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1 **Distribution and abundance of the invasive seagrass *Halophila***
2 ***stipulacea* and associated benthic macrofauna in Carriacou,**
3 **Grenadines, Eastern Caribbean**

4
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13 **ABSTRACT**

14 The invasive seagrass *Halophila stipulacea* has spread throughout the eastern
15 Caribbean since it was first recorded in Grenada in 2002. We quantified the
16 distribution and abundance of *H. stipulacea*, and its associated macroinvertebrate
17 fauna, in sampling stations and transects around the island of Carriacou (a nearby
18 dependency of Grenada) in early 2016. *Halophila stipulacea* occurred in extensive
19 monospecific stands (average bottom cover, 62 %), or smaller mixed stands with
20 native seagrass (*Thalassia testudinum*, *Syringodium filiforme*, *Halodule wrightii*), at 1
21 – 5 m depth in large bays along the leeward (west) coast. It was sparsely distributed on
22 the more wave-exposed east and south coasts, usually in mixed patches with native

23 seagrass. In leeward bays, *H. stipulacea* has largely replaced the native seagrass *H.*
24 *wrightii*, providing a novel biogenic habitat for various filter-feeding invertebrates
25 living within the turf-like leaf canopy (e.g., sponges, ascidians, bivalves, ophiuroids),
26 and sea urchins (mainly *Tripneustes ventricosus*) and a microphagous sea star
27 (*Oreaster reticulatus*) that graze upon it. Populations of the sea star consisted mainly
28 of juveniles indicating the seagrass may serve as a nursery habitat for this endangered
29 species. The spread of *H. stipulacea* along the leeward coast of Carriacou in recent
30 years represents a community-level shift in the shallow subtidal zone, with attendant
31 changes in habitat structure, species composition, and trophic interactions.

32

33 KEYWORDS: Caribbean; Carriacou; *Halophila stipulacea*; invasive species; seagrass;
34 species distribution

35

36 **1. Introduction**

37 Among marine macrophytes, the global spread of invasive seaweeds and their
38 negative impacts on native seaweeds and benthic communities on temperate and
39 tropical coasts are well documented (reviewed by Iderjit et al., 2006; Williams and
40 Smith, 2007). In contrast, only three angiosperms have undergone transoceanic range
41 expansions to become invasive well beyond their native range: 1) *Zostera japonica*,
42 from the temperate and subtropical western Pacific to the eastern Pacific (Harrison
43 and Bigley, 1982); 2) *Halophila stipulacea*, from the Indian Ocean and Red Sea to the
44 Mediterranean via the Suez Canal (Lipkin, 1975) and then across the Atlantic to the

45 Caribbean (Ruiz and Ballantine, 2004); and 3) *H. ovalis*, from the tropical Indo-
46 Pacific to Antigua in the Caribbean (Short et al., 2010). The invasion of *Zostera*
47 *japonica* of estuarine habitats on the northwest coast of North America resulted in the
48 decline and localized displacement of the native congener *Z. marina* (Posey, 1988; Jun
49 Bando, 2006). The gradual spread of *H. stipulacea* throughout the Mediterranean has
50 been thoroughly recorded, and various studies have identified life-history and
51 physiological traits that account for its invasion success in the region (Williams and
52 Smith, 2007). However, the impact of *H. stipulacea* on the native ecosystem remains
53 equivocal (Di Martino et al., 2006, Williams, 2007).

54 In the tropical Atlantic, *H. stipulacea* was first recorded in Grenada in 2002 (Ruiz
55 and Ballantine, 2004), and then in Martinique, Dominica and St Lucia between 2006
56 and 2008 (Willette and Ambrose, 2009; Maréchal et al., 2103). In these locations it
57 forms monospecific stands or mixes with native seagrass (*Thalassia testudinum* and
58 *Syringodium filiforme*) along bed margins. Since then it has been reported widely
59 throughout the eastern Caribbean from Venezuela in the south to St. Maarten and St.
60 John in the north (Willette et al., 2014; van Tuseenbroek et al., 2016; Vera et al.,
61 2014). The introduction and rapid spread of *H. stipulacea* in the Caribbean has been
62 attributed to the transport of plant fragments via yachts (Ruiz and Ballantine, 2004;
63 Vera et al., 2014; Willette et al., 2014). Only sterile or male plants have been found in
64 the region (Vera et al., 2014; Willette et al., 2014).

65 *Halophila stipulacea* is considered invasive in the Caribbean, in view of its rapid
66 expansion and potential to form dense mats that exclude native seagrass (Willette and

67 Ambrose, 2009; 2012; Willette et al. 2014). However, information on the rate of
68 spread of monospecific beds of *H. stipulacea*, and its effect on native seagrass and
69 associated fish and epifaunal invertebrates, is largely restricted to studies in Dominica
70 (Willette and Ambrose, 2009; 2012; Steiner and Willette, 2015). There is evidence
71 that dense mats of *H. stipulacea* increase the nutrient content of sediments and tissues
72 of co-occurring native seagrass (van Tuseenbroek et al., 2016), and increase the
73 abundance of small invertebrate epifauna and the size of associated fish (Willette and
74 Ambrose, 2012). To better assess the potential ecological impact of the recent and
75 rapid expansion of *H. stipulacea* within the Caribbean at large, and the urgency or
76 relevance of conservation or remediation measures to combat the spread of this
77 species, a broader base of research is needed (Rogers et al., 2014).

78 During a long-term study of change in seagrass community composition in relation
79 to changing local and climatic impacts in Carriacou (Grenadines, Grenada) and
80 Barbados, we encountered extensive monospecific beds of *H. stipulacea* along the
81 leeward (west) coast of Carriacou in January 2016. We opportunistically initiated a
82 targeted sampling program to quantify the distribution and abundance of *H. stipulacea*
83 and its associated macroinvertebrate fauna along this coast. We combined this with
84 our island-wide sampling of seagrass beds (part of our broader study) to more fully
85 document the distribution of the invasive seagrass at Carriacou. Although Grenada is
86 believed to be an epicenter of the Caribbean invasion (Ruiz and Ballantine, 2004), and
87 there are reports of *H. stipulacea* in the St. Vincent and the St. Vincent Grenadines,

88 this species has only recently been documented at a single site (Sandy Island Marine
89 Park) in Carriacou (Willette et al., 2014).

90

91 **2. Methods**

92 *2.1. Sampling in leeward bays*

93 Preliminary surveys along the leeward (west) coast of Carriacou revealed dense
94 monospecific beds of *Halophila stipulacea* at Hillsborough Bay, L'Esterre Bay, Tyrell
95 Bay, and Craigston Bay in January/February 2016 (Fig. 1). We used satellite images
96 (Google Earth, © 2015 Google, Inc.), in which seagrass beds appeared as darker bands
97 and patches, to develop a systematic sampling design to quantify the distribution of *H.*
98 *stipulacea* and native seagrasses within these large bays (Table S1). Belt transects
99 were conducted by snorkeling using a hand-held video camera (GoPro Hero4, setting:
100 Video 7.2K/24/Medium) with a plumb line weighted with a 5.0-cm long steel pipe to
101 provide scale and maintain the camera at a fixed height off bottom (up to 2.5 m). At
102 greater depths (up to 5 m at Craigston Bay) a rectangular white plastic slate (8 x 10
103 cm) was placed on bottom for scale. Transect length was estimated from elapsed time
104 on the video record using the mean swim rate of the camera operator (28.2 m min⁻¹ m,
105 n = 4 replicate 10-m long trials, SE = 0.3 m min⁻¹). Transect width was determined
106 from the scaling element in the video record. All video transects (including calibration
107 runs) were conducted under calm sea conditions without noticeable current or wind
108 forces.

109 Transects extended both alongshore and offshore to measure the percentage cover
110 of *H. stipulacea* and native seagrass species (*T. testudinum*, *S. filiforme*) and the
111 density of echinoderm macrograzers (the sea star *Oreaster reticulatus* and sea urchins
112 *Tripneustes ventricosus*, *Diadema antillarum*, and *Lytechinus variegatus*) (Fig. 1,
113 Table S1). Paired alongshore transects, parallel to each other and separated by 10 – 20
114 m, spanned the shallow margin of seagrass beds at ~ 2 m depth (4 – 5 m at Craigston
115 Bay) and followed that margin or depth contour as the snorkeler maintained visual
116 contact with the coastline. To more broadly sample the offshore extent of dense beds
117 of *H. stipulacea* encountered in alongshore transects, 3 – 5 offshore transects, running
118 in parallel and separated by ~ 10 m, extended from the shallow margin of the bed of
119 *H. stipulacea* at Hillsborough Bay and Craigston Bay to the deep margin or limit of
120 visual resolution from the surface (up to ~ 5 m depth).

