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Bottom-up and top-down controls on coral reef sponges: disentangling within-habitat and between-habitat processes

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Abstract. Polarized debates about top-down vs. bottom-up control have given way to more nuanced understanding of control by both resources and consumers in many systems, but coral reef sponges have recently been asserted to differ from other groups in being controlled exclusively top-down. This assertion has been countered by reports of exclusively bottom-up control, with both conclusions based on studies of the same species. Accelerating deterioration of coral reefs motivates knowing the contexts in which either consumers or nutrients or both control key ecosystem role players like sponges. Accordingly, genotype- and size-controlled individuals of 12 common Caribbean reef sponge species were transplanted, in the field, into five circumstances differing in predators, competitors, and the picoplankton consumed by sponges. Growth and survival of the experimental transplants for periods of 1–9 yr revealed context-dependent control of sponges. Primary control of growth was bottom-up, with more picoplankton resulting in consistent and sustained higher growth rates for all 12 of these ecologically and phylogenetically diverse species. Top-down control was not detected within-habitat, on the coral reef. However, between-habitat control was by predation and competition, with reef sponges excluded from adjacent seagrass meadows by spongivorous starfish, and excluded from mangrove prop roots by faster-growing mangrove sponges. These results highlight the strong importance of experimental design details that consider behavior idiosyncrasies, sufficiently long time scales, and appropriate division of species into categories. Diametrically opposite results from studies of the same species also illustrate the inherently greater difficulty of detecting bottom-up processes and the importance of distinguishing within-habitat vs. between-habitat patterns and processes.

Key words: angelfishes; bottom-up; context-dependent; coral reefs; mangroves; seagrass; sponge feeding; sponges; spongivores; top-down; within-habitat vs. between-habitat.

Introduction

Relative importance of top-down and bottom-up trophic interactions that bolster or diminish representation of species in ecological communities has been a key theme since 1960, when Hairston, Smith, and Slobodkin provoked ecologists into considering the implications of a terrestrial world that is green (Hairston et al. 1960). A recent compilation of papers (Terborgh and Estes 2010) illustrates the shift in focus from a polarized debate about single controls to a more nuanced understanding of simultaneous bottom-up and top-down controls of different segments of a trophic web. In the Serengeti, for example, seasonal shortage of suitable food limits populations of large herbivores, while small herbivores are controlled primarily by carnivores (Sinclair et al. 2010). Even in the rocky intertidal, an iconic example of top-down control of community structure and diversity (Paine 1966), the simultaneous importance of bottom-up processes is revealed by regional-scale comparisons among sites that differ in oceanographic parameters such as water column productivity and wave exposure (e.g., Menge 2000), as well as by mechanistic understanding of how context influences particular interactions (e.g., Bracken et al. 2014).

On coral reefs, explicit attention to this theme also dates from 1960 (Stephenson and Searles 1960), and has focused on fleshy seaweeds that, uncontrolled, are capable of overwhelming established corals and inhibiting recruitment by coral larvae. Bottom-up impetus for algal growth comes from increased nutrient inflow due to depleted coastal vegetation and runoff laden with fertilizers and sewage. Top-down control of seaweeds has declined as uninhibited fishing down the food chain (e.g., Pauly and Palomares 2005) has diminished populations of herbivorous fishes and invertebrates. Conclusions from a meta-analysis of 54 marine studies in which both nutrient availability and herbivore pressure were manipulated underscored context-dependency, especially with respect to latitude, functional group of the primary producers, and inherent nutrient availability of the ecosystem (Burkepile and Hay 2006).

Increasing sponge abundance has recently been asserted to threaten coral reefs in a scenario parallel to the macroalgae story, with overfishing the handful of

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spongivores such as angelfishes said to be the primary cause of sponge increase (Pawlik et al. 2013, 2015, Loh and Pawlik 2014). Countering this assertion, Lesser and Slattery (2013) and Slattery and Lesser (2015) have demonstrated control of sponges by abundance of the picoplankton they consume, and reported lack of evidence for predation in their experiments.

Some confusion has been caused by broadly inclusive use of the words "sponges" and "control". "Sponges" is not a homogeneous group, but includes thousands of ecologically diverse species. The more than 20 Orders of sponges represented on coral reefs differ in life history, morphology and chemistry, so that it seems unlikely that what controls some sponges will also control others. Likewise, "control" is not a single process, but can relate to growth rates, abundance, recruitment, population dynamics, and habitat boundaries.

Inherent in controversy about whether or not a problematic increase in sponges is caused by increased nutrients or decreased predators are the assumptions that sponges are actually increasing and that such an increase would be problematic. Sponges can substantially influence coral survival, coral reef water quality, and carbonate balance, in some cases harming and in others benefiting corals and reefs (e.g., Diaz and Rützler 2001, Wulff 2001, 2012, 2016, Rützler 2004, Bell 2008), so it is important to evaluate these assumptions. Although localized, sometimes devastating, but often temporary, increases in a few aggressive encrusting species and excavating species have been reported, especially in response to increased water column nutrients (review in Wulff 2012, pp. 300–301 and 308–312), substantial declines (71–93% of biomass) have been documented in every study in which an entire reef sponge fauna has been censused in time series (Butler et al. 1995, Wulff 2006*a*, 2013, Stevely et al. 2011). So few time-series census studies of coral reef sponges exist that we do not yet know how general these results are. With respect to sponges being problematic: although some sponge species excavate burrows in coral skeletons or overgrow living corals, most play beneficial roles that are not played by other taxa, such as maintaining water clarity, facilitating reef regeneration, and increasing coral survival (e.g., Diaz and Rützler 2001, Wulff 2001, 2016, Bell 2008, Biggs 2013). Conflicting reports of dramatic increases as well as declines, combined with multiple key functional roles, motivates clear understanding of how bottom-up and top-down processes control distribution, abundance, growth and survival for a variety of reef sponge species.

