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► **To cite this version:**

Alexis Paumier, T. Tatlian, Elodie Réveillac, E. Le Luherne, S. Ballu, et al.. Impacts of green tides on estuarine fish assemblages. *Estuarine, Coastal and Shelf Science*, 2018, 213, pp.176-184. 10.1016/j.ecss.2018.08.021 . hal-01917536

**HAL Id: hal-01917536**

<https://institut-agro-rennes-angers.hal.science/hal-01917536v1>

Submitted on 17 Sep 2019

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## Impacts of green tides on estuarine fish assemblages

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### Abstract :

All around the world, an increasing proportion of estuarine systems are facing massive proliferations of green macroalgae, called green tides, in response to nutrient enrichment. The consequences of this perturbation for ichthyofauna that use estuarine systems as essential fish habitats remain understudied. To estimate these consequences, we combined outputs of both macroalgae proliferation and fish community surveys conducted for the European Water Framework Directive in thirteen estuaries in northwestern France, a region where green tides are of great concern. The approach revealed the influence of green tides on estuarine fish communities. The response of each community to the green tides differed according to their functional guild composition. Benthic and marine juvenile guilds were negatively impacted, while demersal and pelagic fish guilds appeared to be more resilient. Green tides, which significantly affect the suitability of fish habitat, change the composition of the fish community and may hinder the future recruitment of marine fish species that rely on estuaries during the juvenile stage.

**Keywords :** Fish community, Estuarine ecology, Green tides, Macroalgae, Nursery

## 25 **1 Introduction**

26 Estuarine systems host a variety of habitats that are associated with high food availability and  
27 represent essential habitats for ichthyofauna (Blaber and Blaber, 1980; Elliott and Dewailly,  
28 1995; Peterson, 2003; Nicolas et al., 2010). These ecosystems provide major ecological  
29 services to fish communities, such as nursery grounds for juveniles, foraging areas for adult  
30 marine fish, permanent habitats for many resident species, and migration corridors for  
31 amphidromous fish (Seitz et al., 2014). Habitat quality and associated ecological services play  
32 a key role in the sustainability and renewal of a large number of estuarine-dependent fish that  
33 rely on estuaries during at least one stage of their life cycle.

34 However, these essential habitats are facing high and increasing anthropogenic disturbances  
35 (Beck and Airoidi, 2007; Brown et al., in press). The excessive input of organic matter and  
36 inorganic nutrients derived from anthropogenic watershed activities represents one of these  
37 disturbances (Diaz and Rosenberg, 2008; Liu et al., 2013; Lyons et al., 2014). The increase in  
38 nitrogen inputs beyond the level of an estuary's self-regulatory capacity (i.e., eutrophication)  
39 often leads to the increased development of a few taxa of fast-growing green macroalgae  
40 (Nixon, 1995; Valiela et al., 1997; Anderson et al., 2015), which causes green tides (GTs). In  
41 recent decades, the abundance and duration of GT events have increased worldwide (Hodgkin  
42 and Birch, 1986; Pihl et al., 1995; Fletcher, 1996; Lehvo and Bäck, 2001, Ye et al., 2011;  
43 Smetacek and Zingone, 2013). While the drivers and processes of these proliferations are  
44 known, their effects on ecosystems have been sparsely described (Lyons et al., 2014). During  
45 a GT, major changes occur in the habitat conditions (Fletcher, 1996). Biogeochemical cycles  
46 (Sfriso and Pavoni, 1994) and habitat structure modifications (Isaksson et al., 1994; Sundbäck  
47 et al., 1996) have been reported to impact invertebrate communities (Quillien et al., 2015) and

48 trophic webs (Raffaelli et al., 1998). However, only a few studies have considered the fish  
49 community, especially in estuarine systems (Raffaelli et al., 1998; Lyons et al., 2014).

50 During recent decades, the intensity of GTs and the number of impacted sites have increased  
51 in northwestern France, with high levels of proliferation observed from mid spring to the end  
52 of summer (Ménesguen and Piriou, 1995). Locally, a small-scale analysis of shallow intertidal  
53 beaches and estuarine mudflats revealed differences in the fish communities between control  
54 and impacted sites during green algae proliferation. Negative impacts for benthic and marine  
55 juvenile fish species begin at a low proliferation rates, and green tides significantly decrease  
56 fish species diversity and overall fish density until the complete disappearance of fish at a  
57 high level of GT (Le Luherne et al., 2016). Proliferations of green macroalgae and fish  
58 communities are both monitored in this region to assess the ecological quality of estuarine  
59 systems and to achieve a status that is compliant with the goals of the European Water  
60 Framework Directive (WFD). Complementing the previous local small-scale approach (Le  
61 Luherne et al., 2016), this study provides a quantitative evaluation of the effects of contrasting  
62 levels of GT proliferation on fish communities in estuaries over a much larger geographic  
63 area. The effects of GTs on fish communities were examined through the analysis of fish  
64 density and species richness collected from thirteen estuaries to explore the following  
65 questions:

- 66 - Is there a significant difference between the fish communities in affected and non-affected  
67 estuaries?
- 68 - At what scale can we detect GT impacts on estuarine fish communities?
- 69 - Do functional groups of fish respond differently to GTs?

## 70 **2 Materials and methods**

### 71 **2.1 General approach**

72 To study the effects of green tides on estuarine fish, a generalized linear model (GLM)  
73 approach was applied (2.5.). We used several survey-based (2.2.) descriptors of the fish  
74 community (2.3). The “natural” environmental variability of fish in estuaries was integrated  
75 by using four major environmental variables that control fish assemblage (i.e., ecoregion,  
76 season, depth, and salinity; Courrat et al., 2009; 2.3.). Then, we tested separately the GT  
77 effect using four descriptors, from a large scale to a local scale (2.4.).

### 78 **2.2 Study area and fish sampling**

79 We investigated the effect of GT in thirteen estuaries located in northwestern France (Fig. 1).  
80 The selection of these study sites allowed the coupling of fish survey and green tide indicator  
81 data. Furthermore, the pressure represented by GTs differed among these estuaries (e.g., from  
82 non-affected to moderately affected. These estuaries qualities were evaluated by ELFI, which  
83 is an indicator of estuarine quality based on the fish metrics (Table 1).  
84 From 2008 to 2014, fish were sampled in thirteen estuaries as part of a monitoring program  
85 that evaluates the ecological status of transitional waters in relation to the WFD (Delpech et  
86 al., 2010). Standardized fish surveys were conducted in spring (between April and June) and  
87 autumn (between September and November) for each site and sampling year (Delpech et al.,  
88 2010). Each survey used a beam trawl with an opening of 1.5 m wide and 0.5 m high and with  
89 a 8-mm stretched mesh in the cod-end (Delpech et al., 2010). The beam trawl was hauled in a  
90 counter-current direction for 15 min at a standard speed of 1.5-3 knots (Delpech et al., 2010).  
91 An average bottom surface of 1100 m<sup>2</sup> was swept during each haul. Salinity and depth were  
92 recorded for each beam trawl haul, the depth ranged between 0.75 and 23 m, and the salinity

93 ranged between 2.5 and 35.1. From 2008 to 2014, 1348 beam trawl hauls have been  
94 conducted, and 85 fish species and 79,125 individuals have been sampled.

