

Drift macroalgal distribution in northern Gulf of Mexico seagrass meadows

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Drift macroalgae, often found in clumps or mats adjacent to or within seagrass beds, can increase the value of seagrass beds as habitat for nekton via added food resources and structural complexity. But, as algal biomass increases, it can also decrease light availability, inhibit faunal movements, smother benthic communities, and contribute to hypoxia, all of which can reduce nekton abundance. We quantified the abundance and distribution of drift macroalgae within seagrass meadows dominated by turtle grass *Thalassia testudinum* across the northern Gulf of Mexico and compared seagrass characteristics to macroalgal biomass and distribution. Drift macroalgae were most abundant in areas with higher seagrass shoot densities and intermediate canopy heights. We did not find significant relationships between algal biomass and point measures of salinity, temperature, or depth. The macroalgal genera *Laurencia* and *Gracilaria* were present across the study region, *Agardhiella* and *Digenia* were collected in the western Gulf of Mexico, and *Acanthophora* was collected in the eastern Gulf of Mexico. Our survey revealed drift algae to be abundant and widespread throughout seagrass meadows in the northern Gulf of Mexico, with likely influences the habitat value of seagrass ecosystems.

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23 ABSTRACT

24 Drift macroalgae, often found in clumps or mats adjacent to or within seagrass beds, can
25 increase the value of seagrass beds as habitat for nekton via added food resources and structural
26 complexity. But, as algal biomass increases, it can also decrease light availability, inhibit faunal
27 movements, smother benthic communities, and contribute to hypoxia, all of which can reduce
28 nekton abundance. We quantified the abundance and distribution of drift macroalgae within
29 seagrass meadows dominated by turtle grass *Thalassia testudinum* across the northern Gulf of
30 Mexico and compared seagrass characteristics to macroalgal biomass and distribution. Drift
31 macroalgae were most abundant in areas with higher seagrass shoot densities and intermediate
32 canopy heights. We did not find significant relationships between algal biomass and point
33 measures of salinity, temperature, or depth. The macroalgal genera *Laurencia* and *Gracilaria*
34 were present across the study region, *Agardhiella* and *Digenia* were collected in the western Gulf
35 of Mexico, and *Acanthophora* was collected in the eastern Gulf of Mexico. Our survey revealed
36 drift algae to be abundant and widespread throughout seagrass meadows in the northern Gulf of
37 Mexico, with likely influences the habitat value of seagrass ecosystems.

38

39 INTRODUCTION

40 Drift macroalgae often originate as attached algae on seagrass leaves and other hard
41 substratum before becoming uprooted by various physical disturbances (e.g., currents, waves)
42 (Norton & Mathieson, 1983; Bell & Hall, 1997; Biber, 2002; Lirman et al., 2003). They are
43 commonly found in small patches within and around the calm, coastal seagrass meadows from
44 early spring to mid-summer (Norton & Mathieson, 1983), with distributions influenced by water
45 currents as well as the roughness of the surrounding substrate (Bell et al., 1995; Bell & Hall,

46 1997; Biber, 2007; Fonseca & Koehl, 2006). The ecosystem benefits of seagrass habitats are
47 strongly correlated with their structural complexity, and macroalgal communities often further
48 increase this complexity 3-100-fold (Morris & Hall, 2001; Kingsford, 1995). Seagrass and
49 macroalgae are major constituents in some of the most productive coastal ecosystems and they
50 enhance fisheries by providing valuable nursery habitat for a variety of finfish and invertebrate
51 fauna (e.g., Carr, 1991; Jackson et al., 2001; Heck, Hays & Orth, 2003; Guido et al., 2004; Bos et
52 al., 2007). In the Mediterranean, seagrass and macroalgal habitats support 30-40% of the
53 commercial fish and 29% of recreational fish during their juvenile life stages (Jackson, Wilding
54 & Attrill, 2015). The structure provided by seagrass and macroalgal communities can enhance
55 feeding and growth rates, while lowering predation rates for many shrimp, crab, and fish species
56 (Orth, Heck & van Montfrans, 1984; Kingsford & Choat, 1985; Bax, 1998; Rooker, Holt & Holt,
57 1998; Nagelkerken et al., 2002). The detached nature of drift macroalgal communities can also
58 aid in dispersal of many small fish and invertebrates utilizing this structure (Astill & Lavery,
59 2001; Holmquist, 1994).

