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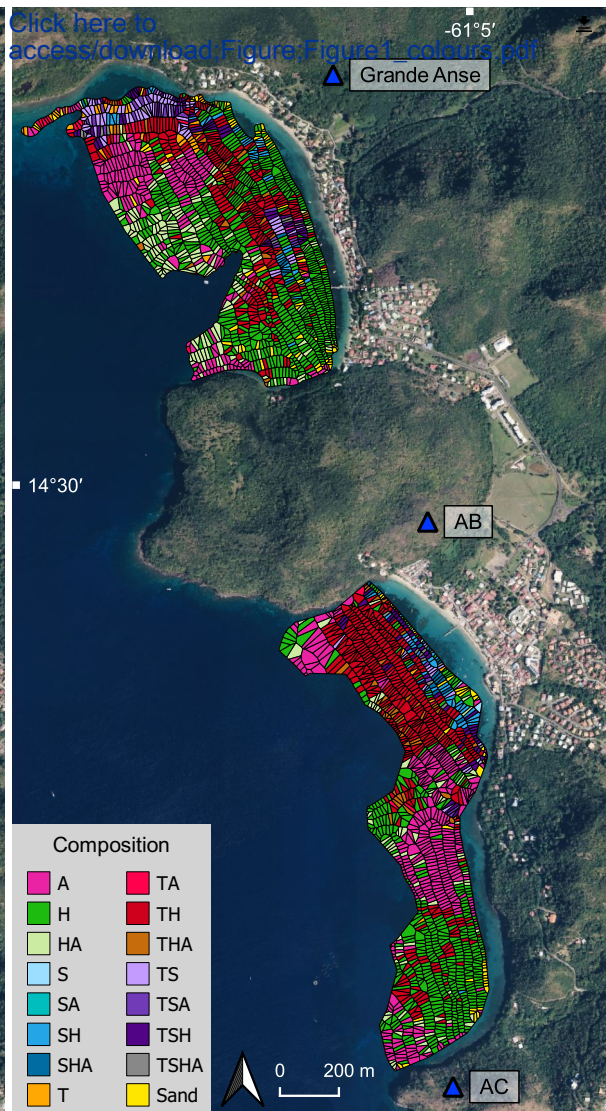
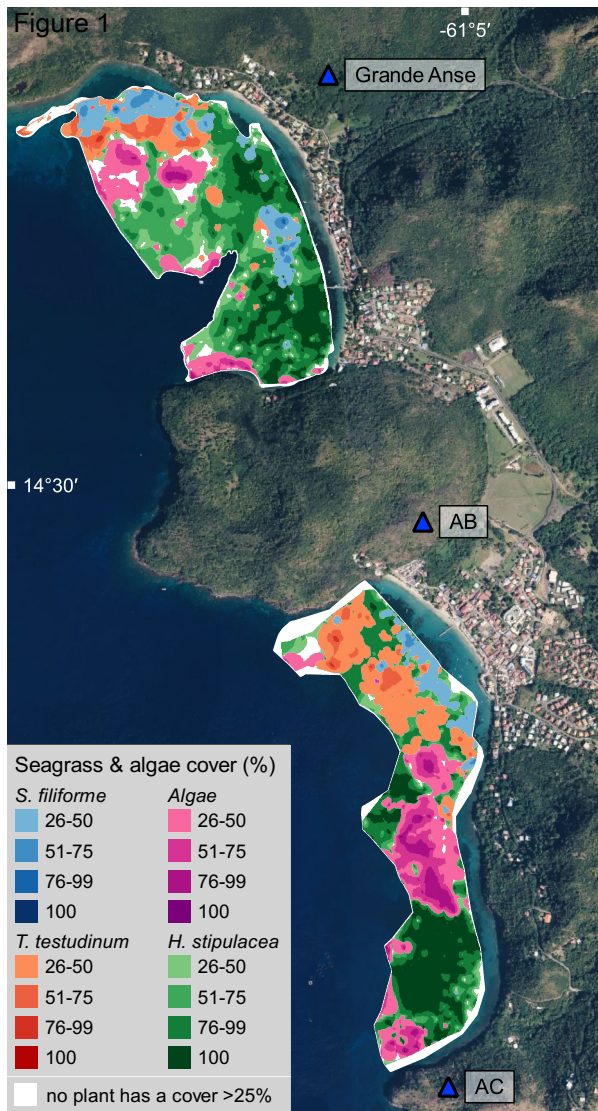
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Food selection and habitat use patterns of immature green turtles (*Chelonia mydas*) on Caribbean seagrass beds dominated by the alien species *Halophila stipulacea* --Manuscript Draft--

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Abstract:	<p>Marine herbivores face rapid changes in the coastal ecosystems where they forage. In the Caribbean, the recent and fast expansion of the invasive phanerogam species <i>Halophila stipulacea</i> is threatening native seagrass ecosystems. So far, <i>H. stipulacea</i> is escaping most Caribbean herbivores, certainly because of its recent introduction or lower nutritional value. We investigated the impact of <i>H. stipulacea</i> invasion on fine-scale foraging habitat selection and food resource selection of immature green turtles at critical foraging sites in Les Anses d'Arlet, Martinique. The analysis of seagrass distribution and nutritional content, together with turtle behaviour and resource selection, showed that <i>H. stipulacea</i> may be of contrasting interest to green turtles. Compositional analysis confirmed the lower nutritional value of <i>H. stipulacea</i> compared to the native species, but the invasive species showed higher digestibility than native ones, which calls into question the energetic advantage of consuming the native plants over the exotic plant. Thus, although green turtles mostly selected the native seagrass <i>Thalassia testudinum</i> in multispecies seagrass beds, some individuals fed on <i>H. stipulacea</i>. Accordingly, in bays entirely invaded by <i>H. stipulacea</i>, one possibility for resident green turtles is to increase foraging on this species, but, if so, the consequences on their growth and survival still remain to be determined. As the expansion of <i>H. stipulacea</i> may have been facilitated by factors such as shipping, anchor scarring and fishing activities, protection of native seagrass beds and immature green turtles from human disturbances is urgently required to ensure the long-term adaptation of green turtles to this new foraging environment.</p>
Suggested Reviewers:	<p>Marjolijn J. A. Christianen, Ph.D. Associate Professor Marine Ecology, Wageningen UR: Wageningen University & Research marjolijn.christianen@wur.nl Dr. Marjolijn Christianen is an expert in Marine Ecology. She has worked on megaherbivore-seagrass interactions, and in particular on the impact of green turtle grazing on seagrass beds, in the context of <i>H. stipulacea</i> expansion in the Caribbean.</p> <p>Karen A. Bjorndal, Ph.D. Distinguished Professor, University of Florida bjorndal@ufl.edu Dr. Karen Bjorndal is well known for her studies on the feeding and nutritional ecology of sea turtles. Her work has included diet selection, digestive processing, the implications of nutrition on organisms' growth and reproductive output, and the roles of sea turtles in marine ecosystems.</p> <p>Dennis J. Russel, Ph.D. Professor of Biology, American University of Sharjah drussell@aus.edu Dr. Dennis Russell is a specialist in Marine Ecology and Botany. He has worked on the ecology of introduced seaweed and seagrass species, and their inclusion in the diet of green turtles over time.</p>



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.

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22 native seagrass beds and immature green turtles from human disturbances is urgently required
23 to ensure the long-term adaptation of green turtles to this new foraging environment.

24
25 **Keywords**

26 Plant-herbivore interactions / Sea turtle / Invasive species / Foraging behavior / Diet /
27 Martinique

28

29

30 **1 Introduction**

31 Investigating foraging habitat use, food selection and underlying strategies in threatened
32 species is essential to understand their ecological roles and trophic relationships and thus
33 develop appropriate conservation measures. Optimal foraging theory postulates that fitness
34 (survival and reproductive success) depends on foraging efficiency and that natural selection
35 has favoured behaviours that maximise energy acquisition (Pyke et al., 1977). Therefore,
36 foraging strategies have evolved in adaptation with the environment, i.e. in response to factors
37 like predation risk, intra- and interspecific competition, as well as food availability and quality
38 (Chevallier et al., 2008; Fritz et al., 1996; Pyke et al., 1977). Rapid changes in the
39 environment can challenge these foraging strategies and affect individuals' fitness,
40 threatening the future of the population. This is especially true for species spending
41 considerable amounts of time on feeding sites over their lifetime, i.e. those with delayed
42 sexual maturity and for which individuals in advanced life stages have high reproductive
43 value or are essential for the survival of young (Braby et al., 2011; Heppell et al., 2002). Thus,
44 foraging ground quality should be considered critical for population recovery.

45

46 **Marine herbivores** have developed adaptive **morphological, physiological and behavioural**
47 **traits to consume algae and seagrass and maximise the nutritional value they get from them.**
48 **For example, sea urchins, parrotfish and surgeonfish use powerful mouthparts to break plant**
49 **fibres and cell walls, while green turtles and some fishes that do not masticate food use a low**
50 **stomach pH to break certain algae or fibres like hemicellulose (Bjorndal, 1985; Steneck et al.,**
51 **2017; Thayer et al., 1984). Sirenians and green sea turtles also depend on their rich gut**
52 **microflora (composed of cellulolytic bacteria) which ensures the partial digestion of plant**
53 **fibres such as cellulose and hemicellulose, by microbial fermentation (Bjorndal, 1980, 1985;**
54 **Thayer et al., 1984). At the behavioural level, one foraging strategy is to regularly revisit the**
55 **same seagrass patches, which allows herbivores to cultivate plots of young leaves (Bjorndal,**
56 **1980). Since regrowths generally have higher protein levels and lower lignin levels (Bjorndal,**
57 **1980; Moran and Bjorndal, 2007), and digestibility of forages is negatively correlated with**
58 **lignin concentration (Moore and Jung, 2001), this strategy improves nutritional content and**
59 **digestibility of the targeted plants. In addition, bite sizes that favour a high surface-to-volume**
60 **ratio of ingesta particles, and thus greater exposure to microbial attack, are likely to maximise**
61 **digestion rates (Bjorndal et al., 1990; Gulick et al., 2021). Reducing ingesta particle size also**
62 **provides a strategy to meet energy requirements in the face of declining food availability,**
63 **whether due to anthropogenic threats or overgrazing (Gulick et al., 2021). Thus, marine**

64 herbivores have adapted to the plant resources that thrive in coastal marine environments, and
65 are largely dependent on the well functioning of these ecosystems. In turn, these herbivores,
66 and especially megaherbivores such as manatees, dugongs and green turtles, can induce
67 structural changes in their foraging habitats and influence their evolution (Thayer et al.,
68 1984). Understanding interactions between these endangered megaherbivores and their
69 ecosystem is therefore crucial for successful conservation strategies.

70
71 Coastal marine ecosystems conservation is even more important given that they face strong
72 anthropogenic pressures and are jeopardised by a rapid reduction in their distribution. This is
73 the case for seagrass meadows, which have suffered a global loss of 29% since 1879, mainly
74 due to coastal human activities, pollution and eutrophication, and climate change (Waycott et
75 al., 2009). The expansion of invasive species such as sea urchins and exotic plants also
76 hinders the development of native seagrasses (Williams, 2007). In particular, the recent
77 implantation of the exotic seagrass species *Halophila stipulacea* in the Caribbean has raised
78 new worries. Originating from the Red Sea, it reached the Western Atlantic Ocean probably
79 transported by boats, and spread rapidly around the Eastern Caribbean islands after a first
80 record in 2002 (Ruiz and Ballantine, 2004; Willette et al., 2014). *H. stipulacea* has been
81 considered an invasive species in the Caribbean due to its rapid expansion and strong
82 competitive ability (Winters et al., 2020), thus contributing to rapidly modifying native plant
83 communities.

84
85 The green turtle (*Chelonia mydas*) is the only sea turtle species with a plant-dominated diet
86 (Bjorndal, 1980; Jones and Seminoff, 2013). Upon recruitment to neritic habitats, juvenile
87 green turtles are indeed known to shift from a carnivorous to a predominantly herbivorous
88 diet (Jones and Seminoff, 2013). Green turtles have been classified as Endangered on the
89 IUCN Red List, mainly due to ongoing harvest and bycatch, and the rapid change in their
90 foraging habitats may represent an additional threat (Seminoff, 2004). While conservation
91 efforts worldwide began in the 1950s, management actions have primarily targeted nesting
92 beaches and protected eggs and hatchlings, as at-sea monitoring of populations remains
93 difficult (Heppell et al., 2002). Yet, stage-based population models on long-lived turtle
94 species have highlighted the importance of reducing mortality in the late life stages (large
95 juveniles, subadults, adults) to promote population recovery (Heppell et al., 2002). Therefore,
96 estimating the impact of changes, particularly in the developmental range of immature green
97 turtles, is important to adapt protection measures for these key habitats.

98

99 Only a few studies mention the presence of non-native plant species in green turtles' diet. In
100 Hawaii, it took 10-12 years for highly invasive species and 20-30 years for slow-growing
101 algae, to become the majority of green turtles' diet (Russell and Balazs, 2015). In the Eastern
102 Caribbean the first occasional grazing events on *H. stipulacea* by green turtles were observed
103 in 2013 (Becking et al., 2014), but the relatively short time since its arrival (Willette et al.,
104 2014) may explain why it was not yet meaningful in turtles' diet. Moreover, these grazing
105 events were always observed within assemblages dominated by the native seagrass *T.*
106 *testudinum*, which was significantly preferred over *H. stipulacea* (Christianen et al., 2018;
107 Whitman et al., 2019). A single study conducted in the U.S. Virgin Islands in 2017/2018 (i.e.
108 within 2 years of the arrival of *H. stipulacea*), highlighted the prevalence of this introduced
109 seagrass in the diet of juvenile green turtles, although it was not a dominant plant in the
110 environment (Gulick et al., 2021). In Martinique (Lesser Antilles), *H. stipulacea* now covers
111 most of the foraging habitats available along the Caribbean coast (Ortolé, 2012). After a first
112 record in 2006, nearly 90% of the changes observed in the benthic communities within 4
113 years benefited *H. stipulacea* (Maréchal et al., 2013). While conservation plans still take little
114 account of invasive plants (Giakoumi et al., 2016), it is important to assess the impact of *H.*
115 *stipulacea* invasion on foraging habitat and food resource selections of immature green
116 turtles. This could provide a better understanding of how turtles have adapted to this rapid
117 change, so that protective measures can be implemented for key seagrass habitats.

