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# Latitudinal variation in spongivorous fishes and the effectiveness of sponge chemical defenses

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**Abstract** It has been proposed that predation pressure declines with increasing latitude and a positive correlation exists between predation intensity and the investment into chemical defenses. However, little direct evidence supports the idea that tropical species are better defended chemically than their temperate counterparts. Temperate reefs of the South Atlantic Bight (SAB) off Georgia, USA, provide a unique opportunity to study tropical sponges in a temperate environment. We documented sponge species richness and abundance, sponge predator density, and examined the ability of eight sponge species to chemically deter predation by fishes on two reefs in the SAB. We used rarefaction analysis and ANOVA to compare our results for sponge species richness and density, respectively, with similar published studies conducted on reefs of the subtropical Atlantic (i.e., Florida Keys). These analyses were combined with similar statistical comparisons for spongivorous fish species richness and density. Results showed that sponge species richness was lower, but sponge density was higher, on the temperate SAB reefs than on the subtropical reefs. Both spongivorous fish diversity and density were lower on the SAB reefs. The greater abundance of sponges and lower density of predators on SAB reefs suggest a lower frequency of predation on sponges on SAB reefs. Of the eight sponge species assayed from the SAB reefs, five possessed chemical extracts that were significantly less deterrent to fish predators than their tropical/subtropical conspecifics. When the results were combined across all sponge species, the chemical deterrence of fish predators was significantly lower for extracts obtained from the temperate sponge community as compared to the tropical/subtropical assemblage. These results support the more general hypothesis that a lower density and diversity of sponge predators occurs at high as compared to low latitudes in the western Atlantic and may contribute to decreased investment in chemical defenses.

**Keywords** Sponge · Chemical defenses · Predation · Atlantic reefs · Secondary metabolites

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## Introduction

A commonly accepted tenet of biogeography is that the intensity of both herbivory and predation are inversely proportional to latitude (Pianka 1966; Vermeij 1978; Bertness et al. 1981; Menge and Lubchencho 1981; Coley and Aide 1991; Pennings et al. 2001). This biogeographic pattern has been attributed to the greater diversity of consumers present at lower latitudes, although evidence supporting this hypothesis is mostly anecdotal (Vermeij 1978; Bertness et al. 1981; Pennings et al. 2001).

Concordant with the concept that the intensity of herbivory and predation are inversely correlated with latitude is the notion that tropical prey species are better defended from predators than those in temperate regions (Bakus and Green 1974; Vermeij 1978; Bolser and Hay 1996; Pennings et al. 2001). Direct support for this idea is rare, but has been provided from studies investigating latitudinal differences

in the palatability of conspecific salt marsh plants spanning a subtropical to high latitude temperate range (Pennings et al. 2001; Salgado and Pennings 2005). These investigators demonstrated that a diversity of herbivores showed a general preference for northern salt marsh plants as opposed to southern salt marsh plants. The evidence supporting this biogeographic pattern in plant defenses at the species level is significant because exceptions to this trend have been documented at higher taxonomic levels in a few orders of plants and marine algae (van Alstyne and Paul 1990; Targett et al. 1992; Swihart et al. 1994; Bolser and Hay 1996).

To date, the majority of studies investigating latitudinal variation in predator–prey interactions have been confined to herbivory on terrestrial plants, marine algae, and seagrasses (van Alstyne and Paul 1990; Coley and Aide 1991; Pennings and Paul 1992; Schupp and Paul 1994; Meekan and Choat 1997). Only a few studies have investigated the biogeographic relationship between the intensity of carnivory and the presence of prey defenses (Bakus and Green 1974; Vermeij 1978; Bertness et al. 1981; Menge and Lubchencho 1981). Although results of these studies suggest a decrease in both predation pressure and the prevalence of prey defenses with increased latitude, none of the above cited comparisons have quantified predator abundance nor tested the palatability of conspecific prey across regions. In fact, the only study that has compared prey chemical defenses against carnivores over a latitudinal gradient used predators and prey from different longitudes (i.e., western Pacific versus Mediterranean Sea) and suggests that prey species from temperate regions are as well defended as those from the tropics (Becerro et al. 2003). The paucity of information in this area, as well as the contradictory results obtained for those studies that have been completed, highlights the need for additional comparisons to determine how the intensity of carnivory and the incidence of prey defenses correspond with latitude.

