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

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Highlights

► We investigated the effects of green tides on juvenile flatfish trophic ecology. ► Across species, flatfish displayed more opportunistic foraging at the impacted site. ► Plaice displayed a lower diet shift than sand sole and turbot at the impacted site. ► Species-specific responses seem driven by prey detection method and foraging time. ► Plaice and sand sole but not turbot derived part of their energy from *Ulva*.

Keywords : eutrophication, foraging behavior, fish diet, macrobenthic invertebrates, stable isotopes, trophic niche, *Pegusa lascaris*, *Pleuronectes platessa*, *Scophthalmus maximus*, North-East Atlantic

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25 1. Introduction

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

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

47 Shifts in fish assemblages have been related to GT (Paumier et al., 2018; Pihl et al., 1995;
48 Quillien et al., 2018; Wennhage and Pihl, 2007), and benthic fish species, such as flatfish, have been
49 found to be the most negatively impacted, with generally lower densities reported at sites with GT (De
50 Raedemaecker et al., 2012; Le Luherne et al., 2017, 2016). Overall, opportunistic macroalgae blooms can
51 decrease the quality of flatfish nurseries (De Raedemaecker et al., 2012; Jokinen et al., 2016), potentially
52 leading to lower annual recruitment rates to the adult stock (Pihl et al., 2005). Meio- and macrobenthic
53 invertebrates, the main prey of juvenile flatfish (Amara et al., 2001; Cabral et al., 2002), are also modified
54 by macroalgae blooms in terms of their taxonomic richness, composition, abundance, biomass and

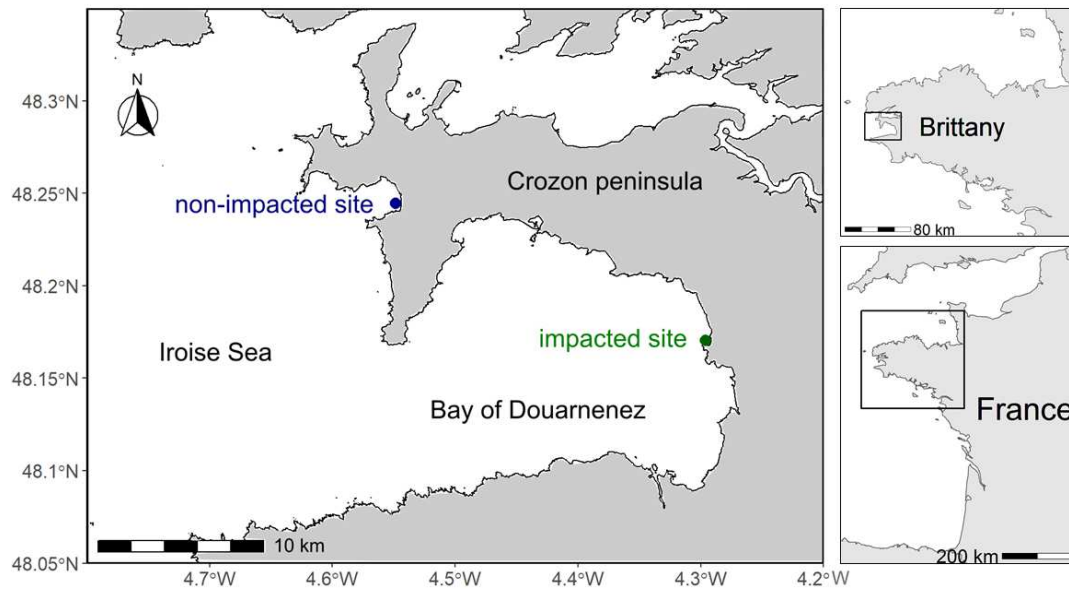
55 functional groups (Carrigo et al., 2013; Pihl et al., 1995; Quillien et al., 2015a, 2015b). Furthermore,
56 juvenile flatfish can experience lower foraging success when drifting macroalgae are added to bare sand,
57 as shown experimentally for *Platichthys flesus* and *S. maximus* (Aarnio and Mattila, 2000; Nordström and
58 Booth, 2007). Consequently, GT could modify flatfish trophic ecology (*e.g.* diet, prey preference, energy
59 intake) through their effects on flatfish prey and on flatfish foraging, first leading to lower body conditions
60 and growth rates (Andersen et al., 2005; Le Luherne et al., 2017; Pihl, 1994) and ultimately to lower
61 recruitment rates (Pihl et al., 2005), through food limitation (Le Pape and Bonhommeau, 2013).

62 Nonetheless, opportunistic and short-term macroalgae blooms can provide an additional source
63 of organic matter (*i.e.* basal resource) for sandy-beach invertebrates (Quillien et al., 2016; Robertson and
64 Lenanton, 1984) and lead to higher benthic invertebrate densities (Bolam et al., 2000; Quillien et al.,
65 2015a, 2015b). Consequently, opportunistic macroalgae (*e.g.* *Ulva* spp.) could represent an additional
66 source of energy for juvenile flatfish via their benthic prey (Robertson and Lenanton, 1984), one that is
67 traceable using stable isotopes. Indeed, *Ulva* spp. have distinctly ¹³C-enriched carbon isotopic
68 compositions relative to marine suspended particulate organic matter (SPOM) (*i.e.* mainly phytoplankton)
69 and sediment organic matter (SOM) (*i.e.* detritus, microphytobenthos, deposited phytoplankton) (Dubois
70 and Colombo, 2014; Quillien et al., 2016), the two main basal resources available at bare sandy beaches.
71 Furthermore, the presence of extensive *Ulva* mats can modify the carbon isotopic compositions of
72 dissolved inorganic carbon (Van Alstyne et al., 2015), leading to ¹³C enrichment of SPOM (Quillien et al.,
73 2016).

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

83 In this study, the effects of GT (*Ulva* spp.) on the trophic niche, foraging behavior and
84 additional basal resource use of juvenile flatfish were investigated in macrotidal sandy beach nurseries.
85 We combined carbon and nitrogen isotopic compositions of predator (flatfish) and potential prey (benthic
86 macroinvertebrates), predator digestive tract contents and potential prey abundances in an approach
87 comparing a site not impacted by GT to a site impacted by GT. During the early summer GT peak, we
88 focused on three nursery-dependent flatfish species – the sand sole *Pegusa lascaris*, the plaice *P. platessa*

89 and the turbot *S. maximus* (Gibson, 2005) – which co-occur in sandy beach nurseries in western Brittany,
 90 France (Déniel, 1981; Quillien et al., 2018). For *P. lascaris*, which remains in the coastal nurseries for
 91 over a year (Déniel, 1981), we also investigated temporal dynamics of its trophic ecology relative to the
 92 early summer GT peak.



