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

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Short title: Green macroalgae and juvenile flatfish trophic ecology

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1. Introduction

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

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

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

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

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

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

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

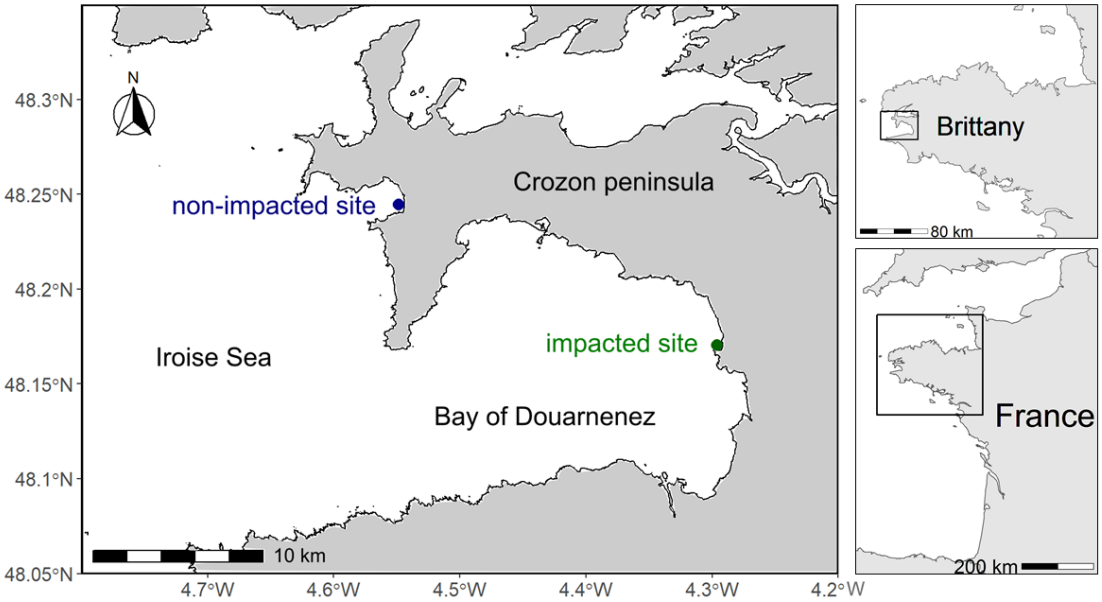

Figure 1. Location (Brittany, France) of the two study sites: the sandy beach not impacted by green tides at the western end of the Crozon peninsula (blue) and the sandy beach impacted by green tides on the eastern side of the bay of Douarnenez (green).

2. Materials and methods

2.1. Study system and GT

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

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

2.2. Sampling

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

Flatfish were sampled during the day at rising tide, using a beach trawl (5 m wide, 0.3 m high, with an 8 mm stretched mesh net in the cod-end) developed by Quiniou (1986). The beach trawl was towed at least once along each beach by two operators in 50 cm deep water, sampling an area of 400-1300 m² (Quillien et al., 2018). The flatfish were identified on site to the species level, counted and individually measured (total length). A subsample was collected for digestive tract analysis and preserved in 4% buffered formalin, while a second subsample was collected for stable isotope analysis and preserved at -20°C. The remaining flatfish were immediately released after being counted and measured. Only a limited number of

