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# Green macroalgae blooms (*Ulva* spp.) influence trophic ecology of juvenile flatfish differently in sandy beach nurseries

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1 **Green macroalgae blooms (*Ulva* spp.) influence trophic ecology of juvenile flatfish differently in sandy**  
2 **beach nurseries**

3 **Short title:** Green macroalgae and juvenile flatfish trophic ecology

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16

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## 23 1. Introduction

24 Sandy beaches are the most common littoral ecosystem, covering 70% of the global coastline free  
25 from ice (McLachlan and Brown, 2006). This ecosystem, regulated mainly by tides, is characterized by  
26 extreme environmental conditions (*e.g.* temperature, exposure to wind and waves, loose nature of the  
27 substratum) (Defeo and McLachlan, 2005). Despite these conditions, specialized and diverse invertebrate  
28 and vertebrate fauna are associated with the surf zone of sandy beaches (McLachlan and Brown, 2006).  
29 During their first year of life, many flatfish species (*e.g.* *Pleuronectes platessa*, *Scophthalmus maximus*)  
30 concentrate (Iles and Beverton, 2000) along sandy beaches (Gibson, 1994; McLachlan and Brown, 2006)  
31 that function as nursery grounds (Beck et al., 2001). Flatfish nurseries are characterized by suitable abiotic  
32 conditions over large spatial scales (*e.g.* temperature, depth, substratum) (Able et al., 2005), while local  
33 biotic conditions (*e.g.* prey and predator abundance) determine their quality (Le Pape et al., 2007; Vinagre  
34 et al., 2006). Overall, juvenile flatfish growth and survival are promoted in these habitats (De Raedemaeker  
35 et al., 2012), whose quantity and quality strongly influence the annual recruitment of juveniles to the adult  
36 stock (Gibson, 1994; Rochette et al., 2010).

37 Since the 1970s, blooms of opportunistic macroalgae have increased in frequency and intensity  
38 worldwide (Smetacek and Zingone, 2013), affecting sandy beaches mostly during spring and summer, when  
39 the algae are ultimately stranded and accumulate (Morand and Merceron, 2005). These short-lived  
40 macroalgae blooms are a symptom of coastal eutrophication caused by excessive discharge of nitrate and  
41 phosphate into aquatic ecosystems (Teichberg et al., 2010), related mainly to agricultural fertilization and  
42 waste disposal (Cloern, 2001). Opportunistic macroalgae blooms are called green tides (GT) when they are  
43 composed of seaweeds from the Phylum Chlorophyta (Smetacek and Zingone, 2013; Van Alstyne et al.,  
44 2015).

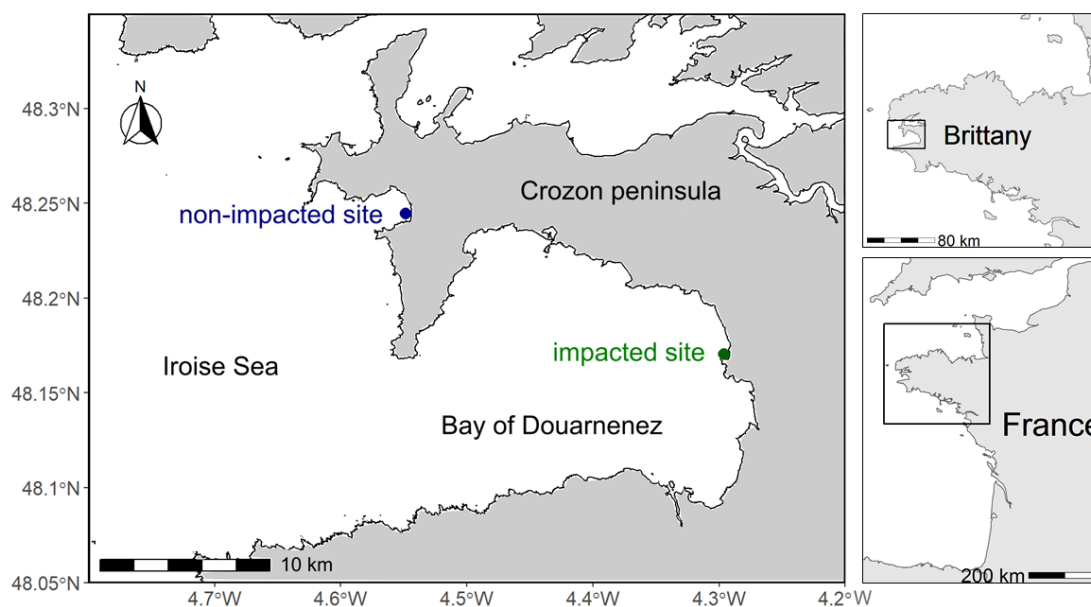
45 Shifts in fish assemblages have been related to GT (Paumier et al., 2018; Pihl et al., 1995; Quillien  
46 et al., 2018; Wennhage and Pihl, 2007), and benthic fish species, such as flatfish, have been found to be the  
47 most negatively impacted, with generally lower densities reported at sites with GT (De Raedemaeker et  
48 al., 2012; Le Luherne et al., 2017, 2016). Overall, opportunistic macroalgae blooms can decrease the quality  
49 of flatfish nurseries (De Raedemaeker et al., 2012; Jokinen et al., 2016), potentially leading to lower annual  
50 recruitment rates to the adult stock (Pihl et al., 2005). Meio- and macrobenthic invertebrates, the main prey  
51 of juvenile flatfish (Amara et al., 2001; Cabral et al., 2002), are also modified by macroalgae blooms in  
52 terms of their taxonomic richness, composition, abundance, biomass and functional groups (Carriço et al.,  
53 2013; Pihl et al., 1995; Quillien et al., 2015a, 2015b). Furthermore, juvenile flatfish can experience lower  
54 foraging success when drifting macroalgae are added to bare sand, as shown experimentally for *Platichthys*  
55 *flesus* and *S. maximus* (Aarnio and Mattila, 2000; Nordström and Booth, 2007). Consequently, GT could  
56 modify flatfish trophic ecology (*e.g.* diet, prey preference, energy intake) through their effects on flatfish

57 prey and on flatfish foraging, first leading to lower body conditions and growth rates (Andersen et al., 2005;  
58 Le Luherne et al., 2017; Pihl, 1994) and ultimately to lower recruitment rates (Pihl et al., 2005), through  
59 food limitation (Le Pape and Bonhommeau, 2013).

60           Nonetheless, opportunistic and short-term macroalgae blooms can provide an additional source  
61 of organic matter (*i.e.* basal resource) for sandy-beach invertebrates (Quillien et al., 2016; Robertson and  
62 Lenanton, 1984) and lead to higher benthic invertebrate densities (Bolam et al., 2000; Quillien et al., 2015a,  
63 2015b). Consequently, opportunistic macroalgae (*e.g.* *Ulva* spp.) could represent an additional source of  
64 energy for juvenile flatfish via their benthic prey (Robertson and Lenanton, 1984), one that is traceable  
65 using stable isotopes. Indeed, *Ulva* spp. have distinctly <sup>13</sup>C-enriched carbon isotopic compositions relative  
66 to marine suspended particulate organic matter (SPOM) (*i.e.* mainly phytoplankton) and sediment organic  
67 matter (SOM) (*i.e.* detritus, microphytobenthos, deposited phytoplankton) (Dubois and Colombo, 2014;  
68 Quillien et al., 2016), the two main basal resources available at bare sandy beaches. Furthermore, the  
69 presence of extensive *Ulva* mats can modify the carbon isotopic compositions of dissolved inorganic carbon  
70 (Van Alstyne et al., 2015), leading to <sup>13</sup>C enrichment of SPOM (Quillien et al., 2016).

71           To our knowledge, few studies have investigated *in situ* effects of opportunistic macroalgae  
72 blooms or related phenomenon (*e.g.* hypoxia) on the trophic ecology of juvenile flatfish (Andersen et al.,  
73 2005; Pihl, 1994; Robertson and Lenanton, 1984). Those that have were based on digestive tract contents,  
74 which provide direct information about the prey ingested by a predator in the last hours or days before  
75 sampling, depending on the predator's digestion rate (Nielsen et al., 2018). However, this source of  
76 information can be biased by small sample sizes, asynchrony between a predator's foraging time and the  
77 sampling time, and prey digestibility (Baker et al., 2014). Carbon and nitrogen isotopic compositions can  
78 reflect the trophic resources assimilated by a consumer over much longer periods (Nielsen et al., 2018), as  
79 well as strong environmental signals such as GT (Quillien et al., 2016).

80           In this study, the effects of GT (*Ulva* spp.) on the trophic niche, foraging behavior and additional  
81 basal resource use of juvenile flatfish were investigated in macrotidal sandy beach nurseries. We combined  
82 carbon and nitrogen isotopic compositions of predator (flatfish) and potential prey (benthic  
83 macroinvertebrates), predator digestive tract contents and potential prey abundances in an approach  
84 comparing a site not impacted by GT to a site impacted by GT. During the early summer GT peak, we  
85 focused on three nursery-dependent flatfish species – the sand sole *Pegusa lascaris*, the plaice *P. platessa*  
86 and the turbot *S. maximus* (Gibson, 2005) – which co-occur in sandy beach nurseries in western Brittany,  
87 France (Déniel, 1981; Quillien et al., 2018). For *P. lascaris*, which remains in the coastal nurseries for over  
88 a year (Déniel, 1981), we also investigated temporal dynamics of its trophic ecology relative to the early  
89 summer GT peak.



90  
 91 **Figure 1.** Location (Brittany, France) of the two study sites: the sandy beach not impacted by green tides at  
 92 the western end of the Crozon peninsula (blue) and the sandy beach impacted by green tides on the eastern  
 93 side of the bay of Douarnenez (green).

94

95 **2. Materials and methods**

96 *2.1. Study system and GT*

97 We sampled the intertidal zone of two known flatfish nursery areas (Déniel, 1981; Quillien et al.,  
 98 2018; Quiniou, 1986) located in the same part of the Iroise Sea (Fig. 1). This water mass is located just off  
 99 the western tip of Brittany at the junction of the English Channel, Celtic Sea and Bay of Biscay. The non-  
 100 impacted site is a 2.3 km long sandy beach located at the western tip of the Crozon peninsula ( $48^{\circ} 14.682'$   
 101  $N$ ,  $4^{\circ} 32.908'$   $W$ ) that has never been impacted by GT (NIm). The impacted site (Im) is a 2.8 km long sandy  
 102 beach located on the eastern side of the Bay of Douarnenez ( $48^{\circ} 10.22'$   $N$ ,  $4^{\circ} 17.775'$   $W$ ) that has been  
 103 impacted by GT every year since the 1970s due to the presence of intensive agricultural areas in the  
 104 neighboring catchment (Perrot et al., 2014). These two beaches have a similar mean breaking-wave height  
 105 (1.4 m) and mean tidal regimes (6.5 m), which classify them as ultra-dissipative. Both also are characterized  
 106 by fine sand, gentle slopes (1.5%) and wide intertidal zones (up to 500 m during spring tides). These  
 107 similarities allow them to be compared in relation to the presence or absence of GT (Quillien et al., 2018).  
 108 All the environmental parameters that describe the morphology, sediment and overlaying water at each site  
 109 (Table S1) were retrieved from Quillien et al. (2015a, 2015b).

110 The GT at the Im site have been surveyed every month from April-October since 2007 (until  
111 present) by the CEVA (Centre d'Etude et de Valorisation des Algues), using aerial overflight and field  
112 sampling, and in November 2012 by the authors of this study. These regular surveys led to the state of the  
113 Bay of Douarnenez being classified as “poor” for the opportunistic macroalgae index of the European Union  
114 Water Framework Directive in a 2012-2017 evaluation ([Atlas DCE Loire-Bretagne, IGN/SHOM/Ifremer](#)).  
115 Based on the total area (ha) of the intertidal zone covered by green macroalgae calculated by the CEVA,  
116 temporal dynamics of the GT has been characterized at the Im site in 2012 (Fig. 2). The period before June,  
117 with low *Ulva* cover, was considered “Pre GT”. The period from June to mid-July, with peak *Ulva* cover,  
118 was considered “Peak GT”. Finally, the two periods from mid-July to October and after October, with  
119 decreasing *Ulva* cover and little to no *Ulva* cover, respectively, were considered “Post GT1” and “Post  
120 GT2”, respectively (Fig. 2). The four periods identified at the Im site were also applied to the NIm site.