118

119 Our study focused on the seagrass beds of Les Anses d'Arlet, Martinique, a green turtle
120 foraging hotspot where immatures spend many years until reaching sexual maturity
121 (Chambault et al., 2018; Siegwalt et al., 2020). We assessed seagrass bed composition and
122 determined nutritional content and digestibility of plants. In parallel, we recorded turtle
123 behaviour and movements to analyse foraging habitat selection, and analysed turtle bite
124 counts to infer diet and food preferences. Because Martinique's multispecies seagrass
125 meadows are dominated by *H. stipulacea*, and given the high fidelity of immature green
126 turtles to their feeding grounds (Siegwalt et al., 2020), we hypothesised that they might now
127 consume significant proportions of *H. stipulacea*.

128

129 **2 Materials and Methods**

130 **2.1 Study site**

131 We conducted our study in Martinique, French West Indies, France, in five bays of Les Anses
132 d'Arlet (14°30'9.64"N, 61°5'11.85"W): Anse Noire, Anse Dufour, Grande Anse, Anse du
133 Bourg and Anse Chaudière (see Fig. S1 and S2 for details). Grande Anse (~75 ha), Anse du
134 Bourg (~30 ha) and Anse Chaudière (~40 ha) are large bays where algae, and the three main
135 phanerogams found in Martinique (i.e. two native species, *Syringodium filiforme* and
136 *Thalassia testudinum*, and one invasive species, *Halophila stipulacea*) are present. Anse
137 Noire (~8 ha) and Anse Dufour (~10 ha) are only covered by *H. stipulacea* and algae.

138 2.2 Benthic composition and resource availability

139 Macroalgae and seagrass species composition of each bay was assessed during 2016 and
140 2018. No precise mapping was done in Anse Noire and Anse Dufour, as *H. stipulacea*
141 covered nearly 100% of the meadows, with few algae on the rocky banks. In Grande Anse,
142 Anse du Bourg and Anse Chaudière, meadows between 2 and 15-20 m depth were entirely
143 surveyed, at predefined points located every ten metres along GPS-based transects. At each
144 sampling point, a close picture of the ground was taken within 1 m² quadrats, either using an
145 underwater camera linked to a monitor on a boat or by scuba-divers using GoPro Hero 4
146 Silver cameras. The benthic vegetal composition and cover percentages of Algae (which, in
147 our study, mainly include the following macroalgae species: *Acanthophora spicifera*,
148 *Avrainvillea fulva*, *Avrainvillea nigricans*, *Caulerpa cupressoides*, *Caulerpa sertularioides*,
149 *Cerarium ciliatum*, *Cladophora prolifera*, *Dictyota prolifera* and other *Dictyota sp.*,
150 *Halimeda incrassata*, *Peniculus capitatus*, *Sargassum fluitans*, *Sargassum histrix var.*
151 *buxifolium*, *Ulva fasciata*), and seagrass species (*H. stipulacea*, *S. filiforme*, and *T.*
152 *testudinum*), were recorded on the pictures *a posteriori*. To determine coverage of algae and
153 each seagrass species, we adapted the Braun-Blanquet scale (Braun Blanquet, 1932) and
154 defined different categories according to the percentage of species coverage. To the initial
155 categories, we added the two categories '0%' and '100%' to indicate that a species was either
156 absent or covered a whole quadrat (as it was important for us to identify areas without or only
157 with *H. stipulacea*). Finally, rather than using one '5-25%' category and several '<5%'
158 categories, two categories between 1 and 25% ('1-12%' and '13-25%') were created to
159 facilitate the use of an interpolation scheme in QGIS. As a result, on each plot, we estimated
160 and classified plant coverage in seven categories (0%, 1-12%, 13-25%, 26-50%, 51-75%, 76-
161 99%, 100%).

162

163 Using the ‘natural neighbor’ interpolation scheme (Cueto et al., 2003) available in QGIS
164 (version 3.16.5, QGIS Development Team, 2022), we created raster maps for each plant and
165 for both years. Once vectorised, surface areas of all polygons composing each of the
166 percentage classes were extracted and multiplied by the corresponding median class
167 percentage to determine the total area available equivalent to a 100% cover. Maps of algae
168 and each seagrass species were then combined into a single map representative of the
169 coverage of macroalgae and seagrass species. Finally, Voronoi polygons were constructed in
170 QGIS using the sampling points as references to map the presence/absence of the different
171 plants and thus represent the different vegetation communities on a composition map.

172 2.3 Video recording of feeding events

173 Field observations were performed in the five bays from May to September 2016, from
174 December 2016 to May 2017, in February, April and June 2018, and from June to October
175 2019. Three snorkelers prospected a bay daily either from 7:00 to 12:00, or 11:00 to 14:00 or
176 14:00 to 19:00 to ensure data collected were evenly distributed across daylight hours. Once a
177 turtle was spotted, the snorkelers video-recorded its behaviours with GoPro Hero 4 Silver
178 cameras, using the focal sampling technique (Altmann, 1974), at a minimal distance of 4
179 meters. The bays being highly frequented, most turtles are used to human presence and their
180 behaviour usually seems unaffected by the presence of snorkelers. Nevertheless, if snorkelers’
181 presence appeared to stress a turtle (which displayed a change in behaviour, location or
182 direction), they moved away. Snorkelers' GPS location (recorded 30 to 60 times/min) was
183 used as a proxy for turtle location. In 2018-2019, a few individuals were also equipped with
184 on-board cameras with GPS as part of the study of Jeantet et al. (2020, 2021), which allowed
185 us to obtain additional behavioural data. From all video recordings, we identified six
186 behavioural categories: Swimming, Surfacing, Resting, Feeding, Interacting, and Scratching
187 (Table S1). Video recordings were analysed by observers and behaviours were labelled with
188 exact start and end times annotated. A total of 235 hours of recordings were obtained during
189 254 follows, of which 117 hours of sequences with feeding activity were extracted and
190 analysed.

191 2.4 Foraging habitat selection

192 Foraging habitat selection was investigated for turtles foraging in bays with multispecific
193 seagrass beds (Grande Anse, Anse du Bourg/Anse Chaudière) and not in the bays where only
194 monospecific seagrass meadows of *H. stipulacea* were present (Anse Noire/Anse Dufour).

195 Using behavioural and trajectory data obtained from direct observations, GPS-derived
196 locations were associated with the behavioural category recorded at the same time. Data from
197 individuals monitored less than one minute were discarded. The tracks of 62 individuals
198 monitored in Grande Anse in 2016-17 (n=44) and 2018-19 (n=12), and in Anse du
199 Bourg/Anse Chaudière in 2016-17 (n=2) and in 2018 (n=4) were analysed to investigate fine-
200 scale foraging habitat selection.

201
202 We performed a compositional analysis of habitat use (Aebischer et al., 1993), with R
203 software (v.4.0.0, R Core Team, 2021) and adehabitatHS package (Calenge, 2020), to test
204 whether immatures preferentially selected specific vegetation communities during foraging
205 activities. Based on the Voronoi composition maps (see 2.2) we identified fifteen distinct
206 plant communities that we gathered into four main habitat types: monospecific seagrass
207 meadows of *H. stipulacea* (H), algal meadows (A), communities composed of *H. stipulacea*
208 and algae (HA), and all other compositions with at least one native species in a monospecific
209 or mixed meadow (M). The composition maps were used to calculate the relative abundance
210 (so-called ‘availability’) of the different habitat types at the site scale, while habitat use by
211 each GPS-tracked turtle was calculated using the proportion of locations within each of these
212 habitat types. A habitat was considered ‘preferred’ if individuals used it more than expected
213 from its availability. Random habitat use (i.e. no habitat preference) was tested with a chi-
214 square test before communities were ranked in order of preference based on pairwise t-tests.

215 **2.5 Diet composition and food selectivity**

216 Individual-level diet composition was inferred from bite count. A bite corresponds to a
217 directed head/jaws movement towards a food item with evident intent to remove and ingest all
218 or most of it, and exclude movements associated with chewing only (Thomson et al., 2018).
219 From the video recording analysis and for each foraging bout, bites were counted and
220 assigned a prey category: *H. stipulacea*, *S. filiforme*, *T. testudinum*, Algae (any species of
221 macroalgae) or Other (typically animal prey, and occasionally squid or fish discards, or food
222 scraps such as eggshells). We did not consider bites for which prey could not be identified and
223 according to Thomson et al. (2018), only individuals with ≥ 30 confidently identified bites
224 (n=61; 27 in monospecific sites, and 34 in multispecific sites) were considered (see Table S2
225 for exact total observation time, total feeding time and time over which bites were counted for
226 each individual).

227

228 In the multispecific bays (Grande Anse and Anse du Bourg/Anse Chaudière), to investigate
229 food selection of immature green turtles at the population level (n=34), we used the
230 compositional analysis similarly to foraging habitat selection. Except for the category Other,
231 for which availability was unknown, we compared the proportion of bites on each resource to
232 their availability at the site scale based on the composition maps of the corresponding year. At
233 the individual level, resource use was also tested using the Manly's selection ratio w_i (Manly
234 et al., 2002), with the 'widesIII' function of the adehabitatHS R package (Calenge, 2020). For
235 each individual, this index was calculated as $w_i = \frac{o_i}{\pi_i}$, where o_i is the proportion of bites on
236 the i item and π_i the proportion of i in the study site. The index gives values between zero and
237 ∞ . Values equal to 1 indicate random feeding, values under 1 indicate negative selection, or
238 avoidance, and values above 1 indicate positive selection, or preference.
239

240 **2.6 Nutritional composition and digestibility of native and invasive plants**

241 **2.6.1 Plant sampling and processing**

242 Between 2015 and 2020, we collected macroalgae (see 2.2 for species details) and seagrass
243 species (leaves of *T. testudinum*, *S. filiforme* and leaves and rhizomes of *H. stipulacea*, as its
244 rhizomes are easily accessible for feeding) at several sampling points in Grande Anse and
245 Anse Noire to assess nutritional composition. *S. filiforme* and algae being rarer, fewer samples
246 were collected to avoid affecting their dynamics. Once collected, samples were rinsed three
247 times in fresh water to remove debris, invertebrates, epiphytes and excess salt. Excess water
248 was removed using a salad spinner and a clean cloth, and the fresh weight (FW) of each
249 sample was determined (± 0.1 g). Samples were dried in an oven at 50°C for 48 h and packed
250 in airtight bags for transport to the laboratory. Samples were then freeze-dried until constant
251 mass, i.e. successive weighing did not differ by more than 0.1%, to determine the dry weight
252 (DW). Dried samples were ground to pass through a 1 mm grid in a Retsch ultra-centrifugal
253 mill (model ZM200), in the same way as in Moran and Bjorndal (2007).

254 **2.6.2 Nutritional composition and digestibility determination**

255 Samples were freeze-dried again before analyses to eliminate any traces of water that might
256 have appeared during grinding. They were analysed in duplicate except when their mass was
257 too low. For analyses, samples were weighed to the nearest 0.001 g:

- 258 a) Energy content was determined on 1 g pellets using a Parr 6200 calorimeter (Parr
259 Instrument Company) calibrated with benzoic acid.
- 260 b) Total mineral content: 1 g samples were burned at 500°C for 24 hours and
261 reweighed to quantify remaining ashes.
- 262 c) Carbon (C) and nitrogen (N) content: we used a Flash (2000 or EA 1112) elemental
263 analyser (Thermo Fisher Scientific), which performed the dynamic flash combustion
264 method (derived from Dumas method, see Dumas, 1831), followed by gas detection
265 using a thermal conductivity detector. These measurements were translated into %C
266 and %N in the sample using Eager software, which allowed the calculation of C:N
267 ratios.
- 268 d) Soluble carbohydrates content: soluble carbohydrates (polysaccharides) were
269 measured on a continuous flow chain, using the neocuproin method, adapted from
270 Brown (1961). The method consists in extracting the water-soluble sugars from the
271 plant tissues and then hydrolysing them with an acid to obtain simple carbohydrates.
272 Monosaccharides' reducing power is then used to reduce, after heating, a cupric-
273 neocuproin chelate into a red copper-neocuproin complex, which absorbs at 460 nm.
274 The determination of reducing sugars is carried out using an auto-analyser and a
275 glucose standard curve, allowing the results to be expressed in glucose equivalent.
- 276 e) Fibre content: the Van Soest sequential fibre solubilisation method, adapted from
277 Goering and Van Soest (1970), classifies the cell wall components of a plant into
278 three types of insoluble residues: neutral detergent fibre (NDF), acid detergent fibre
279 (ADF), and acid detergent lignin (ADL) residues. Neutral soluble detergent (NDS)
280 added with amylase (which allows starch to be degraded) first allows separating
281 cytoplasmic compounds from all insoluble fibres (NDF). After filtration, soluble
282 acid detergent (ADS) helps extracting soluble fibres (ADF), before sulphuric acid is
283 used to retain ADL only. After each of the three phases, the fractions are passed
284 through a desiccator and then weighed. Until the last stage, mineral matter is present
285 in all three fractions NDF, ADF and ADL. A mineralisation stage at 500°C thus
286 allows the proportion of ash to be determined in relation to the proportion of lignin.
287 Once the ash-free ADL is expressed as a percentage of dry matter, the quantity of
288 the three types of fibre can be determined as follows: Lignin = (ash-free) ADL,
289 Cellulose = ADF – ADL, Hemicellulose = NDF – ADF.
- 290 f) In vitro enzymatic digestibility: based on a method adapted from Aufrère et al.
291 (2007), we estimated the potential digestibility of plant samples through the action

292 of enzymes: pepsin, cellulase, amyloglucosidase. These enzymes were chosen to
293 replace the ruminant rumen fluid originally used to measure organic matter
294 fermentability in vertebrates (see Moran and Bjorndal, 2007). The samples were
295 first incubated at 40°C with pepsin (a gastric enzyme whose role is to break down
296 proteins in the food bolus). The starch was then gelatinised at 80°C before being
297 degraded by amyloglucosidase during a second incubation. This led to the release
298 of glucose molecules. Meanwhile, cellulose was degraded by cellulase. Finally,
299 solubilised fractions were incubated at 70°C for 48 h and then, weighed. The
300 proportion of solubilised plant material represents the fraction degraded by the
301 enzymes.

