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# Facilitation of coral reef biodiversity and health by cave sponge communities

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ABSTRACT: Marine caves are understudied ecosystems that are frequently associated with coral reef communities; many are tidally influenced and may host a highly diverse sponge fauna. Although each cave represents a distinct habitat likely structured by site-specific hydrographic processes, a more complete understanding of the ecology of these communities requires comparative studies. Based on a gradient of sponge cover within 5 Bahamian caves, we conducted a natural experiment in sponge-derived nutrient enrichment of nearby patch reefs. We tested the hypothesis that water exiting the cave during low tide provides a nutrient-rich resource that facilitates the diversity and health of nearby reef communities. The percent cover and diversity of corals surrounding the openings of caves were significantly higher than in similar habitats farther removed from these communities. There was a significant correlation between percent sponge cover within the caves and nitrate concentrations in seawater flowing out of the caves, and $\delta^{15}N$ stable isotope signatures indicated enrichment of the nearby reefs by sponge-derived nitrate. Zooxanthellae abundance and total protein concentration were higher in corals from reefs near cave entrances, suggesting that those corals benefited more from cave nutrients than did corals farther from cave openings. In addition to corals, percent algal cover increased near cave entrances, but these potential competitors of corals were kept in check by increased levels of herbivory relative to sites removed from cave mouths. As global environmental changes continue to impact coral reef ecosystems, diversity 'hot spots', such as these marine caves, could serve as refuges and 'seed-banks' for nearby dwindling reef habitats.

KEY WORDS: Facilitation · Nutrients · Sponges · Biodiversity · Coral health · Caves · Herbivory



## INTRODUCTION

To date, most research aimed at explaining patterns and processes on coral reefs has focused on inherently detrimental effects such as abiotic stressors, predation, competition, and pathogenesis. However, positive interactions between species, or facilitation, can also be important to coral reef community structure and function (Bruno & Bertness 2001). For example, the presence of conspecifics or heterospecifics might provide a refuge from abiotic stressors (Bertness et al. 1999), predators (Stachowicz & Hay 1999, Gochfeld 2010), or competitors (Pennings & Callaway 1996). Mangroves and seagrasses are similarly facilitated by the metabolic nitrogenous contributions of associated sponges and mussels, respectively (Ellison et al. 1996, Peterson & Heck 2001), and growth rates of the corals *Acropora palmata, Pocillopora eydouxi* and *Porites furcata* are facilitated by nitrogenous wastes released by damselfishes and grunts (Meyer et al. 1983, Holbrook et al. 2008). Thus, facilitation may be an important mechanism by which coral reefs maintain diversity and function under stressful or nutrient-limited conditions.

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Tropical oceanic waters are typically low in inorganic nitrogen and phosphorous, yet coral reef communities exhibit high productivity and diversity. This 'paradox of the reef' is due to significant recycling of nutrients from various compartments within the coral community (Szmant 2002). Filter feeding provides a metabolic carbon source for many marine invertebrates, including sponges (e.g. Lesser 2006), and their waste products can be converted to biologically useful nitrogen, such as nitrate, by microbes (Taylor et al. 2007, Fiore et al. 2010). Recent incubation and *in situ* experiments have demonstrated that sponges represent a significant source of the total dissolved inorganic nitrogen (DIN) on coral reefs (Corredor et al. 1988, Southwell et al. 2008). However, these studies overlook the contribution of cryptic species that live in the interstices of the reef (equivalent to cave-dwelling species), which represent a considerable proportion of the total sponge biomass, and a significant carbon sink for the coral reef community (Richter & Wunsch 1999, de Goeij et al. 2008). Nutrient enrichment, primarily by crevice-dwelling sponges, can exceed the nitrogen imported into coral reef ecosystems by cross-shelf pathways, fish waste, and nitrogen fixation combined (Richter et al. 2001). Many Caribbean reefs exhibit high levels of nutrient enrichment due to benthic sponge cover (e.g. Southwell et al. 2008); however there is also a need to assess the contribution of the cryptic sponge community to nutrient sources and sinks. While eutrophication may present its own problems to coral reefs (e.g. phase shifts: McCook 1999; disease: Bruno et al. 2003; but see Gochfeld et al. 2012 for evidence that eutrophication does not impact sponge disease), this study underscores the importance of cryptic sponge communities to the overall coral reef nitrogen budget.

Marine caves are marginal ecosystems of coral reef communities which may include one or more of the following conditions: (1) absence of light, (2) finite/episodic food supply mediated by tidal cycles, (3) unusual biogeochemical seawater attributes, and (4) potential barriers to gene flow (Sket 1996). Sponges dominate the biodiversity and biomass of many marine caves (Gili et al. 1986, Bussotti et al. 2006), and they exhibit distinct zonation patterns due to steep environmental gradients (Gili et al. 1986). In fact, marine caves have the potential to act as larger analogs of the framework interstices of the reef, and as such they provide a more tractable experimental system to understand the sources and sinks of coral reef nutrients (Richter et al. 2001, de Goeij et al. 2008, van Duyl et al. 2011). Cave mouths are often surrounded by patch reefs that support a diverse community of marine invertebrates and fishes, relative to the surrounding substrata (M. Slattery pers. obs.). Based on these observations, we tested the following hypotheses: (1) patch reef biodiversity and percent cover are enhanced with proximity to marine caves, (2) cave sponges release nutrients during ebb tides that are utilized by adjacent reef communities, and (3) coral growth and health near caves are facilitated by the presence of cave sponges.

## MATERIALS AND METHODS

### Study sites

Surveys of 5 caves in the Exuma Cays (Bahamas; Fig. 1) and their associated patch reefs were conducted between 1999 and 2011. The caves, located near the Caribbean Marine Research Center (CMRC; Lee Stocking Island, Bahamas: 23° 46.5′ N, 76° 00.5′ W), included Mystery Cave (MC: 23° 31.5′ N, 75° 45.5′ W), Angelfish Blue Hole (AFBH: 23° 31.5′ N, 75° 45.6′ W), Rolleville Cave (RC: 23° 40.7′ N, 75° 59.9′ W), Sugar Cay Crevasses (SCC: 23° 41.9′ N, 76° 00.3′ W), and Norman's Pond Cay Cave (NPCC: 23° 47.3′ N, 76° 08.5′ W). Based on the gradient of sponge cover among these caves, they represent a 'natural experiment' (sensu Diamond 1986) in potential sponge-derived nitrate effects on nearby patch reefs. MC and AFBH are both located near the back of a natural 'hurricane basin' (i.e. a small harbor) on Stocking Island. However, the entrance of MC is effectively a diagonal shaft cut into the limestone wall of the island just below the low tide level, whereas the entrance of AFBH is a vertical shaft at a depth of 10 m, including a cavern zone from 6 to 10 m, in the middle of the bay surrounded by soft sediment and small patch reefs. The diver-accessible depth range of these caves is 3 to 65 m and 10 to 65 m, respectively. RC (depth range 3 to 15 m) is a sinkhole located in a shallow mangrove channel about 3 m below the surface; like AFBH, this cave is surrounded by soft sediment and small patch reefs, as well as seagrass beds and mangroves. SCC are paired sink holes (depth range 3 to 15 m) in the limestone hardpan; the entrances measure about 20 × 3 m, located approximately 1.5 m below sea level, and they are surrounded by a shallow coral community. NPCC (depth range 3 to 65 m) was once an inland blue hole separated from the shoreline by a narrow limestone sill and consequently isolated from marine faunal dispersal (LaPointe et al. 2004); however, this barrier recently collapsed, allowing semidiurnal