Sponges are important contributors to marine benthic communities at all latitudes (Dayton et al. 1974; Alvarez et al. 1990; Bell and Barnes 2000) and many parallels have been drawn between predation on sponges and herbivory. For example, both plants and sponges are abundant, diverse, and often conspicuous. Both lack behavioral defenses, but possess chemical compounds that deter consumers (Bertness et al. 1981; McClintock 1987; Coley and Aide 1991; Schulte and Bakus 1992; Pawlik et al. 1995; Becerro et al. 2003). To date, there is no evidence supporting the hypothesis that sponges at lower latitudes are subjected to more intense predation than species at higher latitudes because carnivore abundance has never been quantified outside of the tropics. Likewise, no comparisons have been conducted within species to determine if an inverse relationship between sponge chemical defenses and latitude exists.

Temperate reefs in the South Atlantic Bight (SAB) of the United States provide an excellent opportunity to examine the relationship between predation pressure and chemical defenses in sponge species that have been studied at a similar longitude in tropical and subtropical coral reef systems. Several subtropical Atlantic and Caribbean sponge species and spongivorous fish predators are present on SAB temperate reefs (Ruzicka 2005). By concentrating on sponge species that co-occur on reefs at different latitudes, the goals of this study were to: (1) quantify the abundance of sponges and spongivorous fish predators on temperate reefs of the SAB, (2) test the palatability of sponge secondary metabolites to generalist fishes of SAB reefs, and (3) compare statistically the results obtained in this temperate system with similar studies conducted on the same sponge species in the tropics/subtropics. Thus, this study provides an initial assessment of how the abundance of sponge predators and chemical deterrence of conspecific sponges may vary with latitude.

## Materials and methods

### Study sites

Two reefs in the SAB, Gray's Reef National Marine Sanctuary (GRNMS; 31°36.056′ N, 80°47.431′ W) and J Reef (31°36.056′ N, 80°47.431′ W), were used for this study. Both reefs are rocky ledge outcrops consisting of consolidated sand, shell, and mud and are typical of the temperate western Atlantic continental shelf. These reefs provide between 1 and 2 m of vertical relief along a narrow ridge. On the elevated side of the ledge the hard substrate becomes flat and quickly transitions into an extensive area of soft substrata due to a shifting layer of sediment 1–5 cm thick. SAB reefs are colonized by a variety of epifaunal species, which together with the substrate form a three-dimensional habitat occupied by a diversity of invertebrates and small cryptic fishes. GRNMS and J Reef are separated by 15 km and have similar depth profiles averaging 18–20 m. Although water temperatures reach 26°C during summer, many tropical species cannot survive the winter temperatures that can be as low as 11°C (Hunt 1974).

### Sponge 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. To provide the best estimate of sponge and fish populations on these reefs, 25- and 50-m transects, respectively, were run parallel and

perpendicular to the ledge. For sponge distributional data, we recorded the total number of individuals for each species present in 0.25-$m^2$ quadrats haphazardly placed alongside the 25-m-long transects. A total of one hundred and four 0.25-$m^2$ quadrats were sampled at both GRNMS and J Reef: 52 quadrats for the sponge population on top of the narrow ridge and 52 for the adjacent sponge community on the elevated soft sediment habitat.

Spongivorous fish populations were assessed with a 50-m swim transect in which divers recorded all spongivorous fishes present along the transect for 30 min. Although many fish species incorporate sponges as a minor component of their diet, we concentrated our surveys on the few specialist fishes in the families Pomacanthidae (angelfish), Monacanthidae (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). 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 on 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.

To determine if sponge community structure and predator abundance are similar between GRNMS and J Reef, mean sponge species richness, sponge species density, sponge density, and spongivorous fish density were compared between reefs with a Student's *t*-test. If no significant differences occurred between reefs, the data were combined so that these parameters could be compared to results for mean sponge species richness and sponge and spongivorous fish densities published from studies conducted at lower latitude.

To determine if sponge species richness, species density (number of species $m^{-2}$), and density (number of individuals $m^{-2}$) differ between reefs at different latitudes, the results of this study were compared to a survey completed by Schmahl (1990) in the Florida Keys. Schmahl (1990) collected distributional information for sponges occurring along three depth contours in the Florida Keys; however, for the purposes of our comparison, only data he obtained from the fore reef at a depth similar to GRNMS and J Reef (i.e., 13–18 m) were used. Likewise, our results for spongivorous fish species richness and density were compared with those obtained by Hill (1998) in the Florida Keys. In our surveys and these published studies, the density of sponges and spongivorous fishes was enumerated as the number of individuals per square meter. Schmahl (1990) used 1-$m^2$ quadrats to quantify sponge populations in the tropics so we pooled the data obtained from every four consecutive 0.25-$m^2$ quadrats to put our sponge distributional data on the same scale.