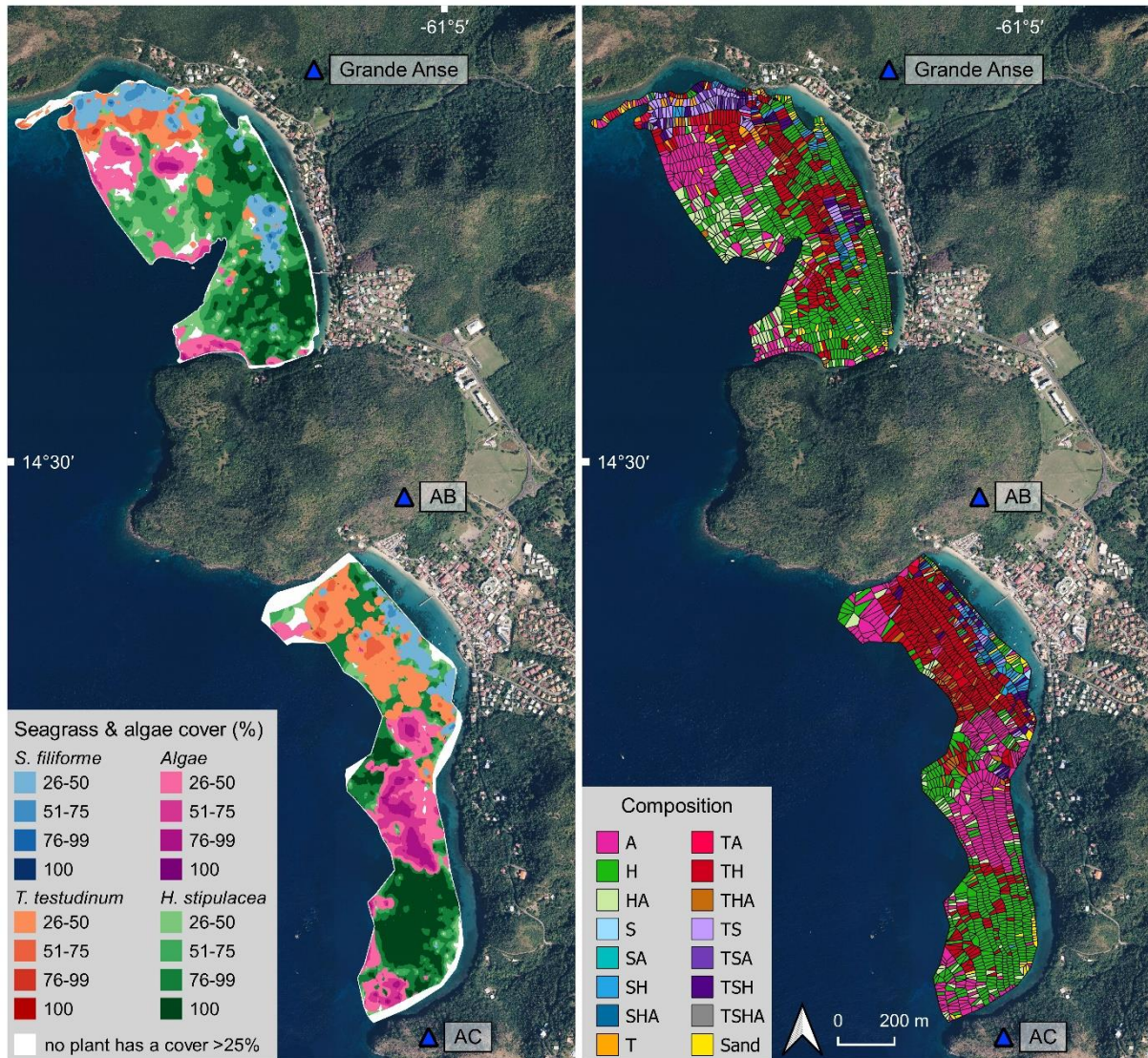
302
303 Differences in plant nutritional content and digestibility between groups were analysed with R
304 software (R Core Team, 2021) using Student's t tests and Kruskal-Wallis tests to consider
305 non-normality of some variables. When a significant difference was raised when comparing
306 more than two groups, we performed pairwise Mann-Whitney-Wilcoxon tests. P-values for
307 multiple tests were corrected using Holm's method (Holm, 1979) from rstatix package
308 (Kassambara, 2021). We used alpha values set at 0.05. Results are presented as means ±
309 standard errors (SE).

311 **3 Results**

312 **3.1 Benthic composition maps of the multispecific bays**

313 Marine plants covered 89% of Grande Anse area in 2016, and 84% in 2018, while they
314 covered 100% of Anse du Bourg/Anse Chaudière in 2016, and 91% in 2018. From 2016 to
315 2018, we found only small positive or negative variations in terms of coverage of the total
316 area by each plant, ranging from 0.4 to 7.5%. Thus, in 2018, *H. stipulacea* covered 56% and
317 59%, *T. testudinum* 12% and 12%, *S. filiforme* 7 % and 3%, and Algae 9% and 16%, of the
318 total area of Grande Anse and Anse du Bourg/Anse Chaudière, respectively (**Fig. 1**).

319



320
 321 **Fig. 1. Benthic composition maps showing:** macroalgae and seagrass species cover (left)
 322 **and plant communities (right)** of Grande Anse and Anse du Bourg (AB)/Anse Chaudière (AC)
 323 from surveys conducted in 2018. In the left panel, plants are superimposed in order: *H.*
 324 *stipulacea* in background, *T. testudinum*, Algae, and *S. filiforme* in foreground. In the right
 325 panel, the Algae (A), and seagrasses *T. testudinum* (T), *S. filiforme* (S), *H. stipulacea* (H) and
 326 their combinations form fifteen distinct plant communities.

327 **Colours, 2-column fitting image**

328

329 3.2 Foraging habitat selection

330 At the population level, in the multispecific bays (i.e. Grande Anse and Anse du Bourg/Anse
 331 Chaudière), the random habitat use hypothesis was rejected ($\lambda=0.2305$, $\chi^2=90.98$, $p<0.0001$),
 332 meaning that turtles favoured some habitats regardless of habitat availability. The pairwise t-

333 tests and the ranking matrix (**Table S3**) showed that habitats with at least one native species
334 (M) were significantly preferred over habitats composed of *H. stipulacea* or/and algae (H, A,
335 HA). There was no detectable difference in the selection of habitats H and HA, while A was
336 the least selected habitat of the four habitats.

337 **3.3 Diet composition and food selection**

338 The time over which bites considered in the diet assessment were counted was approximately
339 30 min per individual (**Table S2**). With 61 individuals retained in the analyses, this equates to
340 over 30 h of feeding sequences.

341
342 In sites with only monospecific stands of *H. stipulacea* (i.e. Anse Noire and Anse Dufour), 24
343 of the 27 monitored individuals foraged on *H. stipulacea* (**Fig. 2A**). That was overall the most
344 represented item in the diet. In sites with multispecific seagrass meadows (i.e. Grande Anse
345 and Anse du Bourg/Anse Chaudière), 30 of the 34 monitored individuals foraged on *H.*
346 *stipulacea* (**Fig. 2B**), with high variability among individuals. Native seagrasses were the
347 most represented in the diet. Algae and Other items were very rare.

348
349 At the population level, in the multispecific bays (i.e. Grande Anse and Anse du Bourg/Anse
350 Chaudière), the random food use hypothesis was rejected ($\lambda=0.1766$, $\chi^2=58.99$,
351 $p<0.0001$), with *T. testudinum* significantly preferred over *S. filiforme*, *H. stipulacea* and
352 Algae, the latter being the least selected. At the individual level, about 47% of the turtles
353 positively selected more than one food resource (**Table S4**). *T. testudinum* and *S. filiforme*
354 were selected positively by 76% and 44% of the monitored turtles, respectively, while *H.*
355 *stipulacea* and Algae were positively selected by 24% and 3% of them, respectively.

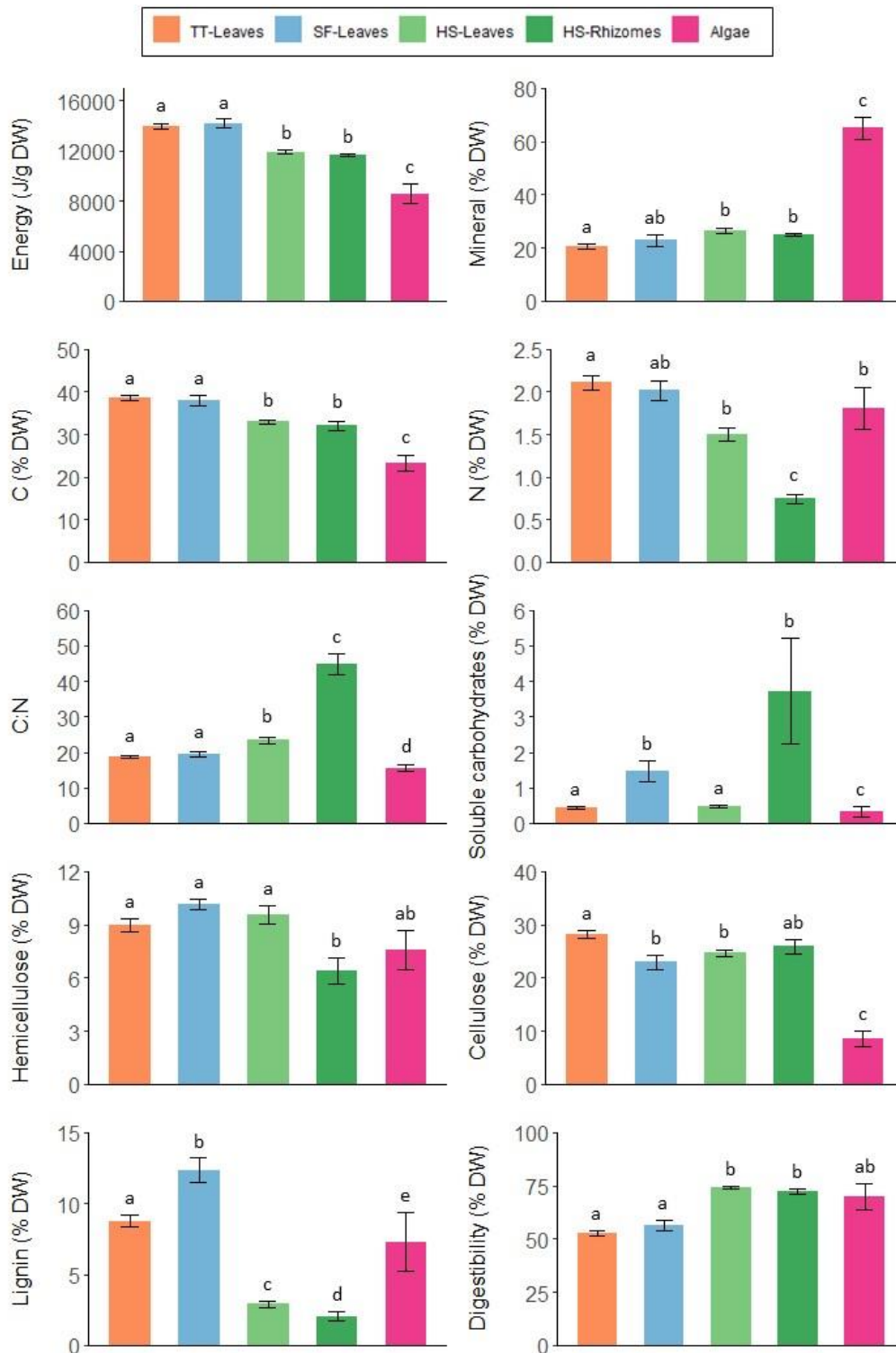
356

373 than *S. filiforme* (5.2 points higher and 3.6 points lower, respectively). Compared to *T.*
374 *testudinum* and *S. filiforme*, the invasive species *H. stipulacea* had a lower energy content
375 (approximately 2 330 j/g DW lower than *T. testudinum* and *S. filiforme*), with lower C
376 contents but higher C:N ratio. *H. stipulacea* rhizomes had also 3 times lower N content and 2
377 times higher C:N ratio than *T. testudinum*. The invasive species contained up to 6 times less
378 lignin than *T. testudinum* and *S. filiforme*. Focusing on *H. stipulacea*, rhizomes had lower N,
379 hemicellulose, and lignin content than leaves (0.8, 3.2, and 0.9 points lower, respectively).
380 There was no significant difference in energy, mineral, C, nor in cellulose content between
381 leaves and rhizomes. However, rhizomes had eight times more soluble carbohydrates and a
382 C:N ratio twice as high as in leaves. The nutritional composition of Algae showed higher
383 variability than seagrasses because of the inclusion of several species. Compared to
384 seagrasses, Algae contained notably more minerals (about 40 points higher), less cellulose
385 (14-20 points lower) and had the lowest C/N ratio.

386
387 Water content (refer to **Fig. S3, Table S5**) was similar in *S. filiforme* and *H. stipulacea*
388 (around 90%). It was lower in *T. testudinum* and Algae (around 87 and 75% FW,
389 respectively). Since the hydrated samples are more representative of the food actually
390 ingested by green turtles, results expressed in fresh weight are also given in the
391 Supplementary material (**Fig. S3, Table S5**). For example, despite leaves of *T. testudinum* and
392 *S. filiforme* had a similar energy content when expressed on a dry weight basis, it was 1.4
393 times higher in the former than in the latter when expressed on a fresh weight basis because of
394 the difference in water content.

395
396 Regarding digestibility (refer to **Fig. 3, Table S5**), *T. testudinum* and *S. filiforme* showed
397 similar values for this parameter ($52.9 \pm 1.3\%$ DW for *T. testudinum* and $56.5 \pm 2.5\%$ DW for
398 *S. filiforme*). However, *H. stipulacea* appeared to be more digestible than both native
399 seagrasses (approx. 20 points higher), and digestibility was similar in leaves and rhizomes of
400 the invasive species ($74.3 \pm 0.7\%$ DW for leaves and $72.2 \pm 1.4\%$ DW for rhizomes). Algae
401 had an intermediate digestibility ($69.9 \pm 6.2\%$ DW) with values between those of native and
402 invasive seagrasses.

