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Indirect effects of overfishing on Caribbean reefs: Sponges overgrow reef-building corals

Tse-Lynn Loh, Steven E McMurray, Timothy P Henkel, Jan Vicente, Joseph Pawlik

Consumer-mediated indirect effects at the community-level are difficult to demonstrate empirically. Here, we show an explicit indirect effect of overfishing on competition between sponges and reef-building corals from surveys of 69 sites across the Caribbean. Removal of sponge-eating angelfishes and parrotfishes resulted in > 3 fold increase in overgrowth of corals by sponges, with coral-sponge contact increasing from 11.0% to 25.6%, and these sponges were mostly species palatable to sponge predators. Palatable species have faster rates of growth or reproduction than defended sponges, which instead make metabolically expensive chemical defenses. On average, overfished sites had lower macroalgal cover, contrary to prevailing assumptions about seaweed control by herbivorous fishes. Coral-sponge competition provides an additional and unambiguous justification for marine protected areas (MPAs) in the Caribbean, where the conceptual model of sponge community ecology and defense trade-offs is notable for the clarity of top-down control and indirect effects across a broad geographic region.

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Authors:

Tse-Lynn Loh[1†], Steven E. McMurray[1], Timothy P. Henkel[2], Jan Vicente[3] & Joseph R. Pawlik[1*]

[1]Department of Biology and Marine Biology and Center for Marine Science, University of North Carolina Wilmington, Wilmington, NC 28409, USA.

[2]Valdosta State University, Department of Biology, 1500 N Patterson St, Valdosta, Georgia 31698, USA.

[3]Institute of Marine and Environmental Technology, University of Maryland Center for Environmental Science, 701 E Pratt St. Suite 236, Baltimore, MD 21202, USA.

†Present address: Daniel P. Haerther Center for Conservation and Research, John G. Shedd Aquarium, Chicago, IL 60605, USA.

[*]Correspondence to Joseph Pawlik, Center for Marine Science, University of North Carolina Wilmington, 5600 Marvin K Moss Lane, Wilmington NC 28409. Tel: 910-9622377, Fax: 910-9622410 pawlikj@uncw.edu

Introduction

Food web dynamics are considered fundamental to the study of ecology (Fretwell, 1987), and are the subject of considerable research despite the theoretical limitations brought by the complexity of natural ecosystems. Policy decisions relevant to the management of living natural resources require an in-depth understanding of ecosystem structure and properties (Hooper et al., 2005; Farber et al., 2006). Among the mechanisms important to ecosystem function are indirect effects, which alter community structure through predation (e.g., trophic cascade) or competition (e.g., indirect mutualism; Wootton, 1994). Indirect effects can be difficult to identify or quantify, particularly for complex ecosystems with demonstrable bottom-up control (Strong, 1992). While a number of examples of indirect effects have been found among both terrestrial and aquatic ecosystems, most of these have been described at the species-level rather than at the community-level (Polis et al., 2000).

Community-level indirect effects have been invoked as an explanation for the negative consequences of overfishing on the competitive interactions between reef-building corals and macroalgae on coral reefs (Knowlton & Jackson, 2008), and this has led to calls for policy action to manage fishing (Jackson & Johnson, 2014). But the coral reefs of the Caribbean are distinctly different than those of the tropical Pacific and Indian Oceans (Roff & Mumby, 2012). The biomass of herbivorous fishes on Caribbean reefs is much lower than on Indo-Pacific reefs, and this situation may have existed before human fishing intensified (Edwards, 2014). There are differing estimates of the baseline cover of macroalgae that occurred on reefs before coral cover began decreasing (Bruno et al., 2014). Caribbean reefs also suffered the catastrophic loss of the sea urchin *Diadema antillarum* RA Philippi, 1845 in the early 1980s, and this species may have played a disproportionate role in herbivory (Shulman & Robertson, 1996) relative to what occurs on Indo-Pacific reefs. Hence, the justification for fishing restrictions on Caribbean reefs for the

purpose of controlling macroalgae seems tenuous, because the top-down effects of herbivorous fishes may be insufficient (Roff & Mumby, 2012).

