

Chemical defenses and resource trade-offs structure sponge communities on Caribbean coral reefs

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Ecological studies have rarely been performed at the community level across a large biogeographic region. Sponges are now the primary habitat-forming organisms on Caribbean coral reefs. Recent species-level investigations have demonstrated that predatory fishes (angelfishes and some parrotfishes) differentially graze sponges that lack chemical defenses, while co-occurring, palatable species heal, grow, reproduce, or recruit at faster rates than defended species. Our prediction, based on resource allocation theory, was that predator removal would result in a greater proportion of palatable species in the sponge community on overfished reefs. We tested this prediction by performing surveys of sponge and fish community composition on reefs having different levels of fishing intensity across the Caribbean. A total of 109 sponge species was recorded from 69 sites, with the 10 most common species comprising 51.0% of sponge cover (3.6–7.7% per species). Nonmetric multidimensional scaling indicated that the species composition of sponge communities depended more on the abundance of sponge-eating fishes than geographic location. Across all sites, multiple-regression analyses revealed that spongivore abundance explained 32.8% of the variation in the proportion of palatable sponges, but when data were limited to geographically adjacent locations with strongly contrasting levels of fishing pressure (Cayman Islands and Jamaica; Curaçao, Bonaire, and Martinique), the adjusted R^2 values were much higher (76.5% and 94.6%, respectively). Overfishing of Caribbean coral reefs, particularly by fish trapping, removes sponge predators and is likely to result in greater competition for space between faster-growing palatable sponges and endangered reef-building corals.

chemical ecology | indirect effects | community structure | marine protected areas | trophic dynamics

Caribbean coral reef ecosystems are threatened by several decades of loss of reef-building corals (1). Sponges are now the dominant benthic animals on most reefs, and there is evidence that sponge abundance is increasing (2–5). Predation is important in this ecosystem; spongivores such as angelfishes and parrotfishes selectively feed on chemically undefended sponge species (6). Although sponges are generally thought to feed by capturing particles, they may also absorb dissolved organic material directly from the seawater they pump through their bodies (7, 8). This feeding versatility may help explain why the bottom-up effects of particulate food availability on sponge growth appear to be negligible, suggesting that sponge communities are primarily structured by top-down factors (9). Although many Caribbean sponge species are chemically defended by secondary metabolites that include alkaloids, terpenoids, and glycosides (10), other species are palatable to sponge predators (9, 11), revealing a resource trade-off between the production and maintenance of chemical defenses versus other life functions. Manipulative experiments have demonstrated that sponge species that are palatable to predators recruit more rapidly than defended sponges (12) and have faster rates of wound healing and tissue growth that act in opposition to grazing by predators (10, 13, 14). These traits allow palatable sponges to persist on reefs alongside chemically defended sponges, which produce secondary metabolites that deter predators, but grow, reproduce, or recruit more slowly than species that lack chemical defenses

(10). Hence, sponges on Caribbean coral reefs provide a relatively uncomplicated ecosystem to examine resource allocation theory because food web dynamics are simplified (primarily top-down control), consumption is limited to a few, large, generalist predatory species (little impact of insect-equivalent, often specialist, mesograzers), the impacts of extinction events or invasive species are minimal, and resource trade-offs are distinct (sponge chemical defense vs. growth or reproduction).

Based on the foregoing, a conceptual model was developed for sponge ecology on Caribbean coral reefs (10). If sponge predators were removed from the system, the higher rates of growth or reproduction of palatable sponge species should result in their greater proportional abundance within the sponge community. The coral reefs of the Caribbean provide a large-scale, long-term, manipulative experiment for testing this conceptual model because many reefs, particularly those off Jamaica, Martinique, and Panama, have been heavily overfished for decades with fish traps that indiscriminately remove not only the usual food-fish targets of groupers and snappers, but smaller fish species that include angelfishes and parrotfishes (15). In contrast, reefs such as those off Bonaire, the Cayman Islands, and parts of the Bahamas have long-established and well-enforced marine protected areas (MPAs) with little or no fishing allowed (15). The variability in fishing pressure and fish densities across the Caribbean provides a gradient against which sponge assemblages can be assessed. In this study, we surveyed sponge communities and spongivorous fish populations on overfished and less-fished Caribbean reefs and compared sponge assemblages across all survey sites and at geographically adjacent groups of sites that have strongly contrasting levels of fishing pressure.