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Fig. 3. Comparison of nutritional composition (mean ± SE) expressed on a dry weight (DW) basis, of seagrasses (TT: *T. testudinum*; SF: *S. filiforme*, HS: *H. stipulacea*) and Algae. Refer to Table S5 for exact values and sample sizes. Kruskal-Wallis tests evidenced significant differences in each case ($p < 0.001$). Groups with the same letter on top are not significantly different (based on multiple pairwise-comparisons). Colours, 1.5 or 2-column fitting image

412

413 4 Discussion

414 4.1 Resource selection in immature green turtles

415 Foraging habitat selection analyses showed that immature green turtles favoured habitats with
416 at least one native species. Moreover, they preferentially selected *T. testudinum* in their diet
417 when available (**Fig. 2B**). These results are consistent with other studies conducted in the
418 Caribbean. Christianen et al. (2018) showed that green turtles selected *T. testudinum* when
419 presented with two other species (*S. filiforme* and *H. stipulacea*) in Bonaire. They also
420 highlighted a change in grazing locations to shallower areas where native seagrass species
421 were still predominant. In Malendure Bay (Guadeloupe), where *T. testudinum* was rarely
422 found in close proximity to foraging green turtles, Whitman et al. (2019) highlighted turtle
423 preference for *S. filiforme* in multispecies seagrass beds. Thus, in these studies, green turtles
424 were still consuming native species about six years after the introduction of *H. stipulacea* and
425 were mainly avoiding the invasive species. Nevertheless, similar to Christianen et al. (2018)
426 and Whitman et al. (2019), we found high inter-individual variability in diet composition,
427 with *H. stipulacea* accounting for 0-100% of the diet, regardless of native plant availability. In
428 multispecies sites, we showed positive selection for *H. stipulacea* in 24% of individuals
429 monitored. However, for the first time, we investigated green turtle food selection at a site
430 where *H. stipulacea* completely replaced native seagrass species. At Anse Noire and Anse
431 Dufour, we observed that the majority of green turtles fed on *H. stipulacea* while some ate
432 Algae (**Fig. 2A**). In addition, a previous study highlighted the high fidelity of green turtles to
433 their capture site in Martinique (Siegwalt et al., 2020). This suggests that individuals observed
434 at Anse Noire and Anse Dufour may spend several years growing in these bays and do not
435 change bays to feed. Therefore, this population appears acclimatised to environmental change
436 and has integrated *H. stipulacea* into its diet.

437

438 Selectivity for food resources may be influenced by several factors, such as forage relative
439 availability (López-Mendilaharsu et al., 2008), nitrogen and phosphorus content (Bjørndal,
440 1980), and energy content (Arthur and Balazs, 2008). On a dry basis, compared to native
441 seagrasses, *H. stipulacea* had globally lower energy, C, and N content (**Fig. 3**). Similarly
442 Christianen et al. (2018) found lower N content and higher C:N ratio for *H. stipulacea*
443 compared to *T. testudinum* and *S. filiforme*. It is likely that the strong preference for native

444 seagrasses, and in particular for *T. testudinum*, could be related to their nutritional benefits.
445 However, Whitman et al. (2019) found no significant differences in these nutritional
446 parameters between *H. stipulacea* and *S. filiforme* at Malendure Bay. To explain the similar
447 nutritional composition of both plants and their high C and N values, Whitman et al. (2019)
448 hypothesised that their feeding area was certainly a very nutrient rich environment. We also
449 expressed the nutritional composition on a fresh basis as it is more representative of the food
450 actually ingested by turtles, and consequently of their foraging effort to meet energetic needs.
451 On this basis, *T. testudinum* had higher energy and N content than the other seagrasses (**Table**
452 **S5, Fig. S3**), which could explain the frequent positive selection for this species, especially in
453 this context of growing juvenile turtles. Nevertheless, at Grande Anse and Anse du
454 Bourg/Anse Chaudière, we observed that some individuals fed on *H. stipulacea* (**Fig. 2B**),
455 while native species were available (**Fig. 1**). If these results can be extrapolated over the long
456 term, this could indicate an advantage to feeding on *H. stipulacea*, first, in terms of energy
457 balance (perhaps related to higher digestibility; or higher ingestion rate, at the expense of
458 longer feeding time), and second, in terms of intraspecific competition (which could be
459 lowered since *H. stipulacea* is abundant in the environment). Moreover, at Anse Noire/Anse
460 Dufour where native seagrasses were no longer present, the majority of the monitored green
461 turtles foraged exclusively on *H. stipulacea* (**Fig. 2A**). Nevertheless, due to its lower
462 nutritional value, the consequences of the massive inclusion of *H. stipulacea* in the diet of
463 green turtles on their growth and survival need to be assessed.

464
465 Fibre content and digestibility are two other important parameters of plant nutritional value
466 that can influence food selectivity of sea turtles (Bjorndal, 1980; Brand-Gardner et al., 1999).
467 Interestingly, we found that *H. stipulacea* was more digestible and had up to 6 times less
468 lignin content than the native species (**Fig. 3, Table S5**). For *T. testudinum* leaves, we found
469 an average digestibility (53% DW) higher than fermentability values previously reported (25-
470 34% DW, Moran and Bjorndal, 2007) (the enzymes we selected being potentially more stable
471 than the rumen juice formerly used for this type of analysis), but consistent with Bjorndal's
472 (1980) apparent organic matter digestibility values. Regarding fibre content, Moran and
473 Bjorndal (2007) found somewhat lower results for *T. testudinum* blades (ligno-cellulose
474 fraction: 25-31% DW), with lower lignin contents than in our study (about 2% DW in their
475 study and 9% DW in ours), while Bjorndal (1980) and Vicente et al. (1980) lignin values
476 accord with ours. According to Moran and Bjorndal (2007), the variability in lignin content
477 may be due to the current flow characteristics of each study site. Yet, while lignin has a higher

478 energy density than cellulose and hemicellulose (between 21 and 27 kJ/g DW, compared to 17
479 kJ/g DW for cellulose and hemicellulose, see Agrawal et al., 2014; Frei, 2013; Murphy and
480 Masters, 1978; Welker et al., 2015), the low digestibility that lignin confers on food (due to its
481 own low digestibility and because it prevents digestive enzymes from breaking down
482 cellulose and hemicellulose completely by complexing with these fibres) precludes it from
483 being an efficient nutrient (Moore and Jung, 2001; Van Soest, 1982). Therefore, although *H.*
484 *stipulacea* showed lower energy content than the native species through nutritional analysis
485 (Fig. 3), its low lignin content and higher digestibility calls into question the measured
486 energetic advantage of native plants over the exotic one. Nevertheless, the digestibility we
487 measured *in vitro* cannot account for all chemical reactions and biological interactions
488 involved in digestion at the whole-body level. In particular, the gut microbiome of green
489 turtles evolves during their growth and notably at their recruitment to the neritic zone with the
490 acquisition of bacteria involved in plant digestion (Campos et al., 2018; Price et al., 2017).
491 Bjorndal (1980) showed that *in vivo* digestibility of hemicellulose and protein increased
492 significantly with turtle's body size, while Campos et al. (2018) highlighted an increase in the
493 taxonomic richness of the gut microbiome as green turtle grow. *H. stipulacea* may therefore
494 be of particular nutritional value for small turtles that have not yet fully adapted their gut
495 microflora to herbivory, but this may diminish for larger individuals. Further research on
496 overall digestibility is needed to accurately test for a difference between native and invasive
497 species considering the body size of individuals.

498
499 Les Anses d'Arlet are considered a critical foraging and developmental habitat for immature
500 green turtles, which spend many years growing until they reach sexual maturity and
501 eventually migrate (Bonola et al., 2019; Chambault et al., 2018; Siegwalt et al., 2020). Due to
502 the lower nutritional value of *H. stipulacea*, inclusion of this seagrass in turtle's diet may have
503 important consequences for the population. Moreover, nitrogen and energy contents of plants
504 have been linked to turtle growth rate and reproductive parameters (Bjorndal, 1980; Wood
505 and Wood, 1981). In Bermuda, Gulick et al. (2021) observed a decline in body mass of
506 growing green turtles related to a decrease in available resources, while Bjorndal et al. (2017)
507 showed a decline in growth rates in three sea turtle species throughout the West Atlantic,
508 linked to an ecological regime shift and probably to an associated decrease in quantity and
509 quality of food resources. Here, we showed that immature green turtles preferentially foraged
510 on the native species when possible, but in bays fully invaded by *H. stipulacea* as in Anse
511 Noire/Anse Dufour, green turtles foraged actually on *H. stipulacea* (Fig 2A). Therefore, for

512 this population, we can expect that a shift from native plants to lower nitrogen and energy
513 plants may reduce turtle's growth rate and delay their sexual maturity. In addition, a previous
514 study showed that residence time in Anse Noire was lower than in Grande Anse (Siegwalt et
515 al., 2020). It has been showed that developmental migrations may be triggered by nutrient
516 limitation and/or reduced growth rates (Bjorndal et al., 2000, 2019; Chaloupka and Limpus,
517 2001). Thus, we can hypothesized that lower nutrient quality of *H. stipulacea* and potentially
518 sub-optimal growth experienced by immature green turtles in Anse Noire/Anse Dufour may
519 force them to move to other more profitable foraging areas. The capture-mark-recapture
520 studies currently conducted in Martinique will allow long-term comparison of growth rate
521 between these multi- and monospecific bays.

522
523 The rapid expansion of *H. stipulacea* in Les Anses d'Arlet have modified the foraging ground
524 of the immature green turtles, which have thus adopted different energetic strategies. Indeed,
525 at Grande Anse, we found a high inter-individual variability in diet composition, with
526 immature green turtles that preferentially foraged for the native species, but also individuals
527 that fed mainly on *H. stipulacea* while native species were available (**Fig. 2B**). It would be
528 interesting to assess whether these individuals feed on *H. stipulacea* occasionally or
529 permanently. Indeed, forager fitness and diet breadth may be affected by increased
530 intraspecific competition for food resources (Svanbäck and Bolnick, 2005). While most turtles
531 selected native plants, whose coverage represented <20% in both multispecific sites (**Fig. 1,**
532 **Fig. 2B**), individuals integrating *H. stipulacea* in their diet or specialising on it may benefit
533 from a lower inter-individual competition for resources. Finally, we can also expect changes
534 in green turtle behaviour when integrating the invasive species into their diet. Thus, turtles
535 may modify their activity budget to adapt to lower energy acquisition by decreasing the time
536 allocated to energy-demanding activities and increasing rest time, or alternatively by
537 increasing the proportion of time devoted to feeding, and thus, the amount of material
538 consumed to meet energy requirements. It would be interesting to compare the activity budget
539 of individuals between Grande Anse and Anse Noire/Anse Dufour to identify potential
540 different energetic strategies used by green turtles to adapt to changes in their environment.

541
542 In this study, we used bite counts from direct observations for estimating the diet composition
543 and the food selection of immature green turtles at the individual level. Direct observation has
544 the advantage of being non-invasive and causing little disturbance, but it is still difficult to
545 monitor free-ranging green turtles over the long term as they move quickly and change

546 environments often. This leads to observation times depending on the goodwill of the green
547 turtles. In this study, we performed behavioural observations during ca. 100 min per follow,
548 and recorded feeding behaviours over an average of 52 min (with standard deviation of 55
549 min, **Table S2**). Thus, this large variability in the recorded duration of feeding activity may
550 result in a bias in diet composition estimation at population level. In addition to the difficulty
551 of monitoring sea turtles, this variability is also due to a high inter-individual variability in the
552 expressed behaviours, with some individuals feeding very little and others feeding during
553 most of the day (Rice et al., 2000, pers. obs.). In addition, the direct observations represented
554 a short period of the turtle's daily time and we cannot exclude that other items were ingested
555 during the rest of the day. Therefore, these limitations highlight the complexity of studying
556 green turtle foraging strategy while direct observation remains an essential first step in
557 identifying the inter-individual variability in diet composition and feeding strategies with
558 minimal disturbance. Thus, although the total time used in our study for the assessment of the
559 diet (ca. 30 h) was quite high compared to the literature (e.g. ca. 8 h in Whitman et al., 2019),
560 further research is needed to improve the precision of these results. Oesophageal content
561 analysis (see in Gulick et al., 2021), is another complementary method that could be
562 implemented to obtain the precise amount of food ingested. However, this method is much
563 more invasive than direct observation and requires capture of the turtles and oesophageal
564 lavage. Stomach and oesophageal contents can also be collected during necropsy, but the
565 body of the dead turtle must not be decomposed, which is rarely the case in Martinique.
566 Finally, the development of on-board cameras with an increasing autonomy represents a
567 promising new method to follow individuals over a longer period of time and thus to go
568 further in the study of feeding strategy of immature green turtles.

569 **4.2 Expansion of *H. stipulacea* in Martinique and conservation implications**

570 **Benthic composition** maps highlighted the dominance of *H. stipulacea* in Les Anses d'Arlet,
571 with a cover >55% in Grande Anse and Anse du Bourg/Anse Chaudière in 2018, while it was
572 the only remaining seagrass species in Anse Noire and Anse Dufour. *H. stipulacea* was first
573 recorded in Martinique in 2006 and spread from North to South (Ortolé, 2012). Its exact time
574 of arrival in Les Anses d'Arlet is unclear, but its presence was reported in Anse Noire in 2011
575 (DEAL Guadeloupe et Martinique, 2011). This fast expansion in Martinique has been
576 observed on other neighbouring islands and is characteristic of the Caribbean (Willette et al.,
577 2014; Winters et al., 2020).

578

579 The introduction and expansion of *H. stipulacea* appears primarily due to anthropogenic
580 factors. While pleasure yachts probably carried *H. stipulacea* from the Mediterranean to the
581 Caribbean, inter-island vessel transit and fishing activities also contributed to its expansion
582 throughout the region by creating vacant spaces for it, and by generating and dispersing
583 fragments (Ruiz and Ballantine, 2004; Willette et al., 2014; Willette and Ambrose, 2012).
584 Some of our study sites where *H. stipulacea* was found in monospecific beds in 2018 (**Fig. 1**)
585 seem to have suffered from bottom-scraping anchors and chains. While the Southern area of
586 Grande Anse is a past authorised anchorage zone (Sermage, 2006), Anse Chaudière still
587 experiences heavy boat traffic (pers. obs.). Indeed, *H. stipulacea* has high ability to colonise
588 bare sand, especially where conditions are not favourable for native species (Winters et al.,
589 2020). In sites with multispecific seagrass meadows, its expansion may have been more
590 difficult and some areas remain dominated by native species (**Fig. 1**). Areas where native
591 meadows were certainly dense and less subject to mechanical disturbances (Sermage, 2006)
592 have been preserved from total invasion by *H. stipulacea*.