Caribbean reefs are also strikingly different from those of the Indo-Pacific in having two- to ten-fold greater biomass of sponges (Wilkinson & Cheshire, 1990). Sponges have been ignored in broader discussions of coral reef community ecology, in part because they were considered to be free of top-down control (Randall & Hartman, 1968). However, a survey of sponge chemical defenses against fish predators revealed that both palatable and defended sponge species were found on reefs (Pawlik et al., 1995). Manipulative field experiments demonstrated that palatable species had faster rates of wound healing, tissue growth, and recruitment that act in opposition to grazing by sponge-eating fishes (primarily angelfishes and parrotfishes), while defended species produced defensive metabolites (Pawlik, 2011). In light of these resource trade-offs, a conceptual model of sponge ecology was proposed that included three trophic levels and indirect effects of sponge competition with reef-building corals and macroalgae (Pawlik, 2011). The consumptive indirect effects of this conceptual model were tested by surveying sites across a gradient of human fishing intensity on Caribbean reefs (Loh & Pawlik, 2014), where a fortuitous long-term manipulative experiment has been ongoing for decades or longer, with some reefs heavily overfished through the use of non-selective fish-traps (e.g., Jamaica, Martinique, Panama), while others have been relatively protected from fishing, either because of low human population density or through the imposition of marine protected areas (MPAs; Bonaire, Cayman Islands, some Bahama Islands). This test of theory was noteworthy not only for its spatial scale, but also because it examined community-level differences in chemical defenses of a taxonomically diverse group across a large geographic region, with identification of the palatability of 109 sponge species. Results of the Caribbean-wide survey showed that, at less-fished reef sites with many sponge predators, there was a high abundance of chemically defended sponge species,

while overfished sites were dominated by palatable species that have faster rates of growth, reproduction or recruitment (Loh & Pawlik, 2014).

In the present study, we used benthic surveys that were performed contemporaneously with the fish and sponge surveys of the previous study (Loh & Pawlik, 2014) to test the indirect effects of overfishing on competition between sponges and reef-building corals. We predicted that removing the top-down control of sponges by overfishing sponge predators would increase competitive sponge-coral interactions, because faster-growing palatable sponges would dominate in the absence of sponge predators. Our surveys also recorded the abundance of other benthic organisms, including macroalgae, at 69 sites across the Caribbean, providing a snapshot of reef community structure and allowing for comparisons of the relative abundances of competitive benthic groups.

Materials and Methods

Descriptions and a map of sites, and methods for surveying sponge-eating fishes have been previously published (Loh & Pawlik, 2014). Spongivore Index (SI) was defined as the sum of total parrotfish and angelfish abundance within a survey volume of 2000 m^3 at each site, with total fish abundance divided by 10 at overfished sites to correct for smaller fish biomass (Loh & Pawlik, 2014). We consider the SI to be a highly conservative measure of fish grazing activities, because literature-based grazing estimates have compared the impact of one large parrotfish (>25 cm TL) to 24 small (5–10 cm TL) parrotfishes (Fox & Bellwood, 2007), and one large (35 cm) to 75 small (15 cm) parrotfishes (Lokrantz et al., 2008).

Surveys of coral reefs were carried out at 69 sites from 12 countries in the Tropical Northwestern Atlantic marine province ("Caribbean") at depths of 10-20 m, except for six sites in Panama and two sites off Florida, USA that were surveyed at 2-7 m (Loh & Pawlik, 2014). Countries surveyed were the Bahamas Islands, Panama, Bonaire, Curaçao, USA (Florida Keys

and Puerto Rico), Martinique, St. Eustatius, St. Lucia, the Dominican Republic, Jamaica, Cayman Islands and Mexico (Yucatan coast). Reef site selection was based on previously published assessments of fishing pressure (Burke & Maidens, 2004), prior to our own surveys of the abundance of sponge-eating fishes and the presence of fish-traps. Survey data validated the selection of the two categories, less-fished (SI = 12.0 - 85.0) and overfished (SI = 0 - 4.2).

At each site, benthic community surveys were carried out by evenly placing a 1x1 m^2 quadrat 5 times along a 20m transect line, with 5 replicate transect lines laid end-to-end at similar depth, and a gap of 5m between each transect (total of 25 quadrats per survey site). The benthos under 25 points within each quadrat were classified into the following categories: reef-building coral, sponge, fire coral (*Millepora* sp. C Linnaeus, 1758), gorgonian, zoanthid, other benthos, bare rock or dead coral, rubble, sand, silt, macroalgae (all erect species, but primarily *Dictyota* JV Lamouroux, 1809; *Halimeda* JV Lamouroux, 1812; *Lobophora* J Agardh, 1894; and *Microdictyon* spp. Decaisne, 1841), turfs (including cyanobacterial mats), and coralline algae. A total of 625 points were recorded at each survey site (Supplemental Information Table S1). Coral-sponge interactions were quantified within the same number of quadrats along the same transect lines. For all coral colonies with at least 50% of their surface areas within each quadrat, we counted coral colonies in 3 categories: (1) those having no contact with sponges, (2) those that were growing adjacent to and in contact with sponges, and (3) those that were overgrown by sponges such that sponge tissue was covering live coral tissue.