121 Video data were analyzed in iMovie (version 9.04, Apple, Cupertino, California,
122 USA) in real-time. Bottom type (sand, rock, *H. stipulacea*, *T. testudinum*, and mixed
123 stands of *H. stipulacea* and *T. testudinum*), sea urchin count (number of *T.*
124 *ventricosus*, *L. variegatus* or *D. antillarum* per frame), and frame width (estimated by
125 overlaying a grid on the video and measuring the width of the scaling element in
126 pixels) were recorded in an Excel macro that was synchronized with the video time.
127 The macro program tabulated records every 1 s. We subsampled these records at 8-s
128 intervals to avoid frame overlap. Frames with more than one bottom type were
129 classified according to the dominant bottom type (> 75 % of frame) or as mixed stands
130 of *H. stipulacea* and *T. testudinum*. We excluded frames where bottom type, sea

131 urchin counts or the width of the scaling element could not be reliably measured due
132 to video quality (< 1 % of all frames).

133 Biomass of *H. stipulacea* was measured in three circular plots (22-cm diameter,
134 0.038 m²) haphazardly placed within dense monospecific beds within areas surveyed
135 by alongshore transects at Hillsborough Bay, L'Esterre Bay and Tyrell Bay, and at
136 Watering Bay on the windward coast (near T4, Fig. 1). Plots were located at 1 – 1.5 m
137 depth and separated by 2 – 3 m. The seagrass “turf” was sheared around the perimeter
138 of the plot, excavated by hand and bagged. Samples were subsequently washed in
139 freshwater and sieved (using a kitchen colander) to remove sediments, then drained
140 and lightly blotted to remove surface water before weighing on a spring-balance. For
141 each site, a haphazard subsample from one plot (~ ¼ of the sample) was manually
142 split into leaf and rhizome, and each component was weighed fresh to estimate the
143 proportion of leaf biomass. Leaf biomass for each sampled plot was estimated from
144 total biomass by multiplying by the proportion of leaf biomass in the subsample.

145 Invertebrate macrofauna in dense monospecific beds of *H. stipulacea* in
146 Hillsborough Bay, L'Esterre Bay and Tyrell Bay were haphazardly sampled by blind
147 toss of 12 quadrats (0.25 m²) within a 5 x 10 m area at 1.5 – 2 m depth. All *H.*
148 *stipulacea* within each quadrat was excavated by hand, and clusters of rhizomes were
149 teased apart and dispersed through water column to reveal associated fauna. Species
150 were counted for each quadrat, photographed *in situ*, and collected for subsequent
151 identification. *O. reticulatus* was sampled on encounter in a dense bed of *H.*

152 *stipulacea* at 2 – 3 m depth in Hillsborough Bay to record feeding activity and body
153 size (radius along the ambulacrum of a single arm, mm).

154

155 2.2 Sampling at stations and line transects around Carriacou

156 To expand our survey of *Halophila stipulacea* across the entire island, 17 stations
157 were sampled in January/February 2016 (Fig. 1, Table S2). One corner of a 10 x 10 m
158 plot was staked, and 12 sampling points were randomly selected on a grid of 2 x 2 m
159 squares. At each point, presence or absence of epibenthic faunal and floral species
160 were recorded within a 0.25 m² quadrat, giving frequency data for the documented
161 species (number of quadrats out of 12 in which a species was observed). Seagrass was
162 further sampled by blind toss of a 0.0625 m² quadrat into the area three times, and
163 collecting seagrass within the quadrat after shearing it at substratum level. The
164 seagrass was bagged, subsequently shaken to remove free water, and weighed fresh.

165 During the same period, line transects were sampled at 13 sites around Carriacou
166 (Fig. 1, Table S2). Transects were conducted by swimming perpendicular to shore,
167 maintaining direction by reference to a wrist compass and/or two aligned targets on
168 shore. Distances and depths (relative to Mean Low Water) were measured with the
169 graduated 2-m pole or a depth gauge for depths over 2 m. The presence of different
170 species of seagrass and epifauna was recorded at 10-m intervals, or at shorter intervals
171 where there were abrupt changes in composition.

172

173 3. Results

174 3.1. Distribution and abundance of *H. stipulacea* and native seagrasses

175 *H. stipulacea* occurred primarily in large sheltered bays (Craigston Bay,
176 Hillsborough Bay, L’Esterre Bay, Tyrell Bay) along the leeward west coast of
177 Carriacou (Fig. 1), where it formed dense monospecific turfs (Fig. 2a) at 1 – 5 m
178 depth. These beds of invasive seagrass extended alongshore for 100s of meters in
179 Craigston Bay, Hillsborough Bay, and Tyrell Bay, and offshore from the shallow
180 beach margin for ~ 100 m in Craigston Bay and Hillsborough Bay (Table S1, Fig. S1),
181 often interspersed with small patches (meters to 10s of meters) of *T. testudinum* and
182 forming mixed stands around the edges of these patches (Fig. S1, 2b). In contrast, *T.*
183 *testudinum* was the dominant seagrass in L’Esterre Bay and *H. stipulacea* occurred in
184 smaller patches (10s to 100s of meters) within extensive beds of *T. testudinum* (Fig.
185 S1). *H. stipulacea* generally graded to *T. testudinum* and sand below ~ 5 m depth, the
186 extent of the offshore belt transects in Craigston Bay and Hillsborough Bay. Although
187 this nearshore seagrass zone previously was dominated by *Halodule wrightii* in
188 Hillsborough Bay and L’Esterre Bay (Scheibling, 1980; Scheibling and Metaxas,
189 2000), *H. wrightii* rarely was observed in these bays in 2016, and then only as sparse
190 rhizomes in the sandy zone inshore of *H. stipulacea* at Hillsborough Bay and Tyrell
191 Bay.

192 The relative abundance of different seagrass species and sand patches (within
193 alongshore belt transects) varied significantly among the four leeward sites (Fig. 3a),
194 as indicated by a G-test of independence (Sokal and Rohlf, 2012) ($\chi^2_{13} = 350.9$, $P <$
195 0.001). The cover of dense monospecific beds of *H. stipulacea* in the nearshore

196 seagrass zone ranged from 29 to 90 % (mean, 62 %) across sites, and was greatest at
197 Craigston Bay and Tyrell Bay (Fig. 3a). Monospecific beds *T. testudinum* accounted
198 for most of the bottom cover in Hillsborough Bay (52 %) and L'Esterre Bay (55 %);
199 mixed stands of *H. stipulacea* and *T. testudinum* accounted for 1 – 8 % of cover across
200 sites (Fig. 3a). Monospecific or mixed stands of *H. stipulacea* extended well beyond
201 the bounds of our alongshore transects at each site, and beyond the outer bound of
202 most offshore transects at Craigston Bay and Hillsborough Bay.

203 On the leeward coast, *H. stipulacea* also was recorded in monospecific beds or
204 mixed stands with *T. testudinum* in one (S24) of two stations in Hillsborough Bay
205 (Fig. 1, 4) and in line transects in Hillsborough Bay (T14), L'Esterre Bay (T13) and
206 Tyrell Bay (T12) (Fig. 1, 3b). Across the windward eastern and southern coasts of the
207 Carriacou, *H. stipulacea* was recorded in monospecific beds or mixed stands with *T.*
208 *testudinum* at a station (S7) in Watering Bay (Fig. 1, 4) and in three line transects in
209 Watering Bay (T2, T3, T4) and one in Manchioneal Bay (T10) (Fig.1, 3b). The cover
210 of *H. stipulacea* in monospecific beds, or in mixed stands with *T. testudinum* and/or
211 *H. wrightti*, in transects on the windward coast (Fig. 1) ranged from 1 to 74 % across
212 the sites where it occurred (Fig. 3b). Seagrass beds in these areas usually were
213 dominated by monospecific or mixed stands of *T. testudinum* and/or *S. filiforme*. Data
214 for stations gave similar results. Frequency of occurrence of native seagrass (*T.*
215 *testudinum* or *S. filiforme*) was 100 % (based on the percentage of quadrats with the
216 species present), except at the station in Hillsborough Bay on the leeward coast, where
217 *H. stipulacea* was 100 % (Fig. 4b).

