Journal of Experimental Marine Biology and Ecology 380 (2009) 36–46

Contents lists available at ScienceDirect

Journal of Experimental Marine Biology and Ecology

journal homepage: www.elsevier.com/locate/jembe

Sponge community structure and anti-predator defenses on temperate reefs of the South Atlantic Bight

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ARTICLE INFO

Article history:
Received 2 March 2009
Received in revised form 12 August 2009
Accepted 12 August 2009

Keywords:
Chemical defenses
Community structure
Sponge
Spongivorous fish
South Atlantic Bight
Structural defenses
Temperate reefs

ABSTRACT

Predator–prey interactions can play a significant role in shaping the structure of both terrestrial and marine communities. Sponges are major contributors to benthic community structure on temperate reefs and although several studies have investigated how abiotic processes control sponge distributions on these reefs, the role of predation is less clear. We investigated the relationship between sponge predators and the distribution of sponges on temperate reefs in the South Atlantic Bight (SAB), off Georgia, USA. We documented sponge species richness and abundance, spongivorous fish density, and examined the ability of 19 sponge species to chemically and structurally deter predation by fishes. We also conducted reciprocal transplant experiments to determine if predation by fishes contributes to the observed zonation of sponge species on these reefs. Our surveys revealed two distinct sponge assemblages: one characterized by amorphous and encrusting sponge morphotypes colonizing the vertical, rocky outcroppings (scarp sponge community), while the other consisted of pedunculate, digitate, and arborescent growth forms occurring on the sediment-laden reef top (plateau sponge community). Spongivorous fishes were more abundant on the scarp than the plateau and scarp sponges were found to be more effective than plateau sponges at chemically deterring generalist fishes. In contrast, plateau sponges were more reliant on structural defenses: a result consistent with the higher spicule content of their skeletons. Transplant experiments confirmed that predators prevent some plateau sponges from colonizing the scarp even though they possess structural defenses. Thus, predation appears to play a role in shaping sponge community structure on SAB reefs by restricting those species lacking adequate chemical defenses to habitats where there is a paucity of spongivores.

1. Introduction

Sponges are important contributors to marine benthic communities at all latitudes and are often abundant, diverse, and conspicuous (Sara and Vacelet, 1973; Dayton et al., 1974; Alvarez et al., 1990; Bell and Barnes, 2000a). They serve as an excellent model for studying the influence of predator–prey interactions on community structure because they are sessile, lack behavioral defenses, and are consumed by a wide diversity of predators including fishes (Wulff, 1994; Dunlap and Pawlik, 1996), echinoderms (Wulff, 1995; McClintock et al., 2005), and turtles (Meylan, 1998).

It is well recognized that sponges produce secondary metabolites to deter predators in tropical (van Alstyne et al., 1994; Bolser and Hay, 1996; Burns et al., 2003), temperate, (Wright et al., 1997; Becerro et al., 2003) and polar communities (McClintock, 1987). Sponges also possess mineralized structural elements believed to irritate the digestive system of predators (Randall and Hartman, 1968) or reduce its dietary attractiveness to predators by inadvertently lowering the nutritional quality of the sponge (Duffy and Paul, 1992; Pennings et al., 1994; Chanas and Pawlik, 1995). Although siliceous spicules or proteinaceous fibers are widespread in many sponge species, the ability of these structural mechanisms to discourage predation has proved less convincing as compared to chemical defenses (Chanas and Pawlik, 1995, 1996; Burns and Ilan, 2003).

Presently, the bulk of our understanding of how predation influences the distributional patterns of sponges comes from studies conducted on tropical (Wulff, 1995; Pawlik, 1998) and polar (McClintock et al., 2005) benthic communities. Specifically, on coral reefs, where predation is believed to reach an apex in marine benthic communities (Vermeij, 1978; Carpenter, 1986), the majority of sponge species possess chemical defenses that discourage predation (Pawlik et al., 1995). In contrast, sponges inhabiting mangrove and seagrass environments, where predation by spongivorous fishes is reduced (Pawlik, 1998; Wulff, 2005), are poorly defended chemically (Pawlik et al., 1995). The consequences of lacking these defenses was experimentally shown when sponge species from seagrass and mangrove habitats were transplanted to coral reefs and were quickly consumed by predators (Dunlap and Pawlik, 1996). As a result, it was

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doi:10.1016/j.jembe.2009.08.011

proposed that sponges inhabiting coral reefs produce unpalatable chemical compounds while those species lacking deterrent metabolites are limited to cryptic habitats on the reef or to environments such as mangroves and seagrasses where the abundance of predators is reduced (Pawlik, 1998).

Although several studies have investigated how sponge distributional patterns on temperate reefs are controlled by abiotic processes (Roberts and Davis, 1996; Bell and Barnes, 2000a,d), the influence of predation on sponge community structure at temperate latitudes is unknown. For two principal reasons temperate reefs located in the South Atlantic Bight (SAB) of the Northwest Atlantic provide an excellent opportunity to study the effects of predation on the distribution of sponges. First, annual water temperatures within this region drop below the threshold for the survival of scleractinian corals resulting in sponge and tunicate dominated benthic communities. Second, hard bottom areas of the SAB consist of two distinct sponge communities immediately adjacent to one another. Temperate reefs of the SAB consist of rocky ledge outcroppings composed of consolidated sand, shell, and mud (Hunt, 1974). These reefs provide between 1–2 m of vertical relief along a narrow ridge (hereafter referred to as the "scarp"), and atop the elevated side of this ridge the hard substrate becomes flat and quickly transitions into an extensive area of soft substrata with a shifting layer of sediment 1–5 cm thick (here after referred to as the "plateau").

In tropical environments, coral reef, seagrass, and mangrove sponge communities are often separated by extensive distances that may limit the foraging patterns of predators (Wulff, 1994, 2005). Conversely, the sponge assemblages occupying the scarp and plateau habitats on SAB reefs lie within several meters of one another and appear equally susceptible to predation by free-swimming predators (i.e. spongivorous fishes). If the influence exerted by predators on sponge assemblages is consistent across scarp and plateau habitats, we would expect this to be reflected in the distribution of anti-predator defenses. Thus, the goals of this study were to: (1) compare sponge community structure between scarp and plateau habitats, (2) compare abundances of predators between scarp and plateau habitats, and (3) determine if the distribution of sponge chemical and structural anti-predator defenses reflects the predator abundances observed between scarp and plateau habitats.

2. Methods

2.1. Study sites

Two temperate reefs in the SAB, the Monitoring Site at Gray's Reef National Marine Sanctuary (GRNMS; 31° 23.815 N, 80° 53.461 W) and J Reef (31° 36.056 N, 80° 47.431 W), were used for this study. All surveys for sponge and predator distribution, feeding assays, and transplant experiments were conducted at these two sites. Both GRNMS and J Reef are rocky ledge outcroppings with 1–2 m of vertical relief projecting out of the surrounding sand. Surveys conducted within the 58 km^2 area of Gray's Reef National Marine Sanctuary indicate that bottoms of this type comprise <1% of the total area but have the highest biodiversity and house the majority of the biomass of both sessile invertebrates and ichthyofauna (Kendall et al., 2007). GRNMS and J Reef are separated by 15 km and have similar depth profiles averaging 18 to 20 m. Although water temperatures reach 26 °C during summer, many tropical species do not persist through the winter temperatures that can be as low as 11 °C (Hunt, 1974).

2.2. Sponge community structure and predator abundance

Surveys were completed in the summer of 2003 and 2004 at GRNMS and J Reef to assess sponge and spongivorous fish species richness and abundance. For sponge distributional data, we recorded the total number of individuals for each species present in 0.25 m^2 quadrats haphazardly placed alongside 25 m long transects. Scarp sponge populations were quantified by transects that run parallel to and on top of the scarp. Transects on the plateau were laid perpendicular to the scarp and started ~2 m behind the elevated side of the scarp. A total of 104, 0.25 m^2 quadrats were conducted at both GRNMS and J Reef: 52 quadrats for the sponge population atop the scarp and 52 for the adjacent sponge community on the plateau.