Differences in mean sponge species density between the Florida Keys and SAB were compared using individual-based rarefaction analysis (Gotelli and Entsminger 2001). This type of analysis was appropriate for our study because of the taxonomic similarity of the organisms sampled (i.e., restricted to sponges) and the consistencies in sampling design. Rarefaction analysis was not appropriate for latitudinal comparisons of mean spongivorous fish species richness because only two species were observed at J Reef and GRNMS. Statistical comparisons of sponge and spongivorous fish densities between high and low latitude reefs were completed with a one-way ANOVA.

## Palatability of sponge crude organic extracts

Over 20 species of sponges are known to be shared between the tropical and temperate western Atlantic (Wells et al. 1960; van Soest 1984; Alvarez et al. 1998). Eight of these species, *Aiolocroa crassa*, *Aplysina fulva*, *Chondrilla* aff. *nucula*, *Chondrosia collectrix*, *Cinachyrella alloclada*, *Ircinia felix*, *Ptilocaulis walpersi*, and *Scopalina ruetzleri* were abundant enough at GRNMS and J Reef to be collected for extraction of anti-predator compounds. The palatability of chemical extracts from these species was tested against generalist fish predators.

Sponge collections were made from May up to and including December 2004. Samples of sponge tissue, ≤10 ml, were obtained by either subsampling large sponges or removing whole sponges from the substrate. A total of 30 samples was collected for each species with every sample originating from a physiologically distinct individual. Individuals 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 3–4 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). Identifications were confirmed by Dr Rob van Soest, University of Amsterdam.

Methods described by Pawlik et al. (1995) and 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 sponge tissue was 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, Colo.). Freeze-dried samples were crushed with a mortar and pestle into small pieces and extracted 3 times at 4°C for 24 h by immersing the sample in a 1:1 methanol:dichloromethane mixture. All extracts were

combined and passed through filter paper (P8 coarse; Fisher Scientific, 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 solvent was transferred to a pre-weighed 20-ml scintillation vial and concentrated to dryness by vacuum evaporation (model SC210A-115; Thermo Electron, Somerset, N.J.). 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 carrageenan:agar (85:15), and 150 ml distilled water. The amount of powdered squid mantle used in food preparation was based upon the mean protein concentration ($\sim$20.7 mg ml$^{-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 carrageenan:agar, squid mantle, and distilled water were thoroughly mixed and heated in a microwave to the boiling point. Immediately after heating, 4.25 ml food mixture was poured into each scintillation vial containing the 0.75 ml 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 × 1 × 1-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.

For each species, 30 control cubes were also prepared by combining 4.25 ml food mixture with 0.75 ml methanol devoid of sponge extract. When necessary, food coloring was added to control cubes to match the color of the food cube containing the crude extract so predatory behavior of fishes would not be influenced by color. Control cubes were readily consumed by fishes in all feeding assays.

Feeding assays were conducted in situ at GRNMS and J Reef. To be compatible with feeding assays conducted in previous studies (Becerro et al. 2003; Burns et al. 2003; Pawlik et al. 1995), food cubes were dispensed individually to generalist reef fish predators. On our SAB reefs these assemblages consisted predominately of black seabasses (*Centropristus striata*), tomtates (*Haemulon aurolineatum*), and spottail pinfish (*Diplodus holbrooki*). The feeding behavior of these fishes was appropriate for this type of study because they habitually "mouth" or "taste" their prey before consuming it. Thus, these assays should reflect a general pattern of overall predator deterrence by sponges occurring on SAB reefs.

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 fish could not habituate to a systematic pattern of cube release. Divers recorded if the cube was consumed or rejected. A food cube was considered unpalatable if fishes rejected it 3 or more times or if it sank to the bottom uneaten. Thirty samples were tested for each sponge species. The degree of chemical deterrence for each sponge species was computed by dividing the total number of food cubes consumed by the total number of food cubes offered.

To determine if palatability of sponges differs with latitude, levels of food cube consumption obtained in our study were compared to published data for feeding assays conducted with the same eight sponge species collected in Belize, Bahamas, and Florida Keys (Pawlik et al. 1995). The bluehead wrasse, *Thalassoma bifasciatum*, was used as the predator in this tropical and subtropical study. Although extract palatability was assessed in aquaria rather than in the field, both our study and this earlier one tested the deterrence of sponge extracts to resident, common generalist predators that had ready access to food cubes that were dispensed. It has been demonstrated that overall patterns of generalist fish behavior are similar between tropical and temperate reefs (Becerro et al. 2003; Burns et al. 2003; Burns and Ilan 2003) and, thus, measures of deterrence should be on a scale appropriate for each region making the results comparable. For the feeding assays conducted by Pawlik et al. (1995) as well as those performed in our study, all control cubes were consumed. This result justifies making direct comparisons of consumption rates for food cubes containing chemical extracts from conspecific sponges used in both studies. Latitudinal differences in sponge extract palatability were compared for each species with a $\chi^2$-test with a William's correction (Sokal and Rohlf 1995). We used the number of food cubes consumed and rejected for each species in Pawlik et al. (1995) as the expected ratio of cubes to be consumed and rejected in our assays. To determine if chemical deterrence differs at the sponge community level between the high and low latitude sites, a Wilcoxon signed-ranks test (Sokal and Rohlf 1995) was used to compare the combined deterrence of all eight species.

