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Biogeography of sponge chemical ecology: comparisons of tropical and temperate defenses

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Abstract Examples from both marine and terrestrial systems have supported the hypothesis that predation is higher in tropical than in temperate habitats and that, as a consequence, tropical species have evolved more effective defenses to deter predators. Although this hypothesis was first proposed for marine sponges over 25 years ago, our study provides the first experimental test of latitudinal differences in the effectiveness of sponge chemical defenses. We collected 20 common sponge species belonging to 14 genera from tropical Guam and temperate Northeast Spanish coasts (Indo-Pacific and Mediterranean biogeographic areas) and conducted field-based feeding experiments with large and small fish predators in both geographic areas. We use the term global deterrence to describe the deterrent activity of a sponge extract against all of the predators used in our experiments and to test the hypothesis that sponges from Guam are chemically better defended than their Mediterranean counterparts. Sympatric and allopatric deterrence refer to the average deterrent activity of a sponge against sympatric or allopatric predators. All of the sponges investigated in this study showed deterrent properties against some predators. However, 35% of the sponge species were deterrent in at least one but not in all the experiments, supporting the idea that predators can respond to chemical defenses in a species-specific manner. Tropical and temperate sponges have comparable global, sympatric, and allopatric deterrence, suggesting not only that chemical defenses from tropical and temperate sponges are equally strong but also that they are equally effective against sympatric and allopatric predators. Rather than supporting geographic trends in the production of chemical defenses, our data suggest a recurrent selection for chemical defenses in sponges as a general life-history strategy.

Keywords Anti-predatory defenses · Defense effectiveness · Mediterranean vs Indo-Pacific · Latitudinal gradient · Predator–prey relationships

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Introduction

Predation is a significant source of mortality in natural communities with strong effects on community structure (Paine 1994; Carpenter 1997; Hixon 1997). Resistance to predation influences population dynamics of both producers and consumers (Lubchenco and Gaines 1981; Crawley 1983; Rhoades 1983) and it is a heritable trait subject to natural selection (Dimock et al. 1976; Rousi et al. 1991). Although there are several mechanisms to prevent predation (e.g., behavioral or structural defenses), chemically based deterrence seems widespread in marine environments (e.g., Paul 1992; Hay 1996; McClintock and Baker 2001, and references therein). Because there is ample evidence that secondary metabolites effectively deter predators, secondary chemistry may have evolved in response to predation, which seems to act as a driving force in the evolution of groups as diverse as butterflies (Berenbaum 1983; Feeny 1991), birds (Martin 1995), and mollusks (Cimino and Ghiselin 1998).

Chemical defenses may be particularly important in tropical environments because of the greater predation pressure associated with tropical ecosystems (Paine 1966; Pianka 1966). For example, herbivory is significantly greater in tropical than in temperate forests (Coley and Aide 1991), as are concentrations of plant defenses such as alkaloids (Levin and York 1978) and phenolic compounds (Coley and Aide 1991). Although marine systems appear to be more prey-dominated than freshwater or terrestrial communities (Warren and Gaston 1992), tropical reefs are thought to suffer greater predation pressure than any other marine or terrestrial community (Vermeij 1978; Carpenter 1986), creating greater potential for the evolution of chemical defenses. Bakus and Green (1974) found an inverse relationship between latitude and ichthyotoxicity in sponges and holothurians, suggesting that fish predators and grazers provide a selective pressure for the production and maintenance of chemical defenses. Similarly, tropical algae seem to be quantitatively and qualitatively better defended than temperate algae, since the former have greater numbers of secondary metabolites (Fenical 1980; Faulkner 1984; Hay and Fenical 1988) and stronger deterrent properties (Bolser and Hay 1996). Herbivorous fishes are more abundant on tropical reefs than on temperate reefs, creating greater herbivore pressure in the tropics (Meekan and Choat 1997), which may have selected for increased defenses in tropical seaweeds (Hay 1991; Bolser and Hay 1996). In addition, tropical grazers may be more tolerant of chemical defenses than temperate grazers (Steinberg et al. 1991; Cronin et al. 1997).

Although most data available in the literature assume that the latitudinal gradient in the production of chemical defenses is a response to increased predation pressure, there is little direct evidence that tropical species are, in fact, better defended against predators than temperate species (but, see Bolser and Hay 1996; Cronin et al. 1997). In addition, several studies have not found support for a latitudinal gradient in chemical defenses (McCaffrey and Endean 1985; McClintock 1987; Steinberg and Paul 1990; Van Alstyne and Paul 1990; Van der Vyver et al. 1990; Targett et al. 1992; Van Alstyne et al. 1999), which reinforces the need for direct tests of this hypothesis (Bolser and Hay 1996; Pennings et al. 2001) and suggests that factors other than predation may act as evolutionary forces on these chemicals (Schmitt et al. 1995; Bolser and Hay 1996; Becerro et al. 1997).