Spongivorous fishes were selected to compare predator abundance across scarp and plateau habitats. Although many fish and invertebrate species incorporate sponges as a minor component of their diet, we concentrated our surveys on the few specialist fishes in the families Pomacanthidae (angelfish), Monocanthidae (filefish), Ostraciidae (boxfishes), and Tetraodontidae (pufferfishes) that are known to rely on sponge prey for >70% of their diet (Randall and Hartman, 1968; Wulff, 1994; Meylan, 1998). Spongivorous fish populations were assessed with timed 50 m transects laid parallel and perpendicular to the scarp. Divers recorded all spongivorous fishes present along the 50 m transect for 30 min. Visual census is an efficient and reliable method of quantifying fish densities at GRNMS and J Reef because the conspicuous anatomical features of spongivorous fishes make identification straightforward, and water turbidity at these sites often limits side to side visibility to 10 m or less, ensuring that fish occurring far a field of the transect are not recorded.

2.3. Sponge collection

A total of 52 sponge species have been documented for SAB temperate reefs (Freeman et al., 2007). We selected a subset of 11 species from the sponge community on the scarp and 8 from the plateau to test for anti-predator chemical and structural defenses. The species selected for sampling reflected the range of sponge morphotypes (e.g. encrusting, amorphous, branching, digitate) common to each habitat and included both common and rare species (Fig. 1). Of the 19 species selected for the chemical and structural palatability assays, 11 were spiculate and 8 were aspiculate species.

All sponges were collected from GRNMS and J Reef by SCUBA divers between May and December 2004. Samples of sponge tissue, ≤10 ml in volume, were obtained by either subsampling large sponges or removing whole sponges from the substrate. A total of 30 samples were collected for each species with every sample coming from a physiologically distinct individual. Sponges sampled within species were always separated by ≥1.0 m. Samples were placed individually into plastic bags and stored on ice in coolers at the surface. Sponges were frozen at −80 °C upon returning to the lab, approximately 3 to 4 h after initial collection. Sponges were identified on the basis of morphology or spicule and tissue preparations (Wells et al., 1960; Wiedenmayer, 1977; Alvarez et al., 1998) and all identifications were confirmed by Dr. Rob van Soest, University of Amsterdam.

2.4. Chemical defenses

Methods described by Becerro et al. (2003) were followed to isolate crude organic extracts and formulate foods for testing the palatability of sponge secondary metabolites to fishes. For each sample, approximately 5 ml volumes of sponge tissue were measured by displacement of water in a graduated cylinder. Samples were frozen at −80 °C, lyophilized, and weighed to the nearest milligram on an analytical balance (model APX-60, Denver Instruments, Denver, CO). Freeze dried samples were crushed with a mortar and pestle into small pieces and extracted three times at 4 °C for 24 h by immersing the sample in a 1:1 methanol:dichloromethane mixture. This solution, while less efficient at extracting the most polar compounds, has been shown to work well for extracting a wide range of secondary metabolites because it contains both low (DCM) and high polarity (MeOH) solvents that have the potential to penetrate cell membranes

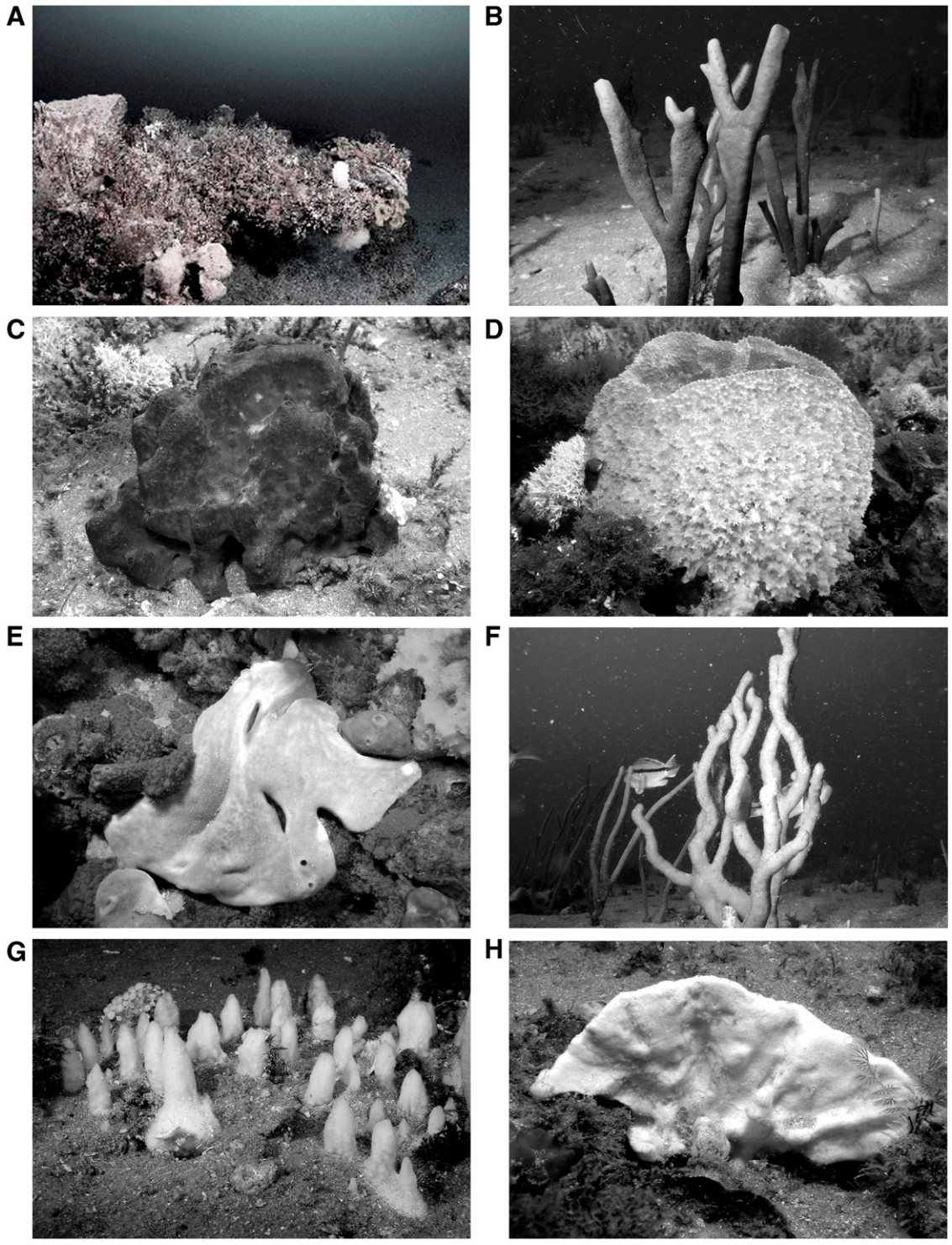

Fig. 1. Examples of the scarp (A) and plateau (B) habitat on SAB reefs and 3 representative scarp sponge phenotypes: C) Amorphous (*I. felix*); D) Vase (*Ircinia campana*); E) Encrusting (*C. collectrix*); and 3 representative plateau sponge phenotypes: F) Arborescent (*P. walpersi*); G) Digitate (*A. ambrosia*); H) Pedunculate (*A. waltonsmithi*); Photographs by Rob Ruzicka (B, E, F, G, H), Greg McFall (A, C, D).

(Cronin et al., 1995). This solvent system also appears to be efficient at extracting lyophilized tissue.

The three extracts obtained above were combined and passed through filter paper (P8 coarse, Fisher Scientific Company L.L.C., Pittsburgh, PA) to remove sponge debris. Excess solvent was removed by rotary evaporation (Brinkmann/Buchi Collegiate, Eppendorf, Germany) at low heat (<30 °C) until approximately 5 ml remained. The remaining 5 ml of solvent was transferred to a pre-weighed 20 ml scintillation vial and concentrated to dryness by vacuum evaporation (model SC210A-115, Thermo Electron Corporation, Somerset, NJ). The dried extract was stored at −80 °C until further use.