60 While macroalgae can enhance the ecosystem services of seagrasses, at sufficiently high
61 biomass, macroalgae can lead to declines in organismal abundance and species diversity (e.g.,
62 Hull, 1987; Bonsdorff, 1992; Zajac & McCarthy, 2015). The degree of this change may be tied
63 to species-specific morphological traits (Bartholomew et al., 2000). Green filamentous
64 macroalgae in the Baltic Sea, for example, is problematic at high concentrations, causing
65 hypoxia and altering the resident benthic communities (Vahteri et al., 2000). Massive influxes of
66 the brown alga *Sargassum* to coastal systems have also led to similar declines in flora and fauna
67 in the Caribbean, causing benthic mortality and decreasing habitat value (Chávez et al., 2020).
68 However, brown algae in New Zealand led to an increase in fish and invertebrate abundance,

69 with higher species abundances relative to attached vegetation and open water areas (Kingsford
70 & Coat, 1985). Understanding the algal composition throughout the northern Gulf of Mexico and
71 seasonal changes in biomass may allow us to better understand the species-specific effects that
72 algae have on seagrass and their associated nekton communities.

73 Algae are classified into three evolutionarily distinct lineages based on variations in their
74 morphological characteristics and tissue pigment composition, and consist of brown algae
75 (Phaeophyceae), green algae (Chlorophyta), and red algae (Rhodophyta), with rhodophytes being
76 the dominant taxa in the northern Gulf of Mexico (Virnstein & Carbonara, 1985; Holmquist,
77 1997). Over the last few decades, seagrass areal coverage has declined in many areas, including
78 the northern Gulf of Mexico and southern Atlantic estuaries of North America (Hall et al., 1999;
79 Peneva, Griffith & Carter, 2008; Carter et al., 2011). Macroalgal blooms have increased in
80 frequency and intensity (e.g., Benz, Eiseman & Gallaher, 1979; Virnstein & Carbonara, 1985;
81 Zieman, Fourqurean & Iverson, 1989; Kopeccky & Dunton, 2006; Fredericq et al., 2009) and are
82 predicted to proliferate under future scenarios of warmer sea surface temperatures and ocean
83 acidification (Brodie et al., 2014). Consequently, the functional role of drift algae may increase
84 in importance in regions where seagrasses have declined. However, drift algae are known for
85 being highly variable across space and time (Benz, Eiseman & Gallaher, 1979; Bell & Hall,
86 1997), with their abundance and movement within estuaries rarely quantified and difficult to
87 track, complicating our understanding of drift algae in seagrass ecosystems. Although
88 underappreciated for their habitat value, drift macroalgae likely augment the value of seagrass
89 beds as habitat for nekton by increasing the physical structure within and adjacent to seagrass
90 beds. We surveyed seagrass meadows across the northern Gulf of Mexico and quantified (1) the

91 abundance of drift macroalgae in early and late summer and (2) the relationship between algal
92 abundance and environmental and seagrass metrics.