218 Mean leaf biomass (fresh weight) in dense beds of *H. stipulacea* in the leeward
219 bays (Hillsborough Bay, L'Esterre Bay, Tyrell Bay) and in a nearshore patch at
220 Watering Bay (near S7) ranged from 1516 to 2714 g m² (Table 1), but did not differ
221 significantly among sites (ANOVA: F_{3,8} = 3.55, P = 0.068). Raw data met assumptions
222 of homoscedasticity (Levene's test: F = 0.505, P = 0.689) and normality (Shapiro's
223 test: W = 0.909, P = 0.206). Leaf biomass of *H. stipulacea* recorded in two stations
224 (S7 and S24) where it was present (53 and 83 g m⁻² respectively) was generally much
225 lower than that of the native seagrass at all other stations (*Thalassia testudinum*: 72 –
226 1877 g m⁻², *Syringodium filiforme*: 0 – 2693 g m⁻²) except S24 in Hillsborough Bay
227 (*T. testudinum*: 59 g m⁻²) (Fig. 4a).

228

229 3.2. Macrofaunal invertebrates associated with dense turfs of *H. stipulacea*

230 A variety of sessile or sedentary filter-feeder macroinvertebrates occurred within
231 the dense turf of *H. stipulacea* in quadrat samples in three leeward bays (Hillsborough
232 Bay, L'Esterre Bay, Tyrell Bay), but at relatively low densities (mean density per
233 species: 0.3 – 4.2 individuals m⁻²) (Table 2). These included sponges (*Amphimedon*
234 *erina*, *Tedania ignis*) and both compound (*Botrylloides nigrum*) and solitary ascidians
235 (*Microcosmus helleri*, *Moluga* sp.) attached to the leaves and rhizomes, and brittle
236 stars (*Ophioderma appressum*) and bivalves (pen shell *Pinna carnea*, eared ark clam
237 *Anadara notabilis*) living within or just below the rhizome mat (Table 2). Cryptically
238 colored juveniles of the microphagous sea star *O. reticulatus* (3 – 6 cm, arm radius)
239 also were found nestled deep into the turf. The herbivorous sea urchin *Tripneustes*

240 *ventricosus* was abundant on the surface of the turf at all three sites (see section 3.3),
241 but was only recorded in quadrats in Tyrell Bay. Also common at Tyrell Bay were the
242 long-spined porcupinefish *Diodon holocanthus*, a nocturnal predator of hard-shelled
243 invertebrates that burrowed into the dense turf of *H. stipulacea*, and goldspotted eel
244 (*Myrichthys ocellatus*).

245

246 3.3. Echinoderm grazers on *H. stipulacea* and native seagrass

247 The sea urchin *T. ventricosus* was common on seagrass beds at all sites in the
248 leeward bays of Carriacou, with mean densities in belt transects (alongshore and
249 offshore, pooled across sites) ranging from 1.0 – 2.4 individuals m⁻² in seagrass
250 habitats (Fig. 5a). Most were adults, but juveniles (< 5 cm horizontal test diameter)
251 occasionally were observed on beds of *H. stipulacea*. The sea urchins *D. antillarum*
252 and *L. variegatus* were an order of magnitude less abundant in these seagrass beds
253 (mean density < 0.1 individual m⁻²); *D. antillarum* was more abundant on sand patches
254 (mainly in Hillsborough Bay) where it reached a mean density (across sites) of 0.8
255 individuals m⁻² (Fig. 5a). *T. ventricosus* also was recorded in 8 out of 17 of stations
256 along the coast of Carriacou. The mean density of *T. ventricosus* across all stations
257 (measured from counts pooled over 12 quadrats per station) was 0.7 individuals m⁻².

258 Chi-square goodness-of-fit tests were used to compare observed distributions of sea
259 urchin species in different habitats (monospecific beds of *H. stipulacea* or *T.*
260 *testudinum*, mixed stands of both species, sand) with those expected by a random
261 distribution (Fig. 5b), for which the number of individuals is proportional to the

262 relative cover of a habitat type (sea urchin counts and the number of frames of each
263 habitat type were concatenated for alongshore and offshore belt transects for each
264 site). The abundance of *T. ventricosus* in different habitat types was not proportional
265 to bottom cover within the survey areas: the sea urchin was more abundant on *T.*
266 *testudinum* and less abundant on *H. stipulacea* than expected by random distribution
267 ($\chi^2_3 = 117$, $P < 0.001$). *D. antillarum* also was not randomly distributed across habitat
268 types and was disproportionately more abundant on sand and less abundant on *T.*
269 *testudinum* ($\chi^2_3 = 41.8$, $P < 0.001$). *L. variegatus* did not show a significant
270 association with a particular habitat type ($\chi^2_3 = 3.2$, $P = 0.348$).

271 The sea star *O. reticulatus* occurred at relatively low density (mean < 0.5
272 individuals 10 m^2) on seagrass beds at all sites in the leeward bays (Craigston Bay,
273 Hillsborough Bay, L'Esterre Bay, Tyrell Bay). The abundance of *O. reticulatus* was
274 proportional to the areal extent of the respective habitat types (seagrass and sand),
275 consistent with expectations of random distribution ($\chi^2_3 = 7.1$, $P = 0.067$) (Fig. 5b).
276 The mean (\pm SD) radius of 56 individuals was $11.1 (\pm 3.1)$ cm; 32 of these (57 %)
277 were < 12 cm, the typical size at reproductive maturity of *O. reticulatus* (Scheibling,
278 1982a). The smallest individuals in this sample (6.0 – 7.9 cm) displayed the cryptic
279 coloration pattern (Fig. 2b) that characterizes juveniles found in seagrass beds
280 (Scheibling, 1980).

281

282 **4. Discussion**

283 *4.1. Distribution and spread of H. stipulacea in Carriacou*

284 Our study is the first to document the distribution and abundance of *H. stipulacea*
285 in Carriacou. Although the species was first reported in neighboring Grenada in 2002
286 (Ruiz and Ballantine, 2004), and throughout the St. Vincent Grenadines by 2013
287 (Willette et al., 2014), the only previous report from Carriacou was a note on its
288 occurrence at 1 – 4 m depth within a popular day-charter anchorage at Sandy Island on
289 the east coast (Willette et al., 2014). In February 2016, we found *H. stipulacea* in a
290 single patch (7 x 50 m) at 2 – 3 m depth on the leeward side of Sandy Island.

291 Interviews with local fishers indicated that expansion of *H. stipulacea* in the adjacent
292 leeward bays (Tyrell Bay, L’Esterre Bay and Hillsborough Bay) had been rapid over
293 the previous 4 – 5 years.

294 Our island-wide sampling indicated that monospecific beds of *H. stipulacea* were
295 largely restricted to the leeward bays. Along the windward east and south coasts, *H.*
296 *stipulacea* occurred sporadically, usually in mixed stands with native seagrass (*T.*
297 *testudinum*, *S. filiforme*, *H. wrightii*) although dense patches of the invasive seagrass
298 were recorded at Watering Bay and Manchioneal Bay. Our belt transects in the
299 leeward bays indicated that extensive and extremely dense beds of *H. stipulacea*
300 currently dominate the nearshore sandy bottom, particularly in Craigston Bay and
301 Tyrell Bay. The leaf biomass of *H. stipulacea* measured in these stands (1.5 – 2.7 kg
302 m⁻², fresh weight) generally exceeded the total leaf biomass measured in stands of
303 native seagrass in our station samples (0.2 – 1.9 kg m⁻² for 16 stations; 3.4 kg m⁻² for
304 one station). Willette and Ambrose (2009) found no difference in dry leaf biomass

305 (0.09 kg m⁻²) between *H. stipulacea* and *S. filiforme* from monospecific stands in
306 Dominica.

307 The occurrence and rapid expansion of monospecific beds of *H. stipulacea* in
308 Dominica also appears to be largely restricted to leeward west coast (Willette and
309 Ambrose, 2009; Steiner and Willette, 2015). A shallow rhizome layer and delicate
310 unbranched roots may render *H. stipulacea* more vulnerable to dislodgement by wave
311 action compared to *T. testudinum* and *S. filiforme*, and likely determines the shallow
312 depth limit (1 – 3 m) of *H. stipulacea* along wave-protected coasts in Carriacou and
313 Dominica (Steiner and Willette, 2015). However, we found dense stands of *H.*
314 *stipulacea* at depths < 1 m on the south (Manchioneal Bay) and east (Watering Bay)
315 coasts of Carriacou, in nearshore areas protected by fringing or barrier reef complexes.
316 Interestingly, large losses of *H. stipulacea* were informally observed by one us (DP) in
317 February 2017 along on the leeward coast of Carriacou. The extensive beds had been
318 heavily eroded in Hillsborough Bay and L’Esterre Bay, and to a lesser extent in
319 Craigston Bay, apparently from heavy storm activity and large swells over the
320 previous few months and continuing into February that left masses of unattached or
321 partially attached *H. stipulacea*.