Significance

Chemical defenses are known to protect some species from consumers, but it is often difficult to detect this advantage at the community or ecosystem levels because of the complexity of abiotic and biotic factors that influence species abundances. We surveyed the community of sponges and sponge predators (angelfishes and parrotfishes) on coral reefs across the Caribbean ranging from heavily overfished sites to protected marine reserves. High predator abundance correlated with high abundance of chemically defended sponge species, but reefs with few predators were dominated by undefended sponge species, which grow or reproduce faster than defended species. Overfishing may enhance competition between palatable sponge species and reef-building stony corals, further impeding the recovery of Caribbean coral reefs.

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Results

Sponge Community Across Caribbean Reefs. A total of 109 sponge species was recorded from surveys conducted at 69 sites (Fig. 1 and [Datasets S1](#) and [S2](#)). Sponge populations in the Caribbean were not dominated by any particular species, with the 10 most common sponges across all sites each comprising 3.6–7.7% of total sponge cover ([Table S1](#), sponge diversity by site in [Dataset S2](#)). Across all sites, 57.5% of sponges recorded were chemically defended, whereas 23.2% were consistently undefended and 19.4% were variably defended; hence, 42.5% were palatable to sponge predators. Of the 109 sponge species, 67 species were chemically defended, 26 species were consistently undefended, and 16 species were variably defended (42 species were palatable) ([Dataset S2](#)). The most common variably defended sponges were the giant barrel sponge *Xestospongia muta* and the green branched sponge *Iotrochota birotulata*. Sponges with unknown chemical defense strategies comprised less than 1% of the total sponge assemblage. An updated list of feeding assay results for 109 species of Caribbean sponges can be found in [Table S2](#), including categorization of chemically defended, consistently undefended, and variably defended species.

Relationship Between Sponge Community and Predator Abundance.

When the number of occurrences of chemically defended, consistently undefended, and variably defended sponges were pooled by location and the relative percentages determined, chemically defended sponges dominated sponge communities at locations with many spongivores (Fig. 2). For Curaçao and Bonaire especially, chemically defended sponges comprised >90% of sponge cover. Sponge assemblages were markedly different on overfished reefs, where >50% of the sponges surveyed were palatable at most locations. The difference in proportions of chemically defended vs. palatable sponges corresponded with spongivorous fish abundance at most locations, with more fishes recorded at locations that were reportedly protected from fishing (including MPAs) compared with locations classified as overfished (Fig. 2). The abundance and types of spongivores recorded at each site are listed in [Dataset S3](#). Images of angelfishes (*Pomacanthus arcuatus* and *Pomacanthus paru*) consuming the consistently undefended sponge species *Callispongia vaginalis* and

Callispongia armigera on Conch Reef, FL (site F1, [Dataset S1](#)), can be seen in [Movie S1](#).

Multiple-regression analysis revealed that the abundance of spongivorous fishes explained 32.8% of the variation in palatable sponge distribution across all sites ([Table 1](#), all sites). The relationship between spongivorous fishes and palatable sponges for all sites was also significant ($P < 0.001$). From the regression, the expected proportion of palatable sponges when no sponge-eating fishes were present is 0.52 ± 0.04 ($P < 0.001$), or about one-half of the sponge population. Two types of spongivorous fishes had significant impacts on the palatable sponge population ([Table 1](#), all sites). Across all sites, for each angelfish within a seawater volume of 2,000 m³ directly above the reef, the percentage of palatable sponges on the reef was reduced by 1.3% (0.013 ± 0.006 ; $P = 0.041$), and for each individual of *Sparisoma viride* (stoplight parrotfish), the percentage was reduced by 0.8% (0.008 ± 0.006 ; $P = 0.033$).