93

94 MATERIALS & METHODS

95 **Study regions.** Five estuaries in the northern Gulf of Mexico, each containing at least 20
96 sites within seagrass meadows, were surveyed twice during the early (May–June) and late
97 (August–September) summer of 2018 (Fig. 1). Sites were selected by overlaying a tessellated
98 hexagonal grid (500 m edge length) on each estuary in ArcGIS (Moore, 2009; Neckles et al.,
99 2012; Wilson & Dunton, 2012). A randomly generated site within each of 20 to 25 grid cells that
100 contained more than 50% seagrass coverage and a minimum of 500 m separation were selected
101 for assessment (Belgrad et al., 2021). Across all regions, turtle grass (*Thalassia testudinum*) was
102 the dominant macrophytic taxon; however, manatee grass (*Syringodium filiforme*) and shoal
103 grass (*Halodule wrightii*) were also common. Star grass (*Halophila engelmannii*) and widgeon
104 grass (*Ruppia maritima*) were present but occurred in <0.01% of surveys and are not considered
105 in this study. *In situ* measurements of seagrass coverage ranged from 0–100%. Measurements
106 were collected across twenty sites within Laguna Madre, TX (LM; 26°08'N, 97°14'W), Corpus
107 Christi Bay, TX (CB; 27°51'N, 97°08'W), and the Chandeleur Islands, LA (LA; 29°54'N,
108 88°50'W). In Florida, measurements were collected from 25 sites at both Cedar Key (CK;
109 29°05'N, 83°01'W) and Charlotte Harbor (CH; 26°04'N, 82°14'W). At each sampling location,
110 abiotic conditions (i.e., temperature, salinity, DO, depth) were recorded, drift macroalgae
111 biomass measured, and seagrass cover/abundance and morphometrics assessed. Because we
112 sampled synoptically using the same methods, we were able to assess both algal biomass and

113 distribution within and among locations across the northern Gulf of Mexico (Table 1; Belgrad et
114 al., 2021; Correia, 2021).

115 **Drift algal abundance assessment.** Within each hexagon, drift algal abundance within
116 seagrass meadows was measured using a flat otter trawl, an epibenthic sled, and 1-m² quadrats.
117 The use of these three sampling techniques provided valuable information about broad and fine
118 scale macroalgal distributions within seagrass habitats. While the trawl covers a larger area than
119 the epibenthic sled, it can quickly become fouled by high biomass of drift algae, making it
120 difficult to standardize trawl lengths. Epibenthic sleds allow for a more standardized comparison
121 between seagrass and macroalgal habitat within a given area. Each sled tow was pulled within
122 seagrass habitats for the same distance allowing for a precise representation of macroalgae
123 within each seagrass bed. Quadrats were used in the same vicinity as the epibenthic sled and
124 trawl to assess seagrass and algal percent cover.

125 A 4.85-m flat otter trawl with a 3.8-cm stretch mesh body and 1.3-cm stretch mesh bag
126 was towed through seagrass beds at an average speed of 3.7–5.6 km h⁻¹ for approximately 2
127 minutes, resulting in linear distances of approximately 116.7 m ± 0.12 SE per trawl. Latitude and
128 longitude were recorded at the beginning, midpoint, and end of each trawl to record the trawl
129 path to obtain accurate distance calculations and provide coordinates for sled and quadrat
130 surveys. Macroalgal abundance was determined as the wet weight of algae present in the trawl,
131 measured using a spring scale. Samples of drift algae were taken from the trawl, bagged, frozen,
132 and later identified to genus using a dissecting microscope (Littler & Littler, 2000). Due to
133 variations in the trawl sampling distance, drift algal weight was standardized to trawl area (g·m⁻²).
134 At the center of each trawl path, environmental parameters including salinity, temperature
135 (°C), and dissolved oxygen (mg L⁻¹) were measured using a YSI Pro 2030 containing a galvanic

136 DO sensor (Model 2002) immediately following the trawl. Water depth (cm) was also measured
137 at the center of the trawl path.

138 We returned to each site to sample using the epibenthic sled, which consisting of an
139 aluminum frame (0.75-m wide and 0.6-m high), with two skids on either side (0.8 m in length),
140 and a 2-mm stretch mesh net. Sled samples were collected near the midpoint of the trawl path.
141 The sled was towed for 13.3 m at approximately 0.5 m sec⁻¹, covering an area of 10 m². Algae
142 from benthic sled samples were bagged, frozen, and transported to the lab where they were later
143 identified to genus and weighed.