322

323 4.2. *Effects of H. stipulacea on native seagrass beds*

324 Dense beds of *H. stipulacea* have effectively replaced those of native *Halodule*
325 *wrightii*, which previously characterized the shallow margin of seagrass meadows
326 along the leeward coast of Carriacou. Our analysis of transects that spanned the

327 shallow margin of seagrass beds in Hillsborough Bay and L'Esterre Bay in 1974
328 (Scheibling, 1980) showed that *H. wrightii* accounted for 65 and 54 % of bottom
329 cover (pooled over transects) at the respective sites (Fig. S2). This species had all but
330 disappeared from these bays in 2016, when cover of *H. stipulacea* in the same areas
331 was 46 and 32 % respectively. Cover of *T. testudinum* (the only other native species)
332 had increased from 33 to 52 % in Hillsborough Bay and from 46 to 55 % in L'Esterre
333 Bay between 1974 and 2016 (Fig. S2, Fig 3a). Overall, there was a near complete
334 cover of seagrass (87 – 98 %) in these nearshore beds at both times (Fig. S2, Fig 3a).

335 *H. stipulacea* also has infiltrated beds of *T. testudinum* and *S. filiforme* around
336 Carriacou to form mixed stands in shallow water (1 – 4 m depth). Similarly, large-
337 scale replacement of *H. wrightii* and *S. filiforme* by *H. stipulacea*, and extirpation of
338 its native congener *H. decipiens*, occurred along the west coast of Dominica between
339 2008 and 2013 (Steiner and Willette, 2015). *H. stipulacea* also replaced *T. testudinum*
340 and colonized nonvegetated substratum in a large protected bay in Bonaire between
341 2011 and 2015 (Smulders et al. 2017). Traits of *H. stipulacea* that may confer a
342 competitive advantage over native species include: broad light tolerance and
343 adaptation to high irradiance (Schwartz and Hellblom, 2002; Sharon et al., 2011),
344 enabling it to inhabit depths ranging from low tide to 50 m (Beer and Waisel, 1981);
345 adaptability to varying sediment quality (Pereg et al., 1994); and rapid vegetative
346 expansion (Duarte, 1991; Willette and Ambrose, 2009). Willette and Ambrose (2012)
347 recorded 92 % survival and lateral expansion rates of 186 % after 12 weeks for 8-cm

348 diameter plugs of *H. stipulacea* transplanted to an adjacent bed of *S. filiforme* in
349 Dominica.

350 Replacement of native seagrass by *H. stipulacea* in the shallow leeward bays of
351 Carriacou may have been facilitated by natural and anthropogenic disturbances that
352 create open space, which can be colonized and rapidly overgrown by drifting
353 fragments of the invasive seagrass with attached roots (Willette and Ambrose, 2012;
354 Smulders et al. 2017). Seasonal increases in wave action or strong storms cause
355 extensive erosion in beds of *H. wrightii* (Scheibing 1980). Stands of *H. stipulacea*
356 may be more resilient to such wave disturbance given their rapid expansion rate
357 (Willette and Ambrose, 2012; Smulders et al. 2017). Increased yachting along this
358 coast also may play a role, as anchor damage creates gaps in seagrass canopies
359 (blowouts) that can take a year or more to close (Patriquin, 1975). The replacement of
360 native seagrass by *H. stipulacea* in Dominica and Bonaire also has been attributed to
361 these kinds of physical disturbances, as well as local trap-fishing practices that
362 disseminate propagules over short distances (Willette and Ambrose, 2012; Smulders et
363 al. 2017).

364

365 4.3. *Effects of H. stipulacea on seagrass-associated invertebrate macrofauna*

366 Given its distinctive morphology and growth form, compared to the dominant
367 native species (*T. testudinum*, *S. filiforme*), *H. stipulacea* presents novel canopy and
368 sub-canopy microhabitats that enhance the structural diversity of seagrass beds and
369 may alter the composition and abundance of associated species (Willette and

370 Ambrose, 2009). The densely packed turf of small leaves and shallow rhizomes of *H.*
371 *stipulacea* forms a complex architecture that accumulates organic-rich sediments and
372 increases nutrient concentrations (van Tussenbroek et al., 2016). Willette and
373 Ambrose (2009) found that small invertebrate epibiota (mainly amphipods and other
374 small crustaceans) were more abundant, and fish that prey on these invertebrates were
375 larger, in beds of *H. stipulacea* compared to *S. filiforme*. We recorded larger sessile or
376 sedentary macroinvertebrates within turfs of *H. stipulacea* (mainly filter-feeders such
377 as sponges, ascidians, bivalves, and brittlestars) that may provide new or additional
378 food sources to seagrass-associated fish predators. This may explain the abundance of
379 long-spined porcupinefish (*Diodon holocanthus*), which prey on hard-shelled
380 invertebrates, in beds of *H. stipulacea* in Tyrell Bay. We also observed southern
381 stingrays (*Dasyatis americana*), which consume similar prey, on beds of *H. stipulacea*
382 in Craigston Bay.

383 Among herbivorous sea urchins commonly found in seagrass beds in the
384 Caribbean, *T. ventricosus* was by far the most abundant in our station and transect
385 samples, occurring mainly in stands of *T. testudinum*. *L. variegatus* rarely was
386 observed and *D. antillarum* typically was associated with patches of sand or coral,
387 although it occasionally occurred in small clusters on *H. stipulacea* (Fig. 2a). These
388 patterns of abundance are consistent with previous records of these sea urchins on
389 native sea grass beds in Carriacou and adjacent Union Island (Chatham Bay) in the
390 Grenadines (Scheibling, 1982b). In the leeward bays, *T. ventricosus* showed a positive
391 association with beds of *T. testudinum*, where the density of the sea urchin (mean: 2.4

392 individuals m⁻²) was more than two times greater than in beds of *H. stipulacea* (Fig.
393 2a). The apparent preference of *T. ventricosus* for beds of *T. testudinum* over those of
394 the invasive seagrass indicates that sea urchin grazing is unlikely to limit the
395 expansion of *H. stipulacea*, and may actually facilitate it by differentially reducing the
396 abundance of its native competitor.

397 The sea star *O. reticulatus* is an omnivorous deposit feeder, consuming microbial
398 films, detrital material and small epiphytic or infaunal species in seagrass beds or on
399 open sand bottoms; it also preys on sponges and sea urchins (mainly *T. ventricosus*),
400 but these are infrequent inclusions to a primarily microphagous diet (Scheibling,
401 1982b). Populations of *O. reticulatus* occurred at low density (mean: 0.33 individuals
402 10 m⁻²) on beds of *H. stipulacea* and *T. testudinum* in our belt transects in the leeward
403 bays of Carriacou. Sea star densities in Hillsborough Bay and L'Esterre Bay were
404 similar to those recorded in beds of *H. wrightii* in these bays in 1974 (0.27 and 0.44
405 individuals 10 m⁻² respectively), when *O. reticulatus* was rare (< 0.03 individuals 10
406 m⁻²) in dense beds of *T. testudinum* (Scheibling, 1980).

407 Beds of *H. stipulacea* appear to provide a favourable new habitat for *O. reticulatus*.
408 Unlike dense beds of *T. testudinum* or *S. filiforme* that impede the foraging
409 movements of *O. reticulatus* (Scheibling, 1980), the sea star moved readily over the
410 dense leaf canopy of *H. stipulacea*, and frequently was observed in its characteristic
411 feeding posture with its disc inflated and cardiac stomach everted (Scheibling, 1982b).
412 The leaves of *H. stipulacea* are covered with small epiphytes and the dense turf
413 accumulates organically rich sediments (van Tussenbroek et al., 2016), as did *H.*

414 *wrightii* in former beds inhabited by the sea star (Scheibling, 1980). Infaunal
415 macroinvertebrates living on and within the canopy of *H. stipulacea* may further
416 enhance the nutritional condition of *O. reticulatus* (Scheibling, 1982b; 2013).

417 Individual size (radius) of *O. reticulatus* on *H. stipulacea* in Hillsborough Bay in
418 2016 (mean: 11 cm) was smaller than that recorded on *H. wrightii* in Hillsborough
419 Bay and L'Esterre Bay in 1974 and 1994 (mean: 14 – 15 cm; Scheibling and Metaxas,
420 2000), reflecting a much higher proportion of juveniles (< 12 cm) in 2016 (57 %) than
421 the previous years (12 – 28 %; Scheibling and Metaxas, 2000). Moreover, the
422 percentage of juveniles in 2016 is an underestimate as it is based on counts of sea stars
423 on the canopy surface and does not include small individuals (< 6 cm) within the leaf
424 canopy. The density of these recent recruits (55.5 individuals 100 m⁻², pooled across
425 three sites) is 1 to 3 orders of magnitude higher than previously recorded for
426 populations of this sea star in any habitat (Scheibling and Metaxas, 2000; 2010). The
427 dense leaf canopy of *H. stipulacea* likely provides a spatial refuge for small and
428 cryptically coloured recruits from predatory fish, similar to dense *T. testudinum*
429 (Scheibling, 1980) or mangrove roots (Scheibling and Metaxas, 2010). Our findings
430 suggest that *H. stipulacea* provides a nursery habitat for populations of this sea star,
431 which has been extirpated or currently is endangered by human activity, throughout its
432 Caribbean range (Scheibling, 2013).