The effect of spongivorous fishes on the proportion of palatable sponges was more pronounced when regression analyses were repeated on subsets of sites that were geographically adjacent and had strongly contrasting impacts of fishing. For sites from the Cayman Islands and Jamaica, the multiple regression for palatable sponges was significant ($P = 0.025$), with an adjusted- R^2 value of 0.765 ([Table 1](#), sites off Cayman Islands and Jamaica). The analysis for sites from Bonaire, Curaçao, and Martinique was also significant ($P = 0.010$), with an adjusted- R^2 value of 0.946, indicating that spongivorous fish abundance explained almost all of the variation in the proportion of palatable sponges at these locations ([Table 1](#), sites off Bonaire, Curaçao, and Martinique). For both regressions, *Sparisoma aurofrenatum* (redband parrotfish) had a significant effect on sponge distributions ([Table 1](#), sites off Cayman Islands and Jamaica, and sites off Bonaire, Curaçao, and Martinique). For the analysis of sites from the Cayman Islands and Jamaica, the percentage reduction of palatable sponges within the survey area by each *S. aurofrenatum* was 2.3% (0.023 ± 0.007 ; $P = 0.022$), whereas for sites from Curaçao, Bonaire, and Martinique, the percentage was 1.2% (0.012 ± 0.002 ; $P = 0.015$). For the latter analysis, angelfishes also had a significant effect, with each



Fig. 1. Map of sites across the Caribbean where surveys were performed of sponge and fish community composition. Shading of site markers indicates abundance of sponge-eating fishes based on survey data using spongivore index (SI) ([Dataset S3](#)). Black, overfished ($SI < 10$); gray, intermediate ($11 \leq SI \leq 20$); white, protected ($SI \geq 21$). Overlapping markers have been displaced for clarity.

