

Impacts of green tides on estuarine fish assemblages

Paumier A.^{1,2,*}, Tatlian T.¹, Reveillac E.¹, Le Luherne Emilie^{1,3}, Ballu S.⁴, Lepage M.²,
 Le Pape Olivier¹

¹ Agrocampus Ouest, INRA, Ecol & Ecosyst Hlth, ESE, F-35042 Rennes, France.

² Irstea, EABX, Aquat Ecosyst & Global Changes, F-33612 Cestas, France.

³ IFREMER, Dept Fisheries Sci & Technol, F-29280 Plouzane, France.

⁴ CEVA, Presquile Pen Lan BP3, F-2610 Pleubian, France.

* Corresponding author : A. Paumier, email address : alexis.paumier@irstea.fr

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 Airolidi, 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 m² 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 Fish metrics ~ environmental variables + GT* (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 Species richness ~ (environmental variables) + (GT*) + ε (link function = log) (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 $Y_{(1/0)} \sim (\text{environmental variables}) + (GT^*) + \varepsilon$ (link function = logistic) (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 $\text{Log}(Y_{(>0)}) \sim (\text{environmental variables}) + (GT^*) + \varepsilon$ (link function = identity) (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)

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

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

2.5.3 Preliminary analysis and modelling options

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

The GLM approach requires linearity in the relations between the response variable and the covariates. This assumption was preliminarily tested before the integration of the environmental variables (e.g., depth and salinity, and ecoregion was a class factor) as linear factors in the GLM. For depths down to 16 m, we observed atypical observations and non-linear effects on fish metrics. Thus, to account for the linear effect of depth, we removed trawl samples 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/m², 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/m² in spring and 0.18 kg/m² 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/m² 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.

408 **5 References**

- 409 Adams, S.M., 2005. Assessing cause and effect of multiple stressors on marine systems. Mar.
410 Pollut. Bull. 51, pp. 649–657. <https://doi.org/10.1016/j.marpolbul.2004.11.040>
- 411 Aitchison, J., 1955. On the Distribution of a Positive Random Variable Having a Discrete
412 Probability Mass at the Origin. J. Am. Stat. Assoc. 50, pp. 901.
413 <https://doi.org/10.2307/2281175>
- 414 Aitchison, J., Brown, J.A.C., 1957. The lognormal distribution, Cambridge University Press.
- 415 Anderson, C.R., Moore, S.K., Tomlinson, M.C., Silke, J., Cusack, C.K., 2015. Living with
416 Harmful Algal Blooms in a Changing World, in: Coastal and Marine Hazards, Risks,
417 and Disasters. Elsevier, pp. 495–561.
- 418 Andrade, R., Gomes, M.P., Pereira-Filho, G.H., Souza-Filho, J.F., Albuquerque, C.Q.,
419 Martins, A.S., 2014. The influence of allochthonous macroalgae on the fish
420 communities of tropical sandy beaches. Estuar. Coast. Shelf Sci. 144, pp. 75–81.
421 <https://doi.org/10.1016/j.ecss.2014.04.014>
- 422 Baden, 1990. Eutrophication on Benthic Communities Including Fish: Swedish West Coast.
423 AMBIO J. Hum. Environ. 19.
- 424 Beck, M., Airolidi, L., 2007. Loss, Status and Trends for Coastal Marine Habitats of Europe,
425 in: Gibson, R., Atkinson, R., Gordon, J. (Eds.), Oceanography and Marine Biology.
426 CRC Press, pp. 345–405.
- 427 Blaber, S.J.M., Blaber, T.G., 1980. Factors affecting the distribution of juvenile estuarine and
428 inshore fish. J. Fish Biol. 17, pp. 143–162. <https://doi.org/10.1111/j.1095-8649.1980.tb02749.x>
- 429 Bowen, J.L., Valiela, I., 2001. The ecological effects of urbanization of coastal watersheds:
430 historical increases in nitrogen loads and eutrophication of Waquoit Bay estuaries.
431 Can. J. Fish. Aquat. Sci. 58, pp. 1489–1500. <https://doi.org/10.1139/f01-094>
- 432 Bray, J.R., Curtis, J.T., 1957. An ordination of the upland forest communities of Southern
433 Wisconsin. Ecol. Monogr. 27, pp. 326–349. doi: 10.2307/1942268
- 434