433

434 4.4. *Ecological implications of the invasion of H. stipulacea*

435 The spread of *H. stipulacea* along the leeward coast of Carriacou, spanning 8.5 km
436 (linear alongshore distance across bays), provides a striking example of a shift in
437 seagrass composition in the shallow subtidal zone, with attendant changes in habitat
438 structure and trophic interactions. Continued spread and vegetative growth of the
439 invasive seagrass would result in increased seagrass species diversity and possibly
440 cover, particularly in more-wave protected areas. The greater small-scale structural
441 complexity of the turf-like canopy of *H. stipulacea* presents novel microhabitats for
442 various small epibiotic invertebrates (Willette and Ambrose, 2012), and filter-feeders
443 such as sponges, bivalves and ascidians (this study) that dwell within the leaves or
444 rhizome layer. Dense turfs of *H. stipulacea* accumulate nutrient rich sediments (van
445 Tussenbroek et al., 2016) that enhance nutritional conditions for these invertebrates
446 and larger microphagous feeders such as the sea star *O. reticulatus*. An increase in
447 abundance of small invertebrate prey in beds of *H. stipulacea*, compared to native
448 seagrass, also appears to be associated with larger body size of fish and a trend
449 towards their increased abundance in these beds (Willette and Ambrose, 2012). *H.*
450 *stipulacea* also provides an alternate food source for green turtles *Chelonia mydas*
451 (Becking et al., 2016; Smulders et al. 2017), and a spatial refuge for recruits of *O.*
452 *reticulatus*, which may aid in recovery of endangered populations. Given the rapid
453 expansion of *H. stipulacea* in Carriacou and elsewhere in the Caribbean, this invasive
454 species may have wide-ranging consequences for the structure and functioning of
455 seagrass ecosystems and the services they provide.

456

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462

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561

562 **Table 1.** Mean (\pm SE) biomass (g m^{-2} , fresh weight) of *Halophila stipulacea* at
 563 sampling sites in the leeward bays, Hillsborough Bay (HB), L'Esterre Bay (LB), and
 564 Tyrell Bay (TB), and in Watering Bay (WB) on the windward coast of Carriacou.
 565 Biomass data are for 3 circular plots (380 cm^2) at each site.

566

Site	Total biomass	Prop. leaf	Leaf biomass
HB	2419 ± 150	0.63	1516 ± 94
TB	4593 ± 281	0.59	2714 ± 166
LB	4164 ± 88	0.51	2137 ± 454
WB	4869 ± 358	0.50	2435 ± 179

567

568 Table 2. Density (individuals 0.25 m⁻²) of macrofaunal invertebrates associated with
 569 turfs of *Halophila stipulacea* at sampling sites in the leeward bays of Carriacou:
 570 Hillsborough Bay (HB), L'Esterre Bay (LB), and Tyrell Bay (TB). Data are mean ±
 571 SE; n = 12 quadrats (0.25 m²).
 572

Taxon	HB	LB	TB
Porifera			
<i>Amphimedon erina</i>	0.42 ± 0.23	0.50 ± 0.23	
<i>Tedania ignis</i>	0.08 ± 0.08		
Mollusca, Bivalvia			
<i>Anadara notabilis</i>	0.08 ± 0.08		0.17 ± 0.11
<i>Pinna carnea</i>		0.08 ± 0.08	
Echinodermata			
<i>Ophioderma appressum</i>	1.00 ± 0.39		0.33 ± 0.14
<i>Oreaster reticulatus</i>		0.25 ± 0.13	0.17 ± 0.11
<i>Tripneustes ventricosus</i>			0.33 ± 0.14
Chordata, Ascidiacea			
<i>Botrylloides nigrum</i>	0.25 ± 0.13	0.08 ± 0.08	
Unidentified sp.*	0.83 ± 0.32	0.58 ± 0.19	
Unidentified sp.*		1.08 ± 0.40	

573 * Unidentified solitary ascidians are those classified in the field as morpho-species;
 574 subsequent identification indicated they included *Microcosmus helleri*, a *Moluga* sp.
 575 and possibly others.
 576

577

578 **Figure Captions**

579

580 Fig. 1. Map of Carriacou showing locations of sampling stations (circles) and line
581 transects or belt-transects (triangles), and presence of monospecific or mixed stands of
582 the invasive *Halophila stipulacea* (blue) or non-invaded stands of native seagrass
583 *Thalassia testudinum* and/or *Syringodium filiforme* (light green). See Table S1 for
584 belt-transect (CB, HB, LB, TB) locations and sampling details; Table S2 for station
585 (S) and transect (T) locations and sampling details. Also shown is Sandy Island where
586 *H. stipulacea* was surveyed in the area where it was first recorded.

587

588 Fig. 2. a) Dense monospecific turf of *Halophila stipulacea* in Hillsborough Bay with
589 small cluster of black long-spine sea urchins *Diadema antillarum* in foreground (~ 7
590 cm horizontal diameter) and numerous white short-spine sea urchins *Tripneustes*
591 *ventricosus* in background (~ 9 cm horizontal diameter). b) Early juvenile of the sea
592 star *Oreaster reticulatus* (~ 4 cm arm radius) nestled into dense turf of *H. stipulacea*
593 in Tyrell Bay, with characteristic cryptic coloration of juveniles in seagrass beds.
594 Photo credit: Robert Scheibling.

595

596 Fig. 3. Cover of seagrass substrata (% of bottom) a) pooled over duplicate alongshore
597 belt transects at Craigston Bay (CB), Hillsborough Bay (HB), L'Esterre Bay (LB), and
598 Tyrell Bay (TB), and b) from line transects around Carriacou. See Table S1 for belt-

599 transect locations and sampling details; Table S2 for line transect locations and
600 sampling details.

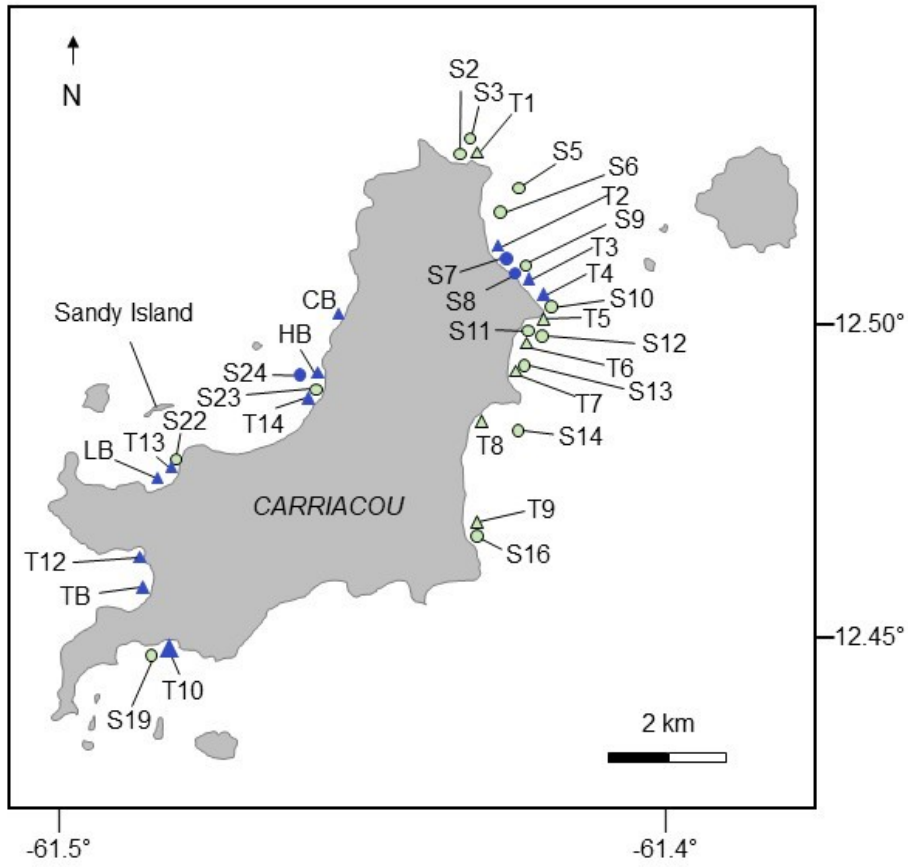
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602 Fig. 4. *Halophila stipulacea* and native seagrass species (*Thalassia testudinum*,
603 *Syringodium filiforme*) at sampling stations: a) biomass (kg m^{-2} , fresh weight) and b)
604 frequency of occurrence (proportion of 12 quadrats sampled). See Table S2 for station
605 locations and sampling details. Note: *Halodule wrightii* is not included since biomass
606 and frequency of occurrence were minimal at stations.

