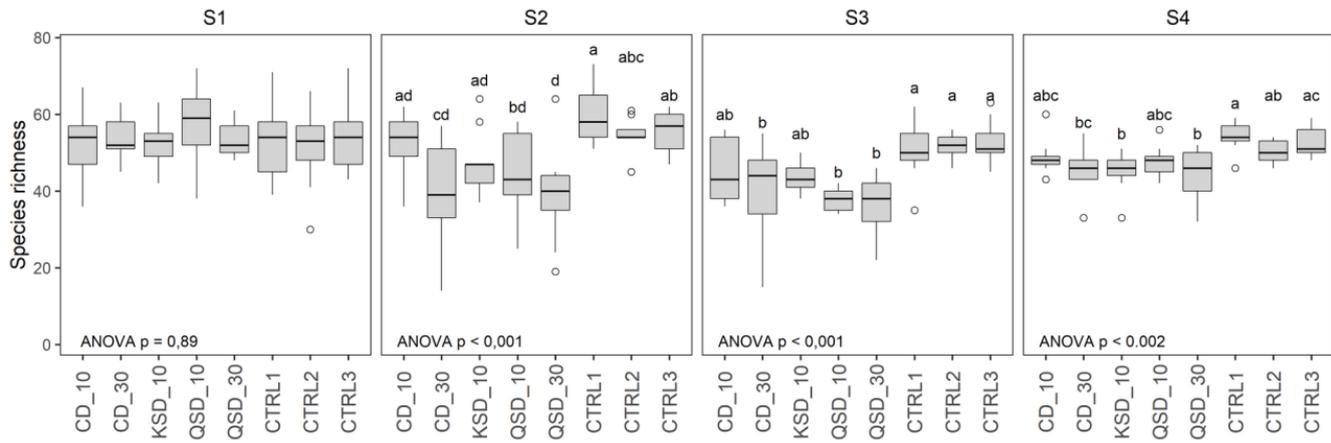
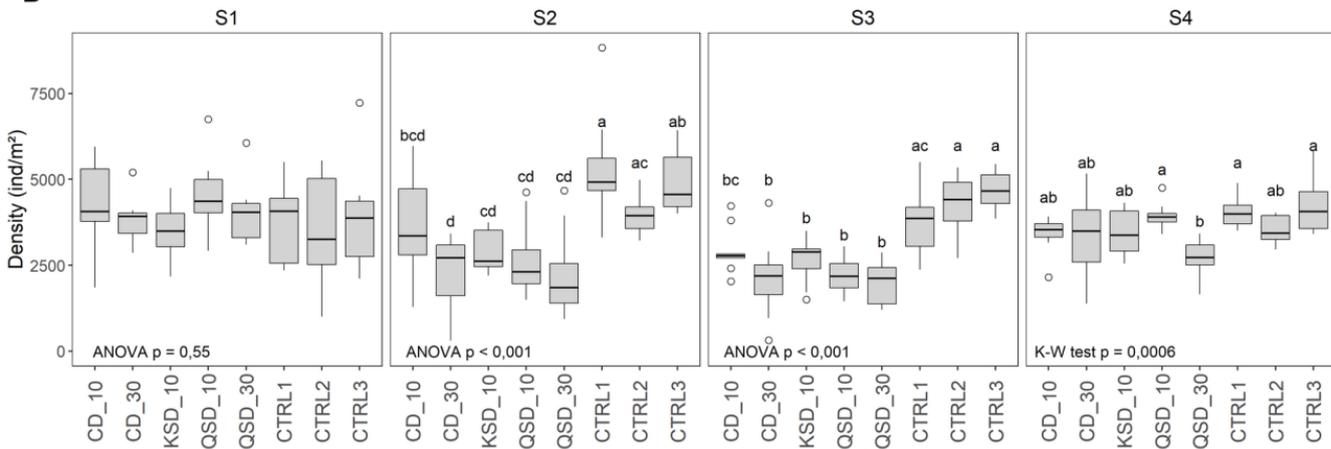