SI and the percentage of coral colonies having no contact with sponges, growing adjacent to sponges, and overgrown by sponges at each site were plotted in a non-metric multi-dimensional scaling (nMDS) ordination with Bray-Curtis distances, followed by ANOSIM (analysis of similarity) to compare coral-sponge interactions between overfished and less-fished sites (Clarke, 1993). Benthic occurrence data were square-root transformed for an nMDS ordination, and individual variables were then correlated with the scores of axes 1 and 2. With

111 square-root transformed data, ANOSIM was used to compare benthic occurrences between
112 overfished and less-fished sites, with SIMPER (percentage similarity) to determine which benthic
113 categories contributed most to group differences (Clarke, 1993). Additionally, we performed
114 linear regressions to examine the effect of SI on cover of palatable sponges, the percentage of
115 coral overgrown by sponges and macroalgal cover, and to relate cover of palatable sponges with
116 coral overgrowth. . All analyses were carried out in R v2.15.2 and PRIMER v6.

117 **Results**

118 The mean Spongivore Index (SI), corrected total density of parrotfishes and angelfishes,
119 for less-fished sites was 42.5 ± 2.8 (SE) within the survey volume of 2000 m^3 (n=44 sites), while
120 overfished sites had a mean corrected density of 2.1 ± 0.3 per 2000 m^3 (n=25 sites). Coral
121 colonies on reefs that were less impacted by fishing (n=22,827 colonies, 44 sites) had little
122 interaction with sponges, with 11.0% of colonies growing either adjacent to sponges (8.8 ± 0.9%)
123 or overgrown by sponges (3.2 ± 0.5%). The incidence of coral-sponge interactions was more than
124 double on overfished reefs (n=11,278 colonies, 25 sites), with 25.6% of corals growing next to
125 sponges (14.9 ± 1.5%) or overgrown by sponges (10.7 ± 2.9%) (Figs. 1, 2). Accordingly, in an
126 non-metric multi-dimensional scaling (nMDS) plot of sponge-coral interactions, survey sites
127 assembled into two groups (stress=0.05, Fig. 3): (1) sites with low spongivore numbers and
128 higher proportions of coral-sponge interactions (e.g. Jamaica, Martinique, Panama); and (2) sites
129 with high spongivore numbers and corals that were less frequently in contact with sponges (e.g.
130 Bonaire, Cayman Islands, Florida Keys). Analysis of similarity (ANOSIM) between overfished
131 (n=25) and less-fished (n=44) reefs indicated that coral-sponge interactions and the density of
132 sponge-eating fishes were significantly different at p=0.001, with a Global R of 0.65.

On less-fished reefs with high abundances of sponge-eating fishes, most of the sponges that overgrew corals were slow-growing, chemically defended species (70.9%), reflecting their greater abundance on reefs where predation pressure is high (Loh & Pawlik, 2014). The chemically defended *Aplysina cauliformis* HJ Carter, 1882 (Fig. 1A), also the most common sponge on Caribbean reefs (Loh & Pawlik, 2014), had the highest number of encounters with corals, accounting for 14.3% of overgrowth interactions (Table 1). On overfished reefs, 43.2% of the sponges that overgrew corals were the faster-growing, palatable species (Loh & Pawlik, 2014), with the palatable sponge *Niphates erecta* P Duchassaing & G Michelotti, 1864 most frequently recorded overgrowing corals (9.7%, Table 1). Sponges with unknown chemical defense strategies accounted for only 0.2% and 0.1% of sponges overgrowing corals on less-fished and overfished reefs, respectively.

Linear regression analysis of all sites confirmed that palatable sponge cover was negatively correlated with SI ($p<0.001$; $r^2=0.280$; Fig. 4A). Also, linear regression analysis indicated that a higher percentage of coral colonies were overgrown by sponges as the cover of palatable sponges increased ($p<0.001$, $r^2=0.551$). Correspondingly, there was a significant negative relationship between the percentage of corals overgrown by sponges and SI ($p=0.010$, $r^2=0.095$, Fig 4B).