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

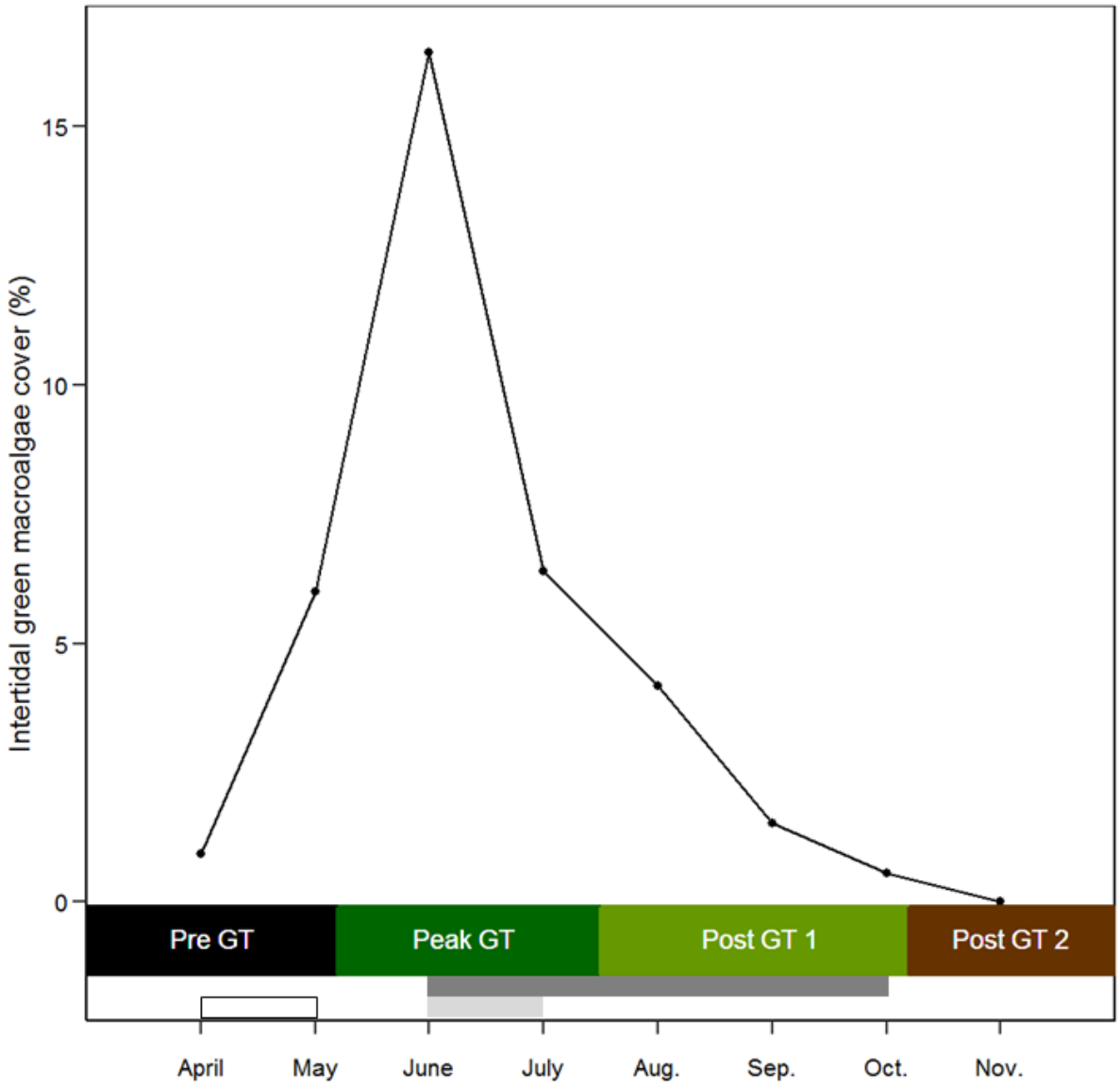

Figure 2. Monthly intertidal cover (%) of green macroalgae from April-November 2012 at the site impacted by green tides (GT), calculated as the percentage of the intertidal zone covered by the sum of the beach area covered by stranded macroalgae and the area of the breaking-wave zone with macroalgae.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

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

2.3. Sample preparation and analyses

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

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

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 $\delta^{13}C$ and $\delta^{15}N$ 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 $\delta^{13}C$ and $\delta^{15}N$ 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