144 **Seagrass and algal vegetative sampling (quadrats).** The structural complexity of
145 seagrass meadows and percent cover of drift algae were assessed using a 1-m² quadrat divided
146 into 100, 10-cm x 10-cm cells. Twelve quadrats were haphazardly thrown along each trawl: four
147 quadrats at the beginning, middle, and end of each trawl path. The percent cover, shoot count,
148 and canopy height of each seagrass species present in a quadrat was recorded. Seagrass percent
149 cover by species, as well as the cover of drift algae, were measured by counting the number of
150 grid cells within each quadrat that contained a particular vegetation type (0–100 grids quadrat⁻¹).
151 The shoot count was calculated for each seagrass species by counting the number of shoots
152 within a random quadrat grid cell. Canopy height was defined as the mean of three randomly
153 selected canopy height measurements.

154 **Statistical analysis.** SAS© was used for all statistical analyses. When comparing algal
155 biomass across the northern Gulf of Mexico, analyses were performed using General Linear
156 Models (GLM) in SAS© with region (CB, CH, CK, LA, and LM) and sampling period (early or
157 late summer) as fixed factors. The algal biomass within the trawl and epibenthic sled samples
158 were log-transformed to mitigate skewness and achieve normality. Comparisons of algal weight

159 across early and late summer were then performed using procedure GENMOD with link function
160 gamma to analyze continuous variables and $\alpha = 0.05$ was maintained in all *post hoc* testing.

161 To compare algal percent cover to environmental and seagrass variables within the
162 quadrats, a multiple linear regression with backward elimination model selection was performed
163 using procedure REG in SAS[®], maintaining $\alpha = 0.05$ during model selection. Variables included
164 in this regression were shoot count, average canopy height, salinity, temperature, dissolved
165 oxygen, and the percent cover of *T. testudinum*, *H. wrightii*, and *S. filiforme* from the quadrats.

166

167 RESULTS

168 **Macroalgal biomass across the northern Gulf of Mexico.** Drift macroalgae were
169 present in both the early and late summer sampling times, reaching biomasses of over 50 g m⁻² in
170 one site in Charlotte Harbor, FL (Fig. 2). Regional comparisons of trawl samples showed no
171 significant changes in the overall algal biomass in Corpus Christi Bay, TX or Cedar Key, FL
172 between early and late sampling times ($p = 0.49$ and 0.29 , respectively; Table 2). Charlotte
173 Harbor, FL had significantly higher biomass of drift macroalgae in the late summer when
174 compared to the early summer months ($p < 0.001$; Table 2). Meanwhile, Laguna Madre, TX and
175 Chandeleur Islands, LA both had significantly less macroalgae in the late summer months
176 compared to the early summer ($p = 0.05$ and 0.01 , respectively; Table 2). Macroalgal biomass
177 collected in the epibenthic sled followed a similar pattern among regions and sampling times
178 (Fig. 2, Table 2).

179 **Macroalgal species composition across the northern Gulf of Mexico.** Drift algal
180 community composition varied across region. Macroalgae identified in Laguna Madre, TX
181 consisted of the genera *Agardhiella*, *Amphiroa*, *Dictyota*, *Digenia*, *Gracilaria*, *Hypnea*, and

182 *Laurencia*. Corpus Christi Bay, TX had similar algal genera comprised of *Agardhiella*,
183 *Chondria*, *Dictyota*, *Digenia*, *Gracilaria*, and *Laurencia*. Macroalgae found in Chandeleur
184 Islands, LA consisted of *Agardhiella*, *Chondria*, *Gracilaria*, *Laurencia*, and *Spyridia*. Cedar
185 Key, FL consisted of *Acanthophora*, *Dictyota*, *Digenia*, *Gracilaria*, *Laurencia*, *Polysiphonia*,
186 and *Ulva*. Charlotte Harbor, FL were mainly comprised of *Acanthophora*, *Cladophora*,
187 *Gracilaria*, and *Spyridia* genera, and *Hypnea*, *Laurencia*, and *Ulva* were also present.

188 **Macroalgal percent cover in relation to seagrass and abiotic parameters.** Within the
189 quadrat surveys, *T. testudinum* percent cover and average canopy height both significantly
190 related to drift algal percent cover ($p = 0.03$ and $p < 0.001$, respectively; Fig. 3), whereas the
191 seagrass shoot counts, salinity, temperature, and percent cover of *H. wrightii* and *S. filiforme* did
192 not significantly contribute to the drift algae cover in these areas ($p > 0.05$; Table 3). Drift algal
193 cover increased with increasing *T. testudinum* cover, and algae were most dense in areas with
194 intermediate seagrass canopy heights around 400 mm tall (Fig. 3).