Sponges are widely distributed in marine systems and successfully inhabit hard- and soft-bottom communities from tropical to polar latitudes, littoral to abyssal habitats, and fresh- to saltwaters, being one of the major groups in both biomass and number of species in hard-bottom communities (Sara and Vacelet 1973). Sponges use chemical defenses against predators (Uriz et al. 1992a; Pawlik et al. 1995) and are among the richest sources of secondary metabolites for marine natural products chemists (Faulkner 2000 and references therein). Although structural defenses are also extremely effective as anti-predator defenses in both terrestrial and marine environments (Coley 1983; Adler and Harvell 1990; Pennings and Paul 1992) and may be subject to the same selective pressures and follow the same patterns as chemical defenses (Harvell 1990; Coley and Aide 1991), they seem to contribute little to defense against predators in sponges (Chanas and Pawlik 1995). Since sponges rely mostly on secondary chemistry to deter predators, their chemical defenses may be more abundant or more potent in environments with higher levels of predation (tropical reefs) than in environments with lower levels of predation (temperate reefs). Although this hypothesis was first proposed over 25 years ago (Bakus and Green 1974), it remains to be experimentally tested.

Our study tested the hypothesis that tropical sponges have evolved more effective chemical defenses than temperate sponges. Many factors at multiple scales affect the production of chemical defenses (Steinberg and van Altena 1992; Harvell et al. 1993; Becerro et al. 1995, 1998), but our hypothesis examines the effect of evolution in distinct geographic regions on the effectiveness of chemical defenses. Thus, we collected tropical (Indo-Pacific) and temperate (Mediterranean) sponge species that are phylogenetically closely related to test whether their deterrent properties significantly differ. Predator behavior and preference may also determine the outcome of feeding experiments, clearly affecting how we perceive the deterrent properties of our samples (Pennings et al. 1994; Schupp and Paul 1994; Cronin et al. 1997; Becerro et al. 1998). To avoid a species-specific pattern generated by a single predator, we conducted two sets of feeding experiments in the field that targeted different members of the fish community. We conducted these experiments in both tropical and temperate habitats to evaluate the deterrent properties of the sponges against predators that interact or do not interact with the sponges. Therefore, our approach allowed testing for differences between geographic areas not only from a producer (sponge) perspective but also from a consumer (generalist fish predator) perspective and at both local and global scales. From a producer perspective, we addressed the following questions: (1) Are chemical defenses from tropical sponges more effective than those from their temperate counterparts? (2) Are sympatric (i.e., co-occurring with the predators) chemical defenses more effective than allopatric (i.e., not sharing habitat with the predators) chemical defenses? From a consumer perspective, we also asked: (3) Do tropical and temperate predators respond similarly to the same chemical defenses? And if not, (4) are tropical predators less deterred than temperate predators?

Materials and methods

Geographic areas: sponge fauna and predators

We collected tropical and temperate sponges from multiple locations on Guam, western Pacific Ocean (13° 25' N, 144° 55' E), and Spain, western Mediterranean Sea (41° 43.2' N, 2° 56' E). Coral reefs are generally restricted to areas washed by warm

Table 1 Percentage yield of crude organic extracts obtained from temperate and tropical (*) sponges. We compared predator deterrence for 11 pairs of sponges, with some species taking part in more than one pair

Order	Family	Genus/species	Percent crude extract
Halichondrida	Axinellidae	*Acanthella acuta*	14.55
Halichondrida	Axinellidae	*Acanthella cavernosa**	25.16
Agelasida	Agelasidae	*Agelas oroides*	15.68
Agelasida	Agelasidae	*Agelas* sp.*	23.25
Verongida	Aplysinidae	*Aplysina aerophoba*	19.40
Verongida	Ianthellidae	*Ianthella basta**	23.76
Halichondrida	Axinellidae	*Axinella damicornis*	11.95
Halichondrida	Axinellidae	*Axinella* sp.*	5.26
Dictyoceratida	Thorectidae	*Cacospongia mollior*	13.91
Dictyoceratida	Thorectidae	*Cacospongia* sp.*	22.36
Dictyoceratida	Thorectidae	*Cacospongia scalaris*	6.55
Dictyoceratida	Thorectidae	*Cacospongia* sp.*	22.36
Poecilosclerida	Crambiidae	*Crambe crambe*	19.64
Halichondrida	Axinellidae	*Stylissa massa**	27.67
Halichondrida	Dictyonellidae	*Dictyonella obtusa*	20.59
Halichondrida	Axinellidae	*Stylissa massa**	27.67
Dendroceratida	Dysideidae	*Dysidea avara*	15.63
Dendroceratida	Dysideidae	*Dysidea* sp.*	9.86
Dictyoceratida	Irciniidae	*Ircinia fasciculata*	8.08
Dictyoceratida	Irciniidae	*Ircinia* sp.*	10.31
Haplosclerida	Petrosiidae	*Petrosia ficiformis*	21.53
Haplosclerida	Petrosiidae	*Xestospongia exigua**	23.08