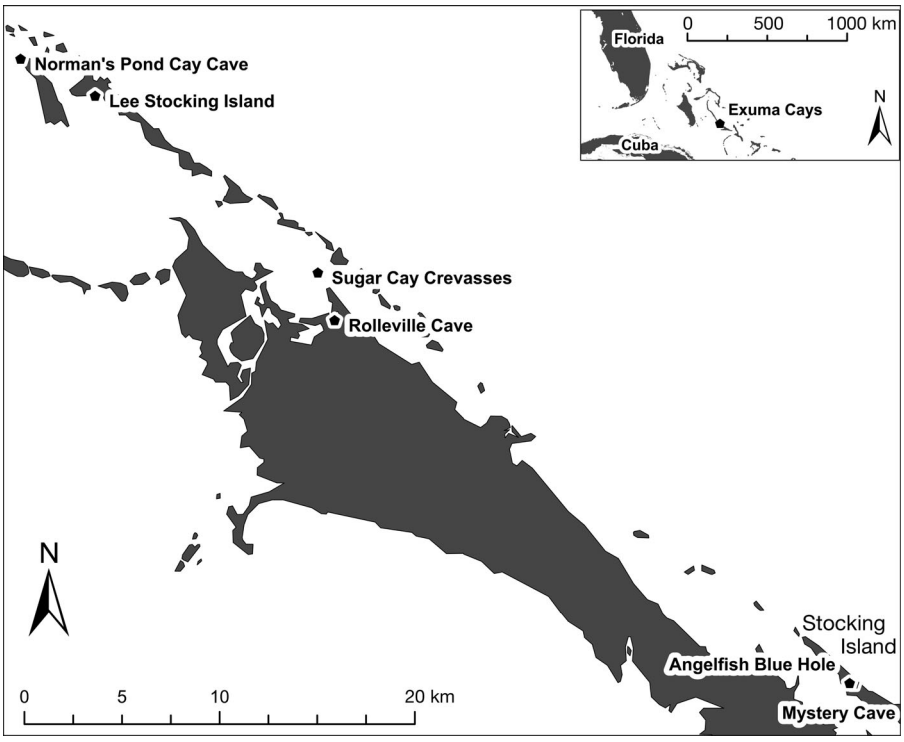


Fig. 1. Study site in the Exuma Cays, Bahamas. Five caves, and their local patch reefs, were examined between 2000 and 2010. From north to south: Norman's Pond Cay Cave (NPCC), Sugar Cay Crevasses (SCC) Rolleville Cave (RC), Angelfish Blue Hole (AFBH), and Mystery Cave (MC). Note: the entrances of AFBH and MC are about 150 m apart despite apparent overlap at this scale. In addition, corals were collected off Lee Stocking Island for a transplant experiment

tidal flushing and the recent colonization by a few sponges (M. Slattery pers. obs.). The shoreline surrounding NPCC is karst limestone and elevated hardpan, while the nearby shallow benthic substrate is fine-grained sand. Given the relative absence of sponges within NPCC, this cave represents the 'control' for our natural experiment of nitrate sources and sinks. The surface area within these caves is very difficult to estimate given the presence of numerous side passages (many too small to be accessed by divers), but a conservative estimate based on the measured lengths of the main passages, assuming that each cave passage represents a cylinder of constant diameter, indicates that the surface area of MC is approximately 4147 $m^2$. In comparison to the size of MC, we estimated the surface areas of the other caves to be >16 000 (NPCC), ~4150 (AFBH) and ~1400 $m^2$ (SCC and RC each).

### Surveys

Macro-benthic percent cover of the cave walls and the nearby patch reefs was assessed using 0.25 and 1 $m^2$ quadrats, respectively. Within each cave, 30 quadrats near the mouth, center, and back of the cave were assessed annually between 2000 and 2005. These cave zones are characterized by distinct fauna, including cryptic shallow reef sponge species (mouth), unique speleophilic sponges (back), and a transition zone consisting of both faunas (center) (M. Slattery pers. obs.). While biomass may be a more appropriate measure for sponges in many communities (Wulff 2001), most cavity-dwelling and/or cave sponges are encrusting, and therefore percent cover is a reasonable metric in these systems. Percent cover was measured as the area of sponge in contact with the cave walls; however, about a third of the sponge cover included other growth morphologies (e.g. 'rope'), so we collected sponge volumetric data, as described by Wulff (2001), on a limited subset of the quadrats (n = 10 per cave) in 2000. Quadrats were haphazardly positioned on the walls of the caves at randomly selected distances from the cave opening along a transect tape. The percent sponge cover and number of sponge species within each quadrat were recorded, as was the percent non-living substrate. In addition, beginning in May 2003 (6 mo after a harbour dredging event that led to considerable sedimentation), replicate (n = 30) 0.25 $m^2$ quadrats representative of the sediment scour were identified and marked, using stainless steel spikes hammered into the cave walls. These permanent quadrats were sampled, as described previously, from May 2003 to 2005, and again in May 2009 and 2010 to assess sponge recovery. At 'near sites' adjacent to each cave

mouth, 10 quadrats were haphazardly positioned on the hard substrata to assess percent cover of corals, sponges, and algae/cyanobacteria, and biodiversity (*H'*) of corals and fish. The numbers of sea urchins and diseased corals were also counted in these quadrats. In addition, 10 quadrats at 'far sites' (located at a linear distance of 25 m from the cave mouths at the hard substrate sites [MC, SCC, and NPCC], or on the first 10 patch reefs encountered at least 25 m from the cave mouths in soft bottom communities [AFBH and RC]) were assessed.

Fish surveys were conducted at each cave, both near and far from the cave mouths. Over a period of 15 min, all fish swimming over a haphazardly positioned 1 $m^2$ quadrat were recorded by divers situated at least 1.5 m from the quadrat. This observation procedure reduced the probability of fish avoiding the divers, but it arbitrarily omitted small fish (e.g. blennies and gobies) from the censuses because they could not be accurately identified from a distance. Likewise, damselfishes were also excluded since they rarely ventured outside their territories and across our observation station. Nonetheless, the larger fish species that were recorded represent the majority of the biomass of potential grazers within these patch reefs (M. Slattery, pers. obs.). To reduce redundant count bias, these procedures were replicated through time between 2000 and 2005, and again in 2009 and 2010 (n = 48 replicates in total). In addition, divers followed individuals of 3 of the dominant herbivores (*Acanthurus coeruleus*, *Scarus vetula*, and *Sparisoma viride*) and recorded the number of bites taken during 10 min observation periods. All species surveys presented are based on data collected in May of each year, and each survey was timed to coincide with the morning slack tide to provide relatively consistent conditions through time.

### Nutrient analyses

Replicate seawater samples (n = 10) were collected for nutrient analyses outside the caves at 'near' and 'far' distances, and within the caves near the mouth, center, and back regions annually from May 2000 through 2005. Divers carried 1 l nalgene bottles and opened these at the specified locations to collect seawater for subsequent analyses. Water column oceanographic profiles within each cave were collected during May 2002 using a moored Hydrolab® DataSonde III. This multiprobe station provided a continuous 24 h recording of temperature, dissolved oxygen, salinity and pH. Individual seawater samples were collected near the moored Hydrolab, which was positioned at the interface between the mouth and center cave zones, at 12 time points over the 24 h sampling period in order to assess finer-scale temporal changes in nitrate variability. Water samples were also collected as a function of time relative to ebb and flood tidal cycles during May 2002, and these were analyzed for nitrate ($NO_3$) as well as particulate organic carbon (POC). For these samples, divers entered the cave 2 h before slack tide (flood), at slack tide, and 2 h after slack tide (ebb) to collect water samples within each zone of the caves. All seawater samples were maintained in coolers on ice until they could be processed at CMRC.

Nitrate was measured using 2 colorimetric procedures based on kits designed by Hach®. In both cases, pre-formulated reagent packets were allowed to incubate for 2 min in the seawater samples, and the color change was quantified using either a color wheel (prior to 2004) or the Hach® DR890 colorimeter (2004 and later). In order to standardize these results, water samples were again collected in 2009, tested using both aforementioned procedures, and normalized to nitrate concentrations recorded using the LACHAT QuickChem® Method 31-107-04-1-E (e.g. Corredor et al. 1988). Following nitrate analyses in 2002, the remaining water samples were filtered onto 0.22 µm GF/F filters and combusted to assess POC levels (Moran et al. 1999) using a Perkin Elmer® 2400 Series II CHNS/O Elemental Analyzer.

$\delta^{15}N$ stable isotope analyses were performed on replicate colonies of the common mounding coral *Siderastrea radians* (n = 5) collected near and far from the mouths of MC, SCC, and NPCC in 2005. *S. radians* is a ubiquitous species within the Caribbean basin, and it is often found in shallow marginal habitats and/or patch reefs (Lewis 1989, Vermeij 2005). The holobiont tissue was removed using a Waterpik and isolated on pre-combusted glass fiber filters. These were immediately frozen at –40°C and held for approximately 1 mo prior to additional processing. Samples were subsequently dried and combusted in a LECO elemental analyzer coupled to a Finnigan® Stable Isotope Ratio Mass Spectrometer (SIR MS) for the analysis of $\delta^{15}N$. In addition, replicate samples of the massive sponge *Haliclona implexiformis* (n = 5) were collected inside MC and SCC at the interface between the mouth and center of the caves. *H. implexiformis* is a common species within mangrove communities of the Caribbean Basin and exhibits facultative nutrient transfer with the mangrove roots (Ellison et al. 1996). These were processed as described for the coral but without tissue removal pro-

cedures. Water samples (n = 3) were also collected from the entrance of the caves during flood tide to assess $\delta^{15}N$ enrichment of the particulate organic matter (POM).