From our benthic surveys, macroalgae comprised the most abundant benthic organisms on Caribbean coral reefs, with an overall cover of 28.6%. Sponges and reef-building corals were next with total cover of 15.9% and 16.2%, respectively (composition of benthos by survey site listed in Table S1). Reef-building corals were more abundant on reefs off Bonaire, Curaçao, the Dominican Republic, and Panama, with cover ranging from 22.1 - 33.3% by location. At other locations, coral cover was less than 15%. The highest cover of macroalgae by location was found on overfished reefs off Jamaica (15.4 - 68.0%, mean = 50.4%). However, sites having abundant

sponge-eating fishes, such as Mira Por Vos Cays (Bahamas, 50.6%), Lac Cai (Bonaire, 36.2%), Banco Chinchorro (Mexico, 14.2 - 54.9%, mean = 39.3%), the Cayman Islands (35.2 - 51.7%, mean = 45.1%) and Desecheo Island (Puerto Rico, 50.2%), also had high macroalgal cover.

While all less-fished sites grouped together in the nMDS, several overfished sites had benthic communities similar to less-fished sites (stress=0.16, Supplemental Information Fig. S1). Sponge and zoanthid cover was inversely correlated with Axis 1 (r = -0.86 and -0.74 respectively), while macroalgal cover was positively correlated with Axis 1 (r = 0.80) (Table S2). For Axis 2, sites were sorted based on turf (r = 0.86) and rock cover (r = -0.64). Based on correlations with the ordination axes, reef-building coral cover did not contribute to the overall variation in community composition among survey sites (r = -0.16 and 0.08 respectively). From the ANOSIM, the benthic communities at less-fished sites were significantly different from overfished sites at p=0.001, with a Global R of 0.34. Percentage similarity (SIMPER) analysis showed that less-fished sites were characterized by higher macroalgal, rock, reef-building coral and coralline algal cover, and less turf and sponge cover (Table 2). Linear regression analysis of all sites also indicated that SI was not correlated with macroalgal cover (p=0.528, r^2=0.006; Fig. 4C).

Discussion

From the standpoint of Caribbean coral reef conservation, our study provides compelling justification for fishing restrictions to protect sponge-eating fishes (angelfishes and parrotfishes) in order to decrease competitive interactions between reef-building corals and sponges. The three-fold difference in overgrowth of corals by sponges between less-fished and overfished sites was substantial, particularly when over 25% of coral colonies at overfished sites were in contact with, or overgrown by, sponges. In a previous study, we demonstrated that a palatable sponge species, *Mycale laevis* HJ Carter, 1882, is restricted to refugia when sponge-eating fishes are

abundant, but overgrows living coral tissue when sponge predators are absent or rare (Loh & Pawlik, 2012) (Fig. 1B). Here, we were able to observe this phenomenon at the community-level and across an entire geographic region. The competitive superiority of sponges over reef-building corals has been well documented, and is likely due to a combination of shading, physical inhibition of water flow and gas exchange, and the use of allelopathic secondary metabolites to kill coral tissue (Porter & Targett, 1988; Thacker et al., 1998; Aronson et al., 2002; Pawlik et al., 2007) (Fig. 1). Because allelopathic metabolites are present in the mucus or exudates of some sponge species, mere proximity to reef-building corals may be sufficient to negatively impact coral physiology and reproduction, making affected colonies more susceptible to bleaching or pathogenesis (Sullivan, Faulkner & Webb, 1983). With the recent announcement that five species of Caribbean reef-building corals are proposed for listing as "threatened species" under the United States Endangered Species Act (NOAA, 2014), the results of this study should be useful in justifying regulations to protect sponge-eating fishes.

While the evidence for indirect effects of overfishing on Caribbean reef sponge communities is robust (Loh & Pawlik, 2014), as are the competitive effects of sponges on reef-building corals (this study), the same cannot be said for the effects of overfishing on macroalgae. We recorded overall higher levels of macroalgal cover on less-fished reefs, contrary to previous studies (Newman et al., 2006), and in support of the emerging recognition that there is equivocal evidence for top-down control of macroalgae by herbivorous fishes on Caribbean reefs (Roff & Mumby, 2012). Our surveys of fishes enumerated spongivores, but they included the dominant parrotfish species, which eat both sponges and macroalgae. We are confident in extrapolating our data to include the additional herbivorous fishes common to Caribbean reefs (primarily acanthurids) because the fishing methods used at most of the overfished sites indiscriminately targeted fishes larger than the mesh-size of fish-traps. Further, parrotfish size and abundance has

recently been cited as an excellent proxy for general fishing pressure across the Caribbean (Vallès & Oxenford, 2014). The abundant macroalgal cover at geographically isolated, less-fished sites in the SE Bahamas or Banco Chinchorro, Mexico, could be attributed to the continued absence of the echinoid *Diadema antillarum*, or to differences in macroalgal species and palatability among sites. For example, the unpalatable *Microdictyon* spp. (Lapointe et al., 2004) and *Dictyota* spp. (Hay, 1991) were common in our surveys of these sites and are generally avoided by fish grazers. While we did not enumerate *D. antillarum* in this study, it may be that populations of this important herbivore are rebounding faster on overfished reefs where urchin predators have been removed by fish trapping, along with herbivorous and spongivorous fishes. If true, this may explain the generally lower levels of macroalgae on overfished reefs observed in this study.