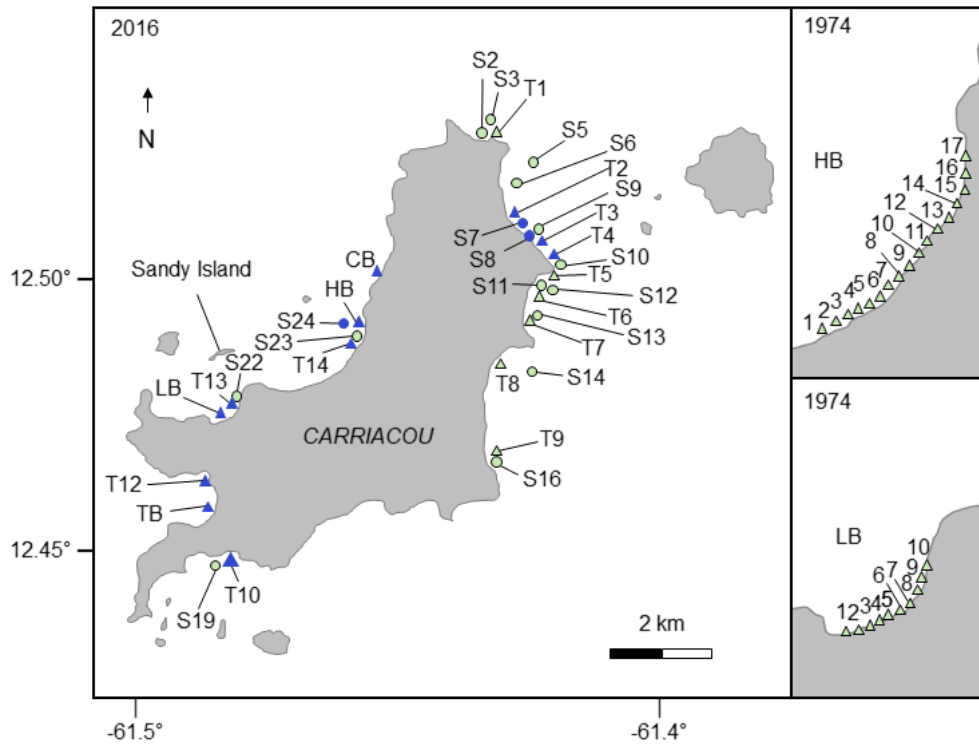
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608 Fig. 5. Distribution and abundance of echinoderms on seagrass and sand substrata
609 based on frames pooled across alongshore and offshore (where applicable) belt
610 transects in Craigston Bay, Hillsborough Bay, L'Esterre Bay, and Tyrell Bay. a) Mean
611 (\pm SE) density of sea urchins (*Tripneustes ventricosus*, *Lytechinus variegatus*,
612 *Diadema antillarum*; individuals m^{-2}) and sea stars (*Oreaster reticulatus*; individuals
613 10 m^{-2}) and b) difference between observed and expected (random distribution across
614 substratum types) counts per substratum type. Total number of frames: sand, 42;
615 *Thalassia testudinum*, 353; mixed *Halophila stipulacea*, 53; *Halophila stipulacea*,
616 579.

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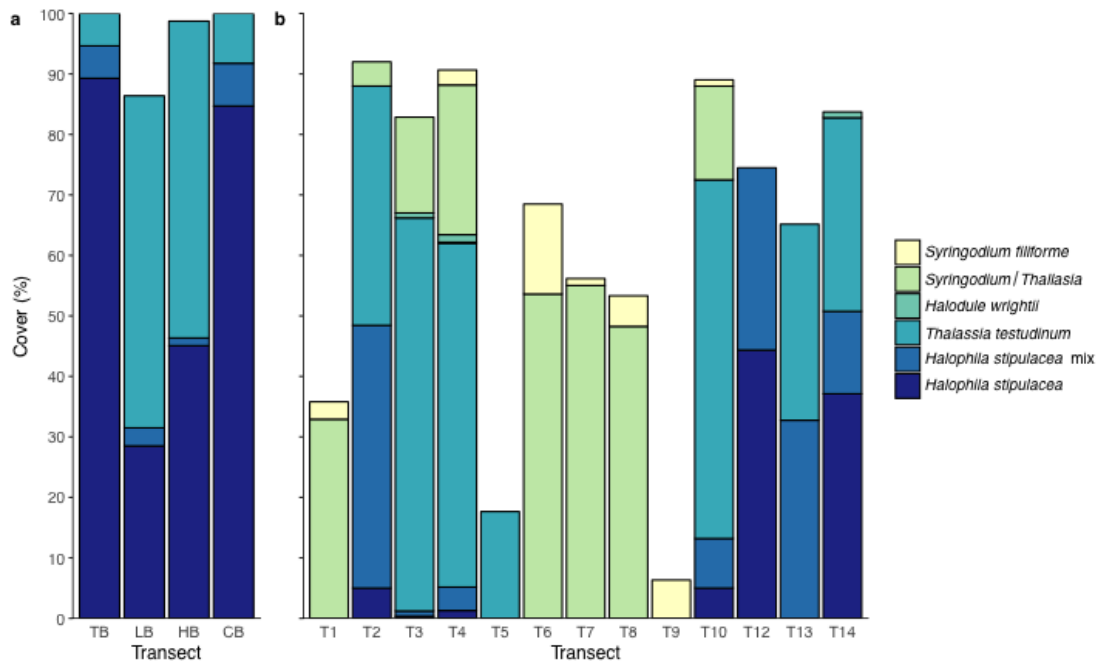
Fig. 1. Map of Carriacou showing locations of sampling stations (circles) and line transects or belt-transects (triangles), and presence of monospecific or mixed stands of the invasive *Halophila stipulacea* (blue) or non-invaded stands of native seagrass *Thalassia testudinum* and/or *Syringodium filiforme* (light green). See Table S1 for belt-transect (CB, HB, LB, TB) locations and sampling details; Table S2 for station (S) and line transect (T) locations and sampling details; Insets show locations of transects conducted in 1974 at Hillsborough Bay (HB) and L'Esterre Bay (LB) (Scheibling, 1980). Also shown is Sandy Island where *H. stipulacea* was surveyed in the area where it was first recorded.



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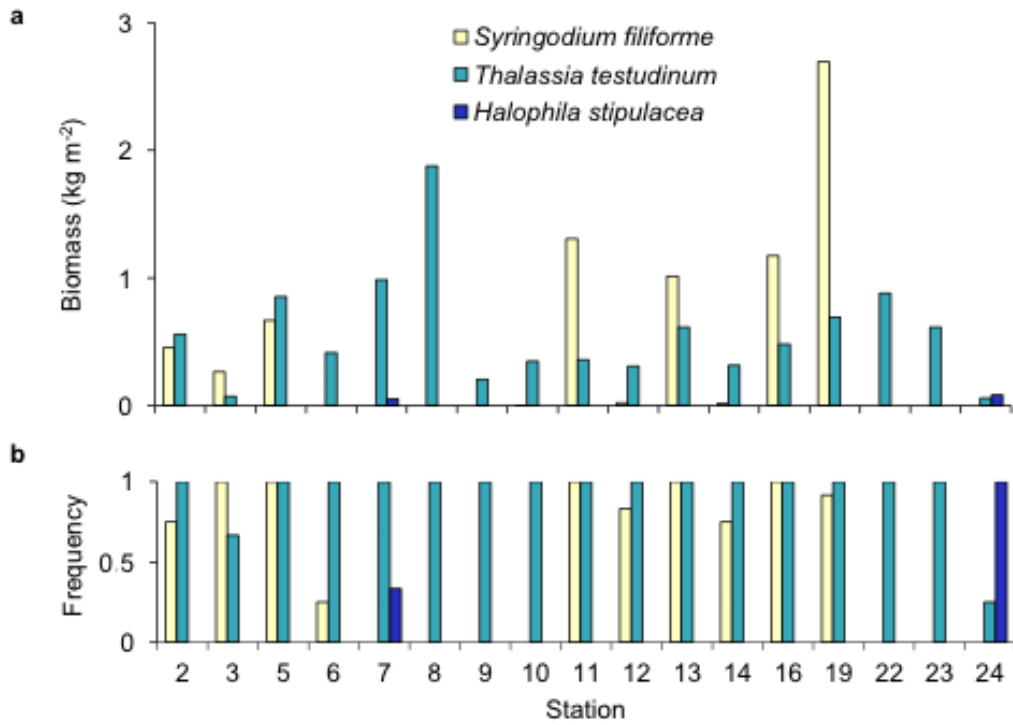
Fig. 2. a) Dense monospecific turf of *Halophila stipulacea* in Hillsborough Bay with small cluster of black long-spine sea urchins *Diadema antillarum* in foreground (~ 7 cm horizontal diameter) and numerous white short-spine sea urchins *Tripneustes ventricosus* in background (~ 9 cm horizontal diameter). b) Early juvenile of the sea star *Oreaster reticulatus* (~ 4 cm arm radius) nestled into dense turf of *H. stipulacea* in Tyrell Bay, with characteristic cryptic coloration of juveniles in seagrass beds. Photo credit: Robert Scheibling.