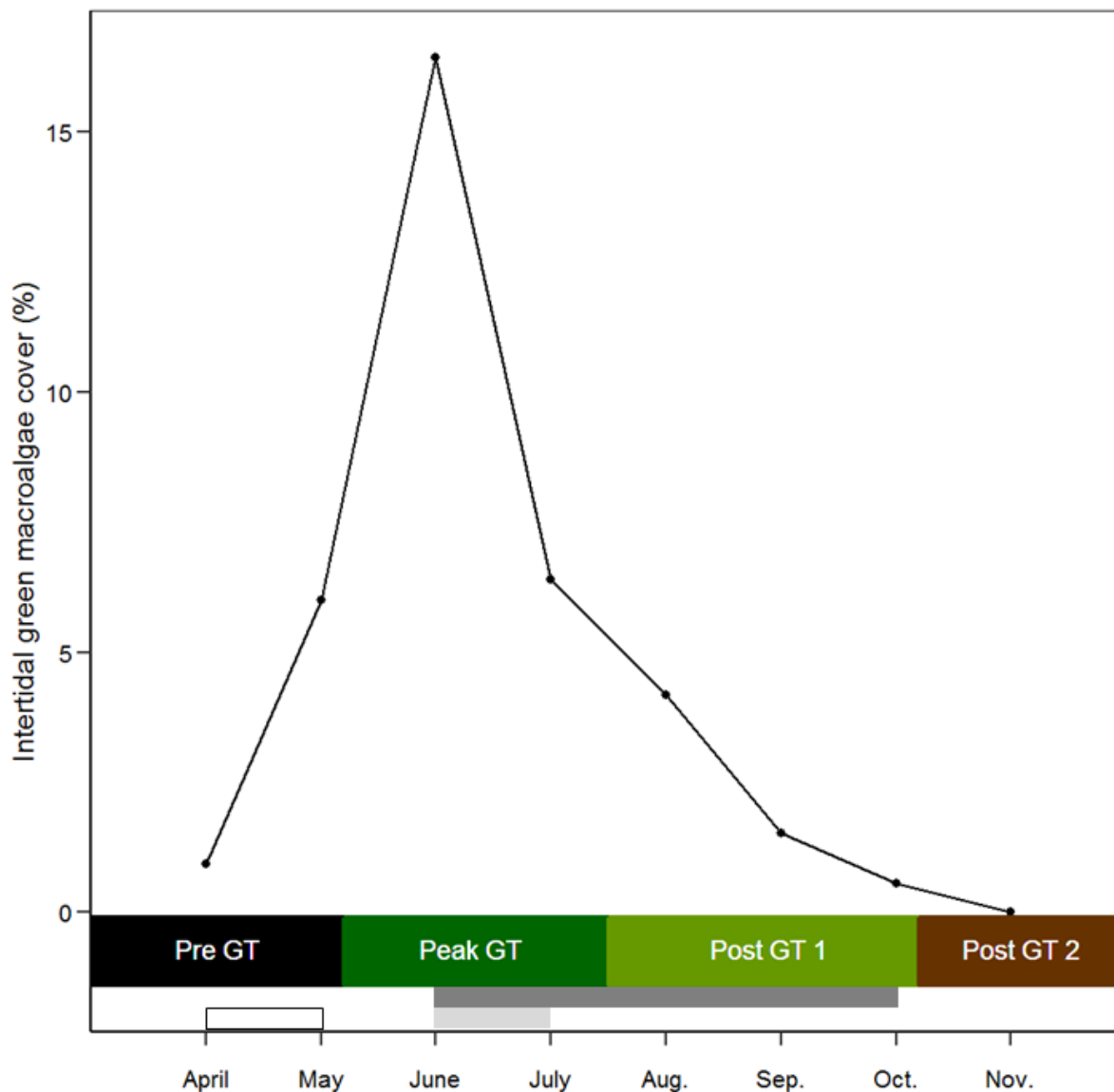
121

## 122 2.2. Sampling

123 Macroinvertebrates, representing the flatfish prey reservoir, were sampled once during the 2012 Pre  
124 GT (early May), Peak GT (early July), Post GT1 (early September) and Post GT2 (early November) periods  
125 at both sites during low tide. To determine macroinvertebrate composition and abundance, nine replicate  
126 sediment cores were randomly sampled on each sampling date along the NIm and Im beaches using a tube  
127 corer (total area = 0.09 m<sup>2</sup>). Samples were then sieved (1 mm mesh size) to retrieve the macroinvertebrates,  
128 which were preserved in 4% buffered formalin (Quillien et al., 2018). Later at the lab, the sediment samples  
129 were sorted, and the macroinvertebrates were identified to the lowest taxonomic level (usually species) and  
130 counted to determine their abundance. To consider potential intra-site variability in macroinvertebrate  
131 isotopic compositions, infaunal organisms were sampled at three points along each beach (min 500 m  
132 between each point) by digging up organisms from the sand and sieving large volumes of sediment (*ca.* 4  
133 L) with a 1 mm mesh sieve. Vagile epibenthic organisms were caught along each beach using a dip net.  
134 Later at the lab, these organisms were sorted and identified before being stored at -20°C for stable isotope  
135 analysis (Quillien et al., 2016).

136 Flatfish were sampled during the day at rising tide, using a beach trawl (5 m wide, 0.3 m high, with  
137 an 8 mm stretched mesh net in the cod-end) developed by [Quiniou \(1986\)](#). The beach trawl was towed at  
138 least once along each beach by two operators in 50 cm deep water, sampling an area of 400-1300 m<sup>2</sup>  
139 (Quillien et al., 2018). The flatfish were identified on site to the species level, counted and individually  
140 measured (total length). A subsample was collected for digestive tract analysis and preserved in 4% buffered  
141 formalin, while a second subsample was collected for stable isotope analysis and preserved at -20°C. The  
142 remaining flatfish were immediately released after being counted and measured. Only a limited number of

143 fish could be collected according to the regulations of the National Marine Park of the Iroise Sea, where the  
 144 study sites are located.



145  
 146 **Figure 2.** Monthly intertidal cover (%) of green macroalgae from April-November 2012 at the site impacted  
 147 by green tides (GT), calculated as the percentage of the intertidal zone covered by the sum of the beach area  
 148 covered by stranded macroalgae and the area of the breaking-wave zone with macroalgae. The temporal GT  
 149 pattern at the impacted site is divided into four periods: the period before the GT (Pre GT), the peak GT  
 150 period (Peak GT) and two periods after the GT (Post GT1 and Post GT2). Data come from the Centre  
 151 d'Etude et de Valorisation des Algues. White, light gray and dark gray bands indicate the settlement periods  
 152 of *P. platessa*, *S. maximus* and *P. lascaris*, respectively, in the coastal nurseries of the Bay of Douarnenez  
 153 (Déniel, 1981).

154 Since *P. lascaris* juveniles stay in the intertidal zone for up to two years (Déniel, 1981), individuals  
155 at both sites were sampled during the four GT periods, as reported by Quillien et al. (2018). Conversely, we  
156 did not sample *P. platessa* during Post GT2, since juveniles had already moved to deeper waters, or *S.*  
157 *maximus* during Pre GT, since larvae only arrive in June (Déniel, 1981). Consequently, we restricted  
158 temporal investigation of the effects of GT on juvenile flatfish trophic ecology to *P. lascaris* and investigated  
159 species-specific effects of GT only during Peak GT, when all three species were sampled at both sites. All  
160 *P. platessa* and *S. maximus* sampled during Peak GT were categorized as young-of-the-year (G0) based on  
161 a total length less than 130 mm and 110 mm, respectively (Déniel, 1981). During Post GT2, we sampled  
162 G0 *P. lascaris* (total length  $\leq 90$  mm) that had settled in 2012, while during Pre GT, the G0 *P. lascaris*  
163 sampled (total length  $\leq 90$  mm) had settled in 2011 (Déniel, 1981; Quillien et al., 2018). During Peak GT  
164 and Post GT1, we sampled G0 (total length  $\leq 90$  mm) and G1 (total length  $> 90$  mm) *P. lascaris* that had  
165 settled in 2012 and 2011, respectively.

166

### 167 2.3. Sample preparation and analyses

168 For the stable isotope analysis, muscle tissue was sampled for large prey species (bivalves,  
169 echinoderms, some polychaetes) and the flatfish, while for the smallest prey species, pooled individuals (5-  
170 300 individuals), from which the gut had been removed, were used. For small echinoderms and crustaceans  
171 that contained calcium carbonate, a subsample was acidified (10% HCl) and used to determine carbon  
172 isotopic compositions, while a second subsample was kept intact and used to determine nitrogen isotopic  
173 compositions. All samples were then rinsed with Milli-Q water, oven-dried (48 h at 60°C), ground to powder  
174 and encapsulated in ultra-clean tin capsules. Isotope ratios of carbon and nitrogen were reported using the  
175 standard  $\delta$  notation of parts per thousand (‰) relative to international reference standards:  $\delta X =$   
176  $\left[ \left( \frac{R_{\text{sample}}}{R_{\text{reference}}} \right) - 1 \right] \times 1000$ , where  $X = {}^{13}\text{C}$  or  ${}^{15}\text{N}$ , and  $R = {}^{13}\text{C}:{}^{12}\text{C}$  or  ${}^{15}\text{N}:{}^{14}\text{N}$ . Vienna-Pee Dee  
177 Belemnite limestone and atmospheric nitrogen were used as reference standards for carbon and nitrogen,  
178 respectively. The analytical precision for both carbon and nitrogen was  $< 0.1\text{‰}$ . Full description of the  
179 stable isotope analysis is available in Quillien et al. (2016). According to laboratory studies, juvenile white  
180 fish muscle has an average isotopic turnover rate between a few days and a few weeks, depending on  
181 temperature and growth rate (Bosley et al., 2002; Suzuki et al., 2005).

182 To characterize the flatfish prey, individuals were dissected, their digestive tract (stomach + gut)  
183 was fixed in 4% buffered formalin and the organisms present were identified to the lowest taxonomic level  
184 using a binocular magnifier. Some prey items were in an advanced phase of digestion (e.g. polychaetes),  
185 which limited our ability to identify them beyond their order.

186

187



## 188 2.4. Data analyses

### 189 2.4.1. Potential flatfish prey

190 The macroinvertebrates considered as potential flatfish prey were grouped into “tropho-orders”  
191 according to (1) their dominant trophic group (carnivore = CAR, omnivore = OMN, deposit feeder = DF or  
192 suspension feeder = SF) following [Fauchald and Jumars \(1979\)](#), [Guerra-García et al. \(2014\)](#), [Jumars et al.](#)  
193 [\(2015\)](#), [Navarro-Barranco et al. \(2013\)](#), [Quillien et al. \(2018\)](#) and online trait databases (*i.e.* Marine Species  
194 Identification Portal, MarLIN, BIOTIC) and (2) their taxonomic order in the World Register of Marine  
195 Species (<http://www.marinespecies.org>). The taxa included in each tropho-order and according to each  
196 dataset (stable isotope, benthic community and digestive tract data sets) are shown in Table S2. Because  
197 spatio-temporal changes in the isotopic composition of a consumer can be traced to the isotopic composition  
198 of its assimilated prey (Nielsen et al., 2018; Yeakel et al., 2011), we tested the combined effect of time and  
199 GT (2 sites: NIm and Im) on the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of the tropho-orders for which we had sufficient data ( $n \geq 3$   
200 for each site, Table S3). Depending on the tropho-order, we performed one-way Type II analysis of variance  
201 (ANOVA) with one period and the two sites or two-way crossed ANOVAS (Type II or III) with multiple  
202 periods and the two sites using the ‘car’ package of R software version 3.4.0 (R Core Team, 2019). Type II  
203 or III ANOVAs were used to account for the unequal sample sizes of each group, and their results were  
204 reported if the interaction term was non-significant or significant, respectively (Shaw and Mitchell-Olds,  
205 1993). If an interaction term was significant, Tukey HSD post-hoc tests were performed using the ‘lsmeans’  
206 package. For each model, residuals were checked visually for normality using a histogram and for  
207 homoscedasticity by plotting them against the fitted values.

208

### 209 2.4.2. Trophic ecology description and comparisons of trophic metrics

210 To test if the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of G0 and G1 *P. lascaris* were significantly different according to time  
211 (four periods: Pre GT, Peak GT, Post GT1 and Post GT2) and GT (2 sites: NIm and Im), we performed  
212 multiple pairwise comparisons (t-tests) using a permutation procedure and the Hommel p-value adjustment  
213 method for multiple tests (‘rcompanion’ package). Multiple pairwise comparisons were chosen instead of  
214 ANOVA because G1 and G0 *P. lascaris* were sampled only during certain periods (“missing cells”).  
215 Permutation tests are non-parametric tests that address observations that are not normally distributed, which  
216 was the case for several groups (Legendre and Legendre, 2012). The Hommel adjustment method was  
217 chosen because it controls for family-wise error, does not assume that observations are normally distributed  
218 and is more powerful than Holm’s and Hochberg’s adjustment methods (Shaffer, 1995). Finally, for  
219 permutation tests with unequal sample sizes and unequal variances, a p-value of 0.05 is too liberal only if  
220 the group with the smaller sample size has the larger variance (Mewhort et al., 2009), which never occurred  
221 in our data. Consequently, a p-value of 0.05 was chosen without the risk of increasing Type I error. The

222 same procedure was used to test if the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of flatfish were significantly different according to  
223 group (G0 *P. lascaris*, G0 *P. platessa*, G0 *S. maximus* and G1 *P. lascaris*) and GT (2 sites: NIm and Im)  
224 during Peak GT. All differences in results were considered significant at  $\alpha = 0.05$ .

225 The digestive tract data were used to calculate each flatfish group's (a combination of site, period,  
226 species and age-class) vacuity rate (percentage of digestive tracts that were empty) and to characterize its  
227 diet according to each tropho-order's frequency of occurrence (percentage of digestive tracts in which the  
228 tropho-order was found) and relative abundance (percentage of tropho-order prey items out of total prey  
229 items). We also used the digestive tract data to measure the dietary similarity (DS) of two flatfish groups by  
230 calculating their proportional similarity index (Schoener, 1970), as recommended by Wallace (1981). DS  
231 was calculated as  $1 - 0.5 (\sum |p_{xi} - p_{yi}|)$ , where  $p_{xi}$  and  $p_{yi}$  are the mean proportions of tropho-order  $i$  ingested  
232 by group  $x$  and  $y$ , respectively and standardized between 0 and 1 ('spaa' package) with 1 indicating perfect  
233 dietary similarity.

234 The macroinvertebrates (potential prey) were sampled a few weeks before the flatfish (their  
235 predators) at each period. Consequently, the flatfish white muscle isotopic composition of a given period  
236 reflect that of their prey sampled at the same given period. To visualize potential trophic changes (isotopic  
237 niche width and position relative to tropho-orders) of *P. lascaris* (G0 and G1) in time and relative to the  
238 GT,  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of macroinvertebrate tropho-orders and *P. lascaris* at both sites (NIm and Im) were  
239 plotted for each of the four GT periods. To represent each group's total isotopic niche width, we added the  
240 convex hull polygons which encompass all the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of each *P. lascaris* group (Layman et al.,  
241 2007). We chose to represent the convex hull polygons instead of the standard ellipse area because it is  
242 easier to visualize on figures. The same kind of figure was plotted to visualize potential trophic changes in  
243 the four co-occurring flatfish groups (G0 *P. lascaris*, G0 *P. platessa*, G0 *S. maximus* and G1 *P. lascaris*)  
244 during Peak GT.