## Results

### Sponge and predator abundance

A total of 32 sponge species were recorded at GRNMS and J Reef. Of these, 29 were present at both sites while three species, *Myriastra* sp., *Aplysilla longispina*, and *Cliona celata*, were only recorded at J Reef. Two species of

spongivorous fishes, *Holacanthus bermudensis* and *Cantherhines macrocerus*, were recorded at both reefs. No significant differences in mean sponge species density (number of sponge species $m^{-2}$), sponge density (number of individuals $m^{-2}$), and spongivorous fish density were detected between GRNMS and J Reef (Table 1). Therefore, richness and density data from these two sites were combined and the means for SAB reefs were compared to published results from the Florida Keys (Schmahl 1990; Hill 1998).

Rarefaction analysis showed that sponge species richness is lower on SAB reefs than Florida Keys reefs, with significant differences evident even at sample sizes <100 individuals (Fig. 1). In contrast, both the density of sponge species and individuals was significantly higher on SAB reefs than on the Florida Keys reefs (Table 2). The greater abundance of sponges on SAB reefs is largely explained by three encrusting species that occur at both latitudes, *Chondrilla* aff. *nucula, Chondrosia collectrix*, and *S. ruetzleri*. Collectively, these species account for >60% of the sponge population on SAB reefs with a mean density of 42.5 (±44.5 SD) individuals $m^{-2}$ (Ruzicka 2005). On Florida Keys reefs, each of these species have a density of <1 $m^{-2}$ (Schmahl 1990).

Both spongivorous fish species richness and density were lower on SAB as opposed to Florida Keys reefs (Table 2). Although other species, such as *Pomacanthus paru* and *Pomacanthus arcuatus*, have been observed on SAB reefs, their occurrence is rare and they were not recorded during our surveys.

### Palatability of sponge crude organic extracts

Chemical extracts obtained from all eight SAB sponge species assayed in this study deterred generalist reef fishes to some degree; however, effectiveness was highly variable across species. *A. fulva* was the most deterrent species while *Cinachyrella alloclada*, *P. walpersi*, and *Chondrosia collectrix* all showed high palatability (Fig. 2). The other sponge species showed intermediate levels of deterrence.

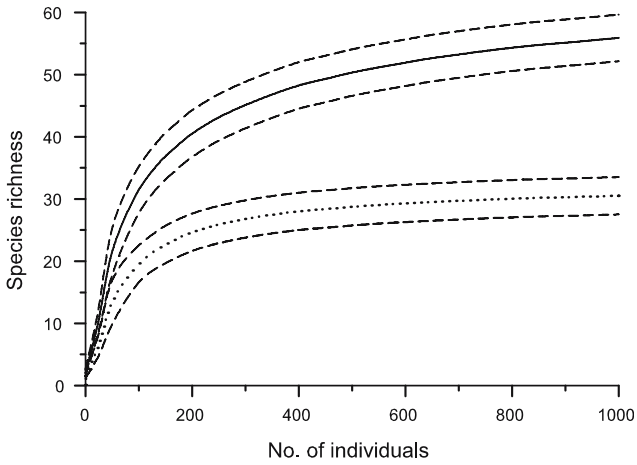


**Fig. 1** Sponge species richness (mean species density ± 95% confidence interval) in Florida Keys (*solid line*) and South Atlantic Bight (SAB; *dotted line*) reefs using individual based rarefaction. Data from the Florida Keys (Florida) are based on Schmahl (1990) while data from the SAB (Georgia) were collected in this study

Of the eight species tested from the SAB, chemical extracts from five of them (*P. walpersi*, *S. ruetzleri*, *C. alloclada*, *I. felix*, and *A. crassa*) were significantly less deterrent to generalist fish predators than their tropical/subtropical conspecifics (Fig. 2). No significant differences in sponge extract palatability were detected between the two geographic regions for *Chondrilla* aff. *nucula, Chondrosia collectrix*, and *A. fulva* (Fig. 2). Overall food cube consumption across the eight species assayed showed that the mean deterrence of fishes by chemical extracts was significantly lower (Wilcoxon signed-ranks test, $T_s = 0$, $P = <0.0039$) for temperate SAB (64% of treated food cubes consumed) as compared to tropical/subtropical (32% of treated food cubes consumed) sponges (Fig. 2).