### 95 **2.3 Fish community metrics and environmental variables**

96 Fish density and species richness were selected as indicators of the fish community status  
97 because they are assumed to decrease with an increase in habitat disturbances (Gibson, 1994;  
98 Delpech et al., 2010). Species richness was estimated based on the number of species captured  
99 in each trawl haul, and the total density was defined as the number of individuals captured per  
100 hectare. In addition, to evaluate the impact of GTs on the use of fish habitat, each species was  
101 classified into functional guilds, including: 3 vertical distribution guilds (i.e., pelagic,  
102 demersal and benthic) and 2 ecological guilds (i.e., marine juvenile and resident) (Franco et  
103 al., 2008; Potter et al., 2015). Vertical distribution guilds describe the spatial distribution of  
104 fish in the water column and illustrate the dependence of the organism on the substratum  
105 (Table 2). Ecological guilds describe the use of estuaries during the species' life cycle (Table  
106 2). Other ecological fish guilds, such as amphidromous or marine adventive species (Elliott  
107 and Quintino, 2007), were not well sampled in the beam trawl surveys; thus, our approach did  
108 not account for these guilds. The fish densities for each of these five guilds were calculated  
109 for each trawl haul.

110 Because estuaries are exposed to strong environmental gradients, it was necessary to consider  
111 the natural source of environmental variability (Elliott and Quintino, 2007; Courrat et al.,  
112 2009; Nicolas et al., 2010) before providing a reliable assessment of the green tide impacts on  
113 estuarine fish communities. Four main environmental variables were considered: the sampling  
114 season of the survey, the ecoregion where the estuary is located, the salinity and the depth  
115 during the trawl haul. Preliminary tests have shown that these four sources of environmental  
116 variability were not correlated.

117 - Fish communities change dramatically between spring and autumn (Elliott and Quintino,  
118 2007). The most marked shift was observed for marine juveniles, whose density decreased  
119 drastically from spring to autumn, revealing a high mortality rate after settlement (Courrat et  
120 al., 2009; Le Pape and Bonhommeau, 2015). These density variations and the seasonality of  
121 GT proliferations led us to separate spring and autumn analyses.

122 - A biogeographic classification based on the Marine Ecoregions of the World (Spalding et  
123 al., 2007) was used to separate the thirteen estuaries into two ecoregions: “North Brittany”  
124 and “South Brittany” (Fig. 1).

125 - Salinity and depth, which are among the main drivers structuring fish communities in  
126 estuaries, were (Courrat et al., 2009) also considered.

## 127 **2.4 Green tide monitoring in WFD and GT index computation**

128 To quantify the intensity of the GTs, we used four indicators provided by the Center for Study  
129 and Promotion of Algae (CEVA, France) and the WFD (Table 3). Three of these indicators  
130 (GT1, GT2 and GT3) were based on quantitative maps of GT, and the last indicators (GT4)  
131 was based on a WFD indicators (Table 3). The quantitative maps were obtained by  
132 combination of orthophotographies and field monitoring. Orthophotographies were obtained  
133 from an aircraft during low tide, and field monitoring was performed to determine the  
134 associated density of macroalgae. The quantitative maps represented the macroalgal  
135 proliferation as a percentage of algal cover. The first three indicators of GTs were derived  
136 from these maps at different spatio-temporal scales (Table 3):

137 - At a large scale (i.e., the estuary scale), the ecological quality ratios (EQRs) were used  
138 (GT1). The EQR index is a validated indicator of estuarine quality in terms of macroalgal  
139 proliferation that is applied in the WFD (Wilkes et al., 2014). The EQR index is composed of  
140 four scores: poor, moderate, good and high. Inside each of the thirteen estuaries, a low

141 variability of the EQR was observed over the period of 2008-2014 (Supp. Fig. 1.1). Among  
142 the thirteen estuaries, some were almost clear of green macroalgae (high), while others were  
143 impacted by GTs (moderate, Table 1). No poor EQR were recorded within the studied  
144 estuarine.

145 - At a local scale (i.e., the trawl haul scale), we used two indicators based on the same data  
146 (Table 3): (i) the macroalgal mat surface ratio within the trawl hauls (GT2), and (ii) the  
147 macroalgal mat surface ratio near the trawl hauls (GT3). The macroalgal mat surface ratio  
148 within the trawl hauls (GT2) was computed using QGis software by combining the  
149 quantitative maps of macroalgal proliferation with the trawling location from 2008 to 2014  
150 (which was the same period as the fish trawl surveys). Preliminary analysis and expert  
151 knowledge validated the inter-annual steadiness of this distribution. The macroalgal mat  
152 surface ratio near the trawl samples (GT3) was also computed by combining the quantitative  
153 maps of macroalgal proliferation with the trawl haul location. To achieve this, a surface buffer  
154 was calculated around each beam trawl haul (Supp. Fig. 2.1). Several surface buffers were  
155 calculated to compute the index of the macroalgal surface ratio near the trawl hauls with  
156 different buffer distances (i.e., from 100 to 1000 m). Inside each buffer, the proportion of sea  
157 surface (excluding land cover) covered by green macroalgae was calculated up to a certain  
158 threshold (i.e., >25%, >50% and >75%) (Supp. Fig. 2.1). The influence of the buffer distances  
159 and thresholds was assessed in preliminary analysis before the GT3 was integrated as  
160 explaining covariates in the models of fish metrics. We screened the correlation levels  
161 between the GT index in the vicinity of trawl hauls according to the different buffer distances  
162 that were defined around the beam trawl hauls (ranging from 100 to 1000 m) and the different  
163 algal cover thresholds (> 25%; > 50% and > 75%).



164 In addition, at a local scale, we tested a fourth GT descriptor on a restricted dataset. The *Ulva*  
165 spp. density per beam trawl (GT4) was estimated from an additional protocol added to the  
166 WFD trawl surveys in 2013 and 2014 (Table 3). These data were available for 227 beam trawl  
167 hauls and were collected using a WFD standardized protocol (Scanlan et al., 2007)  
168 The influence of each of these four indicators on fish metrics was tested separately to  
169 determine the most appropriate scale for assessing the effect of GTs on estuarine fish.

## 170 **2.5 Modelling the effect of GTs on the fish community**

171 The multi-scalar approach used for the GT indicators allowed us to explore the appropriate  
172 scale for detecting the impacts of GTs on fish communities. Because there is no optimal scale  
173 to describe an ecological phenomenon (Levin, 1992; Wheatley and Johnson, 2009), we chose  
174 to compare the response of the fish community to these four GT indexes in separate analyses.  
175 The modelling approach integrated the response of fish to the natural variability and the four  
176 GT indexes used in four separate models (Eq. 1):

$$177 \quad \text{Fish metrics} \sim \text{environmental variables} + \text{GT}^* \quad (\text{Eq. 1})$$

178 where the environmental variables represent the four natural drivers (i.e. ecoregion + salinity  
179 + depth), and “GT\*” corresponds to one of the four GT metrics (Table 3).

### 180 **2.5.1 Species richness**

181 The species richness was modelled using GLM with a Poisson distribution (Eq. 2). This  
182 distribution is most commonly used for analysing count data in trawl surveys (Courrat et al.,  
183 2009).

$$184 \quad \text{Species richness} \sim (\text{environmental variables}) + (\text{GT}^*) + \varepsilon \quad (\text{link function} = \log) \quad (\text{Eq. 2})$$

185 where the environmental variables represent the four natural drivers, and “GT\*” corresponds  
186 to one of the four GT metrics (Table 3).

