

Targeted predator defenses of sponges shape community organization and tropical marine ecosystem function

JANIE L. WULFF^{1,2,3}

¹*Department of Biological Science, Florida State University, Tallahassee, Florida 32306-4295 USA*

²*Smithsonian Tropical Research Institute, Balboa, Republic of Panama*

Citation: Wulff J. L. 2020. Targeted predator defenses of sponges shape community organization and tropical marine ecosystem function. *Ecological Monographs* 00(00):e01438. 10.1002/ecm.1438

Abstract. Defenses that target particular consumers often influence community organization, ecosystem function, and diversity maintenance. In coral reef, mangrove, and seagrass ecosystems, sponges affect substratum stability, water clarity, diversity of associated species, and survival of habitat-providing organisms, key roles not duplicated by other organisms. Whether and how predators control sponges are much disputed. Substantial ecosystem consequences of losing or gaining sponges motivated definitive experiments on how predators control sponge distribution and abundance. Caribbean sponges of 94 species representing 13 taxonomic orders and three linked habitats (coral reefs, mangroves, and seagrass meadows) were exposed to seven predator species representing different habitats and degrees of spongivory in 4,493 *in situ* trials. The resulting data force reassessment of popular interpretations of several patterns and processes. Contrary to extract pellet assays that declare most sponges deterrent, 78% of these 94 species were eaten by at least one predator. But “palatability” is consumer dependent: a sponge species eaten by one predator can be rejected by other predators, and predator species differed in what sponges they ate in 55.4% (214/392) of pairwise comparisons between predators. Because spongivore species are usually restricted to particular habitats, they impose abrupt boundaries on sponges’ habitat distributions, reflecting inverse relationships between accessibility and palatability to each predator. Thus a seagrass-dwelling starfish eats only 9% of seagrass sponge species, but 70% of coral reef species, and 78% of mangrove species. Reef-dwelling angelfishes completely consume only 13% of reef species, but 29% of seagrass species, and 63% of mangrove species. Defenses that target specific predators reveal that spongivore influence on community organization cannot be inferred from extract pellet/omnivore assays that assume defenses target all predators equally. In fact, pellet data wrongly predicted actual consumption of living sponges of that pellet’s species in 43% of field experiments with spongivores. In contrast with herbivore–plant interactions, opportunistic spongivory is at least as important as routine spongivory for community organization and ecosystem function. Potential for loss of key functional roles of sponges, if opportunistic predators gain access to sponge species that lack defenses against them, must inform conservation plans for coral reef, mangrove, and seagrass ecosystems.

Key words: *angelfish; Caribbean; coral reefs; mangroves; opportunistic feeding; parrotfish; seagrass; sponges; spongivory; starfish; top-down control; trunkfish.*

INTRODUCTION

No prey’s defenses are proof against all consumers. This fundamental aspect of ecology and evolution shapes our understanding of resource allocation trade-offs, community structure and dynamics, evolution of defenses and their circumvention, and mechanisms by which species diversity is generated and maintained (Forister et al. 2015). By far the most thorough explorations have been focused on terrestrial plants and marine algae (Coley et al. 1985, Lewis 1985, Weis and Berenbaum 1988, Hay 1992, Paul 1992, van Alstyne

2001, Cornell and Hawkins 2003, Kursar and Coley 2003, Steneck et al. 2017). As patterns have been discovered in specific systems, hypotheses have been developed to guide predictions of relative effectiveness of coping with consumers by resisting, tolerating, or evading them (Tiffin 2000, Cronin 2001, Agrawal and Fishbein 2006), and for how such strategies play out in community organization, mechanisms of speciation, and explanations of diversity patterns (Fine et al. 2013, Coley and Kursar 2014, Agrawal and Weber 2015, Becerra 2015).

Comparisons of defense strategies between taxonomic groups have been instructive in the search for general rules. Contrasts of studies of marine algae with terrestrial plants have revealed similarities but also important differences (Hay et al. 1987, Hay and Fenical 1988, Hay

Manuscript received 1 July 2020; accepted 7 August 2020.
 Corresponding Editor: Geerat J. Vermeij.

³ E-mail: wulff@bio.fsu.edu

1992, 2016, Hay and Steinberg 1992, Cronin and Hay 1996, Cronin 2001, Rasher et al. 2015, Steneck et al. 2017). A comprehensive study of defenses of 81 species of polychaete worms pointed out differences between sessile and mobile prey (Kicklighter and Hay 2006) that influence relative effectiveness of resistance, tolerance, and evasion strategies. Exploration of defense specificity in sessile clonal animals that are constrained, like plants, to strategies that do not involve running away, and able, like plants, to regrow after being partially consumed, would further clarify which aspects of developing theory are most robust (Berenbaum 1995). But the comprehensive data sets required have not existed.

Sponges are brightly colored, soft-bodied, sessile animals that are abundant and diverse in many marine ecosystems. Their conspicuous presence on coral reefs, and associated seagrass meadow and mangrove ecosystems, suggests effective defenses against co-occurring predators; and in fact most predators do not consume sponges at all. Gut contents of 212 Caribbean reef fish species revealed only 11 species with more than 6% sponge material (Randall and Hartman 1968), but some of those species are dedicated spongivores. Urgent questions about what processes might control sponge populations (Wulff 2016, 2017) are raised by dramatic mass mortalities of entire faunas (Butler et al. 1995, Wulff 2006a, 2013, Stevely et al. 2011), aggressive overgrowth of corals by a few species (Vicente 1990, Rützler and Muzik 1993, Antonius and Ballesteros 1998, Macintyre et al. 2000, Benzoni et al. 2008, Wang et al. 2012), assertions that human capture of spongivores is allowing sponges to overgrow reefs (Loh and Pawlik 2014, Loh et al. 2015), and cross-ocean invasions (Coles and Eldredge 2002, Cerrano et al. 2006). Beneficial functional roles of sponges, which include efficient filtering of bacteria from the water column, harboring hundreds of species of symbionts, increasing coral survival by binding living corals to the reef frame, facilitating reef regeneration, and protecting coral skeletons and mangrove prop roots from damage by excavating organisms (reviews in Díaz and Rützler 2001, Wulff 2001, 2012, 2016, Bell 2008), impel understanding of the relative influence of spongivores vs. other agents on sponge distribution, abundance, and diversity.

Elegant experiments that for many years have characterized studies of marine herbivores with algae (Lewis 1985, Hay 1992, van Alstyne 2001, Rasher et al. 2013, Shantz et al. 2020) and insects with plants (Root 1973, Coley 1983, Berenbaum et al. 1989, Bhattarai et al. 2017) are difficult to apply to sponges and their predators, neither of which thrive in captivity. Dense, continuously grazing populations of herbivores facilitate field observation, but vertebrate spongivores (e.g., angel-fishes, trunkfishes, and hawksbill turtles) feed sporadically and are less abundant. High species diversity of sponges (typically 100–300 species in a local area, accessible from a field station or research vessel anchorage, in the tropical western Atlantic: e.g., Reed and Pomponi

1997, Lehnert and Fischer 1999, Zea 2001) imposes a need for expertise in quick and accurate field identification in order to record prey choices. These challenges have resulted in reliance on proxies for evaluating palatability, in particular lab assays in which a sponge species is declared “palatable” if more than 6 of 10 extract/feeding-attractant pellets are consumed by a non-sponge-feeding omnivore (Pawlik et al. 1995, review in Paul and Puglisi 2004). Apparent ease of analysis when sponge species are simply dichotomized into “palatable” vs. “deterrent” has popularized these assays in spite of the untested underlying assumptions that sponge defenses do not target particular predators, defenses are entirely chemical, and defensive chemistry is not altered by handling, extraction, lyophilization, and hardening. Previous field studies of living sponges show that different spongivores consume different sets of sponge species (e.g., Wulff [1995] for starfish; Randall and Hartman [1968], Hourigan et al. [1989], Wulff [1994] for angel-fishes and trunkfishes; Meylan [1988, 1990], van Dam and Diez [1997], Leon and Bjørndal [2002] for hawksbill turtles; and Dunlap and Pawlik [1996], Wulff [1997a] for parrotfishes), but these studies have not been integrated, and they cover a limited number of species. A comprehensive data set of exactly which predators eat which sponges would provide a solid base for future studies focused on evolution of sponge defenses and their circumvention by spongivores, and would straight away allow clear-cut analyses of how sponge defenses influence community organization and ecosystem function.

Consumption of 94 of the most common and ubiquitous tropical western Atlantic sponge species was evaluated by experimental manipulations in the field. To distinguish influences of clade membership vs. habitat context and ecological characteristics, sponge species were chosen to represent 13 taxonomic orders of sponges and three distinct but adjacent habitats: mangroves, seagrass meadows, and coral reefs (exposed surfaces and cryptic spaces within the reef frame). Seven predator species, representing three teleost families and one asteroid family, were chosen to represent these habitats as well as a range of sponge consumption, from sponge specialists that routinely eat sponges, to a microphagous feeder and herbivores that only consume sponges opportunistically. The data address hypotheses relating to controls on distribution and abundance of sponge species, top-down effects on community organization and diversity, evolution of sponge defenses, and predator circumvention of those defenses to answer the following questions: (1) Do sponge defenses specifically target particular predators, or are they effective against predators in general? (2) What are the phylogenetic patterns of effective defenses and defense circumvention; i.e., are these traits evolutionarily constrained or relatively labile? Do related predators consume the same sponge species? Are related sponge species defended against the same spongivores? (3) Does routine sponge consumption differ from opportunistic sponge

consumption with respect to community and ecosystem consequences? (4) Can quick and easy lab assays with omnivores and extract/feeding-attractant pellets serve as an accurate proxy for time-consuming field experiments with spongivores and living sponges? (5) How do comprehensive data on sponge species eaten or avoided by different spongivores alter predictions underlying management, conservation, and restoration strategies for mangroves, seagrass meadows, and coral reefs? (6) And ultimately, what are the consequences of targeted sponge defenses for community organization and ecosystem function?

METHODS

Field sites

Field experiments were conducted at three Caribbean sites: in Belize (Twin Cayes mangrove caye, and shallow reefs in the Blue Ground Range and near the Smithsonian Institution field station on Carrie Bow Caye, map in Rützler et al. [2000]), in Guna Yala, Panama (Guigalutupo and Ulag Sukun, both near San Blas Point, map

in Wulff [1995]), and in Bocas del Toro, Panama (near the Smithsonian Tropical Research Institute station on Isla Colón). At each site, adjacent shallow coral reefs, seagrass meadows, and mangroves facilitated transfer of living sponges among habitats, allowing presentation to unmanipulated predators, in the field, of sponge species that are not normally available to them, as well as direct observations of feeding on co-occurring sponge species.

Sponge species

All experiments were done with healthy living sponges that were never removed from the water. Sponge species were chosen to represent a variety of higher taxa (Fig. 1; 13 of the extant orders of the Class Demospongiae recognized in Morrow and Cárdenas [2015]), and three distinct but interdependent ecosystems: coral reefs (exposed surfaces and cryptic spaces within the reef frame), seagrass meadows/rubble flats, and mangrove roots. A total of 94 sponge species, of diverse growth forms, associations with symbionts, and life histories were used in the feeding choice experiments. In some cases, species tested in previously published work were

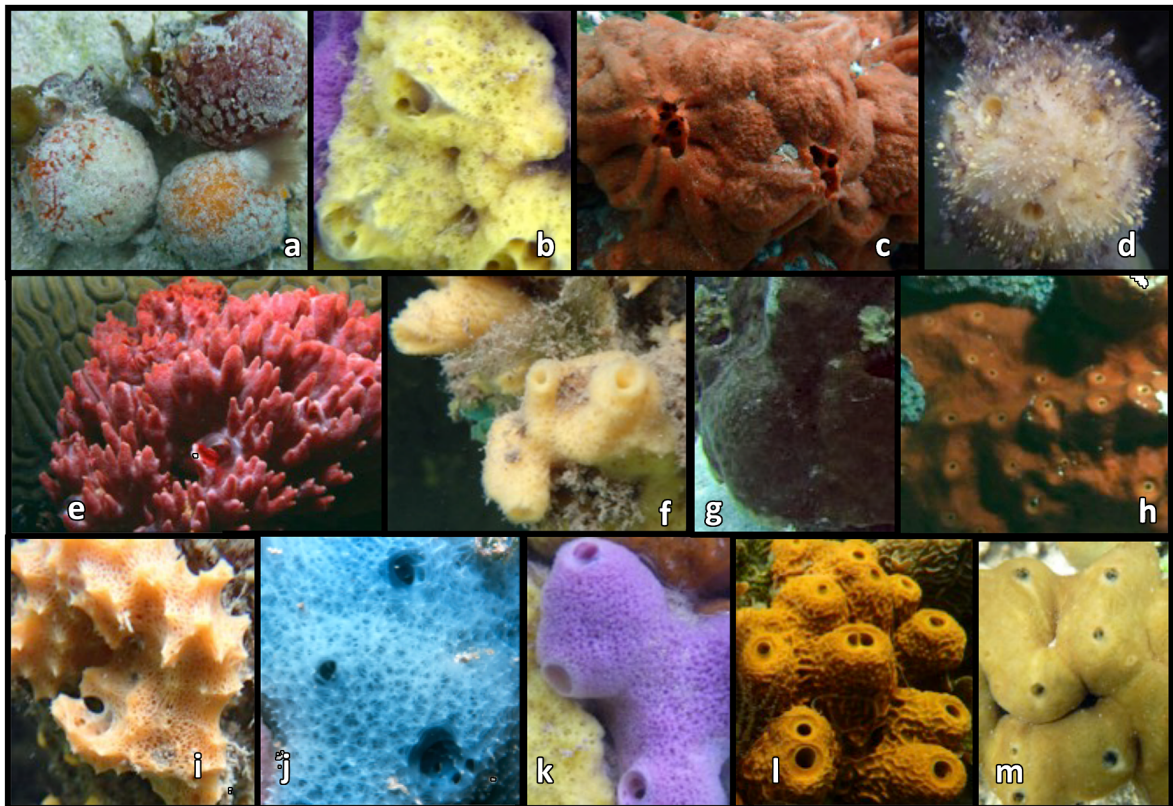


FIG. 1. A representative of each of the 13 Orders of Demospongiae included in experiments. (a) *Tethya actinia*, O. Tethyida; (b) *Halichondria magniconulosa*, O. Suberitida; (c) *Spirastrella hartmani*, O. Clionaida; (d) *Cinachyrella alloclada*, O. Tetractinellida; (e) *Monanchora arbuscula*, O. Poecilosclerida; (f) *Biemna caribea*, O. Biemnida; (g) *Agelas dispar*, O. Agelasida; (h) *Ectyoplasia ferax*, O. Axinellida; (i) *Scopalina ruetzleri*, O. Scopalinida; (j) *Dysidea etheria*, O. Dictyoceratida; (k) *Haliclona implexiformis*, O. Haplosclerida; (l) *Verongula rigida*, O. Verongiida; (m) *Chondrilla caribensis*, O. Chondrillida.

re-tested, to check consistency of results in different contexts and at different field sites. The constraint of using only healthy living sponges, and observing predators in the field, as well as making daily returns to the sites, meant that not all combinations of sponge and predator species could be tested.