## Discussion

Few studies have been conducted to test the hypotheses that: (1) an inverse relationship exists between predation intensity and latitude, and (2) that a lower incidence of predation at

**Table 1** Total sponge species richness, mean (± SD) sponge species density, mean (± SD) sponge density, and spongivorous fish species richness and mean (± SE) density on two South Atlantic Bight (SAB) reefs. Differences between sites in mean sponge species density, sponge density, and spongivorous fish density were compared using a Student's *t*-test. For sponge distributional data $n = 104$ quadrats (each 0.25 $m^2$) for each site. For spongivorous fish data, $n = 4$ transects (each 50 m long) for each site. *GRNMS* Gray's Reef National Marine Sanctuary

| Location | Sponge | | | Spongivorous fish | |
|---|---|---|---|---|---|
| | Species richness | Species $m^{-2}$ | Individuals $m^{-2}$ | Species richness | Individuals $m^{-2}$ |
| GRNMS | 28 | 10.0. ± 1.4 | 73.2 ± 45.0 | 2 | 0.14 ± 0.04 |
| J Reef | 31 | 9.3 ± 1.5 | 69.6 ± 48.1 | 2 | 0.20 ± 0.08 |
| Significance | – | $P = 0.10$ | $P = 0.46$ | – | $P = 0.62$ |
| *t* | – | 1.642 | 0.737 | – | 0.525 |

**Table 2** Sponge species richness, mean (±SD) sponge species density, mean (± SD) sponge density, and spongivorous fish species richness and mean (± SE) density on Florida Keys and SAB reefs. Florida Keys data for sponge composition is modified from Schmahl (1990) and for spongivorous fishes from Hill (1998). Data for sponge distributions and spongivorous fish densities only include surveys completed on Florida Keys reefs at 13–18 m depth because this depth is comparable to SAB reefs. Differences between mean sponge species density, sponge density, and spongivorous fish density were compared using one-way ANOVA. For sponge distributional data $n = 160$ quadrats (each 1 $m^2$) for the Florida Keys and $n = 208$ quadrats (each 0.25 $m^2$; 52 $m^2$ in total) for the SAB reefs. For spongivorous fish data, $n = 26$ transects for the Florida Keys, and $n = 8$ transects (each 50 m long) for SAB surveys

| Location | Sponge | | | Spongivorous fish | |
|---|---|---|---|---|---|
| | Species richness | Species $m^{-2}$ | Individuals $m^{-2}$ | Species richness | Individuals $m^{-2}$ |
| Florida Keys | 84 | 8.0 ± 3.2 | 12.8 ± 6.35 | 5 | 0.29 ± 0.05 |
| SAB | 32 | 9.7 ± 1.5 | 71.4 ± 46.9 | 2 | 0.18 ± 0.02 |
| Significance | – | $P = 0.004$ | $P < 0.001$ | – | $P < 0.001$ |
| $F$ | – | 8.598 | 75.902 | – | 17.696 |

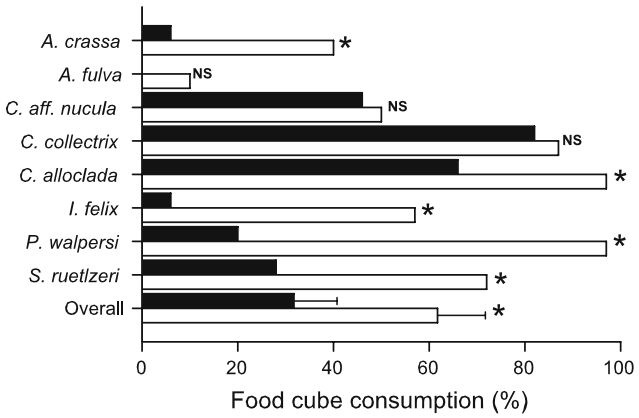


**Fig. 2** Reef fish consumption of food cubes containing the crude organic extracts of eight sponge species, *Aiolocroa crassa, Aplysina fulva, Chondrilla* aff. *nucula, Chondrosia collectrix, Cinachyrella alloclada, Ircinia felix, Ptilocaulis walpersi, Scopalina ruetzleri*, and overall consumption (mean ± SE) of these eight species in tropical/subtropical (*solid bars*) and temperate (*open bars*) reefs. Conspecific sponge palatability equals the total number of treated food cubes consumed divided by the total number of treated food cubes offered. Overall palatability represents the mean percentage of consumption for all eight species combined. Tropical/subtropical assays used *Thalassoma bifasciatum* as the predator while temperate assays used natural assemblages of reef fish on SAB reefs. Significant differences between tropical/subtropical and temperate conspecific sponge palatability were determined with a $\chi^2$ analysis (*NS* non significant; *asterisk* = $\chi^2 \geq 3.85$, $P < 0.05$). For all conspecific comparisons, $n \geq 30$ food cubes offered for both tropical/subtropical and temperate assays. A Wilcoxon signed-ranks test indicated overall consumption was significantly less for the conspecific sponges tested from tropical/subtropical locations (*asterisk*: $T_s = 0$; $P = 0.0039$). Data for sponge palatability on tropical/subtropical reefs are from Pawlik et al. (1995)