187        2.5.2 Fish density

188 The fish survey data were characterized by a large proportion of zeros (Supp. Fig. 1.2.a).  
189 According to this zero-inflated distribution, we used a delta distribution (Aitchison and  
190 Brown, 1957). This approach is appropriate for the analysis of fish survey data (Stefansson,  
191 1996; Le Pape et al., 2003). The delta model (Aitchison, 1955; Pennington, 1983) combines  
192 two distinct GLMs: one sub-model for fish presence and absence (Eq. 3), and one sub-model  
193 for positive density (Eq. 4).

194 - Binomial sub-models for fish presence

195             $Y_{(1/0)} \sim (\text{environmental variables}) + (GT^*) + \varepsilon \quad (\text{link function} = \text{logistic}) \quad (\text{Eq. 3})$

196 where  $Y_{(1/0)}$  represents the presence or absence of fish (i.e., 1 or 0). The area under the curve  
197 (ROC) was used as a criterion to validate the goodness-of-fit of each sub-model (Manel et al.,  
198 2002; Vasconcelos et al., 2013).

199 - Sub-models for positive fish density

200             $\text{Log}(Y_{(>0)}) \sim (\text{environmental variables}) + (GT^*) + \varepsilon \quad (\text{link function} = \text{identity}) \quad (\text{Eq. 4})$

201 where  $Y_{(>0)}$  is the density of fish when at least one fish was caught. The log-transformed  
202 positive densities satisfy the conditions of a linear distribution and the homogeneity of  
203 variance for these sub-models (Supp. Fig. 3.1.). The value of the actual data vs. the predicted  
204 relationship was used as a criterion to validate the goodness-of-fit of these sub-models (Manel  
205 et al., 2002; Vasconcelos et al., 2013).

206 - Coupling

207 The two sub-models (Eqs. 3 and 4) were coupled (Eq. 5) to estimate fish density (Stefansson,  
208 1996). A correction was applied to the positive sub-models to obtain unbiased estimations  
209 from log-transformed data (Laurent, 1963).

$$\hat{Y} = Y_{(1/0)} * e^{\ln(Y_{(>0)})} * e^{\frac{\alpha^2(\ln(Y_{(>0)}))}{2}}$$

(Eq. 5)

210

211 where  $\hat{Y}$  is the fish density estimated by the delta model;  $Y_{(1/0)}$  is the probability of the  
 212 presence of fish provided by the binomial model;  $Y_{(>0)}$  is the logarithmic density of fish  
 213 provided by the log-normal model; and  $\alpha^2(\ln(Y_{(>0)}))$  is the standard error associated with the  
 214 log-normal model.

215 To quantify the uncertainty that accounts for the combination of the two sub-models' errors,  
 216 we used a random sampling approach. We predicted the presence of fish on 5,000 subsamples  
 217 that were randomly generated with the binomial model, and we log-transformed the densities  
 218 of 5,000 subsamples that were generated with the GLM model using positive density values.  
 219 Then, these predictions were coupled, and we computed the 10%, 50% and 90% quantiles of  
 220 the 5,000 predictions (Courrat et al., 2009).

### 221 2.5.3 Preliminary analysis and modelling options

222 There was a single exception to the use of the delta model, and it concerned the pelagic fish  
 223 guild. The proportion of non-null observations of pelagic fish was too low to allow for fitting  
 224 a positive sub-model. As a result, a single binomial model (Eq. 3) was developed for this  
 225 guild (Table 4).

226 The GLM approach requires linearity in the relations between the response variable and the  
 227 covariates. This assumption was preliminarily tested before the integration of the 2  
 228 environmental variables (e.g., depth and salinity, and ecoregion was a class factor) as linear  
 229 factors in the GLM. For depths down to 16 m, we observed atypical observations and non-linear  
 230 effects on fish metrics. Thus, to account for the linear effect of depth, we removed trawl samples  
 231 that were deeper than 16 m. By doing so, we narrowed the data set by less than 1% of the survey

232 data. In a few other cases where we found non-linear patterns, we integrated the  
233 environmental variable as a class factor in the GLMs (see pelagic fish in Table 4).  
234 The models were run using R software (R Core Team 2016). For both sub-models, the  
235 selected level of statistical significance of the four environmental variables and the GT  
236 indexes of the GLM was 5% (i.e., only the environmental variables that were significant at the  
237 5% level were retained, and the same was applied to GT\*). Both the explained percentage of  
238 deviance and the Akaike information criterion (AIC) were used to assess the effects of the  
239 environmental variables and the GTs on the fish metrics.

## 240 **3 Results**

### 241 **3.1 Fish community and its environmental variables**

242 The majority of fish caught belonged to the demersal (71.5%) and benthic (26.6%) guilds,  
243 while a minority of fish were pelagic (1.9%). For the ecological guilds, the residents were the  
244 most frequently caught species (70%), followed by the marine juveniles (13%). Other  
245 ecological guilds were poorly represented and were, thus, not included. Globally, the  
246 statistical significance of depth and ecoregion were high in the models, and the salinity  
247 appeared to be a structuring factor for the density of the benthic and marine juvenile guilds in  
248 spring (Table 4). Selected models had satisfying goodness-of-fit values (Supp. Table 3.1;  
249 Supp. Fig. 3.1).

### 250 **3.2 GT index computation**

251 The study revealed that few beam trawls were conducted within the algal mat: 54 trawl hauls  
252 occurred in spring and 71 hauls occurred in autumn (i.e., 9% of the fish community data).  
253 Furthermore, the macroalgal mat surface ratio (GT2) was very low at these 125 beam trawl  
254 hauls. Accordingly, the green macroalgae density accumulated per beam trawl haul, which

255 was available in 2013 and 2014 (GT4), was very low (mean biomass = 0.0035 kg/m<sup>2</sup>, Supp.  
256 Fig. 1.2.b).

257 The macroalgal mat surface ratio near the beam trawl haul (GT3) differed among the  
258 threshold and buffer combinations. For identical buffer distances, the different algal cover  
259 thresholds were correlated (more than 80%; Supp. Fig. 2.2.). In the radius range of 300-800  
260 m, the levels of correlation were also high between the GT indexes for the different buffer  
261 sizes and the algal cover thresholds (Supp. Fig. 2.2.). We selected a single combination of  
262 buffer distance and algal cover to compute the macroalgal mat surface ratio near the beam  
263 trawl hauls (GT3): the 25% threshold of algal cover within the 500 m buffer.

### 264 **3.3 Large-scale effect of GTs**

265 Accounting for the statistical significance of the environmental variables (Table 4), the  
266 significant effects of the EQR (GT1) were detected for 13 of the 14 models in spring and for  
267 11 of the 14 models in autumn (Table 4). However, a single fish metric – the density of  
268 benthic fish in spring – had a monotonous relationship with GT1 (i.e., a continually  
269 decreasing density associated with a decreasing gradient of the EQR). Moreover, the deviance  
270 explained by GT1 for the density of benthic fish was the highest (32% for the presence-  
271 absence model and 2% for the positive density model). Furthermore, the confidence bands  
272 around the prediction associated with the average and high EQR scores did not overlap, and  
273 there was a distinguishable difference in density (Fig. 2). GTs negatively impacted the benthic  
274 guild in spring. The deviance explained for the other fish metrics was less than 10%.  
275 According to this low signal at the estuarine scale, there was no significant correlation  
276 between GT1 and ELFI.