currents (>20 °C). While Guam's waters have a temperature range from 28 °C to 30 °C that allows the formation of a highly diverse coral reef system (Paulay 1997), western Mediterranean waters have a temperature range from 11 °C to 25 °C (with 9 months per year below the 20 °C threshold for coral formation), with seasonal changes for many environmental variables that determine the characteristics of the Mediterranean benthic community (Margalef 1985).

Guam's tropical reefs support a highly diverse sponge community with over 100 species described (UOGML Systematic Collection). Sponges can be the most landscape-dominant benthic group on some reefs (Thacker et al. 1998). Similarly, sponges are important components on western Mediterranean rocky bottoms, with over 500 species described in the area (Pulitzer-Finali 1983; Boury-Esnault et al. 1994), where they can occupy most of the available substrate (Vacelet 1979; Uriz et al. 1992b). To test the hypothesis that tropical sponges are chemically better defended than temperate sponges, we selected tropical and temperate species that belong to the same genus and are major contributors to the composition of their respective hard-bottom communities (Uriz et al. 1992b; Kelly et al. 2002). We avoided selecting rare tropical or temperate species that would not represent the extent to which tropical or temperate sponges (as a group) are defended against predators. We therefore compared the phylogenetically closest and ecologically most common sponges that have evolved under the distinct environmental parameters of tropical and temperate habitats. When congeners could not be found, we selected species belonging to the same family or order. One comparison was an exception, *Stylissa massa* (synonymous with *Stylotella aurantium*; G. Paulay, personal communication) and *Crambe crambe*, which we paired because of structural similarities in their secondary metabolites (both contain guanidine alkaloids; Jares-Erijman et al. 1993; Kinnel et al. 1998). In our assays, we paired a tropical species with its temperate counterpart (e.g., tropical *Acanthella cavernosa* with temperate *Acanthella acuta*) and offered these species and their respective controls to predators in the field to test for their deterrent properties in both tropical and temperate communities. This procedure allowed us to test whether or not deterrence significantly differs between the two sponge species in the assay (see "Sampling procedures and field experiments" below). We tested a total of 20 sponge species in 11 species pairs (some species were included in more than one species pair; Table 1).

Guam's reefs provide habitat for over 600 fish species including generalist fish predators and spongivores (Hiatt and Strasburg 1960; Amesbury and Myers 1982). We conducted assays at Western Shoals, Apra Harbor, a 3- to 5-m-deep reef with a mixture of coral patches and rocky boulders. The most abundant generalist fish species that fed during our assays at this site included *Pomacentrus amboinensis*, *Amblyglyphidodon curacao*, *Abudefduf sexfasciatus*, *Scarus schlegeli*, *Naso vlamingii*, and *Cheilinus fasciatus*. In western Mediterranean benthic communities, predatory fishes can be locally abundant, especially in protected areas. We conducted assays at Cabrera Island National Park, inside a protected harbor. The most abundant generalist fish predators at this site included *Atherina boyeri*, *Boops salpa*, *Chromis chromis*, *Coris julis*, *Diplodus* spp., *Mugil* spp., and *Oblada melanura*.

Sampling procedures and field experiments

All sponge samples were collected while snorkeling or scuba diving at depths between 0 and 30 m. Samples consisted of several specimens of the same species (5–20) from one or several locations in an attempt to compensate for extremely low or high concentrations of secondary metabolites due to intraspecific variation (Becerro et al. 1995, 1998). For each species, we performed a bulk extraction that included all of the replicates to obtain the mean percent yield extract concentration to use in the assays (see next paragraph). Sponge species were collected independently and placed in separate plastic bags underwater. Once in the laboratory, we removed any foreign material before measuring volume (water displacement) and wet mass of every species. We froze (–40 °C), freeze-dried, and weighed our samples to obtain the species dry mass. We then chopped the sponges into small (<1 cm^3) pieces and soaked them in a mixture of 1:1 dichloromethane/methanol (DCM/MeOH) for 2–3 h. Solvents were changed two additional times to ensure an exhaustive extraction of the secondary metabolites in our samples. The three fractions were combined, dried, and weighed to obtain crude extract mass. Percent yield of crude extract was calculated as the mass of extract divided by the mass of dried sponge, multiplied by 100.