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

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

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

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

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

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

3. Results

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

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

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

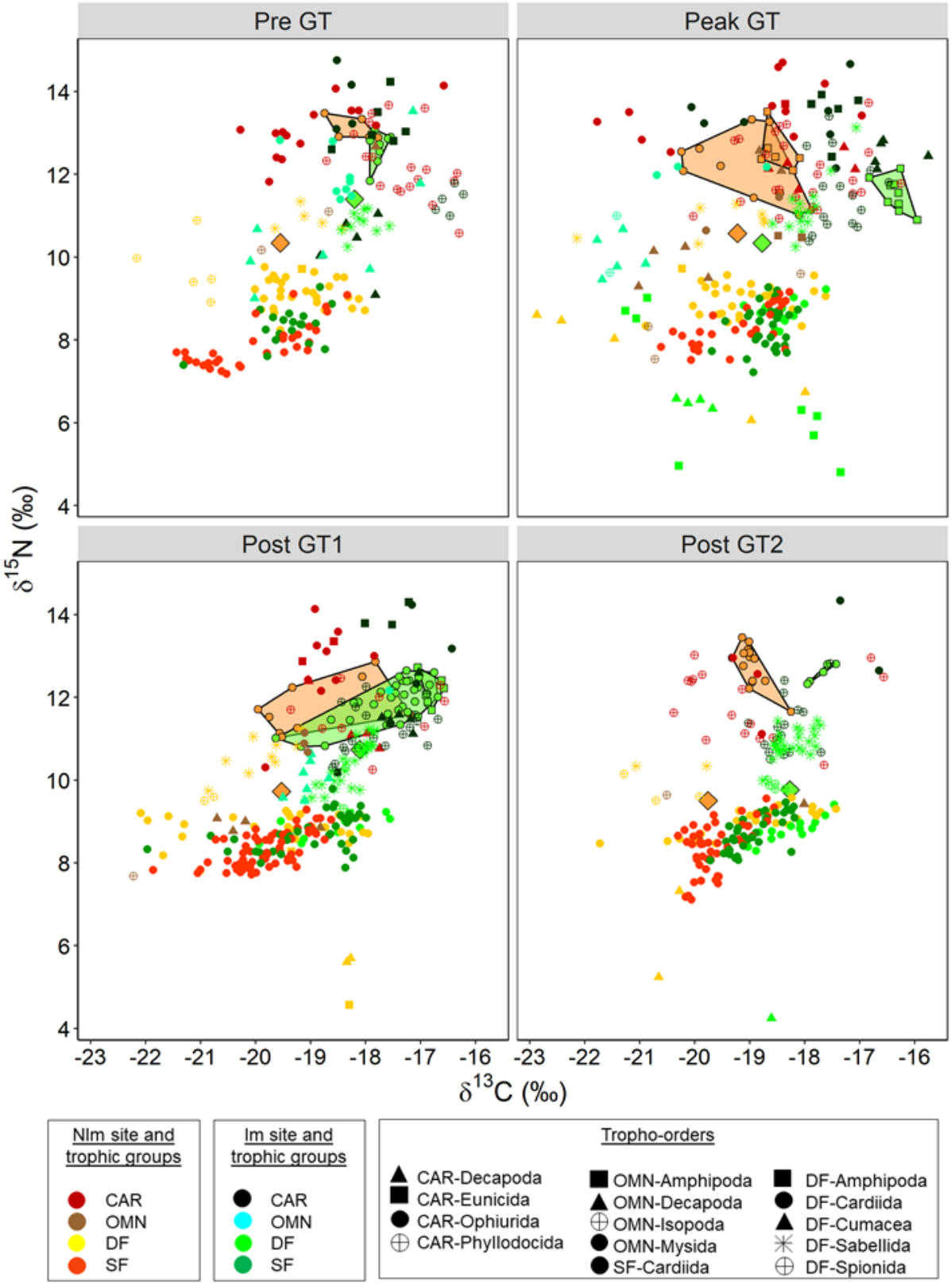

Figure 3. $\delta^{13}C$ and $\delta^{15}N$ (‰) of *Pegusa lascaris* age class 0 (blacklined circles) and age class 1 (black lined squares) at the sandy beach not impacted by green tides (orange, NIm site) and the sandy beach impacted