### 277 **3.4 Local-scale effect of GT**

278 Accounting for the statistical significance of the environmental variables, the two indexes of  
279 proliferation at beam trawl locations (GT2 and GT4) were not statistically significant for  
280 either the spring or autumn surveys.

281 Conversely, statistically significant effects (Table 4) were observed for the algal cover near  
282 the beam trawl haul (GT3). In spring, the probability of the presence of the resident guild  
283 responded to GTs positively. In autumn, statistical significance was detected for 6 of the 12  
284 models. Positive effects of the GTs were observed on total fish density, demersal fish density,  
285 and resident fish density. In contrast, GTs had a negative effect on the benthic and marine  
286 juvenile fish densities. The density of marine juveniles was halved when 20% of the surface at  
287 an area less than 500 m from a beam trawl haul had a green macroalgae cover greater than  
288 25% (Fig. 3).

## 289 **4 Discussion**

290 This study provided evidence on the effects of GTs on estuarine fish communities, and it  
291 focused on thirteen estuarine systems with contrasting levels of GTs. It appeared that GTs had  
292 both negative and positive effects on the fish communities. Benthic fish were especially  
293 sensitive and negatively impacted, and marine juveniles appeared to be dramatically more  
294 sensitive than were resident fish. This confirmed previous findings from coastal areas (Howell  
295 et al., 1999; Jokinen et al., 2015; Le Luherne et al., 2016), and enabled us to extend these  
296 conclusions to estuaries.

### 297 **4.1 Can we consider correlations to GT indexes as causal links to GTs?**

298 Fish that inhabit estuaries have adapted to strong environmental gradients (e.g., “estuarine  
299 quality paradox” theory; Elliott and Quintino, 2007). Thus, it was critical to consider the

300 environmental constraints before providing a reliable assessment of the impacts of GTs on the  
301 estuarine fish communities (Nicolas et al., 2010). Accounting for these “natural” factors that  
302 structure fish communities at different scales (time: seasonal patterns; space: ecoregion at a  
303 mesoscale, depth and salinity at a local scale) allowed us to account for a part of the “natural”  
304 variability and autocorrelations in the fish survey data, which enabled a reliable assessment of  
305 the effects of GTs.

306 In addition, the potential effects of the other anthropogenic pressures potentially combined  
307 with the effects of GTs were not considered. The lack of an exhaustive assessment of the  
308 ecological status of these thirteen estuaries in the WFD, e.g., with regard to the concentration  
309 of xenobiotics, prevents the present approach from accounting for them. These potential  
310 confounding factors smooth the strength of the conclusions based on analysis at the estuarine  
311 scale. However, the use of local-scale GT indexes, especially GT3, allows for a thin-scale  
312 analysis of the link between GTs and fish metrics, with a dramatically less probable influence  
313 of potential confounding factors.

#### 314 **4.2 Large-scale impacts of GT**

315 At the large scale, a single negative effect of GTs was revealed on the benthic guild. It was  
316 previously demonstrated that this guild was the most sensitive to green macroalgae  
317 proliferation (Bowen and Valiela, 2001; Bricker et al., 2008; Le Luherne et al., 2016, 2017).  
318 However, there was no further signal of change in the fish community in relation to GT1. The  
319 relatively low intensity of GTs in these estuaries, the minimum score of EQR encountered in  
320 this survey was a moderate status of estuarine quality in terms of macroalgal proliferation,  
321 prevents dramatic changes in the fish communities at the global scale of estuaries.

### 322 4.3 Local-scale impacts of GT

323 First, we analysed the effects of GTs directly at the trawling location using two indicators  
324 (i.e., macroalgal mat surface ratio on beam trawl hauls, GT2, and *Ulva* spp. density per beam  
325 trawl haul, GT4). From previous restricted small-scale analysis, these two indicators of the  
326 local intensities of GTs were expected to have significant effects on the fish community.

327 However, none of the fish metrics presented a significant response to the GT descriptors at the  
328 trawling locations. This lack of response was explained by the fish sampling protocol. Indeed,  
329 during the WFD survey, trawl hauls were conducted beside the algal mats to avoid the  
330 clogging of the net. Consequently, the surfaces and biomasses of algae were low at the  
331 trawling locations. The maximum *Ulva* spp. density per beam trawl haul recorded was 0.05  
332 kg/m<sup>2</sup> in spring and 0.18 kg/m<sup>2</sup> in autumn. These low algal densities explain the absence of  
333 significant effects on fish metrics. Indeed, Le Luherne et al. (2016) observed a minimum algal  
334 density threshold of 0.30 kg/m<sup>2</sup> from which the fish community was significantly impacted by  
335 expanded blade green macroalgae. The under-sampling of the algal mats during the surveys  
336 explained the inability to provide a clear-cut assessment of the impacts of GTs on fish at the  
337 trawling positions. To improve this assessment, the impacts of the GTs should be analysed  
338 using a dedicated protocol that has been fitted for a before-after control-impact analysis (Le  
339 Luherne et al., 2016).

340 To cope with the under-sampling of the algal mats during the fish surveys, we computed the  
341 macroalgal mat surface ratio near the beam trawl hauls to test the effect of the spread of the  
342 GTs beyond the algal mats. This local descriptor succeeded in detecting the effect of GTs on  
343 estuarine fish.

344 A single significant and positive effect of GTs on resident fish was observed in spring based  
345 on the GT index near the beam trawl hauls. This moderate effect may be caused by the very



346 limited biomass and cover of algae before the proliferation season begins (Adams, 2005;  
347 Andrades et al., 2014). Proliferation occurs between May and September (Merceron et al.,  
348 2007). As a result, a potential scale mismatch between the GT indicator and the fish surveys  
349 may have occurred during the spring campaigns of certain years.

350 Conversely, half of the functional guilds presented a significant response to GT3 in autumn.  
351 Resident and demersal fish responded positively to moderate algal cover in their vicinity  
352 (Adams, 2005; Andrades et al., 2014). However, benthic and marine juvenile fish were  
353 negatively impacted. This sensitivity of benthic and marine juvenile fish was already observed  
354 during GTs, with a dramatic decrease in their density even during moderate proliferation (Pihl  
355 et al., 2005; Le Luherne et al., 2016), as well as a decrease in individual performance (Le  
356 Luherne et al., 2017).

#### 357 **4.4 Generalization on the impact of GTs on fish**

358 The density of benthic fish responded negatively to the GT1 and GT3 indicators of  
359 proliferation, with strong evidence supporting the sensitivity of this guild to GTs. This  
360 sensitivity may be explained by the GT pattern of proliferation. GTs generate physical,  
361 chemical and trophic perturbations that affect the fish community within a small area  
362 (Nordström et al., 2007; Luherne et al., 2016). Physical stress is linked to the degradation of  
363 the physical structure of the habitat. GTs first colonize the estuarine floor, modifying the  
364 structure of the substratum (Solidoro et al., 1997), and then the water column is colonized (Le  
365 Luherne et al., 2016). This modification of the bottom habitat by GTs mainly affects  
366 macrobenthic communities (Quillien et al., 2015), including benthic fish (Le Luherne et al.,  
367 2016, 2017). Trophic perturbations are linked to a decrease in fish foraging efficiency within  
368 the mats of *Ulva* spp (Nordström et al., 2007; Luherne et al., 2016). Finally, chemical  
369 perturbations could occur with anoxic events within the sediment or at the sediment-water

370 interface below the mats of *Ulva* spp. (Baden, 1990; Sundbäck et al., 1996). Therefore, the  
371 benthic fish are the first to be impacted due to the degradation of their habitat (Wennhage,  
372 2002; Wennhage and Pihl, 2007).