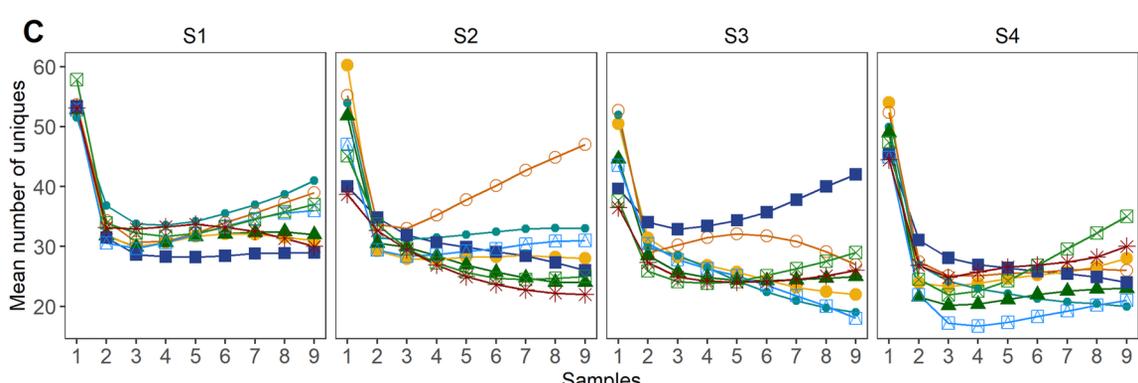
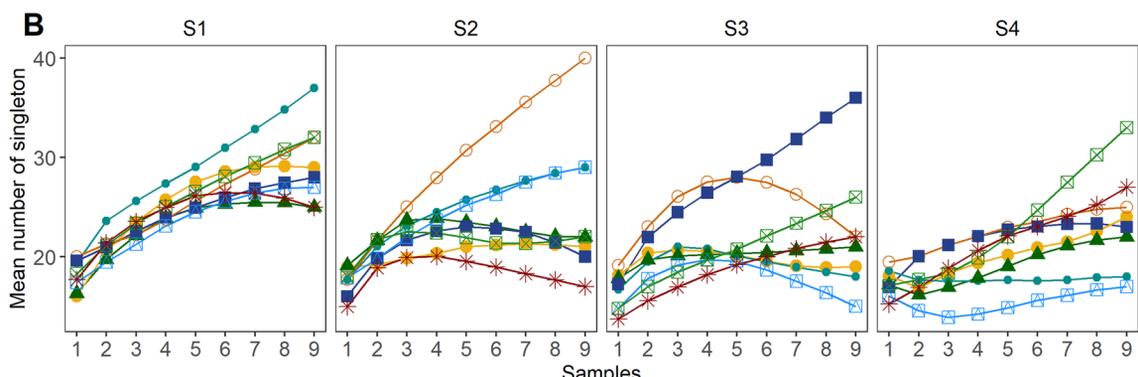
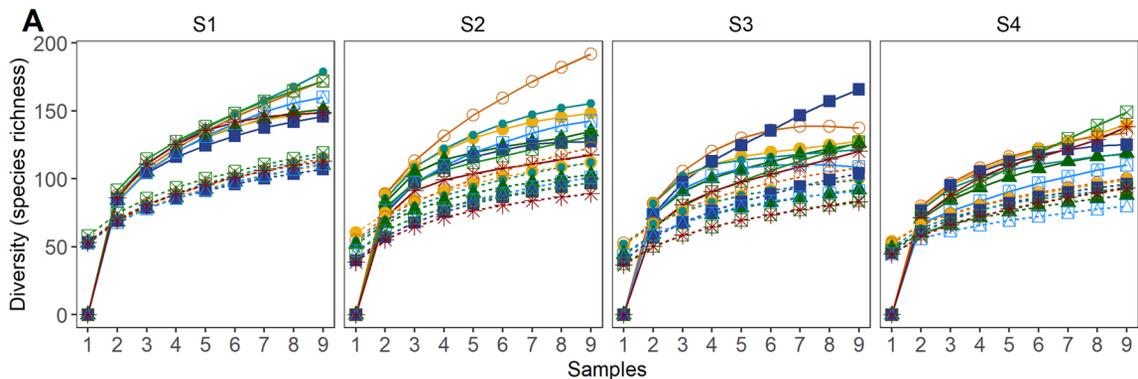






**A****B**

**A****B**



ZONE: ▲ CD10 ● CTRL1 ○ CTRL3 ◻ QSD10

■ CD30 ● CTRL2 ◻ KSD10 ✱ QSD30

DIVERSITY: — Estimated  
 - - - Observed

stress = 0.13