Concentrated crude organic extracts obtained from each sponge were dissolved in 0.75 ml of 100% methanol. Samples were sonicated and visually inspected to ensure the extract had dissolved into solution. Artificial food was created using a mixture of 7.5 g powdered squid mantle, 3.5 g Type I carageenan:agar (85:15), and 150 ml of distilled water. The amount of powdered squid mantle used in food preparation was based upon the mean protein concentration (~20.7 mg ml^{-1}) of 71

Caribbean sponge species surveyed by Pawlik et al. (1995) and matched the amount of squid mantle used in Pawlik's tropical feeding assays. In 25 ml batches, the carageenan:agar, squid mantle, and distilled water were thoroughly mixed and heated in a microwave to the boiling point. Immediately after heating, 4.25 ml of food mixture was poured into each scintillation vial containing the 0.75 ml of methanol and extract. This mixture was stirred and allowed to cool forming a food mold. When cooled, the mold was carefully removed from the vial and cut into $1\times1\times1$ cm cubes for feeding assays. A total of 30 food cubes were prepared for each sponge species assayed. Each food cube contained the chemical extract from a single individual, thus there were 30 independent replicates per sponge species.

To verify whether the food preparation process retained the original weight of the extract, several cubes were lyophilized, extracted, filtered, and placed under vacuum to re-isolate the crude organic extract mass. This extract was weighed and compared to the initial weight of the extract isolated from fresh sponge tissue. No significant differences were found between the extract mass weight obtained from fresh sponge tissue and that re-extracted from food cubes ($t=1.44$, $df=46$, $p=0.08$). This ensured that the volume of crude organic extract in the carrageen-based food matched the naturally occurring extract concentration of the sponge.

For each species, 30 control cubes were also prepared by combining 4.25 ml of food mixture with 0.75 ml of methanol devoid of sponge extract. When necessary, food coloring was added to control cubes to approximate the color of the food cubes containing the crude extract. This was done to reduce biases in predatory behavior of fishes that might result from differences in cube color.

2.5. Structural defenses

Methods developed by Uriz et al. (1996) were used to prepare sponge samples for assays of structural defenses. For each sample, fresh sponge tissue containing a random selection of inner and outer tissue layers was cut into a $1\times1\times1$ cm cube. Thirty samples for each species were placed in a 500 ml beaker and extracted three times for 24 h at 4 °C in 1:1 methanol:dichloromethane. Because intact, non-lyophilized tissue was used for this extraction, water inside the sponge mixed with methanol during extraction resulted in a methanol:water phase that separated from the dichloromethane phase. As a result, samples were shaken a minimum of two times during each extraction to ensure that sponge tissue was exposed to both phases. Thin layer chromatography performed on solutions obtained from a fourth extraction confirmed all compounds soluble in the 1:1 methanol:dichloromethane solvent system had been removed after three treatments. After the third extraction, excess solvent was removed and samples were rinsed three times for one minute with distilled water. Samples were placed on cardboard drying racks to air-dry at room temperature overnight, allowing any remaining solvent to evaporate. All sponge pieces were bagged and stored at −20 °C until further use.

For food preparation, the intact sponge tissue, with all chemical compounds removed, was thawed and rinsed with distilled water. Artificial food was created using a concoction of 2.5 g powdered squid mantle, 1.2 g type I carageenan:agar (85:15), and 50 ml of distilled water. The carageenan:agar powder, squid mantle, and distilled water were thoroughly mixed and heated in a microwave until boiling so the carageenan:agar would set. If necessary, food coloring was added to the mixture to match as closely as possible, the natural color of the sponge. After heating, sponge pieces were added to the food mixture, stirred, and allowed to soak until the mixture was almost solid. Only when the food mixture was slightly viscous were the sponge pieces removed. This method allowed for absorption of artificial food into the sponge tissue and embedded the sponge matrix inside a food cube. This process also ensured that the structural food cubes offered in these feeding assays were of high nutritional quality because they contained natural levels of sponge protein in addition to the protein of the food cube recipe. Therefore, deterrence of fish feeding by these cubes represents inhibition by sponge structural elements rather than avoidance of prey having lower nutritional quality (Duffy and Paul, 1992; Chanas and Pawlik, 1995). Control cubes were prepared in the same manner but without the addition of sponge tissue. For each sponge species assayed, a total of 30 independent replicates and 30 control cubes were prepared.

2.6. Feeding assays

Feeding assays were conducted in situ at GRNMS and J reef. Although spongivorous fishes were used to quantify sponge predator abundance, they were not targeted during the feeding assays because (1) they are not attracted to artificial food released into the water column and (2) are less common than other suites of predators. Instead, food cubes were dispensed individually to generalist reef fish predators. The merits of using generalist predators in studies of anti-predator mechanisms have been outlined in Pawlik et al. (1995) and Becerro et al. (2003). Furthermore these generalist predators provide a reliable measure of deterrence that can be compared across differing sponge communities (Ruzicka and Gleason, 2008) and that are reflective of feeding preferences displayed by spongivorous fishes (Pawlik, 1998). South Atlantic Bight temperate reef fish assemblages consist predominately of black seabasses (*Centropristus striata*), tomtates (*Haemulon aurolineatum*), and spottail pinfish (*Diplodus holbrooki*).The feeding behavior of these reef fishes was appropriate for this study because they habitually “mouth” or “taste” their prey before consuming it.

Feeding assays commenced by releasing several control cubes to initiate feeding activity. This was followed by control and treatment cubes being offered in a random sequence so the fish could not habituate to a systematic pattern of cube release. Divers recorded if the cube was consumed or rejected and the fish species responsible for predation. A food cube was considered unpalatable if fishes rejected it three or more times or if it sank to the bottom uneaten. For each sponge species tested, 30 control and 30 treated samples were offered for both chemical and structural assays.

2.7. Transplant experiments

To further investigate if there is a relationship between predation, anti-predator defenses, and sponge community structure on SAB reefs, reciprocal transplant experiments were carried out between the scarp and plateau sponge communities. Twenty four bricks (20 cm length × 10 cm width × 6 cm height) were deployed at J Reef: 12 each on the scarp and plateau. Six bricks for each habitat were enclosed in Vexar mesh (2.2×2.2 cm opening) to reduce predation by fishes and six remained exposed. Each brick contained predrilled holes in the top and bottom and was secured to the reef with a stainless steel rod. The rods were sunk into holes drilled into the substrate with a pneumatic drill (Chicago Pneumatic, CP785H, Rock Hill, SC) and secured with marine epoxy. Each pair of caged and uncaged bricks was placed within 1 m of each other and labeled with flagging tape.

Three scarp species, *Chondrilla aff. nucula*, *Chondrosia collectrix*, and *Hyrtios violaceaus* were transplanted to the plateau, and 4 plateau species, *Axinella waltonsmithi*, *Axinella pomponiae*, *Desmapsamma anchorata*, and *Ptilocaulis walpersi* were moved to the scarp. The species selected for these experiments were common to their respective habitats, differed in their ability to deter predators both chemically and structurally, and were able to tolerate subsampling (e.g. preliminary transplant experiments revealed rapid mortality in *Ircinia felix* and *I. campana* on caged bricks). Samples, 3–20 ml in size, depending on the species, were carefully removed from larger colonies or, when appropriate, whole colonies were gently uplifted

from the substrate to minimize tissue damage and exposure of inner tissue layers. Samples were placed in plastic bags underwater, brought to the surface, and immediately emptied into large coolers containing aerated seawater. While at sea, the volume of each sample was measured to the nearest 0.5 ml by displacement of seawater in a 100 ml graduated cylinder and returned to the cooler containing the aerated seawater. After sponges for a single caged or uncaged replicate were measured, they were strung on monofilament line (9 kg test) ~2.5 cm apart, and placed into a labeled plastic bag containing aerated seawater. For example, one replicate of sponges transplanted from the plateau to the scarp would contain one individual of each of the following species: *A. waltonsmithi*, *A. pomponiae*, *D. anchorata*, and *P. walpersi*. A total of 6 caged and 6 uncaged replicates were prepared for both the scarp and plateau. Sponges were returned to the bottom and attached with the monofilament line to the appropriate brick within 3 h of initial collection. In caged treatments, the cages were cable tied shut after the sponges were attached. After 9 days, sponges were collected, placed in plastic bags, and measured as described before. This experiment was repeated twice.