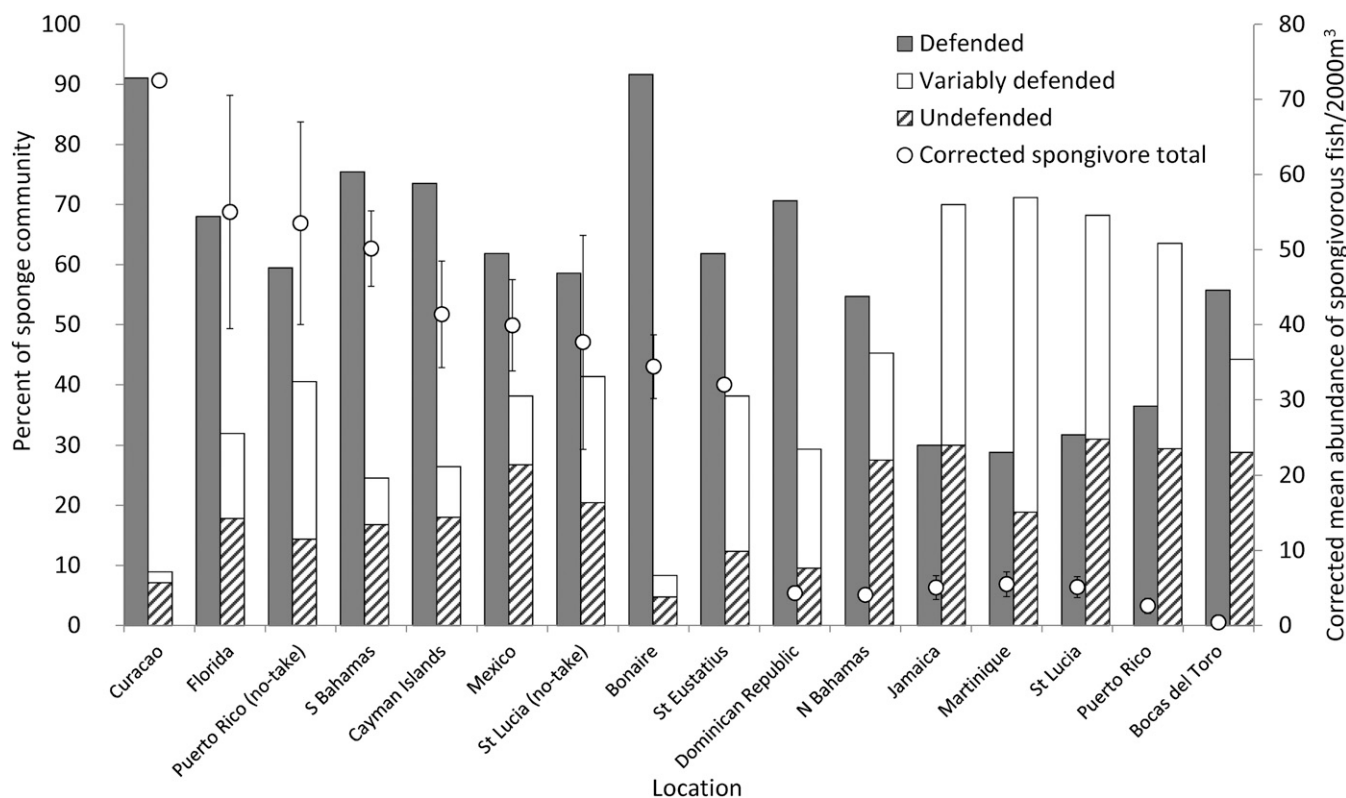


Fig. 2. Pooled percentages of chemically defended, consistently undefended, and variably defended sponges (the last two stacked as palatable sponges) at each survey location with the mean abundance of spongivorous fish (corrected for fish size) within 2,000 m³ of seawater directly above the reef. Sites that were designated as no-take fishing preserves were separated from the other survey sites for Puerto Rico and St. Lucia. Error bars denote SEs.

individual reducing palatable sponge cover by 8.6% (0.086 ± 0.015 ; $P = 0.010$).

In terms of sponge community composition, survey sites were more differentiated by spongivorous fish abundance than by geographic location (Fig. S1). The two-dimensional nonmetric multidimensional scaling (nMDS) ordination of the survey sites by abundance of the 10 most common sponge species returned a stress value of 0.16. When all sponge species were used in the nMDS ordination, rare species (those only recorded at one site) dominated the plot pattern by placing sites with rare species at the fringes of the nMDS plot and compressing all other sites toward the center of the plot. The ordination also approached a random pattern with a stress value >0.25 . Relatively less-fished sites from Bonaire, Cayman Islands, Bahamas, and Mexico grouped together and were characterized by higher abundances of *Aiolochoira crassa*, *Amphimedon compressa*, and *Aplysina cauliformis*, which are all chemically defended. Sites from Jamaica, Martinique, and Panama, which were rated as overfished (15), comprised the other group and had high occurrences of the sponges *Mycale laevis*, *Niphates erecta* (both consistently undefended), and *Iotrochota birotulata* (variably defended).

When sites were assessed using correspondence analysis (CA) of the number of occurrences of all sponges in each of the three defense categories in relation to corrected spongivore densities from fish surveys, survey sites grouped into the following: (i) sites with a high abundance of consistently undefended sponge species and low densities of sponge predators, (ii) sites with a mix of chemically defended and variably defended sponges and high densities of sponge predators, and (iii) sites that had a high density of variably defended sponges, mostly *Xestospongia muta* and *Iotrochota birotulata*, and a moderate density of sponge predators (Fig. 3). The abundance of consistently undefended sponges was inversely correlated with the total number of predators;

however, the abundances of chemically defended and variably defended sponges were not strongly correlated with the abundance of consistently undefended sponges or the total number of sponge predators (Fig. 3).

Discussion

Within the complex framework of food web dynamics (16), empiricists have attempted to determine the resource allocation strategies that individual species, or groups of species, use to persist in response to the challenges of top-down or bottom-up effects, such as the provision of energy to chemical or physical defenses against consumers (17, 18), or to alternative mechanisms for the uptake of nutrients or food (19, 20). Tests of resource allocation theory at the community or ecosystem levels have been hampered by the complexity of most food webs and the interactions of top-down and bottom-up effects (21). The community of sponges on Caribbean coral reefs provides a simpler system for testing resource allocation theory across a large biogeographic region, perhaps because of the relative lack of bottom-up effects (9). Although previous research revealed the existence of top-down control and resource trade-offs using experimental manipulations with individual sponge species (9, 12–14), this study demonstrates that interspecific differences in sponge chemical defenses correlate with community-level differences in sponge community structure that can be detected across a large biogeographic region. The abundance of palatable sponges was inversely related to the abundance of sponge-eating fishes at most locations regardless of the species composition of sponges at each location (Fig. 3). Furthermore, undefended sponges on reefs lacking spongivores were among the largest individuals observed for their species within our surveys because these sponges were not being grazed by predators. On reefs protected from fishing, bite marks were frequently observed on