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

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

3.2.1. Flatfish isotopic compositions and associated metrics

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

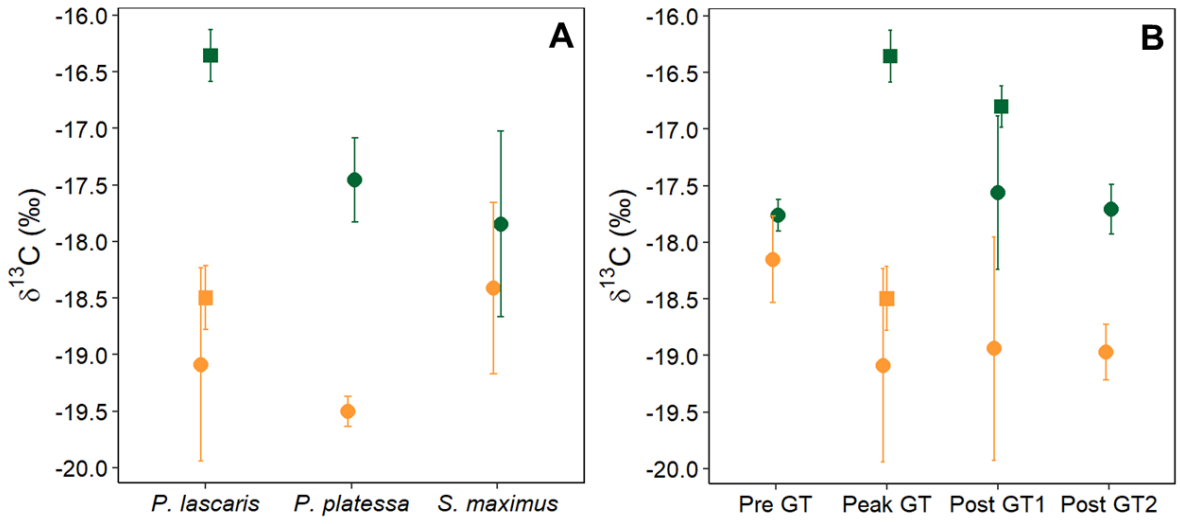

Figure 4. Mean and standard deviation of the $\delta^{13}C$ of (A) age class 0 *P. lascaris* (circles) and age class 1 *P. lascaris* (squares) during the four green tide periods (Pre GT, Peak GT, Post GT1 and Post GT2) and (B) age class 0 flatfish (circles) and age class 1 flatfish (squares) during the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