2.8. Statistical analysis

Differences in sponge community structure between GRNMS and J Reef were compared with a two-way ANOVA using reef (GRNMS or J Reef) and habitat (scarp or plateau) as factors for the following variables: sponge species density (number of sponge species m^{-2}), sponge density (number of individuals m^{-2}), and the density of individual sponge species if the species was recorded at 3 or more sites (i.e. GRNMS-scarp, J Reef-scarp, GRNMS-plateau, J Reef-plateau). When a species was recorded at only two sites, a one-way ANOVA was used to compare the density of that species between sites. Shannon–Weaver diversity (H') and Pielou's evenness were also calculated to compare sponge assemblage similarity across reef and habitat (Sokal and Rohlf, 1995). Spongivorous fish densities were only compared between reefs with a one-way ANOVA because no fish were recorded during plateau surveys.

The ability of an individual sponge species to chemically and structurally deter fish predators was calculated by dividing the total number of food cubes rejected by the total number of food cubes offered. While food cubes used in these palatability assays contained extracts from sponges collected at both GRNMS and J Reef, no distinctions between reef of origin were made during feeding trials. Therefore, statistical analyses assessing the palatability of sponge chemical extracts and structural components to fishes represented the combined results of food cubes prepared from sponges collected at both GRNMS and J Reef. The ability of each species to chemically or structurally deter predators was assessed with a chi-square test with a William's correction.

At the community level, the mean chemical and structural deterrence of predators for each sponge assemblage was calculated by combining the results of the 11 scarp or 8 plateau sponge species tested in the feeding assays. Significant differences between the mean chemical and structural deterrence of fishes by sponges within the scarp or the plateau community was determined with a Wilcoxon paired-sample test. The combined mean deterrence of the scarp and plateau sponge assemblages was calculated by combining the chemical and structural deterrence for all sponge species assayed for that particular habitat. Differences in the combined mean deterrence of the scarp and plateau sponge communities were investigated by ranking the deterrence for each species and subjecting these to a Kruskal–Wallis test. To investigate if potential trends in mode of defense (e.g. chemical vs. structural deterrence) corresponded with sponge morphology we compared the ability of the 8 aspiculate and 11 spiculate sponge species to chemically or structurally deter predators with a Wilcoxon paired-sample test.

Finally, to determine if predation on sponges by fishes helps shape the structure of scarp and plateau sponge communities, changes in volume (initial–final) for sponges used in the reciprocal transplant experiments were compared. Only samples where visible predation could be confirmed were included in these analyses. For example, several samples of *H. violaceaus*, *C. collectrix* and *C. aff. nucula* became disconnected from the monofilament line during the experiment and were not recovered. To avoid over-estimating the impact of predation on our experiment, we did not attribute wholly missing replicates to predation, but instead omitted them from the analysis. Thus, our results present a conservative estimate of predation. A Wilcoxon paired-sample test was used to identify significant differences in sponge volume changes between caged and uncaged pairs for each sponge species. To identify if handling effects contributed to decreases in sponge volume, a paired t-test was used to compare the initial and final volume of the caged replicates.

3. Results

3.1. Sponge community structure and predator abundance

Both sponge species density (number of sponge species 0.25 m^{-2}) and sponge density (number of individuals 0.25 m^{-2}) were similar across GRNMS and J Reef (Fig. 2, Table 1). Within reefs, no significant differences in sponge species density occurred between the scarp and plateau habitat, however, sponge density was significantly higher on the scarp than on the plateau (Fig. 2, Table 1). No significant interaction effect was detected between reef and habitat for mean sponge species density and sponge density (Table 1).

A total of 32 species were recorded from both reefs: 31 at J Reef and 29 at GRNMS. Twenty-eight of the 32 species were present at both reefs, three (*Aiolochroia crassa*, *Cliona celata*, and *Myriastra sp.*) were

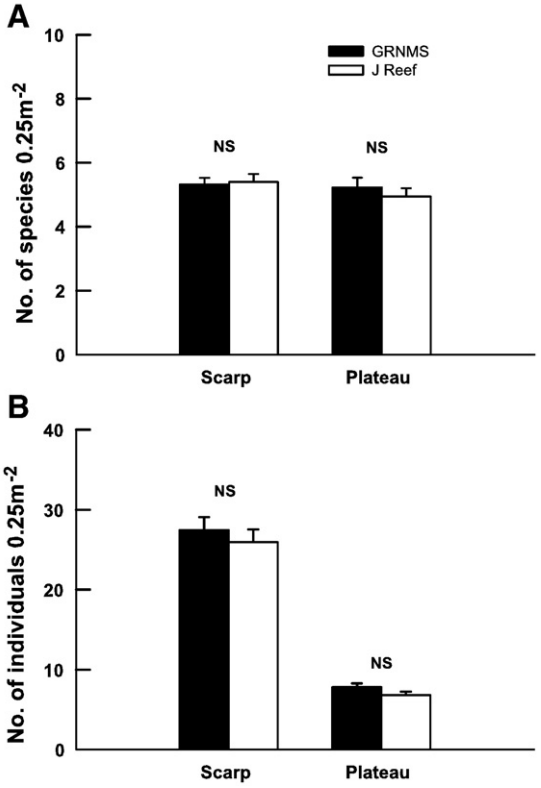

Fig. 2. A) Mean (±SE) sponge species density and B) mean (±SE) sponge density on the scarp and plateau habitats for GRNMS and J Reef. Each bar represents results from 52 quadrats of 0.25 m^2. Tests for significant differences between reefs and habitats were carried out with a two factor ANOVA. For results of these analyses refer to Table 1.

Table 1
Two-way ANOVA results for sponge species density (number of sponge species 0.25 m^{-2} and sponge density (number of individuals 0.25 m^{-2}) at two reefs (GRNMS and Reef) and two habitats (scarp and plateau) within each reef.

Variable	Sponge species density				Sponge density			
	SS	df	F	P	SS	df	F	P
Reef, *R*	0.58	1	0.17	0.67	81.25	1	1.17	0.28
Habitat, *H*	4.04	1	1.198	0.27	19578.48	1	282.49	<0.001
R×*H*	1.73	1	0.514	0.47	3.76	1	0.05	0.81
Within	688.01	204			14138.42	204		
Total	694.37	207			33801.92	207		

only recorded at J Reef, and one (*Geodia gibberosa*) was seen solely at GRNMS. Significant differences in the abundance of 7 species (two way ANOVA; $p \leq 0.05$ when a species occurred at three or more sites; one way ANOVA; $p \leq 0.05$ when a species occurred at only two sites) were detected between reefs (*Dysidea fragilis, Spirastrella sp., Clathria prolifera, A. pomponiae, Higginsia strigilata, Cliona sp.* and *Raspailia sp. B*) and all of these were more common at GRNMS. Within reefs, of the 32 total species recorded, 21 were observed on the scarp and 24 on the plateau. However, species exhibited high habitat fidelity. Sixteen of the 32 species recorded on SAB reefs occurred solely in one habitat: 8 on the scarp and 8 on the plateau (Tables 2 and 3). Of the remaining 16 sponge species, 7 were significantly more abundant on the scarp and 7 on the plateau (one and two way ANOVA; $p \leq 0.05$; Table 3). Only two species (*C. celata* and *Aplysilla longispina*) had similar densities across both habitats (Table 3). In terms of morphology, the majority of the sponge species resident on the scarp were amorphous or encrusting, while the predominant growth forms on the plateau were arborescent, pedunculate, and digitate (Tables 2 and 3). Adjusted for abundance, 94% of the sponges occupying the scarp were amorphous or encrusting while 80% of the plateau sponges were pedunculate, arborescent, or digitate (Table 2).