245 The standard ellipse area corrected for small sample sizes ( $\text{SEA}_C$ ) developed by Jackson et al. (2011)  
246 and the diet richness (number of prey tropho-orders) were calculated ('SIAR' and 'SIBER' packages) to  
247 estimate the isotopic niche width and diet niche width, respectively, of each flatfish group (population level).  
248 The  $\text{SEA}_C$  (strictly positive,  $\text{‰}^2$ ), which encompasses 40% of the isotopic compositions of each flatfish  
249 group, was preferred to Layman's convex hull (Layman et al., 2007) because extreme isotopic compositions  
250 bias it less (Brind'Amour and Dubois, 2013). This metric provides information on the level of isotopic prey  
251 diversity assimilated by a flatfish group during a given period function of the isotopic turnover rate, without  
252 providing any information on the intra-individual trophic diversity (*i.e.* individual specialization). To  
253 compare the size of two flatfish groups'  $\text{SEA}_C$ s, we considered their Bayesian distributions (Jackson et al.,  
254 2011) and calculated the probability that one  $\text{SEA}_C$  was smaller or larger than the other  $\text{SEA}_C$  ('SIAR' and  
255 'SIBER' packages). Furthermore, to help interpret variations in flatfish isotopic niches, we calculated the

256 potential prey isotopic niches (macroinvertebrate  $SEA_C$ ), excluding CAR-Nemerta (Table S2), CAR-other  
257 (*Planaria* sp.) and DF-other (*Orbinia* sp.) because species of these tropho-orders were never mentioned in  
258 studies of the diet of *P. lascaris*, *P. platessa* or *S. maximus* (e.g. Amara et al., 2001; Beyst et al., 1999;  
259 Cabral et al., 2002).

260 Finally, we estimated the amount of potential prey isotopic diversity assimilated by a flatfish group  
261 as the ratio of a flatfish group's  $SEA_C$  to the macroinvertebrate  $SEA_C$  ( $SEA_C$  ratio), expressed as a  
262 percentage. Following Kempf et al. (2008), we also calculated the proportional similarity index (Schoener,  
263 1970) between the digestive tract contents of a flatfish group and the benthic community to measure the  
264 extent to which a flatfish group used the potential prey community (benthic community dataset in Table  
265 S2). This measure, which we termed the dietary opportunism index (DO), was calculated as  $1 - 0.5 (\sum |p_{ij} -$   
266  $q_j|)$ , where  $p_{ij}$  is the mean proportion of the  $j^{\text{th}}$  tropho-order in the  $i^{\text{th}}$  flatfish group and  $q_j$  is the mean  
267 proportion of the  $j^{\text{th}}$  tropho-order in the sediment, and standardized between 0 and 1 ('spaa' package). A  
268 group has either opportunistic foraging behavior (DO close to 1) or selective foraging behavior (DO close  
269 to 0).

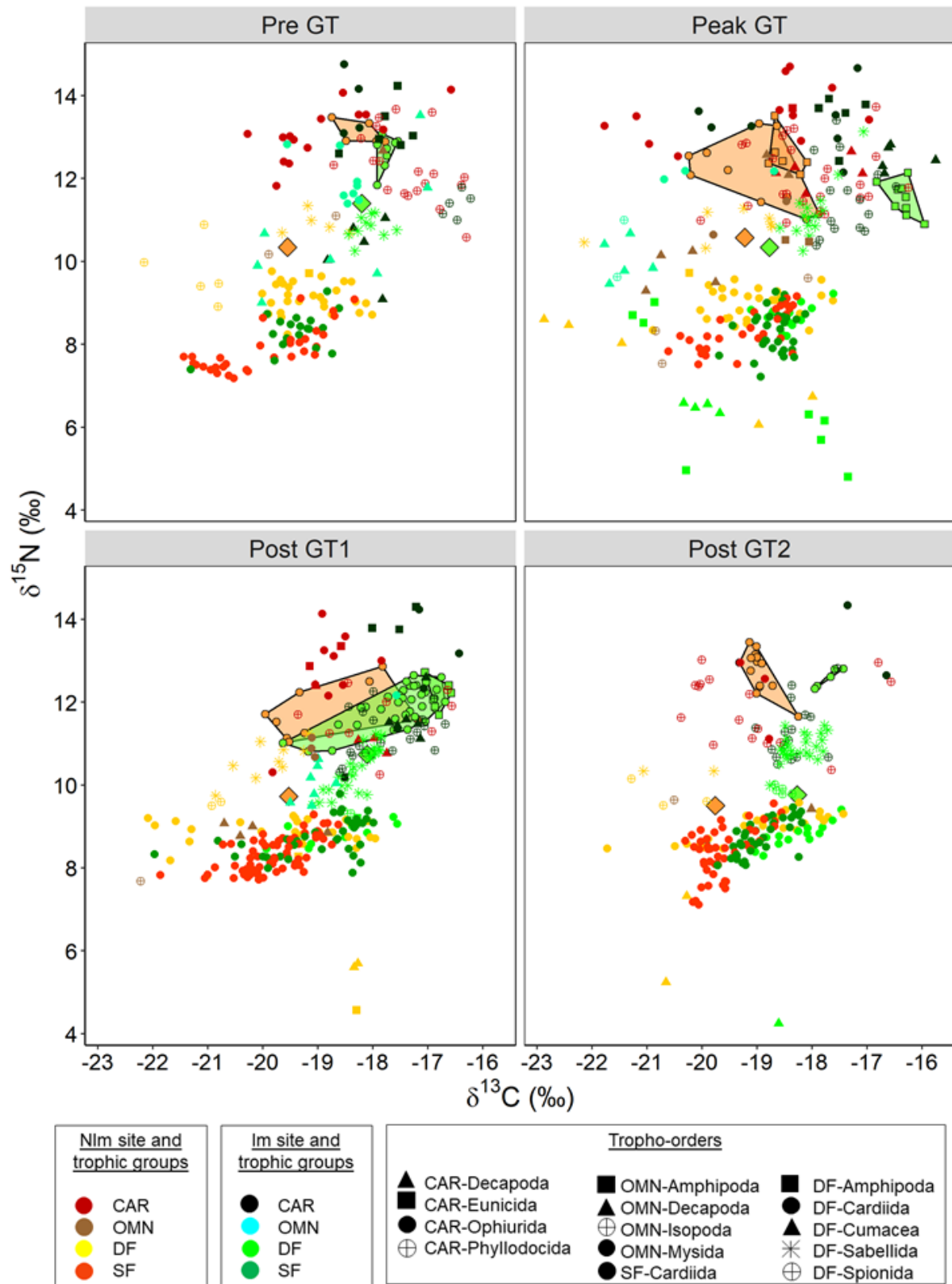
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### 271 3. Results

#### 272 3.1. Isotopic compositions of the flatfish potential prey (macroinvertebrates)

273 Across sites and periods,  $\delta^{13}C$  of macroinvertebrate tropho-orders ranged from -24‰ to -16‰ and  
274  $\delta^{15}N$  ranged from 4 to 15‰. Despite no statistical testing, primary consumers (SF and DF) had the lowest  
275  $\delta^{13}C$  and  $\delta^{15}N$ , secondary consumers (CAR) had the highest values, and OMN had intermediate and often  
276 highly variable values across sites and periods (Fig. 3, Table S3).

277 Seven of the nine tropho-orders investigated presented significantly higher mean  $\delta^{13}C$  at the Im than  
278 at the NIm site. The two bivalve tropho-orders, SF- and DF-Cardiida, presented this signal during all four  
279 periods or from Peak GT-Post GT2, respectively. All the CAR tropho-orders investigated also presented it,  
280 either during all four periods (Phyllodocida, Ophiurida) or during Peak GT and Post GT1 (Decapoda).  
281 OMN-Decapoda did not present this signal during Peak GT or Post GT1, and DF-Cumacea did not present  
282 it during Peak GT; conversely, DF-Sabellida did present it from Pre GT-Post GT1. Five of the nine tropho-  
283 orders showed no significant difference in mean  $\delta^{15}N$  between sites. CAR-Phyllodocida and DF-Cardiida  
284 presented significantly lower mean  $\delta^{15}N$  at the Im than at the NIm site, while the opposite was observed for  
285 CAR-Ophiurida. SF-Cardiida presented significantly higher mean  $\delta^{15}N$  at the Im than at the NIm site during  
286 Pre GT, Post GT1 and Post GT2 but not during Peak GT.



287

288 **Figure 3.**  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  (‰) of *Pegusa lascaris* age class 0 (blacklined circles) and age class 1 (black lined  
 289 squares) at the sandy beach not impacted by green tides (orange, NIm site) and the sandy beach impacted

290 by green tides (green, Im site) during the four green tide periods (Pre GT, Peak GT, Post GT1 and Post  
 291 GT2), with the corresponding convex hulls (orange and green polygons for the NIm and Im site,  
 292 respectively). The  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of the macroinvertebrates sampled at the same site and period are  
 293 represented using a combination of color (site and trophic group) and symbol (tropho-order). The orange  
 294 and green diamonds represent the centroid of the macroinvertebrate community at the NIm and Im sites,  
 295 respectively. CAR = carnivore, OMN = omnivore, DF = deposit feeder, SF = suspension feeder.

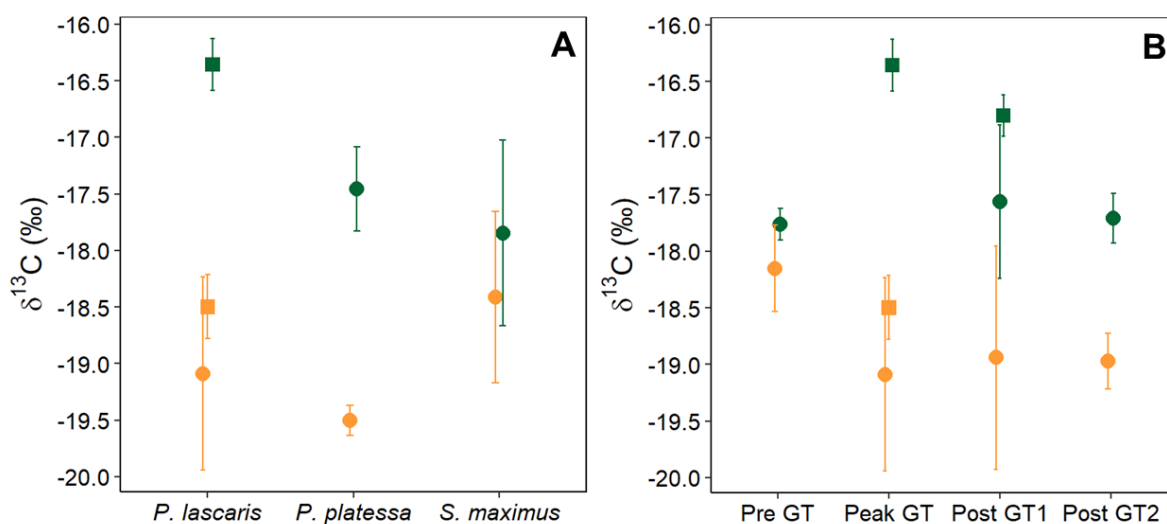
296

### 297 3.2. Species-specific trophic ecology during Peak GT and changes linked to GT

#### 298 3.2.1. Flatfish isotopic compositions and associated metrics

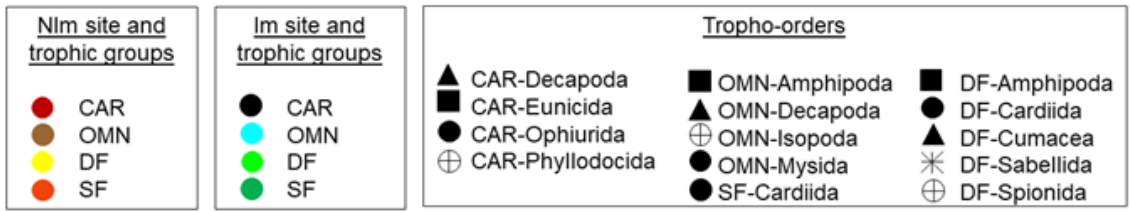
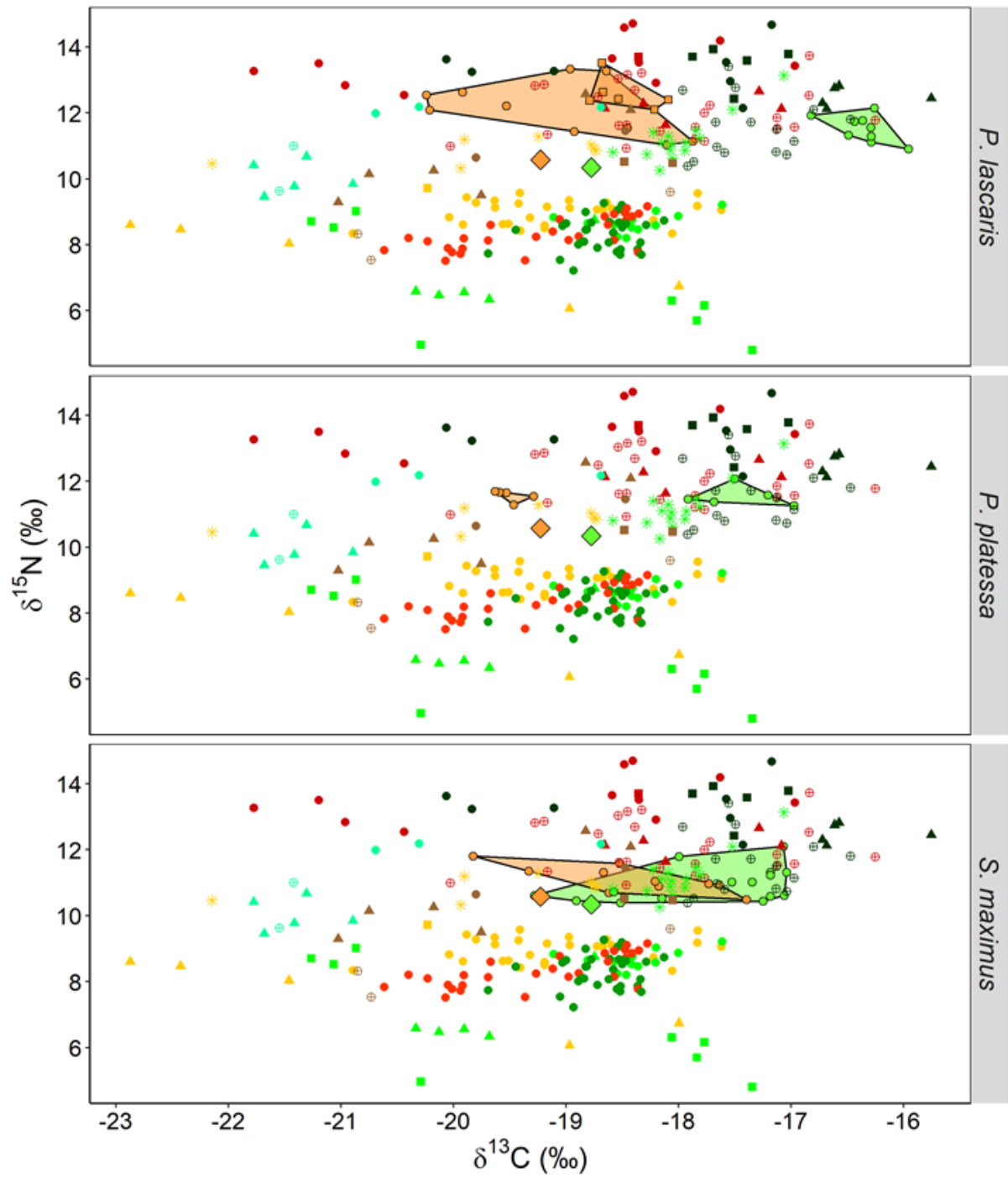
299 During the Peak GT, the isotopic composition of flatfish ranged from -20.2‰ to -16‰ for  $\delta^{13}\text{C}$  and  
 300 from 10.4‰ to 13.5‰ for  $\delta^{15}\text{N}$  (Figs. 4A and 5). At the NIm site, the flatfish groups had similar mean  $\delta^{13}\text{C}$   
 301 and  $\delta^{15}\text{N}$  with variable ranges (Figs. 4A and 5). Two inter-group differences were significant: G1 *P. lascaris*  
 302 had significantly higher  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  than *P. platessa* (t-stat = 2.92, adj. p = 0.03) and *S. maximus* (t-stat  
 303 = 3.35, adj. p = 0.01), respectively. Age-class 0 *P. lascaris* had the widest isotopic niche ( $\text{SEA}_C$ ), followed  
 304 by *S. maximus*, G1 *P. lascaris*, and then *P. platessa* (Bayesian probabilities > 0.83).