- 435 Bricker, S.B., Longstaff, B., Dennison, W., Jones, A., Boicourt, K., Wicks, C., Woerner, J.,
436 2008. Effects of nutrient enrichment in the nation's estuaries: A decade of change.
437 Harmful Algae 8, pp. 21–32. <https://doi.org/10.1016/j.hal.2008.08.028>
- 438 Brown, E.J., Vasconcelos, R.P., Wennhage, H., Bergström, U., Støttrup, J.G., van de
439 Wolfshaar, K., Millisenda, G., Colloca, F., Le Pape O. (in press). Conflicts in the
440 coastal zone: A rapid assessment of human impacts on commercially important fish
441 species utilizing coastal habitat. *Ices Journal of Marine Science*.
442 <https://doi.org/10.1093/icesjms/fsx237>
- 443 Courrat, A., Lobry, J., Nicolas, D., Laffargue, P., Amara, R., Lepage, M., Girardin, M., Le
444 Pape, O., 2009. Anthropogenic disturbance on nursery function of estuarine areas for
445 marine species. *Estuar. Coast. Shelf Sci.* 81, pp. 179–190.
446 <https://doi.org/10.1016/j.ecss.2008.10.017>
- 447 Delpech, C., Courrat, A., Pasquaud, S., Lobry, J., Le Pape, O., Nicolas, D., Boët, P., Girardin,
448 M., Lepage, M., 2010. Development of a fish-based index to assess the ecological
449 quality of transitional waters: The case of French estuaries. *Mar. Pollut. Bull.* 60, pp.
450 908–918. <https://doi.org/10.1016/j.marpolbul.2010.01.001>
- 451 Diaz, R.J., Rosenberg, R., 2008. Spreading Dead Zones and Consequences for Marine
452 Ecosystems. *Science* 321, pp. 926–929. <https://doi.org/10.1126/science.1156401>
- 453 Elliott, M., Dewailly, F., 1995. The structure and components of European estuarine fish
454 assemblages. *Neth. J. Aquat. Ecol.* 29, pp. 397–417.
455 <https://doi.org/10.1007/BF02084239>
- 456 Elliott, M., Quintino, V., 2007. The Estuarine Quality Paradox, Environmental Homeostasis
457 and the difficulty of detecting anthropogenic stress in naturally stressed areas. *Mar.*
458 *Pollut. Bull.* 54, pp. 640–645. <https://doi.org/10.1016/j.marpolbul.2007.02.003>
- 459 Fletcher, R.L., 1996. The Occurrence of “Green Tides”— a Review, in: Schramm, D.W.,
460 Nienhuis, P.D.P.H. (Eds.), *Marine Benthic Vegetation, Ecological Studies*. Springer
461 Berlin Heidelberg, pp. 7–43.
- 462 Franco, A., Elliott, M., Franzoi, P., Torricelli, P., 2008. Life strategies of fishes in European
463 estuaries: the functional guild approach. *Mar. Ecol. Prog. Ser.* 354, pp. 219–228.
464 <https://doi.org/10.3354/meps07203>

- 465 Gibson, R.N., 1994. Impact of habitat quality and quantity on the recruitment of juvenile
466 flatfishes. Neth. J. Sea Res. 32, pp. 191–206. [https://doi.org/10.1016/0077-
467 7579\(94\)90040-X](https://doi.org/10.1016/0077-7579(94)90040-X)
- 468 Hastie, T., Tibshirani, R., 1999. Generalized additive models. Chapman & Hall/CRC, Boca
469 Raton, Fla.
- 470 Hodgkin, E.P., Birch, P.B., 1986. No simple solutions: Proposing radical management options
471 for an eutrophic estuary. Mar. Pollut. Bull. 17, pp. 399–404.
472 [https://doi.org/10.1016/0025-326X\(86\)90317-6](https://doi.org/10.1016/0025-326X(86)90317-6)
- 473 Howell, P.T., Molnar, D.R., Harris, R.B., 1999. Juvenile winter flounder distribution by
474 habitat type. Estuaries Coasts 22, pp. 1090–1095.
- 475 Hull, S.C., 1987. Macroalgal mats and species abundance: a field experiment. Estuar. Coast.
476 Shelf Sci. 25, pp. 519–532. [https://doi.org/10.1016/0272-7714\(87\)90112-0](https://doi.org/10.1016/0272-7714(87)90112-0)
- 477 Isaksson, I., Pihl, L., van Montfrans, J., 1994. Eutrophication-related changes in
478 macrovegetation and foraging of young cod (*Gadus morhua* L.): a mesocosm
479 experiment. J. Exp. Mar. Biol. Ecol. 177, pp. 203–217. [https://doi.org/10.1016/0022-
480 0981\(94\)90237-2](https://doi.org/10.1016/0022-0981(94)90237-2)
- 481 Jokinen, H., Wennhage, H., Lappalainen, A., Ådjers, K., Rask, M., Norkko, A., 2015. Decline
482 of flounder (*Platichthys flesus* (L.)) at the margin of the species' distribution range. J.
483 Sea Res. 105, pp. 1–9. <https://doi.org/10.1016/j.seares.2015.08.001>
- 484 Laurent, A.G., 1963. The Lognormal Distribution and the Translation Method: Description
485 and Estimation Problems. J. Am. Stat. Assoc. 58, pp. 231–235.
486 <https://doi.org/10.1080/01621459.1963.10500844>
- 487 Le Luherne, E., Le Pape, O., Murillo, L., Randon, M., Lebot, C., Réveillac, E., 2017.
488 Influence of Green Tides in Coastal Nursery Grounds on the Habitat Selection and
489 Individual Performance of Juvenile Fish. Plos one 12,
490 <https://doi.org/10.1371/journal.pone.0170110>
- 491 Le Luherne, E., Réveillac, E., Ponsero, A., Sturbois, A., Ballu, S., Perdriau, M., Le Pape, O.,
492 2016. Fish community responses to green tides in shallow estuarine and coastal areas.
493 Estuar. Coast. Shelf Sci. 175, pp. 79–92. <https://doi.org/10.1016/j.ecss.2016.03.031>