Predator species

Sponge-feeding predators included in this study represent coral reefs, mangroves, and seagrass meadows, and several styles and levels of sponge eating. On Caribbean coral reefs, angelfishes of the genus *Pomacanthus* focus their feeding on sponges. Gut content analysis by Randall and Hartman (1968) revealed 70.2% and 74.8% sponges by volume for Gray angelfish, *P. arcuatus* (Linnaeus 1758) and French angelfish, *P. paru* (Bloch 1787); and those fishes were observed in the field to take 89.7% and 71.2% of their total number of bites from sponges (Wulff 1994). Caribbean *Pomacanthus* spp. consume a large proportion of the sponge species available to various extents (Randall and Hartman 1968, Hourigan et al. 1989, Wulff 1994). In this study, groups of mixed *P. arcuatus* and *P. paru*, or solely *P. arcuatus*, were studied on shallow reefs in Belize and Panama.

Trunkfishes feed on sponges to a lesser degree, and Randall and Hartman (1968) found only 6–30% sponge material in trunkfish gut contents, although most of the bites observed by Wulff (1994) in the field were on sponges. No other previous reports of trunkfish spongivory have been published. In this study, experiments and observations of sponge-feeding focused on two members of the family Ostraciidae, the scrawled trunkfish, *Acanthostracion quadricornis* (Linnaeus 1758), in seagrass meadows, and the spotted trunkfish, *Lactophrys bicaudalis* (Linnaeus 1758), among mangrove roots.

A few species of herbivorous parrotfishes typical of coral reefs opportunistically consume a handful of sponge species that they do not normally encounter because the sponges inhabit mangrove prop roots or cryptic spaces within the reef frame (Wulff 1988, 1997a, Dunlap and Pawlik 1996, 1998, Pawlik 1998, Wulff 2005). *Sparisoma aurofrenatum* (Valenciennes 1840) and *S. viride* (Bonnaterre 1788) were the species most often attracted to feed on sponges in this study. Another opportunistic sponge predator, the large Caribbean starfish, *Oreaster reticulatus* (Linnaeus 1758), inhabits seagrass meadows and is an omnivore that normally consumes microalgae in sediment (Scheibling 1980, 1981, 1982), but consumes sponges readily if it encounters species that lack defenses against it (Scheibling 1979, Wulff 1995, 2000, 2008, 2017).

Some species of known vertebrate spongivores were not included. Hawksbill turtle diets have been well characterized at several locations, and studies are in agreement on the few sponge species that they consume regularly (Meylan 1988, 1990, van Dam and Diez 1997,

Leon and Bjorndal 2002). Hawksbills were not observed at any of the sites in this study, nor was evidence of their feeding (which is readily identified, e.g., van Dam and Diez 1997) observed. Spadefish were only encountered at a site that was too distant for daily checks on experiments. The tiny sharpnose puffer, *Canthigaster rostrata*, feeds on sponges less (only 15% sponge in gut contents; Randall and Hartman 1968), and as it was never encountered at sites lacking angelfishes, distinguishing their feeding when observers were absent was not possible. Queen angelfish, *Holocanthus ciliaris*, and rock beauties, *H. tricolor*, were never found at sites that lacked *Pomacanthus* angelfish species, impeding distinction of their feeding during times when observers were not on the reef, and they were much less abundant in general.

General procedures

In each of the three main habitats (coral reef, mangroves, and seagrass meadows), sponge species typical of all three habitats were made available (via reciprocal transplant experiments) to potential predators in situations that were as natural as possible. Sponges were cut to a uniform size (7–12 cm³ for most species) and cut surfaces were allowed to heal for several days in the field (protected inside cages) before they were used in experiments, ensuring that exposure to potential predators was maximally realistic. From previous work (Wulff 1995, 1997a) it was known that consumption or rejection in experiments does not depend on what other species are available simultaneously, and so the assortment of five sponge species used in each trial was determined randomly from those available. Species were removed from the pool after sufficient trials, and a total of 4,493 trials were completed. The large amount of underwater time required, caused by limits on how many sponge and predator individuals can be accurately observed simultaneously, imposed a lengthy data accumulation period: 20 yr, from January 1998 to May 2018. Previously collected data on natural foraging of angelfishes, trunkfishes, and parrotfishes on a reef in Guna Yala, Panama (Wulff 1994, 1997a) and Pacific pufferfish consumption of Caribbean sponges (Wulff 1997b) were reanalyzed for explicit comparison with these experimental data.

Seagrass-dwelling starfish

Individual *Oreaster reticulatus*, with radius at least 10 cm, were enclosed for 24 h in cages of 32 × 42 cm, height 16 cm (meshes 5 × 7 cm allowed free flow of water) that were anchored in seagrass meadows, the normal habitat of the starfish. For each trial, the cage was stocked with five sponge pieces, each of a different species, attached to the cage base with small cable ties. From previous experiments, it was known that *Oreaster* are capable of entirely consuming all five sponge pieces in 24 h, if all are palatable to it (Wulff 1995). Between 6

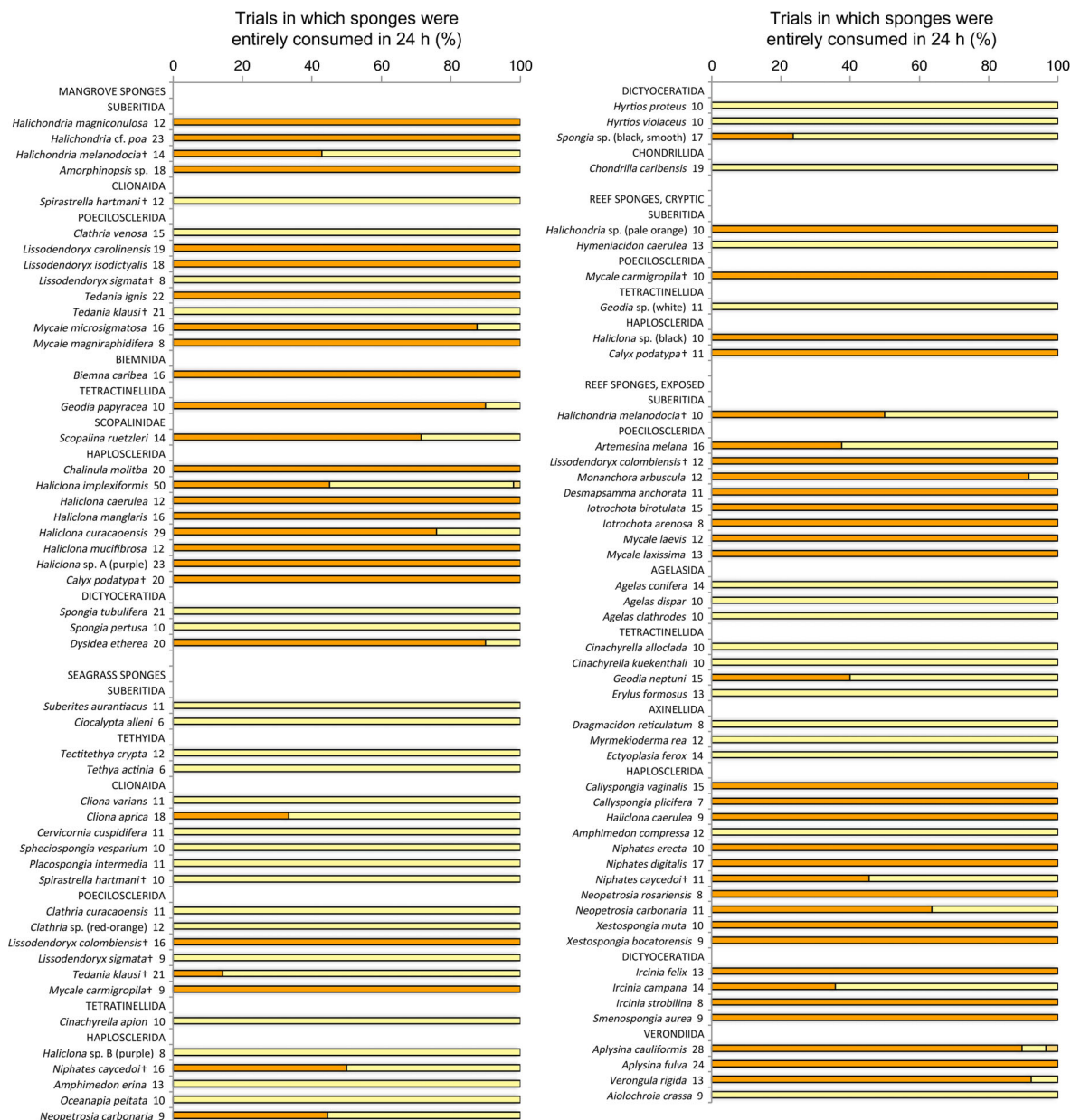


FIG. 2. Percentage of trials in which sponges were entirely consumed in 24 h (dark orange), consistently rejected (pale yellow), or intermediately (light orange). The species are grouped by taxonomic order within groupings by habitat. Number of trials with each species is given after the species name. In the field (seagrass meadows), individual large starfish, *Oreaster reticulatus*, were enclosed for 24 h in cages with small pieces of five different sponge species affixed to the bottom. Most of the 89 sponge species were only found in only one habitat; the eight that were found in more than one habitat are marked with †.

and 50 trials were run with each of 27 typical mangrove-dwelling sponge species, 26 seagrass species, and 44 coral reef species, for a total of 89 species (numbers of species in the three habitats add to 97 because eight species were collected from more than one habitat). All species names, habitats in which they were collected, and numbers of trials are given in Fig. 2. Authors of all species are provided in Fig. 8.

Reef-dwelling angelfishes and parrotfishes

For experiments with coral reef-dwelling angelfishes, sponges were presented on inconspicuous and stable natural substrata. Each sponge was attached with narrow (1–2 mm in diameter) clear cable ties to a piece of coral rubble bound to a Tygon tubing-covered stainless steel stake that was inserted into the reef. Between 6 and 34

trials were run for each of 27 sponge species typical of mangroves, 24 species typical of seagrass, and 47 species typical of coral reefs, for a total of 90 species (numbers of species from the three habitats add to 98 because eight species were collected in more than one habitat). Five sponges, each of a different species, were presented in each trial, as this was the maximum number for which observers could keep clear track of, and record, every bite. All species names, habitats in which they were collected, and sample sizes are given in Fig. 3; and authors of all species are in Fig. 8. One reef species, *Mycale laevis*, was presented with its surface intact, as well as sliced off to expose the inner tissue, because this had influenced parrotfish responses in previous experiments (Wulff 1997a). Feeding was observed continuously for the first hour, and sponges remaining were then checked at 24-h intervals. The same procedure was followed for presenting sponges to parrotfishes, but sites were chosen that lacked angelfishes. At sites with both angelfishes and parrotfishes, the sponge consumption of each was readily distinguished during the first hour, when observations were continuous. A total of 90 sponge species were used in parrotfish trials (Fig. 8).

Bites were only recorded when the observer could clearly see the bite wound on the sponge and it was clear that the fish had swallowed the bite. To avoid spurious records of palatability caused by the typical behavior of fishes testing novel sponges by biting them on their initial encounter (Fig. 9h, Wulff 2017), data from the first two experimental presentations of each species at each site during each field trip were excluded from the data compilations.

Mangrove-dwelling trunkfish, seagrass-dwelling trunkfish

Trunkfish tend to be relatively rare, requiring different approaches to acquiring adequate data on their sponge-feeding. This study combined transplants of common sponge species between habitats with careful daily inspection of both transplanted and resident sponges for recent (not yet healed) bite marks that were unambiguously made by trunkfishes (easily recognized rectangular bites, 4 × 8 mm to 5 × 9 mm, Fig. 9e). Twelve to 16 individuals of each of 13 common coral reef species and 6 common seagrass meadow species were made available to mangrove-dwelling trunkfish, *L. bicaudalis*, by attaching them to prop roots and to CPVC pipes (30.5 cm long) suspended among the prop roots lining the main channel in Twin Cays, Belize. These 19 sponge species from other habitats augmented the natural mangrove root fauna of 42 sponge species (Sponge Haven list in Rützler et al. [2000]). Transplanted reef and seagrass sponges were inspected on 10 consecutive days during each of five field trips (i.e., 50 d), and all of the many hundreds of mangrove sponges in a 10 m long stretch of mangrove roots where the transplants were attached were inspected for bite marks. Direct observations of feeding trunkfish were always confirmed by checking

that a bite was actually removed from the sponge and swallowed. Published data on abundance (volume and number of individuals) of the resident mangrove sponge species (Wulff 2009) were used to compare bite rates to relative prey abundance (i.e., electivity).

In seagrass meadows, surveys for trunkfish bite marks were made on all sponges within 1 m on each side of six transects, each 7 m long, on five days during each of five field trips (i.e., 25 surveys of 84 m² each). In order to compare bite rates on different sponge species with relative abundance of those species (i.e., electivity), all sponges within the six transects, as well as an additional six transects (i.e., a total of 168 m²) were identified to species and their volume measured. Mangrove-dwelling sponges of 10 of the most common species were made available to seagrass-dwelling trunkfish, *A. quadricornis*, by attaching pieces of 12–30 cm³ ($n = 10$ for each species) with cut surfaces healed, to stakes that were stabilized in the sediment and protected from *Oreaster* grazing by a barrier of seagrass meadow sponge species that had been previously determined to deter *Oreaster* feeding (Wulff 1995, 2008).

RESULTS

Starfish spongivory

Seagrass-inhabiting starfish, *Oreaster reticulatus*, consistently rejected 80.8% (21/26) of the seagrass/rubble bed sponge species that coexist with the starfish, but rejected only 22.2% (6/27) of sponge species from the mangroves and 29.5% (13/44) from the coral reefs that are normally inaccessible to the starfish (Figs. 2, 4). The proportion of sponges deemed palatable by *Oreaster* differed significantly among the three habitats (G test, $P < 0.001$). Results for all species were consistent among trials, not varying from site to site or with other species that were offered simultaneously; and for the eight species collected in more than one habitat the results were consistent regardless of habitat. Most (78/88) species were either consistently consumed or consistently rejected, but 10 species were consumed in less than a significant majority of trials, or were partially consumed (Figs. 2, 8). For the three of these species that were collected from two habitats, this intermediate result was consistent across habitats. Only two sponge species typical of the seagrass meadows inhabited by *Oreaster* were consistently consumed: one of them (*Mycale carmi-gropila*) persists in seagrass by living tucked within piles of coral rubble or mollusc shells, and the other (*Lissodendoryx colombiensis*) is protected by being overgrown or surrounded by sponge species that are rejected by *Oreaster* (Wulff 2008).