### Coral growth

*Siderastrea radians* was the only coral species that occurred at all of our study sites, thus we used it as a model for comparative growth and physiological measurements. At each cave site, 11 to 15 similar-sized *S. radians* colonies were tagged near the cave mouths, and 8 to 15 were tagged at far sites. These individuals were monitored for growth at least twice each year between 2000 and 2005. A measuring tape was used to quantify the circumference of each coral, at each point in time, to assess areal growth. Small core samples (6 mm diameter) were collected using a submersible air-powered drill in 2000, 2002, 2003, and 2005 to measure zooxanthellae abundance and protein content within these corals using procedures described in Slattery & Paul (2008). Regeneration of the coral tissue over the cored area was complete by the following year (M. Slattery pers. obs.).

Harbor dredging between September and November of 2002 resulted in considerable sedimentation at our MC site, but not at the nearby AFBH site. The impacts of this anthropogenic disturbance experiment were evident during the January 2003 survey, and one consequence was a significant loss of sponge cover on the cave walls due to sediment scour, which abraded the colonies from walls near the mouth and smothered sponges near the center and back of the cave. We expected that the reduction in MC sponge abundance might reduce nutrient levels on nearby reefs, and consequently impact the remaining coral communities. Thus, we performed a transplant experiment from January 2003 to May 2005 to compare growth and health of the corals near the mouth of MC relative to undisturbed sites. We transplanted 15 individual *Siderastrea radians* (~5 cm diameter) to the mouth of MC (3 m depth), and 15 individuals to the mouth of AFBH (6 m depth). AFBH was chosen as a control site for MC transplants since, post-scour, the percent cover of sponges in both of these similar-sized caves was comparable, and proximity was such that hydrographic conditions (e.g. flow) were expected to be similar, although the depth differences constituted a 12% change in irradiance (Lesser et al. 2009). Corals were collected as intact individuals from patch reefs near CMRC (3 m depth), segregated into Ziploc® bags containing filtered seawater, and transported in coolers directly to MC and AFBH. The corals were randomly assigned to the sites, and attached to the substrate using Woolsey/Z-Spar Splash Zone epoxy (Kop-Coat). Initial areal sizes of each coral were measured as described previously, and subsequent growth measurements were made twice each year (January and May) through 2005. Zooxanthellae and protein content of these corals were assessed in cores collected at the start of this experiment (January 2003) and in May of 2003, 2004 and 2005 when all transplants were recovered. Growth rate, zooxanthellae abundance and protein content were also assessed on 30 control *S. radians* collected from the same patch reef source populations as the transplants; 15 were back-transplanted to CMRC and 15 were tagged at the site but not handled.

### Statistical analyses

Percent cover of the macro-benthic community on the cave walls and nearby patch reefs, as well as the sponge volume within caves, were analyzed using 2-way nested ANOVAs with cave and time as the fixed factors, and distance from the cave mouth as the nested random effect. Scheffe's test was used as a post hoc comparison between treatment blocks. The recovery of the MC sponge community was analyzed using a repeated measures ANOVA with sedimentation as the fixed factor. The diversity and abundance of corals on patch reefs near and far from cave mouths was assessed using a 2-way nested ANOVA, with cave and time as the fixed factors, and distance from the cave mouth as the nested random effect. Herbivore abundance near and far from the cave mouths was compared using unpaired *t*-tests, as were the bite rates of 3 common herbivorous fish species on patch reefs near and far from the cave mouths; however, fish diversity was not inclusive of all species in the communities, so $H'$ was not compared between caves. The percent cover of sponges and algae/cyanobacteria at MC was compared before and after dredging using a repeated measures ANOVA. The number of herbivorous fish at MC and AFBH was also assessed using a 2-way ANOVA with time and site as fixed factors. Nitrate concentrations associated with each cave were analyzed using 2-way nested ANOVAs, with cave and time as fixed factors, and distance from the cave mouth as the nested random effect. The influence of sponge percent cover on cave nitrate concentration was

assessed using simple linear regression. The $\delta^{15}N$ content of POM, the sponge *Haliclona implexiformis*, and the coral *Siderastrea radians* was compared using a 1-way ANOVA with distance as a fixed factor. Nitrate and POC levels at MC during 3 tidal periods were analyzed using repeated measures ANOVAs with distance from the cave mouth as a fixed factor. Coral growth, zooxanthellae abundance, and protein content of annually-monitored *S. radians*, as well as transplant and control individuals from the CMRC 'common garden', were assessed using repeated measures ANOVAs. All data were *a priori* tested for assumptions of normality and equal variance; where these assumptions failed, the data were arcsin transformed, re-tested, and analyzed using JMP 8.0 with the appropriate non-parametric test. The data are presented as the mean ± 1 SE.

## RESULTS

Percent cover of sponges inside 5 caves near Lee Stocking Island, Bahamas, varied significantly, ranging from 13.2 ± 2.2 (in SCC) to 65.2 ± 5.4% (in MC) (Tables 1 & 2, Fig. S1A in the supplement at www.int-res.com/articles/suppl/m476p071_supp.pdf). NPCC sponge cover consisted of 3 small crusts of *Spirastrella* sp. near the cave mouth, all outside of our quadrats, and thus unrepresented in the quantitative results. There were also significant differences in sponge percent cover as a function of distance from the cave mouth (with overall fewer sponges at the cave mouth than in the center of the cave) and through time (e.g. Fig. S1B), and there were significant interaction effects (Table 2). There were significant differences in sponge volume between the 5 caves; ranging from 0.2 ± 0.1 l $m^{-2}$ (in SCC) to 2.2 ± 0.2 l $m^{-2}$ (in MC) (Tables 1 & 2, Fig. S2), although there was no effect of distance from the cave mouth and no interaction effect. Similarly, there were significant differences in the percent cover of corals, sponges and algae between reefs near the mouths of these caves and far sites at all caves except NPCC (Fig. 2). The percent cover was significantly higher near the cave mouths for coral, sponges and algae (Table 2), with 2 exceptions: At RC the percent cover of algae was higher farther from the cave mouth, and there was no significant effect of distance on sponge cover at this site (Scheffe's $p \geq 0.6261$). There were also significant cave effects on corals, sponges, and algae, and the interactions for each of these functional groups (Table 2). In addition to percent cover, the diversity of corals near the mouths of the caves was significantly higher than at further patch reefs at all sites except for NPCC (Tables 2 & 3). Coral diversity was significantly different at each cave site, and the interactions were significant (Table 2). Numbers of herbivores also varied as a function of distance from the mouths of these caves; in general there were significantly more fish and urchins near the mouths of MC, AFBH, RC, and SCC (*t*-tests: $p \leq 0.0117$; Table S1 in the supplement), but there were similar numbers of these herbivores at sites near and far from NPCC (*t*-tests: $p \geq 0.2432$). Bite rates of 3 common herbivorous fish species, *Acanthurus coeruleus*, *Scarus vetula*, and *Sparisoma viride*, indicated that grazing was typically enhanced near the cave mouths, where algal percent cover was highest (*t*-tests: $p \leq 0.0469$; Fig. S3). There was no significant difference in the percent of diseased corals as a function of distance from cave mouths (*t*-tests: $p \geq 0.5560$; range 0.005 to 1.7%). The percent cover of algae increased dramatically through time when herbivores were absent (Table 2, Fig. S4). Algae represented 7.6 ± 0.7% of the benthic substrate at MC prior to dredging operations in late 2002; by May 2003 algae cover had tripled at this site and by 2009 it was the dominant component of our quadrats. However, in 2010 the percent cover of algae/cyanobacteria had dropped to 13.1 ± 2.9% with return of herbivorous fishes (Table 2, Fig. S4). The number of herbivorous reef fishes (acanthurids and scarids) at MC and AFBH varied through time and between sites; there was also a significant interaction effect (Table 2, Fig. S4).