Table 1. Output of multiple-regression analyses with the proportion of palatable sponges per site as the response variable and the corrected abundance of spongivorous fishes within 2,000 m³ of seawater along the reef transect as factors

Multiple regression output	Coefficient	SE	P value
Palatable sponges, all sites			
Adjusted R ²	0.328		
Regression ANOVA	P < 0.001*		
Intercept*	0.523	0.035	<0.001
Filefishes	0.010	0.023	0.659
Trunkfishes	0.002	0.009	0.853
Redband parrotfish	-0.003	0.002	0.087
Redtail parrotfish	-0.004	0.008	0.642
Stoplight parrotfish*	-0.008	0.004	0.033
Angelfishes*	-0.013	0.006	0.041
Palatable sponges, Cayman Islands and Jamaica			
Adjusted R ²	0.765		
Regression ANOVA	P = 0.025*		
Intercept*	0.731	0.076	<0.001
Filefishes	-0.018	0.024	0.490
Trunkfishes	-0.196	0.103	0.114
Redband parrotfish*	-0.023	0.007	0.022
Redtail parrotfish	-0.031	0.016	0.099
Stoplight parrotfish	0.035	0.018	0.109
Angelfishes	-0.032	0.022	0.202
Palatable sponges, Bonaire, Curaçao, and Martinique			
Adjusted R ²	0.946		
Regression ANOVA	P = 0.010*		
Intercept*	0.728	0.067	0.002
Filefishes	0.019	0.041	0.664
Trunkfishes	-0.013	0.014	0.440
Redband parrotfish*	-0.012	0.002	0.015
Redtail parrotfish	0.088	0.039	0.112
Stoplight parrotfish	0.002	0.003	0.665
Angelfishes*	-0.086	0.015	0.010

Shown are separate analyses of all sites, sites off Cayman Islands and Jamaica, and sites off Bonaire, Curaçao, and Martinique.
*Denotes factors that are significant at P < 0.05.

undefended sponges or individuals grew in refuge locations, such as in close proximity to, or among, fire corals, gorgonians, chemically defended sponges (Movie S1), or between branches or plates of stony corals, with the last tactic particularly used by the common and chemically undefended sponge *Mycale laevis* (Table S1) (22). These direct observations of predation, or of undefended sponges in refuge locations, are not possible to represent in our data, which are limited to relative abundance as a proportion of benthic cover. From our analyses, spongivorous fish also had an effect on variably defended sponges, presumably on individuals within the population that were less well defended.

Most of the sponges on the reefs we surveyed were protected from predators by secondary metabolites, with over 60% of species chemically defended and over 57% of the sponge community across all sites chemically defended. Because sponges of the genera *Aplysina* and *Aiolochoxia* are the most abundant sponges among defended species (Table S1), brominated tyrosine-derived alkaloids are the most common defensive secondary metabolites among Caribbean reef sponges (23, 24). Furthermore, with *Aplysina cauliformis* representing 7.7% of the sponge community across all sites (Table S1), the metabolite fistularin 3 is likely the most abundant defensive metabolite among Caribbean sponges (Fig. 4). For tissue samples of *A. cauliformis* from the Florida Keys and Bahamas Islands, fistularin 3 occurred at 2.4 mg/mL of sponge volume (SD = 1.1, n = 59) and, unlike

other *Aplysina* species, had very low levels of other related metabolites in its tissues (24, 25). Other *Aplysina* species, including *Aplysina fulva*, which ranked sixth most abundant across all sites, also had fistularin 3 as a dominant chemical defense (24).