Angelfish spongivory

Angelfishes in the genus *Pomacanthus* distinguished sponge species by degrees of acceptability ranging from

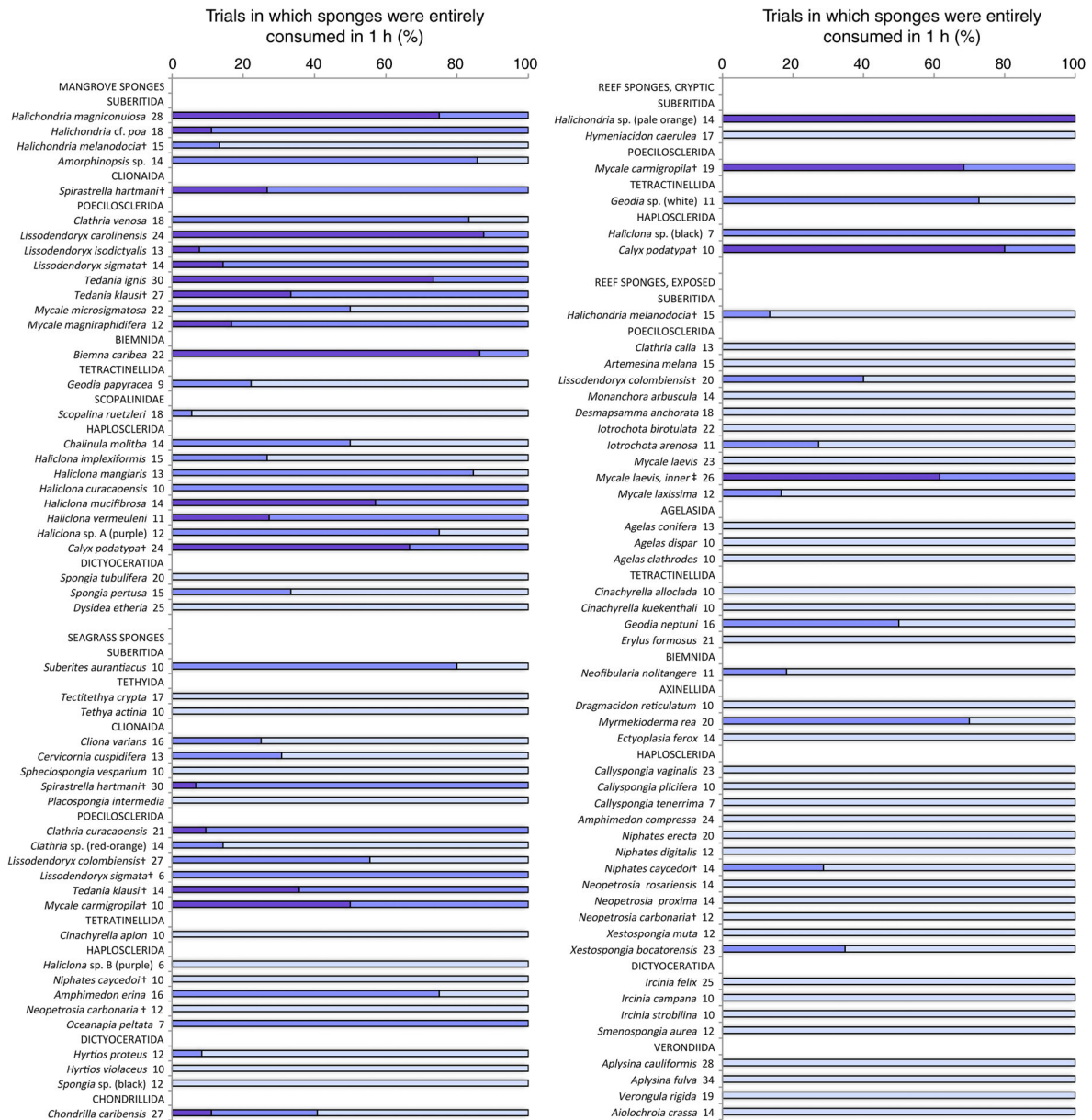


Fig. 3. Percentage of trials in which sponges were entirely consumed in 1 h (dark purple), 24 h (medium purple), or consistently rejected (pale lavender) by angelfishes, *Pomacanthus arcuatus* and *P. paru*. The species are grouped by taxonomic order within groupings by habitat. Number of trials with each species is given after the species name. In the field (coral reefs), sponges were made available to naturally foraging angelfishes by attaching them to coral rubble on stakes that were inserted into the reef. Most of the 90 sponge species were only found in only one habitat; the eight that were found in more than one habitat are marked with †. One species, *Mycale laevis*, marked ‡, was presented with its surface intact, and also with its surface cut off.

“always consumed within 10 minutes” to “never consumed for many years after the experiments were set up” (Figs. 3, 5). Data for congeners *P. paru* and *P. arcuatus* were combined on field data sheets after the first few years of the study because their behavior was not distinguishable when they fed in a mixed group. They ate and rejected the same sponge species, and they both chased conspecific and heterospecific angelfishes away from

especially desirable sponges with equal vigor. Feeding of these *Pomacanthus* spp. was also indistinguishable during a previous 12 yr study of their unmanipulated feeding (Wulff 1994).

Within 24 h, angelfishes consistently ate 63% (17/27) of the mangrove species, and 29.2% (7/24) of the seagrass meadow species, but only 12.8% (6/47) of the coral reef species (Fig. 5). Proportions of species typical of these

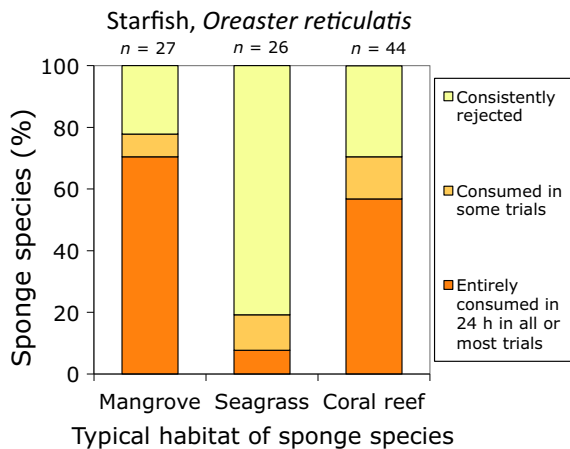


FIG. 4. Percentage of sponge species for which entire pieces were consumed or not by the large starfish *Oreaster reticulatis* when presented five species at a time attached to the bottom of in situ cages in which starfish were confined for 24 h. The proportion of sponges that were consistently rejected is significantly different in the three habitats (G test, $P < 0.001$).

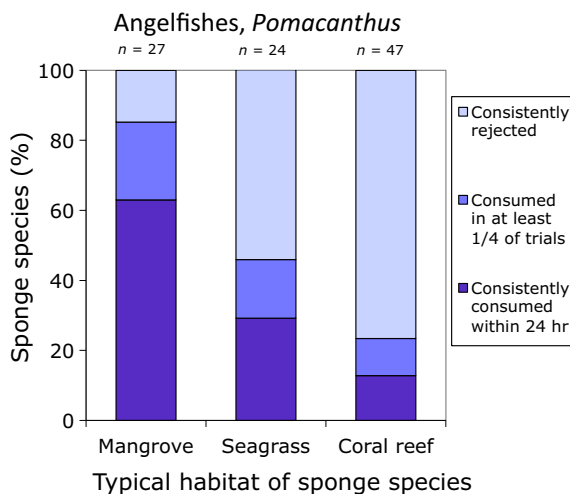


FIG. 5. Percentage of sponge species for which entire pieces were consumed or not by the angelfishes *Pomacanthus paru* and *P. arcuatus*, when presented four to six species at a time attached to coral rubble stabilized by stainless steel stakes covered by tygon tubing. The proportion of sponge species that were consistently rejected is significantly different in the three habitats (G test, $P < 0.05$).

three habitats that angelfishes ate differed significantly (G test, $P < 0.05$). Of the six reef species consumed within 24 h, five live entirely enclosed in cryptic spaces within the reef frame (Figs. 3, 8). The sole non-cryptic reef species consumed, *Myrmekioderma rea*, tends to be semi-cryptic and the surface obscured by fouling so that it is not readily available for grazing. Another semi-cryptic reef species, *Mycale laevis*, was consumed within 24 h when its surface was sliced off (Fig. 9a, b), but not when the surface was intact. *Chondrilla caribensis* (Fig. 1m),

collected in the seagrass, was often missing from its stake after 24 h, but some of the missing sponges were found rolling loose on the bottom with just one or two bites taken, and this species was entirely consumed in fewer than one-half of the trials. Angelfishes were observed attempting unsuccessfully to bite *Chondrilla*, which has a slippery surface and firm texture. One mangrove species, *Biemna caribea* (Fig. 1f), was consumed quickly and steadily until it was gone within 10 minutes in most trials, but all other sponge species were consumed in a rotating pattern during at least the first hour, when observations were continuous: an individual fish was never observed to consume more than six bites from a particular sponge before moving away altogether or switching to feed on a sponge of a different species.

Experimental results could be compared with data from field observations of unmanipulated angelfishes feeding at a site where every sponge was mapped, identified to species, and its volume measured (Wulff 1994). These data were originally published as ranks, but the raw data are here re-analyzed as an additional check on feeding habits and preferences. Bites were only recorded if the bite mark could be seen on the sponge, and the fish was seen to swallow the bite. Data from *P. paru* and *P. arcuatus* were combined because their sponge feeding was indistinguishable. Ivlev's Index of Electivity (see Lorders et al. [2018] for a sponge example) was calculated for each sponge species from the percent of the total bites taken by *Pomacanthus* spp. on that species, and the percent represented by that species of the total sponge volume in the area in which feeding was observed (mean of two census periods spanning four years during the feeding data accumulation period; Wulff 2006a). Volume was chosen as the appropriate metric for sponge availability because nutrition gained by a predator scales with sponge volume rather than numbers of individuals or percent cover. Interpretation of electivity indices must be informed by detailed understanding of foraging behaviors for each predator. Of particular importance is that purposeful dietary diversification, i.e., "smorgasbord feeding," results in rarer species being eaten more frequently than predicted by their relative abundance (Table 3 in Wulff 1994). Thus positive electivity indices of rare species do not necessarily indicate that they are more "palatable" to angelfishes, but simply confirm purposeful dietary diversification. For this reason, positive electivity indices were only considered indicative of angelfish preference for sponge species represented by at least 0.5% of the total volume, i.e., *Spirastrella hartmani*, *Lissodendoryx colombiensis*, *Iotrochota birotulata*, *Niphates erecta*, *Xestospongia proxima*, *Xestospongia bocatorensis*, and *Verongula rigida*.

Parrotfish spongivory

The reef-inhabiting parrotfishes, *Sparisoma aurofrenatum* and *S. viride*, consumed only 3/25 of the mangrove species offered, and took no bites from any of the 22

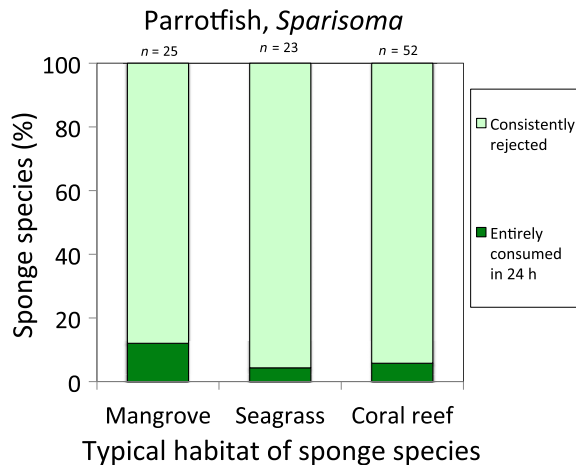


FIG. 6. Percentage of sponge species for which entire pieces were consumed or not by the parrotfishes *Sparisoma aurofrenatum* and *S. viride*, when presented four to six species at a time, attached to coral rubble stabilized by stainless steel stakes covered by tygon tubing. All of the seagrass meadow and coral reef sponges that were consumed inhabit protected microhabitats of cryptic spaces within the reef frame or mutualistic associations.

seagrass species and 46 reef species that live on exposed surfaces (Fig. 6). Of the species that live tucked into cryptic spaces within the reef frame, parrotfishes quickly and completely consumed two, as well as another species that lives in cryptic spaces both on the reef and in seagrass. When any of these three mangrove species and three cryptic reef or seagrass species were made available, the parrotfishes continued to take bites until the sponges were gone, vigorously chasing away heterospecific and conspecific *Sparisoma* spp. equally. But parrotfishes did not consume 84 of the 90 sponge species offered at all, either in experiments or during observations of natural feeding. There was one exception: although they ignored

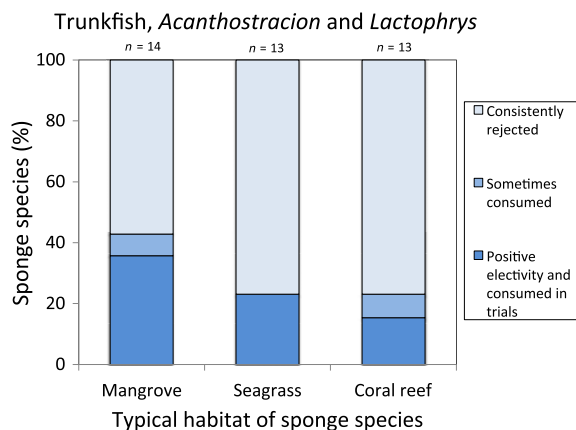


FIG. 7. Percentage of sponge species consistently rejected, sometimes consumed, or with positive electivity and consumed in experiments by the trunkfishes *Lactophrys bicaudalis* and *Acanthostracion quadricornis*. Proportion of sponge species that were consistently rejected did not differ significantly (G test, $P > 0.1$) among habitats.

the semi-cryptic reef species *Mycale laevis* when its surface was intact, they readily consumed the pale grey inner tissue exposed by slicing off part of the surface. Even then they did not eat the orange surface, leaving it behind like the discarded rind of an orange (Fig. 9a, b).

Trunkfish spongivory

This is the first report of sponge feeding in the field by the spotted trunkfish, *Lactophrys bicaudalis*, so behavioral details are provided. Individual *L. bicaudalis* patrolled a long strip of mangrove-lined coastline, and were occasionally observed where reef and seagrass sponges had been transplanted to the mangroves. During each of five 10-d observation periods, they fed very selectively (Table 1). Spotted trunkfish were observed to take bites from, or recent (preceding 24 h; Wulff 2010) trunkfish bite scars were seen on, 6 of the 42 sponge species recorded as residents on the mangrove roots by Rützler et al. (2000). Volume measurements were made of all sponges at this site in the course of time-series censuses (Wulff 2009), allowing calculation of electivity. Ivlev's Index of Electivity demonstrated positive electivity of five of these species: *Halichondria magniconulosa*, *Lissodendoryx isodictyalis*, *Mycale magniraphidifera*, *Bienna caribea* (Fig. 1f), *Haliclona implexiformis* (Fig. 1k), and *H. curacaoensis* (Table 1, summary Fig. 8). No trunkfish feeding was observed on the mangrove sponge species that were most abundant (Wulff 2009) by total volume (*Tedania ignis*) or number of individuals (*Haliclona manglaris*).

Of the 19 sponge species transplanted to the mangroves from the reef and seagrass, spotted trunkfish fed most on two reef species, *Aplysina fulva* and *A. cauliformis* (respectively 48% and 44% of the 109 bites observed on reef sponges), and to a much lesser extent on the reef species *Verongula rigida* (8%; Figs. 11, 9d) and the seagrass species *Clathria curacaoensis* (Fig. 9e) and *Amphimedon erina* (46% and 54% of 16 bites observed on seagrass sponges). The trunkfish concentrated their feeding only on some individuals of *A. fulva* and *A. cauliformis* (5/12 and 5/13 individuals, respectively), and every time the trunkfish returned they fed on these same *Aplysina* individuals, avoiding the others. The consistency with which the spotted trunkfish avoided most (i.e., 14/19) of the reef and seagrass species transplanted to the mangroves (Table 1, Fig. 8) was striking because representatives of all transplanted species were within a few m of each other at many places. For example, branches of one *A. fulva* individual, from which trunkfish took a few bites each day for 5 d, grew adjacent to a *Callyspongia vaginalis* individual, from which no bites were taken; and many bites were taken from *Aplysina* spp. individuals that were surrounded by large mangrove sponges, such as *T. ignis*, from which no bites were taken (Fig. 9g).