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

97

98 2. Materials and methods

99 2.1. Study system and GT

100 We sampled the intertidal zone of two known flatfish nursery areas (Déniel, 1981; Quillien et al.,
 101 2018; Quiniou, 1986) located in the same part of the Iroise Sea (Fig. 1). This water mass is located just off
 102 the western tip of Brittany at the junction of the English Channel, Celtic Sea and Bay of Biscay. The non-
 103 impacted site is a 2.3 km long sandy beach located at the western tip of the Crozon peninsula ($48^{\circ} 14.682'$
 104 N , $4^{\circ} 32.908'$ W) that has never been impacted by GT (NIm). The impacted site (Im) is a 2.8 km long
 105 sandy beach located on the eastern side of the Bay of Douarnenez ($48^{\circ} 10.22'$ N , $4^{\circ} 17.775'$ W) that has
 106 been impacted by GT every year since the 1970s due to the presence of intensive agricultural areas in the
 107 neighboring catchment (Perrot et al., 2014). These two beaches have a similar mean breaking-wave height
 108 (1.4 m) and mean tidal regimes (6.5 m), which classify them as ultra-dissipative. Both also are

109 characterized by fine sand, gentle slopes (1.5%) and wide intertidal zones (up to 500 m during spring
110 tides). These similarities allow them to be compared in relation to the presence or absence of GT (Quillien
111 et al., 2018). All the environmental parameters that describe the morphology, sediment and overlaying
112 water at each site (Table S1) were retrieved from Quillien et al. (2015a, 2015b).

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

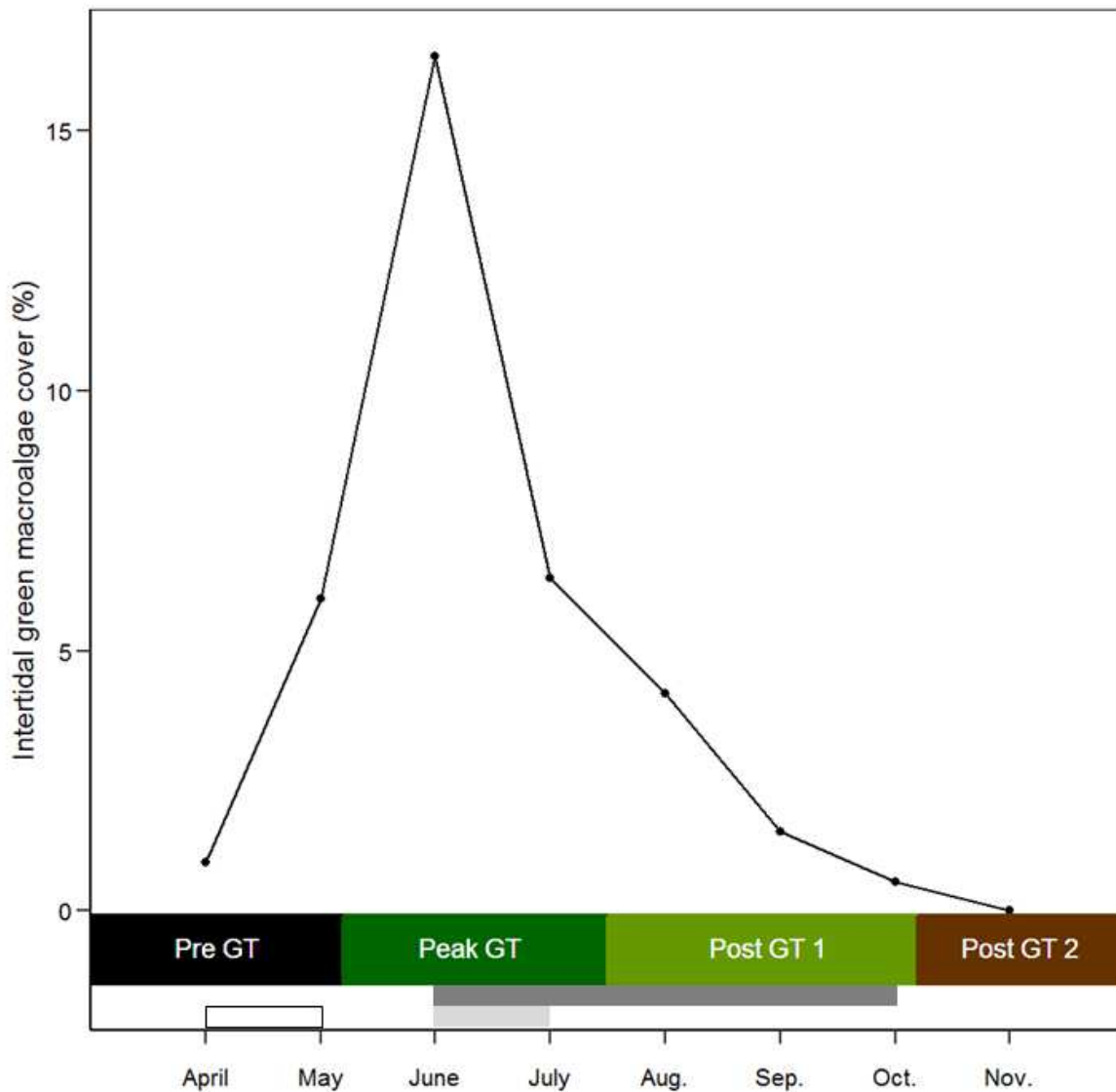
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126 2.2. Sampling

127 Macroinvertebrates, representing the flatfish prey reservoir, were sampled once during the 2012
128 Pre GT (early May), Peak GT (early July), Post GT1 (early September) and Post GT2 (early November)
129 periods at both sites during low tide. To determine macroinvertebrate composition and abundance, nine
130 replicate sediment cores were randomly sampled on each sampling date along the NIm and Im beaches
131 using a tube corer (total area = 0.09 m²). Samples were then sieved (1 mm mesh size) to retrieve the
132 macroinvertebrates, which were preserved in 4% buffered formalin (Quillien et al., 2018). Later at the lab,
133 the sediment samples were sorted, and the macroinvertebrates were identified to the lowest taxonomic
134 level (usually species) and counted to determine their abundance. To consider potential intra-site
135 variability in macroinvertebrate isotopic compositions, infaunal organisms were sampled at three points
136 along each beach (min 500 m between each point) by digging up organisms from the sand and sieving
137 large volumes of sediment (*ca.* 4 L) with a 1 mm mesh sieve. Vagile epibenthic organisms were caught
138 along each beach using a dip net. Later at the lab, these organisms were sorted and identified before being
139 stored at -20°C for stable isotope analysis (Quillien et al., 2016).

140 Flatfish were sampled during the day at rising tide, using a beach trawl (5 m wide, 0.3 m high,
141 with an 8 mm stretched mesh net in the cod-end) developed by Quiniou (1986). The beach trawl was
142 towed at least once along each beach by two operators in 50 cm deep water, sampling an area of 400-1300

143 m² (Quillien et al., 2018). The flatfish were identified on site to the species level, counted and individually
 144 measured (total length). A subsample was collected for digestive tract analysis and preserved in 4%
 145 buffered formalin, while a second subsample was collected for stable isotope analysis and preserved at -
 146 20°C. The remaining flatfish were immediately released after being counted and measured. Only a limited
 147 number of fish could be collected according to the regulations of the National Marine Park of the Iroise
 148 Sea, where the study sites are located.