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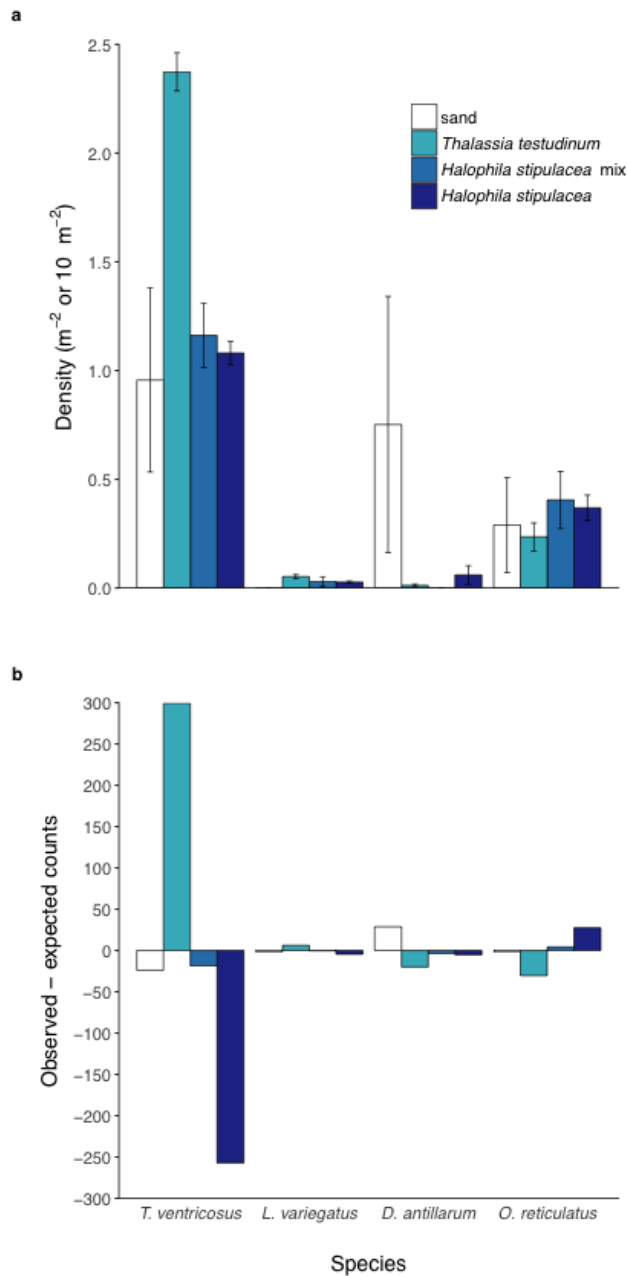
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Fig. 3. Cover of seagrass substrata (% of bottom) a) pooled over duplicate alongshore belt transects at Craigston Bay (CB), Hillsborough Bay (HB), L'Esterre Bay (LB), and Tyrell Bay (TB), and b) from line transects around Carriacou. See Table S1 for belt transect locations and sampling details; Table S2 for line transect locations and sampling details.



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Fig. 4. *Halophila stipulacea* and native seagrass species (*Thalassia testudinum*, *Syringodium filiforme*) at sampling stations: a) biomass (kg m⁻², fresh weight) and b) frequency of occurrence (proportion of 12 quadrats sampled). See Table S2 for station locations and sampling details. Note: *Halodule wrightii* is not included since biomass and frequency of occurrence were minimal at stations.



655
 656 Fig. 5. Distribution and abundance of echinoderms on seagrass (*Halophila stipulacea*,
 657 *Thalassia testudinum*, and mixed stands of both species) and sand substrata based on frames
 658 pooled across alongshore and offshore (where applicable) belt transects in Craigston Bay,
 659 Hillsborough Bay, L'Esterre Bay, and Tyrell Bay. a) Mean (\pm SE) density of sea urchins
 660 (*Tripneustes ventricosus*, *Lytechinus variegatus*, *Diadema antillarum*; individuals m⁻²) and sea
 661 stars (*Oreaster reticulatus*; individuals 10 m⁻²) and b) difference between observed and
 662 expected (random distribution across substratum types) counts per substratum type. Total
 663 number of frames: sand, 42; *Thalassia testudinum*, 353; mixed *Halophila stipulacea*, 53;
 664 *Halophila stipulacea*, 579.

666 **Online Supplementary Material**

667 Table S1. Belt transects from video surveys of leeward bays of Carriacou: Hillsborough Bay (HB), L’Esterre
 668 Bay (LB), Tyrell Bay (TB), and Craigston Bay (CB). Transect length is estimated from swim time; transect
 669 width is estimated from a scaling element in the video record. Start coordinates and approximate direction
 670 relative to shore were obtained from 2015 Google Earth images. For alongshore transects (Along), offshore
 671 distance of alongshore transects was estimated by the observer (RES). Offshore transects (Off) were oriented
 672 perpendicular to shore, starting at the shallow margin of the *Halophila stipulacea* (Hs) bed, where it abuts
 673 beach sand. Direction Depth range across all transects was recorded with a graduated plumb line or dive
 674 computer. The maximum extent of beds of *H. stipulacea* (including small patches of sand or native seagrass)
 675 in each transect was calculated as a proportion of the total length based on swim time.
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Transect	Date 2016	Lat.	Long.	Direction rel. shore	Length (m)	Width (m)	Offshore dist. (m)	Depth (m)
HB1	Feb 19	12.485241	-61.457309	Along (NE)	595	0.6–0.7	30–50	1.5–2.5
HB2	Feb 19	12.485273	-61.457373	Along (NE)	588	0.7	35–55	2.5–3
HB3	Feb 28	12.487410	-61.455300	Off (WNW)	112	0.7–0.9	Hs/sand	13.5
HB4	Feb 28	12.487607	-61.455193	Off (WNW)	88	0.6–0.7	Hs/sand	13.5
HB5	Feb 28	12.487859	-61.455064	Off (WNW)	115	0.6–0.7	Hs/sand	13.5
LB1	Feb 19	12.474414	-61.479166	Along (SW)	482	0.7	30–50	1.5–2.5
LB2	Feb 19	12.474454	-61.479244	Along (SW)	360	0.7–0.8	30–50	1–2
TB1	Feb 24	12.456948	-61.483374	Along (SSW)	307	0.6–0.9	5–10	1–2.5
TB2	Feb 24	12.456984	-61.483542	Along (SSW)	327	0.6–0.7	10–15	2–2.5
CB1	Mar 1	12.499353	-61.453178	Along (NE)	176	0.4–0.5	50	4–4.5
CB2	Mar 1	12.499437	-61.453335	Along (NE)	144	0.4–0.5	60	4.5–5
CB3	Mar 1	12.499352	-61.452922	Off (NW)	77	0.4–0.5	Hs/sand	4–5
CB4	Mar 1	12.499556	-61.452797	Off (NW)	80	0.4–0.6	Hs/sand	4–5
CB5	Mar 1	12.499738	-61.452655	Off (NW)	94	0.4–0.5	Hs/sand	4–5
CB6	Mar 1	12.499908	-61.452502	Off (NW)	140	0.4–0.6	Hs/sand	4–5
CB7	Mar 1	12.500075	-61.452342	Off (NW)	140	0.4–0.7	Hs/sand	4–5

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679 Table S2. Dates, locations and depths of (a) stations and (b) line transects around Carriacou.
 680 Dist. for stations is distance from shore. Direction for line transects is bearing from shore. Site
 681 coordinates are from 2015 Google Earth images. Depths, measured with a calibrated 2-m pole
 682 or a depth gauge for depths over 2 m, were adjusted (approximately) to mean low water level
 683 by reference to tide tables and charts for Carriacou; mean low water level was calculated from
 684 daily low water values over 1 year (2016).
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686 **a) Stations**