Scrawled trunkfish, *Acanthostracion quadricornis*, in the seagrass meadow took bites from, but did not





| SPONGE SPECIES: | | SPONGIVORES: | | | |
|---|-------|---|--|---|---|
| | |  |  |  |  |
| SUBERITIDA | | | | | |
| <i>Suberites aurantiacus</i> (Duchassaing & Michelotti) | S | | | | |
| <i>Halichondria magniconulosa</i> Hechtel | M | | | | |
| <i>Halichondria melanodocia</i> de Laubenfels | M,R | | | | |
| <i>Halichondria</i> cf. <i>poa</i> (de Laubenfels) | M | | | | |
| <i>Halichondria</i> sp. A (yellow) | RC | | | | |
| <i>Ciocalypta alleni</i> de Laubenfels | S | | | | |
| <i>Amorphinopsis</i> sp. | M | | | | |
| <i>Hymeniacidon caerulea</i> Pulitzer-Finali | RC | | | | |
| TETHYIDA | | | | | |
| <i>Tectitethya crypta</i> (de Laubenfels) | S | | | | |
| <i>Tethya actinia</i> de Laubenfels | S | | | | |
| CLIONAIDA | | | | | |
| <i>Cliona varians</i> (Duchassaing & Michelotti) | S | | | | |
| <i>Cliona delitrix</i> Pang | R | | | | |
| <i>Cervicornia cuspidifera</i> Rützler & Hooper | S | | | | |
| <i>Spheciospongia vesparium</i> (Lamarck) | S | | | | |
| <i>Placospongia intermedia</i> Sollas | S | | | | |
| <i>Spirastrella hartmani</i> Boury Esnault, et al. | M,S,R | | | | |
| POECILOSCLERIDA | | | | | |
| <i>Clathria venosa</i> (Alcolado) | M | | | | |
| <i>Clathria curacaoensis</i> Arndt | S | | | | |
| <i>Clathria</i> sp. A (red-orange) | S | | | | |
| <i>Clathria calla</i> (de Laubenfels) | R | | | | |
| <i>Artemesina melana</i> van Soest | R | | | | |
| <i>Lissodendoryx isodictyalis</i> (Carter) | M | | | | |
| <i>Lissodendoryx carolinensis</i> Wilson | M | | | | |
| <i>Lissodendoryx sigmata</i> (de Laubenfels) | M,S | | | | |
| <i>Lissodendoryx colombiensis</i> Zea & van Soest | S,R | | | | |
| <i>Monanchora arbuscula</i> (Duchassaing & Michelotti) | R | | | | |
| <i>Desmapsamma anchorata</i> (Carter) | R | | | | |
| <i>Iotrochota birotulata</i> (Higgin) | R | | | | |
| <i>Iotrochota arenosa</i> Rützler et al. | R | | | | |
| <i>Tedania ignis</i> (Duchassaing & Michelotti) | M | | | | |
| <i>Tedania klausii</i> Wulff | M,S | | | | |
| <i>Mycale laevis</i> (Carter) | R | | | | |
| <i>Mycale microsigmatosa</i> Arndt | M | | | | |
| <i>Mycale magniraphidifera</i> van Soest | M | | | | |
| <i>Mycale carmigropila</i> Hajdu & Rützler | S,RC | | | | |
| <i>Mycale laxissima</i> (Duchassaing & Michelotti) | R | | | | |
| AGELASIDA | | | | | |
| <i>Agelas conifera</i> (Schmidt) | R | | | | |
| <i>Agelas dispar</i> Duchassaing & Michelotti | R | | | | |
| <i>Agelas clathrodes</i> (Schmidt) | R | | | | |
| TETRACTINELLIDA | | | | | |
| <i>Cinachyrella apion</i> (Uliczka) | S | | | | |
| <i>Cinachyrella alloclada</i> (Uliczka) | R | | | | |
| <i>Cinachyrella kuekenthali</i> (Uliczka) | R | | | | |
| <i>Geodia papyracea</i> Hechtel | M | | | | |
| <i>Geodia neptuni</i> (Sollas) | R | | | | |
| <i>Geodia</i> sp. A (white) | RC | | | | |
| <i>Erylus formosus</i> Sollas | R | | | | |

FIG. 8. Comparison of consumption, in the field, of 94 common sponge species by four predator taxa: (1) starfish *Oreaster reticulatus*, (2) angelfishes *Pomacanthus paru* and *P. arcuatus*, (3) trunkfishes *Lactophrys bicaudalis* and *Acanthostracion quadricornis*, and (4) parrotfishes *Sparisoma aurefrenatum* and *S. viride*. Experimental data presented in this paper are combined with extensive observations of natural feeding on sponges at sites where relative abundance (in terms of volume of live tissue) of all sponge species was also measured, allowing calculation of electivity indices. Only sponge species for which data were collected for at least two predator taxa are included in this table. Typical habitat of each species is indicated by R, coral reef; RC, cryptic spaces in coral reef; S, seagrass meadows; M, mangroves. Deep blue = consumed within 24 h in a statistically significant majority of trials (for *Oreaster* >80% of trials); light blue = consumed in at least 25% of trials and/or positive electivity (Ivlev's index) of sponge species constituting at least 0.5% of the total volume in their natural community; lavender = at least 5% of bites observed by unmanipulated predators in natural sponge communities in the field; carmine = rejected in at least 75% of experimental trials and/or no observations of natural feeding in communities in which the sponge species ranked in the top 50% of species with respect to total volume (i.e., lack of feeding observations was not due to low abundance); dusky rose, a single species (*Mycale laevis*) was only consumed by fish when its surface was sliced off; gray = predator and prey species were not sufficiently abundant at the same time and place to collect enough data.





| SPONGE SPECIES: | SPONGIVORES: | | | |
|--|---|---|---|---|
| |  |  |  |  |
| BIEMNIDA | | | | |
| <i>Biemna caribea</i> Pulitzer-Finali M | Blue | Blue | Blue | Red |
| <i>Neofibularia nolitangere</i> (Duch. & Michelotti) R | Grey | Red | Grey | Red |
| AXINELLIDA | | | | |
| <i>Dragmacidon reticulatum</i> (Ridley & Dendy) R | Red | Red | Grey | Red |
| <i>Myrmekioderma rea</i> (de Laubenfels) R | Red | Blue | Grey | Red |
| <i>Ectyoplasia ferox</i> (Duchassaing & Michelotti) R | Red | Red | Red | Red |
| SCOPALINIDA | | | | |
| <i>Scopalina ruetzleri</i> (Wiedenmayer) M | Blue | Red | Red | Red |
| HAPLOSCLERIDA | | | | |
| <i>Callyspongia vaginalis</i> (Lamarck) R | Blue | Red | Purple | Red |
| <i>Callyspongia tenerrima</i> (Duchassaing & Michelotti) R | Grey | Red | Grey | Red |
| <i>Callyspongia plicifera</i> (Lamarck) R | Blue | Red | Grey | Red |
| <i>Chalinula molitba</i> de Laubenfels M | Blue | Blue | Red | Red |
| <i>Haliclona implexiformis</i> (Hechtel) M | Blue | Red | Blue | Red |
| <i>Haliclona manglaris</i> Alcolado M | Blue | Blue | Red | Red |
| <i>Haliclona curacaoensis</i> (van Soest) M | Blue | Blue | Blue | Red |
| <i>Haliclona mucifibrosa</i> De Weerd, Rützler & Smith M | Blue | Red | Grey | Red |
| <i>Haliclona</i> sp. A (purple) M | Blue | Blue | Grey | Red |
| <i>Haliclona</i> sp. B (purple) S | Red | Red | Red | Red |
| <i>Haliclona caerulea</i> (Hechtel) R | Blue | Grey | Red | Red |
| <i>Haliclona vermeuleni</i> de Weerd M | Blue | Blue | Grey | Red |
| <i>Haliclona</i> sp. (black) RC | Blue | Red | Grey | Red |
| <i>Niphates erecta</i> Duchassaing & Michelotti R | Blue | Red | Purple | Red |
| <i>Niphates digitalis</i> (Lamarck) R | Blue | Red | Red | Red |
| <i>Niphates</i> sp. A (purple) R | Blue | Purple | Grey | Red |
| <i>Niphates caycedoi</i> (Zea & van Soest) S,R | Blue | Blue | Red | Red |
| <i>Amphimedon erina</i> (de Laubenfels) S | Red | Blue | Blue | Red |
| <i>Amphimedon compressa</i> Duchassaing & Michelotti R | Red | Purple | Purple | Red |
| <i>Calyx podatypa</i> (de Laubenfels) M,RC | Blue | Blue | Grey | Red |
| <i>Oceanapia peltata</i> (Schmidt) S | Red | Red | Grey | Red |
| <i>Neopetrosia carbonaria</i> (Lamarck) S,R | Blue | Purple | Grey | Red |
| <i>Neopetrosia rosariensis</i> (Zea & Rützler) R | Blue | Red | Red | Red |
| <i>Neopetrosia proxima</i> (Duchassaing & Michelotti) R | Grey | Blue | Red | Red |
| <i>Xestospongia muta</i> (Schmidt) R | Blue | Red | Grey | Red |
| <i>Xestospongia bocatorensis</i> Diaz et al. R | Blue | Blue | Red | Red |
| DICTYOCERATIDA | | | | |
| <i>Ircinia felix</i> (Duchassaing & Michelotti) R | Blue | Red | Red | Red |
| <i>Ircinia campana</i> (Lamarck) R | Blue | Red | Grey | Red |
| <i>Ircinia strobilina</i> (Lamarck) R | Blue | Red | Red | Red |
| <i>Ircinia</i> sp. A (brown) R | Grey | Purple | Purple | Red |
| <i>Hyrtios proteus</i> (Duchassaing & Michelotti) S | Red | Purple | Red | Red |
| <i>Hyrtios violaceus</i> (Duchassaing & Michelotti) S | Red | Grey | Red | Red |
| <i>Smenospongia aurea</i> (Hyatt) R | Blue | Red | Red | Red |
| <i>Spongia tubulifera</i> Hyatt M | Red | Red | Red | Red |
| <i>Spongia obscura</i> Hyatt M | Red | Blue | Red | Red |
| <i>Spongia</i> sp. (black, smooth) S | Red | Red | Grey | Red |
| <i>Dysidea etherea</i> de Laubenfels M | Blue | Purple | Grey | Red |
| VERONGIIDA | | | | |
| <i>Aplysina cauliformis</i> Carter R | Blue | Red | Blue | Red |
| <i>Aplysina fulva</i> (Pallas) R | Blue | Purple | Red | Red |
| <i>Verongula rigida</i> (Esper) R | Blue | Blue | Purple | Red |
| <i>Aiolochoxia crassa</i> (Hyatt) R | Red | Red | Grey | Red |
| CHONDRILLIDA | | | | |
| <i>Chondrilla caribensis</i> Rützler, Duran & Piantoni S | Red | Purple | Red | Red |
| TOTALS | 88 | 91 | 47 | 90 |

FIG. 8. Continued

TABLE 1. Consumption of sponges by the trunkfish species *Lactophrys bicaudalis* (in mangroves) and *Acanthostracion quadricornis* (in seagrass meadows) in the context of relative abundance of sponge species in mangrove, seagrass, and coral reef habitats.

| Species | Bites on sponges in the indicated habitat (%) | Sponge volume in the indicated habitat (%) | No. mangrove sponges bitten within 3 d of transplantation to a seagrass meadow | Bites on seagrass sponges transplanted to mangroves (%) | Bites on reef sponges transplanted to mangroves (%) |
|--|---|--|--|---|---|
| Mangrove sponges, <i>n</i> = 91 bites | | | | | |
| Suberitida | | | | | |
| <i>Halichondria magniconulosa</i> | 2.2 | 9.6 | 2/10 | | |
| <i>Halichondria cf. poa</i> | 0 | 5.1 | 0/10 | | |
| Poecilosclerida | | | | | |
| <i>Lissodendoryx isodictyalis</i> | 14.3 | 13.3 | 4/10 | | |
| <i>Tedania ignis</i> | 0 | 48.5 | 0/10 | | |
| <i>Tedania klausii</i> | 0 | 3 | 0/10 | | |
| <i>Mycale microsigmatosa</i> | 0 | 6.4 | | | |
| <i>Mycale magniraphidifera</i> | 44 | <0.01 | | | |
| Biemnida | | | | | |
| <i>Biemna caribea</i> | 4.4 | 2 | 8/10 | | |
| Haplosclerida | | | | | |
| <i>Haliclona implexiformis</i> | 9 | 0.7 | 2/10 | | |
| <i>Haliclona manglaris</i> | 0 | 0.1 | | | |
| <i>Haliclona curacaoensis</i> | 26.4 | 1 | 8/10 | | |
| <i>Haliclona</i> sp. A (purple) | 0 | 0.03 | | | |
| Dictyoceratida | | | | | |
| <i>Spongia tubulifera</i> | 0 | 5.1 | 0/10 | | |
| <i>Spongia obscura</i> | 0 | 5 | 0/10 | | |
| Seagrass sponges, <i>n</i> = 106 bites in seagrass, <i>n</i> = 16 bites in mangroves | | | | | |
| Suberitida | | | | | |
| <i>Suberites aurantiacus</i> | 0 | <1 | | | |
| Tethyida | | | | | |
| <i>Tectitethya crypta</i> | 0 | <1 | | | |
| Clionaida | | | | | |
| <i>Cliona varians</i> | 0 | 0.3 | | | |
| Poecilosclerida | | | | | |
| <i>Clathria curacaoensis</i> | 80.2 | 8.1 | | 46 | |
| <i>Clathria</i> sp. (red-orange) | 5.7 | 2.4 | | 0 | |
| <i>Lissodendoryx colombiensis</i> | 0 | 35.7 | | 0 | |
| <i>Lissodendoryx sigmata</i> | 0 | 0.5 | | | |
| <i>Tedania klausii</i> | 0 | 16.2 | | 0 | |
| Haplosclerida | | | | | |
| <i>Amphimedon erina</i> | 14.2 | 3 | | 54 | |
| <i>Calyx podatypa</i> | 0 | 2.1 | | | |
| Dictyoceratida | | | | | |
| <i>Hyrtios proteus</i> | 0 | 13.9 | | 0 | |
| <i>Spongia</i> sp. (black) | 0 | 0.1 | | | |
| Chondrillida | | | | | |
| <i>Chondrilla caribensis</i> | 0 | 17.7 | | | |
| Reef sponges, <i>n</i> = 2,356 bites on reef, <i>n</i> = 109 bites in mangroves | | | | | |
| Poecilosclerida | | | | | |
| <i>Desmapsamma anchorata</i> | 0 | 0.4 | | | 0 |
| <i>Iotrochota birotulata</i> | 5.8 | 33 | | | 0 |
| <i>Mycale laevis</i> | 1.4 | 6.7 | | | 0 |
| Tetractinellida | | | | | |
| <i>Erylus formosus</i> | | | | | 0 |

TABLE 1. Continued.