- 494 Le Pape, O., Bonhommeau, S., 2015. The food limitation hypothesis for juvenile marine fish.
495 Fish Fish. 16, pp. 373–398. <https://doi.org/10.1111/faf.12063>
- 496 Le Pape, O., Chauvet, F., Mahévas, S., Lazure, P., Guérault, D., Désaunay, Y., 2003.
497 Quantitative description of habitat suitability for the juvenile common sole (*Solea*
498 *solea*, L.) in the Bay of Biscay (France) and the contribution of different habitats to the
499 adult population. J. Sea Res. 50, pp. 139–149. <https://doi.org/10.1016/S1385->
500 1101(03)00059-5
- 501 Lehvo, A., Bäck, S., 2001. Survey of macroalgal mats in the Gulf of Finland, Baltic Sea.
502 Aquat. Conserv. Mar. Freshw. Ecosyst. 11, pp. 11–18. <https://doi.org/10.1002/aqc.428>
- 503 Lepage, M., Harrison, T., Breine, J., Cabral, H., Coates, S., Galván, C., García, P., Jager, Z.,
504 Kelly, F., Mosch, E.C., Pasquaud, S., Scholle, J., Uriarte, A., Borja, A., 2016. An
505 approach to intercalibrate ecological classification tools using fish in transitional water
506 of the North East Atlantic. Ecol. Indic. 67, 318–327.
507 <https://doi.org/10.1016/j.ecolind.2016.02.055>
- 508 Levin, S.A., 1992. The problem of pattern and scale in ecology. Ecology 73, pp. 1943–1967.
- 509 Liu, D., Keesing, J.K., He, P., Wang, Z., Shi, Y., Wang, Y., 2013. The world's largest
510 macroalgal bloom in the Yellow Sea, China: Formation and implications. Estuar.
511 Coast. Shelf Sci. 129, pp. 2–10. <https://doi.org/10.1016/j.ecss.2013.05.021>
- 512 Lyons, D.A., Arvanitidis, C., Blight, A.J., Chatzinikolaou, E., Guy-Haim, T., Kotta, J., Orav-
513 Kotta, H., Queirós, A.M., Rilov, G., Somerfield, P.J., Crowe, T.P., 2014. Macroalgal
514 blooms alter community structure and primary productivity in marine ecosystems.
515 Glob. Change Biol. 20, pp. 2712–2724. <https://doi.org/10.1111/gcb.12644>
- 516 Manel, S., Williams, H.C., Ormerod, S.J., 2002. Evaluating presence-absence models in
517 ecology: the need to account for prevalence: Presence-absence modelling. J. Appl.
518 Ecol. 38, pp. 921–931. <https://doi.org/10.1046/j.1365-2664.2001.00647.x>
- 519 Mason, N.W.H., Mouillot, D., Lee, W.G., Wilson, J.B., 2005. Functional richness, functional
520 evenness and functional divergence: the primary components of functional diversity.
521 Oikos 111, pp. 112–118. <https://doi.org/10.1111/j.0030-1299.2005.13886.x>

- 522 Ménesguen, A., Piriou, J.-Y., 1995. Nitrogen loadings and macroalgal (*Ulva* sp.) Mass
523 Accumulation in Brittany (France). *Ophelia* 42, pp. 227–237.
- 524 <https://doi.org/10.1080/00785326.1995.10431506>
- 525 Merceron, M., Antoine, V., Auby, I., Morand, P., 2007. In situ growth potential of the
526 subtidal part of green tide forming *Ulva* spp. stocks. *Sci. Total Environ.* 384, pp. 293–
527 305. <https://doi.org/10.1016/j.scitotenv.2007.05.007>
- 528 Nicolas, D., Lobry, J., Le Pape, O., Boët, P., 2010. Functional diversity in European estuaries:
529 Relating the composition of fish assemblages to the abiotic environment. *Estuar.
530 Coast. Shelf Sci.* 88, pp. 329–338. <https://doi.org/10.1016/j.ecss.2010.04.010>
- 531 Nixon, S.W., 1995. Coastal marine eutrophication: A definition, social causes, and future
532 concerns. *Ophelia* 41, pp. 199–219. <https://doi.org/10.1080/00785236.1995.10422044>
- 533 Österblom, H., Hansson, S., Larsson, U., Hjerne, O., Wulff, F., Elmgren, R., Folke, C., 2007.
534 Human-induced Trophic Cascades and Ecological Regime Shifts in the Baltic Sea.
535 *Ecosystems* 10, pp. 877–889. <https://doi.org/10.1007/s10021-007-9069-0>
- 536 Pennington, M., 1983. Efficient Estimators of Abundance, for Fish and Plankton Surveys.
537 *Biometrics* 39, pp. 281. <https://doi.org/10.2307/2530830>
- 538 Peterson, M.S., 2003. A Conceptual View of Environment-Habitat-Production Linkages in
539 Tidal River Estuaries. *Rev. Fish. Sci.* 11, pp. 291–313.
540 <https://doi.org/10.1080/10641260390255844>
- 541 Peterson, Summerson, Thomson, Lenihan, Grabowsk, Manning, Micheli, Johnson, 2000.
542 Synthesis of linkages between benthic and fish communities as a key to protecting
543 essential fish habitat. *Bull. Mar. Sci.* 66, pp. 759–774.
- 544 Pihl, L., Isaksson, I., Wennhage, H., Moksnes, P.-O., 1995. Recent increase of filamentous
545 algae in shallow Swedish bays: Effects on the community structure of epibenthic
546 fauna and fish. *Netherland J. Aquat. Ecol.* 29, pp. 349–358.
547 <https://doi.org/10.1007/BF02084234>
- 548 Pihl, L., Modin, J., Wennhage, H., 2005. Relating plaice (*Pleuronectes platessa*) recruitment
549 to deteriorating habitat quality: effects of macroalgal blooms in coastal nursery
550 grounds. *Can. J. Fish. Aquat. Sci.* 62, pp. 1184–1193. <https://doi.org/10.1139/f05-023>