To test the hypothesis that control of sponges by food availability vs. predatory and competitive interactions is context-dependent, 12 ecologically and phylogenetically diverse species were transplanted into circumstances differing in picoplankton, spongivores, sunlight (relevant for photosymbionts), and competitors. The naturally wide range of combinations of these variables offered by coral reefs, seagrass meadows and mangroves was augmented with cages and experimental substrata. Field experiments were imperative because sponges and their predators do not thrive in tanks. Controlling experiments for genotype and initial size allowed explicit comparisons of growth and survival between (1) two levels of picoplankton abundance, (2) with vs. without two suites of predators, and (3) with vs. without spatial competitors; and allowed clear distinction of within-habitat from between-habitat processes.

Methods

Spongivore populations

Spongivore populations were repeatedly estimated at intervals of 4–24 months between 2002 and 2014. On the reef, all spongivores, including angelfishes (*Pomacanthus arcuatus* [Linnaeus, 1758], *P. paru* [Block, 1787], *Holacanthus ciliaris* [Linnaeus, 1758]) and trunkfishes (*Acanthostracion quadricornis* [Linnaeus, 1758], *Lactophrys bicaudalis* [Linnaeus, 1758]) were noted by species and standard length while slowly swimming transects spaced at 2 m apart throughout 900 m^2 at each census (n = 12). Standard lengths and locations in the censused area were used to confirm that each fish was only counted once. In the seagrass, mean arm length of every *Oreaster reticulatus*, the large starfish, within 100 m^2 was recorded at each census (n = 35).

Picoplankton and nutrient concentrations

Ambient water samples were collected in all three habitats in December 2009 and May 2010, and preserved for measurement of total nitrogen and dissolved organic carbon, as well as for flow cytometry quantification of picoplankton consumed by sponges (i.e., cyanobacteria, heterotrophic bacteria, picoeukaryotes, and prochlorophytes; methods details in Strimaitis 2012).

Sponge transplant and caging experiments

Twelve of the most abundant sponge species on shallow Caribbean coral reefs were chosen to represent a range of growth forms, higher taxa (six demosponge orders), and associations with photosymbionts (Table 1). These 12 species are ubiquitous on Caribbean reefs, but they do not normally live in mangroves or seagrass meadows. A shallow coral reef in the Blue Ground Range, Belize Barrier Reef, was the home site from which transplants were made to mangroves and seagrass at nearby Twin Cays. At the start of the experiments, in June 2006, this reef hosted at least 54 sponge species, abundant spongivorous fishes, and diverse corals and gorgonians (Wulff 2013). Habitat-transplant and predator-exclusion experiments were controlled for genotype and initial size to minimize the effect of the great variation in growth rates typical of sponges (e.g., Wulff 2006*b*). For each of the 12 sponge species, 12–17 large healthy individuals were chosen, and from each individual, five pieces were cut as close as

TABLE 1. Twelve common and ubiquitous Caribbean coral reef sponge species that represent a variety of growth forms and demosponge higher taxa. The four species that harbor cyanobacteria (Erwin and Thacker 2007), are indicated by "Cyan".

Orders, species, authors	Growth form; symbionts
Tetractinellida	
Erylus formosus Sollas 1886	Clusters of low mounds
Poecilosclerida	
Mycale laevis (Carter 1882)	Semi-cryptic massive
Iotrochota birotulata (Higgin 1877)	Erect branching
Desmapsamma anchorata (Carter 1882)	Erect branching, irregular
Axinellida	
Ectyoplasia ferox (Duchassaing & Michelotti 1864)	Thick sheets, low mounds
Haploscerida	
Amphimedon compressa Duchassaing & Michelotti 1864	Erect branching
Niphates erecta Duchassaing & Michelotti 1864	Erect branching
Callyspongia vaginalis (Lamarck 1814)	Clusters of tall tubes
Dictyoceratida	
Ircinia felix (Duchassaing & Michelotti 1864)	Clusters of low mounds; Cyan
Verongiida	
Aplysina fulva (Pallas 1766)	Erect branching; Cyan
Aplysina cauliformis (Carter 1882)	Erect branching; Cyan
Verongula rigida (Esper 1794)	Clusters of low mounds; Cyan

possible to the same size and shape, while minimizing wound surface area. This was key to success, as growth is influenced by the amount of regeneration required to heal surfaces and reconstitute overall shape. All fragments were of naturally occurring shapes; e.g., for sponges shaped as clusters of tubes or mounds, only entire tubes or mounds were used. Sample sizes were constrained by availability of sponge individuals that could supply 5 pieces fitting these criteria. Importantly, all sponges used in experiments resided on the reef where the experiments were established, as spongivorous angelfishes can bite abnormally fiercely on sponges that suddenly appear as novelties.