| Species | Bites on sponges in the indicated habitat (%) | Sponge volume in the indicated habitat (%) | No. mangrove sponges bitten within 3 d of transplantation to a seagrass meadow | Bites on seagrass sponges transplanted to mangroves (%) | Bites on reef sponges transplanted to mangroves (%) |
|-------------------------------|---|--|--|---|---|
| Axinellida | | | | | |
| <i>Ectyoplasia ferox</i> | | | | | 0 |
| Haplosclerida | | | | | |
| <i>Callyspongia vaginalis</i> | 0.1 | 1.6 | | | 0 |
| <i>Amphimedon compressa</i> | 1.7 | 18.4 | | | 0 |
| <i>Niphates erecta</i> | 0.3 | 3.1 | | | 0 |
| <i>Niphates digitalis</i> | | | | | 0 |
| Dictyoceratida | | | | | |
| <i>Ircinia felix</i> | 1.1 | 1.9 | | | 0 |
| Verongiida | | | | | |
| <i>Aplysina cauliformis</i> | | | | | 48 |
| <i>Aplysina fulva</i> | 86 | 17.3 | | | 44 |
| <i>Verongula rigida</i> | 0.2 | 2.3 | | | 8 |

Notes: Similar numbers of individuals of all the species of seagrass and reef sponges (i.e., 12-16 per species) were transplanted to the mangroves, so percentage of bites on each indicates relative choice. The data on percentage of bites and percentage of volume for reef sponges on the reef are from Wulff (1994; species without percentage of volume data were not in the censused plot, and bite data that were published as ranks in 1994 are here given as percentage of total number of bites). In this table, only the species in which new data in the form of bites on individuals transplanted to the mangroves are listed; but summary Fig. 8 includes an additional set of 14 species that were in the top 50% by volume on the reef but were never observed to be consumed during 2,356 bites of trunkfishes on sponges (Wulff 1994). Four species of mangrove sponges could not be transplanted to the seagrass because they are thinly encrusting or very small bodied. Relative abundance of resident species was calculated by adding up the volume of every individual within designated areas of seagrass (data given here), reef (Wulff 1994) or mangroves (Wulff 2009). Electivity (Ivlev's index) was positive for the following species that constituted more than 0.1% of the total volume in their home habitat on the reef: *A. fulva*, *A. cauliformis*; in seagrass: *Clathria curacaoensis*, *Clathria* sp. red, *Amphimedon erina*; in mangroves: *Bienna caribaea*, *Mycale magniraphidifera*, *Lissodendoryx isodictyalis*, *Haliclona implexiformis*, *H. curacaoensis*.

completely consume, six mangrove species that were transplanted to the seagrass (Table 1). These are the same species that were consumed by spotted trunkfish while growing on mangrove prop roots, their native habitat. Trunkfish were rare, and not always in the area in which transplants were placed, so from 6 h to 3 d elapsed before bites were observed. Fresh trunkfish bite marks (i.e., pinacoderm not yet reconstituted) were observed on three seagrass meadow species: *Clathria curacaoensis* (80% of 106 bites), *Amphimedon erina* (14%), and *Clathria* sp. (6%) (Table 1). The first two are the same species consumed by spotted trunkfish when the sponges were transplanted to the mangroves. Measurement of relative abundance of seagrass meadow sponge species (in terms of volume, Table 1) allowed calculation of Ivlev's Index of Electivity, which was positive for all three of these species. In a previous study of feeding by *Acanthostracion quadricornis* and also congener *A. polygonius* (honeycomb cowfish) on a coral reef (Wulff 1994), relative rates of feeding on particular reef sponge species were published as ranks, but electivity could be calculated from the raw data of number of bites taken and volume of live tissue for each species (Table 1), and these match the experimental results of the present study (summary Fig. 8): i.e., the sole reef species for which electivity was positive was *Aplysina fulva* (the congener, *A. cauliformis*, was

absent from the reef studied in 1994). Feeding by both *Acanthostracion quadricornis* and *Lactophrys bicaudalis* in this study matched that of the two *Acanthostracion* species in the earlier study (Wulff 1994) in another way, by consistently taking bites from some *Aplysina* spp. individuals and ignoring the others.

Trunkfishes do not appear to have the same level of habitat fidelity that angelfishes, parrotfishes, and the starfish have, and although the mangrove and seagrass sites studied were each inhabited by a single species, Caribbean trunkfishes can be found in coral reef (Fig. 9c), seagrass, and mangrove habitats. As expected if sponge defenses particularly target predators typical of their home habitat, the proportion of sponge species eaten by trunkfish in natural feeding or in experiments did not significantly differ among these three habitats (Fig. 7, *G* test $P > 0.1$).

Consistency of experimental results in different contexts

Reactions by each predator species to each sponge species were consistent, regardless of field site or which other sponges were presented simultaneously. The few sponge species that were consumed in some trials and rejected in others (e.g., *Haliclona implexiformis*, *Halichondria melanodocia*, and *Niphates caycei* for starfish; *Mycale microsigmatosa*, *Amphimedon*



FIG. 9. Spongivores and effects of spongivory (a, b) Inside and outside view of the surface of the semi-cryptic reef sponge *Mycale laevis* remaining after consumption of the inner tissue by *Sparisoma* spp. and *Pomacanthus* spp. (c) Trunkfishes *Acanthostracion quadricornis* and *Lactophrys bicaudalis* on a coral reef in Belize. (d) *Verongula rigida* sporting a healed bite taken the two days earlier as well as a bite taken just before the photo. (e) The seagrass meadow sponge *Clathria curacaoensis* with a single bite removed by trunkfish *A. quadricornis*. (f) The reef sponge *Callyspongia vaginalis*, with a single bite taken by angelfish *P. arcuatus* 4 months previous, and now regenerating. (g) The reef sponge *Aplysina fulva* transplanted to mangroves, with bites taken by trunkfish *L. bicaudalis*, while the mangrove species *Tedania ignis* was not bitten at all. (h) Typical behavior of angelfish, *Pomacanthus arcuatus*, when a researcher is carrying sponges that are novel to them. Once they have sampled novel species, they no longer rush to investigate unless the species are those they consider particularly palatable. (i) Spine damage by parrotfish bites on a starfish, *Oreaster reticulatus*, that strayed onto the edge of a patch reef from its home habitat, the seagrass meadow.

erina, and *Chalinula molitba* for angelfish; and *Aplysina fulva* and *A. cauliformis* for trunkfish; Figs. 2, 3) elicited the same variability in response wherever they were tested. The nine sponge species that were

collected in more than one of the three habitats elicited the same response from each predator, regardless of the habitat where they were growing (Figs. 2, 3).

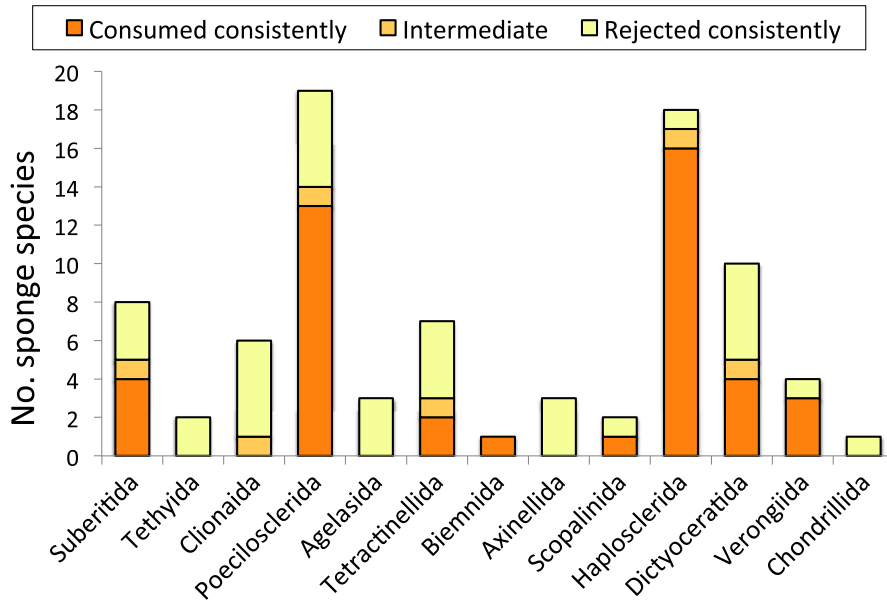


FIG. 10. Number of sponge species in 13 demosponge orders that are consumed to different degrees by the starfish *Oreaster reticulatus* in experiments in the field.

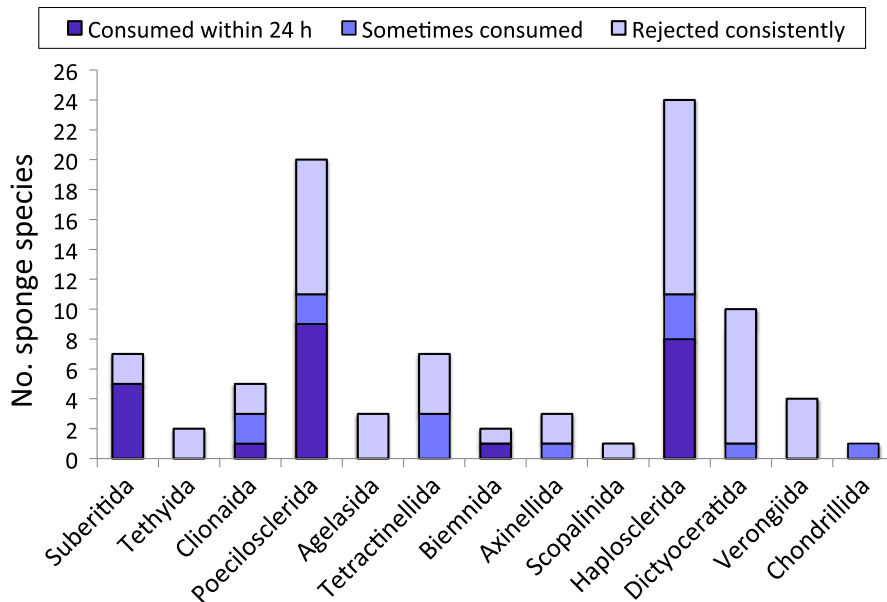


FIG. 11. Number of sponge species in 13 demosponge orders that are consumed to different degrees by the angelfishes *Pomacanthus arcuatus* and *P. paru* in field experiments.

Clade-specific patterns in defenses vs. defense circumvention are asymmetrical

Predator clade membership predicts patterns in defense circumvention well, i.e., spongivorous species within each of the three teleost families studied (i.e., Pomacanthidae, Sparisomatinae, Ostraciidae) made very similar feeding choices, confirming previous reports

(Wulff [1994] for angelfishes and trunkfishes, Wulff [1997a] for parrotfishes).

By contrast, sponge clade membership does not reliably predict vulnerability to consumption. For both angelfish and starfish spongivores, 8 of the 13 sponge orders included a mix of consumed and rejected species (Figs. 10, 11). Too few sponge species were consumed by trunkfishes and parrotfishes for meaningful analysis of









| Predators |  Angelfish |  Trunkfish |  Parrotfish |  Pufferfish |
|---|--|--|---|---|
|  Starfish | 58% <i>n</i> = 85 | 64% <i>n</i> = 44 | 54% <i>n</i> = 84 | 50% <i>n</i> = 9 |
|  Angelfish | | 63% <i>n</i> = 46 | 52% <i>n</i> = 87 | 67% <i>n</i> = 12 |
|  Trunkfish | | | 46% <i>n</i> = 46 | 92% <i>n</i> = 12 |
|  Parrotfish | | | | 50% <i>n</i> = 9 |

FIG. 12. Percentage of sponge species for which the indicated pair of spongivores responded differently, i.e., one consumed and the other rejected sponges of that species (from data compiled in Fig. 8). No importance is ascribed to differences among these percentages, as these in part reflect the assortment of sponge species that were tested for each predator species (e.g., no mangrove or seagrass species were offered to the Pacific pufferfish). Among Caribbean spongivores (i.e., angelfishes, trunkfishes, parrotfishes, starfish), two predator taxa reacted differently to the same sponge species in 55.4% of the 392 paired comparisons. In sea-table experiments (Wulff 1997b) *Arothron hispidus*, a Pacific smooth puffer, rapidly consumed *Halichondria* sp., *Geodia* sp., *Mycale laevis*, *Haliclona* sp., and *Calyx podatypa* in a majority of the trials; rejected *Hymeniacidon caerulea*, *Amphimedon erina*, *Neopetrosia carbonaria*, *Amphimedon compressa*, *Ectyoplasia ferox*, *Aplysina fulva*, and *Verongula rigida* in every trial; and had intermediate responses to *Spirastrella hartmani*, *Lissodendoyx colombiensis*, *Desmapsamma anchorata*, *Iotrochota birotulata*, *Callyspongia vaginalis*, and *Niphates erecta*.

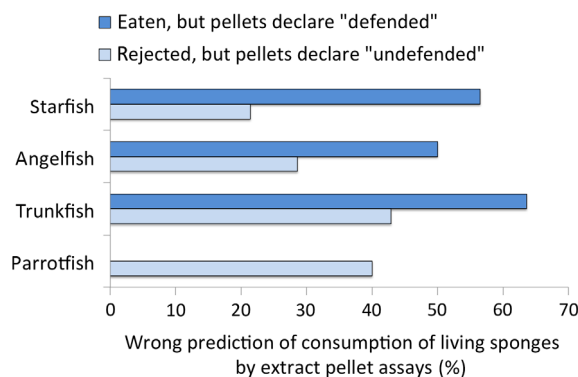


FIG. 13. Percentage of pellet assay/omnivore results that wrongly predict actual consumption of living sponges by spongivores for four predator groups. Pellet data are from Loh and Pawlik (2014), excluding sponge species listed as “variably defended.” Overall, pellet/omnivore lab assays wrongly predicted consumption of live sponges in 43% of direct comparisons.

their feeding across 13 sponge orders. Clade membership fails to reliably predict palatability even at the level of genus. The same predator reacted differently to congeneric species for a third of the genera represented by more than one species (summary Fig. 8).

Predators in different families eat different sets of sponge species

A summary (Fig. 8) of data on 94 sponge species for which degrees of consumption were determined for predators representing at least two different families explicitly shows that different spongivores do not agree on which sponge species are “palatable.” Pairwise comparisons of responses between all four predator groups (three fish families and the starfish *Oreaster*) underscore the degree to which different spongivores eat different sponge species (Fig. 12). Of the 392 pairwise comparisons of responses to the same sponge species, 55.4% were different.

A biogeographic component to comparisons of palatability among predator taxa can be added from sea-table experiments (Wulff 1997b) in which 18 species of living Caribbean sponges were presented as novel prey to a Pacific smooth pufferfish, *Arothron hispidus*, an opportunistically spongivorous fish that is common on coral reefs and rocky shores along the Pacific coast of Central America (Guzmán and Robertson 1989, Allen and Robertson 1994). Of the 459 pairwise comparisons of responses to the same species resulting from adding responses of this Pacific spongivore to the Caribbean data, 56.4% were different.