195

196 **DISCUSSION**

197 Drift macroalgae were found throughout the study region in both the early and late
198 summer months, with lower biomasses observed in the late summer months across Laguna
199 Madre, TX, Cedar Key, FL, and Chandeleur Islands, LA, consistent with previous findings (e.g.,
200 Benz, Eiseman & Gallaher, 1979; Virnstein & Carbonara, 1985). Conversely, macroalgal
201 abundance was higher in the late summer in Charlotte Harbor, FL, and did not significantly
202 change from early to late summer in Corpus Christi Bay, TX. The inconsistent patterns observed
203 in these two estuaries may be the result of tidal and freshwater variations that affect delivery
204 rates of nutrients and/or flushing of drift macroalgae. Corpus Christi Bay, TX is an enclosed

205 system with little direct influence from the Gulf of Mexico and long water residence times (Solis
206 & Powell, 1999; Pulich, 2007). Since macroalgae are commonly flushed by tidal currents, the
207 long water residence time and protection from tidal flushing in Corpus Christi Bay may reduce
208 seasonal algae decline observed in other locations. The high percentage of clay and silt within
209 the benthic sediments of Corpus Christi Bay further indicates differences in the local
210 hydrodynamic regime (Shideler, Stelting & McGowen, 1981), with previous studies showing a
211 direct positive link between algae biomass and the amount of silt-clay in the system (Bell & Hall,
212 1997). In contrast, Charlotte Harbor, FL, has experienced an increase in macroalgal blooms in
213 recent years, particularly on the eastern shore (BTT, 2021). The increase in nutrient
214 concentrations from creeks and streams, as well as the limited water circulation on the east side
215 of Charlotte Harbor, appears to be a major driver of high accumulation of drift algae in these
216 locations. Nutrient inputs from leaking septic systems, fertilizer and agricultural runoff, untreated
217 stormwater, ineffective sewage treatment systems, and altered freshwater inflow have been
218 deemed the primary cause of these algae blooms (Lapointe et al., 2016, BTT, 2021). While
219 seasonal fluctuations often show a decline in algal abundances in the late summer months,
220 localized anthropogenic and hydrodynamic differences may cause localized variations.

221 Drift macroalgae were most dense in areas with higher percent cover of *T. testudinum* but
222 with an intermediate canopy height (~400 mm). Perhaps unsurprisingly, algae are more likely to
223 be entrained within denser seagrass beds (Virnstein & Carbonara, 1985; Bell & Hall, 1997), but
224 this varies depending on location and scale. For example, at smaller spatial scales (m), shoot
225 count and blade length were associated with algal density patterns in Tampa Bay, FL (Bell, Hall
226 & Robbins, 1995). However, when this same location was studied at a larger scale (km), seagrass
227 cover explained 57% of the variation in algal cover, suggesting that spatial scale is important

228 when comparing algal to seagrass communities (Bell & Hall, 1997). The relationship between
229 seagrass canopy height and macroalgal density could be related to light-limiting growth
230 restrictions. When macroalgae reach sufficient biomass, they can restrict the light available to
231 seagrasses, decreasing productivity (Hauxwell et al., 2001; Huntington & Boyer, 2008). This
232 may be why areas with the tallest seagrass canopies also have less macroalgae. Because light is
233 less of a limiting factor, seagrass communities can grow at a faster rate when macroalgae are not
234 present. Conversely, entrapment of algae at intermediate canopy heights could be related to the
235 interaction between the algae and flow conditions. Taller canopies, that extend closer to the
236 surface of the water may be influenced by higher water velocities and turbulence, increasing the
237 likelihood of macroalgae dislodgement.