- 551
552 Potter, I.C., Tweedley, J.R., Elliott, M., Whitfield, A.K., 2015. The ways in which fish use
553 estuaries: a refinement and expansion of the guild approach. Fish Fish. 16, pp. 230–
554 239. <https://doi.org/10.1111/faf.12050>
- 555 Quillien, N., Nordström, M., Gauthier, O., Bonsdorff, E., Paulet, Y., Grall, J., 2015. Effects of
556 macroalgal accumulations on the variability in zoobenthos of high-energy macrotidal
557 sandy beaches. Mar. Ecol. Prog. Ser. 522, pp. 97–114.
558 <https://doi.org/10.3354/meps11151>
- 559 R Development Core Team (2016). R: A language and environment for statistical computing.
560 R Foundation for Statistical Computing, Vienna, Austria. URL [http://www.R-
561 project.org/](http://www.R-project.org/).
- 562 Raffaelli, D.G., Raven, J.A., Poole, L.J., 1998. Ecological impact of green macroalgal
563 blooms. Oceanogr. Mar. Biol. Annu. Rev. 36, pp. 97–125.
- 564 Scanlan, C.M., Foden, J., Wells, E., Best, M.A., 2007. The monitoring of opportunistic
565 macroalgal blooms for the water framework directive. Mar. Poll. Bull. 55, pp. 162–
566 171. <https://doi.org/10.1016/j.marpolbul.2006.09.017>.
- 567 Seitz, R.D., Wennhage, H., Bergstrom, U., Lipcius, R.N., Ysebaert, T., 2014. Ecological
568 value of coastal habitats for commercially and ecologically important species. ICES J.
569 Mar. Sci. 71, pp. 648–665. <https://doi.org/10.1093/icesjms/fst152>
- 570 Sfriso, A., Pavoni, B., 1994. Macroalgae and phytoplankton competition in the central Venice
571 lagoon. Environ. Technol. 15, 1–14. <https://doi.org/10.1080/09593339409385399>
- 572 Smetacek, V., Zingone, A., 2013. Green and golden seaweed tides on the rise. Nature 504,
573 pp. 84–88. <http://dx.doi.org/10.1038/nature12860>.
- 574 Solidoro C, Brando VE, Dejak C, Franco D, Pastres R, Pecenik G, 1997. Long term
575 simulations of population dynamics of *Ulva r.* in the lagoon of Venice. Ecol
576 Model.;102, pp. 259–72.
- 577 Spalding, M.D., Fox, H.E., Allen, G.R., Davidson, N., Ferdaña, Z.A., Finlayson, M., Halpern,
578 B.S., Jorge, M.A., Lombana, A., Lourie, S.A., Martin, K.D., McManus, E., Molnar, J.,
579 Recchia, C.A., Robertson, J., 2007. Marine Ecoregions of the World: A

- 580 Bioregionalization of Coastal and Shelf Areas. BioScience 57, pp. 573–583.
581 <https://doi.org/10.1641/B570707>
- 582 Stefansson, G., 1996. Analysis of groundfish survey abundance data: combining the GLM and
583 delta approaches. ICES J. Mar. Sci. 53, pp. 577–588.
584 <https://doi.org/10.1006/jmsc.1996.0079>
- 585 Stoner, A., Manderson, J., Pessutti, J., 2001. Spatially explicit analysis of estuarine habitat for
586 juvenile winter flounder: combining generalized additive models and geographic
587 information systems. Mar. Ecol. Prog. Ser. 213, pp. 253–271.
588 <https://doi.org/10.3354/meps213253>
- 589 Sundbäck, K., Carlson, L., Nilsson, C., Jönsson, B., Wulff, A., Odmark, S., 1996. Response
590 of benthic microbial mats to drifting green algal mats. Aquat. Microb. Ecol. 10, pp.
591 195–208. <https://doi.org/10.3354/ame010195>
- 592 Valiela, McClelland, Hauxwell, Behr, Hersh, Foreman, 1997. Macroalgal blooms in shallow
593 estuaries: controls and ecophysiological and ecosystem consequences. Limnol.
594 Oceanogr. 42, 1105–1118.
- 595 Vasconcelos, R.P., Le Pape, O., Costa, M.J., Cabral, H.N. (2013) Predicting estuarine use
596 patterns of juvenile fish with Generalized Linear Models. Estuar, Coast. Shelf Sci. 120
597 ,pp. 64-74.
- 598 Villéger, S., Mason, N.W.H., Mouillot, D., 2008. New multidimensional functional diversity
599 indices for a multifaceted framework in functional ecology. Ecology 89, pp. 2290–
600 2301. <https://doi.org/10.1890/07-1206.1>
- 601 Wennhage, H., 2002. Vulnerability of newly settled plaice (*Pleuronectes platessa* L.) to
602 predation: effects of habitat structure and predator functional response. J. Exp. Mar.
603 Biol. Ecol. 269, pp. 129–145. [https://doi.org/10.1016/S0022-0981\(02\)00005-9](https://doi.org/10.1016/S0022-0981(02)00005-9)
- 604 Wennhage, H., Pihl, L., 2007. From flatfish to sticklebacks: assemblage structure of
605 epibenthic fauna in relation to macroalgal blooms. Mar. Ecol. Prog. Ser. 335, pp. 187–
606 198. <https://doi.org/10.3354/meps335187>
- 607 Wheatley, M., Johnson, C., 2009. Factors limiting our understanding of ecological scale. Ecol.
608 Complex. 6, pp. 150–159. <https://doi.org/10.1016/j.ecocom.2008.10.011>