DISCUSSION

Surprises revealed by targeted sponge defenses impel reevaluation of recent assertions about spongivory and community organization

Applying the same field methods to an ecologically and taxonomically comprehensive set of sponges and their spongivores, representative of an entire region, yields a data set with which many questions can finally be addressed with confidence. Some recent assertions require reevaluation; and generalizations based on too few species, or on techniques that may not be pertinent, can now be rectified. The chief conclusions, each discussed in the following sections, are as follows (1) The majority of tropical western Atlantic sponges are consumed by at least one predator species, (2) but spongivores in different families eat different sets of sponge species. Thus, the designations “palatable” or “deterrent” are only meaningful in the context of a particular sponge-species–predator-species pair. (3) Extract pellet assays with captive generalist consumers do not reveal influence of spongivory on community organization and ecosystem function, as these assays fail to match choices of spongivores in 43% of direct comparisons. Popular assertions about negative sponge effects on coral reefs that are based on dichotomous binning of sponges by pellet assays must be reconsidered, and conservation strategies adjusted accordingly. (4) Phylogenetic patterns in specificity are asymmetrical for sponges and spongivores, so although related spongivorous predators eat similar sets of sponge species, (5) clade membership of sponges poorly predicts palatability to a particular predator. (6) Habitat, however, is a reliable predictor of whether or not a sponge species will be palatable to a particular predator, as sponges tend to be defended against predators that share their habitat and palatable to predators that do not normally have access to their habitat. (7) Thus opportunistic sponge-feeding tends to have more dramatic effects than does routine sponge-feeding on distribution and abundance of sponge species, and consequently on community organization and ecosystem function. Routine spongivory within a habitat tends to not be the primary control on resident sponges, but opportunistic spongivory can maintain strict control

of distribution among habitats. (8) Key ecosystem roles contributed uniquely by sponges can be lost, if restrictions on habitat distribution of spongivores are relaxed and they eat sponges lacking defenses against them.

Most Caribbean sponge species are eaten

A majority (78%) of the 94 sponge species studied were eaten by at least one predator species: 51 species were entirely consumed in a significant majority of trials, 13 species were entirely consumed in at least 25% of trials or positively elected by naturally feeding predators, and 9 additional species each received at least 5% of bites of unmanipulated predators. Two very different styles of spongivory are represented: (1) routine sponge-feeding by sponge-focused predators that consume small amounts of most of the sponge species that share their habitat, vs. (2) opportunistic sponge-feeding by omnivores, herbivores, or dedicated spongivores that entirely consume sponge species that are normally unavailable because they live in inaccessible habitats or are protected by mutualistic associations.

These new data confirm previous findings based on three approaches: (1) gut content analysis of spongivores collected in the field after natural feeding (Randall and Hartman 1968, Andréa et al. 2007), (2) field observations of unfettered predators feeding in their natural habitats on resident sponges (Hourigan et al. 1989, Wulff 1994, Lesser and Slattery 2013), and (3) experimental provision, in the field, of sponges that are not normally available to the focal predators (Wulff 1988, 1995, 1997a, 2005, 2017, Dunlap and Pawlik 1996).

These new data invalidate conclusions, based on lab assays, that the majority of Caribbean sponges are deterrent (Pawlik et al. 1995, Loh and Pawlik 2014). In those assays, 69% of 71 sponge species (61.5% of 109 species in the 2014 list) were designated “defended” or “deterrent” because captive wrasses (which do not eat living sponges) ate 6 or fewer of 10 sponge extract/feeding-attractant pellets. By contrast, only 22% of 94 sponge species offered alive in the present study were not eaten by any of the spongivore species studied in the field. Difference in sponge species studied cannot explain divergent conclusions between extract pellet assays (Pawlik et al. 1995, Loh and Pawlik 2014) and field observations with live sponges reported here (Fig. 8), as the lists of species overlap substantially.

Underscoring the conclusion that most Caribbean sponge species are eaten by at least one predator, almost all of the 21 sponge species not consumed by spongivores in this study (Fig. 8) have been reported to be consumed by other spongivores: *Hymeniacidon caerulea* is found in guts of snapping shrimps that live inside it (Ríos and Duffy 1999); *Tethya actinia*, *Cinachyrella* spp., and *Erylus formosus* are eaten by hawksbill turtles (Meylan 1988, Stringell et al. 2016); *Erylus formosus* is also consumed by spadefish (Randall and Hartman 1968)

and *Spongia* spp. by filefishes (Randall and Hartman 1968). Burkepile et al. (2019) reported that parrotfishes eat *Agelas*, although their photo suggests the fish may be squeezing cyanobacteria out of the surface (Clements et al. 2017), rather than removing pieces from the sponge. Gut contents of angelfishes in the genera *Holacanthus* and *Pomacanthus* revealed consumption of *Erylus formosus*, *Ectyoplasia ferox*, and *Neofibularia nolitangere*, as well as species in the genera *Agelas* and *Cinachyrella* (Randall and Hartman 1968); and Reis et al. (2013) found *Clathria calla* in *Holacanthus* guts.

Spongivore species disagree about which sponges are edible—“palatability” depends on the predator species

Jack Spratt could eat no fat, his wife could eat no lean; and so betwixt the two of them, they licked the platter clean.

—Old English nursery rhyme

Although most sponge species were consumed by at least one predator, sponge species consumed readily by one predator were rejected by others. Divergent reactions to the same sponge species by predators in different families (Fig. 12) emphasize the conclusion that “palatable” and “deterrent” can only be defined relative to particular predators. For example, the reef species *Aplysina fulva* is eaten readily by trunkfishes and the starfish *Oreaster*, but is always rejected by parrotfishes. In contrast, parrotfishes that only ate 6 of the 94 species tested readily eat the mangrove species *Halichondria magniconulosa* that trunkfishes avoid. Neither *A. fulva* nor *H. magniconulosa* can be placed in a definitive category of either “palatable” or “defended,” because they can be either, depending on the focal predators.

Over 250 additional examples of different predators’ responses to the same sponge species are listed in summary Fig. 8. Predator species in different families differed in their responses to particular sponge species in 56.4% of the 459 pairwise comparisons of predator responses to sponge species (Fig. 12). This is considered normal for land plants and their herbivores, as different consumers have long been known to focus on different plants (Forister et al. 2015); but in studies of tropical marine sponges it has become popular to dichotomize species as either “palatable/undefended” or “defended/deterrent” based on extract pellet assays with generalists (Pawlik et al. 1995, Sokolover and Ilan 2007, Loh et al. 2015, Helber et al. 2016), that assume all predators have the same preferences. Data showing clear differences among predators in which sponge species they eat have been available for many years (reviews in Wulff 2006b, 2012, 2016). Becerro et al. (2003) explicitly focused attention on different predator responses when extract cubes and pellets made from pairs of 20 related sponge species from tropical (Guam) vs. temperate (northeast Spain) sites evoked significantly different responses in

86% of comparisons with small-medium predators, and in 32% of comparisons with large predators; and reports focused on particular spongivore species have revealed differences in prey choices. The data reported here take the significant steps forward of being: (1) collected from living sponges and their predators in the field, (2) comprehensive with respect to taxonomic representation and the regional sponge fauna, and (3) integrative with respect to simultaneous consideration of sponges and spongivores that represent distinctive adjacent habitats. It is time to stop dichotomizing sponge species as either “palatable” or “defended” and to accept the complex nuances of sponge–spongivore interactions so we can realistically interpret how they influence community organization and dynamics in tropical marine ecosystems.

Consumption of living sponges by spongivores is not accurately assessed by lab assays with extract pellets and a generalist omnivore

Lab assays with extract/feeding-attractant pellets and captive wrasses (which survive well in tanks but never eat living sponges) can be accomplished in a short time, and require only moments in the field for collecting sponges to be extracted. Thus it is an important question whether the quality of information gained during 20 yr of field work justifies the time spent. Explicit comparison of field-collected data on spongivores and living sponges (Fig. 8, this report) with lab pellet assay data (Loh and Pawlik 2014) can be made for 52 sponge species that are included in both studies. Pellet data assess wrongly that a sponge species is palatable (i.e., wrasses ate more than 6/10 pellets but the spongivore rejects the living sponge) in from 21.4% to 42.9% of direct comparisons, depending on the spongivore species (Fig. 13); and pellet data assess wrongly that a sponge species is defended (i.e., wrasses ate six or fewer pellets but the spongivore consumes the species) in from 0% (parrotfish) to 63.6% (trunkfish) of direct comparisons (Fig. 13).

Overall, pellet data wrongly predict whether a sponge species is consumed or rejected by spongivores in 42.9% of 175 direct comparisons using the Pawlik et al. (1995) division of “palatable” from “deterrent” species by whether or not captive wrasses eat more than 6 of 10 pellets. Pellet data on a revised list (Loh and Pawlik 2014), which assigns sponge species whose pellets were eaten by wrasses in only some trials to a “variably defended” category, wrongly predict sponge consumption or rejection by spongivores in 43% of 142 direct comparisons (i.e., not including “variably defended” species). Years of field work are well justified: extract pellet assays with captive wrasses are not reliable proxies for reactions of spongivores to living sponges.

Two examples of common Caribbean sponge species illustrate mismatch between pellet assays and actual sponge consumption by spongivores. The ramifications

for interpreting spongivore influences on communities and ecosystems are discussed in the final two sections of *Discussion*. The coral reef species *Aplysina cauliformis* has often been used as an example of a “deterrent” sponge (Leong and Pawlik 2010, Pawlik et al. 2013) because a mean of only 0.3/10 extract pellets were eaten by captive wrasses (Pawlik et al. 1995). In experiments with living sponges, parrotfishes do not eat it at all (Fig. 8), but it has positive electivity for trunkfish (Table 1), and the starfish *Oreaster* consumes it readily in experiments as well as when it is transplanted to seagrass where *Oreaster* resides (Wulff 2017; Figs. 2, 8). A second example, the coral reef species *Callyspongia vaginalis* has repeatedly been used as a prime example of “palatable” (Pawlik 1997, 2011, Walters and Pawlik 2005, Pawlik et al. 2008, 2013) based on a mean of 9/10 extract pellets consumed by captive wrasses. This species is readily consumed by *Oreaster* (Figs. 2, 8; Wulff 1995) but not by parrotfishes (Fig. 8; Wulff 1997a); and electivity is negative for *Pomacanthus* spp. and trunkfishes (Table 1; Wulff 1994). Trunkfish feeding on reef sponges transplanted to mangroves took many bites from *Aplysina cauliformis*, but not a single bite from an equal number of intermixed *Callyspongia vaginalis*. Pellet assay designation of *A. cauliformis* as “defended” and *C. vaginalis* as “palatable” does not inform understanding of their ecology; and dozens of similar examples emerge from direct comparison of data from living sponges with pellet results.

Assumptions underlying application of sponge pellet assay data to coral reef health and dynamics that have not been adequately tested include (1) defenses are solely chemical, and (2) effectiveness of the compounds is not altered by specimen handling, extraction, lyophilization, and drying (Thoms and Schupp 2007). But two key assumptions are definitively invalidated by the data in this report: (1) prey species preferences of a generalist omnivore represent the preferences of all spongivores, and (2) pellet consumption by a wrasse predicts living sponge consumption by spongivores. Assertions about tropical marine ecosystem dynamics that are based on pellet/omnivore data must now be reevaluated.

It is important to point out that extract pellet assays using appropriate consumers can be useful complements to field studies with living sponges. Extract assays using spongivores can be used to determine the relative importance of physical, chemical, and nutritional defenses, and are essential for avoiding accidental introductions while making biogeographic comparisons. Extract assays have been used successfully for making between-ocean comparisons of sponge defenses (Becerro et al. 2003), and for disentangling relative importance of secondary metabolites and physical characteristics in deterring consumers (Hill et al. 2005, Rohde and Schupp 2011). Duffy and Paul (1992) have used extract assays to investigate complex interactions of nutritional value with chemical defense for two sponge species in Guam and Uriz et al. (1996a), Becerro et al. (1998), Schupp

et al. (1999), and Rohde and Schupp (2011) have compared defenses at different positions within sponge individuals. Schupp et al. (1999) were also able to identify the deterrent compounds using pellets and natural fish assemblages. Uriz et al. (1996b) discovered chemical defenses to be more concentrated in the more nutritionally valuable of two Mediterranean sponge species. Hopefully, the data summarized in Fig. 8, of sponge species consumed or rejected by various spongivores, will motivate focused studies using partitioned pellets to delve into details of sponge defenses as well as the physiological and biochemical mechanisms that serve to circumvent those defenses.

Predator clade predicts patterns in circumvention of sponge defenses: closely related fish species eat similar sets of sponges

Spongivorous fishes within the same genus or family (i.e., Pomacanthidae, Ostraciidae, Scaridae) consumed similar sets of sponges. The two *Pomacanthus* species, the French and gray angelfishes, consistently feed in “smorgasbord” fashion (i.e., taking only small amounts from any particular sponge, and moving among sponges of different species while foraging) on many sponge species, matching reports by Randall and Hartman (1968), Hourigan et al. (1989), Wulff (1994), and Andréa et al. (2007). In a previous observational study, *Pomacanthus paru* and *P. arcuatus* in a mixed group foraged in the same way on the same sponge species (Wulff 1994).

Differences among studies in the sponge species consumed by Caribbean *Pomacanthus* species reflect variation in sponge faunas among sites, as these species consume many of the sponge species with which they coexist, including relatively rare species, as they purposefully diversify their diets. Angelfishes depart from this feeding strategy only when opportunistically eating sponge species from normally inaccessible habitats or microhabitats, such as mangroves or cryptic spaces in the reef frame or under rubble (Figs. 3, 8; Dunlap and Pawlik 1996, Wulff 2005); and under those circumstances the *P. paru* and *P. arcuatus* individuals chase each other away equally, without regard to which competitors are conspecific or heterospecific.

Sponge choices and foraging behavior of trunkfish species in the related genera *Acanthostracion* and *Lactophrys* were indistinguishable (Table 1), even though they were feeding in different contexts. For example, seagrass meadow sponge species that were consumed by scrawled trunkfish foraging in the seagrass were also consumed by the spotted trunkfish when they were transplanted to the mangroves. These data corroborate previous observations of two co-occurring *Acanthostracion* species that fed on the same reef sponge species (Wulff 1994).