305



306  
 307 **Figure 4.** Mean and standard deviation of the  $\delta^{13}\text{C}$  of (A) age class 0 *P. lascaris* (circles) and age class 1 *P.*  
 308 *lascaris* (squares) during the four green tide periods (Pre GT, Peak GT, Post GT1 and Post GT2) and (B)  
 309 age class 0 flatfish (circles) and age class 1 flatfish (squares) during the peak green tide period at the sandy  
 310 beach not impacted by green tides (yellow) and the sandy beach impacted by green tides (green).

311



313 **Figure 5.**  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  (‰) of age class 0 (blacklined circles) and age class 1 (blacklined squares) of the  
 314 three flatfish species at the sandy beach not impacted by green tides (orange, NIm site) and the sandy beach  
 315 impacted by green tides (green, Im site) during the peak green tide period, with the corresponding convex  
 316 hulls (orange and green polygons for the NIm and Im site, respectively). The  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of the  
 317 macroinvertebrates sampled at the same site at the beginning of the peak green tide period are represented  
 318 using a combination of color (site and trophic group) and symbol (tropho-order). The orange and green  
 319 diamonds represent the centroid of the macroinvertebrate community at the NIm and Im sites, respectively.  
 320 CAR = carnivore, OMN = omnivore, DF = deposit feeder, SF = suspension-feeder.

321  
 322 At the Im site, G1 *P. lascaris* had significantly higher mean  $\delta^{13}\text{C}$  than *S. maximus* (t-stat = 3.62, adj.  
 323 p = 0.005) and *P. platessa* (t-stat = 3.22, adj. p = 0.02). All other inter-group differences were non-significant  
 324 for both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ . *S. maximus* had a wider isotopic niche than the two other groups (probabilities >  
 325 0.97), followed by *P. platessa* and then G1 *P. lascaris* (Table 1), with somewhat weaker evidence for *P.*  
 326 *platessa* having a wider isotopic niche than G1 *P. lascaris* (probability = 0.76).

327 None of the flatfish groups presented a similar change in their isotopic metrics at both sites, except  
 328 in their mean  $\delta^{15}\text{N}$ , which did not differ significantly between sites. Only *P. lascaris* and *P. platessa*  
 329 presented significantly higher mean  $\delta^{13}\text{C}$  at the Im than at the NIm site for the same age class (Table 1) and  
 330 different age classes (*P. lascaris*: t-stat = 3.88 adj. p = 0.002). There was strong evidence that *P. platessa*  
 331 and *S. maximus* had a wider isotopic niche at the Im than at the NIm site and that *P. lascaris* had a narrower  
 332 isotopic niche at the Im than at the NIm site (Table 1).

Age class	Species	NIm				Im				Bayesian probability flatfish SEA (Im) < SEA (NIm)	t-stat (adj. p)
		n	TL (mm)	Mean $\delta^{13}\text{C}$ (‰)	SEA <sub>c</sub> (‰ <sup>2</sup> )	n	TL (mm)	Mean $\delta^{13}\text{C}$ (‰)	SEA <sub>c</sub> (‰ <sup>2</sup> )		
G0	<i>P. lascaris</i>	10	18-88	-19.1	2.21	0	NA	NA	NA	NA	NA
G1	<i>P. lascaris</i>	6	95-115	-18.5	0.48	9	100-156	-16.4	0.28	0.80	3.65 (0.004)
G0	<i>P. platessa</i>	5	71-77	-19.5	0.08	5	69-88	-17.5	0.49	0.005	2.91 (0.04)
G0	<i>S. maximus</i>	10	24-56	-18.4	0.67	16	23-70	-17.8	1.25	0.11	1.69 (0.4)

333 **Table 1.** Sample size (n), total length (TL, mm), mean  $\delta^{13}\text{C}$  (‰), and the standard ellipse area corrected for  
 334 small sample sizes (SEA<sub>c</sub>) for age class 0 (G0) and 1 (G1) *Pegusa lascaris* and age class 0 (G0) *Pleuronectes*  
 335 *platessa* and *Scophthalmus maximus* at the sandy beach not impacted by green tides (NIm) and the sandy

336 beach impacted by green tides (Im) during the peak green tide period. The Bayesian probability comparing  
337 the Bayesian SEA of each flatfish group at the two sites and the result of inter-site pairwise comparisons (t  
338 statistic and adjusted p-value) of the  $\delta^{13}\text{C}$  are also shown.

339

### 340 3.2.2. Flatfish digestive tract contents and associated metrics

341 During Peak GT, we identified 15 tropho-orders in the digestive tracts of the flatfish groups.  
342 Bivalves (SF, *Donax* spp.), crustaceans (OMN, e.g. *Gammarus crinicornis* and DF, e.g. *Bathyporeia* sp.,  
343 *Urothoe* sp., Cumacea) and polychaetes (CAR, e.g. *Nephtys* sp., *Glycera* sp. and DF e.g. *Spiophanes*  
344 *bombyx*, *Owenia fusiformis*) were the main prey of *P. lascaris*, *P. platessa* and *S. maximus*. *Ulva* spp. was  
345 never identified in the digestive tracts (Tables 2).

346 At the NIm site, SF-Cardiida was the most frequent (> 75%) and abundant (> 70%) prey in the diet  
347 of G1 *P. lascaris* and *P. platessa*. DF-Cumacea and DF-Amphipoda were the most frequent prey in the diet  
348 of G0 *P. lascaris* (95%) and *S. maximus* (73%), respectively. DF-Cumacea was also a frequent prey for *P.*  
349 *platessa* (79%) and G1 *P. lascaris* (50%), while SF-Cardiida was the second most frequent prey in the diet  
350 of *S. maximus* (64%) and G0 *P. lascaris* (40%) (Table 2). *S. maximus* and G0 *P. lascaris* had the highest  
351 prey richness (8), while *P. platessa* and G1 *P. lascaris* had a lower prey richness (Table 2). All groups had  
352 a low diet similarity with the benthic community (DO < 0.15).

353 At the Im site, DF-Cumacea was the most frequent and abundant prey in the diet of *P. lascaris* and  
354 *S. maximus* (Table 2). Other crustaceans were also abundant prey for these species (> 21%), mainly  
355 amphipods (DF and OMN) for *P. lascaris* and DF-Amphipoda and OMN-Mysida for *S. maximus*. OMN-  
356 Amphipoda and SF-Cardiida were the most abundant (32%) and frequent (94%) prey, respectively, in the  
357 diet of *P. platessa* (Table 2). DF-Cumacea was also frequent prey in the diet of *P. platessa* (50%). *P. platessa*  
358 and *P. lascaris* had higher prey richness than *S. maximus*. Overall, the groups had intermediate diet  
359 similarities with the benthic community (DO > 0.34) (Table 2).

360 All three flatfish groups had higher DO at the Im than at the NIm site. They also relied less on SF-  
361 Cardiida and more on a range of DF and OMN crustaceans, with species-specific differences (Table 2). *P.*  
362 *lascaris* (G1) and *S. maximus* had vastly different diets between the two sites (DS < 0.13), while that of *P.*  
363 *platessa* differed less between sites (DS = 0.52). *P. lascaris* and *P. platessa* had higher prey richness at the  
364 Im than at the NIm site, while *S. maximus* had a lower prey richness (Table 2).

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Species and age class	Peak GT								Post GT2	
	<i>P. las G0</i>		<i>P. las G1</i>		<i>P. pla G0</i>		<i>S. max G0</i>		<i>P. las G0</i>	
<b>Total length (mm)</b>	41-87		101-120		53-82		36-91		34-89	
<b>n (vacuity rate, %)</b>	20 (0%)		4 (0%)		14 (0%)		11 (0%)		19 (17%)	
<b>NIm site</b>	<b>O</b>	<b>A</b>	<b>O</b>	<b>A</b>	<b>O</b>	<b>A</b>	<b>O</b>	<b>A</b>	<b>O</b>	<b>A</b>
CAR-Eunicida	0	0	0	0	0	0	9.1	0.2	0	0
CAR-Perciformes	0	0	0	0	0	0	0	0	0	0
CAR-Phyllodocida*	5.0	0.1	0	0	21.4	0.9	9.1	0.2	5.3	0.1
DF-Amphipoda	25.0	0.8	0	0	0	0	72.7	6.7	10.5	2.4
DF-Cumacea#	95.0	77.3	50.0	3.6	78.6	27.4	45.4	2.5	84.2	27.9
DF-Other	20.0	2.1	0	0	14.3	0.7	0	0	5.3	0.6
DF-Sabellida*	0	0	25.0	0.7	0	0	0	0	5.3	0.1
DF-Spatangoida	0	0	0	0	0	0	0	0	5.3	0.6
DF-Spionida	5.0	0.3	0	0	7.1	0.7	0	0	10.5	1.5
OMN-Amphipoda	5.0	0.1	0	0	0	0	27.3	1.1	10.5	1.8
OMN-Decapoda#	0	0	0	0	0	0	9.1	0.2	0	0
OMN-Isopoda	0	0	0	0	0	0	0	0	0	0
OMN-Mysida	0	0	0	0	0	0	27.3	3.4	5.3	0.6
OMN-Other	5.0	0.1	0	0	0	0	0	0	0	0
SF-Cardiida*	40.0	19.1	75.0	95.7	100	70.2	63.6	85.5	47.4	64.2
Richness	8		3		5		8		10	
DO	0.14		0.11		0.15		0.13		0.32	
<b>Total length (mm)</b>			93-141		70-91		25-79		43-67	
<b>n (vacuity rate, %)</b>	0		9 (0%)		16 (0%)		15 (0%)		10 (29%)	
<b>Im site</b>			<b>O</b>	<b>A</b>	<b>O</b>	<b>A</b>	<b>O</b>	<b>A</b>	<b>O</b>	<b>A</b>
CAR-Eunicida			0	0	0	0	0	0	0	0
CAR-Perciformes			0	0	0	0	6.7	0.9	0	0
CAR-Phyllodocida*			0	0	25.0	6.9	6.7	0.3	10.0	0.1
DF-Amphipoda			77.8	21.2	31.2	5.9	73.3	23.8	60.0	6.5
DF-Cumacea#			88.9	44.8	50.0	25.8	73.3	49.4	20.0	0.5
DF-Other			11.1	2.4	0	0	0	0	0	0
DF-Sabellida*			0	0	0	0	0	0	10.0	0.1
DF-Spatangoida			0	0	6.2	1.6	0	0	0	0
DF-Spionida			22.2	0.8	12.5	0.6	0	0	10.0	0.2
OMN-Amphipoda			22.2	22.0	25.0	32.0	0	0	0	0
OMN-Decapoda#			11.1	0.4	0	0	13.3	0.3	10.0	0.4
OMN-Isopoda			22.2	1.2	6.2	0.6	0	0	0	0
OMN-Mysida			11.1	6.0	18.7	2.0	46.7	25.2	0	0
OMN-Other			11.1	0.4	0	0	0	0	0	0
SF-Cardiida*			11.1	0.8	93.7	24.5	0	0	50.0	92.1
Richness			10		9		6		7	

DO	0.40	0.34	0.35	0.69
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369 **Table 2.** Sample size (n), total length (TL, mm), vacuity rate (%), frequency of occurrence (O, %) and  
 370 relative abundance (A, %) of tropho-orders identified in age class 0 (G0) and age class 1 (G1) flatfish  
 371 (*Pegusa lascaris* (*P. las*), *Pleuronectes platessa* (*P. pla*) and *Scophthalmus maximus* (*S. max*)) sampled at  
 372 the sandy beach not impacted by green tides (NIm site) and the sandy beach impacted by green tides (Im  
 373 site) during the peak green tide (Peak GT) and the second post-green-tide (Post GT2) periods. The number  
 374 of tropho-orders (richness) and the dietary opportunism index (DO) are also shown. Tropho-orders marked  
 375 with \* had significantly higher  $\delta^{13}\text{C}$  at the Im than at the NIm site ( $p < 0.05$  for the main site effect), while  
 376 those marked with # had  $\delta^{13}\text{C}$  that did not differ significantly between the two sites ( $p > 0.05$  for the main  
 377 site effect).