To quantify the anti-predatory properties in the sponges, we conducted two types of field feeding deterrence assays designed to target different assemblages of generalist fish predators. We disregarded specialist sponge predators (e.g., opisthobranchs) since, by definition, a specialist predator will feed exclusively on its prey, which a priori makes them unsuitable to test the general effectiveness of multiple chemical defenses from the diverse species collected at each location. One assay followed methods similar to those used by Becerro et al. (1998) and targeted medium-sized, demersal fish predators such as *Oblada melanura*, *Diplodus* spp., *Mugil* spp., and *Boops salpa* (Spain) and *Cheilinus fasciatus*, *Scarus schlegeli*, and *Naso vlamingii* (Guam). Numerous specimens of these species actively participated in the feeding assays. We added the appropriate amount of extract (in 2 ml of 1:1 DCM/MeOH) from the sponges to an artificial diet consisting of 5 g of ground catfish pellets (Kruse's Perfection brand), 2.5 g of a mixture of agar/carrageenan (15:85), and 80 ml of water. The amount of extract added varied to match the naturally occurring dry mass concentration of extract found in each particular sponge species. Control foods were prepared by adding 2 ml of DCM/MeOH (1:1) to the agar/carrageenan-food diet. The mixture was poured into 1-cm^3 molds to obtain control and treatment food cubes. The integrity of crude extracts following food preparation was examined by thin-layer chromatography. We extracted secondary metabolites from unused food cubes and compared them to the original crude extracts. No decomposition of any compounds was observed, as the number and colors of compounds were similar in the original extracts and in the extracted food cubes. In each trial, we tested the deterrent properties of a tropical species and its temperate counterpart, with their respective controls. We used a minimum of 40 and a maximum of 80 replicates per trial. We offered predators a single cube at a time and recorded whether or not the cube was eaten. In preliminary experiments, control cubes were completely eaten by predators within 15 (tropical predators) and 30 (temperate predators) s. Accordingly, we allowed tropical and temperate predators 15 and 30 s, respectively, to eat each food cube. In each replicate, we offered a treatment cube from one species in the pair followed by a control cube and then the treatment and control cubes for the other species in the pair. We randomly changed the order of the species among replicates and the order of control and treatment cubes within replicates to prevent predators from learning any sequence that may have affected the outcome of subsequent replicates and assays. We recorded a cube as "eaten" when a cube was totally eaten during the 15- or 30-s period, even if it was initially rejected or mouthed several times, and as "rejected" when a cube was continuously rejected and remained uneaten after the 15- or 30-s period. For data analysis information, see "Numerical methods" below.

We designed a second assay to specifically reach the small fish species that live next to the substrate where they feed and look for shelter. Numerous specimens of *Atherina boyeri*, *Coris julis*, and *Chromis chromis* (Spain) and *Pomacentrus amboinensis, Amblyglyphidodon curacao*, and *Abudefduf sexfasciatus* (Guam) actively participated in these assays, although the main predator species (95% of replicates) targeted with this method were *Chromis chromis* and *Pomacentrus amboinensis*. We added an appropriate amount of extract (in 1 ml of 1:1 DCM/MeOH) from the sponges to 0.3 g of food pellets (Sera Granumarin brand) to match the naturally occurring dry mass concentration of extract found in each particular sponge species. When dry, the pellets are 1 mm long rice-like grains, but they become more spherical after absorbing liquids. On average, there are 160 small pellets in 0.3 g. We added the solvent with the extract to a small vial containing the 0.3 g of pellets and let the solvent evaporate so that the pellets absorbed the extract. Some extract stayed behind on the wall of the vial, which makes this assay a slightly conservative one (i.e., natural concentrations are actually slightly higher than those tested). Control foods were prepared by adding 1 ml of DCM/MeOH (1:1) to the small pellets. Each trial tested the deterrent properties of a tropical species and its temperate counterpart with their respective controls. We used a minimum of 100 replicates per trial. Pellets were placed in syringes, from which a diver released them into the water. Another diver observed whether or not predators fed on the pellet. We offered a single pellet at a time and recorded a pellet as "eaten" when a pellet was totally eaten during the 15- or 30-s period, even if it was initially rejected or mouthed several times, and as "rejected" when a pellet was continuously rejected and remained uneaten after the 15- or 30-s period. For data analysis information, see "Numerical methods" below.

Numerical methods

Quantification of deterrence

We calculated a deterrence index to quantify the deterrent effects of a sponge extract towards the predators used in our experiments. The deterrence index (DET) is defined as:

$$\mathrm{DET} = \frac{\frac{\mathrm{EC}}{\mathrm{OC}} - \frac{\mathrm{ET}}{\mathrm{OT}}}{\frac{\mathrm{EC}}{\mathrm{OC}}}$$

where EC is the number of control cubes or pellets eaten by the predators, OC is the total number of control cubes or pellets offered to the predators, ET is the number of treated cubes or pellets eaten by the predators, and OT is the total number of treated cubes or pellets offered to the predators. DET has a maximum value of 1 when predators eat no treated food, i.e., the extract from the sponge totally inhibits feeding by the predators. DET approaches 0 when predators eat the same proportion of treated food as control food, i.e., the extract from the sponge does not inhibit feeding by the predators. By dividing the number of food items eaten by the number of food items offered, we standardized our data and prevented problems associated with the occasional small differences in sample size between controls and treatments.