Based on previous results (Wulff 1995, 2005), sponges on the coral reef and in the seagrass meadow were grown both inside and outside cages; and in the mangroves, sponges were grown on suspended cylindrical substrata (CPVC pipes). One of the five genetically identical and physically similar fragments was attached by narrow cable ties to a pipe suspended among mangrove prop roots at Twin Cays. Four fragments were attached to pieces of coral rubble that were stabilized by seawater-resistant alloy stainless steel stakes covered by biologically inert Tygon tubing. Two of these were transplanted to seagrass at Twin Cays, inside and outside a cage; and two were transplanted on the home reef, inside and outside a cage. Cages (15 × 15 × 15 cm) were designed to maximize internal water flow but minimize dislodgement during storms. Square meshes, 1.5 cm by 1.5 cm, and narrow, transparent cage material minimally impeded water flow and light. The same cage features prevent both spongivore and herbivore access, so a "cage control" would not aid interpretation in this case. The potential problem of protection of macroalgae was alleviated by gentle removal from inside cages at 4–6 months intervals.

Transplant trauma was minimized by keeping all 785 experimental sponges submerged and allowing cut surfaces to heal before moving them. The volume of every sponge was measured by making sufficient external linear measurements to allow accurate, repeatable volume calculation by conglomerations of appropriate geometric solids (Wulff 2001). Experiments were established in August 2006, and sponges were re-measured at intervals of 4–6 months for the first 2 yr, and thereafter at intervals of approximately 12 month for up to 9 yr.

Statistical comparisons of specific growth rates (i.e., increase in volume during a time interval divided by initial volume) were made by Welch's *t*-test for unequal variances. Mortality of one member of some genotype pairs resulted in abandoning pairwise statistical analysis in favor of including all growth data in the analysis. Variation due to genotype differences was nonetheless minimized because the same subset of genotypes was used for all experiments.

RESULTS

Sponge-feeding fishes and starfish

On the coral reef, sponge-specializing fishes were consistently abundant, with an average of 13.3 (SE = 0.8) *Pomacanthus* spp. (*P. paru*, French angelfish, and *P. arcuatus*, gray angelfish), and 8.83 (SE = 0.37), *H. ciliarus* (queen angelfish); as well as 1.15 (SE = 0.47) *L. bicaudalis* (spotted trunkfish), and 0.67 (SE = 0.47) *A. quadricornis* (scrawled trunkfish), in 900 m^2.

The seagrass meadow was inhabited by a mean of 9.2 (SE = 1.88) *Oreaster*, in a 100 m^2 plot. Occasionally a scrawled trunkfish was seen in the seagrass meadow, and

their presence was also indicated by rare observations of their typical oblong bite marks. In the mangroves, the only large spongivores were two spotted trunkfish, observed only at long intervals. No angelfishes were encountered in the seagrass or mangroves.

Picoplankton and nutrient concentrations

Flow cytometry revealed higher picoplankton concentrations in the mangroves than in the other two habitats (#cells/mL $\times 10^{-5}$ were 54.6 ± 1.8, 85.9 ± 1.5, 123.4 ± 2.8 in May and 77 ± 3.1, 33.9 ± 1.2, 150.2 ± 12 in December for respectively the reef, seagrass, and mangroves). Averages of the two time periods were 65.8, 59.9 and 136.8 cells/mL $\times 10^{-5}$ for respectively the reef, seagrass, and mangroves. Water column concentrations were also substantially higher in the mangroves for total nitrogen (in μM: 1.4 ± 0.2 on the reef and 4.2 ± 0.1 in the mangroves) and dissolved organic carbon (in μM: 65.9 ± 0.3 on the reef and 139.2 ± 15.3 in the mangroves).

Reef sponges on the reef: low picoplankton and abundant piscine spongivores

During the first 12 months, growth rates on the reef were not statistically distinguishable for individuals within vs. outside cages for any species (Fig. 1a), although the mean specific growth outside cages was higher for 9 of the 12 species. By 20 months, some caged individuals were outgrowing the cages, disabling the comparison. The 20-month growth rate trajectories of exposed sponges (Fig. 2, diamonds) illustrate the wide range of growth rates for these 12 species in their home habitat, the coral reef: mean specific growth after 12 months ranged from 0.9 to 4.7; and after 20 months from 1.2 to 9.7, with the same species remaining the slowest (*Ectyoplasia ferox*) and fastest-growing (*Desmapsamma anchorata*). Overall lower survival inside vs. outside cages on the reef reflected high mortality of *D. anchorata* inside cages (Fig. 3).

Reef sponges in the seagrass meadow: low picoplankton and abundant starfish spongivores

Mean specific growth rates of sponges inside cages in the seagrass meadow were higher at 12 months than those of the same genotypes grown inside cages on the coral reef for 10 of the 12 species (Fig. 1b), but the difference was statistically significant ($P < 0.05$) for only two species, both of low mound-cluster form (*Verongula rigida* and *Erylus formosus*). Between 12 and 20 months, net growth rate slowed for all but four species, reflecting digestion by *Oreaster* of portions of branching species that protruded from their cages as they grew. Excepting *D. anchorata*, which had all expired by 12 month, survival inside cages was better in the seagrass meadow than on the coral reef (Fig. 3). But, with the sole exception of *A. compressa*, which *Oreaster* rejects (Wulff 1995), *Oreaster* ate all sponges outside cages in the seagrass, so survival was zero for 11/12 species.