373 Following the rapid impact on benthic fish, shifts from a benthic to a pelagic community  
374 could be observed after GT events (Bowen and Valiela, 2001). In the Baltic Sea, a massive  
375 change in fish composition was associated with a decrease in the foraging efficiency of  
376 predatory fish, and this change was induced by a GT (Pihl et al., 2005; Österblom et al.,  
377 2007). In fish survey data from the thirteen studied estuaries, the proportion of pelagic fish  
378 was low (<2%) with regard to previous estimations of European estuarine fish assemblages  
379 (25%; Elliott and Dewailly, 1995). This result revealed that the fish community was not fully  
380 represented in the French WFD surveys. Indeed, the beam trawl is well adapted to sample the  
381 benthic and demersal communities, but this method is inadequate for sampling pelagic fish  
382 (Courrat et al., 2009; Delpech et al., 2010). GTs mainly disturb benthic and demersal species  
383 (Le Luherne et al., 2016, and the present study); thus, the sampling bias did not compromise  
384 the validity of the present approach for these fish guilds. Moreover, the effects of GTs on  
385 pelagic fish occurred at a high level of GT proliferation, which was not observed in the  
386 present data set in the sampled areas. However, potential shifts from a benthic to a pelagic  
387 community after GT events (Bowen and Valiela, 2001) could not be assessed with this  
388 sampling protocol. This type of assessment requires a dedicated protocol to investigate  
389 massive algal mats and sample the whole fish community (Le Luherne et al., 2016).

390 Concerning the ecological guilds, in spite of the moderate level of GTs investigated, the  
391 present approach provided evidence that GTs had negative consequences on marine juvenile  
392 fish. The local productivity of several coastal and estuarine nursery-dependent marine fish  
393 will be reduced with the proliferation of green macroalgae in coastal (Pihl et al., 2005, Brown

394 et al., 2017) and estuarine areas (Peterson et al., 2000; Stoner et al., 2001). The juvenile stage  
395 is a key life stage for fish population size (Stoner et al., 2001; Le Pape and Bonhommeau,  
396 2015), and marine populations of species that are dependent on coastal and estuarine nursery  
397 grounds and the related fisheries could be impacted by GTs, as observed in the Baltic Sea  
398 (Baden, 1990; Jokinen et al., 2015).

### 399 **Acknowledgements**

400 This work was supported by the French Fisheries Organization, France Filière Pêche and the  
401 Loire-Bretagne Water Agency. We would like to thank all the scientific partners involved in  
402 the estuarine fish surveys for the Water Framework Directive in Brittany (France), especially  
403 Eric Thiebaut and Caroline Broudin (Université Pierre et Marie Curie, CNRS, Roscoff,  
404 France), Elena Lucchetti (MNHN, Concarneau, France), Laurent Thieulle (Asconit, Lyon,  
405 France), and Alexandre Carpentier (Université de Rennes 1, MNHN, Dinard, France). We  
406 would also like to thank the three anonymous reviewers and the editor for their numerous  
407 helpful suggestions, improvements and advice.

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615 **Figure captions**

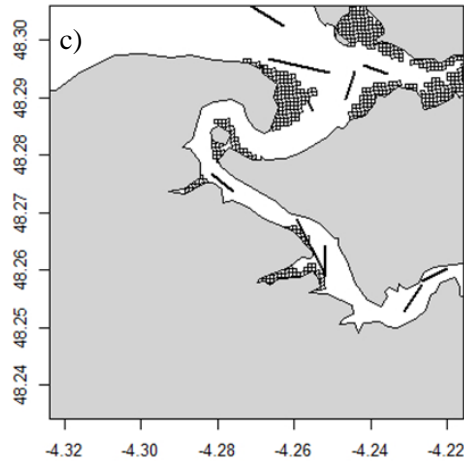
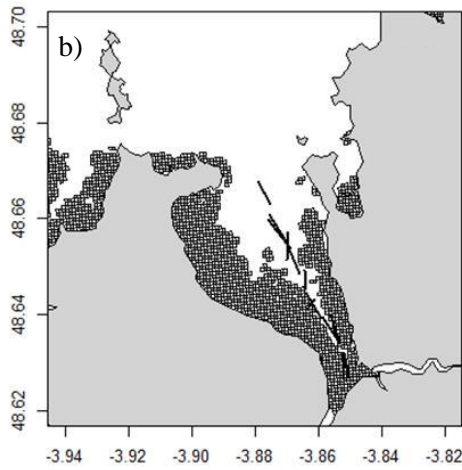
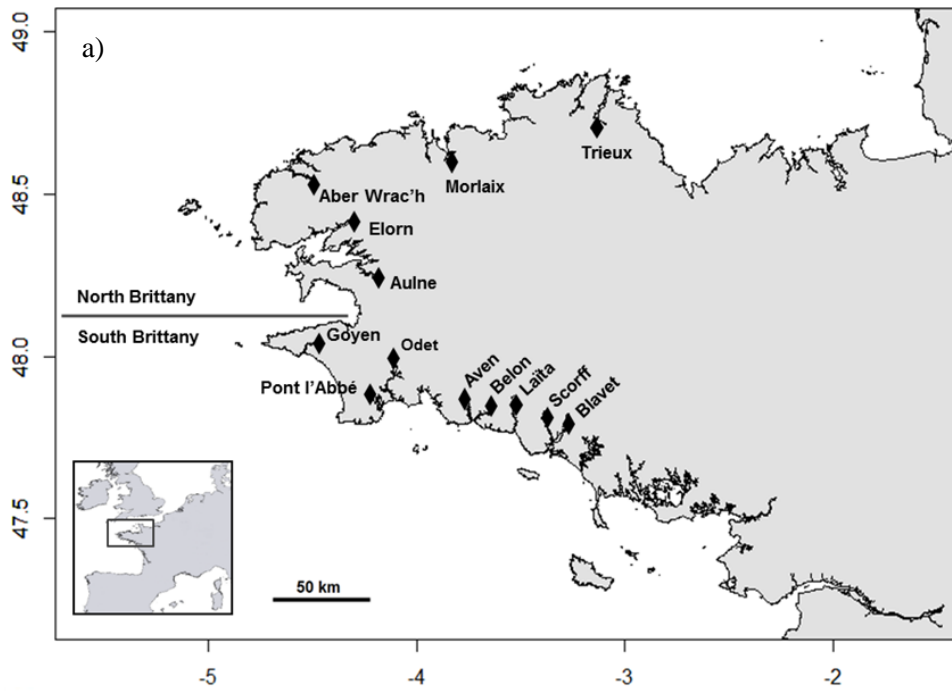
616 Figure 1: a) Locations (in WGS84 coordinates) of the studied estuaries in northwestern France 617  
split into two ecoregions: north and south. The spatial protocol for the fish survey is provided 618 as  
an example for 2 of the thirteen estuaries studied, in (b) the Morlaix Estuary and (c) the 619 Aulne  
Estuary. Lines: the locations of beam trawls; hatched grid: mats of green macroalgae.