- 609 Wilkes, R., Best, M., Scanlan, C., Rossi, N., Kolbe, K., Salas Herrero, F., 2014.
- 610 Intercalibration of opportunistic macroalgae in coastal and transitional waters v4. UE
- 611 Water Framework Directive intercalibration technical report.22p.
- 612 Ye, N., Zhang, X., Mao, Y., Liang, C., Xu, D., Zou, J., Zhuang, Z., Wang, Q., 2011. “Green
- 613 tides” are overwhelming the coastline of our blue planet: taking the world's largest example.
- 614 Ecol. Res. 26, pp. 477-485. <http://dx.doi.org/10.1007/s11284-011- 0821-8>

615 **Figure captions**

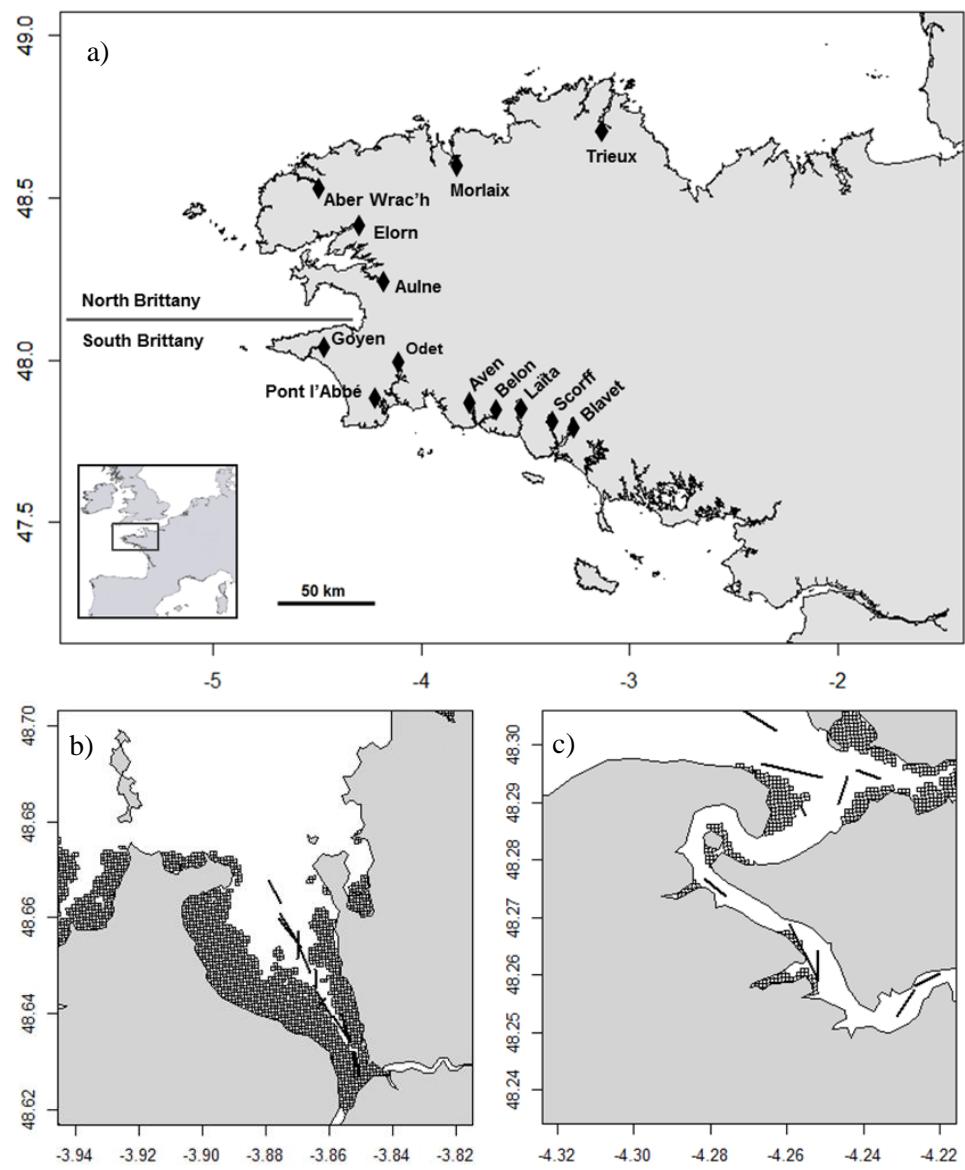
616 Figure 1: a) Locations (in WGS84 coordinates) of the studied estuaries in northwestern France
617 split into two ecoregions: north and south. The spatial protocol for the fish survey is provided
618 as an example for 2 of the thirteen estuaries studied, in (b) the Morlaix Estuary and (c) the
619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

620

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.

625

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.