This study underscores the distinctive ecology of Caribbean coral reefs relative to those in other parts of the world, a concept that is not new (Wilkinson & Cheshire, 1990; Roff & Mumby, 2012), yet often ignored in reviews of coral reef ecosystem function. Sponges dominate benthic communities on Caribbean coral reefs to a greater degree than elsewhere, but this fact is usually obscured by sampling methods. Coral reef ecologists conventionally survey 2-dimensional benthic cover because of the time constraints of scuba diving and the complexity of reef topography. While overall cover of sponges from our surveys was nearly the same as corals (15.9 vs 16.2%), and well behind macroalgae (28.6%), both reef-building corals and macroalgae consist primarily of thin layers of tissue intended to catch light for photosynthesis. The filter-feeding sponges recorded in these surveys were mostly thick-bodied, and in many cases massive or upright branching species, so that the actual biomass of sponges on Caribbean reefs (from reef crest to deep mesophotic reefs and including reef interstices) is likely to be orders of magnitude greater than that of algae or corals. Sponge communities are structured by top-down processes, but may be a rare example of a system unaffected by bottom-up factors (Pawlik et al., 2013;

2015). The primary reason for this may be the nutritional reliance of Caribbean reef sponges on dissolved organic carbon (DOC), which frees sponges from food-limitation and provides a trophic "loop" that returns refractory DOC from the water column to the benthos (de Goeij et al., 2013). A similar nutritional strategy does not appear to be available to sponges on more oligotrophic Indo-Pacific coral reefs (Wilkinson & Cheshire, 1990).

Conclusions

Validating our conceptual ecosystem model (Pawlik, 2011), Caribbean reef sponges provide a rare example of indirect effects at the community level, in which a group of consumer species (primarily angelfishes and parrotfishes) act upon a diverse community of sponges to alter the relative abundance and competitive interactions of sponges with other benthic organisms. In the present study, indirect effects are propagated from human fishing activities, but this role may have been played by higher-level predatory fishes in the past, likely from two trophic levels (requiem sharks - large groupers and snappers), although probably not as effectively as human fish-trapping removes sponge predators. On the other end of the model, palatable sponges compete with corals on overfished reefs, but also appear to compete with macroalgae, as the abundance of the two were inversely correlated. In contrast to this model system, most commonly cited examples of indirect effects are simple ecosystems with trophic levels often identified as individual species (e.g., orca – sea otter – urchin – kelp; wolf – elk – aspen – songbirds, Wootton, 1994; Hebblewhite et al., 2005). Despite the high species-diversity at each level, the clarity of indirect effects observed for the Caribbean reef sponge ecosystem is likely due to the simplicity of the interactions relative to other, particularly terrestrial, ecosystems (Polis et al., 2000): abiotic influences on the system are minimal, top-down effects are dominant, sponge community composition is similar across the entire biogeographic region, insect-equivalent mesograzers are unimportant, and the influences of extinctions and invasions are minimal (Pawlik, 2011; Loh &

Pawlik, 2014). The clarity and predictive capability of this model system runs contrary to the perception that recent contributions to the ecological literature have been increasingly complex and decreasing in explanatory power (Low-Décarie, 2014).

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Table 1 (on next page)

Percentage of the ten most common sponge species overgrowing reef-building corals on less-fished and overfished reefs, indicating the chemical defense category of each species.

Less-fished			Overfished		
Species	**%**	**Defense**	**Species**	**%**	**Defense**
Aplysina cauliformis	14.29	D	*Niphates erecta*	9.72	P
Mycale laevis	12.44	P	*Amphimedon compressa*	8.34	D
Ircinia felix	6.76	D	*Aplysina cauliformis*	8.17	D
Svenzea zeai	6.45	D	*Mycale laevis*	8.08	P
Amphimedon compressa	5.07	D	*Chondrilla nucula*	7.66	P
Agelas citrina	3.84	D	*Iotrochota birotulata*	5.42	P
Xestospongia muta	3.38	P	*Xestospongia proxima*	4.91	P
Aplysina fistularis	3.07	D	*Aplysina fulva*	4.82	D
Aiolochroia crassa	2.76	D	*Amphimedon erina*	2.75	D
Niphates erecta	2.76	P	*Haliclona walentinae*	2.58	D

D = chemically defended, or P = palatable (including chemically undefended and variably defended species). Defense category based on previous research (Pawlik et al., 1995; Loh & Pawlik, 2014).

