Fish-derived nutrient hotspots shape coral reef benthic communities

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Abstract. Animal-derived nutrients play an important role in structuring nutrient regimes within and between ecosystems. When animals undergo repetitive, aggregating behavior through time, they can create nutrient hotspots where rates of biogeochemical activity are higher than those found in the surrounding environment. In turn, these hotspots can influence ecosystem processes and community structure. We examined the potential for reef fishes from the family Haemulidae (grunts) to create nutrient hotspots and the potential impact of these hotspots on reef communities. To do so, we tracked the schooling locations of diurnally migrating grunts, which shelter at reef sites during the day but forage off reef each night, and measured the impact of these fish schools on benthic communities. We found that grunt schools showed a high degree of site fidelity, repeatedly returning to the same coral heads. These aggregations created nutrient hotspots around coral heads where nitrogen and phosphorus delivery was roughly 10 and 7 times the respective rates of delivery to structurally similar sites that lacked schools of these fishes. In turn, grazing rates of herbivorous fishes at grunt-derived hotspots were approximately 3 times those of sites where grunts were rare. These differences in nutrient delivery and grazing led to distinct benthic communities with higher cover of crustose coralline algae and less total algal abundance at grunt aggregation sites. Importantly, coral growth was roughly 1.5 times greater at grunt hotspots, likely due to the important nutrient subsidy. Our results suggest that schooling reef fish and their nutrient subsidies play an important role in mediating community structure on coral reefs and that overfishing may have important negative consequences on ecosystem functions. As such, management strategies must consider mesopredatory fishes in addition to current protection often offered to herbivores and top-tier predators. Furthermore, our results suggest that restoration strategies may benefit from focusing on providing structure for aggregating fishes on reefs with low topographic complexity or focusing the restoration of nursery raised corals around existing nutrient hotspots.

Key words: *biogeochemical hotspots; bottom-up; coral reefs; coral restoration; grunt fish; nutrient cycling; nutrient hotspots; nutrients; subsidies; top-down.*

Introduction

Mobile animals can influence the availability of limiting nutrients across landscapes through the consumption and excretion of resources (Vanni 2002, Estes et al. 2011). Ungulates (McNaughton et al. 1997), seabirds (Croll et al. 2005), and fishes (Burkepile et al. 2013) are just a few examples of animals that accelerate nutrient cycling and enhance nitrogen (N) and phosphorus (P) availability within their habitats. Animals that move between systems also transport nutrients, serving as nutrient sinks in the systems in which they feed and nutrient sources in the systems where waste is excreted. For example, seabirds move nutrients from marine to terrestrial systems, alleviating nutrient limitation in plants and changing plant community structure and ecosystem processes (Croll et al. 2005). Such animals act as mobile links between systems and can provide recipient systems with nutrient subsidies that often exceed abiotic sources of nutrients, ultimately altering nutrient storage and rates of primary productivity in the recipient systems (Vanni 2002, Lundberg and Moberg 2003, Vanni et al. 2013).

Aggregations of animals within a landscape can lead to spatial or temporal variation in nutrient delivery, potentially creating nutrient "hotspots" (McClaine et al. 2003). These spatially heterogeneous patches of nutrients can influence the abundance and distribution of primary producers by altering species performance and competitive interactions (Chesson 2000, John et al. 2007). Nutrient hotspots may also attract herbivores and intensify grazing pressure as herbivores seek out high quality resources (Steinauer and Collins 2001, Anderson et al. 2010). Despite the well recognized importance of animal-derived nutrients in both terrestrial (e.g., McNaughton et al. 1997, Hilderbrand et al. 1999, Croll et al. 2005) and freshwater systems (e.g., Larkin and Slaney 1997, Moore 2006, McIntyre et al.

2008), the potential influence of animal-mediated nutrient hotspots in structuring marine communities have rarely been demonstrated (but see Layman et al. 2013).

In marine systems, the majority of studies investigating nutrient subsidies focus on nutrients derived from nitrogen fixation, physical processes such as upwelling or run-off, or anthropogenic sources (e.g., Welsh 2000, Leichter et al. 2003, Schaffelke et al. 2005). However, fishes can be important sources of nutrients, particularly in oligotrophic systems such as tropical seagrass beds and coral reefs (Layman et al. 2011, Burkepile et al. 2013). For example, in the Florida Keys, fishes are one of the most important sources of N on reefs and can impact algal and coral abundance on a reef-wide scale (Burkepile et al. 2013). Many species of carnivorous fishes, particularly grunts (family Haemulidae), shelter on reefs during the day but forage in adjacent seagrass, sand-flat, and mangrove habitats at night, thereby vectoring nutrients to reefs when they return daily. Because these fishes show high fidelity toward specific shelter sites, often returning to the same coral heads (Ogden and Quinn 1989, Heck et al. 2008), they may create consistent nutrient hotspots that could alter primary production and benthic community composition. Furthermore, fish-derived nutrients affect corals in fundamentally different ways than anthropogenic sources, with nutrients from fishes often facilitating coral growth and anthropogenic nutrients often slowing coral growth (Shantz and Burkepile 2014). Given the high biomass of fishes on pristine coral reefs (e.g., Friedlander et al. 2010), the rates and patterns of fish excretion may strongly influence the dynamics of reef communities and be important components of healthy reef systems. Yet, we know very little about how the distribution of fishes and their nutrients within the reef landscape impacts ecological processes or community structure.