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621 Figure 2: GLM prediction (with the 10-90% confidence intervals) of the estuarine benthic fish 622  
density (number/ha) according to the salinity and the two scores of the ecological quality ratio 623  
(moderate in grey and high in black) in an estuary located in South Brittany that was sampled 624 in  
spring.

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626 Figure 3: GLM prediction (with the 10-90% confidence intervals) of the estuarine marine 627  
juvenile density (number/ha) according to the percentage of the surface that had more than 628 25%  
algal cover and was within 500 m, in an estuary located in South Brittany that was 629 sampled in  
autumn.

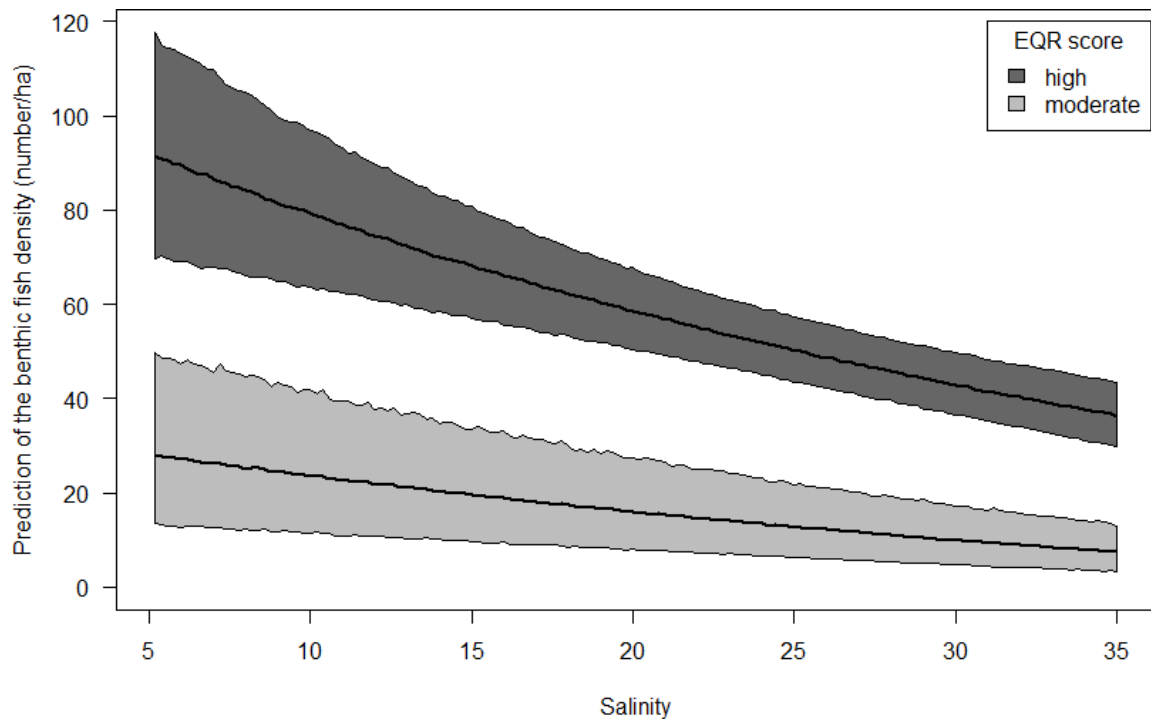


630

631 FIGURE 1

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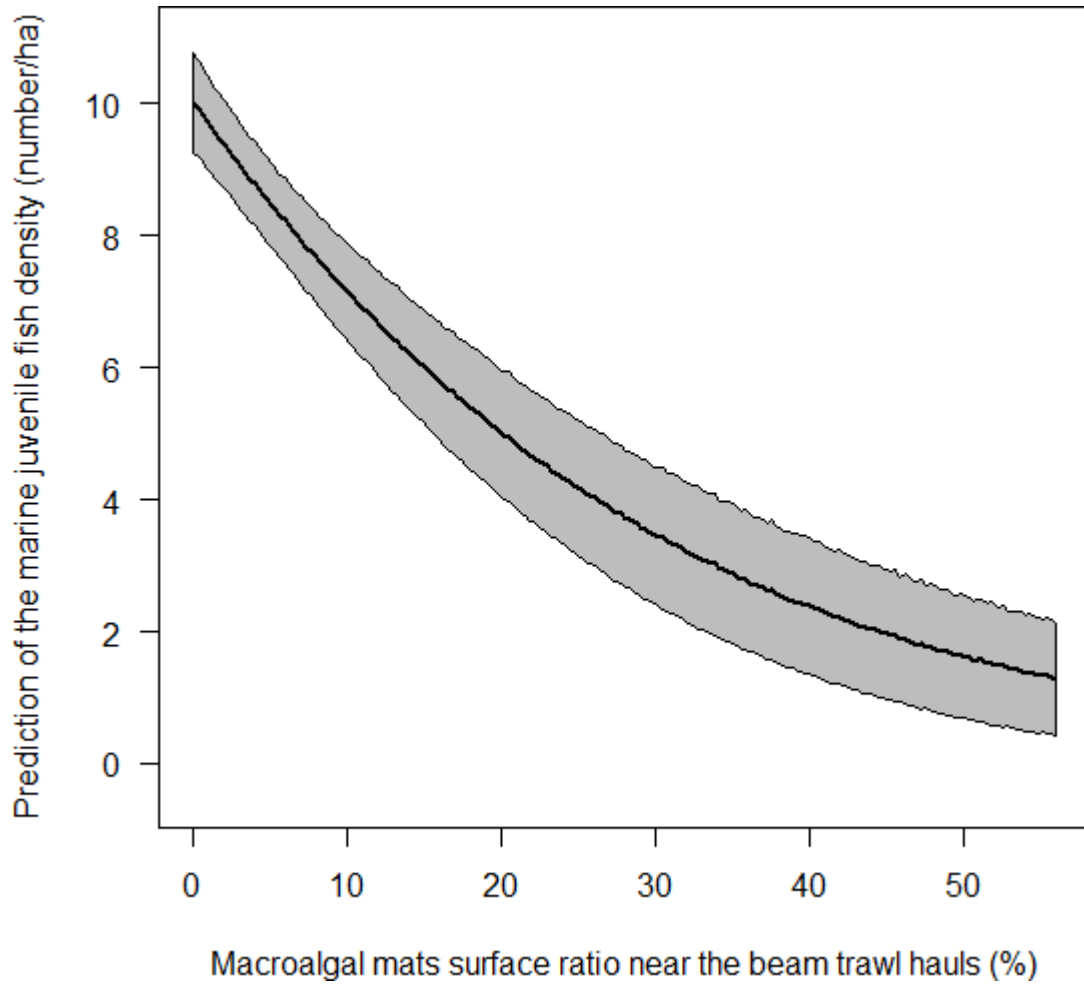
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635 FIGURE 2

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638 FIGURE 3



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640 Table 1: Total estuary area and intertidal area (ha) (Teichert et al, 2018), mean ecological 641 quality ratio (EQR) and the Estuarine and Lagoon Fish Index (ELFI, Delpech et al. 2010, 642 Lepage et al. 2016) and the associated scores for the thirteen studied estuaries.