378

### 379 3.3. Temporal changes in the trophic ecology of *P. lascaris* and changes linked to GT

#### 380 3.3.1. *P. lascaris* isotopic compositions and associated metrics

381 At the NIm site, G0 individuals were sampled during all four periods, but G1 were sampled only  
 382 during Peak GT. At the Im site, G0 individuals were sampled during Pre GT, Post GT1 and Post GT2, while  
 383 G1 were sampled during Peak GT and Post GT1 (Table 3). The isotopic composition of *P. lascaris* (G0 and  
 384 G1) ranged from -20.2‰ to -16‰ for  $\delta^{13}\text{C}$  and from 10.8‰ to 13.5‰ for  $\delta^{15}\text{N}$  (Fig. 3). During Peak GT  
 385 (NIm site) and Post GT1 (Im site), G1 had a narrower isotopic niche ( $\text{SEA}_C$ ) than G0 (probabilities  $> 0.99$ ).  
 386 Age-class G1 also had higher  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  than G0 (but not significantly so) (Figs. 3 and 4B) and lower  
 387  $\text{SEA}_C$  ratios than G0 (Table 3).

388 At the NIm site, G0 *P. lascaris* had the highest mean  $\delta^{13}\text{C}$  during Pre GT (Fig. 4B), a difference that  
 389 was significant only when compared to Post GT2 values (t-stat = 3.51, adj. p = 0.012), and the highest mean  
 390  $\delta^{15}\text{N}$  during Pre GT and Post GT2 (but not significantly so). The  $\text{SEA}_C$  of G0 *P. lascaris* increased from Pre  
 391 GT to Peak GT, and decreased from Post GT1 to Post GT2, with maximum values measured during Peak  
 392 GT and Post GT1. The  $\text{SEA}_C$  ratio followed the same trend (Table 3).

393 At the Im site, *P. lascaris* had the highest  $\delta^{13}\text{C}$  during Peak GT (Fig. 4B). The differences were  
 394 significant when compared to the values from all other periods (adj. p  $< 0.015$ ), except for G1 during Post  
 395 GT1 (t-stat = 2.77, adj. p = 0.09). *P. lascaris* had the highest mean  $\delta^{15}\text{N}$  during Pre GT and Post GT2 (Fig.  
 396 3). The only significant differences were between Pre GT and Peak GT values (t-stat = 3.31, adj. p = 0.03)  
 397 and between Pre GT and Post GT1 (G0) values (t-stat = 3.41, adj. p = 0.03).

398

Age class	Period	NIm						Im						Bayesian probability SEA (Im) < SEA (NIm)	t-stat (adj. p)
		n	TL (mm)	Mean $\delta^{13}\text{C}$ (‰)	Flatfish SEA <sub>C</sub> (‰ <sup>2</sup> )	Macro invert. SEA <sub>C</sub> (‰ <sup>2</sup> )	SEA <sub>C</sub> ratio (%)	n	TL (mm)	Mean $\delta^{13}\text{C}$ (‰)	Flatfish SEA <sub>C</sub> (‰ <sup>2</sup> )	Macro invert. SEA <sub>C</sub> (‰ <sup>2</sup> )	SEA <sub>C</sub> ratio (%)		
G0	Pre GT	6	65-79	-18.1	0.31	6.87	4.5	8	35-80	-17.8	0.18	5.62	3.20	0.84	2.21 (0.3)
G0	Peak GT	10	18-88	-19.1	2.21	8.06	27.4	0	NA	NA	NA	8.04	NA	NA	NA
G1	Peak GT	6	95-115	-18.5	0.48	8.06	5.6	9	100-156	-16.4	0.28	8.04	3.50	0.80	3.65 (0.008)
G0	Post GT1	9	17-69	-18.9	1.94	6.25	31.0	34	9-90	-17.6	0.75	2.80	26.80	0.99	3.07 (0.04)
G1	Post GT1	0	NA	NA	NA	6.25	NA	6	119-162	-16.8	0.26	2.80	9.30	NA	NA
G0	Post GT2	14	26-85	-19.0	0.28	4.16	6.7	5	48-64	-17.7	0.05	2.14	2.3	0.96	3.93 (0.003)

399 **Table 3.** Sample size (n), total length (TL, mm), mean  $\delta^{13}\text{C}$  (‰), and the standard ellipse area corrected for small sample sizes (SEA<sub>C</sub>) for age class  
400 0 (G0) and age class 1 (G1) *Pegusa lascaris* and the macroinvertebrate community (macroinvert.) at the sandy beach not impacted by green tides  
401 (NIm) and the sandy beach impacted by green tides (Im) during the four green tide periods (Pre GT, Peak GT, Post GT1 and Post GT2). The ratio of  
402 the SEA<sub>C</sub> of *P. lascaris* to the macroinvertebrate SEA<sub>C</sub>, the Bayesian probability comparing the Bayesian SEA of *P. lascaris* at the two sites, and  
403 inter-site pairwise comparisons (t statistic and adjusted p-value) of the  $\delta^{13}\text{C}$  are also shown.

404 The SEA<sub>C</sub> was low during all four periods, except for G0 during Post GT1. The SEA<sub>C</sub> ratio was lowest  
 405 during Pre GT, Peak GT and Post GT2, with higher values during Post GT1 (Table 3).

406 During all four periods, there was strong evidence for *P. lascaris* having a narrower isotopic niche  
 407 (SEA<sub>C</sub>) at the Im than at the NIm site when comparing the same age class (Table 3) and different age classes  
 408 (Peak GT probability = 1.00, Post GT1 probability = 0.99). From Peak GT-Post GT2, *P. lascaris* presented  
 409 a significantly higher mean  $\delta^{13}\text{C}$  at the Im than at the NIm site when comparing the same age class (Table  
 410 3) and different age classes (Peak GT t-stat = 3.88 adj. p = 0.004, Post GT1 t-stat = 3.07 adj. p = 0.04). No  
 411 significant inter-site differences were observed in mean  $\delta^{15}\text{N}$  for *P. lascaris*, although  $\delta^{15}\text{N}$  for G1 were  
 412 lower at the Im than at the NIm site during Peak GT (Fig. 3).

413

### 414 3.3.2. *P. lascaris* digestive tract contents and associated metrics

415 During Peak GT, only G1 were sampled at the Im site, while G0 and G1 were sampled at the NIm  
 416 site. During Post GT2, G0 were sampled at both sites. We identified 13 tropho-orders in the digestive tracts  
 417 of *P. lascaris*. The main prey of *P. lascaris* were bivalves (SF), crustaceans (OMN and DF) and polychaetes  
 418 (CAR and DF). *Ulva* spp. was never identified in the digestive tracts (Tables 2).

419 At the NIm site, SF-Cardiida was the most frequent (75%) and abundant prey (96%) in the G1 diet  
 420 during Peak GT. DF-Cumacea was the most frequent and abundant prey (>77%) in the G0 diet during the  
 421 same period (Table 2), resulting in a low diet similarity between age-class (DS = 0.23). Age-class G1  
 422 consumed a much lower diversity of tropho-orders than G0, and the diet of both age classes had a low  
 423 similarity with the benthic community (DO < 0.14). During Post GT2, DF-Cumacea and SF-Cardiida were  
 424 the most frequent (84%) and abundant prey (64%) in the G0 diet, respectively. *P. lascaris* consumed a  
 425 higher diversity of tropho-orders and had a slightly higher diet similarity with the benthic community than  
 426 during Peak GT (Table 2).

427 At the Im site, DF-Cumacea was the most frequent (89%) and abundant prey (45%) in the G1 diet  
 428 during Peak GT. DF-Amphipoda was also a frequent prey (78%). During Post GT2, SF-Cardiida and DF-  
 429 Amphipoda were the most abundant (92%) and frequent prey (60%) of G0, respectively. *P. lascaris* had  
 430 lower prey richness and higher DO during Post GT2 than Peak GT (Table 2).

431 During Peak GT and Post GT2, *P. lascaris* had higher DO at the Im than at the NIm site (Table 2).  
 432 Inter-site differences were period-specific for the other diet metrics. During Peak GT, G1 switched from a  
 433 diet dominated in abundance by SF-Cardiida (96%) to a diet dominated by DF-Cumacea (45%) and  
 434 Amphipoda (21-22%), resulting in a very low inter-site diet similarity (DS = 0.04). The dietary change was  
 435 smaller for G0 at the NIm site, and the inter-site diet similarity was higher (DS = 0.49). Regardless of the  
 436 age class, *P. lascaris* had higher prey richness at the Im than at the NIm site. During Post GT2, the abundance  
 437 of SF-Cardiida in the diet of *P. lascaris* was higher at the Im site (92%) than at the NIm (64%), and the diet

438 similarity was high (DS = 0.68). Age-class G0 had lower prey richness at the Im than at the NIm site (Table  
439 2).

440

#### 441 4. Discussion

442 We presented data for juvenile flatfish and their potential prey (benthic macroinvertebrates) sampled  
443 at one sandy beach that has never been impacted by GT (NIm site) and another that has been impacted by  
444 GT every year since the 1970s (Im site) (Perrot et al., 2014), separated by 20 km. Since juvenile flatfish  
445 have high fidelity for their nursery, moving alongshore no more than 4 km over the course of several months  
446 (Burrows et al., 1994; Le Pape and Cognez, 2016; Riley, 1973), movement between the two beaches should  
447 be non-existent, preventing any potential mixing of individuals. Among the environmental parameters  
448 measured by Quillien et al. (2015a) in 2012, algal mat density, organic matter content and two sediment  
449 characteristics (median grain size and sorting index) were the only ones that differed significantly between  
450 the two sites. According to these authors, these two beaches generally have fine and well-sorted sediment  
451 with less than 6% organic matter (low effect sizes, Table S1). Since algal mat density had the largest effect  
452 size (Quillien et al., 2015a), we considered GT to be the main effect explaining the changes in juvenile  
453 flatfish trophic ecology observed between sites. Nonetheless, these changes could also be due to parameters  
454 that were not measured, such as nutrient concentrations, which differ between the inshore waters of the two  
455 beaches studied (Dussauze and Menesguen, 2008) and generally cause coastal eutrophication and associated  
456 GT (Cloern, 2001; Teichberg et al., 2010).

457

##### 458 4.1. Relating consumer isotopic compositions and niche to diet data

459 Determining accurate proportions of prey in a predator's diet using isotopic compositions is  
460 especially challenging when the predator has a diversified diet and its potential prey have similar isotopic  
461 compositions (Yeakel et al., 2011), like in this study and others (Déniel, 1974; Kostecki et al., 2012;  
462 Rodriguez, 1996). According to the optimal foraging theory (Gill, 2003), juvenile flatfish are most likely to  
463 consume organisms that maximize their energy gain relative to the capture effort. Such organisms are  
464 expected to be highly vulnerable and energy-rich macroinvertebrates with relatively high *in situ* abundances  
465 (Table S4).

466 Furthermore, comparing flatfish isotopic niche width and digestive tract data can help assess the  
467 accuracy of the diet results, which may be biased by predator feeding time (*e.g.* nocturnal feeding, but  
468 diurnal sampling) and prey digestibility (Baker et al., 2014). For example, prey with hard structures (*e.g.*  
469 bivalves, crustaceans) are identifiable for a longer period than prey with softer structures (*e.g.* polychaetes)  
470 (Macdonald et al., 1982). According to Yeakel et al. (2016), a consumer's isotopic niche width ( $SEA_C$ ) is a  
471 function of the isotopic distribution of its potential prey and its dietary strategy (*i.e.* degree of specialization).

472 This relation holds for a given isotopic space that encompasses all potential prey available to the consumer  
473 (macroinvertebrate  $SEA_C$ ) and when the individuals in the consumer group have close mean isotopic  
474 compositions (isotopic variance lower than *ca.* 2‰). In a static framework, a consumer's  $SEA_C$  is predicted  
475 to peak when it is moderately specialized on prey that have a large offset; the offset being calculated as the  
476 prey isotopic mean minus the centroid of the potential prey mixing space (Layman et al., 2007). In a  
477 temporal framework, the  $SEA_C$  of a consumer group is expected to peak during gradual diet transitions.

478

#### 479 4.2. Juvenile flatfish trophic ecology in a non-impacted sandy beach nursery

##### 480 4.2.1. Species-specific trophic ecology during Peak GT

481 During Peak GT, *P. platessa* foraged on a low diversity of tropho-orders (5), and all individuals  
482 consumed SF-Cardiida (high specialization *sensus* Yeakel et al. (2016)), a tropho-order relatively close to  
483 the potential prey centroid in the isotopic niche space (low offset). In this case, the isotopic niche of *P.*  
484 *platessa* should be narrow (Yeakel et al., 2016), as we observed. In the Mont Saint Michel Bay and Wadden  
485 Sea, *P. platessa* also has a diet dominated by bivalves and cumaceans (Braber and De Groot, 1973; Kostecki  
486 et al., 2012) but generally forages on a much higher diversity of prey (Beyst et al., 1999; Kostecki et al.,  
487 2012), a difference potentially caused by classifying prey into tropho-orders.

488 *S. maximus* foraged on a higher diversity of tropho-orders (8), with DF-Amphipoda and SF-Cardiida  
489 observed in 73% and 64% of the digestive tracts, respectively. As both tropho-orders had low offsets, the  
490 isotopic niche of *S. maximus* should be narrow and due to a lower specialization (Yeakel et al., 2016), wider  
491 than that of *P. platessa*, as we observed. Bivalves and amphipods were reported as frequent prey items for  
492 juvenile *S. maximus* along the German coast (De Groot, 1971) and in the Bay of Douarnenez (Déniel, 1974),  
493 respectively. Conversely, bivalves were rarely recorded by Déniel (1974) but frequently recorded in this  
494 study, a difference possibly related to their local availability, as each study sampled a different nursery.