Nitrate levels varied as a function of distance from the cave mouth (Table 2, Fig. S5 in the supplement). Specifically, nitrate concentrations were higher near the mouths of MC, AFBH, RC and SCC, but not NPCC, than at far sites. There were also significant differences among the concentrations of nitrate released from each of the 5 caves (Table 2). Nitrate concentration was significantly correlated with the

Table 1. Sponge cover and volume from 4 caves in the Exuma Cays, Bahamas. Data represent the mean ± 1 SE percent cover or volume (liters of sponge per $m^2$ surface area) within each cave (MC: Mystery Cave; AFBH: Angelfish Blue Hole; RC: Rolleville Cave; SCC: Sugar Cay Crevasses). Note: Norman's Pond Cay Cave is not included since the few small sponges that had recently invaded this cave did not occur in any of our quadrats.

| | MC | AFBH | RC | SCC |
|---|---|---|---|---|
| Cover (%) | 65.2 ± 5.4 | 39.8 ± 4.7 | 50.0 ± 4.3 | 13.2 ± 2.2 |
| Volume (l $m^{-2}$) | 2.2 ± 0.2 | 1.8 ± 0.2 | 0.6 ± 0.1 | 0.2 ± 0.1 |

Table 2. Summary of ANOVA results, showing the *F*-statistic, degrees of freedom and p-value for each treatment factor. Factors include: cave (5 sites throughout Exuma Cays), time (semi-annual sampling between 2000 and 2010), distance (from mouth of cave to back, or patch reefs near and far from the cave mouth). Datasets refer to specific metrics collected during this project; the right-hand column indicates the corresponding figure or table in the paper or in the supplement at www.int-res.com/articles/suppl/m476p071_supp.pdf (Figs. S1, S4–S9). Only significant factors are reported. MC: Mystery Cave; POC: particulate organic carbon; POM: particulate organic matter

| Dataset/factors | ANOVA test | *F* | df | p | Figure/table |
|---|---|---|---|---|---|
| **Sponge cover** | 2-way nested | | | | Fig. S1A |
| Cave | | 910.133 | 3, 71 | <0.0001 | |
| Time | | 32.147 | 15, 71 | <0.0001 | |
| Distance | | 3185.9 | 2, 71 | <0.0001 | |
| Interaction (cave × time) | | 33.665 | 45, 71 | <0.0001 | |
| **Sponge volume** | 2-way nested | | | | Fig. S2 |
| Cave | | 26.279 | 3, 28 | <0.0001 | |
| **Reef cover near/far from caves** | 2-way nested | | | | Fig. 2 |
| Cave- corals | | 113.896 | 8, 59 | < 0.0001 | |
| Cave- sponges | | 158.596 | 8, 59 | < 0.0001 | |
| Cave- algae | | 228.098 | 8, 59 | < 0.0001 | |
| Distance- corals | | 451.126 | 1, 59 | < 0.0001 | |
| Distance- sponges | | 220.031 | 1, 59 | < 0.0001 | |
| Distance- algae | | 21.755 | 1, 59 | < 0.0001 | |
| Interaction (cave × distance) | | 4.289 | 8, 59 | < 0.0005 | |
| **Coral diversity near/far from caves** | 2-way nested | | | | Table 3 |
| Cave | | 15.05 | 4, 50 | < 0.0001 | |
| Distance | | 100.849 | 1, 50 | < 0.0001 | |
| Interaction (cave × distance) | | 21.437 | 4, 50 | < 0.0001 | |
| **Algal cover near MC pre-/post-dredging** | Repeated measures | | | | Fig. S4 |
| Time | | 195.728 | 7, 72 | < 0.0001 | |
| **Sponge cover in MC pre-/post-dredging** | Repeated measures | | | | Fig. S1B |
| Time | | 260 | 7, 72 | < 0.0001 | |
| **Herbivorous fishes pre-/post-dredging** | 2-way | | | | Fig. S4 |
| Time | | 4.645 | 1, 7 | 0.0002 | |
| Cave | | 49.639 | 1, 7 | < 0.0001 | |
| Interaction (time × cave) | | 14.468 | 1, 7 | < 0.0001 | |
| **Nitrate concentration associated with caves** | 2-way nested | | | | Fig. S5 |
| Cave | | 1502.21 | 4, 149 | < 0.0001 | |
| Distance | | 5920.77 | 4, 149 | < 0.0001 | |
| **$NO_3$/POC levels over tidal cycle** | Repeated measures | | | | Figs. 4, S6 |
| Time- $NO_3$ | | 338.536 | 2, 135 | < 0.0001 | |
| Distance- $NO_3$ | | 113.694 | 4, 135 | < 0.0001 | |
| Interaction (time × distance) | | 21.469 | 8, 135 | < 0.0001 | |
| Time- POC | | 1062.28 | 2, 135 | < 0.0001 | |
| Distance- POC | | 177.326 | 4, 135 | < 0.0001 | |
| Interaction (time × distance) | | 749.493 | 8, 135 | < 0.0001 | |
| **$\delta^{15}N$ content of POM, corals and sponges** | 1-way | | | | Table 4 |
| Distance | | 292.389 | 7, 30 | < 0.0001 | |
| **Coral growth** | Repeated measures | | | | Figs. 5, S7 |
| Monitored | | 38.675 | 4, 113 | < 0.0001 | |
| Transplanted | | 3.705 | 3, 56 | 0.0167 | |
| **Zooxanthellae abundance** | Repeated measures | | | | Figs. 5, S8 |
| Monitored | | 17.123 | 4, 113 | 0.0003 | |
| Transplanted | | 14.105 | 3, 56 | < 0.0001 | |
| **Total protein** | Repeated measures | | | | Figs. 5, S9 |
| Monitored | | 4.584 | 4, 113 | 0.0411 | |
| Transplanted | | 21.076 | 3, 56 | < 0.0001 | |

percent cover of sponges within the caves (simple regression: $F_{1,149}$ = 270.858, p < 0.0001; Fig. 3). The different methods of measuring nitrate that were used over time accounted for less than 0.2% variability between samples ($R^2$ = 0.998). Nitrate levels varied over a typical tidal cycle at MC, and were apparently influenced by POC concentrations (Fig. 4, Fig. S6). During flood tide, nitrate levels near the

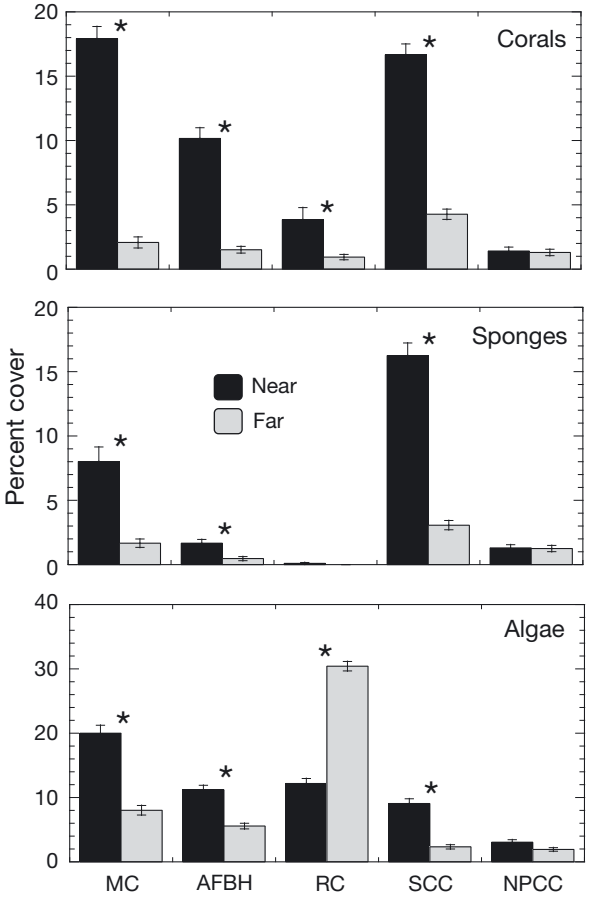


Fig. 2. Percent cover of corals, sponges and algae on patch reefs near the mouths of caves. Data were collected annually between 2000 and 2005 from 10 quadrats near the cave mouth ('near sites'), and 10 quadrats ~25 m from the cave mouth ('far sites'). There was no significant time effect by ANOVA, so the samples from all years were pooled. Data are mean ± 1 SE in 1 $m^2$ quadrats (n = 60 per distance, except MC where n = 50 since the 2003 data were excluded due to sediment scour). (*) significant difference (Scheffe's test, $p \leq 0.05$) between near and far sites. Note difference in scales

mouth of the cave were at their lowest (~2 mg $l^{-1}$), and the water entering the cave had relatively high concentrations of POC (~50 µg $l^{-1}$). During slack tide, POC levels entering the cave were reduced and nitrate levels increased. During ebb tide, the water leaving the caves was low in POC and rich in nitrate (Fig. 4). Nutrient levels also varied significantly with distance from the cave mouth, and the Time × Distance interactions were significant (Table 2). $\delta^{15}N$ varied between POM, cave sponge tissue, and *Siderastrea radians* collected near and far from the mouths of MC and SCC (Tables 2 & 4) but not NPCC. Overall, the cave sponge *Haliclona implexiformis* had higher $\delta^{15}N$ levels than corals or POM, and *S. radians* from near the cave mouths of MC and SCC had higher levels of $\delta^{15}N$ that those collected farther from those caves. In contrast, $\delta^{15}N$ levels in *S. radians* did not vary with distance from NPCC.