Estuary	Total area (ha)	Intertidal area (ha)	EQR (mean)	EQR score	ELFI (mean)	ELFI (Score)
Aber Wrach	699	594	0.60	Good	0.46	Moderate
Aulne	1831	973	0.60	Good	0.59	Moderate
Aven	166	116	0.74	Good	0.88	Good
Belon	183	128	0.96	High	0.88	High
Blavet-Scorff	1531	863	0.47-0.8		0.67	High
Elorn	631	324	0.66	Good	0.96	Good
Goyen	155	111	0.93	High	0.65	Moderate
Laita	247	125	1.00	High	0.77	Good
Morlaix river	1361	1146	0.48	Moderate	0.44	Good
Odet	900	529	0.82	High	0.21	Good
Pont l'Abbe	646	545	0.43	Moderate	0.67	High
Trieux	777	478	0.55	Moderate	0.67	Bad

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645 Table 2: Definition of the three vertical distribution guilds and the two selected ecological 646 guilds (based on Franco et al., 2008; Potter et al., 2015).

Guild	Criterion	Definition
Pelagic	Vertical distribution	Species living in the water column
Demersal	Vertical distribution	Species living in the water layer just above the bottom
Benthic	Vertical distribution	Species living on the substratum
Marine juvenile	Ecology	Species using the shallow coastal waters and estuaries primarily as nursery grounds
Resident	Ecology	Species spending their whole life cycle in shallow coastal waters and estuaries

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649 Table 3: Description of the four indicators of green tide proliferation.

Indicator	Spatial scale	Variable	Green tide indicator	Available data
GT1	Large scale	Factor	Ecological quality ratio (EQR)	2008-2014
GT2	Local scale	Continuous	Macroalgal mat surface ratio on the trawl haul (percentage)	2008-2014
GT3	Local scale	Continuous	Macroalgal mat surface ratio near beam trawl hauls (percentage)	2008-2014
GT4	Local scale	Continuous	<i>Ulva</i> spp. density per beam trawl haul (kg.m <sup>-2</sup> )	2013-2014

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653 Table 4: Statistical significance of the generalized linear models of the fish metrics for the probability of presence, the positive densities and the 654 species richness, and for the two GT indicators (large scales: GT1 and local scale: GT3). NS: nonsignificant; p-value: \* $\leq$ 5%, \*\* $\leq$ 1% and 655 \*\*\* $\leq$ 0.1%.

Fish metrics	Model	Spring				Autumn			
		Environmental drivers	+ Large-scale effect (GT1)	Or +	Local-scale effect (GT3)	Environmental drivers	+ Large-scale effect (GT1)	Or +	Local-scale effect (GT3)
Density	Pres-abs	Depth (***) + Ecoregion (***)	*		NS	Depth (***)		NS	NS
	>0	Depth (***) + Ecoregion (**)	*		NS	Depth (***)	***		*
Species richness		Depth (***) + Ecoregion (**)	***		NS	Ecoregion (***) + Depth (*)	***		NS
Benthic guild density	Pres-abs	Ecoregion (***) + Salinity (***)	***		NS	Ecoregion (***)	*		NS
	>0	Ecoregion (***) + Salinity (***)	**		NS	Ecoregion (***)	***		*
Demersal guild density	Pres-abs	None	***		NS	Depth (***)	NS		NS
	>0	None	***		NS	Depth (***)	***		***
Pelagic guild density	Pres-abs	Class of salinity (***) + depth (**)	***		NS	None	***		NS
Resident guild density	Pres-abs	Depth (***)	***	*		Depth (***)	**		NS
	>0	Depth (***)	***		NS	Depth (***)	***		***
MJ guild density	Pres-abs	Salinity (***) + Ecoregion (**)	***		NS	None	**		***
	>0	Ecoregion (***) + Salinity (***)	**		NS	None	***		**

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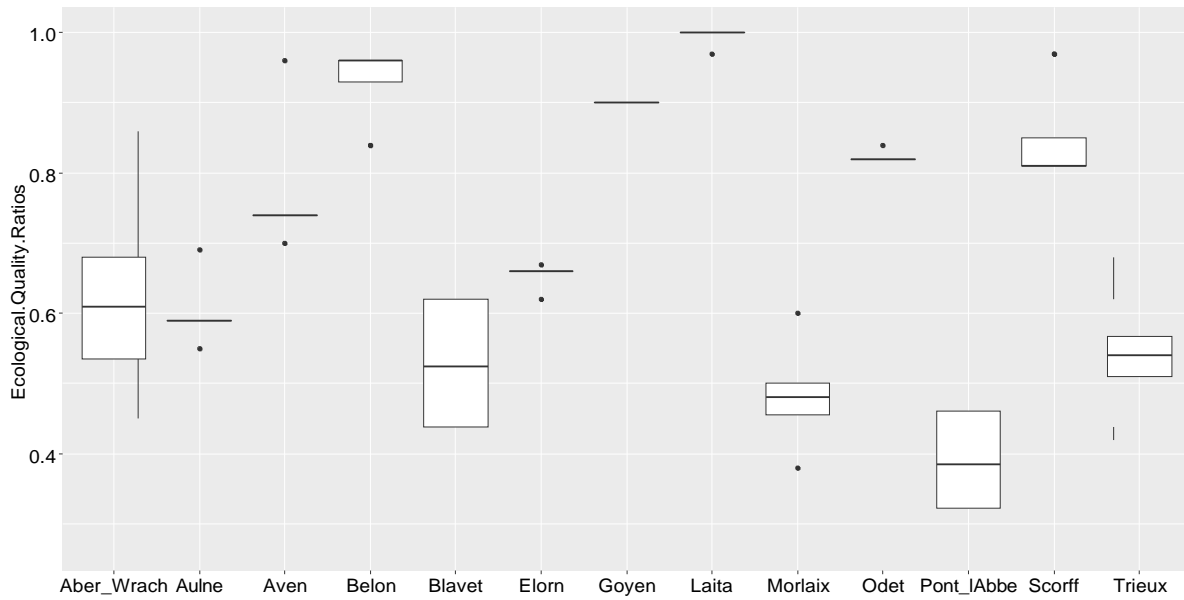
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659 **Appendix**

660 **Appendix 1**

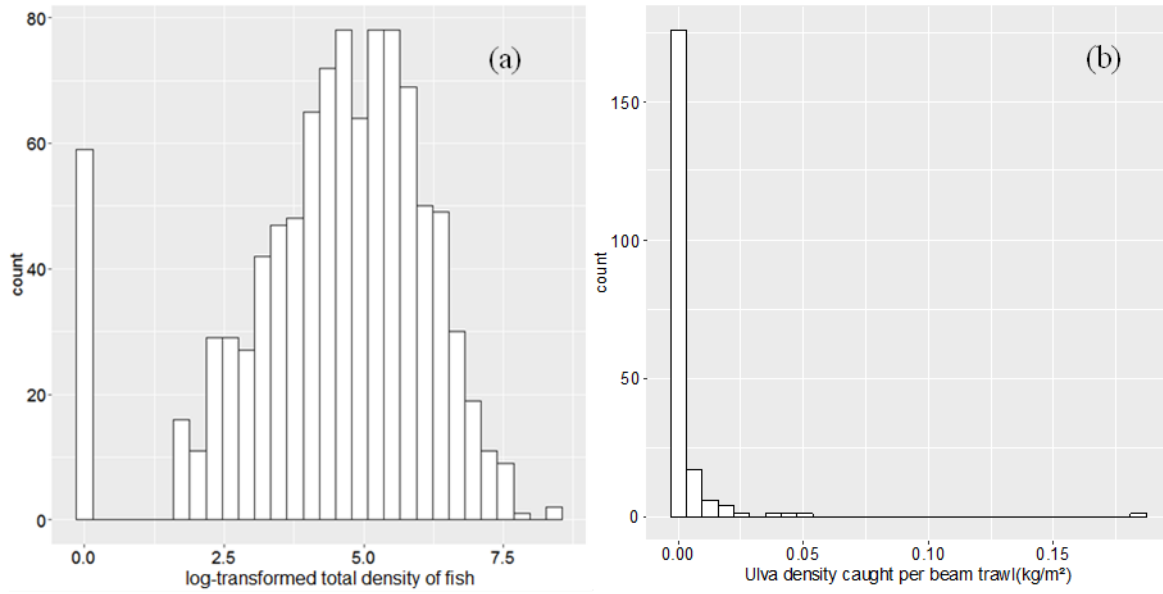
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663 **Supp. Fig. 1.1 Ecological quality ratios of the thirteen estuaries from 2008 to 2014**  
664 **(boxplots: thick line: median; box: from the 0.25 quartile to the 0.75 quartile; whiskers:**  
665 **1.5 times the distance between the quartiles; circles: outlier values).**