We calculated DET for all of the assays conducted in our study, so there are four DET values for each sponge, i.e., one for each assay type (or targeted predator) and geographic location. We defined the global deterrence (GD) of a sponge as the average of its four DET values. The GD value of a sponge is based upon the deterrent properties of the extract against all of the predators used at both geographic locations, which makes GD an appropriate deterrence value to test the hypothesis that tropical sponges are chemically better defended than their temperate counterparts.

We defined the sympatric deterrence (SD) of a sponge as the average of its two DET values from the same geographic area where the sponge lives. Similarly, we defined allopatric deterrence (AD) of a sponge as the average of its two DET values from the geographic area where the sponge does not live. Since the SD and AD values are exclusively based upon the deterrent properties of the extract against sympatric (SD) or allopatric (AD) predators, SD is appropriate to test whether or not tropical sponges are more effective against sympatric predators than are temperate sponges, while a comparison of SD and AD values tests whether or not chemical defenses are more effective against predators that share habitat with a sponge than against predators that do not. We used Pearson's correlation among GD, SD, and AD values of tropical and temperate sponges to investigate whether their deterrent properties were related.

Contingency table analyses of sponge deterrence

We tabulated our data with comparison (the 11 pairs of species tested), geographic area of origin (tropical vs temperate region), treatment (control and treated food), and consumption (eaten or rejected) as factors and the number of occurrences (cubes or pellets) in each category as observed cell frequencies. We used two-way log-linear models (factors: treatment and consumption) to test whether sponges were deterrent and three-way log-linear models (factors: origin, treatment, and consumption) to test whether deterrence significantly differed between a tropical species and its temperate counterpart (Sokal and Rohlf 1995).

Effect of geographic area

We used four-way log-linear models (factors: comparison, origin, treatment, and consumption) to test whether the deterrent properties of sponges depend on their geographic origin. To test the hypothesis that tropical sponges are chemically better defended than their temperate counterparts, we compared the GD of tropical and temperate related species using paired *t*-tests. We tested whether or not tropical defenses are more deterrent than temperate defenses against sympatric predators by comparing the SD of tropical species and their temperate counterparts (paired *t*-tests, one-tailed *P*-values). We also tested the hypothesis that chemical defenses are more effective against sympatric predators than against allopatric predators by comparing the SD and AD of the sponges (paired *t*-test). One-tailed alternative hypotheses (i.e., that tropical species are more deterrent) are the ones of interest in our study, and their use diminishes the type II error and increases the power of our analyses (should the null hypothesis be accepted) as compared to two-tailed hypotheses (Sokal and Rohlf 1995). We checked for normality and equal-variance assumptions (Levene's test) and, if necessary, we ranked transformed data prior to running any parametric analysis (Potvin and Roff 1993).

Effect of predator groups

To determine whether or not feeding behaviors are correlated among predators, we compared deterrence (DET) against tropical and temperate predators and DET against large and small predators using Pearson's correlation coefficient. We also calculated an acceptance ratio (AR), defined as the amount of treatment food eaten divided by the amount of control food eaten. This ratio estimates predator acceptance (or tolerance) of sponge chemical defenses, as higher AR values indicate that predators eat a higher proportion of treated than control food. We used paired *t*-tests to compare AR between assay areas and predator groups.

Results

Sponge deterrence

All of the species investigated in this study had crude organic extracts that deterred at least one group of generalist fish predators (i.e., large vs small and temperate vs tropical) in the field (two-way log-linear models, Tables 2, 3). Most sponge species (65%) deterred all four groups of predators in the assays, while only 1 of 20 sponges exclusively deterred one predator group (tropical *Axinella* sp. deterred only large temperate predators; Table 2). Fifty-four percent (7 of 13) of the species that deterred all four groups of predators were tropical species (*Acanthella cavernosa*, *Agelas* sp., *Stylissa massa*, *Ianthella basta*, *Ircinia* sp., and *Xestospongia exigua*), and the remaining 46% were temperate species (*Acanthella acuta*, *Agelas oroides*, *Aplysina aerophoba*, *Crambe crambe*, and *Dysidea avara*). However, most sponges (71%) that deterred at least one but not all of the predator groups were temperate species (*Cacospongia mollior*, *Cacospongia scalaris*, *Dictyonella obtusa*, *Irci-*