149
 150 **Figure 2.** Monthly intertidal cover (%) of green macroalgae from April-November 2012 at the site
 151 impacted by green tides (GT), calculated as the percentage of the intertidal zone covered by the sum of the
 152 beach area covered by stranded macroalgae and the area of the breaking-wave zone with macroalgae. The
 153 temporal GT pattern at the impacted site is divided into four periods: the period before the GT (Pre GT),

154 the peak GT period (Peak GT) and two periods after the GT (Post GT1 and Post GT2). Data come from
155 the Centre d'Etude et de Valorisation des Algues. White, light gray and dark gray bands indicate the
156 settlement periods of *P. platessa*, *S. maximus* and *P. lascaris*, respectively, in the coastal nurseries of the
157 Bay of Douarnenez (Déliel, 1981).

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

170

171 2.3. Sample preparation and analyses

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

186 To characterize the flatfish prey, individuals were dissected, their digestive tract (stomach + gut)
187 was fixed in 4% buffered formalin and the organisms present were identified to the lowest taxonomic

188 level using a binocular magnifier. Some prey items were in an advanced phase of digestion (*e.g.*
189 polychaetes), which limited our ability to identify them beyond their order.

190

191

192 2.4. Data analyses

193 2.4.1. Potential flatfish prey

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

212

213 2.4.2. Trophic ecology description and comparisons of trophic metrics

214 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
215 (four periods: Pre GT, Peak GT, Post GT1 and Post GT2) and GT (2 sites: NIm and Im), we performed
216 multiple pairwise comparisons (t-tests) using a permutation procedure and the Hommel p-value
217 adjustment method for multiple tests (‘rcompanion’ package). Multiple pairwise comparisons were chosen
218 instead of ANOVA because G1 and G0 *P. lascaris* were sampled only during certain periods (“missing
219 cells”). Permutation tests are non-parametric tests that address observations that are not normally
220 distributed, which was the case for several groups (Legendre and Legendre, 2012). The Hommel
221 adjustment method was chosen because it controls for family-wise error, does not assume that

222 observations are normally distributed and is more powerful than Holm's and Hochberg's adjustment
223 methods (Shaffer, 1995). Finally, for permutation tests with unequal sample sizes and unequal variances, a
224 p-value of 0.05 is too liberal only if the group with the smaller sample size has the larger variance
225 (Mewhort et al., 2009), which never occurred in our data. Consequently, a p-value of 0.05 was chosen
226 without the risk of increasing Type I error. The same procedure was used to test if the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of
227 flatfish were significantly different according to group (G0 *P. lascaris*, G0 *P. platessa*, G0 *S. maximus* and
228 G1 *P. lascaris*) and GT (2 sites: NIm and Im) during Peak GT. All differences in results were considered
229 significant at $\alpha = 0.05$.

230 The digestive tract data were used to calculate each flatfish group's (a combination of site, period,
231 species and age-class) vacuity rate (percentage of digestive tracts that were empty) and to characterize its
232 diet according to each tropho-order's frequency of occurrence (percentage of digestive tracts in which the
233 tropho-order was found) and relative abundance (percentage of tropho-order prey items out of total prey
234 items). We also used the digestive tract data to measure the dietary similarity (DS) of two flatfish groups
235 by calculating their proportional similarity index (Schoener, 1970), as recommended by Wallace (1981).
236 DS 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
237 ingested by group x and y , respectively and standardized between 0 and 1 ('spaa' package) with 1
238 indicating perfect dietary similarity.

239 The macroinvertebrates (potential prey) were sampled a few weeks before the flatfish (their
240 predators) at each period. Consequently, the flatfish white muscle isotopic composition of a given period
241 reflect that of their prey sampled at the same given period. To visualize potential trophic changes (isotopic
242 niche width and position relative to tropho-orders) of *P. lascaris* (G0 and G1) in time and relative to the
243 GT, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of macroinvertebrate tropho-orders and *P. lascaris* at both sites (NIm and Im) were
244 plotted for each of the four GT periods. To represent each group's total isotopic niche width, we added the
245 convex hull polygons which encompass all the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of each *P. lascaris* group (Layman et al.,
246 2007). We chose to represent the convex hull polygons instead of the standard ellipse area because it is
247 easier to visualize on figures. The same kind of figure was plotted to visualize potential trophic changes in
248 the four co-occurring flatfish groups (G0 *P. lascaris*, G0 *P. platessa*, G0 *S. maximus* and G1 *P. lascaris*)
249 during Peak GT.

250 The standard ellipse area corrected for small sample sizes (SEA_C) developed by Jackson et al.
251 (2011) and the diet richness (number of prey tropho-orders) were calculated ('SIAR' and 'SIBER'
252 packages) to estimate the isotopic niche width and diet niche width, respectively, of each flatfish group
253 (population level). The SEA_C (strictly positive, $\% \sigma^2$), which encompasses 40% of the isotopic compositions
254 of each flatfish group, was preferred to Layman's convex hull (Layman et al., 2007) because extreme
255 isotopic compositions bias it less (Brind'Amour and Dubois, 2013). This metric provides information on

256 the level of isotopic prey diversity assimilated by a flatfish group during a given period function of the
257 isotopic turnover rate, without providing any information on the intra-individual trophic diversity (*i.e.*
258 individual specialization). To compare the size of two flatfish groups' SEA_Cs, we considered their
259 Bayesian distributions (Jackson et al., 2011) and calculated the probability that one SEA_C was smaller or
260 larger than the other SEA_C ('SIAR' and 'SIBER' packages). Furthermore, to help interpret variations in
261 flatfish isotopic niches, we calculated the potential prey isotopic niches (macroinvertebrate SEA_C),
262 excluding CAR-Nemerta (Table S2), CAR-other (*Planaria* sp.) and DF-other (*Orbinia* sp.) because
263 species of these tropho-orders were never mentioned in studies of the diet of *P. lascaris*, *P. platessa* or *S.*
264 *maximus* (*e.g.* Amara et al., 2001; Beyst et al., 1999; Cabral et al., 2002).

265 Finally, we estimated the amount of potential prey isotopic diversity assimilated by a flatfish
266 group as the ratio of a flatfish group's SEA_C to the macroinvertebrate SEA_C (SEA_C ratio), expressed as a
267 percentage. Following Kempf et al. (2008), we also calculated the proportional similarity index (Schoener,
268 1970) between the digestive tract contents of a flatfish group and the benthic community to measure the
269 extent to which a flatfish group used the potential prey community (benthic community dataset in Table
270 S2). This measure, which we termed the dietary opportunism index (DO), was calculated as $1 - 0.5 (\sum |p_{ij} -$
271 $q_j|)$, where p_{ij} is the mean proportion of the j^{th} tropho-order in the i^{th} flatfish group and q_j is the mean
272 proportion of the j^{th} tropho-order in the sediment, and standardized between 0 and 1 ('spaa' package). A
273 group has either opportunistic foraging behavior (DO close to 1) or selective foraging behavior (DO close
274 to 0).