Variably defended sponge species made up the smallest category defined by our feeding assay data (16 of 109 species, or 14.7%; Dataset S2), and species within this category have been the subject of more extensive studies in the past. For example, intrapopulation variation in the chemical defenses of the giant barrel sponge *Xestospongia muta* is very high (26), with differential grazing by parrotfishes on some individuals within a population over others (27). Similarly, the chicken-liver sponge *Chondrilla caribensis* (formerly *Chondrilla nucula*) exhibited highly variable chemical defenses, and undefended individuals were rapidly eaten by angelfishes (28). Finally, individuals of *Iotrochota birotulata* were variably defended in our feeding assays (Table S2), yet this species is a preferred food item for the angelfish *Holacanthus tricolor* (29) and exhibited the rapid growth rates associated with other chemically undefended sponge species (9, 14). Although currently the subject of ongoing research, we suspect that variably defended sponge species recruit into the population with different levels of chemical defenses [a constitutive trait or consequence of different microbial symbionts rather than through induction of defense (28)] and that subsequent predation affects sponge survival. Moreover, we speculate that some undefended individuals may persist within a population despite predation due to a form of automimicry [defended and undefended individuals look alike to predators that learn to avoid chemical defenses using visual cues (30)]. Both *X. muta* and *I. birotulata* were among the 10 most abundant sponge species in our surveys (Table S1), and their common presence in the sponge community likely decreased the percentage of variation explained by the presence of spongivores on undefended sponge species in multiple-regression analyses. These variably defended species would be expected to increase in abundance in the absence of predation, but not necessarily decrease in abundance if predation pressure is high. Therefore, considering the confounding effects of variably defended species, the propensity of consistently undefended species to persist in refuge locations despite high predator abundances, and location-specific differences in fishing pressure, it is remarkable that

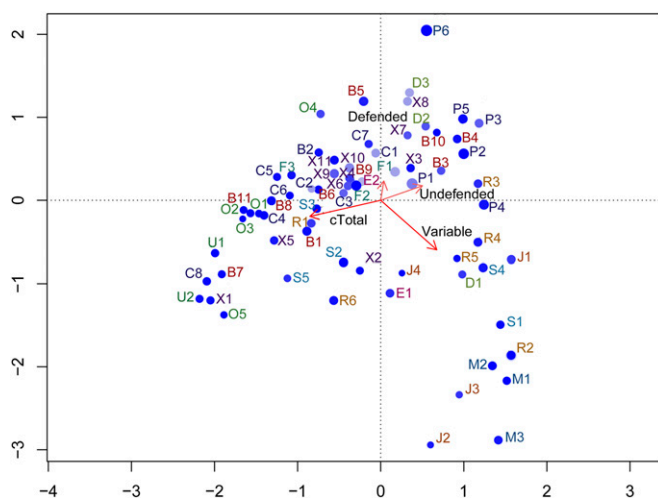


Fig. 3. Correspondence analysis of survey sites for occurrences of chemically defended, consistently undefended, and variably defended sponges, and corrected total abundance of sponge predators within 2,000 m³ of seawater directly above the reef. Prefixes of site names denote the following locations: B, Bahamas; C, Cayman Islands; D, Dominican Republic; E, St. Eustatius; F, Key Largo, FL; J, Jamaica; M, Martinique; O, Bonaire; P, Bocas del Toro, Panama; R, Puerto Rico; S, St. Lucia; U, Curaçao; X, Mexico.

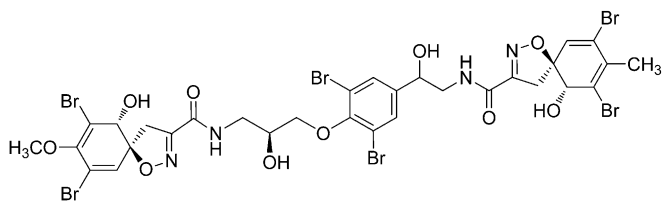


Fig. 4. Fistularin 3, a brominated tyrosine-derived alkaloid and defensive metabolite that has the highest concentration in the tissues of the most abundant sponge, *Aplysina cauliformis*, based on the surveys conducted in this study. This compound and a complex mixture of related metabolites found in species of the genera *Aplysina*, *Aiolochoira*, and *Verongula* (24) constitute the most common chemical defense of Caribbean sponges.

multiple-regression analysis yielded a value as high as 32.8% of the variation in the abundance of palatable sponges on reefs as predicted by the abundance of spongivorous fishes. This value increased to 76.5% and 94.6% when the analyses were restricted to two subsets of geographically adjacent sites that have strongly contrasting levels of fishing pressure: Cayman Islands and Jamaica, and Curaçao, Bonaire, and Martinique, respectively. Within these two subsets, the Cayman Islands, Curaçao, and Bonaire have low human population densities and well-enforced MPA systems, whereas Jamaica and Martinique have high human population densities, few MPAs, and intense fishing practices that include the use of fish traps.