Here, we examined the role of fishes as generators of nutrient hotspots on an Atlantic coral reef and explored how these hotspots influenced benthic community structure. Over three months, we monitored the biomass of fishes sheltering across twenty structurally similar coral heads on a shallow forereef. We estimated the rates of nutrient delivery from fishes and assessed the impact of these nutrients on coral growth, algal community structure, and herbivorous fish grazing at each site. We predicted that aggregations of fishes would create nutrient hotspots around the coral heads where they sheltered and that these fish-derived hotspots would increase coral growth and alter the composition of primary producer communities. Additionally, we predicted that by creating hotspots of important limiting nutrients, fish aggregations would concentrate herbivore grazing on nutrient-enriched algae growing in these hotspots. Herbivory is a fundamentally important process for structuring coral reefs, with high levels of herbivory keeping reefs free of excess harmful algae and facilitating coral recruitment, survivorship, and growth (Hughes et al. 2007, Burkepile and Hay 2008). Accordingly, we expected the cumulative effects of fish-derived nutrients to create distinct benthic communities around hotspots.

MATERIALS AND METHODS

Study species and site

We conducted our research on a shallow forereef (5–7 m deep) in the Florida Keys National Marine Sanctuary, USA (24.992° N, 80.408° W) from May through August of 2013. This site is dominated by primarily dead colonies of the massive, digitate coral *Dendrogyra cylindrus*. During the day, large schools of grunts consistently shelter around some of these *D. cylindrus* colonies, while remaining consistently absent at other colonies.

Experimental setup

In April 2013, we tagged every *D. cylindrus* colony in a 60 × 20 m section of the reef. Over the ensuing month we conducted weekly surveys between 10:00 and 15:00 to record the number, size, and species of fishes within a 0.5-m perimeter of each tagged colony. From these preliminary surveys, we selected 20 study colonies with live tissue, haphazardly distributed across the reef, that consistently sheltered either high or low biomass of fishes and were separated by at least 2 m (*n* = 10 each; see Plate 1; Appendix A). Colonies were interspersed throughout the site to ensure that any large scale abiotic factors such as nutrient delivery from internal waves, which rarely reach these depths in the Florida Keys (Leichter et al. 2003), or land-based sources of pollution, which are negligible at these sites >10 km offshore (Briceño and Boyer 2012), would affect both high and low-biomass colonies equally.

Study colonies ranged in size from 1 × 1 × 0.75 m to 2 × 2 × 2.25 m (length × width × height), with fish tending to shelter at taller colonies. To determine the consistency of fish residency we conducted five-minute surveys between 10:00 and 15:00 at each study colony every seven to nine days from May to mid-August (*n* = 11 surveys) and recorded the number, size, and species of fishes at each colony. Fish were considered residents of the colony if they spent the entirety of the survey within 0.5 m of the colony's perimeter. Each week we began our surveys at a randomly selected colony and surveyed colonies from nearest to the start location to furthest away in order to prevent any artifacts that may have occurred from surveying colonies in the same order. For our analyses, we converted estimates of fish length to biomass using published length–mass relationships (Bohnsack and Harper 1988, Marks and Klomp 2003).

Estimates of nutrient delivery

Fishes excrete nitrogenous waste as ammonia, and to some extent urea, while P is excreted in both soluble and fecal forms (Dosdat et al. 1995). As a result, fish-derived

nutrients are quickly diluted in the water column and rapidly utilized by benthic organisms, making it difficult to capture the signal of fish-derived nutrients in water samples. Therefore, we used bioenergetics models from Burkepile et al. (2013) to estimate nutrient excretion rates from sheltering fishes at each colony. Bioenergetics models use a mass balance approach given a priori knowledge of a fishes' diet, physiology, and the environmental conditions to provide accurate estimates of excretion via linear models (e.g., Vanni 2002, Allgeier et al. 2013, Burkepile et al. 2013). We used these linear models to estimate excretion rates (mg nutrient·[g fish wet mass]$^{-1}$·d^{-1}) of nitrogen and phosphorus based on the biomass of all Haemulid fishes sheltering around $D.$ $cylindrus$ colonies. We focused solely on Haemulid fishes as they represented 99% of the biomass of resident fishes across all study colonies.

We complemented our bioenergetics models to evaluate nutrient output by assessing the nutrient content of macroalgae at the different study colonies, as it reflects ambient nutrient conditions over a relatively long time frame (i.e., weeks to months; Atkinson and Smith 1983). Thus, algae in consistently enriched environments typically show higher tissue nutrients (e.g., Burkepile and Hay 2009, Vega Thurber et al. 2014). During weeks 7 and 14, samples of the macroalga $Dictyota$ $menstrualis$ were collected from within the survey areas at each colony for analysis of N and P content. Samples were immediately placed on ice, transported to the lab, and frozen until processed. Samples were rinsed with deionized water and scraped free of epiphytes before being dried at 50°C to a constant mass and ground to powder. Total carbon and N content was determined via elemental analysis using a CHN analyzer (FlashEA 1112 Series; Thermo Electron Corporation, Waltham, Massachusetts, USA). We measured P content through a standard-oxidation–acid-hydrolysis extraction followed by a colorimetric analysis.

Community structure

To determine how differences in fish-derived nutrients impacted community structure, we established 0.5 × 0.5 m permanent quadrats adjacent to the southwestern side of each study colony. These areas fell within the radius of our fish surveys, and their position was selected to standardize for differences in water motion and light availability that could have occurred based on their position relative to the study colony. To estimate the percent cover of benthic organisms, we took digital photos of each permanent quadrat during the final week of the study. We overlaid a 100-point grid on each photo and identified the organism below each point to the lowest taxonomic level possible. After identification, each point was categorized as either (1) brown macroalgae (>90% $Dictyota$ spp.), (2) red macroalgae (primarily articulated corallines from the genera $Amphiroa$ and $Galaxaura$), (3) green macroalgae ($Halimeda$ spp.), (4) filamentous turf algae, (5) crustose coralline algae

(CCA), (6) turf algae mixed with sediment mats (TAS), (7) cyanobacteria, (8) soft corals, or (9) stony corals. In addition, we pooled all upright algae (brown algae, red algae, green algae, and both turf groups) into a total algae group, as members from these groups can impair coral recruitment and growth (Birrell et al. 2008).

