Sponges facilitate primary producers in a Bahamas seagrass system

Stephanie K. Archer[1]*, Philina A. English[2], Finella M. Campanino[1], Craig A. Layman[3]

1. Louisiana Universities Marine Consortium, Chauvin, Louisiana USA

2. Pacific Biological Station, Fisheries and Oceans Canada, Nanaimo, British Columbia Canada

3. Center for Energy, Environment, and Sustainability, Department of Biology, Wake Forest University, Winston-Salem, North Carolina, United States

*corresponding author: sarcher@lumcon.edu

Abstract

Seagrass beds are important coastal ecosystems worldwide that are shaped by facilitative interactions. Recent theoretical work has emphasized the potential for facilitative interactions involving foundation species to be destabilized in the face of anthropogenic change. Consequently, it is important to identify which taxa facilitate seagrasses. In other ecosystems, sponges contribute to the maintenance of diverse and productive systems through their facilitation of foundation species (e.g., mangroves) and the retention and recycling of energy and nutrients. Sponges are common in tropical and subtropical seagrass beds, yet we know little about how their presence impacts these communities. Here, we examine the impact of the sponge *Ircinia felix* on primary producers in a *Thalassia testudinum* dominated seagrass bed using a long-term field experiment in The Bahamas. We transplanted live sponges into the center of 5 m x 5 m plots and monitored the response of seagrasses and macroalgae. Sponge presence increased seagrass nutrient content and growth, as well as the abundance of macroalgae and non-dominant seagrass species (*Syringodium filiforme* and *Halodule wrightii*). These changes were not seen in the control (unmanipulated) or structure (where we placed a polypropylene sponge replica) plots. We conclude that *I. felix* facilitates seagrass bed primary producers in oligotrophic systems, likely due to nutrients supplied by the sponge. Our study shows that sponges can have a positive influence on seagrass bed foundation species. Further work is needed to understand how

this facilitation impacts the stability of seagrass beds in areas where human activities have increased ambient nutrient levels.

Declarations

Funding: This work was supported by North Carolina State University, NSF OCE 1405198 to Craig Layman, and donations from Win and Tana Archer.

Conflicts of interest: The authors declare they have no conflicts of interest.

Availability of data and material: The data can be found here https://doi.org/10.5061/dryad.qfttdz0gw.

Code availability: The code for all analyses and figures can be found here https://github.com/ecophilina/ircinia.

Authors contributions: SKA and CAL conceived of and designed the experiment. SKA conducted data collection. SKA, PAE, and FC analyzed the data. All authors were involved in the writing and editing of the manuscript.

Introduction

Foundation species are spatially-dominant, structure-forming taxa that form the base of entire ecosystems (Bruno and Bertness 2001; Altieri and van de Koppel 2014). Positive interactions, or facilitation between species, are particularly important in shaping ecosystems formed by foundation species (Bruno et al. 2003; Bulleri 2009; Zhang and Silliman 2019). Traditionally, research has focused on the mechanisms by which foundation species facilitate other species and the consequences for community-level diversity and ecosystem services (e.g., Hughes et al. 2014; Borst et al. 2018; Archer et al. 2020). However, a foundation species can also be the beneficiary of facilitation by members of their assemblages (Peterson et al. 2013; Ellison et al. 1996; Gagnon et al. 2020). Recent theoretical work by van der Heide et al. (2020) showed that the facultative facilitation of foundation species has the potential to create non-linear ecosystem dynamics in response to stressors. Such interactions can increase the range of environmental conditions over which ecosystem degradation will continue once it has begun. Consequently, it is important to understand which species facilitate foundation species, particularly in vulnerable coastal ecosystems.

Seagrass beds are important coastal ecosystems worldwide. They help to attenuate wave energy (Fonseca and Cahalan 1992), stabilize sediments (Folmer et al. 2012), store large amounts of carbon (Fourqurean et al. 2012), and are important sites for nutrient cycling (Hemminga et al. 1991). Seagrass beds also act as hot spots of productivity with diverse and abundant communities of macroalgae, invertebrates, and fish (Duffy 2006). The communities associated with seagrass beds also maintain important links with other coastal ecosystems, such as coral reefs, by acting as a nursery habitat (Heck et al. 2003; Adams et al. 2006) and feeding grounds (Meyer et al. 1983; Yeager et al. 2012). Unfortunately, numerous anthropogenic stressors have resulted in significant worldwide declines in the extent of seagrass habitats (Orth et al. 2006; Waycott et al. 2009).

As foundation species, seagrasses are often facilitated by filter feeders, such as bivalves (Gagnon et al. 2020). Bivalves can facilitate seagrasses through a variety of mechanisms, including decreasing water turbidity (e.g., Wall et al. 2008) and increasing nutrient availability (e.g., Reusch et al. 1994). Sponges, common in tropical and sub-tropical seagrass meadows (Archer et

al. 2015), are also efficient filter feeders (Reiswig 1971, 1974). Although sponges have the potential to strongly impact nutrient availability (Southwell et al. 2008; de Goeij et al. 2013; Archer et al. 2017), how they influence seagrasses and other associated primary producers is generally not well-understood. Despite the paucity of studies, there is some evidence that sponges can influence the growth and abundance of seagrass in a context-dependent manner (Archer et al. 2015, 2018).

In the present study, we investigated the impact of a large sponge, *Ircinia felix*, on seagrass bed primary producers. Using a 1.5 yr field-based experiment, we examined how sponge presence influenced macroalgal abundance and the abundance, growth, and nutrient content of seagrasses. *Ircinia felix* is a high microbial abundance sponge, indicating that it hosts a dense and diverse microbiome (Weisz et al. 2008). As a result, the *I. felix* holobiont (sponge and its associated microbiome) is capable of complex nitrogen (N) and phosphorus (P) transformations (Southwell et al. 2008; Archer et al. 2017). In our study system in The Bahamas, primary production is often co-limited by nitrogen and phosphorus (Allgeier et al. 2010). Therefore, we hypothesize that the presence of the sponge *I. felix* will facilitate both macroalgae and seagrasses resulting in more abundant and faster-growing primary producer communities.

Methods

Study site and experimental design

This study was conducted in a shallow (1.1 m low tide depth) subtidal seagrass bed located off of Southern Great Abaco Island, The Bahamas (26.02610 N, 77.37408 W). Fifteen 5 x 5 m plots were delineated in a continuous seagrass bed on June 9, 2013 by placing wooden stakes at the corners and center of each plot. All plots were separated >2 m. All variables (see below) were measured once before the establishment of the treatments, and again at 1, 5, 12, and 17 months after the treatments were established. After preliminary data were collected, each plot was randomly assigned to one of three treatments: control (n=5), structure (n=5), or sponge (n=5; Fig. S1). Control plots were not manipulated. A polypropylene model of a sponge was placed inside a cage at the center of each structure plot. A single living sponge (*I. felix*, average volume ± standard deviation, 2.5 ± 0.75 L) was placed inside a cage in the center of each sponge plot. Live

sponges were replaced as needed with a total of 3 individual sponge replacements, all occurring within the first month of the experiment.

Response variables

Primary producers (seagrasses and macroalgae) were quantified within three 1 x 1 m quadrats at increasing distances from the center of each plot. The 0 distance quadrat was placed around the sponge or sponge model (sponge and structure plots) or the center (control plots). The 1 m distance quadrat was placed immediately adjacent to the 0 distance quadrat, extending from 0.5-1.5 m from the center point of the plot and the 2 m distance quadrat covered an area 1.5-2.5 m from the center point (Fig. S1). Macroalgae were identified to genus and counts were summed across the three 1 m^2 quadrats. Where individuals were difficult to distinguish (e.g. *Laurencia* spp.) clumps of algae were recorded as individuals. If identification was not possible *in situ*, a representative sample was photographed and subsequently collected. Three species of seagrass were observed in the experimental plots: *T. testudinum*, *Syringodium filliforme*, and *Halodule wrightii*. Shoot densities of these species were counted within four 20 cm x 20 cm "sub-quadrats" that were placed haphazardly within each of the quadrats described above. *S. filliforme* and *H. wrightii* were initially rare and patchily distributed (combined density [mean ± sd] of 149.2 ± 172 shoots m^{-2}, compared to *T. testudinum*'s initial density of 788.1 ± 386.2 shoots m^{-2}). Therefore our counts of *S. filliforme* and *H. wrightii* were pooled, and growth and nutrient content were only measured in *T. testudinum*.

Growth rates of *T. testudinum* shoots were measured at four distances from the center of each plot: the center of the plot or immediately next to the sponge/model sponge (designated as 0 m) and in permanently marked points (using stakes) at 0.5, 1.0, and 2.0 m from the center of the plot. Growth rates were calculated using the standard blade hole punching technique (Zieman 1974) on five short *T. testudinum* shoots per distance. Approximately two weeks after the blades were marked growth was measured *in situ* to minimize disturbance to the plots.

Nutrient content (%C, %N, and %P) was assessed for 10 shoots growing within 0.25 m of the center of each plot, before the beginning of the experiment and again after 1 year. The second youngest blade from each shoot was collected, combined with other blades from the same plot and sampling period, and dried at 60ºC for 48-72 hours. For %C and %N analysis seagrass tissue

was then ground, weighed into tin capsules, and sent to the University of Georgia Stable Isotope Ecology Laboratory for analysis. Percent phosphorus (%P) was determined by dry oxidation acid hydrolysis extraction followed by colorimetric analysis (Fourqurean et al. 1992).

Statistical analysis

Two sampling events occurred in the summer (July, 1 and 12 months into the experiment) and two in the winter (November, 5 and 17 months into the experiment); therefore, all response variables were visually examined for a seasonal effect. If responses differed noticeably between summer and winter, separate factors for season and year of the experiment (1st or 2nd year) were included as explanatory variables in those analyses; otherwise, a continuous effect of months into the experiment was the only temporal variable. In either case, the effects of temporal variables were allowed to interact with experimental treatment (control, structure, or sponge), but season and year were only allowed to interact with each other when included as random slopes (for algal abundance only).

Macroalgal abundances were fit with a negative binomial distribution and a log link. Overall abundance did fluctuate seasonally, so we included fixed effects of treatment, year, and season, and random slopes for the effect of season and year for each taxon. This provides an estimate of the overall treatment effect between years and seasons, as well as taxa-specific differences in these effects.

Shoot densities (counts of shoots m^{-2}) were fit with a quasi-Poisson distribution and a log link. Seagrass shoot counts did not fluctuate between seasons, so we included fixed effects of months into the experiment in a three-way interaction with treatment and distance (a linear covariate representing the center of contiguous 1 m^2 sampling quadrats). Because species-specific shoot counts were not collected for *S. filliforme* or *H. wrightii*, shoot density was modeled for *T. testudinum* alone, as the dominant species, and for *S. filliforme* and *H. wrightii* combined, as sub-dominant species.

T. testudinum growth rate (mm^2 day^{-1}) was analyzed in response to treatment interacting separately with fixed effects of distance, season, and year, as well as stake ID as an additional random factor. We tested for a treatment effect at each distance sampled (0, 0.5, 1, and 2 m) to identify a potential threshold of response. Because an effect was detected at 0 and 0.5 m and not

at the 1 m or 2 m sampling points, the relative distance was included in this model as a factor, with 0 and 0.5 m assigned as "near" and 1 and 2 m assigned as "far."

Finally, we tested for a treatment effect on nutrient concentrations (% of nitrogen, carbon, and phosphorus) in *T. testudinum* shoots one year into the experiment, as compared to samples collected before the experiment.

Plot was included as a random factor in all models, along with any additional random effects as described above. For all response variables, except nutrient concentrations, an offset of the mean values measured before the initiation of the experiment was included (when a log link was used, this value had 1 added to it and was log-transformed). Macroalgal abundance and seagrass shoot densities were assessed using generalized mixed effect models implemented using the glmmTMB package (Brooks et al. 2017); the distribution and link used in each model are described above. All other variables were modeled linear mixed-effects models using the lme4 package (Bates et al. 2015). All analyses were completed in R version 4.0.2 (R Core Team 2020).

Results

Throughout the results, we present effect sizes and 95% confidence intervals rather than test statistics and p-values. All test statistics and p-values can be found in the supplemental material (Tables S1-S7).

Macroalgal abundance

Macroalgal abundances decreased in the winter in all treatments, however, the decrease was only significant in the control (β = -0.83, -1.47 to -0.19). In the sponge treatment, macroalgal abundances increased in year two of the experiment (β = 0.86, 0.12 to 1.59, Fig. 1). This pattern of increased abundance was consistent across most taxa (Fig. S2). Meanwhile, macroalgal abundances in the control and structure plots did not differ from each other (Table S1), but both differed from those in the sponge treatments by year two (β = -0.79, -1.37 to -0.2 and β = -0.64, -1.21 to -0.07 respectively). Macroalgal abundances did not change significantly between the first and second years of the experiment in the control and structure plots (Fig. 1).

183 Shoot densities

184 *Thalassia testudinum* shoot densities decreased similarly in all treatments over time, but this
185 decrease was not significant in sponge plots (control: β = -0.015, -0.028 to -0.003; structure: β =
186 -0.024, -0.036 to -0.011; sponge: β = -0.0098, -0.0226 to 0.0031, Fig. 2). There was no
187 significant effect of distance for any treatment initially or over time (Table S2). *Syringodium*
188 *filiforme* and *H. wrightii* shoot densities did not change in control or structure plots but increased
189 in sponge plots (β = 0.084, 0.055 to 0.112, Fig. 2). The increase in sponge plots was significantly
190 different than both control (β = -0.073, -0.112 to -0.034) and structure plots (β = -0.091, -0.136
191 to -0.047). Initially, *S. filiforme* and *H. wrightii* were more abundant further from the center of
192 sponge plots (β = 0.43, 0.15 to 0.71). However, over time *S. filiforme* and *H. wrightii* increased
193 more near the center of sponge plots (time * distance: β = -0.027, -0.05 to -0.005). There was no
194 significant effect of distance in control or structure plots (Table S3).

195 *Thalassia testudinum* growth

196 Seagrass growth was impacted by treatment at 0 ($F_{2,12}$= 4.29 , p = 0.04) and 0.5 m ($F_{2,12}$= 4.47 , p
197 = 0.04) but this effect had disappeared by 1 m. As a result, we pooled seagrass growth for the
198 near (0 and 0.5 m) and far (1 and 2 m) distances for further analysis. Seagrass growth was slower
199 in the winter (β = -15, -17 to -13) and the decrease in growth during the winter was not different
200 among treatments (Table S4). In sponge plots, seagrass grew slower further from the sponge (β =
201 -8.8, -16.3 to -1.4, Fig. 3). There was no difference in seagrass growth between distances in the
202 control or structure plots. In sponge plots, seagrass grew faster in the second year of the
203 experiment (β = 3.1, 1 to 5.2, Fig. 3). By contrast, seagrass growth declined in the control and
204 structure plots , but this decline was only significant in the control (β = -2.3, -4.4 to -0.2, Fig. 3).

205 *Thalassia testudinum* nutrient concentrations

206 Before the experiment, seagrass in sponge plots had significantly lower nitrogen concentrations
207 than control plots (Fig. 4A, β = -0.35, -0.6 to -0.1) but not structure plots (Table S5). Percent
208 nitrogen in seagrass tissues in both control and structure plots declined similarly over time (Fig.
209 4A), but the decrease was only significant in control plots (β = -0.062, -0.114 to -0.01).
210 Conversely, seagrass % N responded differently in sponge plots than in both the control (β = -

211 0.34, -0.57 to -0.12) and structure (β = -0.28, -0.5 to -0.06) plots. Sponge plots had a higher % N
212 after one year (Fig. 4A); however, this increase was not significant.

213 The pattern was similar for percent carbon; seagrass % C was initially lower in sponge plots than
214 in control (Fig. 4B, β = -3.2, -5.8 to -0.6) and structure plots (β = -2.2, -4.8 to 0.4). Again,
215 percent carbon in seagrass tissue decreased similarly in both control and structure plots (Fig. 4B).
216 However, this decrease was only significant in structure plots (β = -3.1, -5.7 to -0.5). In sponge
217 plots, % carbon showed a slight increase in seagrass tissues, resulting in significantly different
218 response for structure plots (β = -4.6, -8.2 to -0.9) but not for control plots (Table S6).

219 Phosphorus concentrations were similar in all plot types at the beginning of the experiment (Fig.
220 4C). Although % phosphorus in seagrass tissues followed the same patterns as both % nitrogen
221 and % carbon, decreasing in control and structure plots while increasing in sponge plots, none of
222 these changes were significant(Fig. 4C). However, the pattern of change over time was
223 significantly different between control and sponge plots (β = 0.012, 0.002 to 0.022), but not
224 between structure and sponge plots or control and structure plots (Table S7).

225 **Discussion**

226 Facilitation plays an important role in structuring seagrass ecosystems. Although research has
227 largely focused on how seagrasses facilitate other organisms, knowing which taxa facilitate
228 seagrasses will be equally important for understanding long-term seagrass bed dynamics in the
229 face of a changing ocean. We provide the first experimental evidence that the sponge *Ircinia felix*
230 facilitates seagrass bed primary producers. Specifically, we demonstrate that the presence of a
231 sponge resulted in increased nutrient content and growth of the dominant seagrass taxon, as well
232 as an increased abundance of both macroalgae and non-dominant seagrasses.

233 Many sponge holobionts, including *I. felix*, are capable of complex nutrient transformations and
234 often release bioavailable forms of nitrogen and phosphorus into the environment (Southwell et
235 al. 2008; Archer et al. 2017). Because primary producers are typically limited by both nitrogen
236 and phosphorus in Bahamian coastal ecosystems (Allgeier et al. 2010), we hypothesized that the
237 sponges we transplanted would supply these nutrients resulting in the facilitation of seagrass bed
238 primary producers. Consistent with our hypothesis, we saw an increase in seagrass nutrient

content in plots with live sponges relative to our other treatments. This is not the first study to find that sponge-released nutrients can facilitate primary producers. For example, sponges growing on mangrove roots supply nutrients to the trees (Ellison et al. 1996) and sponges can supply nitrogen to macroalgae on coral reefs (Easson et al. 2014). Further, Archer et al. (2015) showed that a sponge (*Halichondria melanadocia*) that grows around the base and leaves of seagrass shoots likely provide nutrients to those shoots. However, to the best of our knowledge, this study is the first to show that a single massive form sponge can increase nutrient content in seagrasses within a 0.25 m radius.

The other changes we documented in the primary producers in our sponge plots are consistent with an increase in nutrient supply in this oligotrophic system. For example, we recorded an increase in *S. filliformе* and *H. wrightii* in sponge plots. Such an increase has been associated with the addition of a novel source of nutrients in similar systems; the addition of nutrients in the form of bird guano shifted the dominant seagrass species in a Florida Bay seagrass bed from *T. testudinum* to *H. wrightii* (Powell et al. 1989; Fourqurean et al. 1995). Concomitantly, we saw an increase in seagrass growth near the transplanted sponges and a general increase in macroalgal abundance in sponge plots. It is possible that the addition of structure to our plots altered water flow and influenced the primary producers. However, similar structures (a sponge replica and holding cage) were added to our structure plots, and the response of the primary producers in control and structure plots did not differ significantly for most responses, whereas in most cases, we saw a significant response in our sponge plots. This suggests that living sponges, rather than the presence of structure, are the cause of increases in seagrass nutrient content and growth, and in the abundance of macroalgae and non-dominant seagrass species (*S. filliformе* and *H. wrightii*).

Seagrasses are often facilitated by other filter feeders increasing nutrient availability (Gagnon et al. 2020). For example, Reusch et al. (1994) found that the blue mussel (*Mytilus edulis*) facilitates seagrass growth via fertilization of sediments through the deposition of biodeposits (feces and pseudofeces). However, this effect appears to be context-dependent. Specifically, in eutrophic conditions mussels cause water column nutrient enrichment and biodeposits that combine to result in high sulfide concentrations in sediments, which in turn drives a reduction in seagrass density (Vinther et al. 2012). The effect of the epiphytic sponge *H. melanadocia* was

also found to be partially determined by the sponge's supply of limiting nutrients (Archer et al. 2015, 2018). Under oligotrophic conditions this sponge-seagrass interaction is commensal, with the seagrass providing an attachment point for the sponge and the seagrass receiving a supply of limiting nutrients. The seagrass in this relationship displayed a net neutral effect of sponge presence, where there was a balance between a negative effect of the sponge shading the seagrass and the positive effect of the sponge releasing bioavailable forms of N and P (Archer et al. 2015). However, this interaction is also context-dependent, with small increases in ambient nutrient levels resulting in a shift from commensalism to parasitism and a reduction of seagrass growth and biomass (Archer et al. 2018).

The context-dependent nature of many facilitative interactions between filter feeders and seagrasses can lead to seemingly unpredictable instability in seagrass ecosystems (van der Heide et al. 2020). For example, these interactions can lower the threshold of nutrient pollution that leads to a decline in seagrass ecosystems, i.e., seagrass loss occurs at lower nutrient levels than would be predicted by studying seagrasses in isolation. At first glance, it may appear that the facilitation of primary producers by *I. felix* would be no different, as this facilitation appears to be based on nutrients supplied by the sponge. However, nutrient processing by the *I. felix* holobiont is also context-dependent. Whereas there is little spatial or temporal variability in *I. felix*'s symbiotic microbiome (Erwin et al. 2012); the active portion of the microbiome appears to be dependent on ambient nutrient concentrations (Archer et al. 2017). As a result the *I. felix* holobiont acts as a source of bioavailable forms of N and P when ambient concentrations of those nutrient species are low, and as a sink when they are high (Archer et al. 2017). This context-dependent nutrient processing has been documented in other sponges (Pawlik and McMurray 2020). The ecosystem-level effects of this context-dependent nutrient processing have not been studied, yet it is reasonable to predict that it should have a stabilizing effect on ambient nutrient levels when sponges are present in sufficient densities. Future work should focus on the impact of *I. felix* presence on seagrass bed primary producers under a range of ambient nutrient levels to better understand if context-dependent nutrient processing by sponges can act as a stabilizing force in seagrass beds.

It is important to understand the facilitation of foundation species, like seagrass, because this can have cascading consequences on local diversity, ecosystem function, and the delivery of

ecosystem services. We studied the effect of *I. felix* in unimpacted seagrass beds and found that sponges can facilitate seagrass bed primary producers, likely through nutrients supplied by the sponge. However, theoretical and empirical work show that interactions involving nutrient-transfer are often context-dependent and that such interactions involving foundation species can lead to non-linear ecosystem dynamics when human activities alter ambient nutrient levels. Therefore, this study represents a first step in understanding how sponges influence seagrass ecosystems. Further work will be necessary to determine if there are impacts on the wider ecosystem and whether the facilitative relationship between sponges and primary producers breaks down in impacted systems.

Acknowledgements

We would like to thank Friends of the Environment (NGO, Abaco, The Bahamas), Diane Claridge and Charlotte Dunn for their logistical support, Erik Archer, Elizabeth Whitman, and Ryann Rossi for their assistance in the field, and Katie Lewia and Jillian Tucker for their assistance in the lab, and the reviewers for their help improving this manuscript. This work was supported by donations from Win and Tana Archer, North Carolina State University, and NSF OCE 1405198.

References

Adams A, Dahlgren C, Kellison G, Kendall M, Layman C, Ley J, Nagelkerken I, Serafy J (2006) Nursery function of tropical back-reef systems. Marine Ecology Progress Series 318:287–301. doi: 10.3354/meps318287

Allgeier JE, Rosemond AD, Mehring AS, Layman CA (2010) Synergistic nutrient colimitation across a gradient of ecosystem fragmentation in subtropical mangrove-dominated wetlands. Limnology and Oceanography 55:2660–2668. doi: 10.4319/lo.2010.55.6.2660

Altieri AH, van de Koppel J (2014) Foundation Species in Marine Ecosystems. In: Bertness MD, Bruno JF, Silliman BR, Stachowicz JJ (eds) Marine Community Ecology and Conservation. Sinauer Associates, Inc., Sunderland, MA, pp 37–56

Archer SK, Stoner EW, Layman CA (2015) A complex interaction between a sponge (*Halichondria Melanadocia*) and a seagrass (*Thalassia Testudinum*) in a subtropical coastal ecosystem. Journal of Experimental Marine Biology and Ecology 465:33–40. doi: 10.1016/j.jembe.2015.01.003

Archer SK, Stevens JL, Rossi RE, Matterson KO, Layman CA (2017) Abiotic conditions drive significant variability in nutrient processing by a common Caribbean sponge, *Ircinia Felix*. Limnology and Oceanography 62:1783–1793. doi: 10.1002/lno.10533

Archer SK, Hensel E, Layman CA (2018) Ambient nutrient availability drives the outcome of an interaction between a sponge (*Halichondria Melanadocia*) and seagrass (*Thalassia Testudinum*). Journal of Experimental Marine Biology and Ecology 503:86–91. doi: 10.1016/j.jembe.2018.02.005

Archer SK, Kahn AS, Thiess M, Law L, Leys SP, Johannessen SC, Layman CA, Burke L, Dunham A (2020) Foundation Species Abundance Influences Food Web Topology on Glass Sponge Reefs. Frontiers in Marine Science 7:549478. doi: 10.3389/fmars.2020.549478

Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48. doi: 10.18637/jss.v067.i01

Borst ACW, Verberk WCEP, Angelini C, Schotanus J, Wolters J-W, Christianen MJA, Van Der Zee EM, Derksen-Hooijberg M, Van Der Heide T (2018) Foundation species enhance food web complexity through non-trophic facilitation. PLOS ONE 13:e0199152. doi: 10.1371/journal.pone.0199152

Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Maechler M, Bolker BM (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. The R Journal 9:378–400.

Bruno JF, Bertness MD (2001) Habitat modification and facilitation in benthic marine communities. In: Bertness MD (ed) Marine Community Ecology. Sinauer, pp 201–218

Bruno JF, Stachowicz JJ, Bertness MD (2003) Inclusion of facilitation into ecological theory. Trends in Ecology & Evolution 18:119–125. doi: 10.1016/S0169-5347(02)00045-9

352 Bulleri F (2009) Facilitation research in marine systems: State of the art, emerging patterns and
353 insights for future developments. Journal of Ecology 97:1121–1130. doi: 10.1111/j.1365-
354 2745.2009.01567.x

355 de Goeij JM, van Oevelen D, Vermeij MJA, Osinga R, Middelburg JJ, de Goeij AFPM,
356 Admiraal W (2013) Surviving in a marine desert: The sponge loop retains resources within coral
357 reefs. Science 342:108–110. doi: 10.1126/science.1241981

358 Duffy J (2006) Biodiversity and the functioning of seagrass ecosystems. Marine Ecology
359 Progress Series 311:233–250. doi: 10.3354/meps311233

360 Easson CG, Slattery M, Baker DM, Gochfeld DJ (2014) Complex ecological associations:
361 Competition and facilitation in a sponge-algal interaction. Marine Ecology Progress Series
362 507:153–167. doi: 10.3354/meps10852

363 Ellison AM, Farnsworth EJ, Twilley RR (1996) Facultative mutualism between red mangroves
364 and root-fouling sponges in Belizean mangal. Ecology 77:2431–2444. doi: 10.2307/2265744

365 Erwin PM, Pita L, Lopez-Legentil S, Turon X (2012) Stability of sponge-associated bacteria
366 over large seasonal shifts in temperature and irradiance. Applied and environmental
367 microbiology 78:7358–7368. doi: 10.1128/aem.02035-12

368 Folmer EO, van der Geest M, Jansen E, Olff H, Michael Anderson T, Piersma T, van Gils JA
369 (2012) Seagrass-Sediment Feedback: An Exploration Using a Non-recursive Structural Equation
370 Model. Ecosystems 15:1380–1393. doi: 10.1007/s10021-012-9591-6

371 Fonseca MS, Cahalan JA (1992) A preliminary evaluation of wave attenuation by four species of
372 seagrass. Estuarine, Coastal and Shelf Science 35:565–576. doi: 10.1016/S0272-7714(05)80039-
373 3

374 Fourqurean JW, Zieman JC, Powell GV (1992) Phosphorus limitation of primary production in
375 Florida Bay: Evidence from C: N: P ratios of the dominant seagrass *Thalassia Testudinum*.
376 Limnology and Oceanography 37:162–171. doi: 10.4319/lo.1992.37.1.0162

Fourqurean JW, Powell GVN, Kenworthy WJ, Zieman JC (1995) The Effects of Long-Term Manipulation of Nutrient Supply on Competition between the Seagrasses *Thalassia Testudinum* and *Halodule Wrightii* in Florida Bay. Oikos 72:349–358. doi: 10.2307/3546120

Fourqurean JW, Duarte CM, Kennedy H, Marbà N, Holmer M, Mateo MA, Apostolaki ET, Kendrick GA, Krause-Jensen D, McGlathery KJ, Serrano O (2012) Seagrass ecosystems as a globally significant carbon stock. Nature Geoscience 5:505–509. doi: 10.1038/ngeo1477

Gagnon K, Rinde E, Bengil EGT, Carugati L, Christianen MJA, Danovaro R, Gambi C, Govers LL, Kipson S, Meysick L, Pajusalu L, Tüney Kızılkaya İ, Koppel J, Heide T, Katwijk MM, Boström C (2020) Facilitating foundation species: The potential for plant-bivalve interactions to improve habitat restoration success. Journal of Applied Ecology 57:1161–1179. doi: 10.1111/1365-2664.13605

Heck K, Hays G, Orth R (2003) Critical evaluation of the nursery role hypothesis for seagrass meadows. Marine Ecology Progress Series 253:123–136. doi: 10.3354/meps253123

Hemminga M, Harrison P, Van Lent F (1991) The balance of nutrient losses and gains in seagrass meadows. Marine Ecology Progress Series 71:85–96. doi: 10.3354/meps071085

Hughes AR, Gribben PE, Kimbro DL, Bishop MJ (2014) Additive and site-specific effects of two foundation species on invertebrate community structure. Marine Ecology Progress Series 508:129–138. doi: 10.3354/meps10867

Meyer JL, Schultz ET, Helfman GS (1983) Fish Schools: An Asset to Corals. Science, New Series 220:1047–1049. doi: 10.1126/science.220.4601.1047

Orth RJ, Carruthers TJB, Dennison WC, Duarte CM, Fourqurean JW, Heck KL, Hughes AR, Kendrick GA, Kenworthy WJ, Olyarnik S, Short FT, Waycott M, Williams SL (2006) A global crisis for seagrass ecosystems. Bioscience 56:987–996. doi: 10.1641/0006-3568(2006)56[987:agcfse]2.0.co;2

Pawlik JR, McMurray SE (2020) The Emerging Ecological and Biogeochemical Importance of Sponges on Coral Reefs. Annual Review of Marine Science 12:315–337. doi: 10.1146/annurev-marine-010419-010807

Peterson BJ, Valentine JF, Heck Jr KL (2013) The snapperGrunt pump: Habitat modification and facilitation of the associated benthic plant communities by reef-resident fish. Journal of Experimental Marine Biology and Ecology 441:50–54. doi: 10.1016/j.jembe.2013.01.015

Powell GVN, Kenworthy JW, Fourqurean JW (1989) Experimental evidence for nutrient limitation of seagrass growth in a tropical estuary with restricted circulation. Bulletin of Marine Science 44:324–340.

R Core Team (2020) R: A language and environment for statistical computing.

Reiswig HM (1971) Particle feeding in natural populations of 3 marine Demosponges. Biological Bulletin 141:568–591. doi: 10.2307/1540270

Reiswig HM (1974) Water transport, respiration and energetics of three tropical marine sponges. Journal of Experimental Marine Biology and Ecology 14:231–249. doi: 10.1016/0022-0981(74)90005-7

Reusch T, Chapman A, Groger J (1994) Blue mussels *Mytilus Edulis* do not interfere with eelgrass *Zostera Marina* but fertilize shoot growth through biodeposition. Marine Ecology Progress Series 108:265–282. doi: 10.3354/meps108265

Southwell MW, Weisz JB, Martens CS, Lindquist N (2008) In situ fluxes of dissolved inorganic nitrogen from the sponge community on Conch Reef, Key Largo, Florida. Limnology and Oceanography 53:986–996. doi: 10.4319/lo.2008.53.3.0986

van der Heide T, Angelini C, de Fouw J, Eklöf JS (2020) Facultative mutualisms: A double-edged sword for foundation species in the face of anthropogenic global change. Ecology and Evolution 00:16. doi: 10.1002/ece3.7044

Vinther H, Norling P, Kristensen P, Dolmer P, Holmer M (2012) Effects of coexistence between the blue mussel and eelgrass on sediment biogeochemistry and plant performance. Marine Ecology Progress Series 447:139–149. doi: 10.3354/meps09505

Wall C, Peterson B, Gobler C (2008) Facilitation of seagrass *Zostera Marina* productivity by suspension-feeding bivalves. Marine Ecology Progress Series 357:165–174. doi: 10.3354/meps07289

Waycott M, Duarte CM, Carruthers TJB, Orth RJ, Dennison WC, Olyarnik S, Calladine A, Fourqurean JW, Heck KL Jr., Hughes AR, Kendrick GA, Kenworthy WJ, Short FT, Williams SL (2009) Accelerating loss of seagrasses across the globe threatens coastal ecosystems. Proceedings of the National Academy of Sciences of the United States of America 106:12377–12381. doi: 10.1073/pnas.0905620106

Weisz JB, Lindquist N, Martens CS (2008) Do associated microbial abundances impact marine demosponge pumping rates and tissue densities? Oecologia 155:367–376. doi: 10.1007/s00442-007-0910-0

Yeager L, Acevedo C, Layman C (2012) Effects of seascape context on condition, abundance, and secondary production of a coral reef fish, *Haemulon Plumierii*. Marine Ecology Progress Series 462:231–240. doi: 10.3354/meps09855

Zhang Y, Silliman B (2019) A Facilitation Cascade Enhances Local Biodiversity in Seagrass Beds. Diversity 11:30. doi: 10.3390/d11030030

Zieman JC (1974) Methods for the study of the growth and production of turtle grass, *Thalassia Testudinum* König. Aquaculture 4:139–143. doi: 10.1016/0044-8486(74)90029-5

Figures

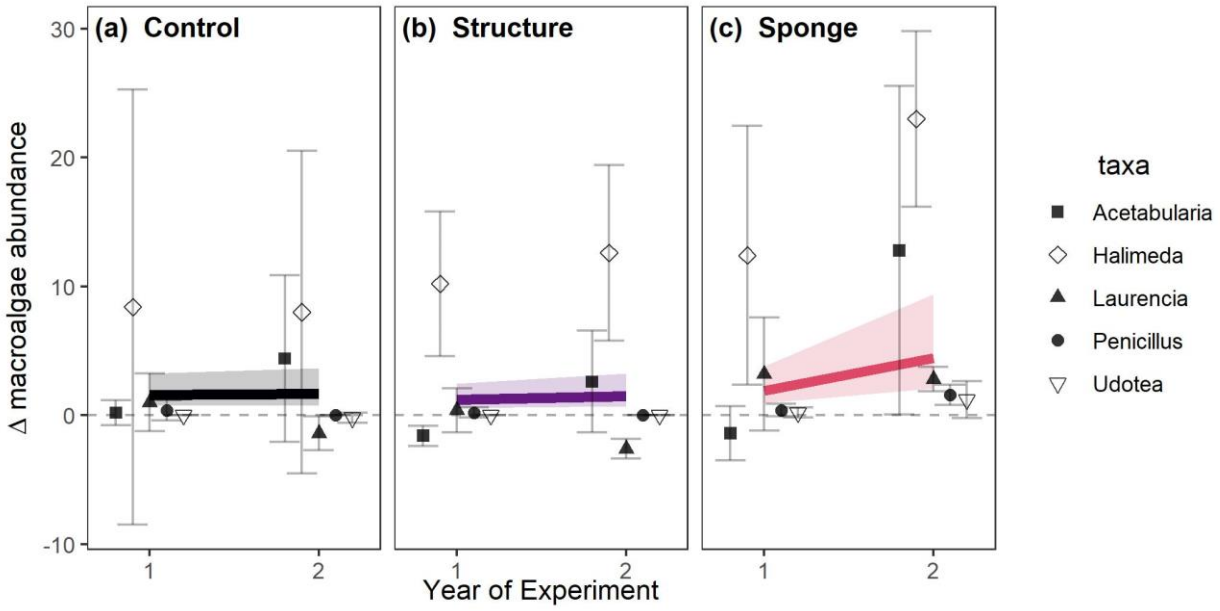
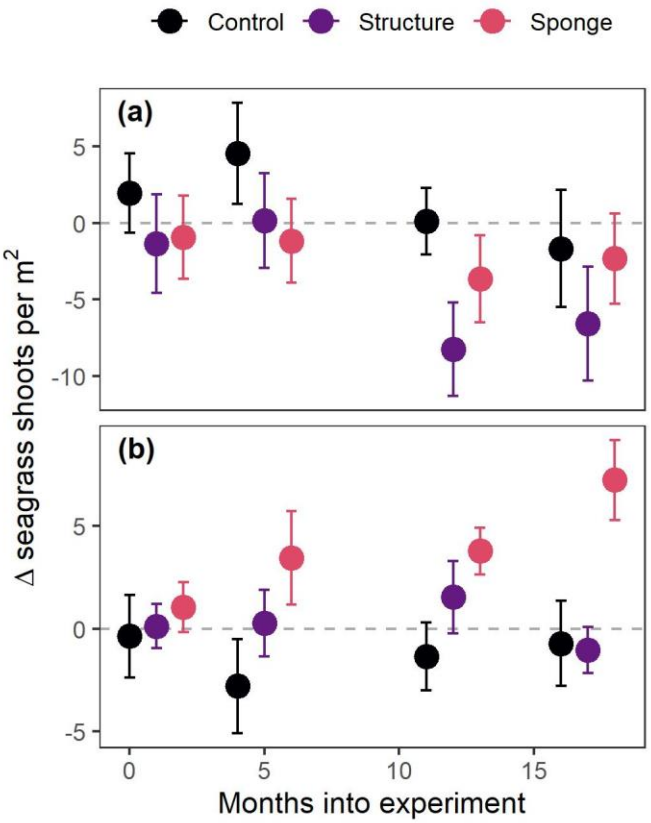
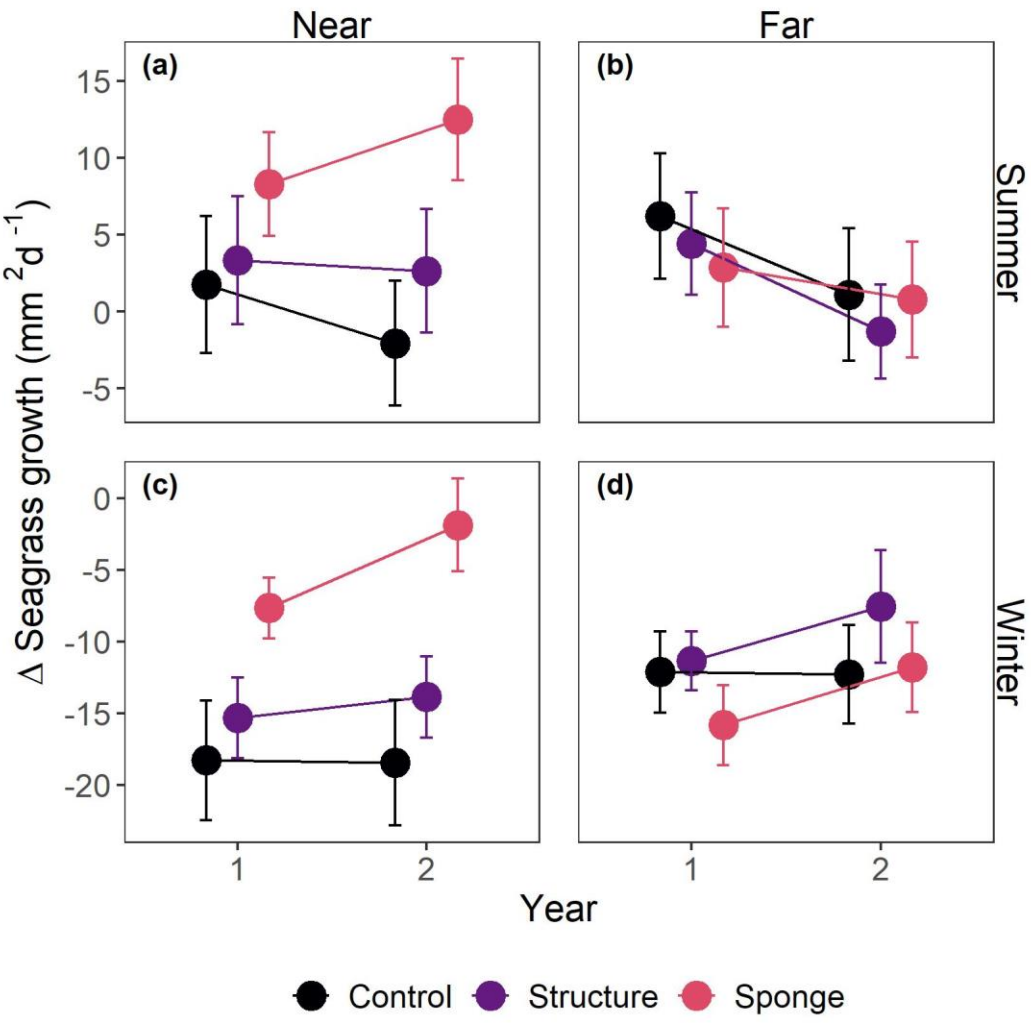


Figure 1: The change in macroalgal abundances relative to counts made immediately before the experiment in (a) control, (b) structure, and (c) sponge plots between summers of year 1 and 2 (1 and 12 months into the experiment). Bold lines represents the global fit for change in summer abundance of an average algae species from a mixed model with random slopes for each species. Observed taxa-specific mean count differences and model estimates are both presented with their 95% confidence intervals.



455

456 Figure 2: Change in seagrass shoot densities (means and 95% confidence intervals) relative to
457 before the experiment of (a) *T. testudinum* and (b) *S. filliforme* and *H. wrightii* combined
458 throughout the experiment.



459

460 Figure 3: Change in seagrass growth rates (means and 95% confidence intervals) relative to
461 summer measurements taken before the experiment for *T. testudinum* shoots growing less than
462 1m (a & c) or between 1 and 2 m (b & d) from the sponge/centre of the plot. Summer sampling
463 (a & b) happened in months 1 and 12 (years 1 and 2 respectively) whereas winter sampling (c &
464 d) occurred in months 5 and 17.

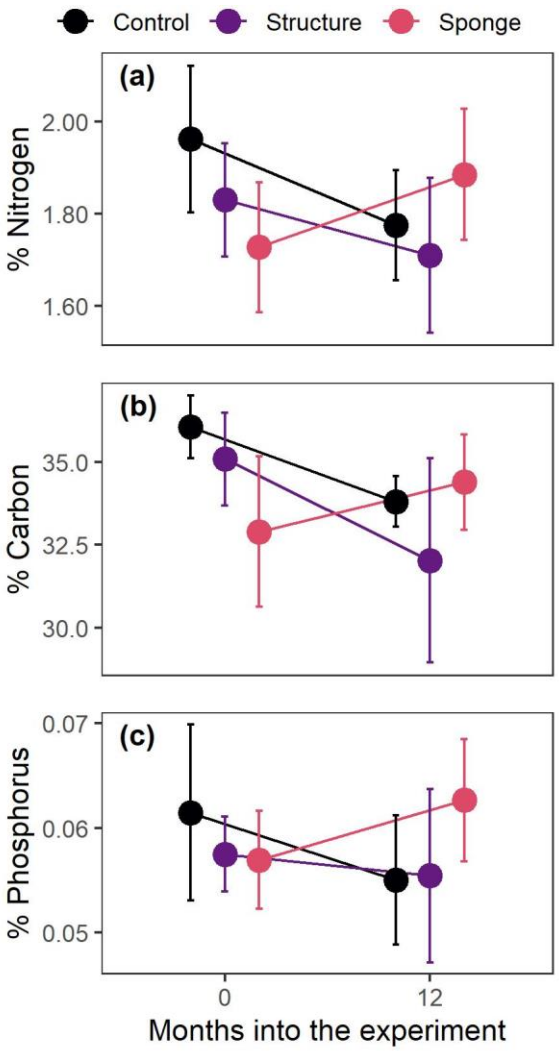


Figure 4: Nutrient concentrations (means and 95% confidence intervals) in *T. testudinum* tissue including (a) percent nitrogen, (b) percent carbon, and (c) percent phosphorus measured before initiation of the experiment and at 1 year (12 months) into the experiment.

Sponges facilitate primary producers in a Bahamas seagrass system

Stephanie K. Archer, Finella Campanino, Philina English, Craig A. Layman

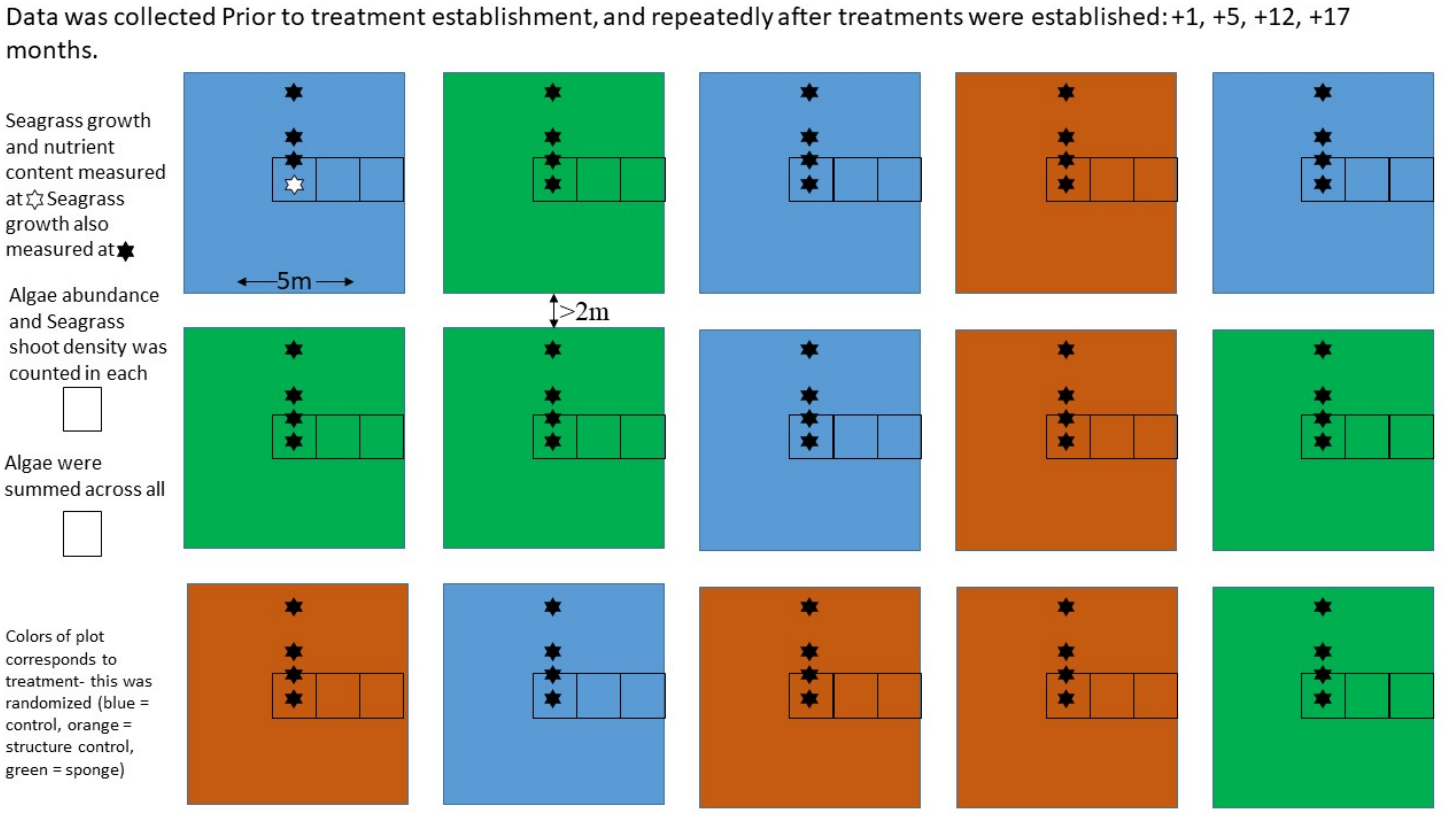


Figure S1. Experimental design and sampling scheme

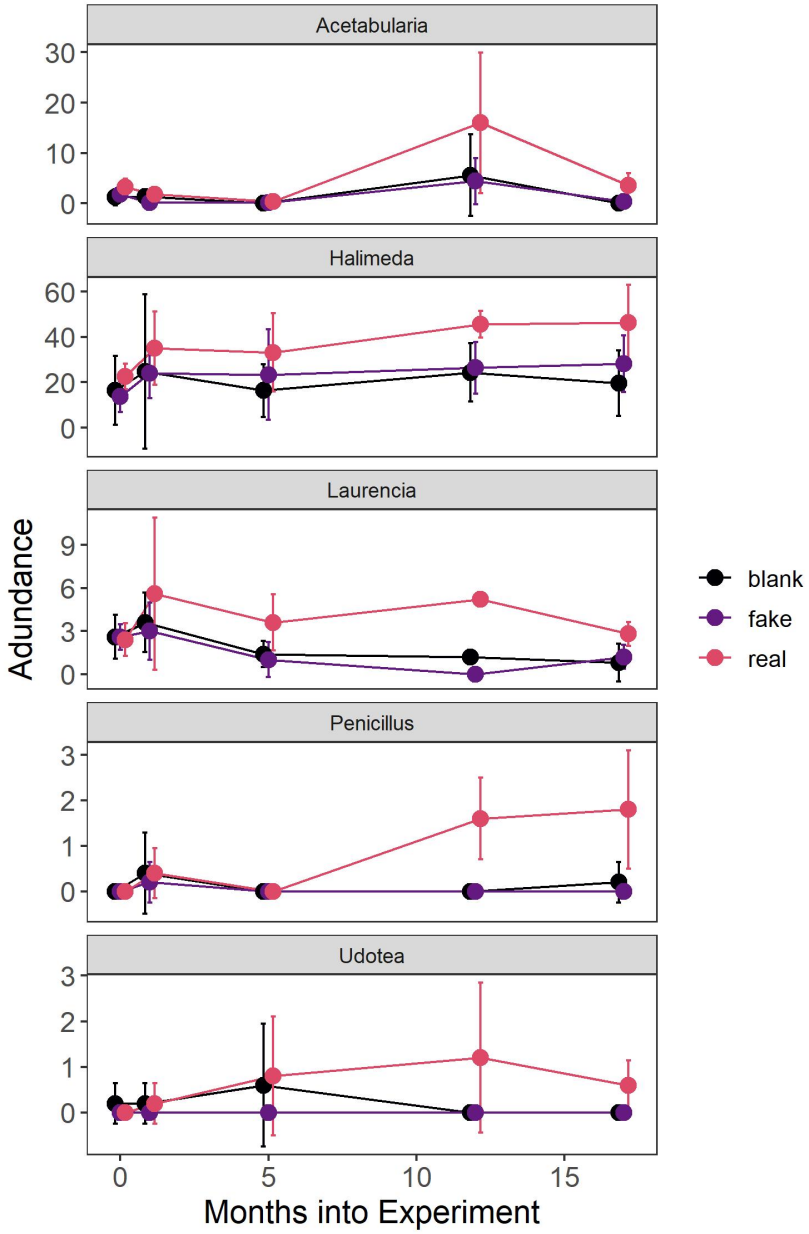

Acetabularia
Halimeda
Laurencia
Penicillus
Udotea
Adundance
Months into Experiment
blank
fake
real

Figure S2. Taxon-specific algal abundance over the course of the experiment.

All results tables have the sponge treatment as the reference level for treatment.

Table S1. Macroalgal abundance model results.

	Estimate	Std. Error	z value	Pr(>|z|)	
Intercept	-1.200	0.62	-2.00	0.0500	*
Treatment [control]	0.610	0.50	1.20	0.2300	
Treatment [structure control]	0.180	0.49	0.37	0.7100	
Year	0.860	0.37	2.30	0.0220	*
Season [winter]	-0.480	0.30	-1.60	0.1100	
Treatment [control] x Year 2	-0.790	0.30	-2.60	0.0086	**
Treatment [structure control] x Year 2	-0.640	0.29	-2.20	0.0290	*
Treatment [control] x Season [winter]	-0.340	0.30	-1.10	0.2500	
Treatment [structure control] x Season [winter]	0.083	0.29	0.29	0.7800	

Table S2. *Thalassia testudinum* shoot density model results.

	Estimate	Std. Error	z value	Pr(>|z|)
Intercept	0.0024	0.0810	0.03	0.98
Treatment [control]	0.0950	0.1100	0.85	0.40
Treatment [structure control]	0.0170	0.1100	0.15	0.88
Sampling	-0.0098	0.0066	-1.50	0.14
Distance from center	-0.0660	0.0570	-1.20	0.25
Treatment [control] x Sampling	-0.0057	0.0090	-0.63	0.53
Treatment [structure control] x Sampling	-0.0140	0.0092	-1.50	0.13
Treatment [control] x Distance from center	0.0750	0.0770	0.97	0.33
Treatment [structure control] x Distance from center	0.0510	0.0760	0.68	0.50
Sampling x Distance from center	0.0065	0.0054	1.20	0.22
Treatment [control] x Sampling x Distance from center	-0.0017	0.0073	-0.23	0.81
Treatment [structure control] x Sampling x Distance from center	0.0014	0.0072	0.19	0.85

Table S3. *Syringodium filliforme* and *Halodule wrightii* shoot density model results.

	Estimate	Std. Error	z value	Pr(>|z|)	
Intercept	-0.3800	0.300	-1.300	2.0e-01	
Treatment [control]	-0.2200	0.410	-0.540	5.9e-01	
Treatment [structure control]	0.0046	0.420	0.011	9.9e-01	
Sampling	0.0840	0.014	5.800	0.0e+00	***
Distance from center	0.4300	0.140	3.000	2.6e-03	**
Treatment [control] x Sampling	-0.0730	0.020	-3.600	2.7e-04	***
Treatment [structure control] x Sampling	-0.0910	0.023	-4.000	5.8e-05	***
Treatment [control] x Distance from center	-0.2500	0.190	-1.300	1.9e-01	
Treatment [structure control] x Distance from center	-0.4300	0.210	-2.100	3.9e-02	*
Sampling x Distance from center	-0.0270	0.012	-2.400	1.8e-02	*
Treatment [control] x Sampling x Distance from center	0.0240	0.016	1.500	1.4e-01	
Treatment [structure control] x Sampling x Distance from center	0.0270	0.018	1.500	1.3e-01	

Table S4. Seagrass growth model results.

	Estimate	Std. Error	df	t value	Pr(>|t|)	
Intercept	5.9	3.1	110	1.90	0.06300	
Treatment [control]	-3.2	4.4	110	-0.71	0.48000	
Treatment [structure control]	-4.1	4.4	110	-0.93	0.36000	
Distance [far]	-8.8	3.8	53	-2.30	0.02400	*
Year 2	3.1	1.1	1100	2.90	0.00430	**
Season [winter]	-15.0	1.1	1100	-14.00	0.00000	***
Treatment [control] x Distance [far]	14.0	5.3	53	2.60	0.01200	*
Treatment [structure control] x Distance [far]	11.0	5.3	53	2.00	0.04900	*
Treatment [control] x Year 2	-5.4	1.5	1100	-3.60	0.00039	***
Treatment [structure control] x Year 2	-3.4	1.5	1100	-2.20	0.02500	*
Treatment [control] x Season [winter]	-1.5	1.5	1100	-0.98	0.33000	
Treatment [structure control] x Season [winter]	1.1	1.5	1100	0.72	0.47000	

Table S5. Percent nitrogen in seagrass tissue model results.

	Estimate	Std. Error	df	t value	Pr(>|t|)	
Intercept	1.70	0.073	21	24.00	0.000	***
Treatment [control]	0.23	0.100	21	2.30	0.034	*
Treatment [structure control]	0.10	0.100	21	0.99	0.330	
Year 2	0.16	0.080	12	2.00	0.071	
Treatment [control] x Year 2	-0.34	0.110	12	-3.10	0.010	**
Treatment [structure control] x Year 2	-0.28	0.110	12	-2.50	0.030	*

Table S6. Percent carbon in seagrass tissue model results.

	Estimate	Std. Error	df	t value	Pr(>|t|)	
Intercept	33.0	0.94	24	35.0	0.000	***
Treatment [control]	3.2	1.30	24	2.4	0.025	*
Treatment [structure control]	2.2	1.30	24	1.7	0.110	
Year 2	1.5	1.30	24	1.1	0.270	
Treatment [control] x Year 2	-3.8	1.90	24	-2.0	0.057	
Treatment [structure control] x Year 2	-4.6	1.90	24	-2.4	0.023	*

Table S7. Percent phosphorus in seagrass tissue model results.

	Estimate	Std. Error	df	t value	Pr(>|t|)	
Intercept	0.05700	0.0033	21	17.00	0.000	***
Treatment [control]	0.00450	0.0046	21	0.98	0.340	
Treatment [structure control]	0.00055	0.0046	21	0.12	0.910	
Year 2	0.00570	0.0037	12	1.50	0.150	
Treatment [control] x Year 2	-0.01200	0.0052	12	-2.30	0.039	*
Treatment [structure control] x Year 2	-0.00780	0.0052	12	-1.50	0.160	