From 2000 to 2005, *Siderastrea radians* near the mouths of MC, AFBH, RC, and SCC increased in size (Fig. S7 in the supplement). In general, *S. radians* increased in circumference by 41.9% near the mouths of these caves and by 31.6% at the far sites. There were significant differences in coral growth rates as a function of cave (Table 2). MC and AFBH corals had statistically identical growth rates (Scheffe's $p \geq 0.2167$), as did RC and SCC corals (Scheffe's $p \geq 0.7043$). Marked individuals near MC and SCC grew faster than conspecifics 25 m distant (Scheffe's $p \leq 0.0431$), but there was no difference in growth rates with distance at AFBH or RC (Scheffe's $p \geq 0.1585$). NPCC corals exhibited the lowest overall growth (Scheffe's $p < 0.0001$), and there was no significant difference related to distance from the cave mouth at this site (Table 2, Fig. S7). Zooxanthellae abundance in *S. radians* declined with distance from the cave mouth at all caves (Table 2) except NPCC (Fig. S8). Specifically, zooxanthellae abundance was 13.2 to 29.2% higher in coral colonies near the cave mouths than in colonies at far sites. The only change in zooxanthellae abundance as a function of time occurred at MC and AFBH (Table 2). A similar temporal pattern was observed for total protein concentration of these coral tissues, with higher protein near all of the cave mouths except NPCC (Table 2, Fig. S9). There was no difference between the 2 groups of *S. radians* at AFBH in 2000 (Scheffe's $p \geq 0.2962$), and there was significantly more protein in the corals further from the mouth of MC after harbor dredging (2003; Table 2, Fig. S9).

Transplanted corals from a 'common garden' near CMRC to patch reefs near the mouth of MC in January 2003 were initially depressed relative to corals transplanted to AFBH, back-transplanted to CMRC, or marked *in situ* at CMRC (i.e. no growth through January 2004: Table 2, Fig. 5). There were also time-dependent differences in coral growth; after 2 yr, growth rates recovered, and the Site × Time interaction was significant (Table 2). Within 4 mo (May 2003), colonies transplanted near the mouth of AFBH exhibited significantly higher abundance of zooxanthellae than the other treatment groups (Table 2, Fig. 5), remaining higher than at the CMRC controls for another 2 yr. Corals transplanted to MC also exhibited significant elevation of zooxanthellae abundance, albeit at a later time point

Table 3. Coral diversity near caves. Mean ±1 SE number of corals per 1 $m^{-2}$ quadrat near each of 5 caves (see Table 1 legend for abbreviations) for each coral species recorded. Within each column, the upper number represents corals at near sites, close to the cave mouth, while the lower number represents corals at far sites, ~25 m from the cave mouth. The total number of corals at near and far sites was used to calculate the Shannon diversity index (*H'*); 2-way nested ANOVA was used to analyze the statistical significance of differences between coral diversity at near and far sites for each cave. n/a: not applicable (i.e. species does not occur at this site)

| Coral species | MC | AFBH | RC | SCC | NPCC |
|---|---|---|---|---|---|
| *Agaricia agaricites* | 1.33 ± 0.33 | 2.67 ± 0.33 | n/a | 8.67 ± 1.2 | n/a |
| | 0 | 0 | | 0.67 ± 0.67 | |
| *A. humilis* | 3.0 ± 1.15 | n/a | 1.0 ± 0.58 | n/a | n/a |
| | 0 | | 0 | | |
| *Colpophyllia natans* | 3.33 ± 0.88 | 0.67 ± 0.67 | 1.0 ± 1.0 | 1.33 ± 0.88 | n/a |
| | 0 | 0 | 0 | 0.33 ± 0.33 | |
| *Dichocoenia stokesi* | 16.0 ± 2.65 | 6.0 ± 1.53 | 5.33 ± 1.86 | 7.67 ± 2.63 | 1.33 ± 0.88 |
| | 0 | 0.33 ± 0.33 | 0.67 ± 0.67 | 1.0 ± 0.58 | 1.33 ± 0.67 |
| *Eusmilia fastigiata* | 1.0 ± 0.58 | n/a | 17.67 ± 6.06 | 16.0 ± 3.61 | n/a |
| | 0 | | 0 | 0 | |
| *Favia fragum* | 0.67 ± 0.67 | 4.0 ± 1.53 | 1.67 ± 0.88 | 3.67 ± 1.2 | 1.0 ± 0.58 |
| | 0.33 ± 0.33 | 0.33 ± 0.33 | 0 | 0.33 ± 0.33 | 0 |
| *Helioseris cucullata* | 4.67 ± 1.2 | 4.33 ± 1.45 | n/a | n/a | n/a |
| | 0 | 0 | | | |
| *Madracis decactis* | n/a | 3.33 ± 0.33 | n/a | 3.67 ± 0.88 | n/a |
| | | 0.33 ± 0.33 | | 0 | |
| *Manicina areolata* | n/a | n/a | 3.0 ± 0.58 | n/a | n/a |
| | | | 5.33 ± 1.45 | | |
| *Montastraea annularis* | n/a | n/a | n/a | 2.31 ± 1.2 | n/a |
| | | | | 2.67 ± 1.33 | |
| *Mycetophyllia lamarckiana* | 8.0 ± 1.53 | 8.0 ± 2.31 | 4.67 ± 1.2 | 4.33 ± 0.88 | n/a |
| | 0 | 0 | 0 | 0 | |
| *Porites branneri* | n/a | n/a | 4.33 ± 1.2 | n/a | n/a |
| | | | 0 | | |
| *P. divaricata* | 3.33 ± 0.67 | 3.33 ± 1.33 | n/a | 0 | n/a |
| | 0.33 ± 0.33 | 0.33 ± 0.33 | | 1.0 ± 0.58 | |
| *P. furcata* | n/a | n/a | n/a | 3.67 ± 0.88 | n/a |
| | | | | 3.33 ± 0.67 | |
| *Scolymia cubensis* | 3.67 ± 0.67 | n/a | n/a | 2.33 ± 1.2 | n/a |
| | 0 | | | 0 | |
| *Siderastrea radians* | 2.33 ± 1.45 | 3.67 ± 0.33 | 11.33 ± 1.45 | 18.67 ± 1.45 | 2.0 ± 1.16 |
| | 1.0 ± 1.0 | 0.33 ± 0.33 | 1.67 ± 0.88 | 3.33 ± 0.67 | 3.0 ± 0.58 |
| *S. siderea* | 3.0 ± 1.53 | 2.67 ± 1.2 | n/a | 6.33 ± 1.2 | 0.67 ± 0.67 |
| | 0 | 0 | | 1.0 ± 0.58 | 1.0 ± 0 |
| *Stephanocoenia intercepta* | n/a | n/a | 3.0 ± 1.0 | 11.33 ± 3.76 | n/a |
| | | | 0 | 1.0 ± 0.58 | |
| *Thalamophyllia riisei* | 0.33 ± 0.33 | 3.0 ± 1.16 | n/a | 10.0 ± 2.08 | n/a |
| | 0 | 0 | | 0 | |
| Coral diversity | | | | | |
| *H'* near | 2.061 ± 0.057 | 2.169 ± 0.069 | 1.831 ± 0.167 | 2.269 ± 0.085 | 0.447 ± 0.775 |
| *H'* far | 0.337 ± 0.584 | 0.462 ± 0.400 | 0.988 ± 0.353 | 1.393 ± 0.264 | 1.043 ± 0.471 |
| 2-way nested ANOVA | p = 0.0008 | p = 0.0019 | p = 0.0202 | p = 0.0049 | p = 0.3188 |

(May 2004), and the Site × Time interaction was significant (Table 2). Protein levels were depressed in each of the handled transplants relative to the source population after 4 mo (Table 2, Fig. 5), and protein levels in the back-transplanted corals remained low even as corals transplanted to the cave sites returned to or surpassed source population levels; the Site × Time interaction for protein content was also significant (Table 2, Fig. 5).