238 This study was limited in its ability to determine species-specific algal effects across
239 varying seagrass characteristics. During sampling, macroalgal species were not separated,
240 identified, and weighed in the field, but were rather weighed collectively and a sample of each
241 species brought back to the lab for later identification. Preliminary site selection was also chosen
242 based on the presence of *T. testudinum* across all site locations, which could have obscured less
243 obvious patterns when comparing algae biomass to *S. filiforme* and *H. wrightii*. Another potential
244 reason for the seagrass species-specific differences are the varying morphological characteristics
245 across *T. testudinum*, *S. filiforme*, and *H. wrightii*, including differences in blade width,
246 thickness, and shoot height (Loria, 2019). Future research should further investigate
247 concentrations of drift macroalgae in *S. filiforme* and *H. wrightii* dominated seagrass meadows to
248 corroborate our nonsignificant findings.

249 Macroalgae proliferate when sufficient light, nutrient availability, and warm temperatures
250 co-occur (EPA, 2013) and can become entrained in seagrass beds in large quantities when

251 seagrasses are dense and water flow is low enough to prevent dislodgement (Bell & Hall, 1997).
252 Although algae can be beneficial by increasing habitat complexity and food resources within
253 seagrass meadows (e.g., Carr, 1994; Kingsford, 1995; Jones, Lawton & Shachak, 1997; Morris &
254 Hall, 2001; Guido et al., 2004), large blooms of macroalgae can displace other benthic habitats
255 and reduce the health of the seagrass meadows (Valiela et al., 1997; Tagliapieta et al., 1998).
256 This study identified several patterns in algal density and composition on a Gulf-wide scale. Data
257 collected during this study also found large abundances of small fish and invertebrates living
258 within these seagrass beds, indicating that the biomass of algae present in the northern Gulf of
259 Mexico do not appear to be detrimental (Belgrad et al., 2021; Correia, 2021). Given the extent
260 that drift algae spatiotemporally vary, research to quantify links between algal genera and faunal
261 community composition could resolve much of the uncertainty surrounding this relationship. As
262 the climate continues to change, macroalgal blooms may become more variable and
263 understanding the interaction between algal-fauna relationships becomes increasingly important.
264 Understanding the role of macroalgae within Gulf of Mexico seagrass beds will allow us to
265 better manage the fisheries and other coastal resources in the future.

266

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424 **Figure 1. Location of the 5 study estuaries (stars) throughout the northern Gulf of Mexico.**

425 Regions include Laguna Madre, TX (LM), Corpus Christi Bay, TX (CB), the northern extent of
426 the Chandeleur Islands (LA), Cedar Key, FL (CK), and Charlotte Harbor, FL (CH). n represents
427 the number of sites that were sampled within each estuary during the early and late summer
428 2018. Map data © 2022 Google.

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431 **Figure 2. Average trawl and sled macroalgal weight in each region. (A)** Average trawl

432 macroalgae weight (g m^{-2}) + SE and (B) benthic sled macroalgae weight (g m^{-2}) + SE sampling

433 across each region during the early (black) and late (grey) summer months. The regions include

434 Laguna Madre, TX (LM, n = 20), Corpus Christi Bay, TX (CB, n = 20), Chandeleur Islands, LA

435 (LA, n = 20), Cedar Key (CK, n = 25), and Charlotte Harbor, FL (CH, n = 25). The asterisk (*)

436 indicates that there is a significant difference between early (May–June 2018) and late (August–

437 September 2018) sampling within that region.

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440 **Figure 3. Vegetation comparisons. (A)** Scatterplots comparing the drift macroalgae percent

441 cover to *T. testudinum* percent cover and (B) average seagrass canopy height from the quadrat

442 dataset. Panel (A) displays drift algae cover increasing with increased *T. testudinum* cover and

443 (B) shows algae percent cover was highest at intermediate canopy heights (~400 mm).

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Figure 1

Location of the 5 study estuaries (stars) throughout the northern Gulf of Mexico.

Regions include Laguna Madre, TX (LM), Corpus Christi Bay, TX (CB), the northern extent of the Chandeleur Islands (LA), Cedar Key, FL (CK), and Charlotte Harbor, FL (CH). n represents the number of sites that were sampled within each estuary during the early and late summer 2018. Map data © 2021 Google.