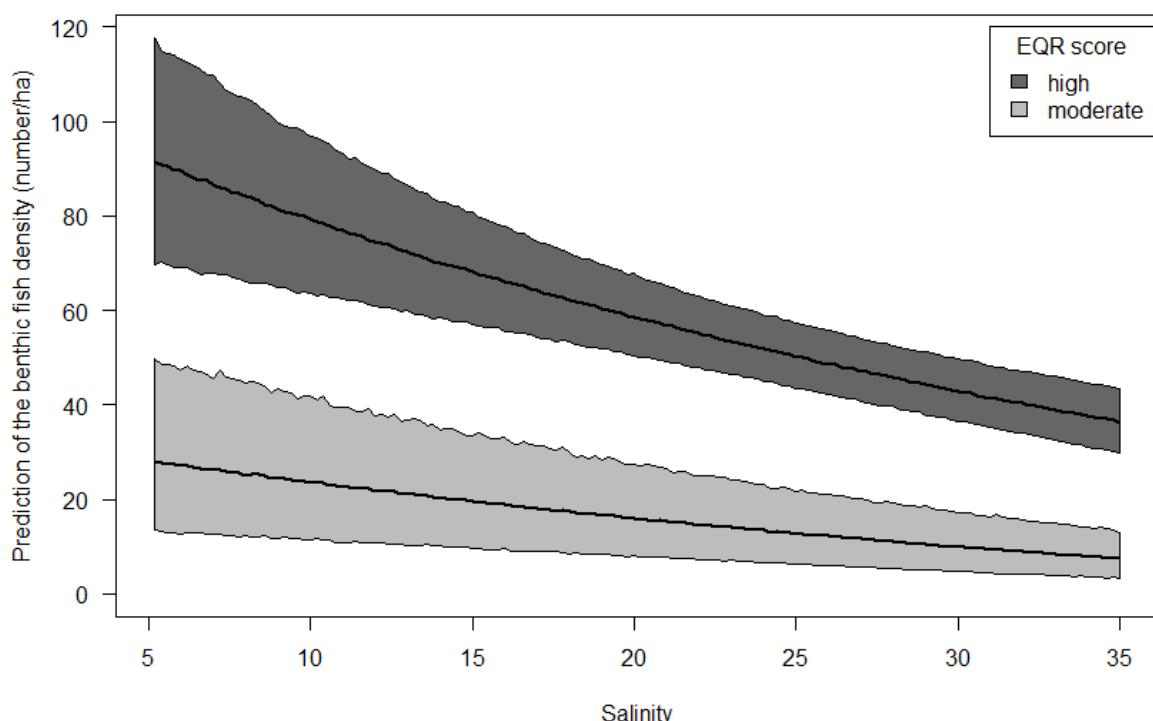


630

631 FIGURE 1

632

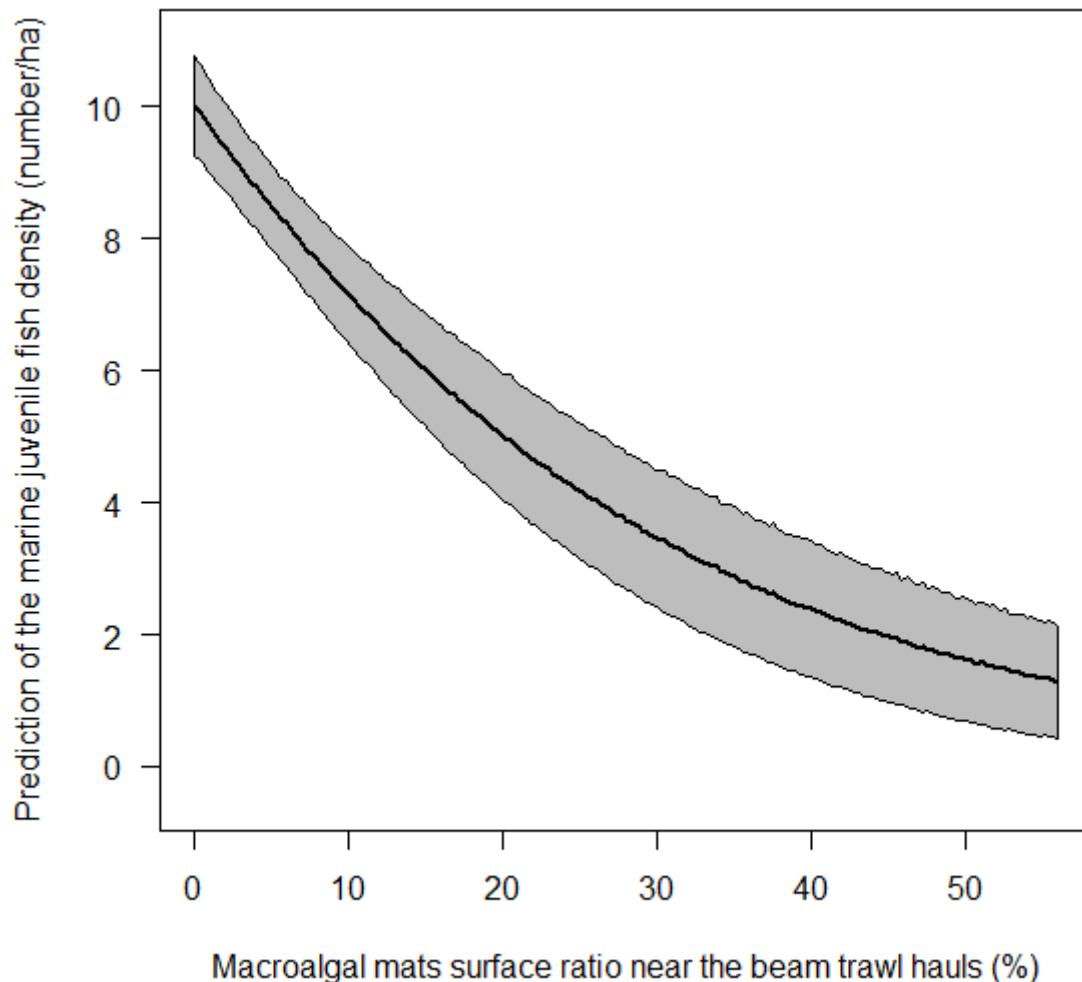
633



634

635 FIGURE 2

636



637

638 FIGURE 3

639

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

643

644

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

647

648

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^{-2})	2013-2014

650