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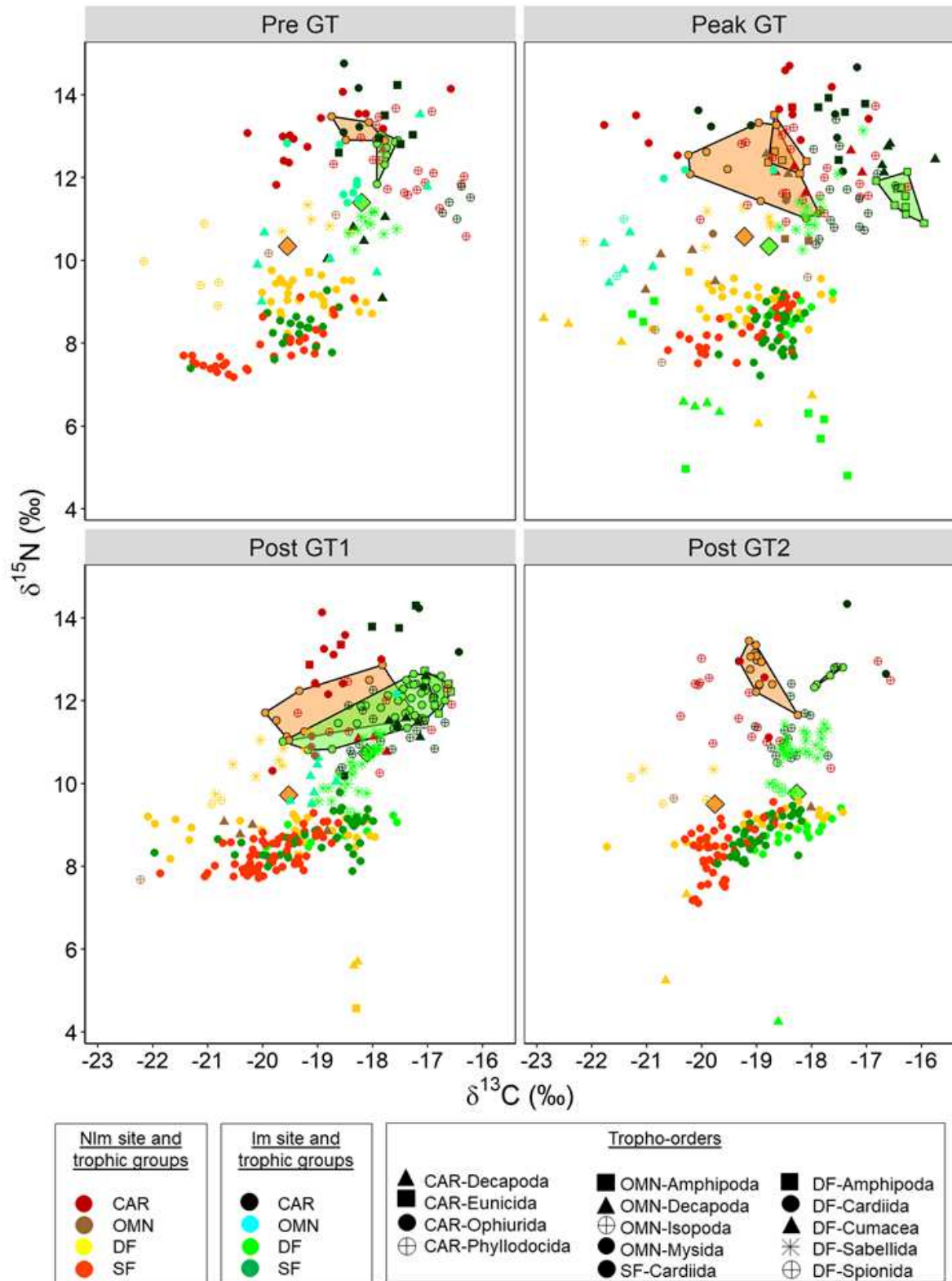
276 3. Results

277 3.1. Isotopic compositions of the flatfish potential prey (macroinvertebrates)

278 Across sites and periods, $\delta^{13}\text{C}$ of macroinvertebrate tropho-orders ranged from -24‰ to -16‰ and
279 $\delta^{15}\text{N}$ ranged from 4 to 15‰. Despite no statistical testing, primary consumers (SF and DF) had the lowest
280 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, secondary consumers (CAR) had the highest values, and OMN had intermediate and often
281 highly variable values across sites and periods (Fig. 3, Table S3).

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

290 opposite was observed for CAR-Ophiurida. SF-Cardiida presented significantly higher mean $\delta^{15}\text{N}$ at the
 291 Im than at the NIm site during Pre GT, Post GT1 and Post GT2 but not during Peak GT.



292

293 **Figure 3.** $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (‰) of *Pegusa lascaris* age class 0 (blacklined circles) and age class 1 (black
 294 lined squares) at the sandy beach not impacted by green tides (orange, NIm site) and the sandy beach
 295 impacted by green tides (green, Im site) during the four green tide periods (Pre GT, Peak GT, Post GT1
 296 and Post GT2), with the corresponding convex hulls (orange and green polygons for the NIm and Im site,
 297 respectively). The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of the macroinvertebrates sampled at the same site and period are
 298 represented using a combination of color (site and trophic group) and symbol (tropho-order). The orange
 299 and green diamonds represent the centroid of the macroinvertebrate community at the NIm and Im sites,
 300 respectively. CAR = carnivore, OMN = omnivore, DF = deposit feeder, SF = suspension feeder.

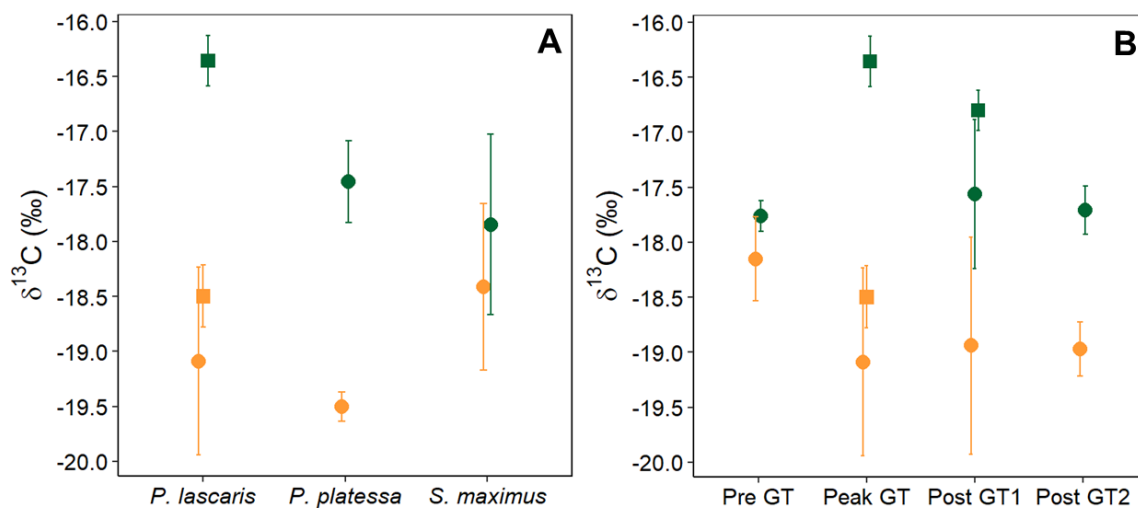
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302 3.2. Species-specific trophic ecology during Peak GT and changes linked to GT