Fish excretion can increase the growth of the corals in which they shelter (Meyer et al. 1983, Shantz and Burkepile 2014). However, it is unclear how fish schools impact corals that they are not directly sheltering in. Therefore, in week 2 of the study, we transplanted four $Acropora$ $cervicornis$ fragments (10 cm each) around each study colony to investigate the effect of fish-derived nutrients on corals around shelter sites. We transplanted two fragments into each permanent benthic quadrat. To examine if potential differences in abiotic forces (e.g., flow rate, shading, sedimentation) could account for variation in coral growth, we transplanted the other two $A.$ $cervicornis$ fragments to the top of dead $D.$ $cylindrus$ pillars on the southwestern edge of each study colony. These corals were within 1 m of those placed in our permanent benthic quadrats, but could have experienced different flow, light, and sedimentation regimes than the corals at the base of the colonies. All corals were tagged, measured, and photographed at the time of outplanting. During weeks 7 and 14, each coral was remeasured and photographed to calculate the total linear extension. Differences between final and initial sizes were used to calculate the percent growth per day.

To assess how fish aggregations impacted herbivore foraging, in weeks 10 and 11, we filmed each study colony for two hours and documented the species, size, and total number of bites taken by herbivorous fishes within each permanent quadrat. All colonies were filmed between 10:00 and 13:00 over the course of two days. When the videos were scored, only bites taken within the permanent quadrats were counted toward the total number of bites taken. To ensure that differences in grazing resulted from nutrient delivery from grunts and the ensuing enrichment of algae on the benthos rather than some other intrinsic factors of the colony, we also transplanted pre-weighed sections of a palatable alga, $Laurencia$ sp., into each permanent quadrat to measure algal biomass removal rates. All $Laruencia$ sp. was collected from an ~3-m^2 area in a nearby backreef location to ensure similar nutrient quality. Prior to deployment, $Laurencia$ sp. was spun dry in a salad spinner and divided into 20 individually weighed portions (initial mass 15.0–20.0 g). Pre-weighed algae were kept in aerated seawater overnight and randomly assigned to a study colony the following day for assays. At each colony, algae were secured to clothespins, attached to the substrate and left for two hours. After two hours, assays were collected in individual bags, returned to the lab, spun dry, and reweighed to determine mass lost during deployment. Half of the assays were filmed using GoPro digital cameras (GoPro, San Mateo, California, USA) to confirm that the mass lost was due to herbivory.
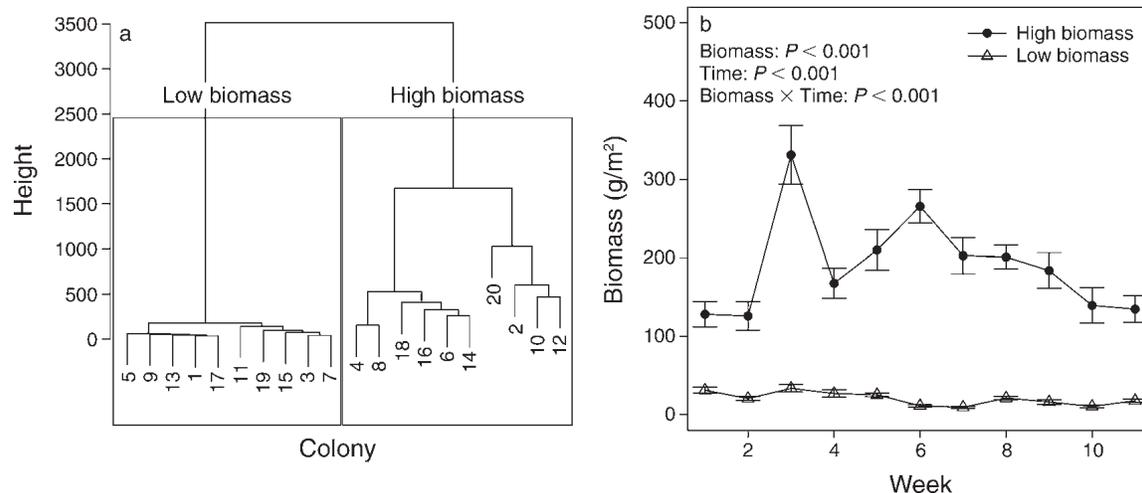
FIG. 1. (a) Results from agglomerative cluster analysis categorizing the 20 study colonies as either high-biomass or low-biomass sites based on the biomass of grunts sheltering at each site during weekly surveys. Numbers below each branch indicate the identification number assigned to each study colony. (b) Biomass of grunts calculated from weekly surveys at high- vs. low-biomass sites throughout the study. *P* values from repeated-measures ANOVA. Data are means ± SE.

Statistical analyses

Because fish biomass tended to cluster at either low or high levels rather than along a continuum of occupation (see *Results*), we used agglomerative hierarchical clustering to categorize study colonies as "high-biomass" or "low-biomass" sites. Biomass status was assigned using the biomass of grunts around each colony throughout the study based on Wards method using Euclidean distances and the cluster library in R (Maechler et al. 2013). Differences in fish biomass based on cluster (high biomass vs. low biomass) and time were assessed by mixed-effects repeated-measures ANOVA with the nlme package in R (Pinheiro et al. 2007). To conform to assumptions of ANOVA, biomass data were log-transformed. Because biomass was significantly and consistently higher at high-biomass vs. low-biomass sites throughout the entirety of the experiment (see *Results*), we used these groups as a treatment variable for all subsequent analyses.

We used mixed-model ANOVAs that considered biomass status (high vs. low) a treatment factor and included a random effect for colony to test for differences in the mean N and P delivery from fishes (as calculated from bioenergetics models), and the algal mass lost from feeding assays. Because grazing rates on the benthos were filmed over separate days, we included an additional treatment factor for day to test for differences in grazing between colonies. Both excretion rates and algal mass loss from feeding assay data were log-transformed, while grazing rate data were square root transformed to meet assumptions of ANOVA. Differences in the N and P content of *D. menstralis* were tested via mixed effects repeated-measures ANOVA.