593

594 Today, it seems urgent to limit the pressures of anthropic origin on the native meadows in
595 order to slow down the expansion of *H. stipulacea*. Thus, prohibiting anchorages and setting
596 up a defined mooring zone (with multiple floating buoys connected to cement blocks by
597 ropes) outside the zones that include native meadows could be a solution. An exhaustive
598 survey at the scale of Martinique, both on the progression of *H. stipulacea* and on the factors
599 likely to favour its expansion (absence of anchorage area, high boat traffic, pollution of
600 anthropic origin) should be conducted annually to take preventive and curative measures to
601 limit its development.

602

603 Furthermore, the effects of climate change on *H. stipulacea* expansion are still very little
604 studied. A recent study showed different responses to sea warming among populations
605 (Nguyen et al., 2020). Increasing sea temperature would reduce *H. stipulacea* meadows in its
606 native regions while facilitating its spread in the Mediterranean Sea, a region invaded 150
607 years ago. It is therefore difficult to predict the future range expansion of *H. stipulacea* in the
608 Caribbean. Species distribution models could help predict the potential range expansion of the
609 invasive species but require accurate data on the current distribution and environment.
610 Consequently, rigorous monitoring of *H. stipulacea*, not only in Martinique but also in the
611 whole Caribbean, should be implemented. Improving knowledge of seagrass is an essential
612 prerequisite to ensure their preservation. This may facilitate a proper growth and adaptation of

613 immature green turtles to changing environments and promote the protection of this
614 threatened species. In turn, this will benefit the entire seagrass ecosystem.

615

616 **5 Conclusion**

617 This study provides a precise assessment of the cover of *H. stipulacea* in an area of South-
618 West Martinique, which is a hotspot of immature green turtles. For the first time, their diet
619 was investigated at sites where native plants were still present, but also at sites where the
620 invasive species had completely replaced native seagrasses. We show that, although green
621 turtles preferentially chose native seagrasses when available, they included *H. stipulacea* in
622 their diet at sites completely or partially covered by this species. We also show that *H.*
623 *stipulacea* was less energetic but more digestible than native plants. In this context, new
624 questions about the impacts of this dietary change on the growth and survival of immature
625 green turtles may be raised. Our study highlights the importance of in-depth dietary analysis
626 (composition, energetics, digestibility, etc.) in ecosystems where resource availability may
627 vary, to gain a broader picture of the causes and consequences of food choices for endangered
628 species like the green turtle.

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660

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1 1 **Food selection and habitat use patterns of immature green turtles (*Chelonia mydas*) on**
2 2 **Caribbean seagrass beds dominated by the alien species *Halophila stipulacea***

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6 6 **Abstract**

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9 9 Marine herbivores face rapid changes in the coastal ecosystems where they forage. In the
10 10 Caribbean, the recent and fast expansion of the invasive phanerogam species *Halophila*
11 11 *stipulacea* is threatening native seagrass ecosystems. So far, *H. stipulacea* is escaping most
12 12 Caribbean herbivores, certainly because of its recent introduction or lower nutritional value.
13 13 We investigated the impact of *H. stipulacea* invasion on fine-scale foraging habitat selection
14 14 and food resource selection of immature green turtles at critical foraging sites in Les Anses
15 15 d'Arlet, Martinique. The analysis of seagrass distribution and nutritional content, together
16 16 with turtle behaviour and resource selection, showed that *H. stipulacea* may be of contrasting
17 17 interest to green turtles. Compositional analysis confirmed the lower nutritional value of *H.*
18 18 *stipulacea* compared to the native species, but the invasive species showed higher digestibility
19 19 than native ones, which calls into question the energetic advantage of consuming the native
20 20 plants over the exotic plant. Thus, although green turtles mostly selected the native seagrass
21 21 *Thalassia testudinum* in multispecies seagrass beds, some individuals fed on *H. stipulacea*.
22 22 Accordingly, in bays entirely invaded by *H. stipulacea*, one possibility for resident green
23 23 turtles is to increase foraging on this species, but, if so, the consequences on their growth and
24 24 survival still remain to be determined. As the expansion of *H. stipulacea* may have been
25 25 facilitated by factors such as shipping, anchor scarring and fishing activities, protection of
26 26 native seagrass beds and immature green turtles from human disturbances is urgently required
27 27 to ensure the long-term adaptation of green turtles to this new foraging environment.
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38 38 **Keywords**

39 39 Plant-herbivore interactions / Sea turtle / Invasive species / Foraging behavior / Diet /
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30 **1 Introduction**

31 Investigating foraging habitat use, food selection and underlying strategies in threatened
32 species is essential to understand their ecological roles and trophic relationships and thus
33 develop appropriate conservation measures. Optimal foraging theory postulates that fitness
34 (survival and reproductive success) depends on foraging efficiency and that natural selection
35 has favoured behaviours that maximise energy acquisition (Pyke et al., 1977). Therefore,
36 foraging strategies have evolved in adaptation with the environment, i.e. in response to factors
37 like predation risk, intra- and interspecific competition, as well as food availability and quality
38 (Chevallier et al., 2008; Fritz et al., 1996; Pyke et al., 1977). Rapid changes in the
39 environment can challenge these foraging strategies and affect individuals' fitness,
40 threatening the future of the population. This is especially true for species spending
41 considerable amounts of time on feeding sites over their lifetime, i.e. those with delayed
42 sexual maturity and for which individuals in advanced life stages have high reproductive
43 value or are essential for the survival of young (Braby et al., 2011; Heppell et al., 2002). Thus,
44 foraging ground quality should be considered critical for population recovery.

45
46 Marine herbivores have developed adaptive morphological, physiological and behavioural
47 traits to consume algae and seagrass and maximise the nutritional value they get from them.
48 For example, sea urchins, parrotfish and surgeonfish use powerful mouthparts to break plant
49 fibres and cell walls, while green turtles and some fishes that do not masticate food use a low
50 stomach pH to break certain algae or fibres like hemicellulose (Bjorndal, 1985; Steneck et al.,
51 2017; Thayer et al., 1984). Sirenians and green sea turtles also depend on their rich gut
52 microflora (composed of cellulolytic bacteria) which ensures the partial digestion of plant
53 fibres such as cellulose and hemicellulose, by microbial fermentation (Bjorndal, 1980, 1985;
54 Thayer et al., 1984). At the behavioural level, one foraging strategy is to regularly revisit the
55 same seagrass patches, which allows herbivores to cultivate plots of young leaves (Bjorndal,
56 1980). Since regrowths generally have higher protein levels and lower lignin levels (Bjorndal,
57 1980; Moran and Bjorndal, 2007), and digestibility of forages is negatively correlated with
58 lignin concentration (Moore and Jung, 2001), this strategy improves nutritional content and
59 digestibility of the targeted plants. In addition, bite sizes that favour a high surface-to-volume
60 ratio of ingesta particles, and thus greater exposure to microbial attack, are likely to maximise
61 digestion rates (Bjorndal et al., 1990; Gulick et al., 2021). Reducing ingesta particle size also
62 provides a strategy to meet energy requirements in the face of declining food availability,
63 whether due to anthropogenic threats or overgrazing (Gulick et al., 2021). Thus, marine

64 herbivores have adapted to the plant resources that thrive in coastal marine environments, and
65 are largely dependent on the well functioning of these ecosystems. In turn, these herbivores,
66 and especially megaherbivores such as manatees, dugongs and green turtles, can induce
67 structural changes in their foraging habitats and influence their evolution (Thayer et al.,
68 1984). Understanding interactions between these endangered megaherbivores and their
69 ecosystem is therefore crucial for successful conservation strategies.

70
71 Coastal marine ecosystems conservation is even more important given that they face strong
72 anthropogenic pressures and are jeopardised by a rapid reduction in their distribution. This is
73 the case for seagrass meadows, which have suffered a global loss of 29% since 1879, mainly
74 due to coastal human activities, pollution and eutrophication, and climate change (Waycott et
75 al., 2009). The expansion of invasive species such as sea urchins and exotic plants also
76 hinders the development of native seagrasses (Williams, 2007). In particular, the recent
77 implantation of the exotic seagrass species *Halophila stipulacea* in the Caribbean has raised
78 new worries. Originating from the Red Sea, it reached the Western Atlantic Ocean probably
79 transported by boats, and spread rapidly around the Eastern Caribbean islands after a first
80 record in 2002 (Ruiz and Ballantine, 2004; Willette et al., 2014). *H. stipulacea* has been
81 considered an invasive species in the Caribbean due to its rapid expansion and strong
82 competitive ability (Winters et al., 2020), thus contributing to rapidly modifying native plant
83 communities.

84
85 The green turtle (*Chelonia mydas*) is the only sea turtle species with a plant-dominated diet
86 (Bjorndal, 1980; Jones and Seminoff, 2013). Upon recruitment to neritic habitats, juvenile
87 green turtles are indeed known to shift from a carnivorous to a predominantly herbivorous
88 diet (Jones and Seminoff, 2013). Green turtles have been classified as Endangered on the
89 IUCN Red List, mainly due to ongoing harvest and bycatch, and the rapid change in their
90 foraging habitats may represent an additional threat (Seminoff, 2004). While conservation
91 efforts worldwide began in the 1950s, management actions have primarily targeted nesting
92 beaches and protected eggs and hatchlings, as at-sea monitoring of populations remains
93 difficult (Heppell et al., 2002). Yet, stage-based population models on long-lived turtle
94 species have highlighted the importance of reducing mortality in the late life stages (large
95 juveniles, subadults, adults) to promote population recovery (Heppell et al., 2002). Therefore,
96 estimating the impact of changes, particularly in the developmental range of immature green
97 turtles, is important to adapt protection measures for these key habitats.

1
2 99 Only a few studies mention the presence of non-native plant species in green turtles' diet. In
3
4 100 Hawaii, it took 10-12 years for highly invasive species and 20-30 years for slow-growing
5
6 101 algae, to become the majority of green turtles' diet (Russell and Balazs, 2015). In the Eastern
7
8 102 Caribbean the first occasional grazing events on *H. stipulacea* by green turtles were observed
9
10 103 in 2013 (Becking et al., 2014), but the relatively short time since its arrival (Willette et al.,
11
12 104 2014) may explain why it was not yet meaningful in turtles' diet. Moreover, these grazing
13
14 105 events were always observed within assemblages dominated by the native seagrass *T.*
15
16 106 *testudinum*, which was significantly preferred over *H. stipulacea* (Christianen et al., 2018;
17
18 107 Whitman et al., 2019). A single study conducted in the U.S. Virgin Islands in 2017/2018 (i.e.
19
20 108 within 2 years of the arrival of *H. stipulacea*), highlighted the prevalence of this introduced
21
22 109 seagrass in the diet of juvenile green turtles, although it was not a dominant plant in the
23
24 110 environment (Gulick et al., 2021). In Martinique (Lesser Antilles), *H. stipulacea* now covers
25
26 111 most of the foraging habitats available along the Caribbean coast (Ortolé, 2012). After a first
27
28 112 record in 2006, nearly 90% of the changes observed in the benthic communities within 4
29
30 113 years benefited *H. stipulacea* (Maréchal et al., 2013). While conservation plans still take little
31
32 114 account of invasive plants (Giakoumi et al., 2016), it is important to assess the impact of *H.*
33
34 115 *stipulacea* invasion on foraging habitat and food resource selections of immature green
35
36 116 turtles. This could provide a better understanding of how turtles have adapted to this rapid
37
38 117 change, so that protective measures can be implemented for key seagrass habitats.

39
40 118
41
42 119 Our study focused on the seagrass beds of Les Anses d'Arlet, Martinique, a green turtle
43
44 120 foraging hotspot where immatures spend many years until reaching sexual maturity
45
46 121 (Chambault et al., 2018; Siegwalt et al., 2020). We assessed seagrass bed composition and
47
48 122 determined nutritional content and digestibility of plants. In parallel, we recorded turtle
49
50 123 behaviour and movements to analyse foraging habitat selection, and analysed turtle bite
51
52 124 counts to infer diet and food preferences. Because Martinique's multispecies seagrass
53
54 125 meadows are dominated by *H. stipulacea*, and given the high fidelity of immature green
55
56 126 turtles to their feeding grounds (Siegwalt et al., 2020), we hypothesised that they might now
57
58 127 consume significant proportions of *H. stipulacea*.

59 128 60 129 **2 Materials and Methods**

61 130 **2.1 Study site**

131 We conducted our study in Martinique, French West Indies, France, in five bays of Les Anses
132 d'Arlet (14°30'9.64"N, 61°5'11.85"W): Anse Noire, Anse Dufour, Grande Anse, Anse du
133 Bourg and Anse Chaudière (see **Fig. S1 and S2** for details). Grande Anse (~75 ha), Anse du
134 Bourg (~30 ha) and Anse Chaudière (~40 ha) are large bays where algae, and the three main
135 phanerogams found in Martinique (i.e. two native species, *Syringodium filiforme* and
136 *Thalassia testudinum*, and one invasive species, *Halophila stipulacea*) are present. Anse
137 Noire (~8 ha) and Anse Dufour (~10 ha) are only covered by *H. stipulacea* and algae.

138 **2.2 Benthic composition and resource availability**

139 Macroalgae and seagrass species composition of each bay was assessed during 2016 and
140 2018. No precise mapping was done in Anse Noire and Anse Dufour, as *H. stipulacea*
141 covered nearly 100% of the meadows, with few algae on the rocky banks. In Grande Anse,
142 Anse du Bourg and Anse Chaudière, meadows between 2 and 15-20 m depth were entirely
143 surveyed, at predefined points located every ten metres along GPS-based transects. At each
144 sampling point, a close picture of the ground was taken within 1 m² quadrats, either using an
145 underwater camera linked to a monitor on a boat or by scuba-divers using GoPro Hero 4
146 Silver cameras. The benthic vegetal composition and cover percentages of Algae (which, in
147 our study, mainly include the following macroalgae species: *Acanthophora spicifera*,
148 *Avrainvillea fulva*, *Avrainvillea nigricans*, *Caulerpa cupressoides*, *Caulerpa sertularioides*,
149 *Cerarium ciliatum*, *Cladophora prolifera*, *Dictyota prolifera* and other *Dictyota sp.*,
150 *Halimeda incrassata*, *Peniculus capitatus*, *Sargassum fluitans*, *Sargassum histrix var.*
151 *buxifolium*, *Ulva fasciata*), and seagrass species (*H. stipulacea*, *S. filiforme*, and *T.*
152 *testudinum*), were recorded on the pictures *a posteriori*. To determine coverage of algae and
153 each seagrass species, we adapted the Braun-Blanquet scale (Braun Blanquet, 1932) and
154 defined different categories according to the percentage of species coverage. To the initial
155 categories, we added the two categories '0%' and '100%' to indicate that a species was either
156 absent or covered a whole quadrat (as it was important for us to identify areas without or only
157 with *H. stipulacea*). Finally, rather than using one '5-25%' category and several '<5%'
158 categories, two categories between 1 and 25% ('1-12%' and '13-25%') were created to
159 facilitate the use of an interpolation scheme in QGIS. As a result, on each plot, we estimated
160 and classified plant coverage in seven categories (0%, 1-12%, 13-25%, 26-50%, 51-75%, 76-
161 99%, 100%).