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Table 2(on next page)

SIMPER dissimilarity matrix for square-root transformed occurrences of benthic categories between less-fished and overfished sites.

Average dissimilarity = 32.77						
	Less-fished	**Overfished**				
Benthic category	**Average abundance**	**Average abundance**	**Average dissimilarity**	**Dissimilarity SD**	**% contribution**	**Cumulative %**
Macroalgae	13.56	10.02	5.34	1.41	16.29	16.29
Turf	6.85	7.02	3.94	1.44	12.03	28.32
Sponge	8.17	11.45	3.43	1.17	10.47	38.79
Rock	8.00	5.78	3.32	1.47	10.12	48.91
Hard coral	9.84	8.99	3.03	1.42	9.24	58.15
Coralline algae	6.49	3.41	2.58	1.42	7.88	66.04
Gorgonian	3.58	2.69	2.24	1.35	6.84	72.88
Sand	5.47	5.51	2.04	1.37	6.21	79.09
Silt	0.86	2.61	1.79	0.89	5.47	84.56
Rubble	2.56	3.22	1.70	1.18	5.18	89.74
Fire coral	1.41	1.19	1.15	1.00	3.50	93.25

% contribution indicates the contribution to dissimilarity between less-fished and overfished groups.

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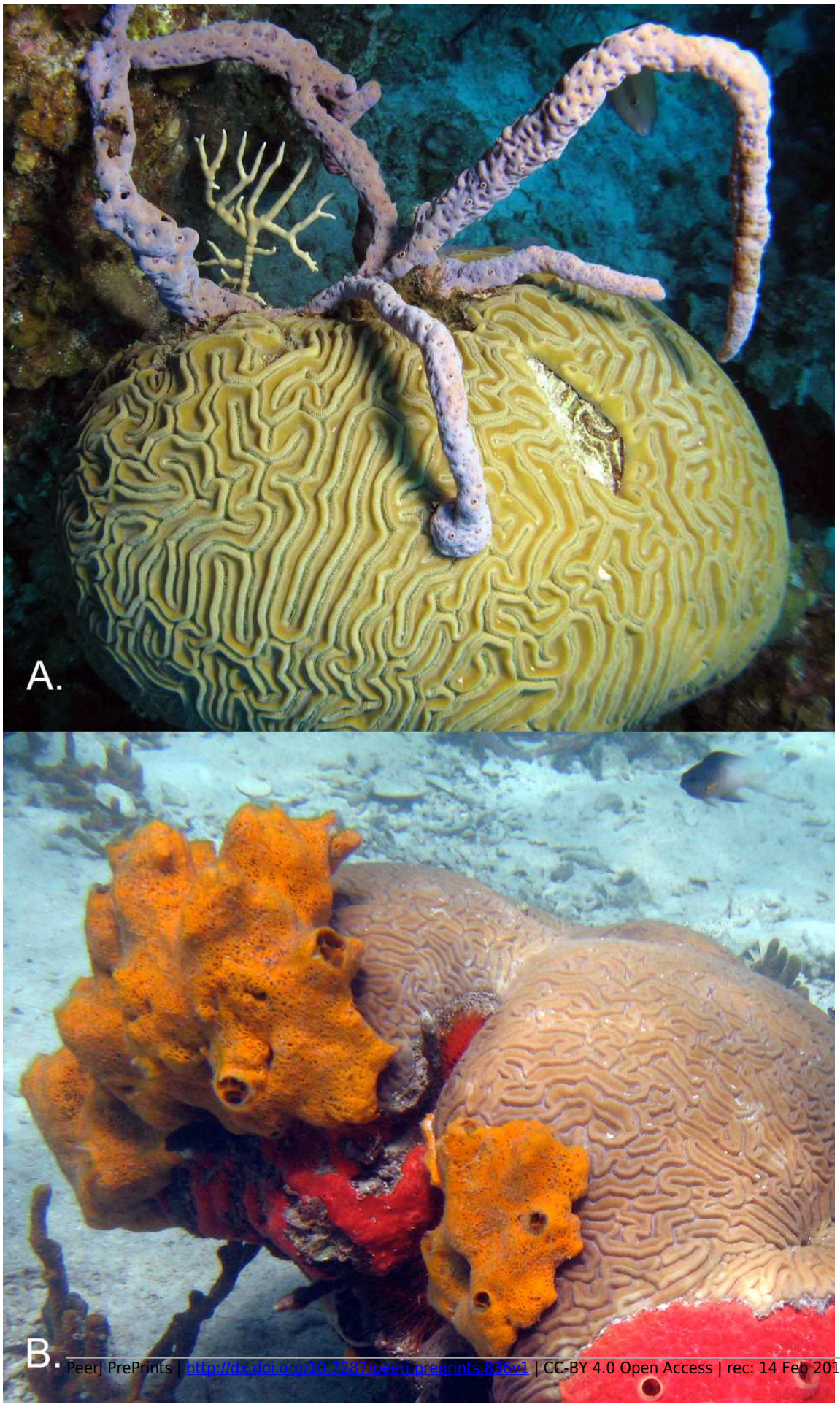
1