higher latitude corresponds with a reduction in prey antipredator defenses (Bertness et al. 1981; Coley and Aide 1991; Pennings et al. 2001). In sponges, the idea that tropical species are better defended chemically than their temperate counterparts was first proposed over 30 years ago (Bakus and Green 1974), but subsequent studies have demonstrated that secondary chemistry is common and important in sponges at all latitudes (McClintock 1987; Pawlik 1997; Becerro et al. 2003; Burns et al. 2003). The data presented here provide an initial assessment of how the chemical deterrence of predators by conspecific prey occurring at both temperate and tropical/subtropical western Atlantic latitudes may be correlated to predator abundance. Although our findings use predator abundance as a proxy for predation intensity, when combined with results from published tropical/subtropical studies from the same region, they support the general hypothesis that a lower density and diversity of sponge predators occurs at higher latitude and may contribute to decreased investment in chemical defenses.

## Sponge and predator abundance

This study found a significantly higher density of sponges and lower density of spongivorous fishes on two temperate western Atlantic reefs of the SAB as compared to the subtropical reefs of the Florida Keys (Table 2). This relationship results in there being approximately 396 and 44 sponges per spongivorous fish on SAB and Florida Keys reefs, respectively. While we do not have a direct measure of predation intensity, these differences in predator and prey density between regions are suggestive of lower attack rates by fishes on sponges residing on SAB reefs.

Evidence for lower predation pressure on SAB reefs is also reflected in the differences in sponge community structure apparent on these subtropical and temperate reefs. For example, sponge populations on SAB reefs are dominated by the encrusting species, *C.* aff. *nucula* (Ruzicka 2005). Considerable evidence suggests that *C.* aff. *nucula* is a favored prey species of spongivorous fishes (Randall and Hartman 1968; Meylan 1998; Pawlik 1998), yet this is the most abundant species occurring on SAB reefs accounting for ~50% of the sponge assemblage (Ruzicka 2005). In comparison, on Florida Keys reefs, the abundance of this

species is low with densities <1 individual $m^{-2}$ (Schmahl 1990). It has been demonstrated that in the absence of spongivorous fish predators, *C.* aff. *nucula* can rapidly overgrow coral reefs and become a top spatial competitor (Hill 1998). No differences in the ability of *C.* aff. *nucula* to chemically deter fish predators were observed across the temperate and tropical/subtropical studies (Fig. 2), thus we hypothesize that the differences in density of *C.* aff. *nucula* between these high and low latitude sites reflects the lower abundance of predators available to consume *C.* aff. *nucula* on SAB reefs.

While the evidence provided above supports the conclusion that predation on sponges is lower on this western Atlantic temperate reef system than it is on subtropical reefs of the Florida Keys, it is worth reiterating that we did not measure predation directly. Obtaining such measures on sponges at multiple sites is not trivial, but will be necessary if future studies are to further clarify the relationship between predation intensity and latitude in this, or any other, group of organisms.

## Palatability of sponge crude organic extracts

We found that five of eight sponge species present on the temperate SAB reefs are less chemically deterrent to fish predators than their counterparts at lower latitude (Fig. 2). Latitudinal differences in the ability of these five species to deter predators may reflect genetically fixed differences in the production of secondary metabolites or plastic responses to differences in predation intensity. Whether the former explanation applies in our study is unclear because the underlying population genetics of these systems have not been adequately investigated. Studies of the genetics of sponge populations and species are certainly warranted. For example, while thought historically to be one cosmopolitan species, allozyme electrophoresis has demonstrated that *C.* aff. *nucula* collected across the Mediterranean, Caribbean, and southwestern Atlantic, consists of at least five distinct genetic forms that show remarkable similarities in morphology (Klautau et al. 1999). Other sponge species, such as those within the *Callyspongia* complex, however, do not show this variability and maintain genetic homogeneity in populations across the Caribbean (Lopez-Legentil et al. 2007).