We tested for differences in the growth rates of *A. cervicornis* transplants via a nested two-way ANOVA that considered biomass status and position (elevated vs.

colony base) as predictors and included an interaction between the two. Transplants suffered high rates of breakage, likely due to the many careless recreational divers visiting the site (A. A. Shantz, *personal observation*). Therefore, we restricted our analysis to transplants that showed no signs of breakage at the time of measurement. This limited our analysis to 46 of the 80 transplants: 18 from high-biomass colonies (8 elevated and 10 at the base of colonies) and 28 from low-biomass colonies (15 elevated and 13 base).

We used mixed-effects ANOVA to test for differences in the percent cover of each benthic category as well as the overall cover of total algae at high- vs. low-biomass colonies. For groups that were rare (i.e., <5% of benthic cover) we used Fisher's exact tests to test for differences in their presence or absence between colonies. We also used ANOSIM and SIMPER analyses to test for similarity in the benthic algal community. We visualized differences in the benthic algal communities via nonmetric multidimensional scaling (NMDS) using a random starting configuration and Bray-Curtis distance based on the percent cover of each benthic category at each colony. ANOSIM and NMDS analyses were conducted using the vegan package in R (Oksanen et al. 2013). All data are reported as means ± SE.

RESULTS

Grunts accounted for the majority of biomass observed at *D. cylindrus* colonies and nearly 99% of the variation between high- and low-biomass colonies. The biomass of resident grunts sheltering among corals varied from 0 to 830 g/m², and agglomerative clustering indicated that colonies could be classified as either high-biomass or low-biomass sites (Fig. 1a). Biomass was relatively consistent at colonies identified as low biomass but showed significant variation through time at high-
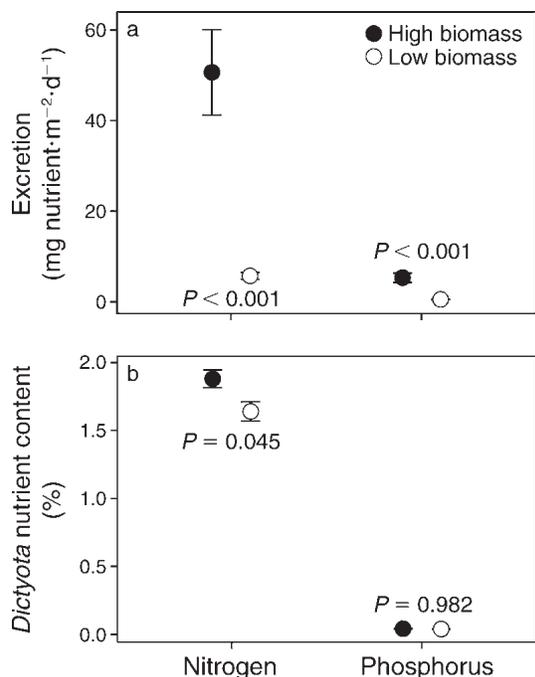
FIG. 2. (a) Daily excretion rates, as calculated by bioenergetics modeling, of nitrogen and phosphorus from grunts around high-biomass and low-biomass sites. (b) Percentage of nitrogen and phosphorus in the tissue of the alga *Dictyota menstrualis* collected from high-biomass vs. low-biomass sites. P values from mixed effects ANOVA. Data are means ± SE.

biomass sites (biomass × time effect, $F_{10, 180} = 3.81$, $P < 0.001$; Appendix B). Despite this variability, grunt biomass remained consistently higher at sites designated as high biomass vs. those designated as low biomass for the entirety of the study (biomass effect, $F_{1,18} = 67.83$, $P < 0.001$; Fig. 1b).

From our bioenergetics models, the average modeled grunt excretion rates of N and P around high-biomass sites were ~10 times greater than at low-biomass sites ($F_{1,16} = 91.07$, $P < 0.001$ and $F_{1,16} = 25.07$, $P < 0.001$ respectively; Fig. 2a). Modeled mean N excretion around high-biomass sites was 50.07 ± 9.43 mg·m^{-2}·d^{-1} (mean ± SE) while P excretion was 5.32 ± 1.01 mg·m^{-2}·d^{-1}. Calculated excretion rates around low-biomass sites also represented a sizable contribution of N and P to the area (5.72 ± 0.72 mg N·m^{-2}·d^{-1} and 0.53 ± 0.08 mg P·m^{-2}·d^{-1}), but were approximately an order of magnitude lower than at high-biomass sites. Additionally, nitrogen content of *D. menstrualis* was roughly 15% higher near high-biomass than low-biomass sites ($F_{1,18} = 4.64$, $P = 0.045$; Fig. 2b), but we found no difference in P content ($F_{1,18} < 0.001$, $P = 0.98$).

ANOSIM showed a significant difference in the benthic algal communities between high- and low-biomass sites ($R = 0.31$, $P = 0.007$). Dissimilarity between sites was driven primarily by TAS (26.7% of dissimilarity), CCA (24.5%), and brown macroalgae (24.0%) (Appendix B). These results were supported by our NMDS analysis, which suggested that high- and low-biomass sites were similar in turf cover, and to some extent red macroalgae, but diverged in percent cover of most other benthic groups (Fig. 3).