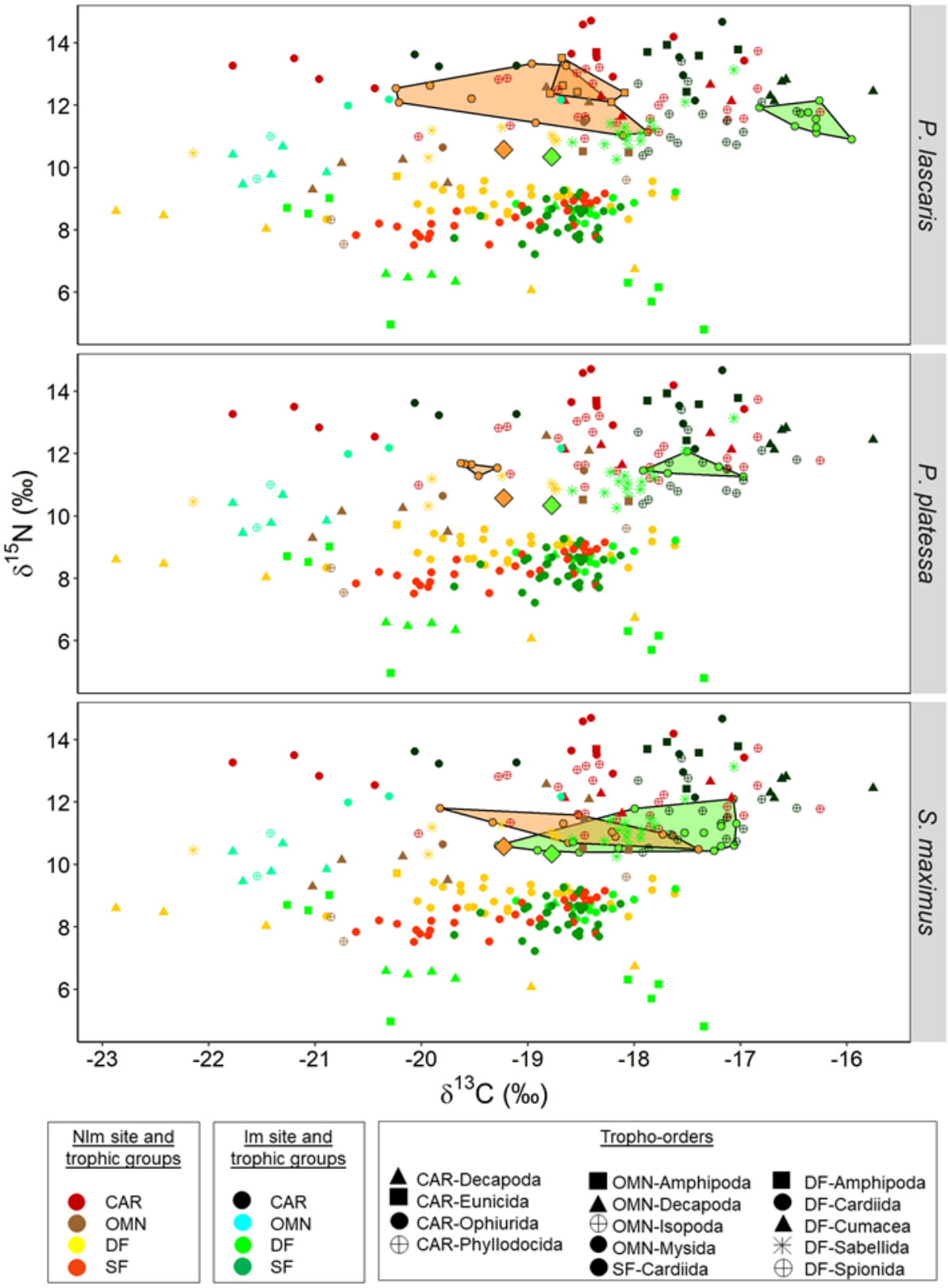
P. lascaris
P. platessa
S. maximus
δ15N (‰)
δ13C (‰)
14
12
10
8
6
-23
-22
-21
-20
-19
-18
-17
-16
NIm site and trophic groups
CAR
OMN
DF
SF
Im site and trophic groups
CAR
OMN
DF
SF
Tropho-orders
CAR-Decapoda
CAR-Eunicida
CAR-Ophiurida
CAR-Phyllodocida
OMN-Amphipoda
OMN-Decapoda
OMN-Isopoda
OMN-Mysida
SF-Cardiida
DF-Amphipoda
DF-Cardiida
DF-Cumacea
DF-Sabellida
DF-Spionida

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

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

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

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

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

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

3.2.2. Flatfish digestive tract contents and associated metrics

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

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

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

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

	Peak GT								Post GT2	
Species and age class	*P. las G0*		*P. las G1*		*P. pla G0*		*S. max G0*		*P. las G0*	
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

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

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

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

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

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

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

Age class	Period	NIm						Im						Bayesian probability SEA (Im) < SEA (NIm)	t-stat (adj. p)
		n	TL (mm)	Mean $\delta^{13}C$ (‰)	Flatfish SEA_C (‰²)	Macro invert. SEA_C (‰²)	SEA_C ratio (%)	n	TL (mm)	Mean $\delta^{13}C$ (‰)	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)

Table 3. Sample size (n), total length (TL, mm), mean $\delta^{13}C$ (‰), and the standard ellipse area corrected for small sample sizes (SEA_C) for age class 0 (G0) and age class 1 (G1) *Pegusa lascaris* and the macroinvertebrate community (macroinvert.) at the sandy beach not impacted by green 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 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 sites, and inter-site pairwise comparisons (t statistic and adjusted p-value) of the $\delta^{13}C$ are also shown.