651

652

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		***	**

656

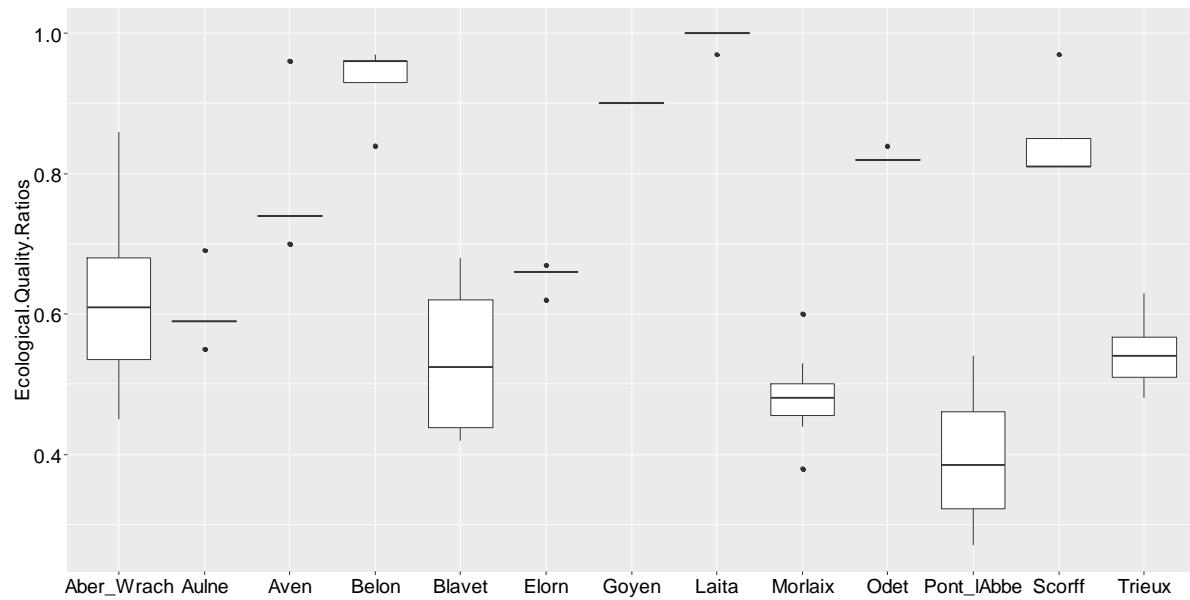
657

658

659 **Appendix**

660 **Appendix 1**

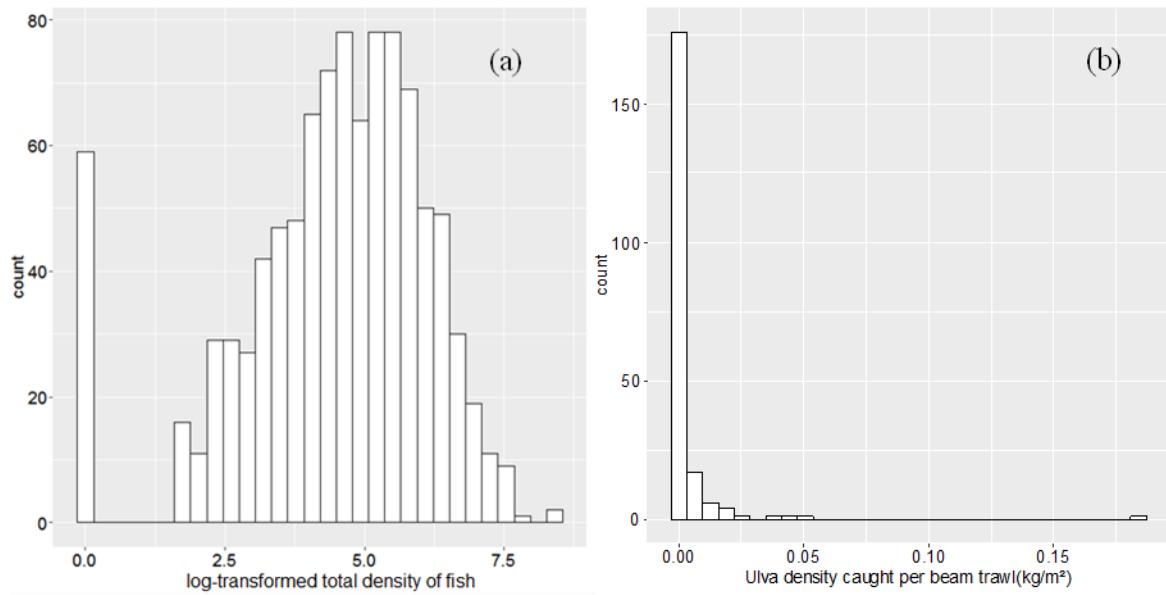
661



662

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).**

666



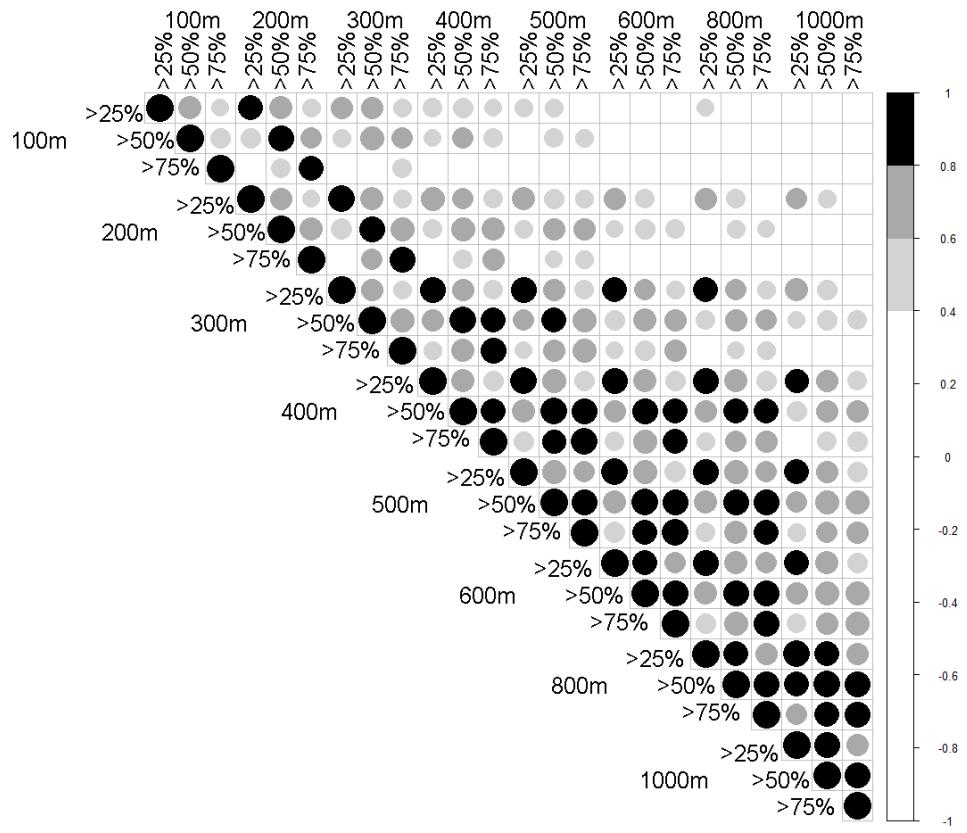
672