Figure 1.

Figure 2

Average trawl and sled macroalgal weight in each region.

(A) Average trawl macroalgae weight (g m^{-2}) + SE and (B) benthic sled macroalgae weight (g m^{-2}) + SE sampling across each region during the early (black) and late (grey) summer months. The regions include Laguna Madre, TX (LM, $n = 20$), Corpus Christi Bay, TX (CB, $n = 20$), Chandeleur Islands, LA (LA, $n = 20$), Cedar Key (CK, $n = 25$), and Charlotte Harbor, FL (CH, $n = 25$). The asterisk (*) indicates that there is a significant difference between early (May–June 2018) and late (August–September 2018) sampling within that region.

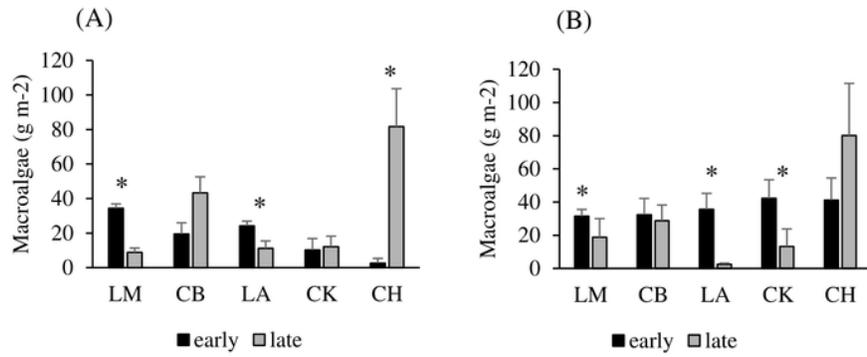


Figure 2.

Figure 3

Vegetation comparisons .

(A) Scatterplots comparing the drift macroalgae percent cover to *T. testudinum* percent cover and (B) average seagrass canopy height from the quadrat dataset. Panel (A) displays drift algae cover increasing with increased *T. testudinum* cover and (B) shows algae percent cover was highest at intermediate canopy heights (~400 mm).

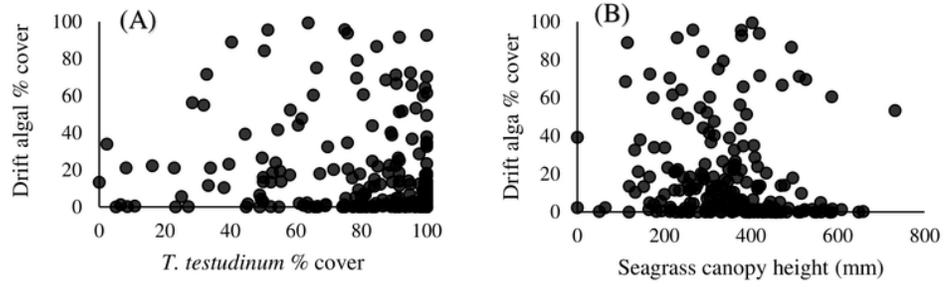


Figure 3.

Table 1 (on next page)

Abiotic variables from each region.

Abiotic variables (Mean \pm SE) measured during the early (May-June) and late (August-September) summer months 2018.

- 1 **Table 1. Abiotic variables from each region.** Abiotic variables (Mean \pm SE) measured during the early (May–June) and late
 2 (August–September) summer months 2018.

Abiotic parameter	Time	Laguna Madre, TX	Corpus Christi Bay, TX	Chandeleur Islands, LA	Cedar Key, FL	Charlotte Harbor, FL
Salinity (ppt)	Early	36.8 \pm 0.06	33.9 \pm 0.16	16.2 \pm 0.49	28.3 \pm 0.59	22.6 \pm 1.22
	Late	37.1 \pm 0.13	34.9 \pm 0.14	27.6 \pm 0.27	25.1 \pm 0.70	19.9 \pm 0.96
Temperature (°C)	Early	28.1 \pm 0.20	27.0 \pm 0.15	29.8 \pm 0.55	29.7 \pm 0.16	30.1 \pm 0.22
	Late	29.7 \pm 0.38	30.2 \pm 0.20	30.8 \pm 0.25	30.1 \pm 0.52	31.8 \pm 0.29
Dissolved Oxygen (mg L ⁻¹)	Early	8.4 \pm 0.43	6.2 \pm 0.32	9.5 \pm 0.58	7.6 \pm 0.30	6.3 \pm 0.24
	Late	6.1 \pm 0.47	11.8 \pm 0.46	8.9 \pm 0.38	6.8 \pm 0.35	7.7 \pm 1.50