303 3.2.1. Flatfish isotopic compositions and associated metrics

304 During the Peak GT, the isotopic composition of flatfish ranged from -20.2‰ to -16‰ for $\delta^{13}\text{C}$
 305 and 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
 306 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ with variable ranges (Figs. 4A and 5). Two inter-group differences were significant: G1 *P.*
 307 *lascaris* 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.*
 308 *maximus* (t-stat = 3.35, adj. p = 0.01), respectively. Age-class 0 *P. lascaris* had the widest isotopic niche
 309 (SEA_C), followed by *S. maximus*, G1 *P. lascaris*, and then *P. platessa* (Bayesian probabilities > 0.83).

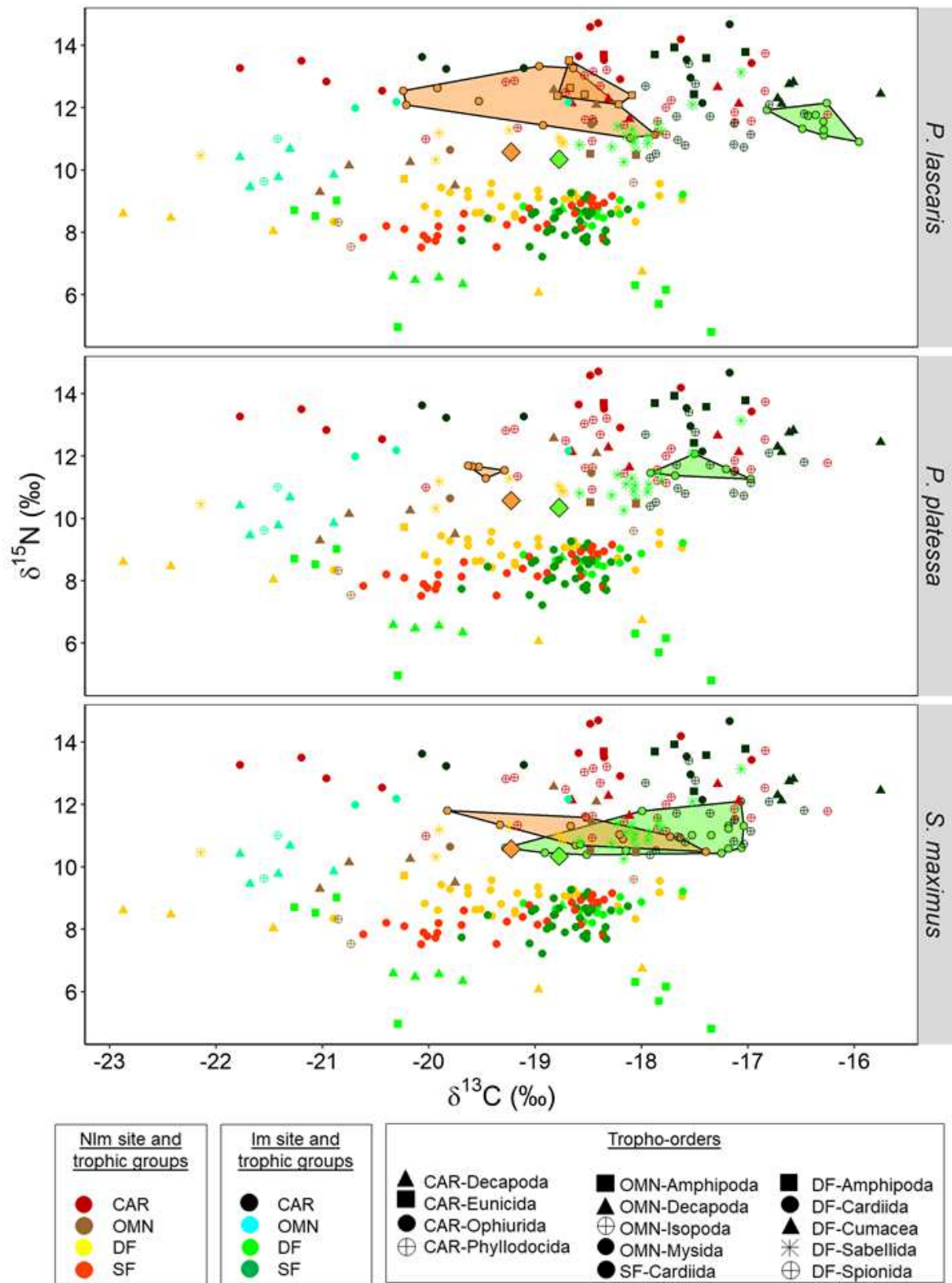
310



311

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

316



317

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

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

332 None of the flatfish groups presented a similar change in their isotopic metrics at both sites, except
 333 in their mean $\delta^{15}\text{N}$, which did not differ significantly between sites. Only *P. lascaris* and *P. platessa*
 334 presented significantly higher mean $\delta^{13}\text{C}$ at the Im than at the NIm site for the same age class (Table 1)
 335 and different age classes (*P. lascaris*: t-stat = 3.88 adj. p = 0.002). There was strong evidence that *P.*
 336 *platessa* and *S. maximus* had a wider isotopic niche at the Im than at the NIm site and that *P. lascaris* had
 337 a narrower 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 _c (‰ ²)	n	TL (mm)	Mean $\delta^{13}\text{C}$ (‰)	SEA _c (‰ ²)		
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)