404 The SEA_C was low during all four periods, except for G0 during Post GT1. The SEA_C 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_C) 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 $\delta^{13}C$ 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 $\delta^{15}N$ for *P. lascaris*, although $\delta^{15}N$ 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 then
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).

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

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

4.2.1. Species-specific trophic ecology during Peak GT

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

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

Age-class G0 *P. lascaris* also foraged on a relatively high diversity of tropho-orders (8), with 95% occurrence of DF-Cumacea, indicating high specialization (Yeakel et al., 2016) on this tropho-order. In this case, the isotopic niche of G0 *P. lascaris* should be relatively narrow (Yeakel et al., 2016), which is not what we observed. Consequently, our sampling likely underestimated the importance of certain tropho-orders in the *P. lascaris* diet due to its nocturnal foraging and rapid digestion (De Groot, 1971). To achieve the wide isotopic niche and the measured $\delta^{13}C$ and $\delta^{15}N$, G0 *P. lascaris* likely had a more generalist diet and foraged more frequently than estimated on tropho-orders with higher mean $\delta^{13}C$ and $\delta^{15}N$, such as CAR-Phyllodocida and CAR-Ophiurida (Table S3), previously reported as prey (Cabral et al., 2002; Rodriguez, 1996). Furthermore, the relatively high specialization of G1 *P. lascaris* on a tropho-order with a low offset (SF-Cardiida) should yield a relatively narrow isotopic niche (Yeakel et al., 2016), as we observed. 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 $\delta^{13}C$ and $\delta^{15}N$ tropho-orders (SF-Cardiida and DF-Cumacea, Table S3), indicating we
507 probably missed important prey with higher mean $\delta^{13}C$ and $\delta^{15}N$ (*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. lacaris*, 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 SEA_C) during
528 Peak GT and Post GT1. In autumn (Post GT2), potential prey isotopic diversity (macroinvertebrate SEA_C)
529 and assimilated prey diversity (flatfish 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 SEA_C) in autumn and maintained this characteristic until the next summer (Peak GT), despite the increase

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

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

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

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

Combining the digestive tract data and benthic community data (nine samples at each site during Peak GT) revealed that flatfish relied more on the *in situ* macroinvertebrates at the Im site, hence displaying a more opportunistic foraging behavior. Studies based on digestive tract data also observed more opportunistic foraging behavior of bottom-feeding fish during GT and hypoxic events (Andersen et al., 2005; Pihl et al., 1992) such as *P. flesus* in a fjord impacted by a GT. Andersen et al. (2005) interpreted this behavior as reflecting a random prey selection linked to a disturbed foraging activity. Experimentally adding habitat complexity (eelgrass) also induced a switch from a positive prey selection to a random feeding in young-of-the-year *Pomatomus saltatrix* (Buckel and Stoner, 2000). In the current study, either the greater 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 $\delta^{13}C$
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

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

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

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

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

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

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

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**

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

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

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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
Wave height (m)	1.3	2.0	0.7	1.4	2.1	0.7
Beach slope (%)	1.6	1.6	1.5	1.4	1.5	1.2
SWT (°C)	14.6	18.9	8.7	14.7	21.4	8.2
Surface water chl *a* concentration ($\mu g.L^{-1}$)	15.8	33.7	5.1	15.8	33.7	5.1
Algal mat density ($kg_{WW}.m^{-2}$)	0.0	0.0	0.0	0.65	4.02	0.0
Dissolved oxygen content (%)	103.4	106.5	99.9	103.9	108.1	100.0
Median grain size (µm)	180.4	260.0	155.0	158.5	180.0	140.0
Sediment organic matter content (%)	4.5	5.4	3.3	4.1	6.2	3.0
Sediment sorting index	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).