Colonies that sheltered large schools of grunts tended to have lower overall cover of total algae and TAS ($P = 0.01$ and 0.001 respectively; Fig. 4) than colonies without large schools of grunts. The percent cover of CCA was also ~70% higher around high-biomass colonies than low-biomass colonies ($P = 0.013$, Fig. 4). There were no significant differences in the percent cover of brown or red macroalgae individually. Green macroalgae cover was low across sites. However, these algae were present at 7 of 10 high-biomass sites but completely absent at all low-biomass sites ($P = 0.003$, two-tailed Fisher's exact test). Other rare benthic groups (e.g., stony coral, soft coral, cyanobacteria) did not differ between sites either in percent cover or presence/absence (Fig. 4).
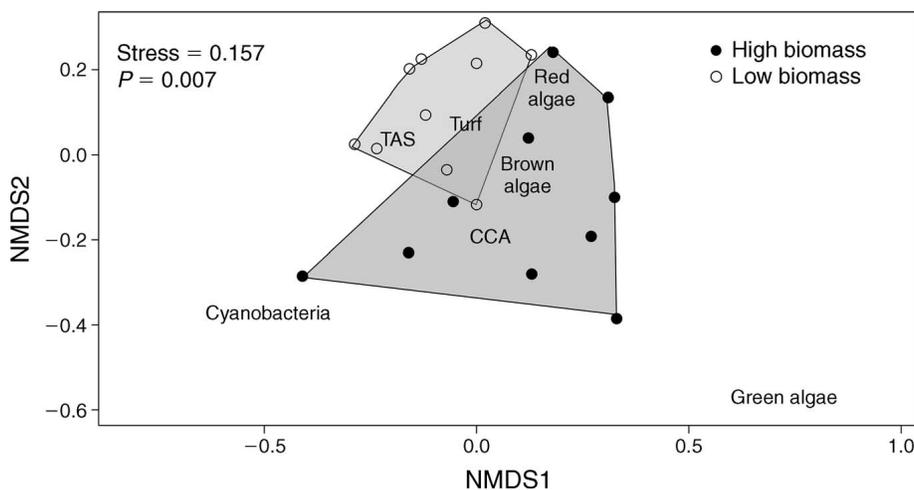

FIG. 3. Results of nonmetric multidimensional scaling (NMDS) depicting algal community structure around high-biomass vs. low-biomass sites. Benthic categories depict the distance relationships between colonies based on the percent cover of the category. P value from ANOSIM. TAS, turf algae mixed with sediment mats; CCA, crustose coralline algae.
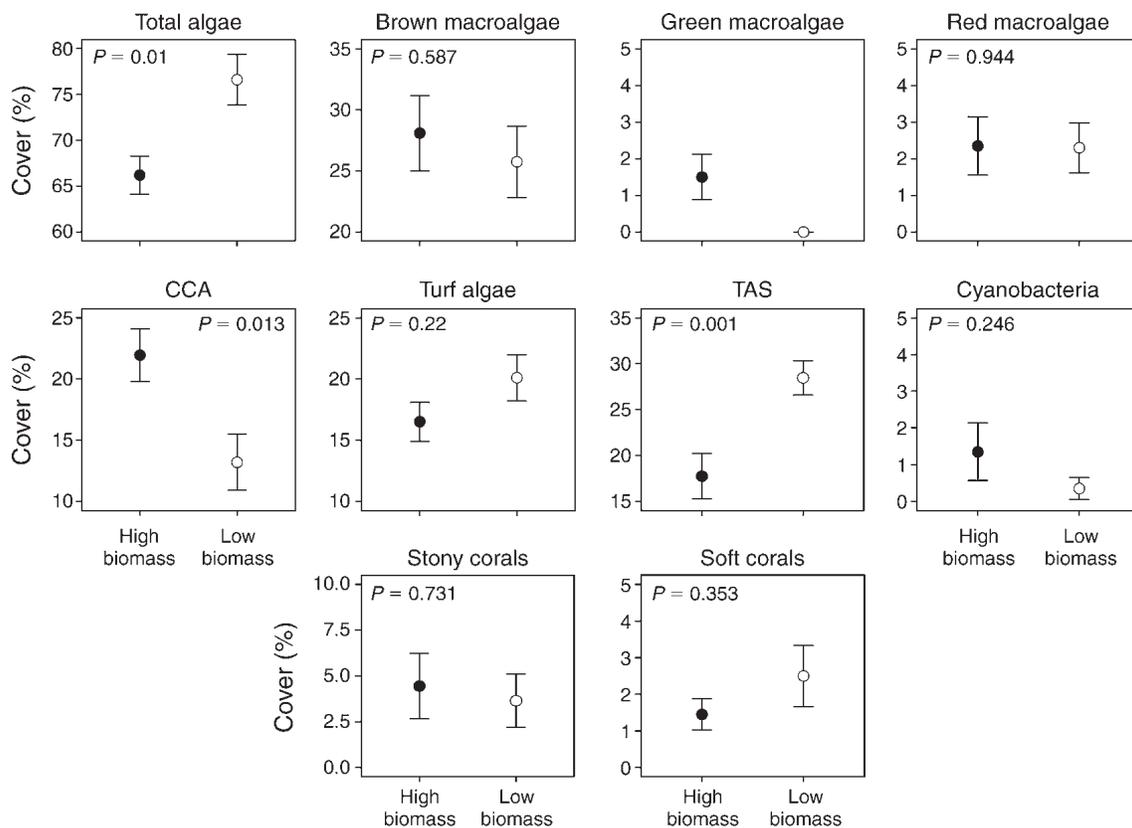
FIG. 4.   Percent cover of different benthic groups at high-biomass vs. low-biomass sites. *P* values from mixed effects ANOVA. Data are means ± SE; CCA, crystose coralline algae; TAS, turf algae mixed with sediment mats.

A. cervicornis transplanted around high-biomass sites grew nearly 75% faster than transplants at low-biomass sites ($F_{1,16} = 6.63$, $P = 0.02$; Fig. 5). We found no difference in growth rates between elevated coral transplants and those at the base of colonies ($F_{1,12} = 0.22$, $P = 0.65$) and no interaction between biomass and position ($F_{1,12} = 0.39$, $P = 0.55$).