Consumption of the same few sponge species by *Sparisoma viride* and *S. aurofrenatum* in this study matches a previous report that three Caribbean

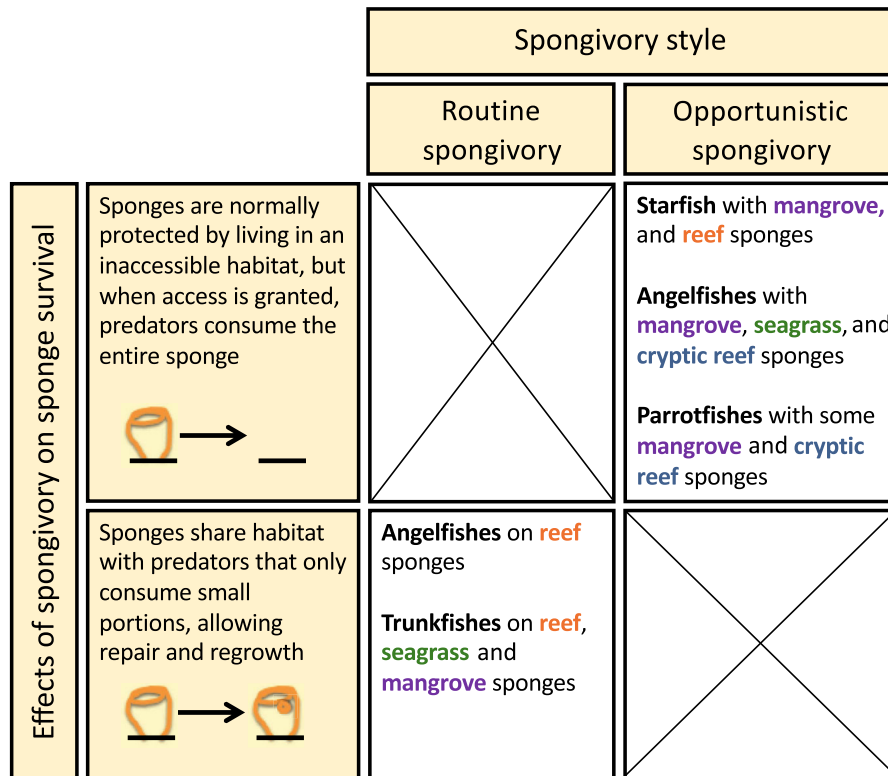


FIG. 14. Routine spongivory and opportunistic spongivory influence survival, and therefore habitat distribution, of prey sponges differently. Spongivorous members of three fish families and one species of starfish are placed in categories according to (1) whether or not they tend to consume an entire sponge individual if they consume any of it vs. only consuming a small portion of a sponge during a given feeding episode; and (2) whether the sponge species consumed live in the same habitat, and are therefore exposed continuously to that predator species vs. the sponge species consumed normally live in a different habitat (or in the same habitat but in crevices or otherwise inaccessible places) and so are not normally available to the predator. Note that angelfishes are listed in two places because they routinely consume only small portions of sponge species with which they coexist, but they consume entire sponges of species that are typically unavailable because they live in other habitats.

Sparisoma species and a fourth parrotfish in the genus *Scarus* ate the same sponge species and had similar sponge-feeding behavior, with the only difference being less of a focus on sponge feeding by the much smaller *Scarus iseri* (Wulff 1997a). This similarity in sponges consumed extends across oceans at the generic level for both predators and prey, with the common eastern Pacific parrotfish *Scarus ghobban* most frequently consuming two cryptic reef species *Geodia* sp. and *Halichondria* sp. congeneric with, and possibly conspecific with (Wulff 1996), the two cryptic reef species most consumed by Caribbean parrotfishes (Fig. 8; Wulff 1997a, b).

Although congeneric sponge-feeding fishes tend to eat the same sponge species, other members of their genera and families do not eat sponges. Two small-bodied Caribbean *Sparisoma* species are browsers in seagrass habitats (Bernardi et al. 2000). And although the large Pacific puffer *Arothron mappa* has sometimes been found with its gut packed with sponges (Hiatt and Strasburg 1960), and *A. hispidus* focuses on sponges when they are available, a third congener, *A. meleagris*, primarily eats corals (Glynn et al. 1972, Guzmán and

Robertson 1989). Sponge-feeding angelfishes in the genus *Holacanthus*, e.g., the Queen angelfish, *H. ciliaris*, also feed in smorgasbord fashion, but may focus on different sets of sponge species from those eaten by *Pomacanthus* angelfishes (Randall and Hartman 1968, Hourigan et al. 1989, Wulff 1994, Andréa et al. 2007). In the tropical eastern Pacific, *Holacanthus passer* feeds on plankton where reefs are devoid of exposed sponges, but opportunistically feeds on cryptic sponge species when these are removed from their hiding places within the reef frame (Wulff 1997b). Comparisons between closely related spongivores and non-spongivores might aid future studies of the physiological and biochemical mechanisms by which spongivores deal with sponge defenses.

Butterflyfish food choices provide an intriguing contrast to the similar sets of species eaten by congeneric spongivores, as their foraging patterns have often demonstrated resource partitioning among closely related species, especially in the highly diverse tropical western Pacific fauna (Lawton et al. 2012, Pratchett 2014, Slattery and Gochfeld 2016). Resource

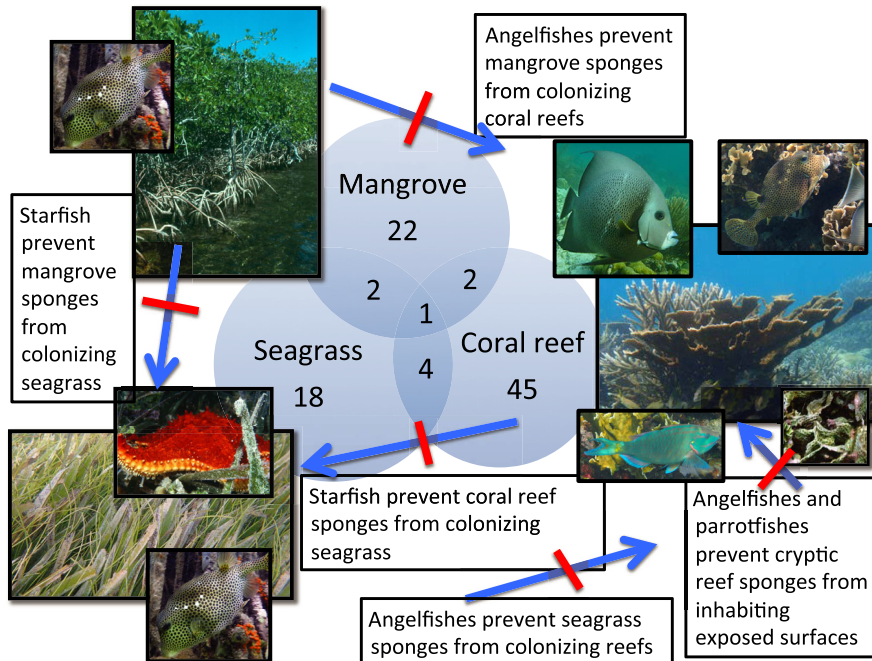


FIG. 15. Opportunistic spongivory helps to maintain habitat-distinct sponge faunas: red bars across the blue arrows indicate that sponge species typical of mangroves, seagrass, and cryptic spaces within the reef frame are prevented from inhabiting reef surfaces by their vulnerability to reef-dwelling angelfishes and parrotfishes; and sponge species typical of reefs and mangroves are prevented from inhabiting seagrass meadows by their vulnerability to seagrass-dwelling starfish. Numbers indicate how many of the 94 sponge species included in this study inhabit one, two, or all three habitats.

partitioning was also demonstrated for two congeneric Caribbean butterflyfishes (Liedke et al. 2018), while another pair of Caribbean congeners was shown to differ in ways reminiscent of the differences between sponge-feeding by angelfishes vs. parrotfishes, with one species, *Chaetodon capistratus*, actively broadening its diet and the congeneric *C. aculeatus* feeding selectively on relatively hidden prey (Birkeland and Neddeker 1981).

Sponge clade membership does not reliably predict predator deterrence on taxonomic levels from genus to order

Sponge species in the same clade often evoke different responses from a particular predator (Fig. 8). At the level of demosponge orders, for which chemistry has aided systematics (Bergquist and Hartman 1969, Hooper et al. 1992, Tribalat et al. 2016), particular predators do not show marked feeding patterns (Figs. 10, 11). Even at the genus level, clade membership does not reliably predict sponge palatability. Reactions of particular predators to congeneric sponge species in the 18 genera represented by two or more species in this study differed (i.e., one sponge species was consumed while a congeneric species was rejected) in 32% (34/105) of pairwise comparisons for starfish, angelfish, and trunkfish feeding (Fig. 8). This result has not previously been demonstrated with living sponges and spongivores, but it is in

accord with conclusions of a comprehensive review of patterns in sponge chemistry, in which Harper et al. (2001) pointed out that matching between particular secondary metabolite chemistry in sponges and effects on predators is often not close.

Of the 48 genera in this study, only two, *Agelas* and *Cinachyrella* (Fig. 1d, g), were uniformly rejected: all six species were rejected by all predators to which they were made available (Fig. 8). Likewise, only two genera were broadly palatable. *Geodia* species were the most uniformly palatable across habitats and predator species in this study (Fig. 8), as well as in other studies on Caribbean reefs (Wulff 1997a), Caribbean mangroves (Dunlap and Pawlik 1996, 1998), and on eastern Pacific reefs and low intertidal cobble beds (Wulff 1997b). A large-bodied reef sponge, *Geodia neptuni*, is among the top four species in hawksbill turtle diets in all studies that provide relative consumption data (Meylan 1988, van Dam and Diez 1997, Leon and Bjorndal 2002). Survival of a seagrass *Geodia* species in the Florida Keys is aided by an epibiotic sponge, *Amphimedon erina*, that seagrass spongivores do not eat (Fig. 2; Ramsby et al. 2012). *Hali-chondria* species also tend to be readily consumed by opportunistic sponge feeders, such as herbivorous parrotfishes (Fig. 8; Dunlap and Pawlik 1996, Wulff 1997a), a microphagous starfish (Table 1; Wulff 1995), an omnivorous Pacific pufferfish, *Arothron hispidus*, the Moorish idol, *Zanclus cornutus* (Linnaeus), and the

eastern Pacific angelfish *Holacanthus passer* Valenciennes, which is also a planktivore (Wulff 1997b).

The more common pattern of divergent predator responses to congeneric sponge species is well illustrated by the speciose genus *Haliclona* (Fig. 8). *Haliclona caerulea* is protected from predators by symbiotic association with erect coralline algae (Wulff 1997b), but when these algae are absent, it is consumed readily by the Caribbean starfish, *Oreaster reticulatus*, the Pacific Moorish idol *Zanclus cornutus*, and by angelfish in both the Caribbean and eastern Pacific. In contrast, angelfishes and parrotfishes rejected *Haliclona implexiformis* (Wulff 2005), and starfish consumed it in only half the trials in this study. An undescribed seagrass-dwelling *Haliclona* species was uniformly rejected, while *Haliclona curacaoensis* was consumed by all but the parrotfishes (Fig. 8). A sister species of the iconic mangrove sponge *Tedania ignis*, *T. klausii*, was distinguished as different (Wulff 2006c) because it deters *Oreaster* feeding, whereas *T. ignis* is consumed readily by *Oreaster*. Variety in predator targeting within sponge genera suggests that sponge defenses may be relatively labile evolutionarily. A practical application of this surprising discovery is that palatability of a sponge species cannot necessarily be predicted from congeneric sponges, but each sponge–spongivore combination must be tested.

Habitat reliably predicts patterns in sponge defenses against predators

Most fishes and invertebrates never eat sponges (Randall and Hartman 1968). For the handful of dedicated and opportunistic spongivores, a sponge species is most likely to deter a particular predator if the predator and sponge species coexist in the same habitat (Figs. 4, 5). Key to this pattern is that most spongivore species tend to be confined to a particular habitat. Coral reef-dwelling angelfishes consume significantly less of a sponge species the easier their access to it (Figs. 3, 5); readily consuming mangrove species that are normally out of their reach, consuming fewer seagrass species, which they may occasionally reach by short and risky forays from the reef, and even fewer coral reef species with which they coexist. Likewise, the seagrass-dwelling starfish *Oreaster* is less likely to find a sponge species edible the easier its access to it: they readily consume mangrove and coral reef species that are normally off limits to them, and generally reject seagrass meadow sponge species with which they coexist (Figs. 2, 4). Experimentally provided reef sponges that were eaten by reef-dwelling angelfishes and experimentally provided seagrass sponges that were eaten by seagrass-dwelling starfish can get away with lacking inherent deterrents because they are normally unavailable due to living in cryptic spaces or mutualistic association with defended sponge species (Wulff 1997a, 2008).

Reef-dwelling herbivorous parrotfishes do not normally consume reef sponge species that inhabit exposed

surfaces. But *Sparisoma aurofrenatum* and *S. viride* can eat a few sponge species typical of mangrove prop roots, where the parrotfishes do not regularly forage, as well as a few of the sponge species that live in cryptic microhabitats that render them inaccessible unless a major storm or curious biologist exposes them by breaking open the reef frame (Fig. 6). These herbivores consume the internal tissue of the semi-cryptic reef species *Mycale laevis* only if the surface is breached (Figs. 8, 9a, b; Wulff 1997a).

Trunkfishes do not disproportionately consume sponge species from a particular habitat (Table 1, Figs. 7, 8) and have never been reported to opportunistically consume entire sponge individuals. This apparent exception to the pattern of inverse relationship between palatability and accessibility actually falls perfectly in line with the conclusion that sponge defenses target predators with which they share habitat, as the relatively uncommon trunkfishes can be found in all three habitats (Fig. 9c).

Opportunistic spongivory exceeds routine spongivory in shaping community organization in coral reef, seagrass, and mangrove ecosystems

Opportunistic spongivory may occur only sporadically, and contribute relatively little to time-averaged nutrition for the predators. But effects on sponges are profound because entire individuals are consumed, eliminating the possibility of recovery and regeneration. As a consequence, benthic community composition is significantly affected as opportunistic spongivory imposes strict habitat boundaries on sponge species whose defenses target predators in their home habitat but are ineffective against predators of adjacent habitats (Fig. 12). Most sponge species typical of coral reefs or mangrove prop roots cannot colonize adjacent seagrass meadows, where the large normally microphagous starfish *Oreaster reticulatus* eats them (Figs. 2, 4, 8; Scheibling 1979, Wulff 1995, 2017). Reef species transplanted to seagrass thrived when protected by cages from *Oreaster* (Wulff 2017), confirming that opportunistic spongivory is the cause of habitat restriction. Most sponge species typical of mangroves or seagrass meadows cannot grow on coral reefs because angelfishes and parrotfishes eat them (Figs. 3, 5, 6, 8; Dunlap and Pawlik 1996, 1998, Pawlik 1998, Wulff 2005, 2017). Mangrove sponges transplanted to coral reefs and protected within cages grew in the presence of spongivorous fishes, but were eaten as soon as the cages were removed (Wulff 2005). Similarly, many sponge species that live tucked into cryptic spaces within the reef frame are unable to live on exposed surfaces because they are eaten (Figs. 2, 3, 8; Bakus 1964, Wulff 1988, 1997a, b, 2006b, Dunlap and Pawlik 1996). Cages maintained over small crevices for 7 months allowed cryptic sponges to grow to protrude above the reef surface (Wulff 1988, 1997a). When the cages were removed, parrotfishes immediately ate the

sponges, confirming their confinement to cryptic spaces by opportunistic sponge-feeding.

In contrast, routine daily feeding on exposed reef sponge species with which reef-dwelling spongivores coexist does not eliminate entire sponge individuals. Angelfishes take only a few bites from each sponge before moving on. Observations of 2,285 bites by naturally feeding angelfishes in the field revealed that they moved on after a mean of 2.8 bites and, in 92% of the cases, the next prey sponge was of a different species (Wulff 1994). Randall and Hartman (1968) reported 70 sponge species to have been consumed by one or more of the 11 fish species with sponge remains in gut contents. They called angelfishes “smorgasbord feeders” because of the variety of sponge species (24–40) in gut contents of individual fish species, with up to nine sponge species in the gut of a single fish. Their work has been well corroborated by other gut content studies (e.g., 16 sponge species in five individuals of *P. paru* by Andréa et al. [2007]) and by direct field observations of angelfishes foraging on coral reefs. In St. Croix, U.S. Virgin Islands, *Pomacanthus* spp. were directly observed (Hourigan et al. 1989) to consume at least 23 sponge species; Lesser and Slattery (2013) observed feeding on means of 19.7–30.4 sponge species/15 minutes; and in Panama, Wulff (1994) recorded feeding by *Pomacanthus* spp. on 64 sponge species, including 36 of the 42 species in a fully censused area (36/39 species after further taxonomic analysis). Trunkfishes also consume only portions of individual sponges, even when feeding on species they prefer (Table 1; Wulff 1994).