495 Age-class G0 *P. lascaris* also foraged on a relatively high diversity of tropho-orders (8), with 95%  
496 occurrence of DF-Cumacea, indicating high specialization (Yeakel et al., 2016) on this tropho-order. In this  
497 case, the isotopic niche of G0 *P. lascaris* should be relatively narrow (Yeakel et al., 2016), which is not  
498 what we observed. Consequently, our sampling likely underestimated the importance of certain tropho-  
499 orders in the *P. lascaris* diet due to its nocturnal foraging and rapid digestion (De Groot, 1971). To achieve  
500 the wide isotopic niche and the measured  $\delta^{13}C$  and  $\delta^{15}N$ , G0 *P. lascaris* likely had a more generalist diet  
501 and foraged more frequently than estimated on tropho-orders with higher mean  $\delta^{13}C$  and  $\delta^{15}N$ , such as CAR-  
502 Phyllodocida and CAR-Ophiurida (Table S3), previously reported as prey (Cabral et al., 2002; Rodriguez,  
503 1996). Furthermore, the relatively high specialization of G1 *P. lascaris* on a tropho-order with a low offset  
504 (SF-Cardiida) should yield a relatively narrow isotopic niche (Yeakel et al., 2016), as we observed.  
505 Nonetheless, the relatively high  $\delta^{13}C$  and  $\delta^{15}N$  of G1 *P. lascaris* cannot be explained by a diet composed

506 mainly of low  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  tropho-orders (SF-Cardiida and DF-Cumacea, Table S3), indicating we  
507 probably missed important prey with higher mean  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  (e.g. CAR-Phyllodocida, Table S3), as  
508 expected with a sample size of 4.

509 Overall, our digestive tract data seem to accurately reflect the diet of *P. platessa* and *S. maximus*,  
510 which are daytime feeders, but probably does not accurately reflect the diet of *P. lascaris*, a nocturnal feeder  
511 (De Groot, 1971). In the future, samples should be collected at night to characterize the diet of *P. lascaris*  
512 correctly and avoid the risk of missing important highly digestible prey such as polychaetes (Macdonald et  
513 al., 1982). Despite their relatively low *in situ* abundance (Table S4), SF-Cardiida appeared to be positively  
514 selected by all three species (at varying degrees), likely due to their high vulnerability and high energy  
515 content (Brey, 2001). Indeed, *Donax* spp., members of SF-Cardiida, live near the sediment surface and  
516 extend their siphons above the sediment to feed on POM (Quillien et al., 2015a, 2015b). which makes them  
517 more vulnerable to predation than the most abundant tropho-order DF-Spionida (mainly *Spiophanes*  
518 *bombyx*, Tables S2 and S5), a sessile polychaete that can quickly withdraw into its tube (Jumars et al., 2015;  
519 Quillien et al., 2015b). Consequently, consumption of SF-Cardiida likely maximizes the energy gain of the  
520 flatfish relative to prey search, detection and capture (Gill, 2003).

521

#### 522 4.2.2. Temporal variability in the trophic ecology of juvenile *P. lascaris*

523 The settlement period of *P. lascaris* larvae (June-October) in the Bay of Douarnenez (Déniel, 1981)  
524 led us to consider our sampling periods according to a different chronology. The G0 sampled from Peak  
525 GT-Post GT2 settled in 2012 and were the youngest individuals, while the G0 sampled during Pre GT and  
526 the sampled G1 settled in 2011 and were older.

527 Considering G0, *P. lascaris* assimilated the most isotopically diversified prey (high  $\text{SEA}_C$ ) during  
528 Peak GT and Post GT1. In autumn (Post GT2), potential prey isotopic diversity (macroinvertebrate  $\text{SEA}_C$ )  
529 and assimilated prey diversity (flatfish  $\text{SEA}_C$ ) were much lower. Based on Yeakel et al. (2016), the  
530 maximum isotopic niche of *P. lascaris* measured during Peak GT could reflect transition from the pelagic-  
531 based diet of the larvae to the benthic-based diet of the juveniles (Gibson, 1997). Similarly, the widening of  
532 Post GT1 isotopic niche could reflect transition from the Peak GT diet to the Post GT2 diet. Juvenile flatfish  
533 are known to go through gradual diet transitions during their first year of life in coastal nurseries (Beyst et  
534 al., 1999; Cabral et al., 2002; Rodriguez, 1996), and the digestive tract data revealed a change in diet  
535 between these two periods. During Post GT2, *P. lascaris* continued to consume DF-Cumacea frequently,  
536 consumed a higher diversity of prey, and shifted to a diet dominated by SF-Cardiida, reflecting the very  
537 strong increase of the *in situ* abundance of SF-Cardiida (Table S4).

538 Considering older individuals, *P. lascaris* switched to a lower isotopic diversity of prey (small  
539  $\text{SEA}_C$ ) in autumn and maintained this characteristic until the next summer (Peak GT), despite the increase

540 in potential prey isotopic diversity (macroinvertebrate SEA<sub>C</sub>). From G0 to G1 age-classes, the diet of *P.*  
541 *lascaris* had lower prey richness and higher dominance in occurrence and abundance of SF-Cardiida, despite  
542 the lower *in situ* abundance of the cardid *Donax* during Peak GT (Table S4). These results tend to disagree  
543 with the continuously narrow isotopic niche observed from Post GT2 onward, which was likely caused by  
544 underestimating less common prey items in the G1 *P. lascaris* diet. From younger to older individuals, the  
545  $\delta^{13}\text{C}$  of *P. lascaris* also increased from *ca.* -19‰ to *ca.* -18‰, probably indicating an increasing assimilation  
546 of prey with higher  $\delta^{13}\text{C}$  by G1 (*e.g.* CAR-Phyllodocida, Table S3).

547 Over time, *P. lascaris* had relatively selective foraging behavior (low DO) that was likely related to  
548 preferential consumption of organisms that maximized its energy intake and to the low vulnerability of the  
549 most abundant tropho-order, DF-Spionida (Table S4). Two energy-rich (Brey, 2001) and more vulnerable  
550 tropho-orders (SF-Cardiida and DF-Cumacea) are preferentially consumed (positive selection) by juvenile  
551 *P. lascaris*, as reported in previous studies (Cabral et al., 2002; Quiniou, 1986; Rodriguez, 1996).

552

#### 553 4.3. Broad changes in juvenile flatfish trophic ecology related to GT

554 Despite the relatively small sample sizes for the diet analyses, we identified broad trophic changes  
555 that juvenile flatfish experience at an exposed and dissipative sandy beach impacted by GT. During Peak  
556 GT, the diet data collected at the two sites indicated that the *Ulva* bloom did not prevent juvenile flatfish  
557 from foraging (vacuity rates of 0% at both sites). At the NIm site, all flatfish preferentially consumed SF-  
558 Cardiida despite its low *in situ* abundance (6%) whereas at the Im site, the flatfish consumed less SF-  
559 Cardiida despite a continuously low abundance (Table S4). Conversely, the flatfish increased their  
560 consumption of amphipods (DF and OMN) and mysids between the NIm and Im site, following the overall  
561 *in situ* abundance increase of these tropho-orders (Table S4). This result suggests that during Peak GT  
562 juvenile flatfish had lower foraging efficiency at the Im site and a preference for more abundant epifauna  
563 and mobile organisms (*e.g.* amphipods, mysids), which may have been easier to detect and capture than  
564 infauna organisms (cardid); a shift in agreement with optimal foraging theory (Gill, 2003).

565 Combining the digestive tract data and benthic community data (nine samples at each site during  
566 Peak GT) revealed that flatfish relied more on the *in situ* macroinvertebrates at the Im site, hence displaying  
567 a more opportunistic foraging behavior. Studies based on digestive tract data also observed more  
568 opportunistic foraging behavior of bottom-feeding fish during GT and hypoxic events (Andersen et al.,  
569 2005; Pihl et al., 1992) such as *P. flesus* in a fjord impacted by a GT. Andersen et al. (2005) interpreted this  
570 behavior as reflecting a random prey selection linked to a disturbed foraging activity. Experimentally adding  
571 habitat complexity (eelgrass) also induced a switch from a positive prey selection to a random feeding in  
572 young-of-the-year *Pomatomus saltatrix* (Buckel and Stoner, 2000). In the current study, either the greater  
573 habitat complexity (Nelson and Bonsdorff, 1990) and/or the exudates released by *Ulva* spp. (Engström-Öst



574 and Isaksson, 2006) may have reduced flatfish foraging efficiency (*i.e.* prey detection and/or capture), as  
575 previously reported for *S. maximus* (Nordström and Booth, 2007) and *P. flesus* (Aarnio and Mattila, 2000).  
576 Consequently, the more opportunistic foraging behavior of flatfish at the Im site is probably the combined  
577 result of (1) changes in the juvenile flatfish potential prey (Table S4), (2) higher vulnerability of abundant  
578 tropho-orders (*e.g.* tube-dweller, shallow infauna and mobile epifauna are expected to be increasingly  
579 vulnerable to visual predatory fish, De Groot, 1971) and (3) decrease in the foraging efficiency of juvenile  
580 flatfish.

581 A seven-year study (2007-2013) of eight exposed sandy beaches (five impacted by GT and three  
582 not impacted) along the Brittany coast revealed consistent and long-lasting effects (six months after the end  
583 of the *Ulva* bloom) of GT on benthic macroinvertebrates (Quillien et al., 2015b). Across sites and years,  
584 DF-Amphipoda (mainly *Urothoe* spp.), DF-Sabellida (mainly *Owenia fusiformis*) and DF-Cardiida  
585 (*Macomangulus tenuis*) benefited from the presence of GT, while SF-Cardiida (*Donax* spp.) was negatively  
586 affected by GT. Consequently, even though we sampled only one site for each treatment (impacted or not  
587 impacted by GT), the replacement of SF-Cardiida with more abundant tropho-orders (*e.g.* small crustaceans)  
588 in the diet of juvenile flatfish can likely be generalized to other exposed sandy beaches impacted by GT.

589

#### 590 4.4. Species-specific trophic changes during the Peak GT

591 Following results in Quillien et al. (2016), we qualified a consumer with a significantly higher  $\delta^{13}\text{C}$   
592 at the Im site than at the NIm site as presenting an “*Ulva* isotopic signal”. A consumer (*e.g.* *P. platessa*,  
593 macroinvertebrate tropho-order) with this signal has derived a significant proportion of its energy from  
594 *Ulva* spp. and/or indirectly from GT-modified SPOM (Quillien et al., 2016) or by foraging on prey  
595 presenting an *Ulva* isotopic signal. Despite their abundance at the Im site, we never identified *Ulva*  
596 fragments in flatfish digestive tracts, meaning flatfish presenting an *Ulva* isotopic signal can only have  
597 acquired it via their prey.

598

##### 599 4.4.1. *P. platessa* is least disturbed by GT

600 The diet of *P. platessa* differed only slightly between the NIm and Im sites. At the Im site, *P.*  
601 *platessa* still relied mainly on SF-Cardiida and DF-Cumacea (with a slight decrease in occurrence and  
602 abundance) but foraged on a higher diversity of tropho-orders, such as epifauna and mobile tropho-orders  
603 (DF-Amphipoda, OMN-Amphipoda, OMN-Isopoda, OMN-Mysida). This small dietary shift suggests that  
604 *P. platessa* was only slightly disturbed in its prey preference by GT, maybe due to its use of both visual and  
605 chemical cues to detect prey (De Groot, 1971) and its April-May settlement period in coastal nurseries  
606 (Déniel, 1981). Indeed, older post-settlement *P. platessa* are exposed to the GT, and tolerance to such

607 environmental disturbance is likely to increase with size, as shown during severe hypoxia (Nilsson and  
608 Ostlund-Nilsson, 2008).

609 *P. platessa* presented an *Ulva* isotopic signal likely due to the high occurrence of SF-Cardiida in its  
610 diet and to the consumption of CAR-Phyllodocida. Indeed, both tropho-orders presented an *Ulva* isotopic  
611 signal acquired directly by consuming GT-modified SPOM (Quillien et al., 2016) for the first and indirectly  
612 by consuming *Ulva* spp. and SPOM for the second (Jumars et al., 2015). Le Luherne et al. (2017) also  
613 reported higher  $\delta^{13}\text{C}$  of *P. platessa* at a GT-impacted beach than at a beach not impacted by GT in another  
614 flatfish nursery (the Bay of Saint-Brieuc), a result confirming this species continues foraging in coastal  
615 nurseries despite GT.

616 Nonetheless, the higher abundance of DF-Amphipoda, a tropho-order that increased in abundance  
617 during Peak GT (Table S4) and across several GT sites (Quillien et al., 2015b), in the diet of *P. platessa*  
618 seems to indicate that this species adapted its foraging behavior to the macroinvertebrates available locally.  
619 Finally, *P. platessa* remained relatively specialized on a tropho-order with a relatively low offset in the  
620 isotopic space (SF-Cardiida), normally resulting in a narrow isotopic niche (Yeakel et al., 2016). Where GT  
621 occur, *P. platessa* had a narrow isotopic niche that was nonetheless wider than that at the NIm site, a small  
622 shift likely related to the increase in prey richness.

623

#### 624 4.4.2. *S. maximus* is strongly disturbed by GT

625 Conversely, at the Im site, *S. maximus* stopped consuming SF-Cardiida, a key prey at the NIm site,  
626 and shifted to a diet based mainly on DF and OMN crustaceans. This dietary shift, confirmed by the small  
627 inter-site diet similarity, suggests that the foraging efficiency of *S. maximus* is strongly disturbed by GT  
628 (Nordström and Booth, 2007). Indeed, the higher structural complexity at the Im site linked to the GT  
629 (Holmquist, 1997) probably hindered the search and detection of prey by *S. maximus*, an exclusively visual  
630 predator (De Groot, 1971). Furthermore, the June-July settlement of *S. maximus* in coastal nurseries (Déniel,  
631 1981), exposes very young post-settlement juveniles to the GT, which are potentially less tolerant to the  
632 disturbance (Nilsson and Ostlund-Nilsson, 2008).

633 At the Im site, *S. maximus* foraged mainly on tropho-orders that did not present an *Ulva* isotopic  
634 signal (DF-Cumacea, OMN-Decapoda) or likely did not present it (*i.e.* small sample size, DF-Amphipoda,  
635 OMN-Mysida), probably explaining the absence of an *Ulva* isotopic signal for *S. maximus*. Consequently,  
636 *S. maximus* derived little or no energy from the additional basal resource (*Ulva* spp), a result possible linked  
637 to its higher dependence on mobile organisms like fish (Déniel, 1974; Quiniou, 1986) that can avoid GT  
638 and potentially benefit less from the additional basal resource. Finally, the high specialization of *S. maximus*  
639 on two tropho-orders – DF-Cumacea and DF-Amphipoda – with relatively high offsets in the isotopic space,  
640 likely explains its wider isotopic niche at the Im than at the NIm site (Yeakel et al., 2016).