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

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

344

345 3.2.2. Flatfish digestive tract contents and associated metrics

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

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

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

365 All three flatfish groups had higher DO at the Im than at the NIm site. They also relied less on SF-
366 Cardiida and more on a range of DF and OMN crustaceans, with species-specific differences (Table 2). *P.*
367 *lascaris* (G1) and *S. maximus* had vastly different diets between the two sites (DS < 0.13), while that of *P.*
368 *platessa* differed less between sites (DS = 0.52). *P. lascaris* and *P. platessa* had higher prey richness at the
369 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>	
Total length (mm)	41-87		101-120		53-82		36-91		34-89	
n (vacuity rate, %)	20 (0%)		4 (0%)		14 (0%)		11 (0%)		19 (17%)	
NIm site	O	A	O	A	O	A	O	A	O	A
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	
Total length (mm)			93-141		70-91		25-79		43-67	
n (vacuity rate, %)	0		9 (0%)		16 (0%)		15 (0%)		10 (29%)	
Im site			O	A	O	A	O	A	O	A
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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374 **Table 2.** Sample size (n), total length (TL, mm), vacuity rate (%), frequency of occurrence (O, %) and
 375 relative abundance (A, %) of tropho-orders identified in age class 0 (G0) and age class 1 (G1) flatfish
 376 (*Pegusa lascaris* (*P. las*), *Pleuronectes platessa* (*P. pla*) and *Scophthalmus maximus* (*S. max*)) sampled at
 377 the sandy beach not impacted by green tides (NIm site) and the sandy beach impacted by green tides (Im
 378 site) during the peak green tide (Peak GT) and the second post-green-tide (Post GT2) periods. The number
 379 of tropho-orders (richness) and the dietary opportunism index (DO) are also shown. Tropho-orders
 380 marked with * had significantly higher $\delta^{13}\text{C}$ at the Im than at the NIm site ($p < 0.05$ for the main site
 381 effect), while those marked with # had $\delta^{13}\text{C}$ that did not differ significantly between the two sites ($p > 0.05$
 382 for the main site effect).

383

384 3.3. Temporal changes in the trophic ecology of *P. lascaris* and changes linked to GT

385 3.3.1. *P. lascaris* isotopic compositions and associated metrics

386 At the NIm site, G0 individuals were sampled during all four periods, but G1 were sampled only
 387 during Peak GT. At the Im site, G0 individuals were sampled during Pre GT, Post GT1 and Post GT2,
 388 while G1 were sampled during Peak GT and Post GT1 (Table 3). The isotopic composition of *P. lascaris*
 389 (G0 and 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
 390 Peak GT (NIm site) and Post GT1 (Im site), G1 had a narrower isotopic niche (SEA_C) than G0
 391 (probabilities > 0.99). Age-class G1 also had higher $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ than G0 (but not significantly so) (Figs.
 392 3 and 4B) and lower SEA_C ratios than G0 (Table 3).

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

398 At the Im site, *P. lascaris* had the highest $\delta^{13}\text{C}$ during Peak GT (Fig. 4B). The differences were
 399 significant when compared to the values from all other periods (adj. p < 0.015), except for G1 during Post
 400 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.
 401 3). The only significant differences were between Pre GT and Peak GT values (t-stat = 3.31, adj. p = 0.03)
 402 and between Pre GT and Post GT1 (G0) values (t-stat = 3.41, adj. p = 0.03).

403

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 _C (‰ ²)	Macro invert. SEA _C (‰ ²)	SEA _C ratio (%)	n	TL (mm)	Mean $\delta^{13}\text{C}$ (‰)	Flatfish SEA _C (‰ ²)	Macro invert. SEA _C (‰ ²)	SEA _C 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)

404 **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_C) for age
405 class 0 (G0) and age class 1 (G1) *Pegusa lascaris* and the macroinvertebrate community (macroinvert.) at the sandy beach not impacted by green
406 tides (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
407 ratio of the SEA_C of *P. lascaris* to the macroinvertebrate SEA_C, the Bayesian probability comparing the Bayesian SEA of *P. lascaris* at the two
408 sites, and inter-site pairwise comparisons (t statistic and adjusted p-value) of the $\delta^{13}\text{C}$ are also shown.

409 The SEA_C was low during all four periods, except for G0 during Post GT1. The SEA_C ratio was lowest
410 during Pre GT, Peak GT and Post GT2, with higher values during Post GT1 (Table 3).

411 During all four periods, there was strong evidence for *P. lascaris* having a narrower isotopic niche
412 (SEA_C) at the Im than at the NIm site when comparing the same age class (Table 3) and different age
413 classes (Peak GT probability = 1.00, Post GT1 probability = 0.99). From Peak GT-Post GT2, *P. lascaris*
414 presented a significantly higher mean $\delta^{13}C$ at the Im than at the NIm site when comparing the same age
415 class (Table 3) and different age classes (Peak GT t-stat = 3.88 adj. p = 0.004, Post GT1 t-stat = 3.07 adj. p
416 = 0.04). No significant inter-site differences were observed in mean $\delta^{15}N$ for *P. lascaris*, although $\delta^{15}N$ for
417 G1 were lower at the Im than at the NIm site during Peak GT (Fig. 3).

418

419 3.3.2. *P. lascaris* digestive tract contents and associated metrics

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

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

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

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

443 and the diet similarity was high ($DS = 0.68$). Age-class G0 had lower prey richness at the Im than at the
444 NIm site (Table 2).

445

446 **4. Discussion**

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

462

463 *4.1. Relating consumer isotopic compositions and niche to diet data*

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

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

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

484

485 4.2. Juvenile flatfish trophic ecology in a non-impacted sandy beach nursery

486 4.2.1. Species-specific trophic ecology during Peak GT

487 During Peak GT, *P. platessa* foraged on a low diversity of tropho-orders (5), and all individuals
488 consumed SF-Cardiida (high specialization *sensus* Yeakel et al. (2016)), a tropho-order relatively close to
489 the potential prey centroid in the isotopic niche space (low offset). In this case, the isotopic niche of *P.*
490 *platessa* should be narrow (Yeakel et al., 2016), as we observed. In the Mont Saint Michel Bay and
491 Wadden Sea, *P. platessa* also has a diet dominated by bivalves and cumaceans (Braber and De Groot,
492 1973; Kostecki et al., 2012) but generally forages on a much higher diversity of prey (Beyst et al., 1999;
493 Kostecki et al., 2012), a difference potentially caused by classifying prey into tropho-orders.

494 *S. maximus* foraged on a higher diversity of tropho-orders (8), with DF-Amphipoda and SF-
495 Cardiida observed in 73% and 64% of the digestive tracts, respectively. As both tropho-orders had low
496 offsets, the isotopic niche of *S. maximus* should be narrow and due to a lower specialization (Yeakel et al.,
497 2016), wider than that of *P. platessa*, as we observed. Bivalves and amphipods were reported as frequent
498 prey items for juvenile *S. maximus* along the German coast (De Groot, 1971) and in the Bay of
499 Douarnenez (Déniel, 1974), respectively. Conversely, bivalves were rarely recorded by Déniel (1974) but
500 frequently recorded in this study, a difference possibly related to their local availability, as each study
501 sampled a different nursery.