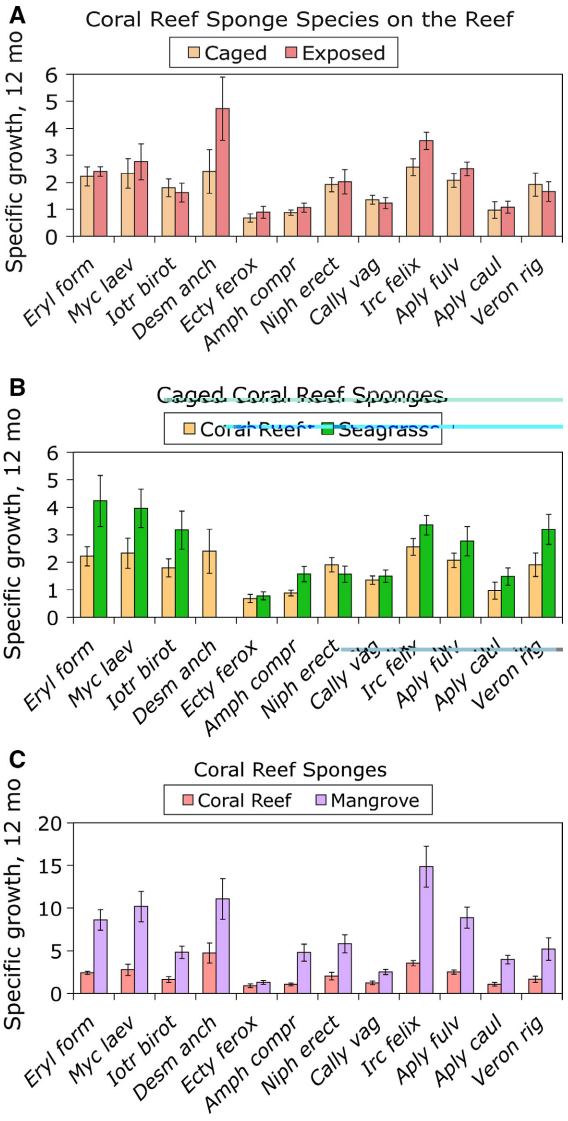

FIG. 1. Specific growth rates, t = 0 to 12 months, of 12 common and ubiquitous species of Caribbean coral reef sponges. Samples sizes are 12–17 for each species, and all experimental transplants into five circumstances (coral reef, in and out of cages; seagrass meadow, in and out of cages; and on cylindrical substrata suspended among mangrove prop roots) were controlled for genotype, initial size and shape. (a) Coral reef sponges, in and out of cages, on their home coral reef. No comparisons were significantly different. (b) Coral reef sponges, in and out of cages, in a seagrass meadow. Only two comparisions were significantly different ($P < 0.05$): *Erylus formosus*, *Verongula rigida*. (c) Coral reef sponges outside of cages on a reef and attached to substrata among mangroves. All comparisons were significantly different ($P < 0.01$) with the exception of *Ectyoplasia ferox*.

Reef sponges in mangroves: high picoplankton, spatial competitors, and low spongivory

Most reef sponges transplanted to pipes in mangroves grew rapidly, exhibiting specific growth rates as high as 14.9 in the first year. Growth rates were significantly