Overgrowth of corals by sponges.

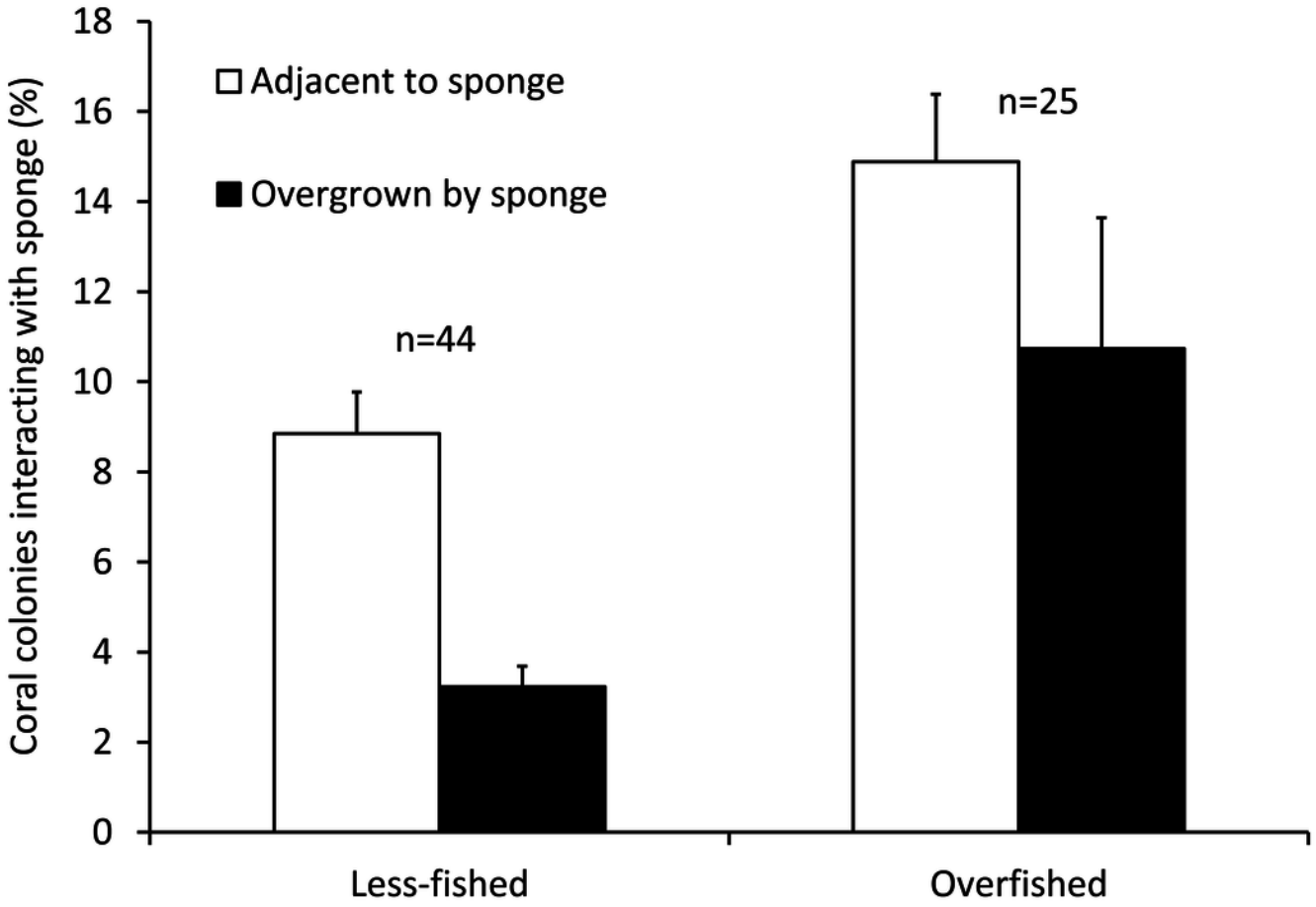
Brain coral *Diploria labyrinthiformis* C Linnaeus, 1758 overgrown by the most abundant Caribbean sponges in the chemically defended category (A) *Aplysina cauliformis*, and in the palatable category (B) *Mycale laevis*. (Hogsty Reef, Bahamas; Bocas del Toro, Panama, respectively).