No herbivorous fishes (e.g., Acanthurids or Scarids) spent enough time around any colony to be considered resident fish. Nonetheless, grazing rates by these herbivores were roughly three times greater at the High-biomass sites than at the low-biomass sites (1.52 ± 0.36 vs. 0.50 ± 0.10 bites per minute, respectively; $F_{1,17} = 8.56$, $P = 0.009$; Fig. 6) and day had no effect ($F_{1,17} = 2.57$, $P = 0.127$). Grazing rates were roughly 1.5–2.0 times higher for all herbivorous fishes except the ocean surgeonfish (*Acanthurus tractus*) and the yellowtail parrotfish (*Sparisoma rubripinne*), which increased grazing roughly 9- and 15-fold in high-biomass sites, respectively, and the queen parrotfish, *Scarus vetula*, which showed no change in grazing rates between sites. In contrast to grazing patterns on the benthos, herbivores consumed similar amounts of *Laurencia* from feeding assays at both high- and low-biomass sites (46.6% ± 10% mass consumed vs. 35.9% ± 8% consumed, respectively, $F_{1,18} = 0.71$, $P = 0.41$).

DISCUSSION

On coral reefs, consumer-mediated nutrient cycling is rarely appreciated as an important driver of community structure. However, we show that fish-derived nutrients from common mesopredators that occupy the middle of food chains can play an important role in dictating community structure. Our bioenergetics models show
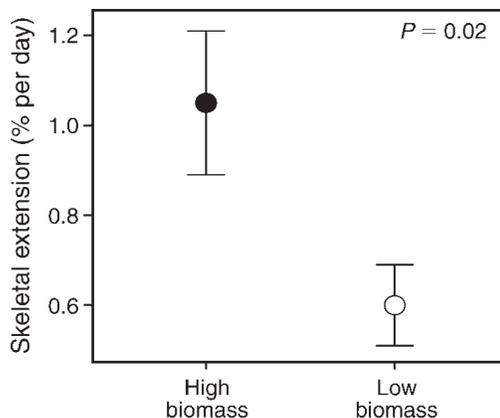

FIG. 5.   Skeletal extension rates, as a percentage of total linear extension per day, for *Acropora cervicornis* transplants located at high-biomass vs. low-biomass sites. *P* value from mixed effects ANOVA. Data are means ± SE.
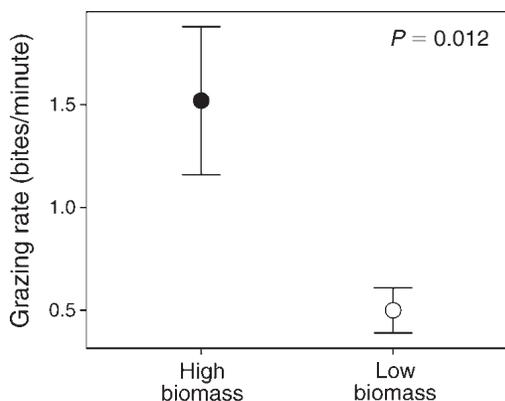
Fig. 6. Grazing rates of herbivorous fishes at high-biomass vs. low-biomass sites. P value from mixed effects ANOVA. Data are means ± SE.

that the high site fidelity of sheltering Haemulid fishes increased the delivery of both N and P around their shelter sites by an order of magnitude. These nutrient hotspots had higher coral growth rates, less harmful algae, and more crustose coralline algae compared to areas where fishes rarely sheltered. Interestingly, the increased input of limiting nutrients at hotspots led to increased feeding by herbivorous fishes, which likely drove much of the difference in benthic community structure at the high-biomass sites. Our data are some of the first to indicate that fish aggregations and their nutrient subsidies can be important determinants of ecosystem processes and community structure on coral reefs.

High rates of nutrient delivery often influence the species composition and dominance of primary producer communities, as well as impact overall rates of production, elemental storage and ecosystem function (Chapin et al. 1997). For example, Burkepile et al. (2013) documented a positive relationship between fish excretion rates and the percent cover of macroalgae across multiple reefs in the Florida Keys, including the site used in this study. However, the spatial distribution of nutrients may be as important as total delivery rates for determining ecological processes. Heterogeneity in resource supply can have profound effects on ecosystems by creating gradients in species performance within the landscape (Chesson 2000) or altering the feeding patterns of consumers (Barboza et al. 2009). At our site, the majority of fish-derived nutrients were not distributed evenly across the reef. Instead, bioenergetics models indicated that large schools of grunts provided, on average, roughly 10 times more N and P to discrete sites where they consistently sheltered. Importantly, our study site had the lowest reef-wide rates of N and P excretion among reefs in the upper Florida Keys, but the consistent aggregation of fishes at specific sites within our study reef created nutrient hotspots where nutrient excretion rates exceeded those of most other reefs in the region (Burkepile et al. 2013).

Thus, fish aggregations appear to be important for determining both within and among reef patterns in nutrient distribution.

High-biomass sites also possessed distinctly different algal communities than structurally similar sites that lacked large schools of grunts (Fig. 3). Low rates of nutrient supply typically favor slow-growing algae that are effective in nutrient acquisition, storage, and use, while high nutrient levels often promote rapidly growing, ephemeral species such as filamentous turf (Herbert and Fourqurean 2008). Surprisingly, we found no difference in the percent cover of turf or macroalgae between sites. Instead, the lower cover of TAS and higher cover of CCA at high-biomass sites accounted for over 50% of the differences between high- and low-biomass sites (Fig. 4; Appendix B). Given that fast growing algae are typically favored by excess nutrients, one might expect the opposite pattern. However, previous experiments manipulating nutrients on reefs have reported that both shorter filamentous turf algae and TAS are mediated by grazing rather than nutrients, while CCA responds positively to nutrient enrichment in the presence of grazers (Burkepile and Hay 2009, Walsh 2011). Our findings are consistent with these patterns and suggest that the nutrient-induced concentration in grazing around nutrient hotspots had more influence on benthic algal communities than did the direct effects of nutrients on algal growth and competition.