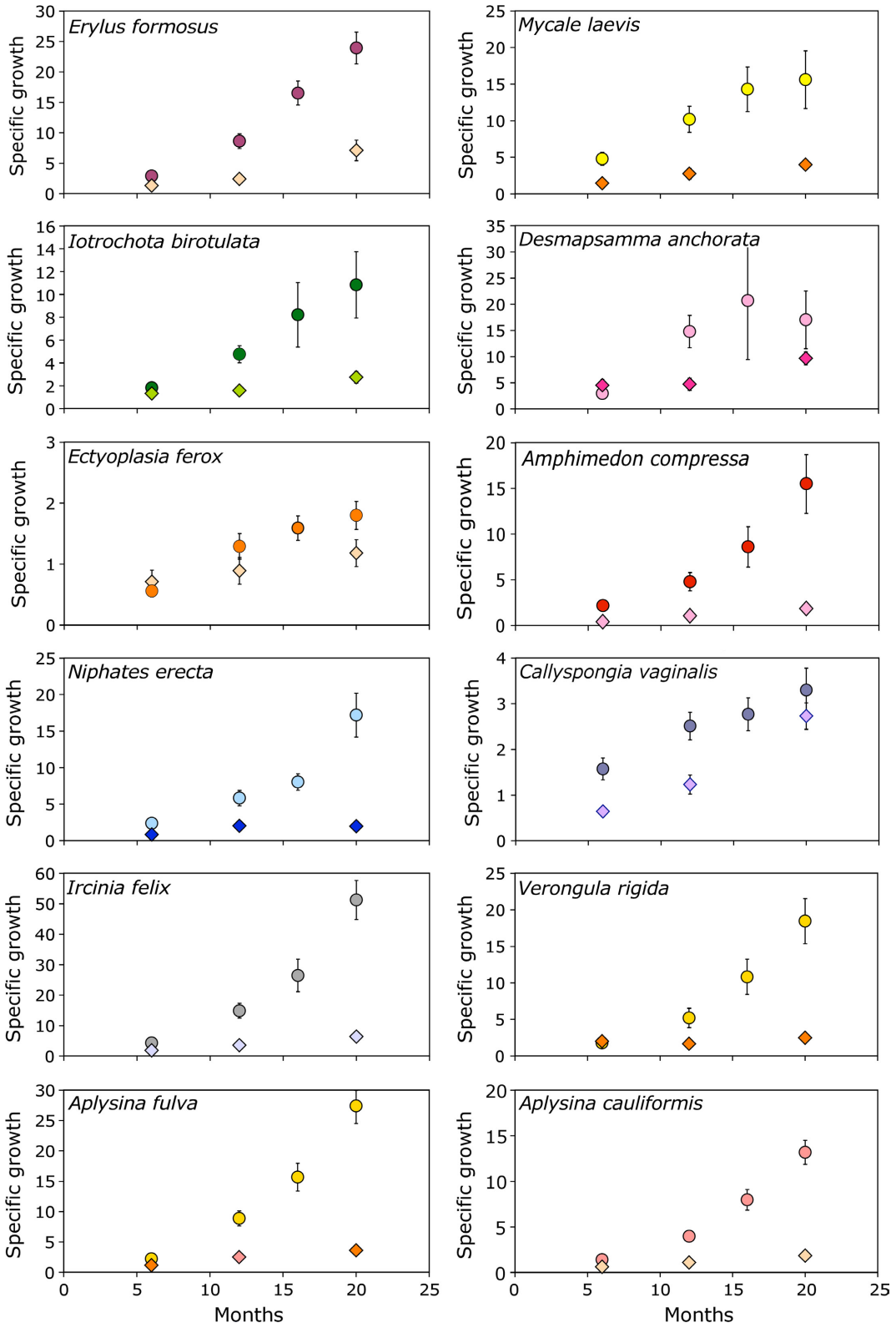

FIG. 2. Specific growth rates during the first 20 months of the same set of genotypes for each of 12 species of common coral reef sponges growing outside cages on a shallow reef (**diamonds**) on the Blue Ground Range and on cylindrical experimental substrata suspended among mangrove prop roots (**circles**) at Twin Cays. Note that *y*-axis scales range from maxima of 3 to 60. [Colour figure can be viewed at wileyonlinelibrary.com]

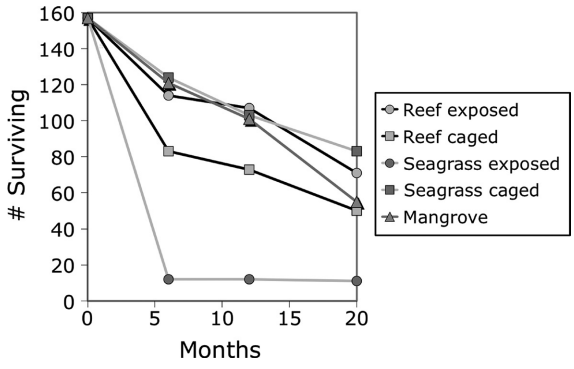

FIG. 3. Mortality rates of sponges of 12 species typical of Caribbean coral reefs in five circumstances (coral reef, in and out of cages; seagrass meadow, in and out of cages; and on cylindrical substrata suspended among mangrove prop roots).

higher in the mangroves than on the reef ($P < 0.01$, Fig. 1c) for all but one (*E. ferox*) of the 12 species; and the same species grew the slowest (*E. ferox*) and the fastest (*D. anchorata*) as on the reef. The reef sponges continued to grow rapidly as long as they were not overgrown by other organisms (Fig. 2, circles). Specific growth at 20 month ranged from 1.8 (*E. ferox*) to 51.3 (*I. felix*); and by 20 month the mean specific growth in the mangroves was over 7× that of counterparts on the reef for half of the species (*N. erecta* 8.8×, *A. compressa* 8.4×, *I. felix* 8×, *A. fulva* 7.6×, *V. rigida* 7.4×, *A. cauliformis* 7.2×).

Sizes achieved by the largest individuals of most species far exceeded sizes of unmanipulated individuals found on the reef. For example, after 4 yr, the largest individuals in the mangroves vs. on the reef were 7,333 cm^3 vs. 553 cm^3 for *M. laevis*, 6,388 cm^3 vs. 1,195 cm^3 for *I. felix*, and 1,296.8 cm^3 vs. 388 cm^3 for *A. fulva*. Surviving reef sponges continued to grow in the mangroves, so that after 9 yr, even very slow-growing *E. ferox* achieved a size of 4,499 cm^3 on mangroves while the largest individual on the reef was 213 cm^3.

Survival in the mangroves was initially excellent for all species, but diminished after 12 months, as members of the the mangrove root-inhabiting sponge and compound ascidian fauna recruited onto experimental substrata. Many reef sponges succumbed (Fig. 3) to overgrowth by these more rapidly growing species (Wulff 2005). Reef sponges that achieved huge sizes evaded demise due to competition by covering all primary space on their pipe, preventing recruitment of competitors.