From the multiple-regression analysis with corrected parrotfish abundance, angelfishes had the largest impact on sponge populations across all sites, with each individual angelfish having approximately the same effect as 1.6 stoplight parrotfishes (*S. viride*). For sites off the Lower Antilles, one angelfish had the equivalent grazing effect on palatable sponges as 7.2 redband parrotfishes (*S. aurofrenatum*). Angelfishes are more specialized spongivores, with a diet composed primarily of sponges [70–90% of gut volume (29)], whereas parrotfishes are usually described as grazers on algae and hard corals (31). The effect of angelfishes on the sponge community was particularly strong in our analysis of geographically adjacent sites having contrasting fishing impacts off the Lower Antilles, with each angelfish recorded within a 2,000-m³ volume above the reef reducing the proportion of undefended and variably defended sponge species by 8.6%. Even though sponges may comprise only a small proportion of the parrotfish diet, we observed a higher density of parrotfishes compared with angelfishes at all survey sites where these fishes were present (Dataset S3). As such, it is possible for *S. aurofrenatum* and *S. viride* to significantly control the proportion of palatable sponges in the sponge community by numerical abundance alone. Evidence of intense fishing activity (e.g., fish traps on reef bottoms, nets, line fishing) was observed at overfished sites off Martinique and St. Lucia, and although the numbers of spongivorous fishes counted at some of these sites were similar to those at less-fished sites, the size of these fishes were markedly smaller on overfished reefs (only individuals that could escape the mesh size of fish traps). Fish size presumably has an important influence on the relative effect of grazing, as larger parrotfishes can remove more sponge volume per unit effort or bite. In particular, large terminal-phase parrotfishes were very rare or absent on overfished reefs.

One alternative predator, the sponge-eating seastar *Oreaster reticulatus*, had an important effect on sponge community structure when spongivorous fishes were absent. This seastar species was only observed at two sites, Adriana's Reef and Rio Grande (Bocas del Toro, Panama), both of which also had no spongivorous fishes recorded in their respective surveys. Despite lacking angelfishes and parrotfishes because of overfishing, the presence of *O. reticulatus* at these two sites kept the proportion of chemically undefended sponges lower than at other overfished

sites (Fig. 2). It is unlikely that *O. reticulatus* is as effective at eating sponges as fishes are because seastars are only able to crawl along the reef bottom and are unable to access undefended sponges on top of topographically complex reef structures. In low-relief habitats such as seagrass beds, *O. reticulatus* can exclude preferred sponge species from the area (32). It seems likely that *O. reticulatus*, which was common before the mid-1900s before being targeted for the ornamental curio trade (33), may have been an important predator of sponges on reefs throughout the Caribbean.

Differences in the rates of growth or reproduction between chemically defended and palatable sponge species are likely to facilitate trophic cascades when sponge predators are removed. As palatable sponges are fast growing, grazing by spongivorous fishes keeps their populations in check by maintaining these sponges at a low proportion of the sponge community. It is therefore likely that the increase in the proportional cover of palatable sponges on overfished reefs will lead to more competitive interactions with other benthic reef organisms. For example, the consistently undefended Caribbean sponge *Mycale laevis* has a thinly encrusting, semicryptic growth form on reefs with numerous spongivorous fish, but a fleshy, apparent form that overgrows and smothers reef-building coral colonies on overfished reefs (34). Overgrowth of coral colonies by *M. laevis* and other palatable sponge species was frequently observed while surveys were being conducted for the present study. The indirect effects of competition with corals from the removal of sponge predators could further impede the recovery of coral reefs that are already impacted by disease, eutrophication, and the effects of climate change.