Given that herbivores are often nutrient limited, they should focus their foraging on high-quality primary producers (Barboza et al. 2009, Lemoine et al. 2014). We found that herbivorous fishes fed at roughly three times greater rates around high-biomass sites than low-biomass sites (Fig. 6). This is similar to large herbivores in terrestrial systems such as bison in tall-grass prairies (Steinauer and Collins 2001) and large ungulates in African savannahs (Anderson et al. 2010) that exhibit higher grazing rates around nutrient hotspots. Accordingly, the increased grazing at high-biomass sites likely explains the absence of higher macroalgal cover associated with high levels of fish-derived nutrients on a reef-wide scale (Burkepile et al. 2013), as more intense herbivory likely compensates for increased algal production at the scale of individual coral heads.

We also found that the high levels of fish-derived nutrients at high-biomass sites promoted coral growth, with extension rates of A. cervicornis approximately 1.5 times greater at these sites than at sites where grunt biomass was low (Fig. 5). This pattern has been documented for corals that shelter fishes directly within their branches. For example, growth of Porites furcata was approximately 1.4 times greater when colonies sheltered schools of grunts (Meyer and Schultz 1985). While this value is similar to the increased growth rates recorded here, our study shows that corals receive benefits from fishes by merely growing in the proximity

($\leq$1 m) of large schools of fishes. Given the high fish biomass on reefs with low fishing pressure (Sandin et al. 2008, Friedlander et al. 2010), corals may be adapted to thrive in areas with high rates of nutrient recycling by fishes, so long as macroalgal cover remains low. Indeed, Allgeier et al. (2014) suggested that fish may deliver nutrients to corals at an optimum N:P ratio for coral growth of around 20:1, a level almost identical to the 20.3:1 calculated in our study. Thus, fish-derived nutrients and nutrient hotspots may be an important positive feedback on coral success that could facilitate coral-dominated communities.

As a result, nutrient hotspots may serve as important nodes for the recovery of degraded reefs. On coral depauperate reefs, diffuse grazing by fishes may be insufficient to consistently suppress macroalgae and facilitate coral recovery (Mumby et al. 2007, Sandin and McNamara 2012). However, we show that nutrient hotspots can focus grazing from herbivorous fishes on discrete patches, leading to decreased cover of upright algae, which can inhibit coral settlement and growth (Birrell et al. 2008), and increased cover of CCA, which can promote the settlement and survival of coral larvae (Harrington et al. 2004). Furthermore, higher coral growth rates around fish-derived hotspots may reduce the time corals spend in smaller size classes, when they are weaker competitors and suffer greater levels of size-dependent mortality (Bak and Meester 1999). Thus, fish-derived nutrient hotspots may not only improve coral settlement but also increase survival rates.

These positive feedbacks are likely important for the recovery of degraded reefs and may be important when considering restoration efforts. For example, reefs with low topographic complexity may benefit from artificial structure to provide aggregation points for fishes. Likewise, on coral depauperate reefs, planting nursery-raised corals around existing fish aggregation sites may improve the growth, survival, and potential reproductive output of transplanted corals. In turn, the increased topographic complexity afforded by restored corals may provide more sheltering habitat for fishes, encouraging a positive feedback that promotes reef recovery (e.g., Mumby and Steneck 2008). Accordingly, the significant positive effects of fish-derived nutrient hotspots on grazing and coral growth rates demonstrated in this study may be an important consideration for coral restoration strategies.

One potential concern with our study is that the sites where grunts aggregated could have coincided with some unique location effects such as different wave exposure, currents, or abiotic nutrient delivery that attracted herbivorous fishes and resulted in different benthic communities but was unrelated to fish-derived nutrients. However, both high- and low-biomass sites were well interspersed over a 20 × 60 m area of reef (Appendix A). This interspersion minimized the chances of any physical forces such as wave exposure or currents

affecting only high- or low-biomass sites. Further, in the Florida Keys, the major sources of abiotic nutrients are typically internal waves (e.g., Leichter et al. 2003) or delivery of nutrients from land-based sources. However, internal waves rarely reach the shallow depths where we were working and are extremely variable in space and time when they do reach these shallow depths (Leichter et al. 2003), which would make them an unlikely explanatory factor for generating very consistent spatial and temporal differences in fish and benthic communities. Further, land-based sources of pollution are quite rare on these outer forereefs that are >10 km offshore (Briceño and Boyer 2012). Even if these abiotic sources were important deliverers of nutrients to our field site, the interspersion of our high- and low-biomass sites would have made it very unlikely that these nutrient sources would have biased our data set in a significant way.

Another potential explanation of differences in increased herbivore foraging around high-biomass sites could be that these sites just attract more types of all fishes regardless of fish-derived nutrients. However, while grunts spend the entire day in shelter sites (Ogden and Quinn 1989), both parrotfish and surgeonfish are roving herbivores with average territory sizes ranging from 100 m^2 to over 1000 m^2 (Mumby and Wabnitz 2002, Catano et al. 2015). Due to the small size of our study site (20 × 60 m), individual parrotfish and surgeonfish would likely range over the majority of our site, including both high- and low-biomass colonies. The fact that we found a threefold increase in foraging on the benthos only around high-biomass colonies strongly suggests that these fishes consistently choose to forage in these areas. In contrast to benthic grazing rates on the existing algal community, there was no difference in consumption of *Laurencia* sp. during feeding assays between high- and low-biomass sites. If grazing at these coral colonies were based on attraction of herbivores to these sites via mechanisms unrelated to fish-derived nutrients, than we would have expected consumption of algae in the feeding assays to follow the same pattern as we saw in grazing on the benthos. However, these data suggest that increased grazing around high-biomass sites was a direct result of nutrient delivery from fishes and the subsequent increase in nutritional quality in naturally occurring algae rather than herbivorous fishes being attracted to high-biomass sites for reasons unrelated to fish-derived nutrients.