Routine vs. opportunistic sponge-feeding is not necessarily determined by predator species identity. The key is whether or not feeding is on normally available sponge species that coexist in the same habitat with the predator (Fig. 14). When angelfishes feed opportunistically on sponges that are not normally available to them, they depart from “smorgasbord feeding” and instead behave like opportunistically sponge-feeding parrotfishes, i.e., chasing each other away and taking bites until the sponge is entirely consumed (Figs. 3, 5, 8).

Differences in individual survival of interactions with predators during opportunistic vs. routine sponge-feeding play out at the community level. Within-habitat control of sponges by routine feeding of predators typical of the same habitat tends to be minimal, with growth rates controlled bottom-up (Wulff 2017). In contrast, opportunistic spongivory can exert uncompromising top-down control on habitat boundaries, resulting in distinct sponge faunas of coral reef exposed surfaces, coral reef cryptic spaces, seagrass meadows, and mangroves (Fig. 15).

Re-evaluating scenarios about coral reef ecosystem dynamics and sponge ecology that are based on pellet assays

In the light of spongivore feeding patterns that reveal how specifically targeted the defenses of sponges are, it

is now possible to reexamine some commonly accepted scenarios about sponges and spongivores that have been built on dichotomous binning of sponge species into “palatable” vs. “defended/deterrent” on the basis of consumption of extract/feeding-attractant pellets by captive wrasses.

Recent assertions that Caribbean corals and reefs are being overgrown by palatable sponge species wherever spongivores have been overfished have been based on a regression analysis in which “the abundance of spongivorous fishes explained 32.8% of the variation in palatable sponge distribution across all sites” (Loh and Pawlik 2014). Their interpretation of this statistical result involves problematic definitions of both “spongivorous fishes” and “palatable sponge species.” “Spongivorous fishes” are defined by Loh and Pawlik as parrotfishes plus angelfishes (with a correction factor applied to sites with very small fishes), but data in Figs. 5, 6, and 8 confirm and augment what previous publications (Randall and Hartman 1968, Wulff 1994, 1997a) have also indicated: effects of parrotfishes on coral reef sponges are relatively trivial and confined to opportunistic feeding on a handful of normally cryptic or otherwise protected species, while angelfishes focus on sponges, and routinely consume many sponge species to at least some degree. “Palatable sponge” is defined by Loh and Pawlik as captive wrasses eating more than 6 of 10 extract/feeding-attractant pellets, but data in Figs. 8, 12 show that palatability is consumer dependent: Caribbean spongivores differ in their assessment of the palatability of particular sponge species in 55.4% of 392 pairwise comparisons (Fig. 12); and extract pellet assays with non-spongivores wrongly assessed palatability of the living sponges to spongivores in 43% of direct comparisons (Fig. 13). A statistical association of two problematic variables is no proper basis for erecting scenarios of coral reef organization and dynamics or for conservation planning.

Another consequence of popular acceptance of unequivocal top-down control of “palatable” sponges on Caribbean coral reefs (Pawlik et al. 2013, Loh and Pawlik 2014, Loh et al. 2015) is that authors of studies with contrasting data have interpreted their data as if they are deviations from the normal. Recognizing that the scenario of palatable sponges (as judged by wrasses eating pellets) overgrowing Caribbean reefs with fewer spongivores may not be a valid standard for comparison motivates reinterpretation of results from these studies in other biogeographic regions.

In Brazil, Lorders et al. (2018) attributed the lack of support their data gave to a scenario of top-down control of reef sponges to differences between Brazil and the Caribbean in diversity, sedimentation, and turbidity. Their thorough three-pronged approach found no correlation of spongivore (angelfishes) abundance with either sponge cover or sponge–coral competitive interactions, and two of the top four sponge choices by Brazilian angelfish were species judged “defended” by pellet assays

with captive wrasses (Pawlik et al. 1995). In the light of the data comparisons in Fig. 13, which invalidate conclusions based on dichotomous split of sponges into “palatable” vs. “defended” by pellet assays, Lorders et al.’s data can be seen to align well with data from field experiments with live sponges that also show no top-down control on a Caribbean reef with abundant spongivores (Wulff 2017).

In Sulawesi, Powell, et al. (2015) were also unable to detect top-down control of sponges: after 6 months, caged vs. exposed sponge assemblages did not differ in abundance or composition at reef sites with many spongivores. They concluded that the apparent discrepancy between their data and the predator-control scenario in the Caribbean (Pawlik et al. 2013, Loh and Pawlik 2014) must mean that Indonesian sponges are better defended. Their Sulawesi data do, however, match those from a Caribbean reef with abundant spongivorous fishes, where caged vs. uncaged individuals of the 12 most abundant sponge species did not differ in net growth over 1 yr (Wulff 2017), alleviating the discrepancy in data sets from different oceans. Similar results from cage experiments on spongivore-inhabited reefs in these two studies provide additional impetus for follow up on Powell et al.’s (2015) encouragement for learning more about spongivore foraging on Indonesian reefs.

In Zanzibar, lack of correlation between deterrence (lab assays with extract/feeding-attractant pellets) and abundance (percent cover) for 10 sponge species, as well as production of deterrent pellets from only three of the species, led Helber et al. (2016) to conclude that spongivorous fishes must be rare. Based on their acceptance of the assertion that Caribbean sponges that produce pellets eaten by wrasses overgrow corals if spongivores are rare (Loh and Pawlik 2014, Loh et al. 2015), they deduced that “chemically undefended sponges dominate the reef at Bawa Island, Zanzibar, subjecting reef-building corals to a higher competitive pressure.” In the absence of data on either sponge-feeding by fish or overgrowth of corals by sponges at Bawa Island, it is not possible at this time to be certain how sponges, corals, and fishes are interrelated on the reefs of Zanzibar. Taking into account the inability of extract pellets to predict consumption of living sponges by spongivores in the Caribbean (Fig. 13), as well as the discharge of untreated sewage near the reef at Bawa, one possibility is that sponge increases are less related to spongivore abundance than to increased food for sponges (e.g., in the Caribbean: Lesser and Slattery 2013, Slattery and Lesser 2015, Wulff 2016, 2017).

In the eastern Mediterranean, Sokolover and Ilan (2007) assessed palatability of 10 sponge species using pellets, and concluded that predation pressure could not explain why all of their sponges were judged “palatable” in pellet assays. They suggested that tough fibers and spicules might explain this puzzling result. Physical defenses may be important, and it will be interesting to see this hypothesis tested. But their mismatch of pellet

results and field observations becomes less puzzling immediately considering that pellet assays do not relate reliably to actual predation on sponges in the Caribbean either.

There are not yet sufficient studies of how sponge–spongivore interactions influence corals and reefs in different biogeographic regions to know if the data will converge on a common story. Conclusions from the studies remarked on above all appear to be compatible with a view of insufficient top-down control of coral reef sponges to warrant concern that coral reefs are endangered by loss of spongivores. But many more data are required before we have an integrated understanding of how sponge–spongivore relationships influence coral reef organization and dynamics under a variety of circumstances. The data summary in Fig. 8 can inform additional Caribbean studies for 94 sponge species and seven spongivores, but in other regions, consumption, or not, of each sponge species must be learned for each spongivore species before we can know the role spongivores play in sponge distribution and abundance.

Spongivory, sponge increases and decreases, ecosystem function, and conservation of tropical marine ecosystems

Whether or not spongivores are important factors in ecosystem function of coral reefs and linked tropical coastal ecosystems depends on which sponge species are consumed, and whether the spongivory is routine or opportunistic. Some sponge species play significantly destructive roles as excavators of solid carbonate or over-growers of living corals, but most sponges play important positive functional roles that are not duplicated by other organisms (reviews in Wulff 2001, 2016, Bell 2008, Schönberg 2008). Sponges maintain water clarity by efficient filtering of bacteria-size plankton from the water column, harbor hundreds of species of symbionts, increase coral survival by binding living corals to the reef frame, facilitate reef regeneration, protect coral skeletons from damage by excavating organisms, and feed hawksbill turtles and angelfishes (reviews in Díaz and Rützler 2001, Wulff 2001, 2012, 2016, Bell 2008). Sponges growing on mangrove prop roots prevent excavations by isopods that can weaken and kill the trees (Ellison et al. 1996). In seagrass meadows, large sponges can shelter juveniles of commercially valuable animals such as spiny lobsters and prevent phytoplankton blooms from impeding seagrass photosynthesis (Butler et al. 1995, Peterson et al. 2006). These significant beneficial functional roles raise the question: Should we be more concerned about sponge losses than gains?

Popular acceptance of the notion that sponges are increasing and growing over corals and reefs appears to be based on a few studies of increases (number of individuals or percent cover) in one or a few species (review in Wulff 2016, Edmunds et al. 2020), in combination with a proposed mechanism of fast-growing palatable sponges growing uncontrolled where spongivores are

scarce (Loh and Pawlik 2014). Plausibility has been added by an apparent parallel with macroalgae increasing where herbivores are scarce. But, as pointed out earlier, the correlation of palatable sponges with diminished spongivores invoked to promote this mechanism (Loh and Pawlik 2014) is problematic in the light of (1) the data summarized in Fig. 8 on consumption of 94 common species by 7 spongivores, (2) angelfish and parrotfish feeding patterns in Figs. 5, 6, and (3) the comparisons of pellets with live sponges in Fig. 13. Even more awkward than a flawed mechanism to explain sponge increases on coral reefs is the lack of data documenting sponge increases on coral reefs. No extended time-series studies of entire coral reef sponge faunas have demonstrated sponge biomass increases (reviews in Wulff 2016, Edmunds et al. 2020), and, perhaps by coincidence, data from the few repeatedly censused sites in which sponges of all species were measured for volume, have identified declines in sponges, sometimes in the form of mass mortalities (Butler et al. 1995, Wulff 2006a, 2013, Stevely et al. 2011; Biggs, B.C. and Strimaitis, A.M., *unpublished manuscript*). Phytoplankton blooms, cold snaps, and disease have been implicated.

Opportunistic feeding on sponges living in habitats that are normally off limits to the predators can also cause sponge losses. Sponge defenses that specifically target only the spongivores in their own habitat leave sponges vulnerable if spongivores that are normally restricted to other habitats gain access. Thus failure of restraints on habitat occupation by spongivores has the potential to wreak havoc on sponge faunas, resulting in loss of the many ways sponges help to maintain their ecosystems (Wulff 2000, 2016, Díaz and Rützler 2001, Bell 2008). For example, if angelfishes can gain access to mangroves, they are capable of stripping the prop roots of typical mangrove species (Figs. 3, 5), eliminating a nutrient-trading mutualism and rendering the trees vulnerable to boring isopods against which the sponges protect them (Ellison et al. 1996). The few places in which close association of corals and mangroves appears to facilitate angelfish living in mangroves bear witness to the loss of typical mangrove sponge species in the presence of angelfishes. At such sites typical reef sponge species have replaced or augmented mangrove species (Rützler et al. 2000, Wulff 2000, 2005, Rogers 2017); with their colonization of the roots likely facilitated by a supply of larvae from nearby adult reef sponges. But sudden angelfish colonization of mangroves distant from reefs could eliminate mangrove sponges quickly and leave mangroves vulnerable for the time it takes reef sponge larvae to disperse distantly, settle, and grow. The seagrass-dwelling starfish *Oreaster* is normally restrained from moving onto coral reefs by parrotfishes biting their spines (Fig. 9i) and butterflyfish biting their tube feet, papillae, and pedicellariae. When parrotfishes were abruptly removed from a reef in Guna Yala, Panama, *Oreaster* moved onto the reef and consumed all reef sponges lacking defenses against them (Figs. 2,

4; Wulff 2006a), greatly diminishing the diversity and abundance of the reef sponge fauna and the ecosystem services this fauna provided. Rather than reducing the reef sponges that inhabit exposed surfaces by eating them, parrotfishes can protect those reef sponges from being eaten by starfish.

Thus an important ramification of sponge defenses that target the predators with which they normally share habitat is that distribution and abundance of sponge species can depend on distribution and abundance of particular predator species. This is a more complex scenario than one in which palatable sponges (identified by pellet assays) overgrow corals and reefs where spongivores are depleted, but it is important that an appealingly simple but misleading story not motivate conservation strategies. Coral reef conservation that is based on the premise that sponges will overgrow corals and overwhelm reefs if there are too few spongivores to eat them will focus on protecting spongivores. Conservation planning that is based on the premise that growth rates of coral reef sponges are primarily controlled bottom-up will consider that overgrowth of corals could be spurred by excess water column nutrients, and therefore focus on wastewater treatment, responsible application of agricultural fertilizers, and integrity of coastal vegetation. Conservation planning motivated by concern about losses of sponges, and their ecosystem roles, due to opportunistic sponge-feeding will focus on maintaining natural habitat constraints on opportunistic sponge-feeders so they do not eliminate sponges that lack defenses against them. These are fundamentally different plans.

The story revealed by knowing spongivore consumption or rejection of 94 common species representing coral reefs, seagrass meadows, and mangroves is complex. Spongivore families differ in what sponge species they eat, although closely related spongivores eat similar sets of sponges. A sponge's defenses target predators of its habitat and are not necessarily effective against predators of other habitats; and the apparent evolutionary lability of sponge defenses precludes inference of defenses from related sponge species. Two contrasting modes of spongivory have very different effects: routine spongivory results in partial mortality that allows recovery and does not appear to be the primary limit on sponges in their normal habitat, while opportunistic spongivory can eliminate entire sponges, thereby confining vulnerable species to habitats that are off limits to opportunistic spongivores. Accepting an assay-based declaration that sponges are either palatable or not is easier than embracing these complexities. But taking into account the complexities and aiming for a nuanced understanding have the advantage of enabling us to be more informed and effective stewards of our tropical coastal ecosystems.

ACKNOWLEDGMENTS

Long days in the water for weeks, months, and years at a time were essential to the success of this project, and these were facilitated by the Caribbean Coral Reef Ecosystems

Program (USNM) and the Smithsonian Tropical Research Institute. I am especially grateful to Ross Robertson, Klaus Rützler, Michael Carpenter, and Zachary Foltz for development and maintenance of remote field stations at Carrie Bow Cay in Belize and in Guna Yala, Panama, where field work is and was supported to an extraordinary degree; and to Gabriel Jacome and Plinio Góndola for support at the STRI Bocas del Toro station. I thank the many volunteer station managers and fellow researchers at Carrie Bow Cay over the 20 yr of this project. I thank a reviewer who improved the manuscript with many thoughtful comments. I am grateful to Egbert Leigh who has given me many opportunities to gain perspective on terrestrial plant–herbivore relationships by hosting me for time on Barro Colorado Island, Panama (STRI) and also provided many insightful comments on this manuscript. This work was supported by the National Science Foundation [grant number 0550599]; the Marine Science Network of the Smithsonian Institution, supported in part by the Hunterdon Oceanographic Research Endowment; and the Caribbean Coral Reef Ecosystems Program (CCRE) of the National Museum of Natural History, Smithsonian Institution.

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