Table 2 Percentage of food eaten by large predators in assays conducted in Guam and Spain. We show for each pair of sponges (1) the percentage of control and treated food eaten and (2) the significance of sponge deterrence and geographic origin of sponges. Sponge deterrence was tested using two-way log-linear models, while differences in deterrence among sponges from different geographic regions were examined using three-way log-linear models

Sponge comparison	Large predators in Guam				Large predators in Spain			
	Percentage eaten		Effects		Percentage eaten		Effects	
	Control	Treated	Deterrence	Origin	Control	Treated	Deterrence	Origin
Acanthella acuta	100.0	6.3	***	n.s.	82.5	5.0	***	n.s.
Acanthella cavernosa	100.0	4.4	***		90.0	0.0	***	
Agelas oroides	100.0	32.6	***	n.s.	85.0	27.5	***	n.s.
Agelas sp.	100.0	34.8	***		85.0	37.5	***	
Aplysina aerophoba	89.8	8.2	***	n.s.	78.5	25.3	***	n.s.
Ianthella basta	94.0	6.0	***		78.5	12.7	***	
Axinella damicornis	100.0	68.8	***	*	75.0	45.0	*	n.s.
Axinella sp.	100.0	93.8	n.s.		92.5	50.0	***	
Cacospongia mollior	100.0	68.9	***	*	65.4	26.9	***	n.s.
Cacospongia sp.	100.0	33.3	***		69.2	15.4	***	
Cacospongia scalaris	100.0	73.3	***	***	55.6	23.6	***	n.s.
Cacospongia sp.	95.7	26.1	***		54.2	19.4	***	
Crambe crambe	94.4	2.8	***	n.s.	57.5	11.3	***	**
Stylissa massa	100.0	2.8	***		68.8	37.5	***	
Dictyonella obtusa	100.0	41.3	***	***	68.8	17.5	***	n.s.
Stylissa massa	97.8	0.0	***		75.0	32.5	***	
Dysidea avara	97.7	27.9	***	n.s.	73.8	20.2	***	n.s.
Dysidea sp.	97.7	34.9	***		66.7	16.7	***	
Ircinia fasciculata	100.0	68.9	***	***	82.5	32.5	***	n.s.
Ircinia sp.	97.8	22.2	***		75.0	10.0	***	
Petrosia ficiformis	97.5	17.5	***	n.s.	71.3	50.0	*	***
Xestospongia exigua	100.0	7.5	***		74.7	3.8	***	

n.s. ($P > 0.05$); * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$

Table 3 Percentage of food eaten by small predators in assays conducted in Guam and Spain. For each pair of sponges tested, the percentage of control and treated food eaten and the significance of the effects of sponge deterrence and geographic origin of the sponges are shown. Sponge deterrence was tested using two-way log-linear models, while differences in deterrence among sponges from different geographic regions were examined using three-way log-linear models

Sponge omparison	Small predators in Guam				Small predators in Spain			
	Percentage eaten		Effects		Percentage eaten		Effects	
	Control	Treated	Deterrence	Origin	Control	Treated	Deterrence	Origin
Acanthella acuta	100.0	96.2	*	***	100.0	90.8	***	***
Acanthella cavernosa	99.2	56.3	***		100.0	54.2	***	
Agelas oroides	94.4	80.2	**	***	100.0	5.0	***	***
Agelas sp.	95.7	28.5	***		100.0	54.1	***	
Aplysina aerophoba	100.0	42.9	***	***	100.0	16.1	***	***
Ianthella basta	100.0	98.7	*		100.0	59.5	***	
Axinella damicornis	100.0	54.4	***	***	100.0	1.5	***	***
Axinella sp.	100.0	98.1	n.s.		100.0	99.2	n.s.	
Cacospongia mollior	100.0	99.4	n.s.	n.s.	100.0	99.3	n.s.	***
Cacospongia sp.	100.0	95.0	**		100.0	59.6	***	
Cacospongia scalaris	100.0	100.0	n.s.	*	100.0	71.8	***	n.s.
Cacospongia sp.	100.0	95.0	**		100.0	57.7	***	
Crambe crambe	100.0	10.2	***	***	100.0	0.0	***	n.s.
Stylissa massa	100.0	31.3	***		100.0	0.0	***	
Dictyonella obtusa	100.0	100.0	n.s.	***	100.0	100.0	n.s.	***
Stylissa massa	100.0	22.1	***		100.0	0.0	***	
Dysidea avara	100.0	33.6	***	***	100.0	91.3	***	**
Dysidea sp.	98.5	56.6	***		100.0	100.0	n.s.	
Ircinia fasciculata	100.0	100.0	n.s.	***	98.6	92.9	n.s.	***
Ircinia sp.	100.0	12.4	***		100.0	69.0	***	
Petrosia ficiformis	100.0	96.8	n.s.	***	100.0	82.0	***	***
Xestospongia exigua	100.0	2.0	***		100.0	0.0	***	

n.s. ($P > 0.05$); * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$

nia fasciculata, and *Petrosia ficiformis*) compared to only 29% (2 of 7) of tropical origin (*Axinella* sp., *Dysidea* sp.).