Sponge diversity (H') and evenness (J) reflected the similarities in sponge community structure observed across reef sites and highlighted the differences between habitats within reefs. Sponge diversity and evenness were similar for GRNMS ($H' = 2.08$; $J = 0.61$) and J Reef ($H' = 2.31$; $J = 0.67$), but the plateau values for these indices were nearly double that of the scarp (Table 2). The lower scarp values were due to 5 sponge species (*C. aff. nucula, I. felix, C. collectrix, Scopalina ruetzleri,* and *Spirastrella sp.*) accounting for >88% of the entire sponge assemblage on the scarp (Table 3). In contrast, plateau species were more evenly distributed with the four most common plateau species, *A. waltonsmithi, A. bookhouti, Cinachyrella alloclada,* and *Axinyssa ambrosia*, only representing 35% of the plateau population (Table 3).

Five species of spongivorous fishes were recorded at GRNMS and J Reef. They were *Holocanthus bermudensis* (blue angelfish), *Cantherhines macrocerus* (orange-spotted filefish), *Lactophrys quadricornis* (scrawled cowfish), *Pomacanthus arcuatus* (gray angelfish), and *Pomacanthus paru* (french angelfish). Of these 5 species, only 2, *H. bermudensis* and *C. macrocerus*, were observed during surveys. No differences in the density of spongivorous fishes occurred between GRNMS and J Reef, however, fish were only found in scarp transects (Fig. 3).

Table 2
Summary of distributional data, morphological classification, Shannon–Weaver diversity (H'), and Pielou's evenness (J) for the 32 sponge species recorded on the scarp and plateau habitats at GRNMS and J Reef.

Classification	Scarp	Plateau
Species that solely occupied this habitat	8	8
Species significantly more abundant in this habitat	7	7
Amorphous and encrusting species	15	8
Arborescent, pedunculate, and digitate species	6	15
Aspiculate species	10	6
Spiculate species	10	17
Diversity (H')	1.40	2.75
Evenness (J)	0.49	0.91

Data presented in this table are combined for GRNMS and J Reef. $N = 104$ quadrats of 0.25 m^2 in each habitat.

Table 3
Distributional data, morphological classification, and skeletal structure for sponge species found at GRNMS and J Reef.

Sponge Species	Habitat	Scarp density	Plateau density	Morphotype	Skeleton
Chondrilla aff. Nucula	Sc	17.5 ± 9.5		E	S
Ircinia felix	Sc	2.4 ± 1.5	0.3 ± 0.6	A	A
Chondrosia collectrix	Sc	1.9 ± 3.1		E	A
Scopalina ruetzleri	Sc	1.4 ± 1.6		E	S
Spirastrella sp.	Sc	1.4 ± 1.8	<0.1 ± 0.1	E	S
Aplysina fulva	Sc	0.7 ± 1.2	0.1 ± 0.7	B	A
Ircinia campana	Sc	0.5 ± 0.8	<0.1 ± 0.1	V	A
Hyrtios violaceaus	Sc	0.5 ± 0.9	<0.1 ± 0.1	A	A
Clathria prolifera	Sc	0.4 ± 0.7	<0.1 ± 0.1	P	S
Dysidea fragilis	Sc	0.2 ± 0.7		A	A
Coscinoderma lanuga	Sc	0.2 ± 0.6		A	A
Smenospongia cerebriformis	Sc	0.1 ± 0.4	<0.1 ± 0.1	A	A
Geodia gibberosa	Sc	<0.1 ± 0.1		E	S
Aiolochroia crassa	Sc	<0.1 ± 0.1		A	A
Myriastra sp.	Sc	<0.1 ± 0.1		E	S
Cliona celata	NS	<0.1 ± 0.1	<0.1 ± 0.1	E/A	S
Aplysilla longispina	NS	<0.1 ± 0.1	<0.1 ± 0.1	E	A
Axinella waltonsmithi	Pl	<0.1 ± 0.1	1.0 ± 1.1	P	S
Cinachyrella alloclada	Pl	<0.1 ± 0.1	0.9 ± 1.3	G	S
Axinella bookhouti	Pl	<0.1 ± 0.1	0.6 ± 0.9	P	S
Raspailia sp. A	Pl		0.5 ± 0.9	D	S
Unidentified sponge	Pl	<0.1 ± 0.1	0.5 ± 0.8	N/C	N/C
Axynissa ambrosia	Pl		0.5 ± 0.8	D	S
Higginsia strigilata	Pl		0.4 ± 0.7	P	S
Raspailia sp. B	Pl		0.4 ± 0.7	D	S
Axinella pomponaie	Pl	<0.1 ± 0.1	0.3 ± 0.6	B	S
Desmapsamma anchorata	Pl	<0.1 ± 0.1	0.3 ± 0.5	B	S
Clathria carteri	Pl		0.2 ± 0.5	P	S
Cliona sp.	Pl		0.2 ± 0.8	E	S
Ciocalypta gibbsi	Pl		0.2 ± 0.5	D	S
Lissodendoryx stigmata	Pl		0.1 ± 0.4	A	S
Ptilocaulis walpersi	Pl	<0.1 ± 0.2	0.1 ± 0.3	B	S

Habitat listed refers to reef zone in which that sponge species was significantly more abundant (one and two way ANOVA; $p \leq 0.05$) or solely occurred: Sc = Scarp, Pl = Plateau, and NS = no significant difference in density across habitats. Reported value equals the mean density (number of individuals 0.25 m^{-2} ± SD) recorded at the 2 scarp sites (GRNMS-scarp, J Reef-scarp) or the 2 plateau sites (GRNMS-plateau, J Reef plateau). $N = 104$ quadrats of 0.25 m^2. Morphological classifications for sponges based on descriptions by Freeman et al. (2007): A = Amorphous, B = Arborescent/Branching, D = Digitate, G = Globular, E = Encrusting, P = Pedunculate, V = Vase, and N/C = not classified. For skeletal structure A = Aspiculate and S = Spiculate. Species listed by habitat and in order of highest to lowest density within habitat.

3.2. Tests for sponge chemical and structural defenses

Food cubes containing chemical extracts or intact sponge tissues devoid of secondary metabolites from 11 and 8 of the predominant scarp and plateau sponge species, respectively, varied widely in their ability to deter predation by fishes. Across the sponge species tested, consumption of food cubes containing crude organic extracts ranged from 9 to 97% of those offered and 27% to 97% for food cubes containing intact sponge tissue without secondary metabolites (Fig. 4). Across reef habitats (i.e., scarp versus plateau) general differences in the mechanisms employed for predator deterrence were observed. Of the 11 scarp species assayed, 5 were significantly less palatable chemically than structurally and six showed no significant differences between chemical and structural palatability. In no instances were structural defenses found to be more effective at deterring fish predators than chemical defenses in the scarp sponge

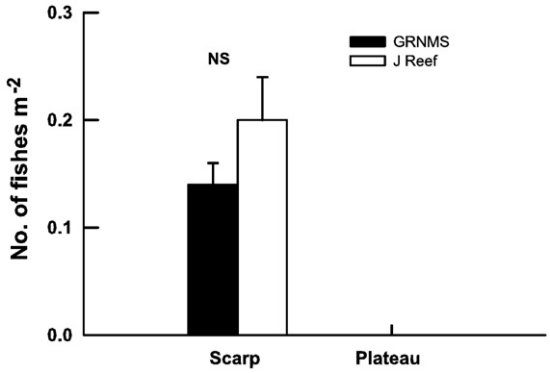

Fig. 3. Mean (±SE) density of spongivorous fishes on the scarp and plateau habitats for GRNMS and J Reef. $N = 4$, 50 m transects for each habitat at each reef site. Significant differences between habitats were tested for with a single factor ANOVA (NS = non significant).