Species-characteristic scopes for growth

Rank order of growth rates for these 12 species on the reef was maintained for individuals transplanted to other habitats (Fig. 4), indicating that scope for growth is a species-specific characteristic, and growth in habitats differing in food availability scales accordingly (the hypothesis that the rank orders of growth rates match between habitats by chance can be rejected, Kendall Rank Correlation, $P < 0.01$). Plotting mean specific growth rate in the picoplankton-rich mangroves as a function of growth on the picoplankton-meager reef (Fig. 5) underscores the degree to which species-specific scope for growth scales with food availability. The sole species that falls off the line, *D. anchorata*, grows unusually rapidly, apparently by minimal investment in skeletal strength. In consequence it also fragments more readily than other branching species (Wulff 2008). On the mangroves, net size increase of *D. anchorata* faltered as branches that grew too large for the flimsy skeleton to support broke off, perishing in the sediment below.

DISCUSSION

Bottom-up control of growth rates and biomass

Growth rates of coral reef sponges are constrained by the relative scarcity of picoplankton in the water column over the reef. All 12 species in this study, representing a variety of growth forms, relationships with photosynthetic symbionts, and higher taxa (six orders), grew faster when exposed to higher picoplankton concentrations. These results concur with higher growth rates reported previously for reef sponges transplanted into habitats with more picoplankton: *Callyspongia vaginalis* moved into deeper water by Trussell et al. (2006), and *I. birotulata*, *A. compressa*, and *A. fulva* moved onto mangrove prop roots by Wulff (2005). These new data extend previous work by demonstrating: (1) a common pattern for 12 ecologically and phylogenetically diverse species, and (2) maintenance of higher growth rates in a higher picoplankton habitat for years, resulting in enormous size disparities between sponges of the same genotype and initial size when grown for the same time period in low vs. high food habitats.

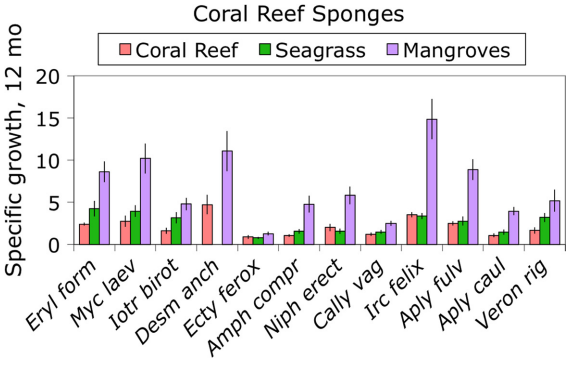

FIG. 4. Specific growth rates over time of sponges of the same set of genotypes for 12 months on a coral reef outside cages, in a seagrass meadow inside cages (sponges outside cages were consumed), and on experimental substrata among mangrove roots. A null hypothesis that rank orders of growth rates match between habitats to this extent by chance can be rejected by Kendall Rank Correlation, $P < 0.01$. [Colour figure can be viewed at wileyonlinelibrary.com]

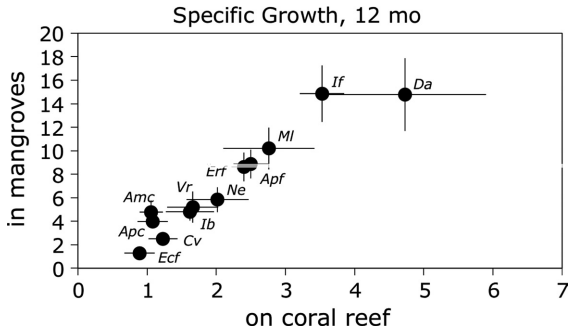

FIG. 5. Means (and SE) of specific growth rates of 12 species of sponges over 12 months. Individuals of the same genotypes and initial sizes that were grown on their home reef and on experimental substrata suspended among mangrove prop roots. The species, in order along the *x*-axis are: *E. ferox*, *A. compressa*, *A. cauliformis*, *C. vaginalis*, *I. birotulata*, *V. rigida*, *N. erecta*, *E. formosus*, *A. fulva*, *M. laevis*, *I. felix*, *D. anchorata*.

Capture and conversion of picoplankton into sponge biomass varies among species, as the efficiency with which sponges filter various components of the picoplankton or absorb dissolved organic matter is influenced by their shape, size, microbial symbionts, and internal morphology (e.g., Reiswig 1971, Weisz et al. 2007, reviews in Rützler 2004, 2012). The 12 species in this study illustrate this variation, with growth rates on the reef spanning a 5.3 fold range. Scope for growth appears to be a species-specific characteristic, as the rank order of growth rates on the coral reef was maintained when all species grew faster in response to twice the picoplankton concentration in the mangroves (Fig. 4). The consistent relationship between specific growth rates on the reef and in the mangroves (Fig. 5) underscores the degree to which these 12 ecologically and evolutionarily diverse sponge species are all influenced similarly by this one environmental variable: amount of food available.