641  
642 4.4.3. *P. lascaris* appears the most disturbed by GT

643 Despite a larvae settlement period normally starting in June in the Bay of Douarnenez (Déniel,  
644 1981), no G0 were sampled during Peak GT at the Im site (July), but over 30 were sampled during Post  
645 GT1 (September), a result close to the one reported in July 2013 by Quillien et al. (2018). This absence  
646 during Peak GT suggests that GT have negative effects on pre-settlement larvae and/or post-settlement  
647 juveniles, probably related to higher mortality rates and/or temporary avoidance of impacted coastal  
648 nurseries. Indeed, experiments have shown that juvenile flatfish prefer unvegetated substrata to vegetated  
649 substrata (Carl et al., 2008; Wennhage and Pihl, 1994) and *Ulva* blooms, which can cause temporary hypoxia  
650 (Cloern, 2001, authors personal observations) and release exudates (Van Alstyne et al., 2015), are known to  
651 increase the mortality of crab larvae and juveniles (Johnson and Welsh, 1985; Van Alstyne et al., 2015),  
652 *Clupea harengus* eggs (Aneer, 1987) and *P. platessa* larvae (Larson, 1997).

653 The diet of G1 *P. lascaris* shifted from the NIm to the Im site (very low inter-site diet similarity):  
654 they nearly stopped consuming SF-Cardiida, consumed more DF-Cumacea (in occurrence and abundance)  
655 and seven new tropho-orders (e.g. DF-Amphipoda, OMN-Amphipoda) at the Im site. This seems to indicate  
656 that GT disturbed the foraging of G1 *P. lascaris* strongly, likely due to the low nocturnal dissolved oxygen  
657 concentrations that often occur during *Ulva* blooms (Johnson and Welsh, 1985) (August 2012: 6%, authors  
658 personal observations). Since, temporary hypoxia decreases locomotor activity of *Solea solea* (Dalla Via et  
659 al., 1998), another Soleidae and decreases predation efficiency of juvenile *P. flesus* (Tallqvist et al., 1999),  
660 nocturnal hypoxia could reduce prey search activity (i.e. swimming to search for prey) and foraging  
661 efficiency of *P. lascaris* (Tallqvist et al., 1999), a nocturnal predator (De Groot, 1971). As a result, *P.*  
662 *lascaris* probably foraged more randomly and consumed the most abundant and vulnerable (e.g. mobile  
663 epifauna) tropho-orders, as indicated by the more opportunistic foraging behavior.

664 The G1 *P. lascaris* also presented an *Ulva* isotopic signal, which can not be explained by the main  
665 tropho-orders identified in the digestive tracts. Furthermore, the specialization of *P. lascaris* on DF-  
666 Cumacea and DF-Amphipoda (high offset) at the Im site rather than on SF-Cardiida (lower offset) at the  
667 NIm site should have widened its isotopic niche (Yeakel et al., 2016) and not, as we observed, narrowed it.  
668 These results suggest that we missed important prey for *P. lascaris* at the Im site. Based on the isotopic data,  
669 we hypothesize that, despite the GT, G1 *P. lascaris* continued to forage at the Im site and additionally  
670 consumed DF-Sabellida and CAR-Phyllodocida, two previously identified prey, using chemical cues (De  
671 Groot, 1971). Indeed, both tropho-orders are more abundant at the Im site than at the NIm site (Quillien et  
672 al., 2015b) (Table S4) and have *Ulva* isotopic signals acquired directly by consuming *Ulva* spp. (Quillien et  
673 al., 2016) for the first and indirectly via *Ulva* spp. and SPOM for the second (Jumars et al., 2015).

674

#### 675 4.5. *P. lascaris* adapts its foraging behavior to the GT context

676 During all four periods, the narrower isotopic niche of *P. lascaris* at the Im than at the NIm site  
677 likely reflects the generally lower potential prey offset at the former, related to the narrower  
678 macroinvertebrate isotopic niche (Yeakel et al., 2016). The *Ulva* isotopic signal detected during all periods  
679 except before the GT, suggests that *P. lascaris* derives via its prey a significant proportion of its energy  
680 from *Ulva* spp. and from GT-modified SPOM.

681 Due to the later arrival of G0 *P. lascaris* at the Im site (after Peak GT), their wide isotopic niche  
682 measured during Post GT1 is likely the result of transitioning from a pelagic to a benthic-based diet (Gibson,  
683 1997). As *P. lascaris* also presented an *Ulva* isotopic signal during this period, its new benthic diet probably  
684 included grazing on DF-Sabellida crowns, on parts of CAR-Phyllodocida and on SF-Cardiida siphons,  
685 tropho-orders which are relatively abundant in the sediment (Table S4) and present *Ulva* isotopic signals.

686 During Post GT2, *P. lascaris* appeared to consume mainly SF-Cardiida and DF-Amphipoda at the  
687 Im site, two tropho-orders that cannot solely explain the *Ulva* signal of *P. lascaris*. Consequently, *P. lascaris*  
688 likely foraged more on DF-Sabellida and CAR-Phyllodocida, than suggested by the digestive tract contents.  
689 Overall, the diet of *P. lascaris* at the Im site was likely composed of the most abundant *in situ* tropho-orders,  
690 as found at the NIm site (Post GT2). *P. lascaris* also appeared to have more opportunistic foraging behavior  
691 at the Im than at the NIm site, probably linked to the higher vulnerability of the dominant tropho-orders  
692 (Table S4) at the Im site (SF-Cardiida) than at the NIm site (DF-Spionida). The narrow isotopic niche  
693 measured during Post GT2 is probably linked to the very low isotopic diversity of potential prey  
694 (macroinvertebrate SEA<sub>C</sub>).

695 From G0 to G1 age-classes, *P. lascaris* shifted from a diet dominated by SF-Cardiida and DF-  
696 Amphipoda to one dominated by DF-Cumacea and DF-Amphipoda (which probably present no *Ulva*  
697 signal), probably explaining the isotopic niche widening (Yeakel et al., 2016) and the absence of an *Ulva*  
698 signal during Pre GT. Finally, during Peak GT and Post GT1, the isotopic niche of G1 *P. lascaris* was wider  
699 than that during Pre GT. This increase may have been related to the higher isotopic diversity of potential  
700 prey during Peak GT and the assimilation of tropho-orders with *Ulva* isotopic signals during Peak GT and  
701 Post GT1, such as the relatively abundant DF-Sabellida and CAR-Phyllodocida (Table S4).

702 Over time, *P. lascaris* appeared to present more opportunistic behavior at the Im than at the NIm  
703 site, likely because during Peak GT its foraging behavior was disturbed and because the benthic community  
704 shifted from less vulnerable (DF-Spionida or DF-Cardiida) to more vulnerable tropho-orders during the  
705 other periods (e.g. DF-Amphipoda during Pre GT, SF-Cardiida during Post GT1 and Post GT2).

706

707 **Conclusion**

708 Combining stable isotopes, digestive tract data and benthic community data revealed that *Ulva*  
709 blooms modified the trophic ecology of the three flatfish species. The GT directly and indirectly resulted in  
710 dietary changes and more opportunistic foraging behavior of flatfish juveniles. These changes were likely  
711 caused by (1) potential prey shifts (tropho-order abundance) and (2) reduced foraging efficiency of juvenile  
712 flatfish related to environmental changes associated with the GT (e.g. structural complexity, *Ulva* exudates,  
713 temporary hypoxia). More precisely, the flatfish relied less on SF-Cardiida and more on DF-Cumacea and  
714 DF-Amphipoda where the GT occurred, a shift that could result in lower body conditions for the flatfish  
715 (De Vlas, 1979; Veer et al., 2010). Indeed, small crustaceans content less energy than bivalves (Brey, 2001;  
716 De Vlas, 1979) and the juvenile flatfish likely spend more energy to forage (harder prey detection and/or  
717 capture for *P. platessa* and *S. maximus*) or reduce their prey search activity (*P. lascaris*) in nurseries  
718 impacted by GT.

719 Based on the literature, we hypothesize that the investigated flatfish species respond differently to  
720 the GT mainly according to the dominant sense they use to detect prey (vision or olfaction) and to when  
721 they forage (day or night), with potentially an additional effect of when they settle relative to the GT peak.  
722 GT appeared to strongly disturb the larval settlement of *P. lascaris* and the juvenile foraging behavior of *P.*  
723 *lascaris* and *S. maximus*, while *P. platessa* appeared to be overall less disturbed by the GT. Furthermore, *P.*  
724 *platessa* and *P. lascaris* likely derived significant proportions of their energy from the new basal resource  
725 (*Ulva* spp.) via their prey, while *S. maximus* did not seem to do so. Our findings challenge the use of a broad  
726 “benthic fish” or “flatfish” category when investigating impacts of human disturbances, such as  
727 eutrophication (Le Luherne et al., 2016; Paumier et al., 2018), on the functioning of coastal ecosystems.

728

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737

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## Supplementary data

**Table S1.** Environmental characteristics measured monthly at the non-impacted sandy beach (NIm) and at the sandy beach impacted by green tides (Im) from April to December 2012 and expressed as means, maximal and minimal values.

	NIm			Im		
	Mean	Max.	Min	Mean	Max	Min
<b>Wave height (m)</b>	1.3	2.0	0.7	1.4	2.1	0.7
<b>Beach slope (%)</b>	1.6	1.6	1.5	1.4	1.5	1.2
<b>SWT (°C)</b>	14.6	18.9	8.7	14.7	21.4	8.2
<b>Surface water chl <i>a</i> concentration (µg.L<sup>-1</sup>)</b>	15.8	33.7	5.1	15.8	33.7	5.1
<b>Algal mat density (kg<sub>ww</sub>.m<sup>-2</sup>)</b>	0.0	0.0	0.0	0.65	4.02	0.0
<b>Dissolved oxygen content (%)</b>	103.4	106.5	99.9	103.9	108.1	100.0
<b>Median grain size (µm)</b>	180.4	260.0	155.0	158.5	180.0	140.0
<b>Sediment organic matter content (%)</b>	4.5	5.4	3.3	4.1	6.2	3.0
<b>Sediment sorting index</b>	1.2	1.6	1.1	1.1	1.2	1.0

Wave height was retrieved from the PREVIMER public database considering the WW3 model (grid = 200m) and one monthly value was obtained for each site. Monthly surface water chlorophyll *a* concentration was also retrieved from the PREVIMER database which provides estimates of plankton concentration using the ECO-MARS-3D model (grid = 4 km). Beach slope was calculated by Quillien et al. (2015a) for each site on one occasion by dividing the maximal tide by the shore width. Seawater temperature (SWT) and dissolved oxygen content were measured monthly just above the sediment using a YSI-OMS v2 probe by Quillien et al. (2015a). One monthly measure was obtained for each site. Algal mat density was calculated by dividing the 1 min drained *Ulva* biomass (monthly field sampling by Quillien et al. (2015a) by the monthly surface covered by *Ulva* estimated by the CEVA aerial surveys. Median grain size, sediment organic matter content and sediment sorting index were measured by Quillien et al. (2015a) using a single sediment core (inner diameter: 11.3 cm; depth: 15 cm) sampled monthly at each site. “Grain sizes were measured by dry-sieving, using a series of 16 sieves from 63 to 10 000 µm. The sorting index was calculated based on the first and third quartile ratio of the sediment grain size (Trask sorting index) and the median was equal to the second quartile of the sediment grain size value. Organic matter content was measured by weight loss after combustion at 450°C for 5 h” (Quillien et al., 2015a).

**Table S2.** Macroinvertebrate species or taxonomic entities (family, order) included in each tropho-order according to the data set considered. The first data set is composed of the macroinvertebrates sampled in the sediment to determine their carbon and nitrogen isotopic compositions (stable isotope data set). The second data set is composed of the macroinvertebrates sampled in the sediment to determine the potential prey community (benthic community data set). The third data set is composed of the macroinvertebrates identified in the flatfish digestive tracts (digestive tract data set).

<b>Tropho-orders</b>	<b>Stable isotope data set</b>	<b>Benthic community data set</b>	<b>Digestive tract data set</b>
<b>CAR-Decapoda</b>	<i>Crangon crangon</i>	<i>Crangon crangon</i>	
<b>CAR-Eunicida</b>	<i>Scoletoma impatiens</i>	<i>Lumbrineris</i> sp.	<i>Lumbrineris</i> sp.
<b>CAR-Nemerta*</b>	<i>Lineus acutifrons</i> Nemertea <i>Amphiphorus langiaegeminus</i> <i>Cerebratulus roseus</i>	<i>Lineus acutifrons</i> Nemertea	
<b>CAR-Ophiurida</b>	<i>Acrocnida brachiata</i>	<i>Acrocnida brachiata</i>	
<b>CAR-Phyllodoceida</b>	<i>Glycera convoluta</i> <i>Nephtys assimilis</i> <i>Nephtys hombergii</i> <i>Nephtys</i> sp. <i>Sigalion mathildae</i> <i>Phyllodoce mucosa</i> <i>Aphroditidae</i>	<i>Glycera tridactyla</i> <i>Mysta picta</i> <i>Nephtys assimilis</i> <i>Nephtys cirrosa</i> <i>Nephtys hombergii</i> <i>Nephtys</i> sp. <i>Eteone longa</i> <i>Pholoe inornata</i> <i>Malmgreniella</i> spp. <i>Sigalion mathildae</i> <i>Phyllodoce lineata</i>	<i>Glycera</i> sp. <i>Mysta</i> sp. <i>Nephtys</i> sp. Syllidae
<b>DF-Amphipoda</b>	<i>Bathyporeia pelagica</i> <i>Urothoe poseidonis</i>	<i>Bathyporeia pelagica</i> <i>Urothoe poseidonis</i> <i>Urothoe pulchella</i> <i>Perrierella audouiniana</i> <i>Haustorius arenarius</i> <i>Melita palmata</i>	<i>Bathyporeia</i> sp. <i>Urothoe</i> sp.
<b>DF-Cardiida</b>	<i>Macomangulus tenuis</i>	<i>Macomangulus tenuis</i>	
<b>DF-Cumacea</b>	<i>Cumopsis fagei</i> <i>Eocuma dollfusi</i>	<i>Cumopsis fagei</i> <i>Cumopsis goodsir</i> <i>Cumopsis longipes</i> <i>Eocuma dollfusi</i>	Cumacea
<b>DF-Sabellida</b>	<i>Owenia fusiformis</i>	<i>Owenia fusiformis</i>	<i>Owenia fusiformis</i>
<b>DF-Spatangoida</b>	<i>Echinocardium cordatum</i>		<i>Echinocardium cordatum</i>
<b>DF-Spionida</b>	<i>Spiophanes bombyx</i> <i>Magelona mirabilis</i>	<i>Spiophanes bombyx</i> <i>Spio martinensis</i> <i>Scolelepis (Scolelepis) squamata</i> <i>Magelona mirabilis</i> <i>Dispia</i> sp.	<i>Spiophanes bombyx</i> Spionidae