We found that global (GD), sympatric (SD), and allopatric (AD) deterrence were not correlated between tropical and temperate sponges (GD: r=−0.058, n=11, P=0.866; SD: r=−0.192, n=11, P=0.571; AD: r=0.067, n=11, P=0.844), indicating that evolutionarily related sponges did not necessarily have similar levels of deterrence. We found significant variation in deterrence in 26 of the 44 (60%) tropical versus temperate species comparisons investigated (three-way log-linear models; Tables 2, 3), again indicating that related sponges often varied in their ability to later predator.

Effect of geographic area

Four-way log-linear models showed a significant effect of the geographic area of origin on the deterrence of sponges against both predator groups at both assay locations (small tropical predators, G=1322.78, df=66, P <0.001; small temperate predators, G=1307.54, df=44, P <0.001; large tropical predators, G=104.92, df=44, P <0.001; large temperate predators, G=92.35, df=44, P <0.001). However, although the area of origin was a significant factor, the particular outcomes did not consistently show higher deterrence of one of the areas, i.e., both tropical sponges (e.g., *Acanthella cavernosa*; Table 3) and temperate sponges (e.g., *Axinella damicornis*; Tables 2 and 3) can be more effective than their respective counterparts. In fact, we found no quantitative differences in global (GD), sympatric (SD), and allopatric (AD) deterrence between tropical and temperate species (GD: t=−1.247, df=10, P=0.121; SD: t=0.753, df=10, P=0.235; AD: t=−1.620, df=10, P=0.136; Fig. 1A, B, C, respectively). Interestingly, we did find significantly higher percent yield of crude extract in tropical than in temperate sponges (t=-2.385, df=10, P=0.019, Fig. 1D).

We also tested the hypothesis that chemical defenses are more effective against sympatric predators than against predators that do not share habitat with the sponge. In both geographic areas, we found no significant difference in efficiency between chemical defenses from sympatric and allopatric sponges (tropical assays: t=0.117, df=10, P=0.455; temperate assays: t=-1.192, df=10, P=0.131).

Effect of predator groups

Considering the geographic area of the predators, tropical and temperate fish predators responded similarly to

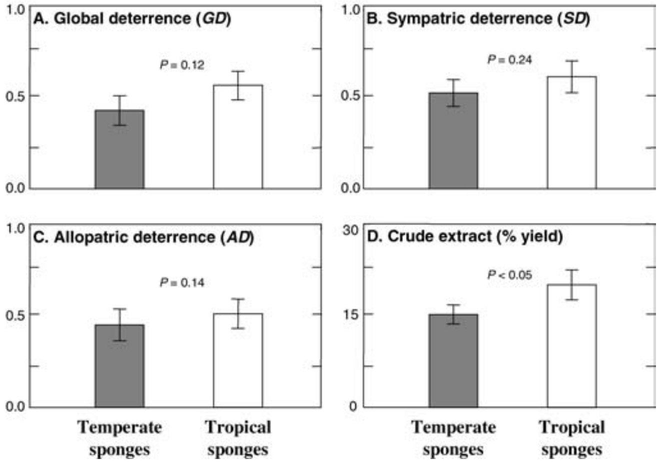

Fig. 1 Mean (±SE) values of the global deterrence (**A**), sympatric deterrence (**B**), allopatric deterrence (**C**), and percent yield of crude extract (**D**) for temperate (*filled bars*) and tropical (*open bars*) sponges. Mean differences between tropical and temperate sponges tested by paired *t*-tests (one-tailed *P*-values indicated)

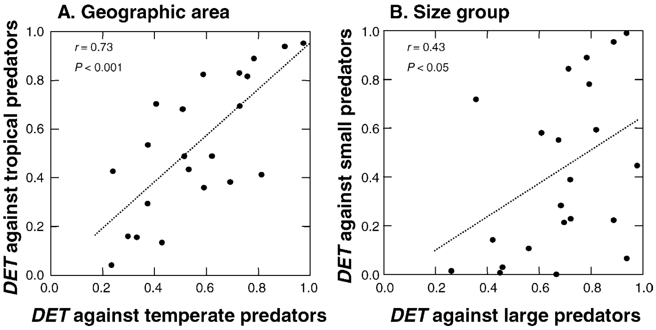

Fig. 2 Relationship between the levels of deterrence between predator groups according to their geographic area (**A**) and size (**B**). Pearson correlations indicated