Materials and Methods

Study Sites and Benthic Community Surveys. Surveys were conducted on coral reefs at 69 sites from 12 countries across the Tropical Northwestern Atlantic marine province (referred to herein as “Caribbean” for brevity) from 2008 to 2012 (site details in Dataset S1). At each location, sponge community data and fish densities were recorded at 3–11 geographically distinct sites (>2 km apart) by a team of three to four that only included personnel from among the same five surveyors to minimize interobserver subjectivity. Transect lines were laid out along a contiguous section of the reef at 10–20 m (except for the shallow reefs off Bocas del Toro, Panama, and two sites off Key Largo, FL, 2–7 m). Surveys of sponge cover were carried out using a technique adapted from past studies (35) by evenly placing a 1 × 1 m² quadrat at 5 points along a 20-m transect line, with 5 replicate transects laid end-to-end at the same depth (total of 25 quadrats and 625 points per survey site). All sponges were identified to species (36), and when necessary, identifications were confirmed by Sven Zea (Universidad Nacional de Colombia, Santa Marta, Colombia) using microscopic examination of spicule mounts or tissue sections. Sponge species were categorized as chemically defended, consistently undefended, or variably defended based on data from laboratory feeding assays using the bluehead, *Thalassoma bifasciatum*, that were either conducted in the past (11, 26, 28) or performed for this study using the same methods (Table S2).

Surveys of Spongivores. The densities of spongivorous fishes were recorded at each survey site as described previously (22) (Dataset S3). The species monitored comprised all angelfish species, parrotfishes of the genus *Sparisoma*, and all species of trunkfishes, filefishes, and pufferfishes. Although the pufferfish *Canthigaster rostrata* was counted, this small, territorial, and very abundant species feeds primarily on small benthic crustaceans (37) and was not included in further analyses. Among all sites, only two, both at Bocas del Toro, Panama, had few fishes but several individuals of the sponge-eating seastar, *Oreaster reticulatus*, and these were included in the spongivore survey.

Data Analyses. The occurrences of the 10 most common sponge species at each site were used to compare sponge diversity among sites using nMDS with Bray–Curtis dissimilarities. This scaling analysis was limited to the 10 most abundant sponge species because this subset included over 50% of all sponges surveyed across all sites, included proportional representation of all three chemical defense categories (defended, undefended, and variably defended; Table S1), and because the inclusion of less common species obscured the underlying pattern in the data (Results).

All other analyses used data from all sponge species present at each site. The number of occurrences of chemically defended, consistently undefended, and variably defended sponges within the sponge assemblage were calculated for each site, and plotted in a CA with the corrected total number of sponge predators (both fishes and seastars) recorded in 2,000 m³ of seawater directly above the reef. Parrotfishes were significantly smaller in overfished areas (31), and to correct for fish size at overfished sites where fishes were small (<20 cm TL) and fish traps were observed, parrotfish abundance was divided by 10. This correction was considered highly conservative, as parrotfishes in these areas were often <10 cm in total length (TL) (the size that allowed them to escape fish traps). Examples of calculations from the literature include equivalent grazing estimates of one large (>25 cm TL) to 24 small (5–10 cm TL) parrotfishes (38), and one large (35 cm) to 75 small (15 cm) parrotfishes (39).

To investigate the relationship between the abundance of spongivorous fishes and sponge community structure, multiple-regression analyses were performed separately for the proportion of consistently undefended sponges and the proportion of palatable species (consistently undefended and variably defended species) within the sponge community at each site as the response variables, and the following sponge predator groups as factors: angelfishes (*Holocanthus* and *Pomacanthus* spp.), redband parrotfish (*Sparisoma aurofrenatum*), stoplight parrotfish (*S. viride*), redtail parrotfish (*Sparisoma chrysopterum*), trunkfish (*Lactophrys* and *Acanthostracion* spp.), and filefish (*Cantherhines* spp.). Numbers of parrotfishes were corrected for body size as previously described. Multiple regressions were also conducted on subsets of data from latitudinally similar regions with contrasting and long-term levels of fishing pressure (subset 1: Cayman Islands

and Jamaica; subset 2: Bonaire, Curaçao, and Martinique). All multivariate analyses were carried out in the program R using the *vegan* and *ca* packages (40, 41).

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