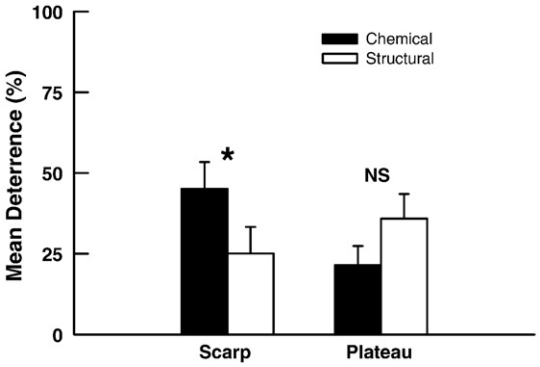

Fig. 5. Mean (±SE) deterrence of reef fishes by food cubes containing the crude organic extracts or natural tissue with the crude organic extracts removed of 11 scarp and 8 plateau sponge species represented at GRNMS and J Reef. Significant differences in mean deterrence between chemical and structural assays were tested with a Wilcoxon paired-sample test (NS = non significant: $T_s = 13$; $p = > 0.05$; *: $T_s = 5$; $p = 0.01$).

species assayed. In contrast, half of the 8 plateau species tested possessed structural defenses that were more effective than their chemical components in deterring predation by fishes (Fig. 4). Two plateau species were significantly less palatable chemically than structurally and 2 species showed no significant differences in their abilities to chemically or structurally deter predation by fishes (Fig. 4). Combining the results obtained for all sponge species within a single habitat showed that chemical defenses were the primary mode of deterrence against fishes for sponges resident on the scarp, while no single mechanism of defense was found to be significantly more common in plateau sponges (Fig. 5). When the results of the chemical and structural assays were combined for each sponge community, no significant differences in the combined mean deterrence between the scarp and plateau communities were detected (Fig. 6).

The differences in deterrence mechanisms observed among habitats, i.e. chemical defenses in scarp sponge species and a greater mix of chemical and structural components on the plateau, appear to be influenced by the predominant skeletal structure of the sponges occupying each reef zone. Aspiculate species tested in our assays relied significantly more on chemicals as an anti-predator mechanism (Fig. 7). These aspiculate species are common on the scarp, but account for <10% of the plateau sponge population (Table 3). On the other hand, spiculate sponge species we tested showed roughly equivalent reliance on chemicals and

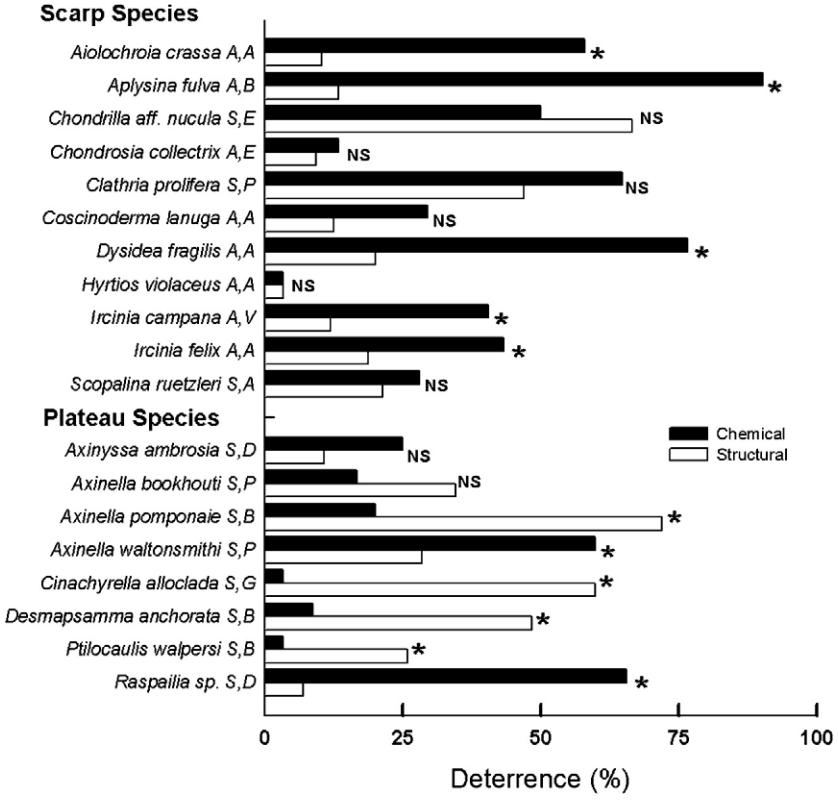

Fig. 4. Reef fish deterrence by food cubes containing crude organic extracts or natural tissue with crude organic extracts removed of 11 scarp and 8 plateau sponge species represented at GRNMS and J Reef. For both chemical and structural assays, sponge deterrence equals the total number of treated food cubes rejected divided by 30 treated food cubes offered. In all assays, fishes consumed all 30 control cubes. Significant differences between chemical and structural palatability were determined with a chi-square analysis (NS = non significant; * = $x^2 \geq 3.85$, $p < 0.05$). The first letter behind the species name denotes whether the species is aspiculate (A) or spiculate (S). The second letter denotes the species phenotype: amorphous (A), arborescent/branching (B), digitate (D), encrusting (E), globular (G), pedunculate (P), and vase (V).

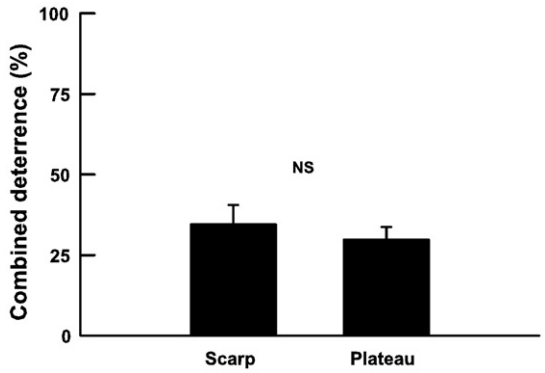

Fig. 6. Combined deterrence (mean ± SE) of reef fishes by food cubes containing the crude organic extracts or natural tissue with the crude organic extracts removed of 11 scarp and 8 plateau sponge species represented at GRNMS and J Reef. Mean deterrence between the scarp and plateau sponge communities was compared with a Kruskal–Wallis test (NS = not significant: $H = 0.170$, $p = > 0.1$).

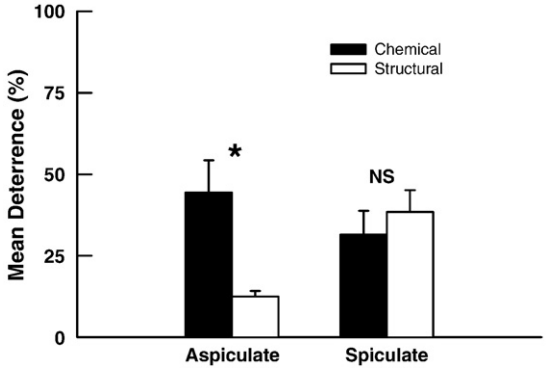

Fig. 7. Mean (±SE) chemical and structural deterrence of reef fishes by food cubes containing the crude organic extracts or natural tissue with the crude organic extracts removed of 8 aspiculate and 11 spiculate sponge species represented at GRNMS and J Reef. Significant differences in mean deterrence between the aspiculate and spiculate sponges were tested with a Wilcoxon paired sample test (NS = non significant: $T_s = 24$, $p = > 0.05$; *: $T_s = 0$; $p = 0.01$).

structure in deterring fish predators (Fig. 7) and compose >90% of the plateau sponge population.

Three species of fish were the primary generalist predators responsible for consumption of food cubes at GRNMS and J Reef. All three species, *C. striata* (black seabass), *H. aurolineatum* (tomtate grunt), and *D. holbrooki* (spottail pinfish), represent the most abundant generalist fish predators encountered on SAB reefs. *C. striata* consumed the greatest percentage of food cubes and consumed chemical and structural cubes in equal proportions (Fig. 8). *H. aurolineatum* consumed a greater number of chemical food cubes than structural, while the reverse was true for *D. holbrooki* (Fig. 8).

3.3. Transplant experiments

All sponges transplanted across habitats showed reductions in volume during the 9 day experiment except caged samples of *C. collectrix* (Fig. 9). Mean reductions in volume were observed on transplanted sponges in both caged and uncaged treatments, but these reductions were significantly larger in uncaged treatments for 3 of the 4 plateau species transplanted to the scarp and one scarp species, *C. collectrix*, transplanted to the plateau (Fig. 9). Handling effects on caged treatments were observed for two species, *A. waltonsmithi* ($t = 2.46$, $df = 11$, $p = 0.03$) and *D. anchorata* ($t = 3.39$, $df = 11$, $p = 0.005$) where the final volume was significantly less than the initial volume at the conclusion of the experiment.