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^2) caught per beam trawl in 2013 and 2014.

673
674

675

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.

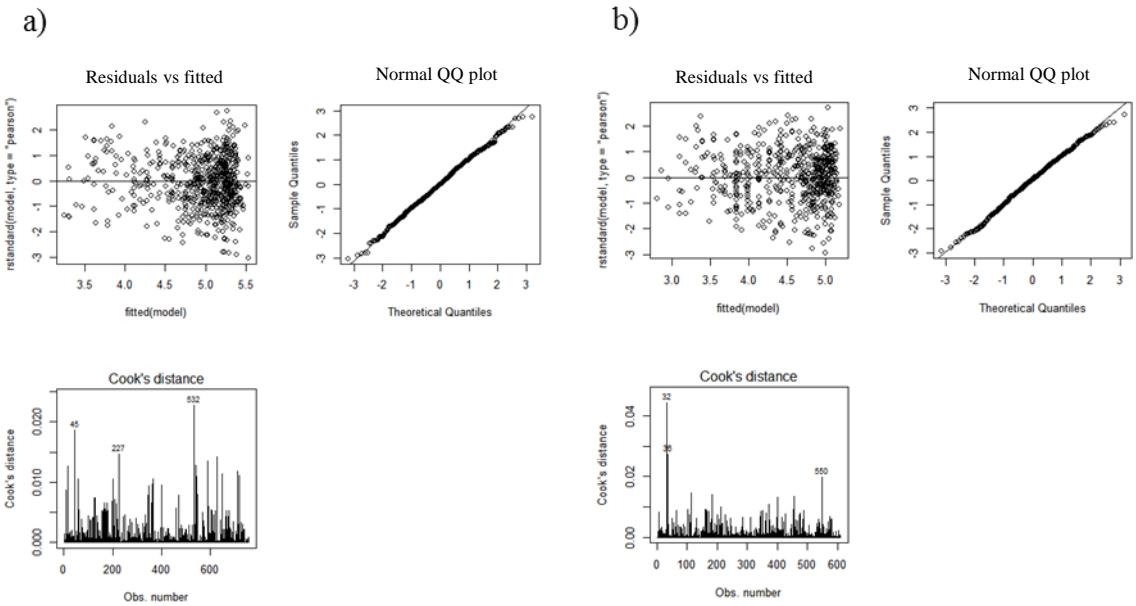
676

677

678

679

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



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.

681
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

684
685
686