Sevenfold greater growth of the same genotypes in the picoplankton-rich mangroves relative to the reef, in 20 months, corroborates previous correlations of sponge biomass and water column productivity across the Great Barrier Reef (Wilkinson and Cheshire 1990), within and between the Caribbean and Great Barrier Reef regions (Wilkinson 1987), along the coast of Colombia (Zea 1994), and between that coast and three remote Colombian atolls (Zea 2001). Lesser (2006) found greater biomass, tube extension rates, and sponge sizes in deep water/more picoplankton relative to shallow water/less picoplankton for the three Caribbean reef species *C. vaginalis*, *Agelas conifera*, and *Aplysina fistularis*; and abundance of sponge species that excavate carbonate or that overgrow living corals has also been positively correlated with water column nutrients (e.g., Rützler 2002, Schönberg 2008, Wulff 2012, 2016).

Extension by this study of previous conclusions (cited above) that growth rates and biomass of reef sponges strongly reflect picoplankton abundance, contrasts with a recent claim that evidence is lacking for bottom-up control of reef sponges (Pawlik et al. 2015). In a comprehensive response to this assertion, Slattery and Lesser (2015) have pointed out that Pawlik et al.'s claim is based on selective citation of previous work and, among other methodological problems, on use of percent cover rather than volume to address hypotheses relating to sponge growth and abundance. In the following sections, I address the alternative claim that reef sponges are controlled top-down.

First however, for completeness it must be pointed out that the relationship between sponge growth and picoplankton concentration is not monotonic. Although growth is inhibited by the normally oligotrophic water over coral reefs, and experiments demonstrate increased growth with increased picoplankton, very dense picoplankton may promote sponge death. Time-series census data have revealed drastic mass mortalities (71–93%) of Caribbean sponges coincident with dense picoplankton blooms spurred by eutrophication (Butler et al. 1995, Stevely et al. 2011, Wulff 2013).

Extreme top-down and sideways control of between-habitat distribution

Habitat-specific distribution patterns of Caribbean sponges are striking, with most species confined to either coral reefs, seagrass meadows, or mangrove prop roots. Previous assumptions that abiotic factors restrict habitat distributions seemed reasonable given obvious abiotic differences between these systems, but experiments have demonstrated control by interactions: seagrass-dwelling starfish prevent many coral reef sponge species from living in seagrass by eating them (Wulff 1995), coral reef-dwelling spongivorous fishes prevent many mangrove root- dwelling sponge species from living on coral reefs (Dunlap and Pawlik 1996, Wulff 2005), normally herbivorous fishes prevent some sponge species typical of cryptic spaces within the reef from living on exposed surfaces (Dunlap and Pawlik 1996, Wulff 1997), and competition from mangrove root inhabitants puts otherwise suitable mangrove roots off limits to coral reef sponges (Wulff 2005).

Swift elimination of sponges transplanted to other habitats without protection from predators or competitors demonstrates control by interactions, but does not answer the question "would habitat distributions change if enemies were absent, or is ultimate control by abiotic factors?". At least for the species and sites in this study, long-term monitoring confirmed the primary role of interactions in controlling between-habitat distribution. When protected by cages from the opportunistic spongivore *Oreaster* (Wulff 1995), 11/12 reef sponge species thrived in a seagrass meadow (Figs. 1b, 4), only inhibited when starfish digested portions that out-grew their cages. And all 12 species grew faster in the more productive water around mangroves, only halted (Fig. 3) when overgrown by members of the faster-growing mangrove fauna as they colonized the initially bare experimental substrata.

Minimal top-down control of net growth and abundance on the coral reef

Caribbean reef sponges that inhabit exposed surfaces – i.e., the vast majority of species, and the bulk of sponge biomass – were first demonstrated to evade primary control by coral reef predators by Randall and Hartman (1968). Their comprehensive gut contents data showed that only 11 of 212 Caribbean reef fish species (angelfishes, trunkfishes, a filefish, and spadefish) eat sponges; and that the chief spongivores, angelfishes, consume many sponge species. Randall and Hartman found 70 sponge species in guts of four angelfish species, and individual angelfish had eaten as many as nine species shortly before being speared for science. Field observations of unmanipulated angelfishes feeding on live sponges have unambiguously confirmed that angelfish consume small amounts of many species in rotation. Hourigan et al. (1989) recorded 23 species consumed, Lesser and Slattery (2013) observed consumption of means of 19.7–30.4 sponge species/15 min, and Wulff (1994) observed consumption of 64 sponge species, including 36 of the 42 species in a fully censused plot. Observations of feeding sequences (2,285 bites, 75% of them on sponges) confirmed that angelfishes moved on after a few (mean of 2.8) bites, and in 92% of the time the subsequent prey sponge was a different species (Wulff 1994).

A recent assertion that control of Caribbean coral reef sponges is entirely by predators was based on greater growth of two of five species inside cages on Conch Reef, Florida Keys (Pawlik et al. 2013), and on an inverse correlation across 69 sites of spongivore abundance with percent cover of sponges deemed palatable by pellet assays (Loh and Pawlik 2014). Those cage data contrast with the statistically indistinguishable growth inside and outside cages for all 12 species in this study (4 of them among the 5 species in Pawlik et al. 2013). Differences in spongivore density do not explain the discrepancy, because spongivores were denser on the Belize reef than on Conch Reef (i.e., 9.2 angelfishes per 500 m^2 in Belize vs. only 3.2 and 7.5 angelfishes per 500 m^2 at two depths on Conch Reef). Interpretation of the across-site correlation results of Loh and Pawlik (2014) is difficult because of how both sponge and fish species were assigned to the categories "palatable" and "spongivore": (1) "palatable" was defined by pellet assays (Pawlik et al. 1995) which do not always match results from spongivores and living sponges (Wulff 1994, 1995, 2005, 2006*b*, Lesser and Slattery 2013); and (2) "spongivore" counts included three parrotfishes in the genus *Sparisoma*, which do not normally eat sponge species that live on exposed reef surfaces (Randall and Hartman 1968, Dunlap and Pawlik 1996, 1998, Wulff 1997).