163 Using the ‘natural neighbor’ interpolation scheme (Cueto et al., 2003) available in QGIS
164 (version 3.16.5, QGIS Development Team, 2022), we created raster maps for each plant and
165 for both years. Once vectorised, surface areas of all polygons composing each of the
166 percentage classes were extracted and multiplied by the corresponding median class
167 percentage to determine the total area available equivalent to a 100% cover. Maps of algae
168 and each seagrass species were then combined into a single map representative of the
169 coverage of macroalgae and seagrass species. Finally, Voronoi polygons were constructed in
170 QGIS using the sampling points as references to map the presence/absence of the different
171 plants and thus represent the different vegetation communities on a composition map.

172 **2.3 Video recording of feeding events**

173 Field observations were performed in the five bays from May to September 2016, from
174 December 2016 to May 2017, in February, April and June 2018, and from June to October
175 2019. Three snorkelers prospected a bay daily either from 7:00 to 12:00, or 11:00 to 14:00 or
176 14:00 to 19:00 to ensure data collected were evenly distributed across daylight hours. Once a
177 turtle was spotted, the snorkelers video-recorded its behaviours with GoPro Hero 4 Silver
178 cameras, using the focal sampling technique (Altmann, 1974), at a minimal distance of 4
179 meters. The bays being highly frequented, most turtles are used to human presence and their
180 behaviour usually seems unaffected by the presence of snorkelers. Nevertheless, if snorkelers’
181 presence appeared to stress a turtle (which displayed a change in behaviour, location or
182 direction), they moved away. Snorkelers' GPS location (recorded 30 to 60 times/min) was
183 used as a proxy for turtle location. In 2018-2019, a few individuals were also equipped with
184 on-board cameras with GPS as part of the study of Jeantet et al. (2020, 2021), which allowed
185 us to obtain additional behavioural data. From all video recordings, we identified six
186 behavioural categories: Swimming, Surfacing, Resting, Feeding, Interacting, and Scratching
187 (**Table S1**). Video recordings were analysed by observers and behaviours were labelled with
188 exact start and end times annotated. A total of 235 hours of recordings were obtained during
189 254 follows, of which 117 hours of sequences with feeding activity were extracted and
190 analysed.

191 **2.4 Foraging habitat selection**

192 Foraging habitat selection was investigated for turtles foraging in bays with multispecific
193 seagrass beds (Grande Anse, Anse du Bourg/Anse Chaudière) and not in the bays where only
194 monospecific seagrass meadows of *H. stipulacea* were present (Anse Noire/Anse Dufour).

195 Using behavioural and trajectory data obtained from direct observations, GPS-derived
196 locations were associated with the behavioural category recorded at the same time. Data from
197 individuals monitored less than one minute were discarded. The tracks of 62 individuals
198 monitored in Grande Anse in 2016-17 (n=44) and 2018-19 (n=12), and in Anse du
199 Bourg/Anse Chaudière in 2016-17 (n=2) and in 2018 (n=4) were analysed to investigate fine-
200 scale foraging habitat selection.

201
202 We performed a compositional analysis of habitat use (Aebischer et al., 1993), with R
203 software (v.4.0.0, R Core Team, 2021) and adehabitatHS package (Calenge, 2020), to test
204 whether immatures preferentially selected specific vegetation communities during foraging
205 activities. Based on the Voronoi composition maps (see 2.2) we identified fifteen distinct
206 plant communities that we gathered into four main habitat types: monospecific seagrass
207 meadows of *H. stipulacea* (H), algal meadows (A), communities composed of *H. stipulacea*
208 and algae (HA), and all other compositions with at least one native species in a monospecific
209 or mixed meadow (M). The composition maps were used to calculate the relative abundance
210 (so-called ‘availability’) of the different habitat types at the site scale, while habitat use by
211 each GPS-tracked turtle was calculated using the proportion of locations within each of these
212 habitat types. A habitat was considered ‘preferred’ if individuals used it more than expected
213 from its availability. Random habitat use (i.e. no habitat preference) was tested with a chi-
214 square test before communities were ranked in order of preference based on pairwise t-tests.

2.5 Diet composition and food selectivity

216 Individual-level diet composition was inferred from bite count. A bite corresponds to a
217 directed head/jaws movement towards a food item with evident intent to remove and ingest all
218 or most of it, and exclude movements associated with chewing only (Thomson et al., 2018).
219 From the video recording analysis and for each foraging bout, bites were counted and
220 assigned a prey category: *H. stipulacea*, *S. filiforme*, *T. testudinum*, Algae (any species of
221 macroalgae) or Other (typically animal prey, and occasionally squid or fish discards, or food
222 scraps such as eggshells). We did not consider bites for which prey could not be identified and
223 according to Thomson et al. (2018), only individuals with ≥ 30 confidently identified bites
224 (n=61: 27 in monospecific sites, and 34 in multispecific sites) were considered (see **Table S2**
225 for exact total observation time, total feeding time and time over which bites were counted for
226 each individual).

228 In the multispecific bays (Grande Anse and Anse du Bourg/Anse Chaudière), to investigate
229 food selection of immature green turtles at the population level (n=34), we used the
230 compositional analysis similarly to foraging habitat selection. Except for the category Other,
231 for which availability was unknown, we compared the proportion of bites on each resource to
232 their availability at the site scale based on the composition maps of the corresponding year. At
233 the individual level, resource use was also tested using the Manly's selection ratio w_i (Manly
234 et al., 2002), with the 'widesIII' function of the adehabitatHS R package (Calenge, 2020). For
235 each individual, this index was calculated as $w_i = \frac{o_i}{\pi_i}$, where o_i is the proportion of bites on
236 the i item and π_i the proportion of i in the study site. The index gives values between zero and
237 ∞ . Values equal to 1 indicate random feeding, values under 1 indicate negative selection, or
238 avoidance, and values above 1 indicate positive selection, or preference.

240 2.6 Nutritional composition and digestibility of native and invasive plants

241 2.6.1 Plant sampling and processing

242 Between 2015 and 2020, we collected macroalgae (see 2.2 for species details) and seagrass
243 species (leaves of *T. testudinum*, *S. filiforme* and leaves and rhizomes of *H. stipulacea*, as its
244 rhizomes are easily accessible for feeding) at several sampling points in Grande Anse and
245 Anse Noire to assess nutritional composition. *S. filiforme* and algae being rarer, fewer samples
246 were collected to avoid affecting their dynamics. Once collected, samples were rinsed three
247 times in fresh water to remove debris, invertebrates, epiphytes and excess salt. Excess water
248 was removed using a salad spinner and a clean cloth, and the fresh weight (FW) of each
249 sample was determined (± 0.1 g). Samples were dried in an oven at 50°C for 48 h and packed
250 in airtight bags for transport to the laboratory. Samples were then freeze-dried until constant
251 mass, i.e. successive weighing did not differ by more than 0.1%, to determine the dry weight
252 (DW). Dried samples were ground to pass through a 1 mm grid in a Retsch ultra-centrifugal
253 mill (model ZM200), in the same way as in Moran and Bjorndal (2007).

254 2.6.2 Nutritional composition and digestibility determination

255 Samples were freeze-dried again before analyses to eliminate any traces of water that might
256 have appeared during grinding. They were analysed in duplicate except when their mass was
257 too low. For analyses, samples were weighed to the nearest 0.001 g:

- 258 a) Energy content was determined on 1 g pellets using a Parr 6200 calorimeter (Parr
1 259 Instrument Company) calibrated with benzoic acid.
- 3 260 b) Total mineral content: 1 g samples were burned at 500°C for 24 hours and
4 261 reweighed to quantify remaining ashes.
- 7 262 c) Carbon (C) and nitrogen (N) content: we used a Flash (2000 or EA 1112) elemental
8 263 analyser (Thermo Fisher Scientific), which performed the dynamic flash combustion
9 264 method (derived from Dumas method, see Dumas, 1831), followed by gas detection
10 265 using a thermal conductivity detector. These measurements were translated into %C
11 266 and %N in the sample using Eager software, which allowed the calculation of C:N
12 267 ratios.
- 18 268 d) Soluble carbohydrates content: soluble carbohydrates (polysaccharides) were
19 269 measured on a continuous flow chain, using the neocuproin method, adapted from
20 270 Brown (1961). The method consists in extracting the water-soluble sugars from the
21 271 plant tissues and then hydrolysing them with an acid to obtain simple carbohydrates.
22 272 Monosaccharides' reducing power is then used to reduce, after heating, a cupric-
23 273 neocuproin chelate into a red copper-neocuproin complex, which absorbs at 460 nm.
24 274 The determination of reducing sugars is carried out using an auto-analyser and a
25 275 glucose standard curve, allowing the results to be expressed in glucose equivalent.
- 32 276 e) Fibre content: the Van Soest sequential fibre solubilisation method, adapted from
33 277 Goering and Van Soest (1970), classifies the cell wall components of a plant into
34 278 three types of insoluble residues: neutral detergent fibre (NDF), acid detergent fibre
35 279 (ADF), and acid detergent lignin (ADL) residues. Neutral soluble detergent (NDS)
36 280 added with amylase (which allows starch to be degraded) first allows separating
37 281 cytoplasmic compounds from all insoluble fibres (NDF). After filtration, soluble
38 282 acid detergent (ADS) helps extracting soluble fibres (ADF), before sulphuric acid is
39 283 used to retain ADL only. After each of the three phases, the fractions are passed
40 284 through a desiccator and then weighed. Until the last stage, mineral matter is present
41 285 in all three fractions NDF, ADF and ADL. A mineralisation stage at 500°C thus
42 286 allows the proportion of ash to be determined in relation to the proportion of lignin.
43 287 Once the ash-free ADL is expressed as a percentage of dry matter, the quantity of
44 288 the three types of fibre can be determined as follows: Lignin = (ash-free) ADL,
45 289 Cellulose = ADF – ADL, Hemicellulose = NDF – ADF.
- 58 290 f) In vitro enzymatic digestibility: based on a method adapted from Aufrère et al.
59 291 (2007), we estimated the potential digestibility of plant samples through the action

292 of enzymes: pepsin, cellulase, amyloglucosidase. These enzymes were chosen to
293 replace the ruminant rumen fluid originally used to measure organic matter
294 fermentability in vertebrates (see Moran and Bjorndal, 2007). The samples were
295 first incubated at 40°C with pepsin (a gastric enzyme whose role is to break down
296 proteins in the food bolus). The starch was then gelatinised at 80°C before being
297 degraded by amyloglucosidase during a second incubation. This lead to the release
298 of glucose molecules. Meanwhile, cellulose was degraded by cellulase. Finally,
299 solubilised fractions were incubated at 70°C for 48 h and then, weighed. The
300 proportion of solubilised plant material represents the fraction degraded by the
301 enzymes.

302
303 Differences in plant nutritional content and digestibility between groups were analysed with R
304 software (R Core Team, 2021) using Student's t tests and Kruskal-Wallis tests to consider
305 non-normality of some variables. When a significant difference was raised when comparing
306 more than two groups, we performed pairwise Mann-Whitney-Wilcoxon tests. P-values for
307 multiple tests were corrected using Holm's method (Holm, 1979) from rstatix package
308 (Kassambara, 2021). We used alpha values set at 0.05. Results are presented as means ±
309 standard errors (SE).

311 **3 Results**

312 **3.1 Benthic composition maps of the multispecific bays**

313 Marine plants covered 89% of Grande Anse area in 2016, and 84% in 2018, while they
314 covered 100% of Anse du Bourg/Anse Chaudière in 2016, and 91% in 2018. From 2016 to
315 2018, we found only small positive or negative variations in terms of coverage of the total
316 area by each plant, ranging from 0.4 to 7.5%. Thus, in 2018, *H. stipulacea* covered 56% and
317 59%, *T. testudinum* 12% and 12%, *S. filiforme* 7 % and 3%, and Algae 9% and 16%, of the
318 total area of Grande Anse and Anse du Bourg/Anse Chaudière, respectively (**Fig. 1**).