502 Age-class G0 *P. lascaris* also foraged on a relatively high diversity of tropho-orders (8), with 95%
503 occurrence of DF-Cumacea, indicating high specialization (Yeakel et al., 2016) on this tropho-order. In
504 this case, the isotopic niche of G0 *P. lascaris* should be relatively narrow (Yeakel et al., 2016), which is
505 not what we observed. Consequently, our sampling likely underestimated the importance of certain
506 tropho-orders in the *P. lascaris* diet due to its nocturnal foraging and rapid digestion (De Groot, 1971). To
507 achieve the wide isotopic niche and the measured $\delta^{13}C$ and $\delta^{15}N$, G0 *P. lascaris* likely had a more
508 generalist diet and foraged more frequently than estimated on tropho-orders with higher mean $\delta^{13}C$ and
509 $\delta^{15}N$, such as CAR-Phyllodocida and CAR-Ophiurida (Table S3), previously reported as prey (Cabral et
510 al., 2002; Rodriguez, 1996). Furthermore, the relatively high specialization of G1 *P. lascaris* on a tropho-

511 order with a low offset (SF-Cardiida) should yield a relatively narrow isotopic niche (Yeakel et al., 2016),
512 as we observed. Nonetheless, the relatively high $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of G1 *P. lascaris* cannot be explained by a
513 diet composed mainly of low $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ tropho-orders (SF-Cardiida and DF-Cumacea, Table S3),
514 indicating we probably missed important prey with higher mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (e.g. CAR-Phyllodocida,
515 Table S3), as expected with a sample size of 4.

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

528

529 4.2.2. Temporal variability in the trophic ecology of juvenile *P. lascaris*

530 The settlement period of *P. lascaris* larvae (June-October) in the Bay of Douarnenez (Déniel,
531 1981) led us to consider our sampling periods according to a different chronology. The G0 sampled from
532 Peak GT-Post GT2 settled in 2012 and were the youngest individuals, while the G0 sampled during Pre
533 GT and the sampled G1 settled in 2011 and were older.

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

545 Considering older individuals, *P. lascaris* switched to a lower isotopic diversity of prey (small
546 SEA_C) in autumn and maintained this characteristic until the next summer (Peak GT), despite the increase
547 in potential prey isotopic diversity (macroinvertebrate SEA_C). From G0 to G1 age-classes, the diet of *P.*
548 *lascaris* had lower prey richness and higher dominance in occurrence and abundance of SF-Cardiida,
549 despite the lower *in situ* abundance of the cardid *Donax* during Peak GT (Table S4). These results tend to
550 disagree with the continuously narrow isotopic niche observed from Post GT2 onward, which was likely
551 caused by underestimating less common prey items in the G1 *P. lascaris* diet. From younger to older
552 individuals, the $\delta^{13}C$ of *P. lascaris* also increased from *ca.* -19‰ to *ca.* -18‰, probably indicating an
553 increasing assimilation of prey with higher $\delta^{13}C$ by G1 (*e.g.* CAR-Phyllodocida, Table S3).

554 Over time, *P. lascaris* had relatively selective foraging behavior (low DO) that was likely related
555 to preferential consumption of organisms that maximized its energy intake and to the low vulnerability of
556 the most abundant tropho-order, DF-Spionida (Table S4). Two energy-rich (Brey, 2001) and more
557 vulnerable tropho-orders (SF-Cardiida and DF-Cumacea) are preferentially consumed (positive selection)
558 by juvenile *P. lascaris*, as reported in previous studies (Cabral et al., 2002; Quiniou, 1986; Rodriguez,
559 1996).

560

561 4.3. Broad changes in juvenile flatfish trophic ecology related to GT

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

573 Combining the digestive tract data and benthic community data (nine samples at each site during
574 Peak GT) revealed that flatfish relied more on the *in situ* macroinvertebrates at the Im site, hence
575 displaying a more opportunistic foraging behavior. Studies based on digestive tract data also observed
576 more opportunistic foraging behavior of bottom-feeding fish during GT and hypoxic events (Andersen et
577 al., 2005; Pihl et al., 1992) such as *P. flesus* in a fjord impacted by a GT. Andersen et al. (2005)
578 interpreted this behavior as reflecting a random prey selection linked to a disturbed foraging activity.

579 Experimentally adding habitat complexity (eelgrass) also induced a switch from a positive prey selection
580 to a random feeding in young-of-the-year *Pomatomus saltatrix* (Buckel and Stoner, 2000). In the current
581 study, either the greater habitat complexity (Nelson and Bonsdorff, 1990) and/or the exudates released by
582 *Ulva* spp. (Engström-Öst and Isaksson, 2006) may have reduced flatfish foraging efficiency (*i.e.* prey
583 detection and/or capture), as previously reported for *S. maximus* (Nordström and Booth, 2007) and *P.*
584 *flesus* (Aarnio and Mattila, 2000). Consequently, the more opportunistic foraging behavior of flatfish at
585 the Im site is probably the combined result of (1) changes in the juvenile flatfish potential prey (Table S4),
586 (2) higher vulnerability of abundant tropho-orders (*e.g.* tube-dweller, shallow infauna and mobile epifauna
587 are expected to be increasingly vulnerable to visual predatory fish, De Groot, 1971) and (3) decrease in the
588 foraging efficiency of juvenile flatfish.

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

598
599 *4.4. Species-specific trophic changes during the Peak GT*

600 Following results in Quillien et al. (2016), we qualified a consumer with a significantly higher
601 $\delta^{13}\text{C}$ at the Im site than at the NIm site as presenting an “*Ulva* isotopic signal”. A consumer (*e.g.* *P.*
602 *platessa*, macroinvertebrate tropho-order) with this signal has derived a significant proportion of its
603 energy from *Ulva* spp. and/or indirectly from GT-modified SPOM (Quillien et al., 2016) or by foraging
604 on prey presenting an *Ulva* isotopic signal. Despite their abundance at the Im site, we never identified
605 *Ulva* fragments in flatfish digestive tracts, meaning flatfish presenting an *Ulva* isotopic signal can only
606 have acquired it via their prey.

607
608 *4.4.1. P. platessa is least disturbed by GT*

609 The diet of *P. platessa* differed only slightly between the NIm and Im sites. At the Im site, *P.*
610 *platessa* still relied mainly on SF-Cardiida and DF-Cumacea (with a slight decrease in occurrence and
611 abundance) but foraged on a higher diversity of tropho-orders, such as epifauna and mobile tropho-orders
612 (DF-Amphipoda, OMN-Amphipoda, OMN-Isopoda, OMN-Mysida). This small dietary shift suggests that

613 *P. platessa* was only slightly disturbed in its prey preference by GT, maybe due to its use of both visual
614 and chemical cues to detect prey (De Groot, 1971) and its April-May settlement period in coastal nurseries
615 (Déniel, 1981). Indeed, older post-settlement *P. platessa* are exposed to the GT, and tolerance to such
616 environmental disturbance is likely to increase with size, as shown during severe hypoxia (Nilsson and
617 Ostlund-Nilsson, 2008).