		<i>Laonice</i> sp. Spionidae	
<b>OMN-Amphipoda</b>	<i>Gammarus crinicornis</i> <i>Gammarus</i> sp. <i>Pontocrates arenarius</i>	<i>Dexamine spinose</i> <i>Gammarus crinicornis</i> <i>Pontocrates arenarius</i> <i>Synchelidium maculatum</i>	<i>Gammarus crinicornis</i>
<b>OMN-Decapoda</b>	<i>Diogenes pugilator</i> <i>Liocarcinus</i> sp. <i>Portumnus latipes</i>	<i>Diogenes pugilator</i> <i>Liocarcinus holsatus</i> <i>Portumnus latipes</i>	Paguridae <i>Portumnus latipes</i>
<b>OMN-Isopoda</b>	<i>Idotea baltica</i> <i>Idotea pelagica</i> <i>Eurydice pulchra</i>	<i>Idotea linearis</i> <i>Eurydice pulchra</i> <i>Lekanesphaera</i> sp.	<i>Idotea neglecta</i> <i>Eurydice pulchra</i>
<b>OMN-Mysida</b>	Mysida	<i>Acanthomysis longicornis</i> <i>Gastrosaccus sanctus</i> <i>Haplostylus normani</i> <i>Schistomysis parkeri</i> Mysida	Mysida
<b>SF-Cardiida</b>	<i>Donax vittatus</i> <i>Donax trunculus</i>	<i>Donax vittatus</i> <i>Donax trunculus</i>	<i>Donax vittatus</i> <i>Donax trunculus</i> <i>Donax</i> spp. (siphons/feet) <i>Donax</i> spp.
<b>CAR-other*</b>	<i>Planaria</i> sp.	<i>Actiniaria</i> sp. <i>Planaria</i> sp.	
<b>DF-other*</b>	<i>Orbinia</i> sp.	<i>Sipunculus nudus</i> <i>Capitella</i> sp. <i>Phylo foetida</i> <i>Scoloplos armiger</i> Orbiniidae <i>Paradoneis armata</i> <i>Chaetozone gibber</i>	Harpacticoida
<b>OMN-other</b>		<i>Apseudes talpa</i>	Crustacea (larva) Ostracoda
<b>SF-other</b>	<i>Ensis</i> sp. <i>Chamelea gallina</i> <i>Mactra stultorum</i> <i>Mactra</i> sp.	<i>Lucinella divaricata</i>	

The tropho-orders with a \* were not included in the calculation of the macroinvertebrate isotopic niche and centroid because we didn't find mention of these species in juvenile flatfish diet and so we didn't consider them as potential prey.

**Table S3.** Mean (and standard deviation = SD) of the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values measured for the different organic matter sources at the base of each food web (marine suspended particulate organic matter = SPOM, sediment organic matter = SOM and *Ulva* spp. = ULV), the macroinvertebrate tropho-orders (see Table S3) and age 0 (0G) and age 1 (1G) flatfish species (*Pegusa lascaris*, *Pleuronectes platessa* and *Scophthalmus maximus*) sampled at the non-impacted sandy beach (NIm) and at the sandy beach impacted by green tides (Im) during the pre green tide (Pre GT), the peak green tide (Peak GT) and the two post green tide periods (Post GT1 and Post GT2).

Period		NIm			Period		Im		
		$\delta^{13}\text{C}$ (SD)	$\delta^{15}\text{N}$ (SD)	n			$\delta^{13}\text{C}$ (SD)	$\delta^{15}\text{N}$ (SD)	n
<b>Pre GT</b>	POM	-25.09 (0.51)	6.54 (0.67)	3	<b>Pre GT</b>	POM	-24.52 (0.05)	6.61 (0.69)	3
	SOM	-21.37 (1.68)	6.34 (0.37)	8		SOM	-21.05 (1.37)	6.23 (0.92)	9
	CAR-Nem.	-18.29 (0.61)	14.17 (0.56)	14		ULV	-19.06 (0.00)	7.19 (0.13)	3
	CAR-Oph.	-18.94 (0.98)	13.09 (0.64)	14		CAR-Dec.	-18.19 (0.43)	10.29 (0.77)	5
	CAR-Phy.	-17.36 (0.67)	12.25 (0.83)	19		CAR-Eun.	-17.77 (0.47)	13.19 (0.59)	6
	DF-Amph.	-19.16	8.36	1		CAR-Nem.	-16.74	14.65	1
	DF-Card.	-19.17 (0.60)	9.13 (0.36)	28		CAR-Oph.	-18.39 (0.16)	13.81 (0.79)	4
	DF-Sab.	-19.03 (0.46)	10.91 (0.27)	5		CAR-Phy.	-16.48 (0.19)	11.37 (0.31)	5
	DF-Spi.	-21.20 (0.56)	9.73 (0.75)	5		DF-Sab.	-18.08 (0.26)	10.82 (0.28)	10
	OMN-Amph.	-24.09	8.08	1		OMN-Dec.	-18.71 (1.37)	10.66 (1.53)	7
	OMN-Dec.	-17.82	12.68	1		OMN-Mys.	-18.54 (0.43)	11.94 (0.57)	8
	OMN-Iso.	-19.29 (0.86)	10.64 (0.65)	2		SF-Card.	-19.42 (0.59)	8.32 (0.45)	19
	SF-Card.	-19.98 (0.90)	8.01 (0.93)	33		0G <i>P. lascaris</i>	-17.76 (0.14)	12.64 (0.40)	8
	SF-other	-19.01 (1.21)	9.70 (1.16)	3					
	0G <i>P. lascaris</i>	-18.15 (0.38)	13.08 (0.26)	6					
POM	-21.46 (1.18)	6.93 (0.51)	3	POM	-20.09 (0.05)	6.75 (0.92)	3		

	SOM	-21.59 (1.60)	5.62 (0.83)	9		SOM	-20.02 (0.23)	6.12 (0.55)	9
	CAR-Dec.	-17.89 (0.68)	12.16 (0.37)	5		ULV	-18.14 (1.08)	11.91 (2.50)	6
<b>Peak GT</b>	CAR-Eun.	-18.35	13.7	1	<b>Peak GT</b>	CAR-Dec.	-16.47 (0.40)	12.49 (0.30)	5
	CAR-Nem.	-18.09 (0.57)	13.77 (0.47)	12		CAR-Eun.	-17.50 (0.32)	13.48 (0.61)	5
	CAR-Oph.	-19.18 (1.61)	13.56 (0.70)	11		CAR-Nem.	-16.94 (0.36)	13.02 (1.08)	4
	CAR-Phy.	-18.08 (0.91)	12.06 (0.79)	24		CAR-Oph.	-18.39 (1.24)	13.35 (0.76)	7
	DF-Amph.	-20.23	9.72	1		CAR-Phy.	-17.38 (0.44)	11.54 (0.90)	15
	DF-Card.	-19.12 (0.77)	8.99 (0.37)	27		DF-Amph.	-19.31 (1.70)	6.77 (1.72)	8
	DF-Cum.	-21.31 (2.38)	7.74 (1.08)	6		DF-Card.	-18.39 (0.38)	8.67 (0.30)	12
	DF-Sab.	-19.64 (1.22)	10.86 (0.36)	7		DF-Cum.	-19.76 (0.62)	6.94 (1.02)	5
	DF-Spat.	-18.58	11.44	1		DF-Sab.	-17.99 (0.35)	11.20 (0.68)	15
	OMN-Amph.	-20.64 (4.12)	9.86 (1.11)	3		OMN-Dec.	-21.41 (0.35)	10.03 (0.50)	5
	OMN-Dec.	-19.83 (1.04)	10.64 (1.37)	6		OMN-Iso.	-21.48 (0.09)	10.32 (0.97)	2
	OMN-Iso.	-19.87 (1.57)	8.49 (1.04)	3		OMN-Mys.	-19.90 (1.06)	12.12 (0.11)	3
	OMN-Mys.	-19.14 (0.94)	11.05 (0.57)	2		SF-Card.	-18.70 (0.33)	8.31 (0.51)	31
	SF-Card.	-19.23 (0.74)	8.34 (0.49)	28		SF-other	-17.4	9.25	1
	SF-other	-19.39 (0.98)	8.90 (1.20)	2		1G <i>P. lascaris</i>	-16.36 (0.23)	11.53 (0.40)	9
	DF-other	-19.26 (0.18)	9.84 (0.31)	2		0G <i>P. platessa</i>	-17.46 (0.37)	11.55 (0.32)	5
	0G <i>P. lascaris</i>	-19.09 (0.85)	12.12 (0.83)	10		0G <i>S. maximus</i>	-17.84 (0.82)	10.92 (0.51)	16
	1G <i>P. lascaris</i>	-18.50 (0.28)	12.57 (0.49)	6					
	0G <i>P. platessa</i>	-19.50 (0.13)	11.57 (0.16)	5					
	0G <i>S.</i>	-18.41 (0.76)	11.11 (0.41)	10					



<i>maximus</i>									
<b>Post GT1</b>	POM	-22.79 (1.28)	7.61 (0.25)	3	<b>Post GT1</b>	POM	-21.04 (1.15)	7.73 (0.14)	3
	SOM	-20.16 (0.17)	4.28 (0.56)	3		SOM	-20.14 (0.13)	6.76 (0)	3
	CAR- Dec.	-18.26 (0.56)	11.34 (0.72)	4		ULV	-18.51 (1.14)	9.95 (0.78)	10
	CAR- Eun.	-18.86 (0.40)	13.11 (0.34)	2		CAR- Dec.	-17.36 (0.25)	11.58 (0.47)	7
	CAR- Nem.	-18.45 (0.25)	13.82 (0.62)	4		CAR- Eun.	-17.81 (0.57)	13.00 (1.90)	4
	CAR- Oph.	-18.79 (0.52)	12.71 (1.09)	9		CAR- Nem.	-17.18 (0.63)	13.38 (0.75)	6
	CAR- Phy.	-17.87 (0.99)	11.60 (0.67)	9		CAR- Oph.	-16.89 (0.4)	13.25 (0.95)	3
	DF- Amph.	-18.83 (0.75)	6.42 (2.61)	2		CAR- Phy.	-17.77 (0.64)	11.21 (0.55)	19
	DF- Card.	-20.16 (2.04)	8.75 (0.28)	31		DF- Amph.	-18.29	9.2	1
	DF- Cum.	-19.22 (1.57)	6.37 (1.24)	3		DF- Card.	-18.63 (0.79)	8.84 (0.27)	10
	DF- Sab.	-19.89 (0.56)	10.59 (0.46)	9		DF- Sab.	-18.30 (0.37)	10.39 (0.55)	27
	DF- Spio.	-20.85 (0.12)	9.55 (0.07)	2		DF- Spio.	-18.43 (0.09)	9.67 (0.55)	3
	OMN- Dec.	-20.03 (0.83)	8.93 (0.14)	4		OMN- Dec.	-19.07 (0.25)	10.02 (0.43)	7
	OMN- Iso.	-22.23	7.68	1		OMN- Mys.	-17.57	12.17	1
	OMN- Mys.	-19.10 (0.03)	10.90 (0.24)	3		SF- Card.	-19.01 (0.91)	8.74 (0.45)	36
	SF- Card.	-19.81 (0.63)	8.32 (0.41)	63		CAR- other	-19.01 (0.33)	9.78 (0.41)	3
OG <i>P.</i> <i>lascaris</i>	-18.94 (0.99)	11.76 (0.64)	9	OG <i>P.</i> <i>lascaris</i>	-17.56 (0.68)	11.91 (0.48)	34		
				1G <i>P.</i> <i>lascaris</i>	-16.80 (0.18)	12.16 (0.37)	6		
<b>Post GT2</b>	POM	-22.86 (0.17)	6.77 (0.14)	3	POM	-21.75 (0.16)	7.22	3	
	SOM	-20.30 (0.19)	4.16 (0.41)	3	SOM	-20.08 (0.13)	4.79 (0.86)	3	
	CAR- Nem.	-17.09	14.99	1	ULV	-16.72 (0.29)	9.74 (0.82)	7	

CAR-Oph.	-18.98 (0.28)	12.22 (0.97)	3	CAR-Nem.	-17.37 (0.32)	13.36 (0.37)	3
CAR-Phy.	-19.08 (1.17)	11.84 (0.81)	16	CAR-Oph.	-17.00 (0.50)	13.49 (1.19)	2
DF-Amph.	-20.03	8.49	1	CAR-Phy.	-18.36 (0.37)	11.30 (0.69)	16
DF-Card.	-18.86 (1.07)	9.04 (0.32)	21	DF-Card.	-18.26 (0.49)	8.80 (0.29)	14
DF-Cum.	-20.47 (0.27)	6.28 (1.47)	2	DF-Cum.	-18.61	4.25	1
DF-Sab.	-20.43 (0.91)	10.34 (0.00)	2	DF-Sab.	-18.24 (0.30)	10.90 (0.31)	27
DF-Spio.	-20.64 (0.69)	9.76 (0.34)	3	DF-Spio.	-18.56 (0.12)	9.88 (0.09)	5
OMN-Dec.	-18.98 (1.36)	9.04 (0.54)	2	SF-Card.	-18.96 (0.43)	8.74 (0.41)	37
OMN-Iso.	-20.51	9.64	1	0G <i>P. lascaris</i>	-17.71 (0.22)	12.59 (0.22)	5
SF-Card.	-19.63 (0.45)	8.39 (0.60)	47				
0G <i>P. lascaris</i>	-18.97 (0.24)	12.77 (0.50)	14				