2

Coral-sponge interactions for reef sites that were less-fished (n=44) and overfished (n=25).

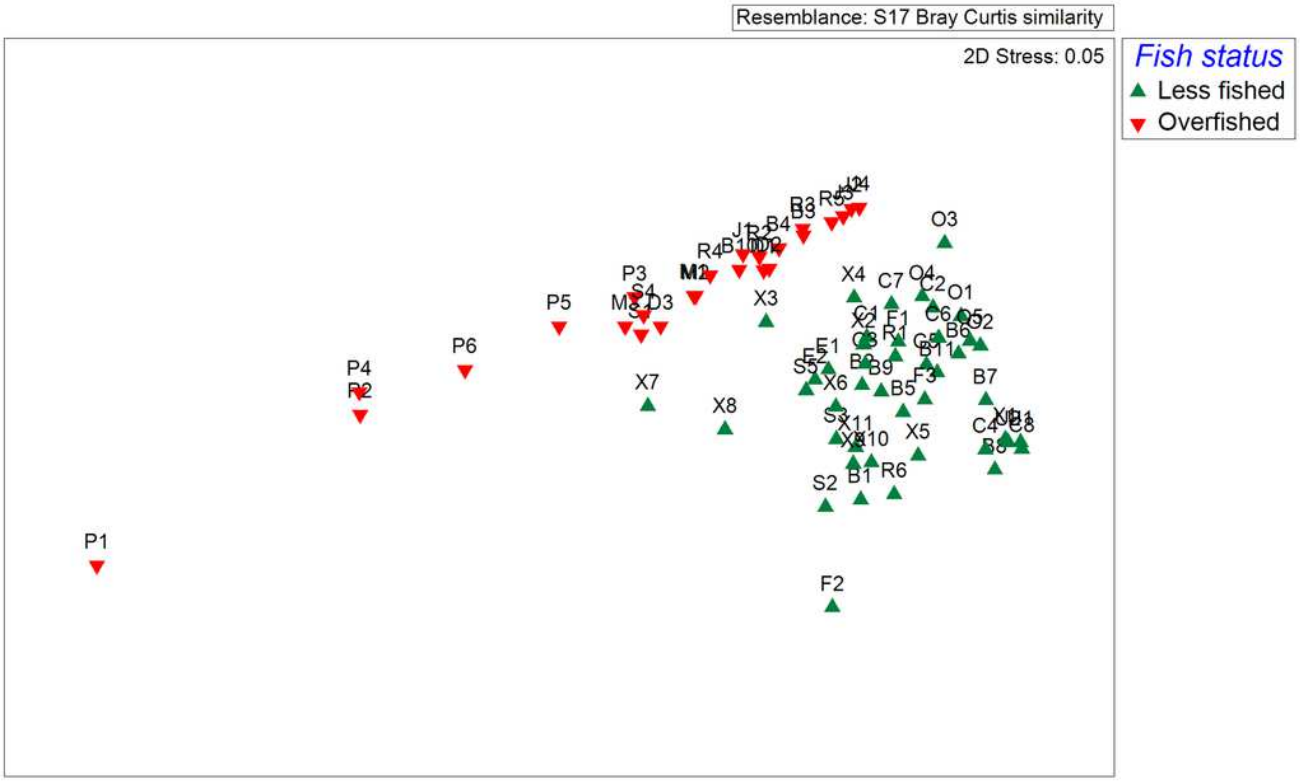
Mean percentage of coral colonies surveyed that were growing adjacent to, or overgrown by, sponges. Error bars denote standard errors.



3

nMDS plot of survey sites relating the percentage of coral colonies that had no interaction with sponges, growing adjacent to sponges and overgrown by sponges, and Spongivore Index (SI) at each site.

Sites labeled green are less-fished, and sites labeled red are overfished. 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.



4

Linear regression plots of benthic cover vs. SI

(A) Palatable sponge cover, (B) percentage of corals overgrown by sponges and (C) macroalgal cover vs. SI. Cover is defined as the number of occurrences in 625 benthic survey points at each site.