## DISCUSSION

As sponges become a more dominant component of Caribbean coral reefs (Diaz & Rutzler 2001, Pawlik 2011), there has been a greater appreciation of their roles in community structure and function (reviewed in Wulff 2006, Pawlik 2011). Recent studies have highlighted the potential negative consequences of sponge-mediated eutrophication on coral reef resili-

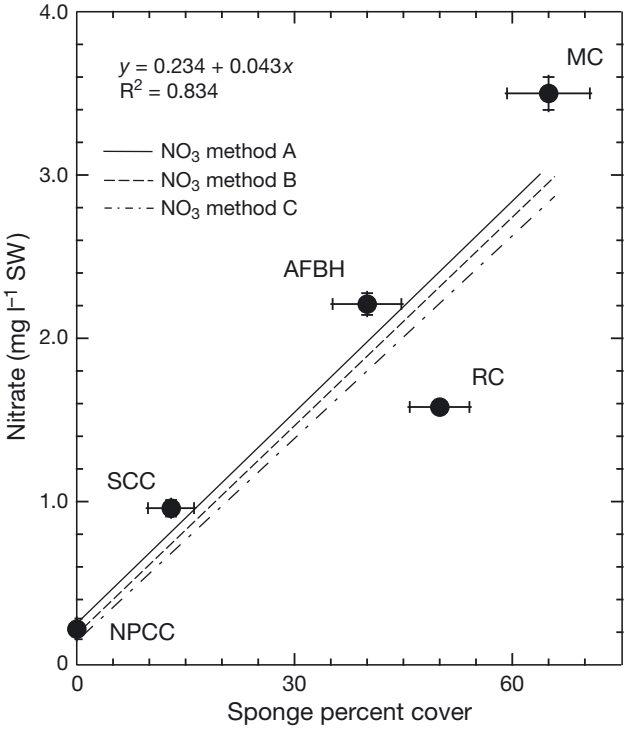


Fig. 3. Correlation between mean (±1 SE) nitrate concentration in seawater collected at the cave mouth annually from May 2000 to 2005 and percent sponge cover (combined percent cover throughout each of the cave zones [i.e. mouth, center and back]) within caves. Note that the 3 nitrate methods (A: LACHAT QuickChem, B: Hach colorimeter, C: Hach color wheel) accounted for less than 0.2% of the variation. See Table 1 for cave name definitions

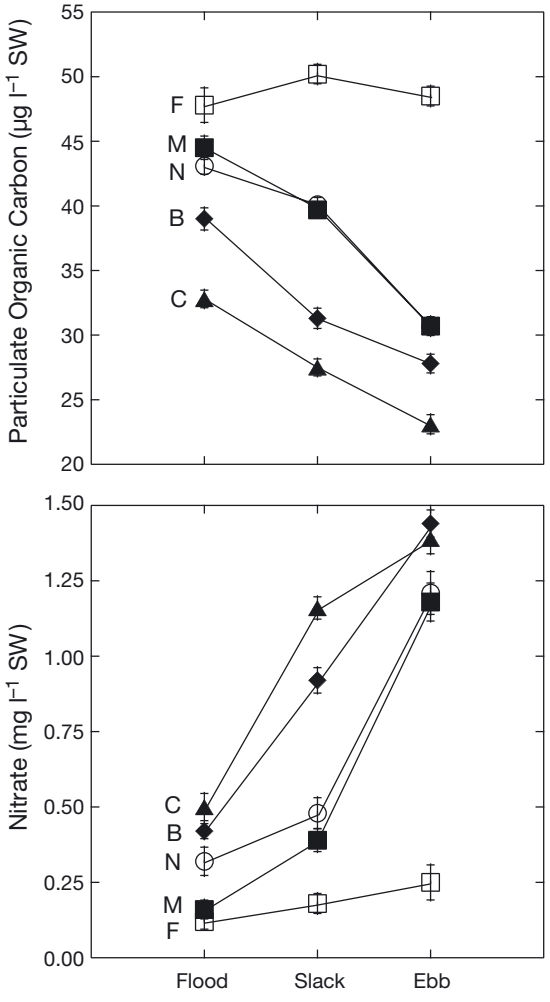


Fig. 4. Mean (± 1 SE) particulate organic carbon and nitrate concentrations in seawater within Mystery Cave (n = 10 replicates per site) during each of 3 tidal conditions (flood, slack, and ebb) in May 2002. F: Far sites outside cave, approximately 25 m from mouth; N: near sites outside cave mouth; M: inside cave mouth; C: center of cave; B: back of cave. See 'Materials and methods: Surveys' for further clarification of these cave zones

Table 4. $\delta^{15}N$ sources and sinks at 3 Bahamian caves. Particulate organic matter (POM) was collected during flood tide near the mouth of Mystery Cave (MC). The sponge *Haliclona implexiformis* was collected inside MC and Sugar Cay Crevasses (SCC), while the coral *Siderastrea radians* was collected at near sites close to the mouths of MC, SCC, and Norman's Pond Cay Cave (NPCC) and at far sites ~25 m from the cave mouths. For the sponges and corals, n = 5; for the POM samples, n = 3. Different letters indicate significantly different groups (Scheffe's $p \leq 0.05$)

| Species | Mean $\delta^{15}N$ | SE | Scheffe's post hoc |
|---|---|---|---|
| POM | 2.77 | 0.10 | A |
| *H. implexiformis* | | | |
| MC | 5.25 | 0.14 | B |
| SCC | 5.08 | 0.13 | B |
| *S. radians* | | | |
| MC near | 3.22 | 0.14 | C |
| MC far | 2.72 | 0.12 | A |
| SCC near | 3.04 | 0.11 | C |
| SCC far | 2.69 | 0.10 | A |
| NPCC near | 2.62 | 0.07 | A |
| NPCC far | 2.69 | 0.07 | A |

ence to phase shifts (Southwell et al. 2008). Specifically, the 'fertilization' of foliose algae can increase their competitive edge over corals (Bruno et al. 2009). In contrast, our data suggest that cave sponge-derived nutrients may facilitate coral reef biodiversity and health, albeit in the presence of a robust grazer community. These data rely on a gradient of sponge cover across 5 caves as the source of nitrate released to nearby patch reef communities, as the likely cause of the health of those communities. This natural experiment suffers from the lack of a true control (i.e. each cave may be distinguished by a unique set of site-specific environmental variables), which confounds the experimental treatment and