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

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

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 $\delta^{13}C$ and $\delta^{15}N$ 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**		
		$\delta^{13}C$ (SD)	**δ^{15N} (SD)**	**n**			**$\delta^{13}C$ (SD)**	**δ^{15N} (SD)**	**n**
Pre GT	POM	-25.09 (0.51)	6.54 (0.67)	3	**Pre GT**	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 *P. lascaris*	-17.76 (0.14)	12.64 (0.40)	8
	SF-other	-19.01 (1.21)	9.70 (1.16)	3					
	0G *P. lascaris*	-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
Peak GT	CAR-Eun.	-18.35	13.7	1	**Peak GT**	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 *P. lascaris*	-16.36 (0.23)	11.53 (0.40)	9
	DF-other	-19.26 (0.18)	9.84 (0.31)	2		0G *P. platessa*	-17.46 (0.37)	11.55 (0.32)	5
	0G *P. lascaris*	-19.09 (0.85)	12.12 (0.83)	10		0G *S. maximus*	-17.84 (0.82)	10.92 (0.51)	16
	1G *P. lascaris*	-18.50 (0.28)	12.57 (0.49)	6					
	0G *P. platessa*	-19.50 (0.13)	11.57 (0.16)	5					
	0G *S.*	-18.41 (0.76)	11.11 (0.41)	10					

	maximus								
Post GT1	POM	-22.79 (1.28)	7.61 (0.25)	3	**Post GT1**	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
	0G *P. lascaris*	-18.94 (0.99)	11.76 (0.64)	9		0G *P. lascaris*	-17.56 (0.68)	11.91 (0.48)	34
						1G *P. lascaris*	-16.80 (0.18)	12.16 (0.37)	6
Post GT2	POM	-22.86 (0.17)	6.77 (0.14)	3	**Post GT2**	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 *P. lascaris*	-17.71 (0.22)	12.59 (0.22)	5
SF-Card.	-19.63 (0.45)	8.39 (0.60)	47				
0G *P. lascaris*	-18.97 (0.24)	12.77 (0.50)	14				

Table S4. Mean density (ind/m²) and relative abundance (%) of the sediment macroinvertebrates grouped by tropho-orders during the four periods (pre green tide period (Pre GT), peak green tide period (Peak GT), first post green tide period (Post GT1), second post green tide period (Post GT2)) at the non-impacted sandy beach (NIm) and at the sandy beach impacted by green tides (Im). See appendix S2 for the species considered in each tropho-order.

	Pre GT				**Peak GT**				**Post GT1**				**Post GT2**			
	NIm		Im		NIm		Im		NIm		Im		NIm		Im	
	ind/m²	%	ind/m²	%	ind/m²	%	ind/m²	%	ind/m²	%	ind/m²	%	ind/m²	%	ind/m²	%
CAR-Decapoda	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
CAR-Eunicida	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
CAR-Nemerta	1	1	4	2	9	2	6	3	4	1	10	1	6	1	11	1
CAR-Ophiurida	2	1	2	1	6	1	1	1	7	2	4	0	7	1	1	0
CAR-Other	0	0	0	0	0	0	1	1	0	0	4	0	0	0	2	0
CAR-Phyllodocida	1	1	7	4	23	5	17	9	25	6	40	4	23	4	22	3
DF-Amphipoda	48	21	78	44	12	3	62	31	51	12	57	6	15	3	44	5
DF-Cardiida	75	34	10	6	44	10	7	4	58	14	7	1	54	9	16	2
DF-Cumacea	17	8	6	4	27	6	12	6	65	15	23	2	9	2	5	1
DF-Other	0	0	0	0	2	1	5	2	10	2	5	1	9	2	1	0
DF-Sabellida	0	0	5	3	2	1	31	15	1	0	246	26	1	0	172	21
DF-Spionida	1	1	33	19	269	61	20	10	49	12	47	5	242	42	33	4
OMN-Amphipoda	15	7	0	0	17	4	7	4	7	2	0	0	57	10	0	0
OMN-Decapoda	1	1	0	0	1	0	0	0	0	0	19	2	2	0	1	0
OMN-Isopoda	0	0	0	0	0	0	0	0	1	0	0	0	11	2	0	0
OMN-Mysida	0	0	1	1	0	0	10	5	2	1	22	2	0	0	5	1
OMN-Other	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
SF-Cardiida	62	27	27	15	28	6	19	9	147	34	478	50	136	24	522	62
SF-Other	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
SF-Veneroida	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0