Species designations for sponges we collected on the two SAB reefs were not based on genetics, but rather morphological characters including colony shape and texture, size and density of oscules, spicule types, and dermal, subdermal, and endosomal organization. While the possibility exists that our within-species comparisons represent contrasts between cryptic species, published evidence suggests that this would not affect our overall conclusions because the chemical taxonomy of genetically related sponge species (i.e., species within the same family or order) is conserved and is independent of geographic origin (Bergquist and Wells 1983; Pawlik et al. 1995; Thoms et al. 2006).

The latter explanation for the differences in predator deterrence in sponges at these western Atlantic high and low latitude sites (i.e., plasticity in secondary metabolite production) may apply regardless of whether or not these populations at different latitudes are genetically isolated. Synthesis of compounds that deter predators is thought to be metabolically expensive (Paul 1992) and the ability to enhance production after attack may minimize this cost. Although rare in marine systems, the induction of chemical defenses is known for some seaweeds (Harvell 1990; Cronin et al. 1997) and the substantial variability in secondary metabolite production exhibited in some sponge species is suggestive of an inducible defense (Teeyapant and Proksch 1993; Swearingen and Pawlik 1998; Assmann et al. 2000). *Aplysina fistularis* has been shown to increase metabolite production after simulated attack, but it is unclear if this is in response to predation or to prevent infection of the wound (Walker et al. 1985; Thoms et al. 2006). Preliminary data for *I. felix*, a species tested in this study, shows temporal variation in the concentration of anti-predator compounds that may correspond with predator abundance (L. Bates and D. F. Gleason, unpublished data). If production of these compounds represents an inducible defense, and sponges on temperate reefs are subjected to a lower frequency of attack than those in the tropics, plasticity may explain the lower chemical deterrence in temperate sponges.

In contrast to the five species discussed above, no significant differences in predator deterrence between the lower and higher latitude reefs were observed for chemical extracts from three of the eight sponge species (Fig. 2). We attempted to identify some commonalities among the species in these two groups, i.e., those showing lower predator deterrence at higher latitude and those showing no difference, but none were obvious. Species in both groups were diverse in terms of their ability to repel predators ranging from the highly deterrent *Aplysina fulva* to the highly palatable *Chondrosia collectrix* in the group exhibiting no difference and from the deterrent *Aiolocroa crassa* to the palatable *Cinachyrella alloclada* in the group showing lower deterrence on the temperate reefs. Presence and absence of spicules, a structure thought to supplement chemicals in predator deterrence (Hill et al. 2005; Jones et al. 2005), also does not appear to provide any insight into the palatability patterns that we observed: both groups of sponges contain spiculate and aspiculate forms. It should be noted, however, that in no instance were chemical extracts of sponges from the temperate SAB reefs more

**Table 3** Indices of deterrence (*DET*)[a] for sponges tested from several tropical and temperate locations. Only studies that tested the palatability of sponge chemical extracts to fish predators are presented here. Temperate sites are SAB and Mediterranean Sea, tropical/subtropical sites are Guam, Caribbean, Red Sea, and Florida Keys. Whether the feeding assays were conducted in situ with random assemblages of reef fish (*Field*) or in aquaria with a single species (*Lab*) is indicated

| Study | No. of sponge species | Origin of sponges | Origin of predators | Predator | Field/lab | DET |
|---|---|---|---|---|---|---|
| This study | 8 | SAB | SAB | Reef fish assemblage | Field | 0.40 |
| Becerro et al. (2003) | 11 | Mediterranean | Mediterranean | Reef fish assemblage | Field | 0.51 |
| | 11 | Mediterranean | Guam | | | 0.47 |
| | 11 | Guam | Mediterranean | | | 0.50 |
| | 11 | Guam | Guam | | | 0.57 |
| Burns et al. (2003) | 17 | Caribbean | Caribbean | *Thalassoma bifasciatum* | Lab | 0.87 |
| | 17 | Caribbean | Red Sea | *Thalassoma klunzingeri* | Lab | 0.73 |
| | 17 | Red Sea | Red Sea | *T. klunzingeri* | Lab | 0.39 |
| Pawlik et al. (1995) | 71 | Florida Keys/ Caribbean | Florida Keys/ Caribbean | *T. bifasciatum* | Lab | 0.63[b] |
| | 8 | Florida Keys/ Caribbean | Florida Keys/ Caribbean | *T. bifasciatum* | Lab | 0.68[c] |

[a] DET was calculated using the formula in Becerro et al. (2003): DET = [(EC/OC) – (ET/OT)]/(EC/OC), where EC is the number of control food cubes or pellets consumed, OC is the number of control food cubes or pellets offered, ET is the number of treated food cubes or pellets consumed, and EO is the number of treated food cubes or pellets offered. For each study, the DET value represents the difference between the total number of control and treated food cubes or pellets consumed for all sponge species assayed. DET ranges between 0 and 1, with 1 representing the maximum level of deterrence (i.e., predators consumed no treated food cubes), and 0 indicating the minimum level of deterrence, (i.e. predators consumed the same proportion of treated and control food cubes or pellets). This formula corrects for differences in sample size and the number of control food cubes or pellets consumed so that DET values can be compared across studies