Station	Site name	Description	Date 2016	Lat.	Long.	Depth (m)	Distance (m)
2	Petit Carenage inshore	Fringing bed	Feb 21	12.526643	-61.435876	2.0	60
3	Petit Carenage offshore	Offshore patch	Feb 21	12.526862	-61.433699	3.0	200
5	Watering Bay streaks	Mid lagoon sand	Feb 23	12.518372	-61.423202	3.1	750
6	Grand Cay	Offshore patch	Feb 23	12.517743	-61.426857	2.3	375
7	Watering Bay wharf	Fringing bed	Feb 22	12.512812	-61.429159	2.5	100
8	Watering Bay South	Fringing bed	Feb 12	12.506200	-61.425711	1.2	40
9	Watering Bay South	Fringing bed	Feb 12	12.506692	-61.424784	1.2	140
10	Watering/Jew Bay head	Fringing bed	Feb 27	12.500672	-61.419566	1.1	30
11	Jew Bay North	Fringing bed	Jan 29	12.497265	-61.422321	3.3	140
12	Jew Bay offshore	Patchy fringing bed	Feb 26	12.496147	-61.420841	4.6	340
13	Jew Bay South	Fringing bed	Jan 31	12.492453	-61.423829	2.8	150
14	Grand Bay North lagoon	Lagoonal patch	Feb 25	12.483286	-61.424363	3.4	320
16	Grand Bay South	Fringing bed	Feb 25	12.468669	-61.430513	2.7	200
19	Manchioneal Bay	Fringing bed	Feb 20	12.447888	-61.485022	0.9	12
22	L'Esterre Bay	Cobble banks	Jan 24	12.477468	-61.479154	0.5	140
23	Hillsborough inshore	Fringing bed	Jan 27	12.485738	-61.457227	2.5	75
24	Hillsborough offshore	Offshore patch	Feb 17	12.486810	-61.458521	4.5	260

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689 **b) Line transects**

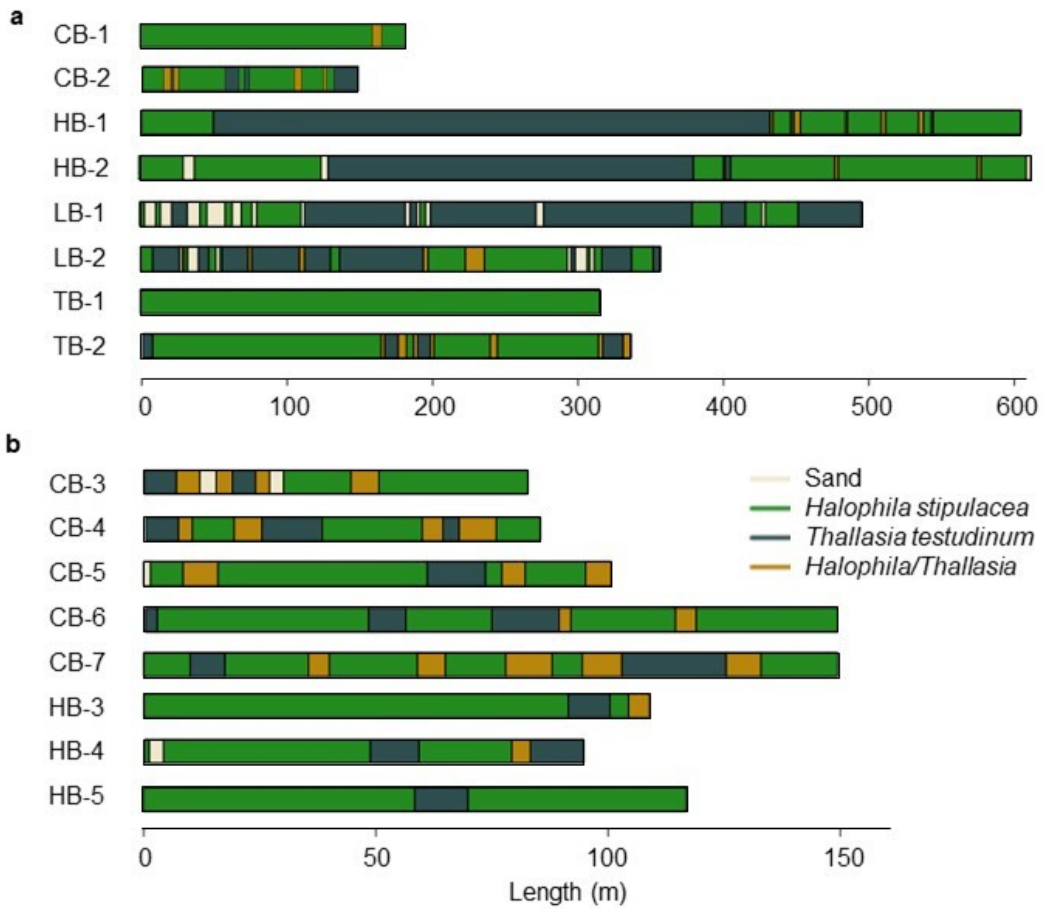
Transect	Site name	Date 2016	Lat.	Long.	Direction (deg)	Length (m)	Depth (m)
1	Petit Carenage	Feb 21	12.526206	-61.436210	36	92	0–2.3
2	Watering Bay North	Feb 22	12.512881	-61.430128	181	180	0–3.7
3	Watering Bay South	Feb 12	12.505801	-61.426082	55	194	0–1.4
4	Watering Bay South	Feb 14	12.505297	-61.425494	83	218	0–1.4
5	Watering/Jew Bay head	Feb 27	12.500645	-61.419880	85	61	0–3.5
6	Jew Bay North	Jan 26	12.498028	-61.423446	124	162	0–3.1
7	Jew Bay South	Jan 31	12.492572	-61.425183	98	157	0–3.3
8	Grand Bay North	Feb 25	12.484747	-61.429249	119	107	0–2.1
9	Grand Bay South	Feb 25	12.468696	-61.432335	92	121	0–4.2
10	Manchioneal Bay	Feb 20	12.448010	-61.484987	184	144	0–2.1
12	Tyrell Bay	Mar 21	12.457063	-61.482992	282	160	0–4.4
13	L’Esterre Bay	Jan 30	12.476246	-61.477468	299	339	0–1.7
14	Hillsborough Bay	Jan 27, Feb18	12.485285	-61.456774	313	360	0–6.1

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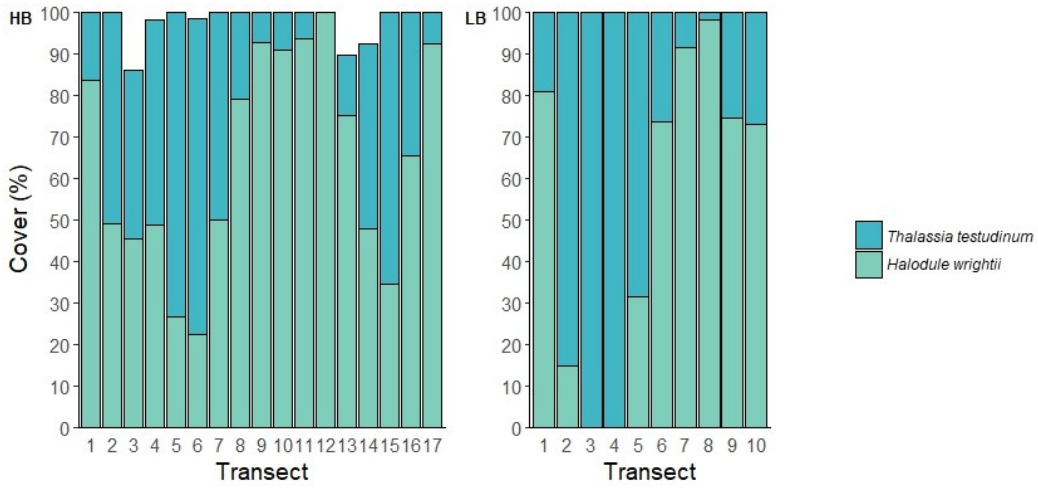
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Fig. S1. Seagrass/substrate composition in alongshore (a) and offshore (b) belt transects at Craigston Bay (CB), Hillsborough Bay (HB), L'Esterre Bay (LB), and Tyrell Bay (TB). See Table S1 for belt transect locations and sampling details.



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Fig. S2. Cover of seagrass substrata (% of bottom) from transects conducted in 1974 at Hillsborough Bay (HB) and L'Esterre Bay (LB) (Scheibling, 1980). Belt transects extended offshore (length x width: 100 x 10 m in HB, 120 x 5 m in HB) and were spaced at 50-m intervals alongshore.