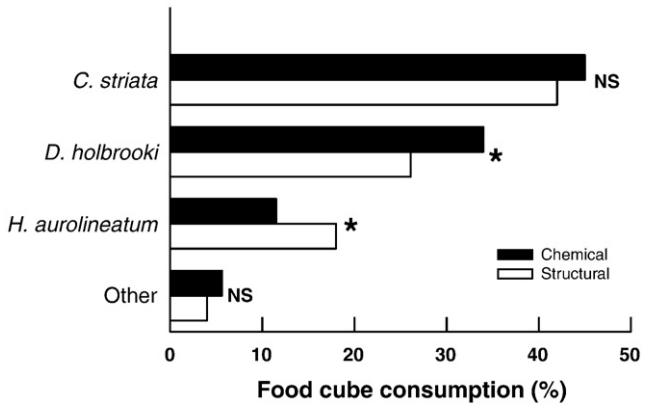

Fig. 8. Consumption by *C. striata*, *D. holbrooki*, *H. aurolineatum*, and other reef fishes of food cubes containing the crude organic extracts or natural tissue with the crude organic extracts removed of 11 scarp and 8 plateau sponge species represented at GRNMS and J Reef. Food cube consumption equals the total number of treated food cubes consumed divided by the total number of food cubes offered. Significant differences between the number of chemical and structural food cubes consumed by each species were determined with a chi-square analysis (NS = non significant; * = $x^2 \geq 3.85$, $p < 0.05$). For both assays, $N = 570$ food cubes offered.

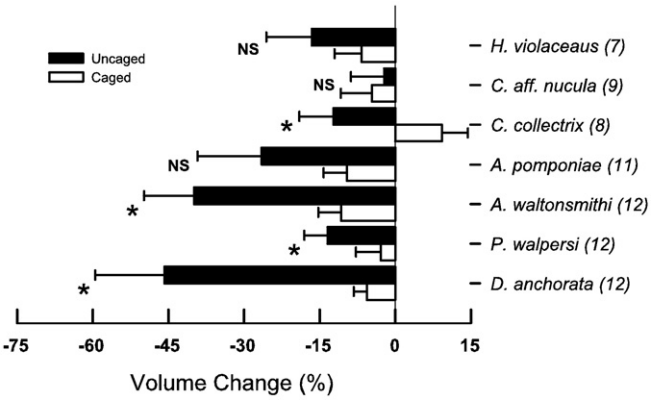

Fig. 9. Mean (±SE) percent change in volume after 9 days for three scarp sponge species (*H. violaceaus*, *C. aff. nucula*, and *C. collectrix*) transplanted from the scarp to the plateau habitat and four plateau species (*A. pomponiae*, *A. waltonsmithi*, *P. walpersi*, and *D. anchorata*) transplanted from the plateau to the scarp habitat. Significant differences in volume between the uncaged and caged treatments were compared using a Wilcoxon paired-sample test (NS = non significant; * = $p < 0.05$). N = number of samples recovered after conclusion of experiment (indicated in parenthesis).

Predation scars were clearly evident on sponges that suffered partial mortality in uncaged treatments. Predation by invertebrates could be distinguished from that by fishes because the fish left large semi-circular bite marks in the sponge tissue while invertebrate grazing often resulted in shallow, irregular scarring along the surface. For the 3 species of sponges that showed significantly greater losses of volume when transplanted from the plateau to the scarp and left uncaged, the type of predation causing the tissue loss differed. Grazing scars caused by invertebrates were apparent on *A. waltonsmithi*, while fish bites were almost exclusively observed on *P. walpersi*. *D. anchorata* was preyed upon by both fishes and invertebrates. Although uncaged samples of *C. collectrix* showed significantly greater losses of volume when transplanted from the scarp to the plateau, the predators responsible were not identified from scarring patterns. Unlike the other sponges tested, significant differences between caged and uncaged treatments of *C. collectrix* resulted from a combination of growth in caged treatments and predation in uncaged treatments. In many instances, recollected samples of *C. collectrix* had firmly reattached to the brick and required removal with a dive knife.

4. Discussion

Sponges are important components of marine benthic communities spanning tropical, temperate, and polar habitats (Dayton et al., 1974; Targett and Schmahl, 1984; Bell and Barnes, 2000a; Becerro, 2008). Historically, abiotic processes like sedimentation, current regimes, and periodic disturbances from storms were considered the major factors influencing sponge distributional patterns on temperate reefs (Roberts and Davis, 1996; Bell and Barnes, 2000a,c). Results presented here demonstrate that predation, as well as the mechanisms used by sponges to deter predators, play a role in shaping sponge community structure on temperate reefs. Our findings, in part, agree with studies performed in the tropics demonstrating that sponges with lower levels of chemical defenses may be relegated to environments where there is a relative paucity of spongivorous predators, while chemically well defended species can persist in habitats where these predators are more abundant (Pawlik et al., 1995; Pawlik, 1998). The results of this study also indicate that sponges on SAB reefs are structurally defended, but these defenses may not be sufficient to allow survival in areas with high spongivore abundance.

Sponge species on SAB reefs are segregated into two assemblages: scarp and plateau. Sixteen of the 32 species we recorded occurred solely within one of these assemblages and 14 other species were significantly more prevalent on either the scarp or plateau habitat (Tables 2 and 3). The morphological characteristics of the predominant sponge species within the scarp and plateau assemblages are consistent with studies documenting the effects of abiotic factors on sponge zonational patterns on temperate reefs (Bell and Barnes, 2000c,d). For example, in this study, more than 90% of the sponges colonizing the scarp possess an amorphous or encrusting phenotype. It is believed these growth forms are able to withstand the scouring and abrasion that occurs along these habitats during periodic disturbances (Schmahl, 1990; Bell and Barnes, 2000b). In contrast, the adjacent sediment-laden plateau most likely restricts the recruitment of many of these species (Zea, 1993). Instead erect arborescent, digitate, and pedunculate growth forms comprise 80% of the plateau sponge assemblage. These phenotypes are known to have lower accumulations of inorganic particles that may cause suffocation of the organism (Trammer, 1983; Bell and Smith, 2004).

In addition to the differences in abiotic factors occurring between the scarp and plateau habitats, our results demonstrate variation in biotic factors that could serve to reinforce the dissimilarities in sponge morphology observed between these two habitats. Spongivorous fish densities were significantly higher on the scarp than on the plateau (Fig. 3) and it appears that spongivorous fishes do not forage along the plateau even though this habitat lies within several meters of the scarp. Angelfishes are known to defend small territorial feeding areas when food is sufficient (Hourigan et al., 1989) and their defense of the more food laden scarp may limit their foraging along the plateau. If predator abundance is used as a proxy for predation intensity (see Ruzicka and Gleason, 2008), sponges occupying the scarp appear more susceptible to attack by spongivorous fishes than those inhabiting the plateau. Thus, while both biotic and abiotic forces appear to play a role in structuring sponge distributional patterns on SAB reefs, the relative contribution of each to sponge community patterns is not known presently and will only become clearer with further study.

Scarp and plateau sponge assemblages show similar abilities to deter fish predators when the results for both chemical and structural assays are combined (Fig. 6), but the primary mechanism of deterrence appears to differ between these habitats. Sponges occupying the scarp rely most heavily on chemical defenses whereas no single mode of deterrence is more effective within the plateau sponge assemblage (Fig. 5). While it appears that there is a positive relationship between the abundance of spongivorous fishes and the effectiveness of chemical defenses on SAB reefs, it should be pointed out that other factors, besides the direct effects of predation, may be selecting for the high levels of chemical defenses observed in scarp sponges. In addition to their anti-predator properties, secondary metabolites in sponges are effective anti-pathogen and anti-fouling agents and may also impede the settlement of competing sessile species (Uriz et al., 1992; Becerro et al., 1994; Becerro et al., 1997; Kubanek et al., 2002). Space for sessile organisms is limited in the scarp habitat and sponge species exhibiting high levels of allelopathy may be at a competitive advantage (Becerro et al., 1995; Thacker et al., 1998). Alternatively, the higher abundance of spongivorous predators on the scarp may result in higher wounding rates for sponges occupying this habitat. If so, secondary metabolites may be produced in high concentrations in scarp sponges to neutralize infections that might occur after attack (Walker et al., 1985; Teeyapant and Proksch, 1993; Thoms et al., 2006). Such responses are not needed for those sponge species occupying the plateau because both competitor and predator densities are much lower than observed on the scarp.