[b] DET value includes all sponge species assayed in Pawlik et al. (1995)

[c] DET value represents the subset of eight sponge species that were used for comparison to our results

deterrent to fish than those from the tropical/subtropical reefs (Fig. 2). Thus, a lower level of chemical defense at the high latitude site is the most parsimonious explanation for the differences in predator deterrence observed between our study conducted on temperate SAB reefs and those in the literature that were completed on tropical/subtropical reefs.

The validity of conclusions we reached by comparing our results to the literature were predicated on the assumption that assays used in different studies were comparable. Our tropical/subtropical to temperate comparisons would be invalid if the generalist fish predators used in our temperate assays were significantly more or less tolerant to sponge chemical extracts than *T. bifasciatum*, the predator used in the subtropical/tropical assays. A survey of the available literature in which sponge chemical extracts were tested against fish suggest that generalist fish predators, regardless of geographic origin, provide a reliable measure of deterrency (Table 3). Specifically, assays conducted by Burns et al. (2003) showed no significant differences in deterrence in 17 pairwise comparisons between the bluehead wrasse, *T. bifasciatum*, and Red Sea wrasse, *Thalassoma klunzingeri*, when both were fed food pellets containing extracts from the same Caribbean sponges (Table 3). Similarly, Becerro et al. (2003) reported no significant differences in deterrence for tropical (Guam) and temperate (Mediterranean) sponges when tested against sympatric and allopatric predators (Table 3).

Interestingly, the overall levels of deterrence we observed for the SAB sponges were more similar to those reported from the Red Sea, Mediterranean, and Guam than the subtropical/tropical western Atlantic (Table 3). In fact, indices reported from the Florida Keys/Caribbean are higher than any of the other regions tested. It is unlikely that this dissimilarity in deterrence values is an artifact of the assays being conducted by different groups of investigators because: (1) techniques used to extract chemicals from sponges and formulate food cubes were similar across studies; and (2) a single group of investigators (i.e., Burns et al. 2003) used the same techniques to investigate predator deterrence in both Red Sea and Caribbean sponges, but found those from the Caribbean to be much more deterrent (Table 3). While the factors accounting for these regional differences are beyond the scope of the current study, it does highlight the point that a full understanding of the biogeographic relationship between predation intensity and anti-predator chemical defenses will require comparisons to be made not only at different latitudes, but also at a variety of longitudes.

Finally, although differences in spongivorous fish diversity and density may account for some, or all, of the variation in sponge extract palatability that we observed,

we would be remiss if we did not acknowledge that the maintenance of secondary chemicals in sponges can be a function of factors unrelated to predation. For example, secondary metabolites in sponges are effective anti-viral, anti-bacterial, and anti-fouling agents and also impede the settlement of spatial competitors (Becerro et al. 1997; Kubanek et al. 2002; Kelly et al. 2005). Given that sponge populations on tropical and temperate reefs are likely subjected to differing levels of spatial competition, temperature, water turbidity, nutrient availability, pathogen exposure, and UV intensity, investigations into the role of these factors in affecting production of secondary compounds is warranted (Becerro et al. 1995; Turon et al. 1996; Targett and Arnold 1998).

## Conclusion

This analysis indicates that the density and diversity of spongivorous fish predators are lower on high latitude than on low latitude western Atlantic reefs. It shows that the sponges occupying SAB reefs are less effective at using chemical defenses to deter predation by sympatric fishes than their tropical/subtropical counterparts. These findings agree with those conducted on gastropods, decapods, and insects indicating predation by carnivores is reduced at higher latitudes (Jeanne 1979; Bertness et al. 1981; Heck and Wilson 1987) and is associated with a concomitant reduction in prey anti-predator defenses (Vermeij 1978). This study also expands on these earlier findings by providing quantitative estimates of the density of carnivores on temperate as opposed to tropical/subtropical reefs and by providing experimental evidence that observed differences in predator density coincide with an overall decrease in chemical defenses for prey species shared across these locations. At the level of individual species, our results corroborate those conducted with plants and marine algae (Targett et al. 1992; Bolser and Hay 1996) showing that differences in chemical deterrence across latitudes do not occur in all prey species. For some species of plants, algae, and sponges, it appears factors unrelated to predation, such as competition (Thacker et al. 1998) and pathogen resistance (Kubanek et al. 2002; Kelly et al. 2005), are proximate causes for the maintenance of these defenses irrespective of their geographic origin.

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