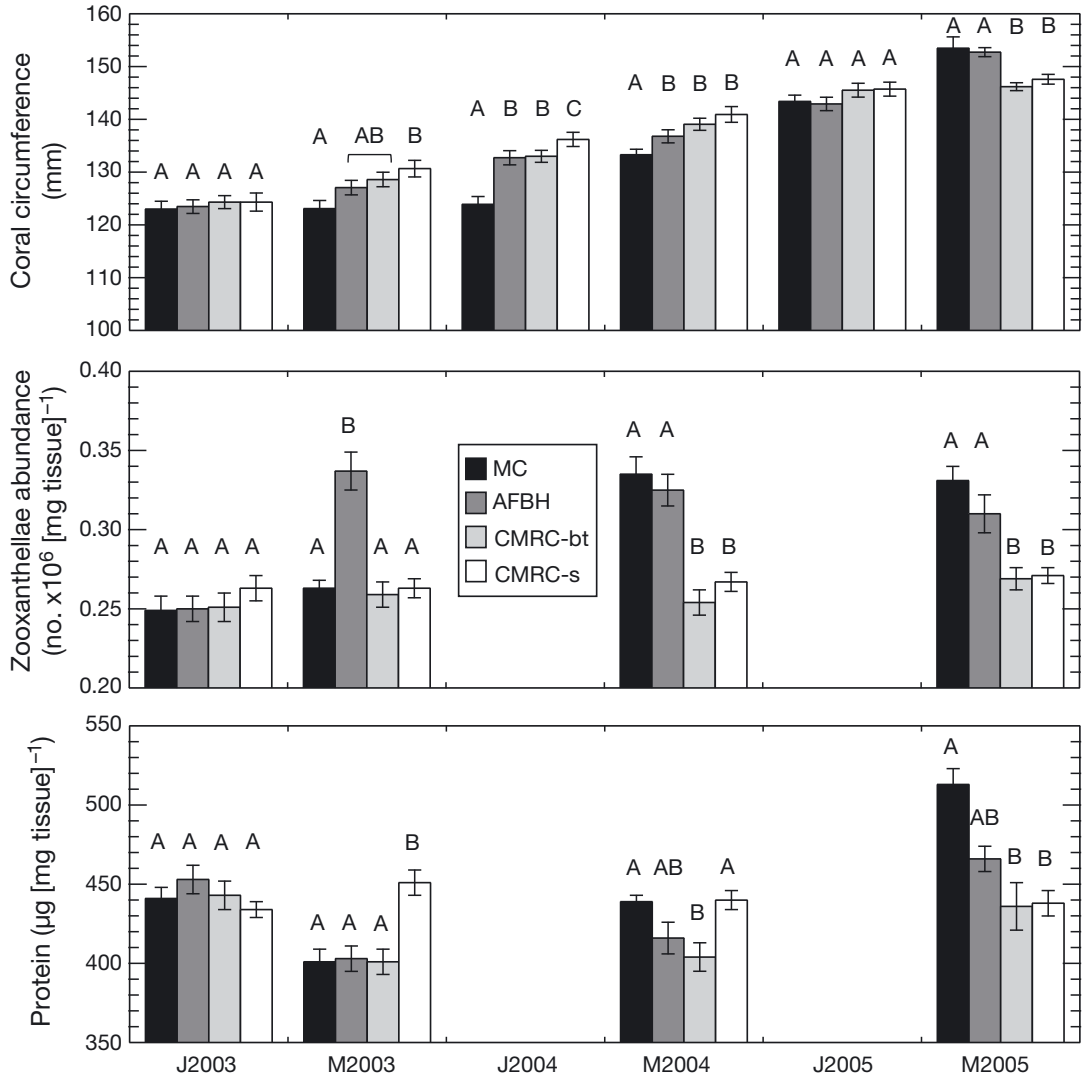


Fig. 5. *Siderastrea radians*. Condition of coral transplants through time. Histograms represent the mean ± 1SE coral circumference, zooxanthellae density, and protein content for marked coral colonies between 2003 and 2005. In January 2003, corals from a source population at the Caribbean Marine Research Center (CMRC) were transplanted to Mystery Cave (MC) and Angelfish Blue Hole (AFBH), back-transplanted (CMRC-bt), or tagged *in situ* but not handled (CMRC-s) (n = 15 colonies at each site). Growth measurements were made in January (J) and May (M) each year, while invasive sampling for zooxanthellae and protein were only conducted once per year in May in order to limit stress and/or repair time relative to growth rates. Transplants that exhibited significant differences (Scheffe's test, $p \leq 0.05$) in circumference, zooxanthellae density, or protein content, are indicated by different letters

constrains conclusions (Diamond 1986); nonetheless, the sponge-nutrient correlations, stable isotope surveys, and transplant experiments support cave sponge facilitation as the most parsimonious explanation for the local patch reef biodiversity and health.

### Biodiversity of cave facilitated patch reefs

Due to recent declines in coral community structure and function, there has been increased interest in discovering biodiversity hotspots, and understanding the specific environmental factors that control these communities (Balvanera et al. 2006). In particular, marginal ecosystems such as seagrass beds and mangroves are recognized as important local sources of coral reef biodiversity (Dorenbosch et al. 2007). The results of this study indicate that patch reefs near marine caves may also represent a local hotspot of biodiversity. Reefs near the mouths of marine caves host greater diversity and percent cover of corals, algae and sponges relative to similar, but disjunct,

reef habitats (Fig. 2). In contrast to seagrass beds and mangroves, which tend to harbor very few corals, coral diversity was up to 4.3 times higher on patch reefs near cave mouths than on reefs further away (Table 3). The diversity and percent cover of algae and sponges near caves were comparable to regional reefs, seagrass beds, and mangroves (M. Slattery pers. obs.) and, while the differences in herbivorous fish diversity were less obvious, the numbers of herbivores were also higher at these sites (Table S1 in the supplement). These patch reefs were relatively stable through time, and they exhibited immunity to an extensive regional bleaching event in 2005 (M. Slattery pers. obs.), likely due to the diel flushing of these communities with cave-cooled seawater (Fig. S6). It is possible that some of the coral health responses (i.e. growth: Fig. S7) may be due to the effect of 'cave'; this could explain some of the significant interaction effects revealed by our analyses. Specifically, in addition to a gradient in cave sponge cover and nitrate, our natural experiment demonstrates variation in other site-specific variables. For example, seawater flow from these caves can vary from day to day, and certainly between sites. While much of the POC is effectively reduced by cave sponge filtration prior to release onto nearby patch reefs (Fig. 3), heterotrophic feeding may enhance coral growth independent of nitrate enrichment (e.g. Lesser 2006, Lesser et al. 2010). In addition, corals on nearby shallow patch reefs, where thermal stress can be high, might benefit from reduced seawater temperatures (Edmunds 2009) and from elevated flow rates that can mediate surficial sediment clearance (Fabricius & Wolanski 2000). It is possible that these factors are responsible for the continued positive growth rates of MC corals, even under reduced zooxanthellae abundance and protein concentration (Figs. S8 & S9, respectively), after dredging operations commenced in October 2002.

### Cave sponge-derived nutrients

Marine caves are primarily influenced by tidal processes that turn over oxygen and nutrients on a semidiurnal basis (Gili et al. 1986, Fichez 1991) and enable filter-feeding communities to thrive (Bussotti et al. 2006). We found a strong correlation between the percent cover of sponges, the dominant filter-feeders (≥95% of the community) in marine caves of the Bahamas, and the concentration of nitrate in ebb-tide seawater collected at the mouths of these caves (Fig. 3). We further examined the change in POC and nitrate over a tidal gradient representing flood, slack, and ebb conditions (Fig. 4). Taken as a whole (Fig. S6 in the supplement), our data are consistent with a model of food delivery to the cave sponges during flood tides, uptake and metabolism of POC by sponge filtration, and transport of nitrogenous waste to local patch reefs during ebb tides. Recent studies indicate that DOC represents over 90% of the total organic carbon removed by coral cavity sponges (de Goeij et al. 2008, van Duyl 2011), and it likely regulates sponge cell turnover under conditions of environmental stress (de Goeij et al. 2009). Moreover, high microbial abundance (HMA) sponges apparently favor DOC, while POC may be more important for low microbial abundance (LMA) sponges (de Goeij et al. 2008). Since both types of bacteriosponge inhabit these caves (Table S2), our POC results provide a very conservative estimate of the carbon flux within these cave communities and the fate of this energetic resource. Additional research has demonstrated the important metabolic nitrogenous resource that shallow coral reef sponges in Florida provide (Southwell et al. 2008). However, water samples from Bahamian patch reefs 25 m away from the caves had very low levels of nitrate (Fig. S5), indicating that these marginal ecosystems behave more like the Red Sea and Curacao, where cryptic sponge biomass is a major source of DIN (Richter et al. 2001, Scheffers et al. 2004), than other Caribbean 'sponge reefs' (Southwell et al. 2008). Bacteria have been linked with the regeneration of nitrate from metabolic nitrogenous waste due to their high biomass and genetic capacity, in some sponge species (Mohamed et al. 2008). We did not examine sponge-associated bacteria in this study, but many of the cave sponge species are known to harbor rich microbial communities (e.g. Weisz et al. 2008; Table S2), so it seems likely that symbiotic bacteria play a critical functional role within the community (Fiore et al. 2010). Nonetheless, there are clearly additional temporal considerations associated with nitrogen delivery to local coral reefs. For example, LaPointe et al. (2004) reported relatively high concentrations (3.5 mM) of 'nitrate-nitrite' at our NPCC site between 1997 and 1999. The highest levels of nitrate we encountered over 10 yr of sampling this cave (including sampling every 2 h during a 24 h period in January 2003 [data not shown]) was about one tenth of this level (Fig. S5). It is possible that structural changes to the NPCC blue hole (i.e. collapse of the barrier sill and resultant tidal flushing) may account for some of the differences in DIN recorded by LaPointe et al. (2004) and in this study.