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Table 2 (on next page)

Comparisons of trawl and sled algal weight across region and sampling time .

Multiple and general linear regression models for macroalgal biomass across region during early (May–June 2018) and late (August–September 2018) summer sampling. Each location was then separated and analyzed individually using generalized estimating equations with sample period as the fixed factor.

1 **Table 2. Comparisons of trawl and sled algal weight across region and sampling time.**

2 Multiple and general linear regression models for macroalgal biomass across region during early
 3 (May–June 2018) and late (August–September 2018) summer sampling. Each location was then
 4 separated and analyzed individually using generalized estimating equations with sample period
 5 as the fixed factor.

	SS	df	F ratio	Prob > F
<i>Trawl algae weight</i>				
Region (LM, CB, LA, CK, CH)	1937715.58	4	6.87	< 0.0001
Sample period (early, late)	142138.139	1	2.52	0.1137
Region*sample period	2547045.91	4	9.03	< 0.0001
<i>Sled algae weight</i>				
Region (LM, CB, LA, CK, CH)	92.383	4	3.38	0.0104
Sample period (early, late)	197.888	1	28.99	< 0.0001
Region*sample period	65.214	4	2.39	0.0521
Algal biomass comparisons across sampling time	Mean estimate		Chi-Square	Pr > ChiSq
<i>Trawl</i>				
LM (early v late)	-479.345		6.51	0.0107
CB (early v late)	3773.820		0.49	0.4859
LA (early v late)	-527.146		3.86	0.0493
CK (early v late)	-1150.98		1.11	0.2921
CH (early v late)	299.2744		14.22	0.0002
<i>Sled</i>				
LM (early v late)	-26.07		4.97	0.7533
CB (early v late)	238.02		0.10	0.3665
LA (early v late)	-13.46		18.31	0.2010
CK (early v late)	-28.12		1.64	< 0.0001
CH (early v late)	88.59		0.82	0.0258

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Table 3(on next page)

Backward regression to compare algae to abiotic and seagrass characteristics.

Multiple linear regression with backward elimination model selection results comparing algal density across abiotic and seagrass variables. The variables included in the model, following selection, include *T. testudinum* density and the average canopy height. Variables that were determined to be insignificant to the model during the selection process were average shoot count, salinity, water temperature, *H. wrightii* density, *S. filiforme* density, and dissolved oxygen.

1 **Table 3. Backward regression to compare algae to abiotic and seagrass characteristics.**

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 3 density across abiotic and seagrass variables. The variables included in the model, following
 4 selection, include *T. testudinum* density and the average canopy height. Variables that were
 5 determined to be insignificant to the model during the selection process were average shoot
 6 count, salinity, water temperature, *H. wrightii* density, *S. filiforme* density, and dissolved oxygen.

	SS	df	F ratio	Prob > F
<i>Final model</i>	4.87	2	7.10	0.0010
<i>Variables in final model</i>				
<i>T. testudinum</i> density	1.73		5.04	0.0258
Average canopy height	4.50		13.11	0.0004
	Model R ²	C(p)	F ratio	Prob > F
<i>Variables removed from the model</i>				
Average total shoot count	0.0760	7.02	0.02	0.8964
Salinity	0.0749	5.26	0.25	0.6182
Temperature	0.0737	3.53	0.27	0.6028
<i>H. wrightii</i> density	0.0702	2.36	0.83	0.3626
Dissolved oxygen	0.0652	1.52	1.18	0.2791
<i>S. filiforme</i> density	0.0604	0.65	1.14	0.2862

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