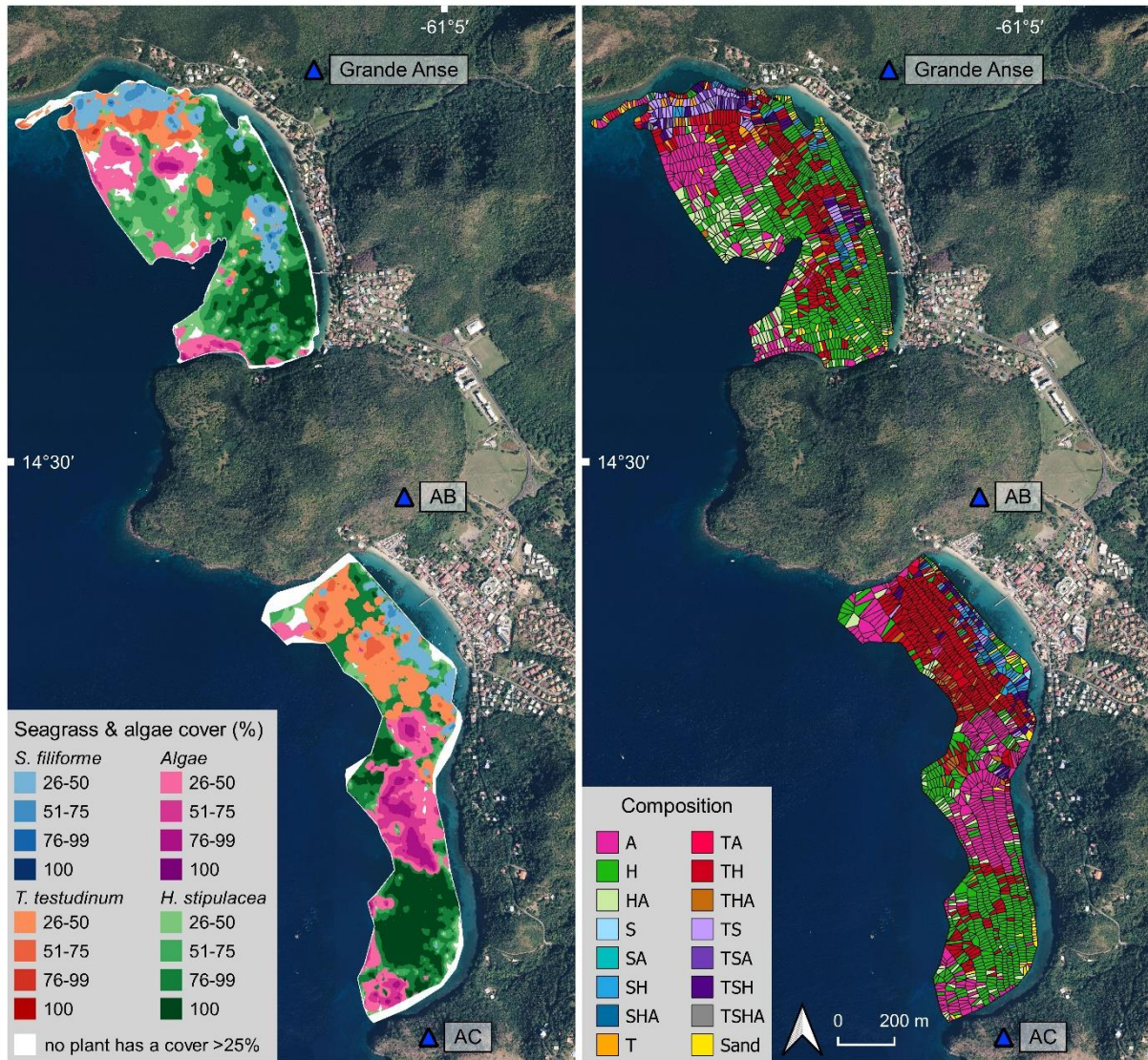


Fig. 1. Benthic composition maps showing: macroalgae and seagrass species cover (left) and plant communities (right) of Grande Anse and Anse du Bourg (AB)/Anse Chaudière (AC) from surveys conducted in 2018. In the left panel, plants are superimposed in order: *H. stipulacea* in background, *T. testudinum*, Algae, and *S. filiforme* in foreground. In the right panel, the Algae (A), and seagrasses *T. testudinum* (T), *S. filiforme* (S), *H. stipulacea* (H) and their combinations form fifteen distinct plant communities.

Colours, 2-column fitting image

3.2 Foraging habitat selection

At the population level, in the multispecific bays (i.e. Grande Anse and Anse du Bourg/Anse Chaudière), the random habitat use hypothesis was rejected ($\lambda=0.2305$, $\chi^2=90.98$, $p<0.0001$), meaning that turtles favoured some habitats regardless of habitat availability. The pairwise t-

333 tests and the ranking matrix (**Table S3**) showed that habitats with at least one native species
334 (M) were significantly preferred over habitats composed of *H. stipulacea* or/and algae (H, A,
335 HA). There was no detectable difference in the selection of habitats H and HA, while A was
336 the least selected habitat of the four habitats.

337 **3.3 Diet composition and food selection**

338 The time over which bites considered in the diet assessment were counted was approximately
339 30 min per individual (**Table S2**). With 61 individuals retained in the analyses, this equates to
340 over 30 h of feeding sequences.

341
342 In sites with only monospecific stands of *H. stipulacea* (i.e. Anse Noire and Anse Dufour), 24
343 of the 27 monitored individuals foraged on *H. stipulacea* (**Fig. 2A**). That was overall the most
344 represented item in the diet. In sites with multispecific seagrass meadows (i.e. Grande Anse
345 and Anse du Bourg/Anse Chaudière), 30 of the 34 monitored individuals foraged on *H.*
346 *stipulacea* (**Fig. 2B**), with high variability among individuals. Native seagrasses were the
347 most represented in the diet. Algae and Other items were very rare.

348
349 At the population level, in the multispecific bays (i.e. Grande Anse and Anse du Bourg/Anse
350 Chaudière), the random food use hypothesis was rejected ($\lambda=0.1766$, $\chi^2=58.99$,
351 $p<0.0001$), with *T. testudinum* significantly preferred over *S. filiforme*, *H. stipulacea* and
352 Algae, the latter being the least selected. At the individual level, about 47% of the turtles
353 positively selected more than one food resource (**Table S4**). *T. testudinum* and *S. filiforme*
354 were selected positively by 76% and 44% of the monitored turtles, respectively, while *H.*
355 *stipulacea* and Algae were positively selected by 24% and 3% of them, respectively.

373 than *S. filiforme* (5.2 points higher and 3.6 points lower, respectively). Compared to *T.*
374 *testudinum* and *S. filiforme*, the invasive species *H. stipulacea* had a lower energy content
375 (approximately 2 330 j/g DW lower than *T. testudinum* and *S. filiforme*), with lower C
376 contents but higher C:N ratio. *H. stipulacea* rhizomes had also 3 times lower N content and 2
377 times higher C:N ratio than *T. testudinum*. The invasive species contained up to 6 times less
378 lignin than *T. testudinum* and *S. filiforme*. Focusing on *H. stipulacea*, rhizomes had lower N,
379 hemicellulose, and lignin content than leaves (0.8, 3.2, and 0.9 points lower, respectively).
380 There was no significant difference in energy, mineral, C, nor in cellulose content between
381 leaves and rhizomes. However, rhizomes had eight times more soluble carbohydrates and a
382 C:N ratio twice as high as in leaves. The nutritional composition of Algae showed higher
383 variability than seagrasses because of the inclusion of several species. Compared to
384 seagrasses, Algae contained notably more minerals (about 40 points higher), less cellulose
385 (14-20 points lower) and had the lowest C/N ratio.

386
387 Water content (refer to **Fig. S3, Table S5**) was similar in *S. filiforme* and *H. stipulacea*
388 (around 90%). It was lower in *T. testudinum* and Algae (around 87 and 75% FW,
389 respectively). Since the hydrated samples are more representative of the food actually
390 ingested by green turtles, results expressed in fresh weight are also given in the
391 Supplementary material (**Fig. S3, Table S5**). For example, despite leaves of *T. testudinum* and
392 *S. filiforme* had a similar energy content when expressed on a dry weight basis, it was 1.4
393 times higher in the former than in the latter when expressed on a fresh weight basis because of
394 the difference in water content.

395
396 Regarding digestibility (refer to **Fig. 3, Table S5**), *T. testudinum* and *S. filiforme* showed
397 similar values for this parameter ($52.9 \pm 1.3\%$ DW for *T. testudinum* and $56.5 \pm 2.5\%$ DW for
398 *S. filiforme*). However, *H. stipulacea* appeared to be more digestible than both native
399 seagrasses (approx. 20 points higher), and digestibility was similar in leaves and rhizomes of
400 the invasive species ($74.3 \pm 0.7\%$ DW for leaves and $72.2 \pm 1.4\%$ DW for rhizomes). Algae
401 had an intermediate digestibility ($69.9 \pm 6.2\%$ DW) with values between those of native and
402 invasive seagrasses.

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404

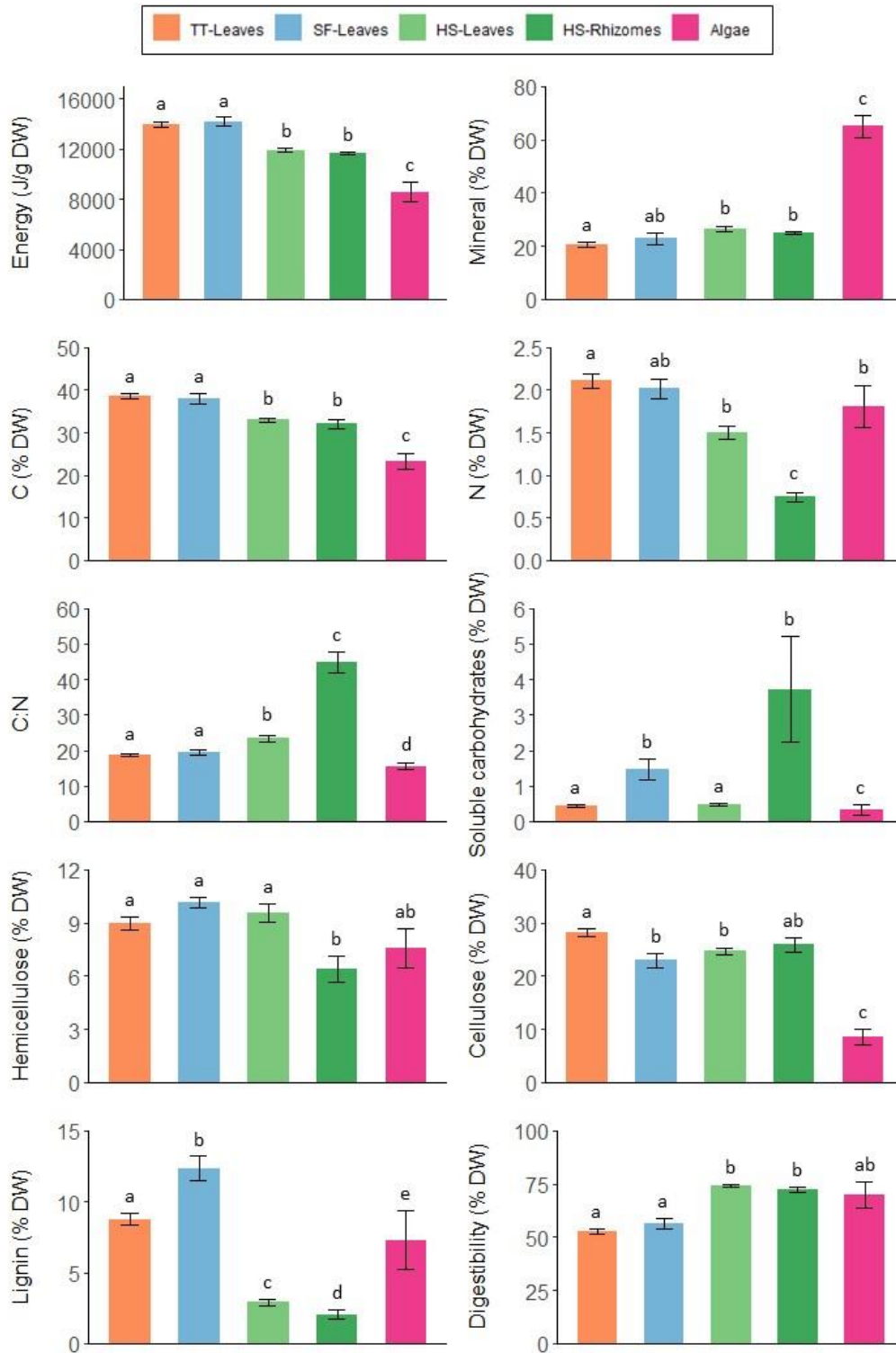


Fig. 3. Comparison of nutritional composition (mean \pm SE) expressed on a dry weight (DW) basis, of seagrasses (TT: *T. testudinum*; SF: *S. filiforme*, HS: *H. stipulacea*) and Algae. Refer to Table S5 for exact values and sample sizes. Kruskal-Wallis tests evidenced significant differences in each case ($p < 0.001$). Groups with the same letter on top are not significantly different (based on multiple pairwise-comparisons). Colours, 1.5 or 2-column fitting image

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4 Discussion

4.1 Resource selection in immature green turtles

Foraging habitat selection analyses showed that immature green turtles favoured habitats with at least one native species. Moreover, they preferentially selected *T. testudinum* in their diet when available (**Fig. 2B**). These results are consistent with other studies conducted in the Caribbean. Christianen et al. (2018) showed that green turtles selected *T. testudinum* when presented with two other species (*S. filiforme* and *H. stipulacea*) in Bonaire. They also highlighted a change in grazing locations to shallower areas where native seagrass species were still predominant. In Malendure Bay (Guadeloupe), where *T. testudinum* was rarely found in close proximity to foraging green turtles, Whitman et al. (2019) highlighted turtle preference for *S. filiforme* in multispecies seagrass beds. Thus, in these studies, green turtles were still consuming native species about six years after the introduction of *H. stipulacea* and were mainly avoiding the invasive species. Nevertheless, similar to Christianen et al. (2018) and Whitman et al. (2019), we found high inter-individual variability in diet composition, with *H. stipulacea* accounting for 0-100% of the diet, regardless of native plant availability. In multispecies sites, we showed positive selection for *H. stipulacea* in 24% of individuals monitored. However, for the first time, we investigated green turtle food selection at a site where *H. stipulacea* completely replaced native seagrass species. At Anse Noire and Anse Dufour, we observed that the majority of green turtles fed on *H. stipulacea* while some ate Algae (**Fig. 2A**). In addition, a previous study highlighted the high fidelity of green turtles to their capture site in Martinique (Siegwalt et al., 2020). This suggests that individuals observed at Anse Noire and Anse Dufour may spend several years growing in these bays and do not change bays to feed. Therefore, this population appears acclimatised to environmental change and has integrated *H. stipulacea* into its diet.