618 *P. platessa* presented an *Ulva* isotopic signal likely due to the high occurrence of SF-Cardiida in
619 its diet and to the consumption of CAR-Phyllococida. Indeed, both tropho-orders presented an *Ulva*
620 isotopic signal acquired directly by consuming GT-modified SPOM (Quillien et al., 2016) for the first and
621 indirectly by consuming *Ulva* spp. and SPOM for the second (Jumars et al., 2015). Le Luherne et al.
622 (2017) also reported higher $\delta^{13}\text{C}$ of *P. platessa* at a GT-impacted beach than at a beach not impacted by
623 GT in another flatfish nursery (the Bay of Saint-Brieuc), a result confirming this species continues
624 foraging in coastal nurseries despite GT.

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

632

633 4.4.2. *S. maximus* is strongly disturbed by GT

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

642 At the Im site, *S. maximus* foraged mainly on tropho-orders that did not present an *Ulva* isotopic
643 signal (DF-Cumacea, OMN-Decapoda) or likely did not present it (*i.e.* small sample size, DF-Amphipoda,
644 OMN-Mysida), probably explaining the absence of an *Ulva* isotopic signal for *S. maximus*. Consequently,
645 *S. maximus* derived little or no energy from the additional basal resource (*Ulva* spp), a result possible
646 linked to its higher dependence on mobile organisms like fish (Déniel, 1974; Quiniou, 1986) that can

647 avoid GT and potentially benefit less from the additional basal resource. Finally, the high specialization of
648 *S. maximus* on two tropho-orders – DF-Cumacea and DF-Amphipoda – with relatively high offsets in the
649 isotopic space, likely explains its wider isotopic niche at the Im than at the NIm site (Yeakel et al., 2016).

650

651 4.4.3. *P. lascaris* appears the most disturbed by GT

652 Despite a larvae settlement period normally starting in June in the Bay of Douarnenez (Déniel,
653 1981), no G0 were sampled during Peak GT at the Im site (July), but over 30 were sampled during Post
654 GT1 (September), a result close to the one reported in July 2013 by Quillien et al. (2018). This absence
655 during Peak GT suggests that GT have negative effects on pre-settlement larvae and/or post-settlement
656 juveniles, probably related to higher mortality rates and/or temporary avoidance of impacted coastal
657 nurseries. Indeed, experiments have shown that juvenile flatfish prefer unvegetated substrata to vegetated
658 substrata (Carl et al., 2008; Wennhage and Pihl, 1994) and *Ulva* blooms, which can cause temporary
659 hypoxia (Cloern, 2001, authors personal observations) and release exudates (Van Alstyne et al., 2015), are
660 known to increase the mortality of crab larvae and juveniles (Johnson and Welsh, 1985; Van Alstyne et
661 al., 2015), *Clupea harengus* eggs (Aneer, 1987) and *P. platessa* larvae (Larson, 1997).

662 The diet of G1 *P. lascaris* shifted from the NIm to the Im site (very low inter-site diet similarity):
663 they nearly stopped consuming SF-Cardiida, consumed more DF-Cumacea (in occurrence and abundance)
664 and seven new tropho-orders (e.g. DF-Amphipoda, OMN-Amphipoda) at the Im site. This seems to
665 indicate that GT disturbed the foraging of G1 *P. lascaris* strongly, likely due to the low nocturnal
666 dissolved oxygen concentrations that often occur during *Ulva* blooms (Johnson and Welsh, 1985) (August
667 2012: 6%, authors personal observations). Since, temporary hypoxia decreases locomotor activity of *Solea*
668 *solea* (Dalla Via et al., 1998), another Soleidae and decreases predation efficiency of juvenile *P. flesus*
669 (Tallqvist et al., 1999), nocturnal hypoxia could reduce prey search activity (i.e. swimming to search for
670 prey) and foraging efficiency of *P. lascaris* (Tallqvist et al., 1999), a nocturnal predator (De Groot, 1971).
671 As a result, *P. lascaris* probably foraged more randomly and consumed the most abundant and vulnerable
672 (e.g. mobile epifauna) tropho-orders, as indicated by the more opportunistic foraging behavior.

673 The G1 *P. lascaris* also presented an *Ulva* isotopic signal, which can not be explained by the main
674 tropho-orders identified in the digestive tracts. Furthermore, the specialization of *P. lascaris* on DF-
675 Cumacea and DF-Amphipoda (high offset) at the Im site rather than on SF-Cardiida (lower offset) at the
676 NIm site should have widened its isotopic niche (Yeakel et al., 2016) and not, as we observed, narrowed
677 it. These results suggest that we missed important prey for *P. lascaris* at the Im site. Based on the isotopic
678 data, we hypothesize that, despite the GT, G1 *P. lascaris* continued to forage at the Im site and
679 additionally consumed DF-Sabellida and CAR-Phyllodocida, two previously identified prey, using
680 chemical cues (De Groot, 1971). Indeed, both tropho-orders are more abundant at the Im site than at the

681 NIm site (Quillien et al., 2015b) (Table S4) and have *Ulva* isotopic signals acquired directly by consuming
682 *Ulva* spp. (Quillien et al., 2016) for the first and indirectly via *Ulva* spp. and SPOM for the second
683 (Jumars et al., 2015).

684

685 4.5. *P. lascaris* adapts its foraging behavior to the GT context

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

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

697 During Post GT2, *P. lascaris* appeared to consume mainly SF-Cardiida and DF-Amphipoda at the
698 Im site, two tropho-orders that cannot solely explain the *Ulva* signal of *P. lascaris*. Consequently, *P.*
699 *lascaris* likely foraged more on DF-Sabellida and CAR-Phyllodocida, than suggested by the digestive
700 tract contents. Overall, the diet of *P. lascaris* at the Im site was likely composed of the most abundant *in*
701 *situ* tropho-orders, as found at the NIm site (Post GT2). *P. lascaris* also appeared to have more
702 opportunistic foraging behavior at the Im than at the NIm site, probably linked to the higher vulnerability
703 of the dominant tropho-orders (Table S4) at the Im site (SF-Cardiida) than at the NIm site (DF-Spionida).
704 The narrow isotopic niche measured during Post GT2 is probably linked to the very low isotopic diversity
705 of potential prey (macroinvertebrate SEA_C).

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

713 Over time, *P. lascaris* appeared to present more opportunistic behavior at the Im than at the NIm
714 site, likely because during Peak GT its foraging behavior was disturbed and because the benthic

715 community shifted from less vulnerable (DF-Spionida or DF-Cardiida) to more vulnerable tropho-orders
716 during the other periods (e.g. DF-Amphipoda during Pre GT, SF-Cardiida during Post GT1 and Post
717 GT2).

718

719 **Conclusion**

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

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

741

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750

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Journal Pre-proof

- We investigated the effects of green tides on juvenile flatfish trophic ecology
- Across species, flatfish displayed more opportunistic foraging at the impacted site
- Plaice displayed a lower diet shift than sand sole and turbot at the impacted site
- Species-specific responses seem driven by prey detection method and foraging time
- Plaice and sand sole but not turbot derived part of their energy from *Ulva*

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Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: