

ARTIFICIAL REEFS CONCENTRATE NUTRIENTS AND ALTER BENTHIC COMMUNITY STRUCTURE IN AN OLIGOTROPHIC, SUBTROPICAL ESTUARY

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ABSTRACT

The construction of artificial reefs in the oligotrophic seagrass meadows of central Florida Bay attracted large aggregations of fish and invertebrates, and assays of nutrient availability indicated increases in availability of nutrients to sediment microalgae, periphyton, and seagrasses around reefs. An average of 37.8 large (> 10 cm) mobile animals were observed on each small artificial reef. The dominant fish species present was the gray snapper (*Lutjanus griseus* Linnaeus, 1758). Four years after the establishment of the artificial reefs, microphytobenthos abundance was twice as high in reef plots ($1.7 \pm 0.1 \mu\text{g chl-}a \text{ cm}^{-2}$) compared to control plots ($0.9 \pm 0.1 \mu\text{g chl-}a \text{ cm}^{-2}$). The accumulation of periphyton on glass periphytometers was four times higher in artificial reef plots ($200.1 \pm 45.8 \text{ mg chl-}a \text{ m}^{-2}$) compared to control plots ($54.8 \pm 6.8 \text{ mg chl-}a \text{ m}^{-2}$). The seagrass beds surrounding the artificial reefs changed rapidly, from a sparse *Thalassia testudinum* (Banks & Soland. ex König) dominated community, which persisted at control plots, to a community dominated by *Halodule wrightii* (Ascherson). Such changes mirror the changes induced in experimentally fertilized seagrass beds in Florida, strongly suggesting that the aggregations of animals attracted by artificial reefs concentrated nutrients in this oligotrophic seascape, favoring the growth of fast-growing primary producers like microphytobenthos and periphyton, and changing the competitively dominant seagrass from slow-growing *T. testudinum* to faster-growing *H. wrightii* in the vicinity of the reefs.

In oligotrophic landscapes, the availability of nutrients can exert control over the biomass and species composition of the primary producer community and a change in the rate of nutrient supply can cause changes in the functioning of those ecosystems (Chapin et al., 1997). Low rates of nutrient supply favor slow-growing species that are effective in nutrient acquisition and use in both terrestrial (Reader et al., 1994; Guo and Berry, 1998) and marine (Valiela et al., 1992; Duarte, 1995; Fourqurean et al., 1995) plant communities. Increases in nutrient supply shift the competitive balance to favor faster-growing species. Fertilized patches within an oligotrophic landscape can become preferred feeding spots for herbivores who seek high-nutrient food as the fast-growing species tend to have higher nutrient content (e.g., McNaughton et al., 1997).

In Florida Bay, a large (2000 km²), subtropical, oligotrophic estuary, defecation by roosting seabirds caused a shift in benthic plant community composition from slow-growing to fast-growing seagrass species (Fourqurean et al., 1995; Frankovich and Fourqurean, 1997), an increase in the nutrient content of seagrass leaves (Powell et al., 1989), an increase in gross primary productivity and respiration rate (Herbert and Fourqurean, 2008), changes in primary producer diversity (Herbert and Fourqurean, 2008) and changes in infaunal community composition (Ferguson, 2008). Experimental fertilization in the most nutrient-limited parts of Florida Bay caused similar changes to species composition and nutrient content of primary producers (Armit-

age et al., 2005), increases in the number and biomass of epibenthic animals, and a change in species composition of the epibenthic community (Gil et al., 2006).

Fish schools aggregate near vertical structures, or reefs that provide shelter and protection from predators. Defecation and urination by resting schools of fish in other coastal ecosystems increase nutrient availability in the water column and sediment (e.g., Geesey et al., 1984; Meyer and Schultz, 1985) and increase the growth rate of benthic organisms at the resting sites (Meyer et al., 1983). The aggregation of large schools of fish can create top-down effects on the surrounding community as well. Herbivorous fish can engage in disproportionately high feeding near the resting habitat and reduce local levels of primary producer biomass (Valentine and Heck, 1999; 2005), and selective feeding on higher nutrient content, fast-growing plant species can control the species composition of the benthic plant community (Armitage and Fourqurean, 2006). Florida Bay, like many estuaries, contains few natural structures other than mangrove prop roots along island shores to harbor fish schools that could concentrate and deposit nutrients.

Artificial structures have been shown to act as refugia for juveniles of many fish species (Gorham and Alevizon, 1989; Pondella and Stephens, 1994; Carassou et al., 2009). These structures mimic the effects of natural reefs by providing a three-dimensional shelter with multiple crevices for small fish to hide from large predators (Polovina, 1994). Placing structure near reefs with large source populations attracts fish whose abundances can become comparable to neighboring natural reefs (Stone et al., 1979; Ogden and Ebersole, 1981; Carr and Hixon, 1997; Grossman et al., 1997). Estuaries like Florida Bay contain large populations of juvenile fish, some of which migrate between feeding grounds in seagrass beds and shelter on reefs at night (Parrish, 1989; Nagelkerken and van de Velde, 2004). Placing artificial structures in an environment normally lacking in vertical refugia creates habitat complexity that may otherwise not occur over large spatial scales. This phenomenon has been successfully used to concentrate fish schools for the purpose of recreational and commercial fishing (Alevizon et al., 1985; Neves Santos and Costa Monteiro, 1998; Pitcher and Seaman, 2000) and to mitigate the loss of natural habitat (Davis, 1985; Pickering et al., 1998).

There is some evidence that artificial reefs in oligotrophic environments cause changes in the benthic communities surrounding the artificial reefs. Dense seagrass beds surround the wreckage of boats and planes that have sunk in Florida Bay since the 1980s in otherwise sparse seagrass habitat (pers. obs.). Further, dense seagrass beds developed in an otherwise sparsely vegetated sand flat around artificial reefs placed to encourage the aggregation of coral reef fishes in the Bahamas (Alevizon et al., 1985; Alevizon, 2002). These observations led us to ask if artificial reefs deployed in oligotrophic Florida Bay would cause patches of higher nutrient availability and therefore changes in the surrounding benthic plant communities. Specifically, we questioned whether artificial reefs would (1) attract a substantial biomass of animals, (2) change nutrient availability immediately adjacent to the reefs, and (3) affect the structure and composition of the seagrass community around the artificial reefs.

METHODS

LOCATION.—Florida Bay is an estuary on the southwestern tip of the state of Florida. The primary producer community is seagrass dominated. The main seagrass species present is

Thalassia testudinum (Banks & Soland. ex König) with lower abundances of *Syringodium filiforme* (Kützing) and *Halodule wrightii* (Ascherson) (Zieman et al., 1989). This subtropical estuary has been shown experimentally to be primarily phosphorus-limited (Powell et al., 1989), but this limitation varies over spatial and temporal scales (Armitage et al., 2005). Phosphorus concentrations are relatively low in the northeastern portions of the estuary, but increase nearer the Gulf of Mexico, the primary source of phosphorus for the estuary (Fourqurean et al., 1992a). The high residence time of estuarine waters, high nitrogen fixation rates and nitrogen concentrations in terrestrial runoff all contribute to high N:P ratios. Consequently, even low levels of phosphorus additions can have significant effects on the primary producer community. *Thalassia testudinum* is relatively slow growing and is competitively dominant in the phosphorus-limited condition. When nutrients are added to the system, the faster growing *H. wrightii* becomes dominant, outcompeting *T. testudinum* (Fourqurean et al., 1995).

Florida Bay is home to a variety of species of juvenile and adult fishes (Thayer and Chester, 1989). Juvenile fishes are primarily found in seagrass patches. Thus Florida Bay, like other seagrass-dominated estuaries around the world, functions as a nursery for many juvenile fish species that upon maturity migrate to the Florida Keys reef tract or to the Gulf of Mexico (e.g. Ley et al., 1999; Gerard and Muhling, 2010).

We constructed artificial reefs near the Bob Allen Keys (ca. 25.03°N, 80.66°W) in the east-central region of Florida Bay. The site is characterized by salinities in the 30–45 range, low water-column and porewater nutrients (Fourqurean et al., 1992b), and sparse *T. testudinum* beds. *Halodule wrightii* is present but is located primarily on shoals and is even more sparse or altogether absent at depths > 2 m. The study site was over 2 km from the nearest mangrove forest and ca. 20 km from the nearest coral patch reef. This study site was chosen because natural seagrass communities here are sparse and phosphorus-limited, and because of a nearby artificial reef created by a small plane wreck in the early 1980s that is home to many fish species including mangrove snappers [*Lutjanus griseus* (Linnaeus, 1758)], French grunts [*Haemulon plumieri* (Lacépède, 1801)], pipefishes [*Syngnathus floridae* (Jordan and Gilbert, 1882)] and nurse sharks [*Ginglymostoma cirratum* (Bonnaterre, 1788)] (pers. obs.). Over the years, the area surrounding the wreckage has developed into a relatively lush seagrass meadow of *T. testudinum* and *H. wrightii* (pers. obs.).

EXPERIMENTAL DESIGN.—On March 4, 2005, we deployed nine artificial reefs constructed from 14 concrete blocks (20 cm × 20 cm × 40 cm) arranged in a pyramid formation, following Davis (1985). This arrangement resulted in an artificial reef approximately 1.7 m in width and length and 1 m in height. The top of the reefs were approximately 1 m below the mean water surface. We also designated nine control plots, for a total of 18 experimental units, which were distributed randomly in a 3 × 6 grid with 5 m spacing between experimental plots. We sampled these 18 experimental plots every other month from May 2005 through May 2006, then we revisited the structures after a sampling hiatus in March 2009.

RESPONSE VARIABLES.—Visual counts of the abundance of large conspicuous fish and invertebrates were performed to ensure that the artificial reefs did in fact serve as the attractants they have proven to be in similar manipulations. Sediment nitrogen and phosphorus concentrations were measured from sediment cores. Chlorophyll *a* (chl-*a*) concentrations in surface sediment were measured as a proxy for benthic microalgal biomass. The abundances and morphology of primary producer species were measured using a modified Braun Blanquet method (Fourqurean et al., 2001). Nitrogen and phosphorus concentrations were measured in the tissue of seagrass species. The abundance of chl-*a* was measured on periphytometers deployed in each plot to determine if a changing nutrient environment might be reflected in increased abundances of periphyton.

FAUNAL ABUNDANCE.—Faunal abundance was measured by visual counts performed by SCUBA divers. We collected data on fish over 10 cm in length and two of the larger benthic invertebrates that inhabit structures in south Florida, the spiny lobster *Panulirus argus*

(Latreille, 1804) and the stone crab *Menippe mercenaria* (Say, 1818). These were collectively referred to as "large mobile fauna." We approached the experimental plots slowly so as to not scare away residents to ensure a more accurate count. We present the faunal abundance data as the total number of target organisms observed in each experimental plot.

SEDIMENT NITROGEN AND PHOSPHORUS.—Sediment cores were collected by divers using 5 cc syringes (1.1 cm diameter) with the tips removed. Eight cores were taken per experimental plot, and the values from these eight subsamples were averaged by plot for each sampling time. We removed 1 cm³ of surface sediment, corresponding to 1 cm depth, and samples were transferred to a 20 ml vial for on-site ice storage and then returned to the lab for processing. Nitrogen concentrations were determined for a subsample of 25 mg of sediment using an elemental analyzer (FISONS NA1500). Phosphorus concentration of the sediment was determined using a dry oxidation-acid hydrolysis extraction followed by a colorimetric analysis (Fourqurean et al., 1992b).

CHLOROPHYLL A.—Microphytobenthos abundance was measured as the chl-*a* content of the surface sediments. Benthic chl-*a* concentrations were determined by taking sediment samples in the same manner as sediment nutrients. Eight samples were also taken for each experimental plot, and the values from these eight subsamples were averaged by plot for each sampling time. Chl-*a* was extracted from the top 1 cm of sediment collected with a 1.1 cm diameter syringe corer. Using acetone as a solvent, the concentration of chl-*a* in the extract was determined fluorometrically (as $\mu\text{g cm}^{-2}$). Relative periphyton abundance was assessed using glass slide periphytometers. These samplers are widely used to estimate algal abundance and growth rate in various water bodies including rivers and estuaries (Uehlinger and Brock, 1991; Matlock et al., 1998; Barbour et al., 1999). A single periphytometer was placed in each plot. Each periphytometer contained 20 2.5 cm \times 7.5 cm microscope glass slides that were approximately 1 mm thick. After 60 d, the periphytometers were collected, and the growth accumulated on each slide was scraped off. Chl-*a* was extracted from the material scraped from slides using acetone and chl-*a* concentrations of the extracts were determined fluorometrically. Total concentration from each periphytometer was divided by the total surface area of the slides to express abundance as $\text{mg chl-}a \text{ m}^{-2}$.

SEAGRASS MORPHOLOGY AND NUTRIENT CONTENT.—Seagrass cover was determined using a modified Braun Blanquet method (Fourqurean et al., 2001). Twelve $\frac{1}{4}$ -m² quadrats-per-plot were surveyed to estimate seagrass cover. In each quadrat, each species of seagrass was scored based on the fraction of bottom enclosed in the quadrat that was obscured by each species. A Braun Blanquet score of 0.1 was assigned if a single shoot of that species was present and it covered < 5% of the quadrat, 0.5 indicated few shoots that covered < 5%, 1 indicated many shoots comprising < 5% cover, 2 = 5%–25% cover, 3 = 25%–50% cover, 4 = 50%–75% cover, and 5 = 75%–100% cover. Quadrat locations were randomized by randomly selecting positions using a grid of 1 m grid cells drawn in a 2 m radius around each artificial reef and in the 25 m² of each control plot; scores for all quadrats at a plot were averaged for each sampling time. Seven shoots of *T. testudinum* and 30 shoots of *H. wrightii* were collected for subsequent nutrient analysis. These shoots were cleaned of epiphytes and measured for length. The leaf material from all shoots of a species within a plot and sampling event were homogenized together prior to analysis. The nitrogen and phosphorus concentration in the seagrass leaf tissue were measured as above for sediment.

STATISTICAL ANALYSIS.—We analyzed the effect of the presence of artificial reefs on the aggregation of larger fish and invertebrates and the nutrient status and composition of the benthic plant community using a repeated measures ANOVA with the plot as the unit of observation (SPSS v.13 software) testing for the changes in the response variables through time and the effect of reef presence on the response variables. We resampled our experiment effort in March 2009 and analyzed those data using a Student's t-test for differences between means at reef and control plots.

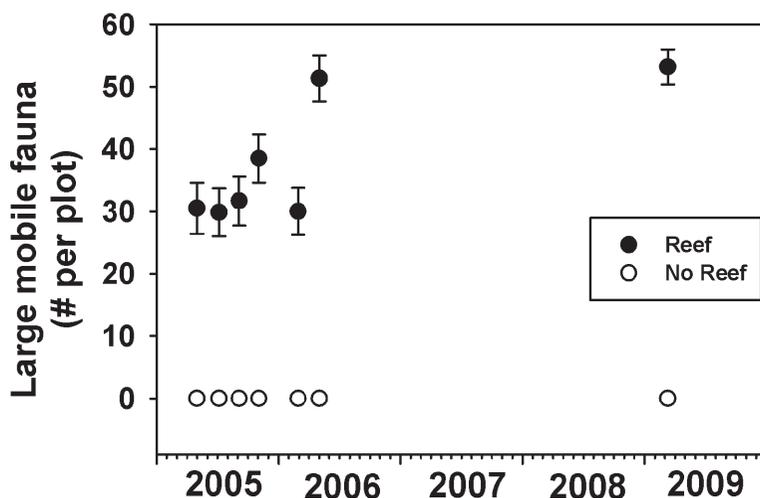


Figure 1. Faunal abundance at artificial reef plots compared to control plots in Florida Bay. Only fish ≥ 10 cm total length and large crustaceans (stone crabs and spiny lobsters) were counted. Error bars indicate ± 1 SE.

RESULTS

FAUNAL RESPONSE.—There were more fish and invertebrates observed in plots containing reefs than control plots (Fig. 1, Table 1; reef main effect in ANOVA). Faunal abundances increased with time (time main effect in ANOVA) and the change in faunal abundance over time depended on the presence of an artificial reef, with no increase in control plots but large increases in reef plots (ANOVA, time \times reef interaction). An average of 37.8 individuals was observed in reef plots. The dominant fish species present was the gray snapper (*L. griseus*). Schools of Atlantic spadefish [*Chaetodipterus faber* Broussonet, 1782] were abundant in the first two sampling periods but were not seen in appreciable numbers thereafter. Other species present in smaller numbers were the red grouper [*Epinephelus morio* (Valenciennes in Cuvier and Valenciennes, 1828)], triggerfish (*Balistes caprisacus* Gmelin, 1789) and the French grunt (*H. plumieri*). Spiny lobsters (*P. argus*) and Florida stone crabs (*M. mercenaria*) took refuge in the inner hollows of the concrete blocks. All fauna present were juveniles of their respective species, consistent with prior assessments of Florida Bay fauna. Fishes were generally observed to swim around the reefs and through the holes in the concrete blocks and did not retreat even in the presence of a diver. There were approximately three lobsters and one stone crab per reef.

SEDIMENT NUTRIENTS.—Averaged across all sampling times, sediment nitrogen content was slightly, but significantly, higher in reef plots than control plots (Fig. 2, Table 1; reef main effect in ANOVA), but sediment N concentration showed different trajectories at reef plots than at control plots (time \times reef interaction). By the end of our observations in 2009, sediment N concentrations were 50% higher in control plots than in reef plots (*t*-test, $t = -8.635$, $P < 0.001$). The presence of artificial reefs had a simpler effect on sediment P concentrations (Fig. 2, Table 1): in reef plots, P

Table 1. Repeated measures analysis of variance of the effect of reef presence and sampling time on response variables related to faunal abundance, nutrient availability, and benthic plant community composition.

Variable	Effect	F	P
Fauna	Reef	258.3	<0.001
	Time	10.8	<0.001
	Reef × time	10.8	<0.001
Sediment N content	Reef	5.5	0.041
	Time	7.3	0.006
	Reef × time	5.3	0.019
Sediment P content	Reef	21.0	<0.001
	Time	34.9	<0.001
	Reef × time	20.23	<0.001
Microphytobenthos chl- <i>a</i>	Reef	5.6	0.039
	Time	53.9	<0.001
	Reef × time	2.1	0.070
Periphyton chl- <i>a</i>	Reef	0.8	0.385
	Time	17.7	0.001
	Reef × time	13.6	0.002
<i>Thalassia</i> leaf N content	Reef	7.1	0.024
	Time	0.3	0.717
	Reef × time	2.2	0.148
<i>Thalassia</i> leaf P content	Reef	11.2	0.007
	Time	125.7	<0.001
	Reef × time	0.0	0.980
<i>Thalassia</i> Braun Blanquet abundance	Reef	1,783.5	<0.001
	Time	2.2	0.050
	Reef × time	5.0	<0.001
<i>Thalassia</i> leaf length	Reef	22.1	0.001
	Time	45.0	<0.001
	Reef × time	54.3	<0.001

concentrations in the sediments increased throughout the experiment, so that by the end of our observations in 2009, P concentrations were three times higher in reef plots than in control plots (t-test, $t = 6.430$, $P < 0.001$).

MICROPHYTOBENTHOS ABUNDANCE.—Averaged across all sampling times, microphytobenthos were more abundant at reef plots than at control plots (Fig. 3, Table 1; reef main effect in ANOVA). While there were differences in microphytobenthos among sampling periods (ANOVA, time main effect), the pattern in abundance over the course of the experiments was the same at reef and control plots (ANOVA, time × reef interaction). At the conclusion of the experiments, microphytobenthos were twice as abundant at reef plots compared to control plots (t-test, $t = 8.968$, $P < 0.001$).

PERIPHYTON ABUNDANCE.—Averaged over all sampling periods, there was no significant difference in the mass of chl-*a* accumulated on periphytometers placed in reef and control plots (Fig. 4, Table 1; reef main effect in ANOVA) but there were significant differences among sampling periods (time main effect in ANOVA), and a significant time × reef interaction indicating that chl-*a* accumulation rates showed different temporal trajectories in reef plots compared to control plots.

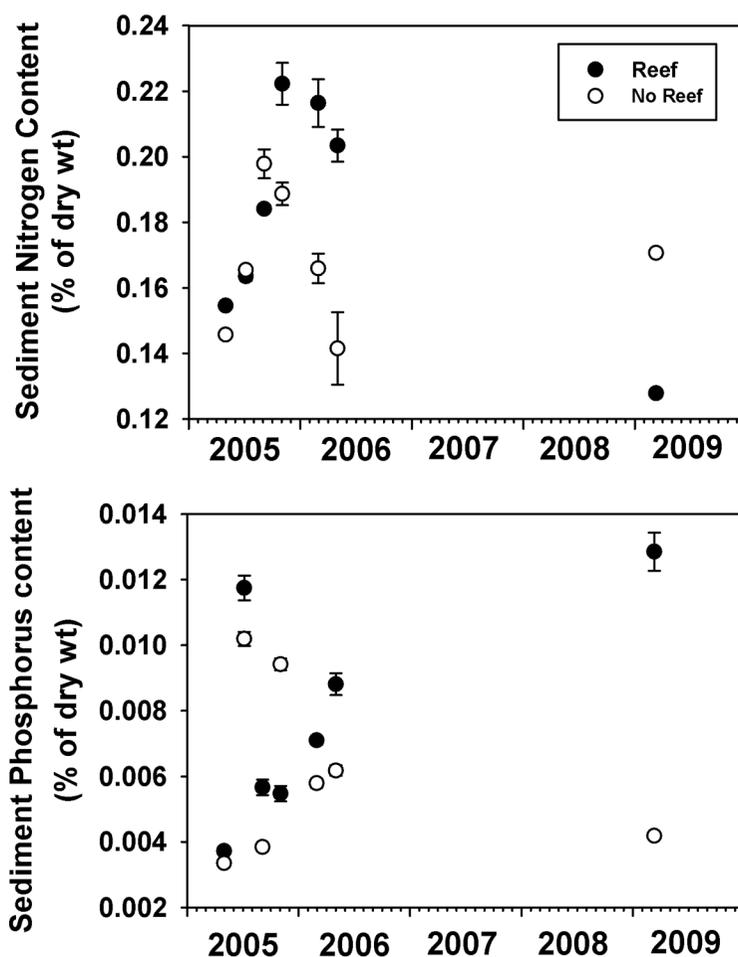


Figure 2. Time series of sediment nutrient content adjacent to artificial reefs and control plots in Florida Bay, beginning when the artificial reefs were constructed. Top panel: effects of artificial reefs on sediment nitrogen content. Bottom panel: effects of artificial reefs on sediment phosphorus content. Error bars indicate ± 1 SE.

Periphytometers deployed in reef plots two months prior to collection in March 2009 accumulated four times as much periphyton chl-*a* as those in control plots (t-test, $t = 3.236$, $P = 0.012$).

SEAGRASS LEAF NUTRIENT CONCENTRATION.—Averaged over all of the sampling periods, the N content of *T. testudinum* leaves was higher in reef plots than controls plots (Fig. 5, Table 1, reef main effect in ANOVA), but the N content did not change over the course of our experiments (insignificant time or reef \times time interaction in ANOVA). Similarly, P content of *T. testudinum* leaves was significantly higher in reef plots than in control plots averaged over the length of the study (Fig. 5, Table 1; reef main effect in ANOVA). P content increased over the course of our observations (time main effect in ANOVA).

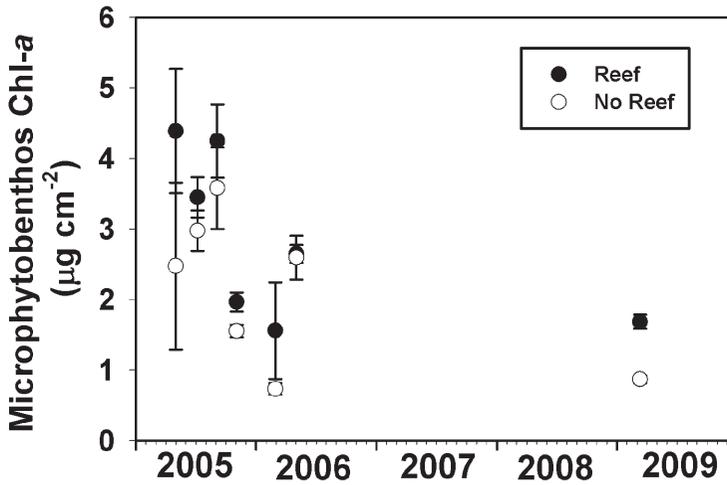


Figure 3. Time series of the abundance of microphytobenthos, as measured by chl-*a* content of the sediments, adjacent to artificial reefs and control plots in Florida Bay, beginning when the artificial reefs were constructed. Error bars indicate ± 1 SE.

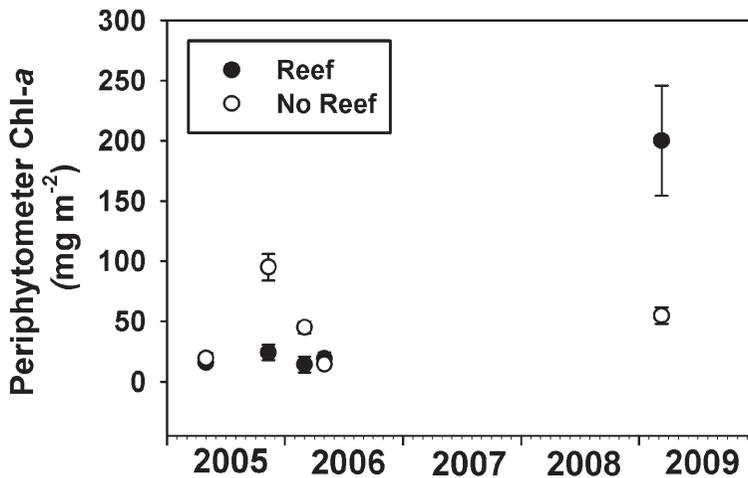


Figure 4. Time series of the concentration of chl-*a* accumulating on glass periphytometers on artificial reefs and in control plots in Florida Bay, beginning when the artificial reefs were constructed. Error bars indicate ± 1 SE.

SEAGRASS COVER AND MORPHOLOGY AND SPECIES COMPOSITION.—Averaged across all sampling times of our experiments, the abundance of *T. testudinum* was lower in reef plots compared to control plots (Fig. 6, Table 1; reef main effect in ANOVA). The differences in abundance were largely driven by the decrease in abundance in reef plots between May 2006 and March 2009 (reef \times time effect in ANOVA). Abundance of *T. testudinum* surrounding the artificial reefs was half the abundance

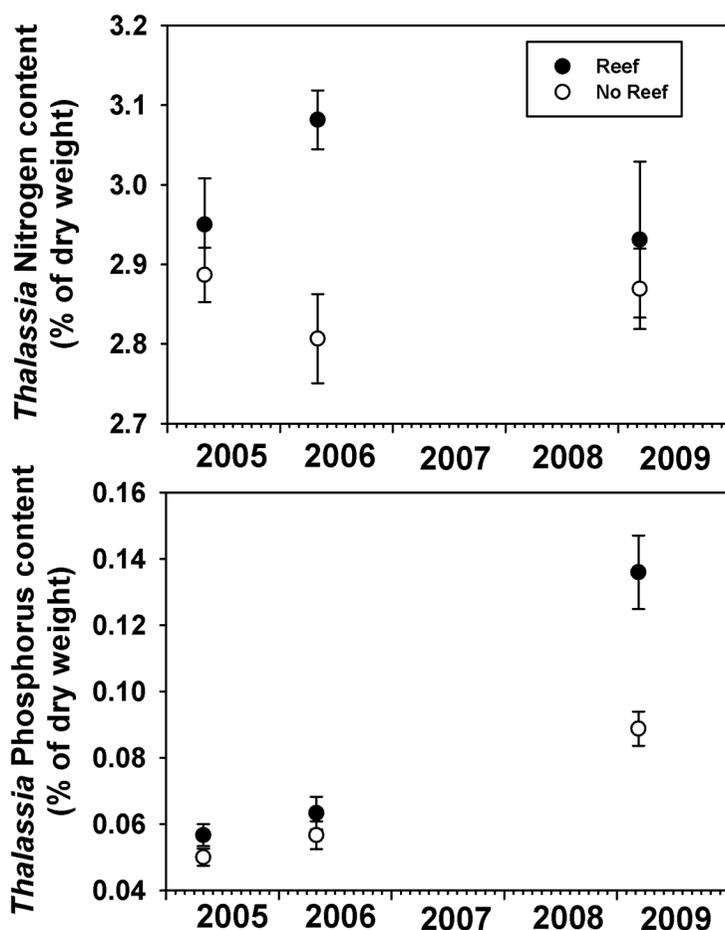


Figure 5. Time series of the concentrations of nutrients in the leaves of the seagrass *Thalassia testudinum* adjacent to artificial reefs and control plots in Florida Bay, beginning when the artificial reefs were constructed. Top panel: nitrogen content. Bottom panel: phosphorus content. Error bars indicate ± 1 SE.

at the control plots in March 2009 (t-test, $t = -4.941$, $P < 0.001$), despite the similarity in *T. testudinum* abundance at reef and control plots at the beginning of the experiment. This difference in abundance, as assessed by Braun Blanquet cover, was not driven by a change in the stature of the remaining short shoots of *T. testudinum*. Averaged over all sampling events, leaves of *T. testudinum* were longer in control plots than in reef plots (Fig. 6, Table 1; reef main effect in ANOVA). However, leaves were longer in the reef plots than in the control plots at the end of the observations (t-test, $t = 3.088$, $P = 0.001$), even though cover was lower in the reef plots.

Reef plots were colonized by the faster growing seagrass *H. wrightii* over the course of our observations, while control plots were not (Fig. 7). In May 2006, a bare area developed around the artificial reefs, possibly as a result of scour, or the grazing by herbivores sheltering on the reefs. *Halodule wrightii* began growing within this area. These new shoots were very sparse and were not registered by our surveys in May

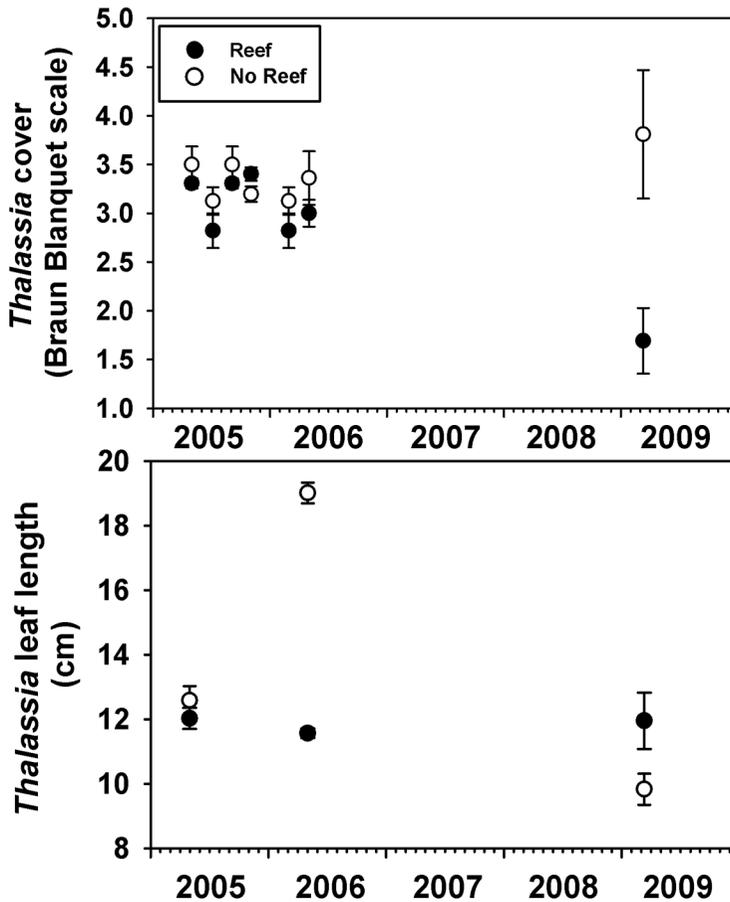


Figure 6. Time series of the abundance and leaf length of the seagrass *Thalassia testudinum* adjacent to artificial reefs and control plots in Florida Bay, beginning when the artificial reefs were constructed. Top panel: mean Braun Blanquet cover scores for plots of each treatment. A Braun Blanquet score of 0.1 is assigned if a single shoot of that species was present and it covered < 5% of the quadrat, 0.5 indicates few shoots that cover < 5%, 1 indicates many shoots comprising < 5% cover, 2 = 5%–25% cover, 3 = 25%–50% cover, 4 = 50%–75% cover, and 5 = 75%–100% cover. Bottom panel: mean leaf length for reef and control plots. Error bars indicate ± 1 SE.

2006, but by March 2009, *H. wrightii* was more abundant around the reefs than *T. testudinum*. *Halodule wrightii* was not present at any of the control treatments at any time during our experiments.

DISCUSSION

The construction of artificial reefs in the oligotrophic seagrass meadows of central Florida Bay attracted large aggregations of fish and invertebrates, and assays of nutrient availability indicated increases in availability of nutrients to sediment microalgae, periphyton, and seagrasses around reefs. The seagrass beds surrounding the artificial reefs changed rapidly, from a sparse *T. testudinum* dominated community,

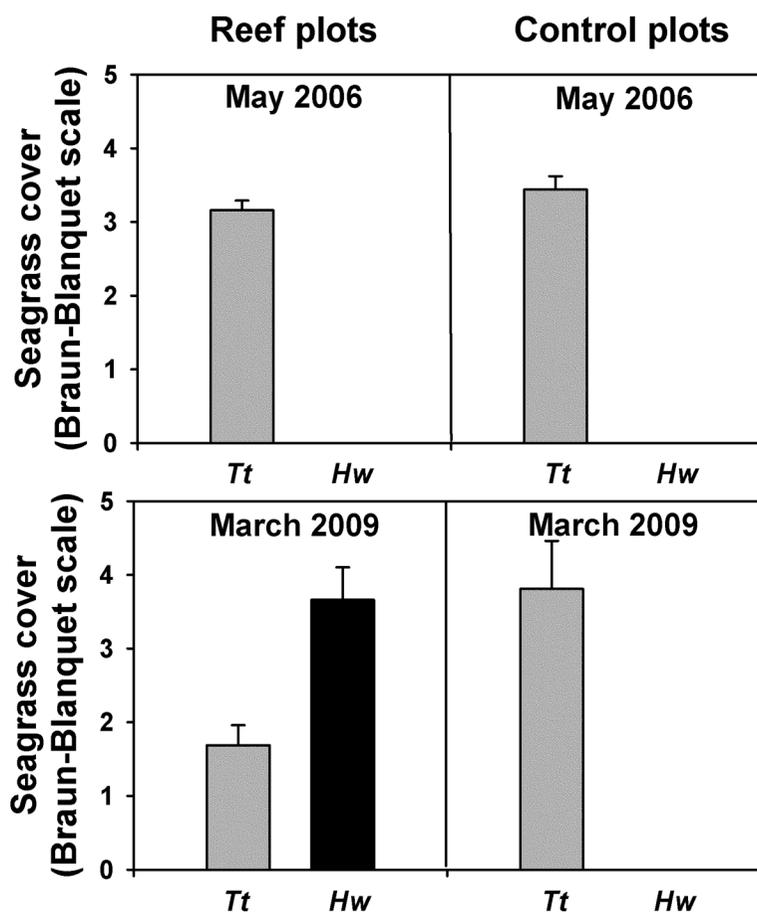


Figure 7. Abundance of the seagrasses *Thalassia testudinum* (*Tt*) and *Halodule wrightii* (*Hw*) in artificial reef and control plots in Florida Bay in May 2006 and March 2009. Values are the mean Braun Blanquet cover score. Error bars indicate ± 1 SE.

which persisted at control plots, to a community dominated by *H. wrightii*. Such changes mirror the changes induced in experimentally fertilized seagrass beds in Florida Bay (Fourqurean et al., 1995; Armitage et al., 2005), strongly suggesting that the aggregations of animals attracted by artificial reefs concentrated nutrients in this oligotrophic seascape and changed the competitively dominant seagrass from slow-growing *T. testudinum* to faster-growing *H. wrightii*.

In other structure-limited marine and estuarine environments, artificial reefs act as an effective attractant for various fish species (Alevizon and Gorham, 1989). The aggregation of fauna in both marine and terrestrial environments can result in both top-down (Randall, 1965) and bottom-up effects (Day and Detling, 1990; Pickering et al., 1998) for the primary producer community. A concentration of herbivores can result in significant biomass removal, to the extent that total ecosystem productivity is severely diminished (Pastor and Naiman, 1992). Such an effect has long been noted around coral reefs—a “halo” of heavily grazed plant communities often surrounds

coral reefs in the Caribbean as a result of the herbivores that shelter on the reef (Ogden and Zieman, 1977; Tribble, 1981). In multilevel food webs, predator concentrations can also have density- or behaviorally-mediated indirect effects on primary producers by influencing the feeding rate of herbivores (e.g., Silliman and Bertness, 2002). There can also be positive effects of the accumulations of animals on reefs for the ecosystem surrounding the reefs. When animals gather, wastes are deposited in the location of the gathering, resulting in nutrient loading. Fecal matter is high in nitrogen and phosphorus and can therefore influence the nutrient content of plants as well as the structure of the plant community. The effect of this nutrient loading on primary producers has been demonstrated experimentally where artificial reefs in different locations also show local increases in seagrasses and algae (Branden et al., 1994; Alevizon 2002).

We believe that the majority of the changes in the nutrient availability and seagrass community composition were a result of the aggregated fish and invertebrates, not because of physical or hydrologic changes caused by the reefs. We feel confident that the biogeochemical and community changes we observed were due to the presence of fauna. Experiments involving artificial reefs and have yielded similar changes among primary producers (Alevizon, 2002). Of course, without experimentally excluding animals from aggregating on artificial reefs, we cannot definitively conclude that the increases in nutrient availability and the resultant changes in benthic plant community structure were solely a response to nutrient accumulation by the animals that took shelter on our artificial reefs. It is possible that there were some effects of the reefs on sediment dynamics and water motion that could have contributed to the increase in the availability of P surrounding the reefs.

It is likely that the benthic plant communities at the artificial reefs responded to the addition of phosphorus, not nitrogen, from the waste product of animals sheltering on the reef. Seagrass (Fourqurean et al., 1992b) and periphyton communities (Frankovich and Fourqurean, 1997; Armitage et al., 2006, Frankovich et al., 2006) in Florida Bay are limited by P availability, and the N content of seagrasses, over 3% by dry weight, is so high as to suggest N saturation at our study site. By March 2009, sediment P was enhanced near reefs compared to control plots and *T. testudinum* P content was higher near reefs than at control plots. However, the N content of sediments decreased near reefs, and the N content of *T. testudinum* was not significantly different between reef and control plots. Both the biomass of benthic microalgae and periphyton accumulation on periphytometers were higher at reef plots than no reef plots. These observations are consistent with an increase in the availability of P leading to enhanced growth of primary producers around the reef plots. Further, owing to the retention of P in seagrass ecosystems in Florida Bay (Herbert and Fourqurean, 2008), it is likely that the increased P availability caused by the presence of the artificial reefs will persist for decades, even if these artificial reefs were removed.

Changes in the structure of the benthic community surrounding the artificial reefs may cascade upwards to higher trophic levels. Fertilization experiments in the system show that benthic infauna abundances increase and species compositions change when nutrient availability is increased (Ferguson, 2008) and epibenthic animal community structure shifts (Gil et al., 2006). Food web structure also changes, with an increase in epiphyte grazers and an increased reliance on the primary production of fast-growing species at fertilized sites (Armitage and Fourqurean, 2009). These changes to community structure are responses to both changes in nutrient

availability and the physical structure of the seagrasses that provide refuge from predation. Seagrasses respond to increased availability by incorporating it into their tissue and changing morphology.

Changes in nutrient content of plants can have higher-order effects, since herbivores in general, and herbivorous marine fish in particular prefer high-nutrient content forage (e.g., Goecker et al., 2005; Armitage and Fourqurean, 2006). We did not collect data on rates of herbivory around our artificial reefs to gauge the magnitude of any top-down effects of faunal aggregations on our artificial reefs. However, we do not think an increase in herbivory around reefs is the reason for the change in the seagrass community structure around the reefs because we did not observe any large herbivorous fish like parrotfishes on our artificial reefs. Further, local herbivorous fish strongly prefer *H. wrightii* over *T. testudinum* (Armitage and Fourqurean, 2006), thus top-down effects would control the biomass of *H. wrightii*, in contrast to our observations. The change from the sparse *T. testudinum*-dominated seagrass beds of the control plots to the *H. wrightii*-dominated communities surrounding the artificial reefs by March 2009 is likely due to the competitive dominance of *H. wrightii* in high nutrient environments (Fourqurean et al., 1995).

Results of this experiment are consistent with other experiments performed in Florida Bay where the effects of nutrient addition were investigated (Powell et al., 1989; Armitage et al., 2005; Gil et al., 2006). Powell et al. (1989) manipulated nutrients via bird feces (birds were incited to defecate via appropriately placed bird stakes), and Armitage et al. (2005) and Gil et al. (2006) directly applied slow-release fertilizer at a variety of sites across the bay. These experiments also showed comparable increases in sediment nutrients, benthic algal biomass, seagrass foliar tissue, and a shift from the normally dominant *T. testudinum* to *H. wrightii*. It is noteworthy that accumulation of large mobile fauna caused localized nutrient loading at rates similar to these previous studies. Loading due to fecal matter from birds was measured to be approximately $52 \text{ mg N m}^{-2} \text{ d}^{-1}$ (Powell et al., 1989). Nutrients loaded in the direct fertilization experiment released nitrogen at $1430 \text{ mg N m}^{-2} \text{ d}^{-1}$ (Armitage et al., 2005; Gil et al., 2006). In aquaculture systems, the defecation rates of *Lutjanus* sp. range from $20\text{--}30 \text{ mg N kg}^{-1} \text{ h}^{-1}$ (Leung et al., 1999). If we assume that each reef harbored ca. 2 kg of sheltering fish and that these fish spent 12 hr d^{-1} resting on the reefs, our experiments resulted in a loading rate of approximately $200 \text{ mg N m}^{-2} \text{ d}^{-1}$. This is roughly the same loading rate as the bird perch experiments of Powell et al. (1989) and Fourqurean et al. (1995) but much less than the loading rates used by Armitage et al. (2005) and Gil et al. (2006), which were based on maximum possible anthropogenic loading from diffuse polluted groundwater inputs to the Florida Keys. The clear implication here is that over sufficient temporal scales, even small nutrient loading rates from accumulations of fish on small artificial reefs can have the same community structure-changing effects as larger loading rates. Considering that the spatial dimensions of the reef limited abundances to approximately 35 fish, we expect that larger artificial structures will have a more pronounced effect.

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