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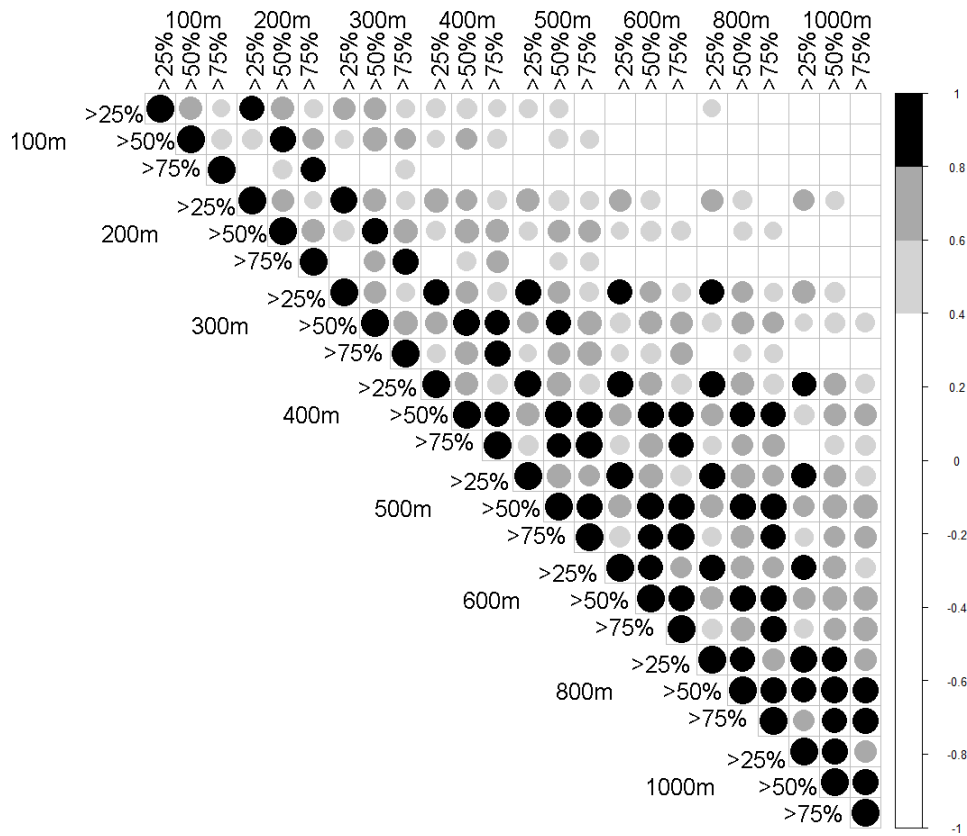
**Supp. Fig. 1.2. (a) Spring distribution of the log-transformed total density of fish from the entire sampling of the thirteen estuaries; (b) distribution of *Ulva* spp. density (kg/m<sup>2</sup>) caught per beam trawl in 2013 and 2014.**

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676 **Appendix 2 – Sensibility analysis for the proximity index**



Supp. Fig. 2.2. Correlation matrix between the radius areas and the different algal density thresholds. The size and the color of circles represent the different levels of correlation.

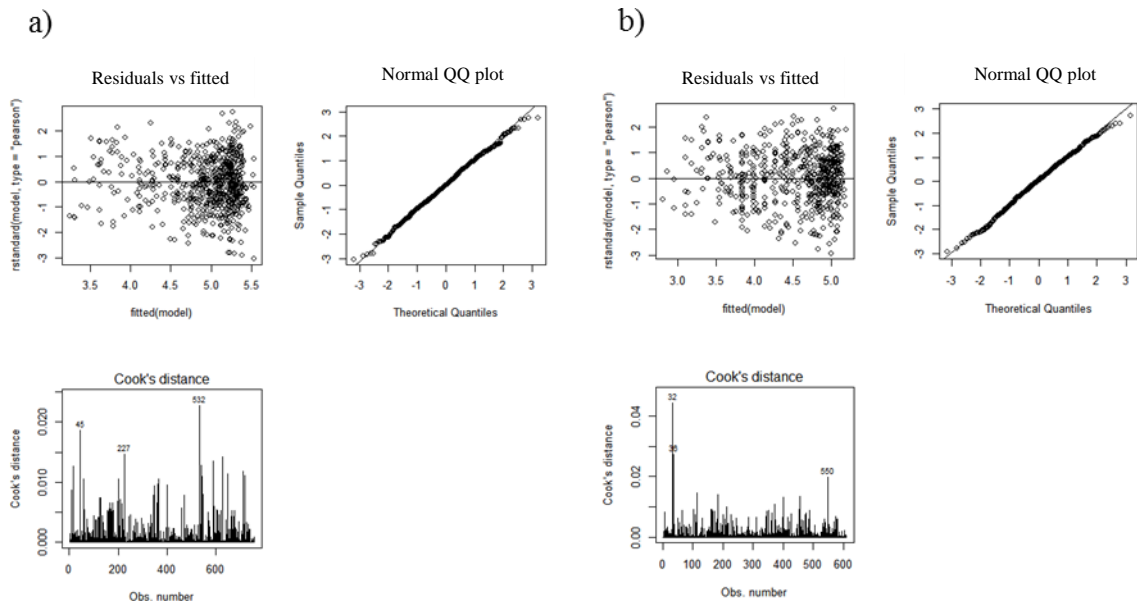
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680 **Appendix 3 – Validation of the GLM models on positive density**



681 **Supp. Fig. 3.1. Validation of the GLMs on the positive density for the total density of fish (log scale) in: (a) autumn, (b) spring.**

682 **Supp. Table 3.1. Goodness-of-fit for the Binomial sub-models. AUC values and the p-**  
 683 **values associated.**

	spring		autumn	
	Area under curve	p value	Area under curve	p value
Presence of fish	0.79	***	0.67	***
Presence of the benthic guild	0.84	***	0.70	***
Presence of the demersal guild	NA	NA	0.67	***
Presence of the pelagic guild	0.67	***	NA	NA
Presence of the resident guild	0.61	***	0.62	***
Presence of the marine juvenile	0.76	***	NA	NA

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