Selectivity for food resources may be influenced by several factors, such as forage relative availability (López-Mendilaharsu et al., 2008), nitrogen and phosphorus content (Bjørndal, 1980), and energy content (Arthur and Balazs, 2008). On a dry basis, compared to native seagrasses, *H. stipulacea* had globally lower energy, C, and N content (**Fig. 3**). Similarly Christianen et al. (2018) found lower N content and higher C:N ratio for *H. stipulacea* compared to *T. testudinum* and *S. filiforme*. It is likely that the strong preference for native

444 seagrasses, and in particular for *T. testudinum*, could be related to their nutritional benefits.
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2 445 However, Whitman et al. (2019) found no significant differences in these nutritional
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4 446 parameters between *H. stipulacea* and *S. filiforme* at Malendure Bay. To explain the similar
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6 447 nutritional composition of both plants and their high C and N values, Whitman et al. (2019)
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8 448 hypothesised that their feeding area was certainly a very nutrient rich environment. We also
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10 449 expressed the nutritional composition on a fresh basis as it is more representative of the food
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12 450 actually ingested by turtles, and consequently of their foraging effort to meet energetic needs.
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14 451 On this basis, *T. testudinum* had higher energy and N content than the other seagrasses (**Table**
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16 452 **S5, Fig. S3**), which could explain the frequent positive selection for this species, especially in
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18 453 this context of growing juvenile turtles. Nevertheless, at Grande Anse and Anse du
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20 454 Bourg/Anse Chaudière, we observed that some individuals fed on *H. stipulacea* (**Fig. 2B**),
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22 455 while native species were available (**Fig. 1**). If these results can be extrapolated over the long
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24 456 term, this could indicate an advantage to feeding on *H. stipulacea*, first, in terms of energy
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26 457 balance (perhaps related to higher digestibility; or higher ingestion rate, at the expense of
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28 458 longer feeding time), and second, in terms of intraspecific competition (which could be
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30 459 lowered since *H. stipulacea* is abundant in the environment). Moreover, at Anse Noire/Anse
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32 460 Dufour where native seagrasses were no longer present, the majority of the monitored green
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34 461 turtles foraged exclusively on *H. stipulacea* (**Fig. 2A**). Nevertheless, due to its lower
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36 462 nutritional value, the consequences of the massive inclusion of *H. stipulacea* in the diet of
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38 463 green turtles on their growth and survival need to be assessed.

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42 465 Fibre content and digestibility are two other important parameters of plant nutritional value
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44 466 that can influence food selectivity of sea turtles (Bjorndal, 1980; Brand-Gardner et al., 1999).
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46 467 Interestingly, we found that *H. stipulacea* was more digestible and had up to 6 times less
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48 468 lignin content than the native species (**Fig. 3, Table S5**). For *T. testudinum* leaves, we found
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50 469 an average digestibility (53% DW) higher than fermentability values previously reported (25-
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52 470 34% DW, Moran and Bjorndal, 2007) (the enzymes we selected being potentially more stable
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54 471 than the rumen juice formerly used for this type of analysis), but consistent with Bjorndal's
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56 472 (1980) apparent organic matter digestibility values. Regarding fibre content, Moran and
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58 473 Bjorndal (2007) found somewhat lower results for *T. testudinum* blades (ligno-cellulose
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60 474 fraction: 25-31% DW), with lower lignin contents than in our study (about 2% DW in their
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62 475 study and 9% DW in ours), while Bjorndal (1980) and Vicente et al. (1980) lignin values
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64 476 accord with ours. According to Moran and Bjorndal (2007), the variability in lignin content
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66 477 may be due to the current flow characteristics of each study site. Yet, while lignin has a higher

478 energy density than cellulose and hemicellulose (between 21 and 27 kJ/g DW, compared to 17
479 kJ/g DW for cellulose and hemicellulose, see Agrawal et al., 2014; Frei, 2013; Murphy and
480 Masters, 1978; Welker et al., 2015), the low digestibility that lignin confers on food (due to its
481 own low digestibility and because it prevents digestive enzymes from breaking down
482 cellulose and hemicellulose completely by complexing with these fibres) precludes it from
483 being an efficient nutrient (Moore and Jung, 2001; Van Soest, 1982). Therefore, although *H.*
484 *stipulacea* showed lower energy content than the native species through nutritional analysis
485 (**Fig. 3**), its low lignin content and higher digestibility calls into question the measured
486 energetic advantage of native plants over the exotic one. Nevertheless, the digestibility we
487 measured *in vitro* cannot account for all chemical reactions and biological interactions
488 involved in digestion at the whole-body level. In particular, the gut microbiome of green
489 turtles evolves during their growth and notably at their recruitment to the neritic zone with the
490 acquisition of bacteria involved in plant digestion (Campos et al., 2018; Price et al., 2017).
491 Bjorndal (1980) showed that *in vivo* digestibility of hemicellulose and protein increased
492 significantly with turtle's body size, while Campos et al. (2018) highlighted an increase in the
493 taxonomic richness of the gut microbiome as green turtle grow. *H. stipulacea* may therefore
494 be of particular nutritional value for small turtles that have not yet fully adapted their gut
495 microflora to herbivory, but this may diminish for larger individuals. Further research on
496 overall digestibility is needed to accurately test for a difference between native and invasive
497 species considering the body size of individuals.

498
499 Les Anses d'Arlet are considered a critical foraging and developmental habitat for immature
500 green turtles, which spend many years growing until they reach sexual maturity and
501 eventually migrate (Bonola et al., 2019; Chambault et al., 2018; Siegwalt et al., 2020). Due to
502 the lower nutritional value of *H. stipulacea*, inclusion of this seagrass in turtle's diet may have
503 important consequences for the population. Moreover, nitrogen and energy contents of plants
504 have been linked to turtle growth rate and reproductive parameters (Bjorndal, 1980; Wood
505 and Wood, 1981). In Bermuda, Gulick et al. (2021) observed a decline in body mass of
506 growing green turtles related to a decrease in available resources, while Bjorndal et al. (2017)
507 showed a decline in growth rates in three sea turtle species throughout the West Atlantic,
508 linked to an ecological regime shift and probably to an associated decrease in quantity and
509 quality of food resources. Here, we showed that immature green turtles preferentially foraged
510 on the native species when possible, but in bays fully invaded by *H. stipulacea* as in Anse
511 Noire/Anse Dufour, green turtles foraged actually on *H. stipulacea* (**Fig 2A**). Therefore, for

512 this population, we can expect that a shift from native plants to lower nitrogen and energy
1 513 plants may reduce turtle's growth rate and delay their sexual maturity. In addition, a previous
2 514 study showed that residence time in Anse Noire was lower than in Grande Anse (Siegwalt et
3 515 al., 2020). It has been showed that developmental migrations may be triggered by nutrient
4 516 limitation and/or reduced growth rates (Bjorndal et al., 2000, 2019; Chaloupka and Limpus,
5 517 2001). Thus, we can hypothesized that lower nutrient quality of *H. stipulacea* and potentially
6 518 sub-optimal growth experienced by immature green turtles in Anse Noire/Anse Dufour may
7 519 force them to move to other more profitable foraging areas. The capture-mark-recapture
8 520 studies currently conducted in Martinique will allow long-term comparison of growth rate
9 521 between these multi- and monospecific bays.
10 522

11 523 The rapid expansion of *H. stipulacea* in Les Anses d'Arlet have modified the foraging ground
12 524 of the immature green turtles, which have thus adopted different energetic strategies. Indeed,
13 525 at Grande Anse, we found a high inter-individual variability in diet composition, with
14 526 immature green turtles that preferentially foraged for the native species, but also individuals
15 527 that fed mainly on *H. stipulacea* while native species were available (**Fig. 2B**). It would be
16 528 interesting to assess whether these individuals feed on *H. stipulacea* occasionally or
17 529 permanently. Indeed, forager fitness and diet breadth may be affected by increased
18 530 intraspecific competition for food resources (Svanbäck and Bolnick, 2005). While most turtles
19 531 selected native plants, whose coverage represented <20% in both multispecific sites (**Fig. 1,**
20 532 **Fig. 2B**), individuals integrating *H. stipulacea* in their diet or specialising on it may benefit
21 533 from a lower inter-individual competition for resources. Finally, we can also expect changes
22 534 in green turtle behaviour when integrating the invasive species into their diet. Thus, turtles
23 535 may modify their activity budget to adapt to lower energy acquisition by decreasing the time
24 536 allocated to energy-demanding activities and increasing rest time, or alternatively by
25 537 increasing the proportion of time devoted to feeding, and thus, the amount of material
26 538 consumed to meet energy requirements. It would be interesting to compare the activity budget
27 539 of individuals between Grande Anse and Anse Noire/Anse Dufour to identify potential
28 540 different energetic strategies used by green turtles to adapt to changes in their environment.
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30 542 In this study, we used bite counts from direct observations for estimating the diet composition
31 543 and the food selection of immature green turtles at the individual level. Direct observation has
32 544 the advantage of being non-invasive and causing little disturbance, but it is still difficult to
33 545 monitor free-ranging green turtles over the long term as they move quickly and change
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546 environments often. This leads to observation times depending on the goodwill of the green
1 547 turtles. In this study, we performed behavioural observations during ca. 100 min per follow,
2 548 and recorded feeding behaviours over an average of 52 min (with standard deviation of 55
3 549 min, **Table S2**). Thus, this large variability in the recorded duration of feeding activity may
4 550 result in a bias in diet composition estimation at population level. In addition to the difficulty
5 551 of monitoring sea turtles, this variability is also due to a high inter-individual variability in the
6 552 expressed behaviours, with some individuals feeding very little and others feeding during
7 553 most of the day (Rice et al., 2000, pers. obs.). In addition, the direct observations represented
8 554 a short period of the turtle's daily time and we cannot exclude that other items were ingested
9 555 during the rest of the day. Therefore, these limitations highlight the complexity of studying
10 556 green turtle foraging strategy while direct observation remains an essential first step in
11 557 identifying the inter-individual variability in diet composition and feeding strategies with
12 558 minimal disturbance. Thus, although the total time used in our study for the assessment of the
13 559 diet (ca. 30 h) was quite high compared to the literature (e.g. ca. 8 h in Whitman et al., 2019),
14 560 further research is needed to improve the precision of these results. Oesophageal content
15 561 analysis (see in Gulick et al., 2021), is another complementary method that could be
16 562 implemented to obtain the precise amount of food ingested. However, this method is much
17 563 more invasive than direct observation and requires capture of the turtles and oesophageal
18 564 lavage. Stomach and oesophageal contents can also be collected during necropsy, but the
19 565 body of the dead turtle must not be decomposed, which is rarely the case in Martinique.
20 566 Finally, the development of on-board cameras with an increasing autonomy represents a
21 567 promising new method to follow individuals over a longer period of time and thus to go
22 568 further in the study of feeding strategy of immature green turtles.

4.2 Expansion of *H. stipulacea* in Martinique and conservation implications

569 Benthic composition maps highlighted the dominance of *H. stipulacea* in Les Anses d'Arlet,
570 with a cover >55% in Grande Anse and Anse du Bourg/Anse Chaudière in 2018, while it was
571 the only remaining seagrass species in Anse Noire and Anse Dufour. *H. stipulacea* was first
572 recorded in Martinique in 2006 and spread from North to South (Ortolé, 2012). Its exact time
573 of arrival in Les Anses d'Arlet is unclear, but its presence was reported in Anse Noire in 2011
574 (DEAL Guadeloupe et Martinique, 2011). This fast expansion in Martinique has been
575 observed on other neighbouring islands and is characteristic of the Caribbean (Willette et al.,
576 2014; Winters et al., 2020).

579 The introduction and expansion of *H. stipulacea* appears primarily due to anthropogenic
580 factors. While pleasure yachts probably carried *H. stipulacea* from the Mediterranean to the
581 Caribbean, inter-island vessel transit and fishing activities also contributed to its expansion
582 throughout the region by creating vacant spaces for it, and by generating and dispersing
583 fragments (Ruiz and Ballantine, 2004; Willette et al., 2014; Willette and Ambrose, 2012).
584 Some of our study sites where *H. stipulacea* was found in monospecific beds in 2018 (**Fig. 1**)
585 seem to have suffered from bottom-scraping anchors and chains. While the Southern area of
586 Grande Anse is a past authorised anchorage zone (Sermage, 2006), Anse Chaudière still
587 experiences heavy boat traffic (pers. obs.). Indeed, *H. stipulacea* has high ability to colonise
588 bare sand, especially where conditions are not favourable for native species (Winters et al.,
589 2020). In sites with multispecific seagrass meadows, its expansion may have been more
590 difficult and some areas remain dominated by native species (**Fig. 1**). Areas where native
591 meadows were certainly dense and less subject to mechanical disturbances (Sermage, 2006)
592 have been preserved from total invasion by *H. stipulacea*.

593
594 Today, it seems urgent to limit the pressures of anthropic origin on the native meadows in
595 order to slow down the expansion of *H. stipulacea*. Thus, prohibiting anchorages and setting
596 up a defined mooring zone (with multiple floating buoys connected to cement blocks by
597 ropes) outside the zones that include native meadows could be a solution. An exhaustive
598 survey at the scale of Martinique, both on the progression of *H. stipulacea* and on the factors
599 likely to favour its expansion (absence of anchorage area, high boat traffic, pollution of
600 anthropic origin) should be conducted annually to take preventive and curative measures to
601 limit its development.

602
603 Furthermore, the effects of climate change on *H. stipulacea* expansion are still very little
604 studied. A recent study showed different responses to sea warming among populations
605 (Nguyen et al., 2020). Increasing sea temperature would reduce *H. stipulacea* meadows in its
606 native regions while facilitating its spread in the Mediterranean Sea, a region invaded 150
607 years ago. It is therefore difficult to predict the future range expansion of *H. stipulacea* in the
608 Caribbean. Species distribution models could help predict the potential range expansion of the
609 invasive species but require accurate data on the current distribution and environment.
610 Consequently, rigorous monitoring of *H. stipulacea*, not only in Martinique but also in the
611 whole Caribbean, should be implemented. Improving knowledge of seagrass is an essential
612 prerequisite to ensure their preservation. This may facilitate a proper growth and adaptation of

613 immature green turtles to changing environments and promote the protection of this
1 614 threatened species. In turn, this will benefit the entire seagrass ecosystem.

3 615

6 616 **5 Conclusion**

8 617 This study provides a precise assessment of the cover of *H. stipulacea* in an area of South-
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10 618 West Martinique, which is a hotspot of immature green turtles. For the first time, their diet
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12 619 was investigated at sites where native plants were still present, but also at sites where the
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14 620 invasive species had completely replaced native seagrasses. We show that, although green
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16 621 turtles preferentially chose native seagrasses when available, they included *H. stipulacea* in
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18 622 their diet at sites completely or partially covered by this species. We also show that *H.*
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20 623 *stipulacea* was less energetic but more digestible than native plants. In this context, new
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22 624 questions about the impacts of this dietary change on the growth and survival of immature
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24 625 green turtles may be raised. Our study highlights the importance of in-depth dietary analysis
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26 626 (composition, energetics, digestibility, etc.) in ecosystems where resource availability may
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28 627 vary, to gain a broader picture of the causes and consequences of food choices for endangered
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30 628 species like the green turtle.

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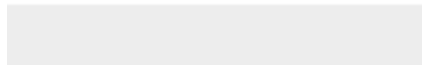
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Food selection and habitat use patterns of immature green turtles (*Chelonia mydas*) on Caribbean seagrass beds dominated by the alien species *Halophila stipulacea*

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