Ideally, we would have been able to conduct a fish removal/addition experiment that would conclusively show that fish aggregations impacted herbivore foraging and benthic dynamics. But, these experiments were not possible at this popular dive site within a national marine sanctuary. However, recent experimental studies have shown that the creation of artificial reefs in oligotrophic seagrass beds promote fish aggregations (especially grunts and snappers) that, in turn, lead to
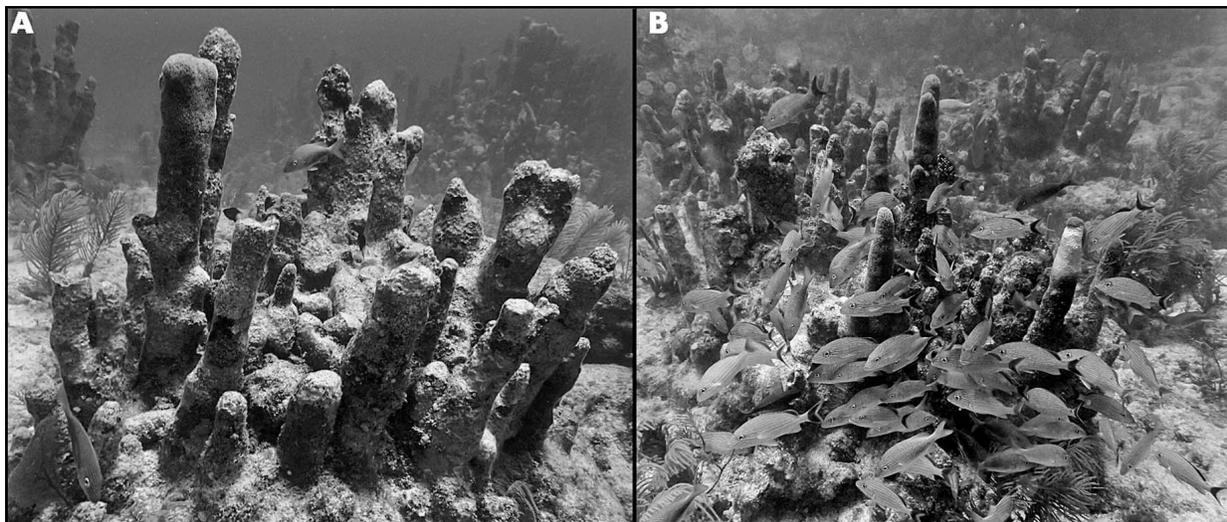
PLATE 1. Examples of *Dendrogyra cylindrus* colonies sheltering (A) low biomass and (B) high biomass of grunts around the colony. Photo credit: A. A. Shantz

increased delivery of fish-derived nutrients, increased primary production, and biomass accumulation (e.g., Dewsbury and Fourqurean 2010, Allgeier et al. 2013, Layman et al. 2013). Thus, in experiments that have directly altered fish aggregations, the impacts on nutrient cycling and benthic dynamics that they show support our hypotheses about the impact of fish-derived nutrients in this reef system.

Finally, the level of increase in the N content of algae around the high-biomass sites that we recorded requires a large and consistent amount of N input to generate. For example, in a recent experiment (Vega Thurber et al. 2014), we enriched plots of reef with ~600 g/m^2 of slow release N+P fertilizer, replaced monthly, for three years. This enrichment increased N and P in the water column approximately six to eight times above ambient levels, although the actual delivery rate was likely higher as some of the N and P was diffused and absorbed before we could measure it. This enrichment experiment resulted in a 20% increase in the N content of *D. menstrualis*, which is very similar to the 15% increase that we documented at high-biomass sites in this study. This indicates that the differences in algal tissue N we report here, between study colonies often separated by just a few meters, requires an extremely substantial, localized, and consistent input of N to achieve. It seems extremely unlikely that differences in physical forcing could generate these differences in algal N content at such small scales given both the interspersion of our sites within the reef and the lack of other physical mechanisms (e.g., internal waves or land-based pollution) that could drive such large differences in nutrient delivery. Thus, the concentration of fish-derived nutrients at high-biomass sites are the mostly likely explanation driving increases in algal N content,

alterations to herbivore foraging, differences in benthic communities, and increases in coral growth.

Human activity is likely to continue to cause biodiversity loss and habitat fragmentation capable of disrupting consumer-mediated nutrient regimes. Accordingly, studies are needed to quantify the importance of animal-derived nutrients on community structure and ecosystem function before important consumer-mediated nutrient pathways are inadvertently broken and valuable ecological processes lost. Our understanding of the impact of fish-derived nutrients on coral reefs is sorely incomplete. This study demonstrates that by creating nutrient hotspots, coral reef mesopredators play an important, yet previously unrecognized, role in shaping coral reef communities. As a result, overfishing of mesopredators may undermine coral reef health by disrupting the natural delivery and distribution of nutrients on reefs. This is noteworthy because management strategies often focus protection on herbivores and apex predators but overlook these mid-level predators. Furthermore, this pattern is likely not unique to reefs and may represent a less recognized threat of overfishing to marine systems. For example, Layman et al. (2011) documented an approximately 500% decline in nutrient delivery in fished vs. unfished tidal creeks in the Bahamas and subsequent declines in primary production with the removal of fishes. Because many mobile-link organisms, including the grunts in this study, cross system boundaries to forage or shelter (Lundberg and Moberg 2003, Heck et al. 2008), conservation must focus not only on the organisms themselves but also on both the donor and recipient ecosystems for the nutrients that they translocate. Our study suggests that whole-system management plans, such as no-take reserves, or targeted protection for these mobile-link species may be needed to retain these important nutrient pathways.

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Supplemental Material

Ecological Archives

Appendices A and B are available online: http://dx.doi.org/10.1890/14-2209.1.sm