The greatest contributor to differences in experimental results from Conch Reef and Belize may be differences in angelfish behavior when faced with novel vs. familiar sponges. Normal angelfish feeding behavior, i.e., taking a few bites and moving to a sponge of another species, requires that they distinguish many species; so they readily sample novel sponges, sometimes causing considerable damage even if bites are not ingested. Once sampled, novel sponges are either ignored or included in normal "smorgasbord" feeding activity. For experiments on Conch Reef (Pawlik et al. 2013), sponges had to be brought from other sites because of collecting restrictions near the underwater habitat. Immediate losses to curious angelfish from sponges placed outside cages on Conch Reef could explain lower net growth of those sponges at the end of the experiments, 9.5 month later, even if angelfish reverted to their normal "smorgasbord" feeding after an initial flurry of sampling. In Belize, where net growth differences between caged and uncaged sponges were not significant (Fig. 1a), experiments (using 4/5 of the same species as Pawlik et al. 2013) were on the home reef of all the sponges used, and no angelfish sampling flurries occurred in response to experimental set-up.

Implications for making conservation decisions about deteriorating coral reefs

Conservation and management decisions based on reports that sponges could over-grow coral reefs if spongivores are over-fished will have little in common with decisions based on reports that sponges could grow faster and become more abundant if nutrients that fuel picoplankton increase. Concern that overfishing will result in sponges overwhelming coral reefs may be unwarranted, based on the results of this study, although the long-ago near elimination of hawksbill turtles from Caribbean reefs may have influenced abundance of the taxonomically narrow set of species they are capable of consuming in large quantities (e.g., Meylan 1988). But the demonstrated left-skewed pattern of bottom-up control directs attention to nutrient inputs. Some release of coral reef sponges from inhibited growth due to meager picoplankton might be beneficial, as the great majority of sponge species play positive roles, including increasing coral survival, filtering the water column, harboring hundreds of symbiont species, participating in nutrient flux, and facilitating reef repair (e.g., Bell 2008, Wulff 2016). With greater nutrient increases, however, the balance could shift so that sponges that play beneficial roles under normal nutrient conditions begin to overgrow corals. Increases in the few species that excavate burrows in coral skeletons or overgrow living corals have been already demonstrated to coincide with increased nutrients (e.g., Rützler 2002, Schönberg 2008). On the other hand, very high nutrient levels spur dense blooms that result in sponge death, with consequences similar to removing mortar from brick walls and filters from aquaria, i.e., nothing to bind live corals to the reef (Wulff and Buss 1979), stabilize broken corals for reef repair (Biggs 2013), or nip incipient phytoplankton blooms in the bud (e.g., Peterson et al. 2006, Stevely et al. 2011).

Implications for distinguishing top-down and bottom-up control

Diametrically opposite results from experiments that are apparently the same (i.e., sponges inside and outside of cages) and overlap in focal species, highlight the importance of experimental design details. For sponges this means keeping them submerged, controlling for genotype and initial size, measuring size by volume, monitoring experiments for more than a year, distinguishing predators that regularly eat small amounts of many sponge species living on exposed surfaces (i.e., angelfishes and trunkfishes) from those that opportunistically eat a few species of normally unavailable sponges (i.e., parrotfishes); and distinguishing vigorous but brief sampling of novel prey from normal feeding on familiar prey. For other groups, the details will differ, but it is clear that results can be inadvertently biased if behavioral details are ignored or subcategories (e.g., of prey and consumers) that respond differently are inappropriately defined.

Bottom-up influence is inherently more difficult to detect than top-down because growth in response to food takes time but loss to predators is immediate. A possible bias in favor of conclusions of top-down control in shorter-term studies was revealed by Smith et al.'s (2010) simultaneous manipulations of nutrients and herbivores, both separately and together, for nearly a year and a half. Not only did their experiments reveal a lag time in community level response to increased nutrients, contrasting with rapid response to herbivore removal; but there was also a lag time in community recovery when herbivores were restored in nutrient enrichment plots.

A developing consensus that top-down and bottom-up control of organisms is generally context-dependent does not after all appear to be flaunted by coral reef sponges. Just as for other groups in other systems, complex interplay between controls that cascade both up and down through a food web are revealed by experiments in which: (1) both consumers and food availability are manipulated, (2) appropriate sub-categories of consumer and consumed species are defined, (3) details of experimental design and metrics chosen for size and abundance take into account physiology, growth form, habitat boundaries, and behavior idiosyncrasies of all focal species, (4) within-habitat patterns and processes are distinguished from between-habitat, and (5) experiments are monitored for long enough that bottom-up influences can be revealed, and frequently enough for mechanisms to be identified.

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