Excess nutrients in coral reef communities have been implicated in the phase shift of coral- to algal-dominated systems (Bruno et al. 2009), and they have been shown to decrease coral fecundity (Koop et al. 2001). Our data demonstrate that marine caves serve as a significant source of nutrients, so why are the mouths of marine caves not algal plains? While nutrient limitation may play some role in the control of algal blooms (LaPointe 1997), there is good experimental evidence to show that herbivory is at least as important in controlling algae (Edmunds & Carpenter 2001, Mumby & Steneck 2008, Burkepile & Hay 2009). We observed greater numbers of grazing fishes and urchins at the mouths of the caves relative to the far sites (with the exception of *Tripneutes ventricosus* which prefers seagrass beds common to some far sites; Table S1 in the supplement), although the biodiversity of herbivores was similar. Many of these fish used the physical structure of the patch reefs around the cave mouth and/or the cave mouth itself as residential habitat; that is to say, they were more site-attached than conspecifics that tended to migrate through the far reef sites (M. Slattery pers. obs.). Thus, although the elevated nutrient levels emanating from the cave mouths enhance algal growth near the caves (LaPointe et al. 2004), corals are likely able to persist on these reefs due to the enhanced levels of grazing by herbivorous fishes and urchins (Fig. S3).

The $\delta^{15}N$ data reinforce our hypothesis of nitrogen enrichment of the cave mouth patch reefs by cave sponge-derived nitrate. There was significant $^{15}N$ enrichment of the cave sponge *Haliclona implexiformis*, compared to flood-tide POM value. Significant enrichment of the cave mouth corals, relative to conspecifics approximately 25 m away, was observed at MC and SCC, but not at NPCC (Table 4). $\delta^{15}N$ can vary over broad vertical and horizontal spatial scales in the marine environment for any given species (Heikoop et al. 2000), but our results indicate similar levels of enrichment across a 49 km region of the Exuma Cays, Bahamas, i.e. the maximal linear distance between these caves (Fig. 1). These data are interesting for 2 additional reasons: (1) NPCC has low sponge biomass (<100 g total within the cave) and thus acts as a natural control for the experimental factor of 'sponge', and (2) $\delta^{15}N$ enrichment at MC was identical to that at SCC at a time when sponge biomass was similar between both caves (based on the adjusted cave surface area-sponge volumes) due to an anthropogenic scour event. Thus, the presence of sponges within these caves appears to be a crucial factor in patch reef nitrogen enrichment, and the level of enrichment is apparently a function of cave sponge volume rather than percent cover (e.g. AFBH vs. RC: Fig. 3, Fig. S2 in the supplement). Moreover, variability in nutrient levels within these caves throughout a tidal cycle (Fig. 4) may be due to the differences in sponge percent cover from the mouth to the back of the cave (Fig. S1A), or to the specific sponge biodiversity within each of these zones (Table S2).

### Cave facilitated patch reef health

Our results suggest that nutrients derived from cave sponge communities likely facilitate the diversity and health of nearby coral reefs. The importance of cave sponge-derived nutrients on cave mouth patch reefs is apparent when *Siderastrea radians* coral growth, zooxanthellae abundance, and protein concentrations are compared near and far from the mouths of the caves (Figs. S7 to S9 in the supplement, respectively). *S. radians* growth rates at MC lagged behind individuals transplanted to AFBH, as well as controls (back-transplants and source population) at CMRC, for at least 16 mo (Fig. 5) after anthropogenic sediment scour caused a significant decline in the MC sponge community. It is possible that cave-specific effects (e.g. lower irradiance at 6 m depth in AFBH vs. 3 m depth in MC) and/or residual dredging effects (e.g. resuspended copper paint which flaked off yacht hulls) accounted for some of this response. However, as the MC sponge community percent cover, and by extension nutrient enrichment, recovered to pre-dredging levels by January 2005, *S. radians* growth rates also recovered and eventually exceeded those of the other treatment groups. We take these data to indicate a nutrient effect at MC given the reduced growth rate of corals at AFBH and in both sets of controls at CMRC. Specifically, irradiance at MC exceeded that of AFBH; yet, under essentially identical nutrient levels when the MC cave sponge cover declined to the level of AFBH due to sedimentation, coral growth at AFBH outpaced that of conspecifics at MC, suggesting that light was not a limiting factor for either cave community. Additionally, irradiance at the CMRC control site was equivalent to that of the MC transplant sites, but MC coral growth rates were much higher in the presence of cave sponge-mediated nutrient enrichment. In the absence of a true control, additional cave-specific factors cannot be ruled out; nonetheless, these data provide compelling evidence for the role of cave sponge-derived nitrate in coral patch reef health.

The reduced nitrate due to dredging-mediated sponge scour at MC appeared to have an immediate impact on zooxanthellae abundance within the transplanted *Siderastrea radians* compared to conspecifics relocated to AFBH. However, within 1 yr, the zooxanthellae abundances at these sites were identical and exceeded the source population levels. All of the handled *S. radians* exhibited a depression in protein concentrations relative to non-handled controls, and this might be partially explained by the reduction in zooxanthellae (Porter et al. 1989, Dove et al. 2006, Slattery & Paul 2008), as protein and zooxanthellae counts from 2004 and 2005 mirrored one another. The difference in zooxanthellae abundance and protein concentration at AFBH in May 2003 may represent a lag in energy transfer from symbiont to host coral (Crossland et al. 1980, Lipschultz & Cook 2002). The sedimentation that impacted the cave sponges also killed some corals and sponges near the mouth of MC. An immediate result of this loss was a decline in the 'resident' fish populations largely due to emigration to other sites (including AFBH, where they apparently kept algal cover in check: Fig. S4 in the supplement) during dredging operations and the subsequent reduction of stable food sources; however, these fish populations were slow to recover due to scour and general disturbance by dredging operations in the area (M. Slattery pers. obs.). The absence of a grazer fauna for several years resulted in a longer-term increase in algal percent cover (Fig. S4). By 2009, the mouth of MC consisted of a thick carpet of algae/cyanobacteria (primarily *Lyngbya* sp.; 272.6 $m^2$ area × 1 m depth). However, these changes slowly reversed themselves; as of May 2010, the MC patch reef community had returned to conditions more similar to its pre-dredged structure and these conditions were stable through May 2010. This apparently reversible phase shift might be due to coral tissue regeneration (Diaz-Pullido et al. 2009), or to new coral recruits (Vermeij 2005), which may have provided a 'cue' for the return of the grazing fish community (M. Slattery pers. obs.), and their subsequent role in re-establishment of stable cave mouth patch reef communities (Edmunds & Carpenter 2001). Alternatively, other cave-specific factors in this 'natural experiment' may have also contributed to the coral health at MC.

These data have potential implications for coral reef management and resilience (Mumby & Steneck 2008). As climate change and other anthropogenic impacts continue to degrade coral reef ecosystems, pristine coral communities are of greater consequence (Hoegh-Guldberg & Bruno 2010). To the extent that these patch reef communities near cave mouths are genetically connected to nearby coral reefs (Harmelin 1997), there is hope that these biodiversity hot spots might act as a seed bank for degraded coral communities. These patch reefs might provide novel genetic stock for coral reef managers to transplant onto degraded reefs. Alternatively, propagules from larval recruitment and/or clonal processes might enhance the resilience of coral reef communities. However, our results also demonstrate the fragile nature of these marine cave ecosystems (Iliffe et al. 1984, this study). Following a harbor-dredging event in 2002, at least one 'downstream' cave was severely impacted by sedimentation, and the impacts were evident for at least 8 yr. Marine cave sponge communities have the potential to facilitate local patch reef biodiversity and growth via shared nutrients, as has been demonstrated in mangrove sponges (Ellison et al. 1996). While our study is by no means the first example of a positive contribution by sponges to coral reef species (see examples in Wulff 2006), we provide compelling evidence for the subtle influences of sponges on coral reef communities. These facilitated patch reefs exist in marginal habitats that represent a greater degree of stressful conditions than other reefs throughout the area, as predicted by Bertness & Callaway (1994). The loss of these unique marine cave ecosystems, the sources and sinks of local nutrients, may have significant implications for longer-term coral reef community resilience; therefore, protection of marine caves is of critical importance.

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