Our results also suggest that structural components within sponge tissue provide some protection from generalist fish predators. Spiculate sponge species exhibited the highest levels of structural deterrence (Fig. 7) and 93% of the plateau species identified in this study were spiculate (Tables 2 and 3). Arborescent, digitate, and pedunculate growth forms are common on the plateau and the species possessing these erect phenotypes often require spicules to stabilize their growth forms (Koehl, 1982). The arborescent, digitate, and pedunculate species we investigated contained aggregations of spicules peripherally arranged throughout their tissue (Wells et al., 1960; Wiedenmayer, 1977; Alvarez et al., 1998). As a result, spicules may provide structural support and assist in deterring generalist predators. Indeed, the idea of skeletal elements serving as an exaptation for predator defense has been proposed before (Gould and Vrba, 1982; Jones et al., 2005).

Results of previous studies investigating the role of sponge structural elements in providing protection from predators have been equivocal (Chanas and Pawlik, 1995, 1996; Burns and Ilan, 2003; Hill et al., 2005). Many of these studies, however, disrupted the integrity of the sponge tissue by investigating the palatability of spicules in isolation or in unnatural orientations (Chanas and Pawlik, 1995; Burns and Ilan, 2003; Hill et al., 2005) whereas this study did not. Two inherent problems may arise from these earlier methodologies. First, spicules in their natural form are often concentrated in a particular region of the sponge skeleton. This organization is disrupted when the skeleton is disassociated and reinserted into food cubes (Burns and Ilan, 2003). Second, additional structural elements such as the outer cortex of the sponge and the fibrous network of spongin are eliminated. We maintained the integrity of the sponge skeletal structure so our results provide a comprehensive test of sponge structural defenses against generalist predators.

To our knowledge, only one other study has tested the anti-predator effectiveness of spicules and spongin skeleton in their natural configuration (Chanas and Pawlik, 1996). This earlier study tested two Caribbean sponge species, *Agelas clathrodes* and *Xestospongia muta*. Although these investigators detected no statistically significant deterrence of fish predators by intact structural components, a trend ($p = 0.06$) in favor of predator avoidance of food pellets containing sponge skeleton from *A. clathrodes* was evident (Chanas and Pawlik, 1996). Given these earlier findings and those of our study, it is clear that further investigation into the role of sponge structural components as predator deterrents is warranted.

As final cautionary notes when interpreting our tests of structural anti-predator defenses in sponges, we would like to address two points. First, sponge tissues used for the structural assays were only devoid of compounds soluble in the 1:1 methanol:dicloromethane solvent system. While, as noted earlier, this solvent combination has been shown to work well for extracting a wide range of secondary

metabolites (Cronin et al., 1995), it is conceivable that low concentrations of some anti-predator compounds were left behind in the sponge tissue and contributed to their deterrence. This possibility seems fairly remote considering the large differences in chemical and structural palatability for many of the sponge species tested, but at this point it cannot be wholly be excluded. Second, our feeding assays did not test the synergistic effect of chemical and structural defenses. It has been demonstrated that the interaction of chemical and structural defenses can enhance predator deterrence and the effectiveness of these defenses may be underestimated when tested individually (Burns and Ilan, 2003; Hill et al., 2005; Jones et al., 2005). The fact that every sponge species we assayed showed some level of deterrence, both chemically and structurally, and that the predator deterred varied by type of defense (e.g. *H. aurolineatum* consumed more chemical than structural food cubes while the opposite was true for *D. holbrooki*; Fig. 8), makes a synergism between chemical and structural defenses an intriguing possibility. Further study in this area is certainly warranted.

The transplant experiments provided evidence that predation occurs on both scarp and plateau sponge assemblages (Fig. 9). In some instances, however, observed losses in volume may have resulted from handling rather than predation. Unfortunately, the lack of reciprocal back transplants (e.g. transplanting plateau spp. back to the plateau) to control for handling effects was not accounted for in this study. For sponges transplanted from the plateau to the scarp, it was clear that both invertebrates and spongivorous fishes participated as consumers. Predation on sponges by invertebrates was confirmed when one set of plateau species transplanted to the scarp was recovered from a nearby crevice within the scarp rather than the brick to which it was initially attached. When removed from the crevice, only the rigid axial core of the sponge *D. anchorata* remained while all peripheral tissue had been consumed. This type of predation was frequently observed on samples of *D. anchorata* and is highly indicative of crab predation.

The fact that both invertebrates and spongivorous fishes consumed the plateau species transplanted to the scarp suggests that predators play a role in restricting the distribution of some sponge species on SAB reefs. Although the plateau species assayed in this study demonstrated a greater ability to deter predators by structural means (Fig. 5), physical defenses may not be as effective as chemical defenses against predators inhabiting the scarp. Indeed, 3 of the 4 species transplanted from the plateau to the scarp (*A. pomponiae, D. anchorata,* and *P. walpersi*) were significantly more deterrent structurally than chemically and all showed significantly greater losses in volume on uncaged as opposed to caged treatments. It has been shown that spongivorous fishes, echinoids, and crabs can tolerate spicules in their diet (Randall and Hartman, 1968; Birenheide and Amemiya, 1993 ; Wulff, 1994; Pawlik, 1998; Hill et al., 2005) and crabs can avoid consuming spicules via their feeding behavior (Waddell and Pawlik, 2000a). Additionally, it has been demonstrated that secondary metabolites are effective deterrents against invertebrate predators (Waddell and Pawlik, 2000b; Waddell and Pawlik, 2000a; Burns et al., 2003; Hill et al., 2005). While sponge structural defenses may deter the generalist predators occurring on the plateau, they may not be sufficient to inhibit the predators inhabiting the scarp that have evolved the ability to either tolerate or bypass the defensive potential of structural components. As a result, chemical defenses may be required for sponges to successfully colonize the scarp.

In summary, in three ways, the results of this study corroborate or expand our understanding of how predation and anti-predator defenses may influence sponge community structure. First, contrary to what has been thought (Chanas and Pawlik, 1995, 1996), structurally intact sponge tissue is an effective defense against generalist reef fishes. Although the primary role of spicules is to stabilize the skeleton of a sponge (Koehl, 1982), these structural components may also serve as an exaptation for defense against generalist reef fishes. Second, while abiotic factors are known to influence sponge community structure on temperate reefs (Bell and Barnes, 2000b,c), our results show that predation by spongivorous predators contributes to the observed patterns. Lastly, the findings presented here agree with those reported from tropical systems that chemical defenses in sponges may be more effective at deterring specialist predators than structural mechanisms (Pawlik et al., 1995; Waddell and Pawlik, 2000a). On temperate reefs, it appears sponge species that are well defended structurally but lack effective chemical defenses may be restricted to habitats where there is a relative absence of specialized predators that can tolerate or circumvent structural defenses.

Acknowledgements

We are indebted to the staff at Gray's Reef National Marine Sanctuary, including G. McFall, K. Golden, and P. Fischel, and the crew of the NOAA ship Nancy Foster who provided the logistical support to make all diving possible. We also express our gratitude to R. Van Soest for his assistance with sponge taxonomy and T. Barsby for his help with isolating sponge chemical compounds. Much appreciation goes to L. Bates, C. Freeman, H. Harbin, G. McFall, S. Mock, N. Jones, P. Erwin, and L. Wagner for field assistance. Lastly, the authors recognize the contributions of A. Harvey, B. Schulte, S. Vives and four anonymous reviewers whose comments and suggestions significantly improved this manuscript. This study was funded by grants from Gray's Reef National Marine Sanctuary, the National Undersea Research Program at the University of North Carolina at Wilmington (Subaward No. SAB-2004-20A and SAB-2005-10B), and the Georgia Southern University Graduate Student Professional Development Fund. **[SS]**

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