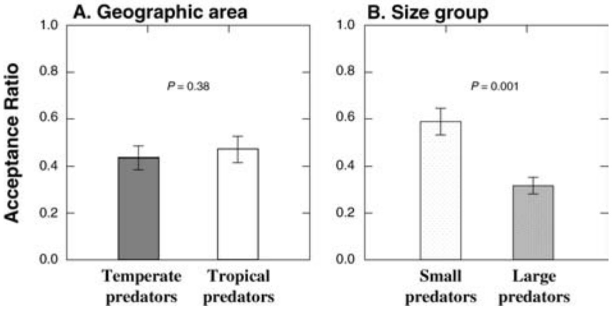

Fig. 3 Differences in the acceptance ratio (amount of treated food eaten divided by amount of control food eaten, mean ± SE) according to the geographic area (**A**) and size (**B**) of the predator. Mean differences between temperate and tropical species and small and large predators tested by paired *t*-tests (one-tailed *P*-values indicated)

sponge chemical defenses. We found a strong positive correlation between the deterrence obtained against tropical and temperate predators (r=0.734, n=22, P <0.001; Fig. 2A) and no significant differences between the amounts of treatment food eaten compared to control food (AR, t=-0.889, df=21, P=0.384; Fig. 3A), indicating comparable tolerance to sponge chemical defenses between the two geographic groups.

In contrast, we found differences in feeding behavior when considering the size of the predators. Although 60% of the related sponge species significantly differed in their deterrence, this proportion greatly changed with the size of predators (Tables 2, 3). Related species significantly differed in 86% (19 of 22) of the sponge comparisons tested against small predators, while only 32% (7 of 22) did so when tested against large predators. As a consequence of this variation in predator response, we found a weak correlation between the deterrence obtained from small and large predators that explained only 19% of the observed variation (r=0.431, n=22, P=0.045; Fig. 2B). Small and large predators also differed in tolerance to sponge chemical defenses, as indicated by the significantly higher amount of treated food eaten by the small predators (AR, t=3.726, df=21, P=0.001; Fig. 3B).

Discussion

A large body of indirect evidence supports the hypothesis that chemical defenses and other adaptive traits against predators increase with decreasing latitude (Bakus and Green 1974; Vermeij 1978; Hay and Fenical 1988; Coley and Aide 1991). Predation also seems to be negatively related to latitude, as supported by data from both terrestrial and marine systems (Pianka 1966; Bertness et al. 1981; Menge and Lubchenco 1981; Coley and Aide 1991; Warren and Gaston 1992; Coates 1998). Coupling these latitudinal gradients in levels of defenses and predation has resulted in a general acceptance that organisms living in environments with higher levels of predation have evolved better defensive mechanisms than have those living in environments with lower levels of predation, despite the paucity of direct evidence available (Bolser and Hay 1996; Cronin et al. 1997; Pennings et al. 2001). In marine systems, this hypothesis was first proposed for sponge chemical defenses over 25 years ago (Bakus and Green 1974) but, to date, there are no experimental data for or against the idea that tropical sponges are chemically better defended than temperate sponges.

We tested chemical extracts from tropical and temperate sponges in feeding deterrence assays with several generalist fish predators, categorized by their size and geographic location. Our approach allowed us to calculate the deterrence of sponge extracts against all of the predators in our tests (global deterrence, GD) and also exclusively against those predators that share (sympatric deterrence, SD) or do not share (allopatric deterrence, AD) a habitat with the sponges. We found no significant differences in the GD of tropical and temperate sponges, suggesting that the defenses of tropical sponges are as effective as those of temperate sponges. We found the same pattern for SD, i.e., tropical sponges deterred tropical predators as effectively as temperate sponges deterred temperate predators. We also found no significant differences between the SD and AD of tropical and temperate sponges, suggesting that, irrespective of their geographic area of origin, sponges equally deterred sympatric and allopatric predators.

Our results indicate that the deterrent effects of chemical defenses from tropical and temperate sponges are equivalent, contrary to what was expected according to the latitudinal gradient hypothesis (Bakus and Green 1974) and contrary to what has been described for algae (Bolser and Hay 1996). Since we did not replicate assay sites within geographic regions, any differences we may have observed are not necessarily due to a latitudinal gradient. However, our finding of no difference in deterrence contradicts the first studies on latitudinal gradients in sponge toxicity (Bakus and Green 1974; Green 1977). More recent data on toxicity from temperate and Antarctic sponges suggest that a simple inverse relationship between toxicity and latitude is questionable (McClintock 1987; Van der Vyver et al. 1990) and that toxicity and deterrence need not be correlated (Pawlik et al. 1995).

Although all of the species investigated in this study deterred some of the predators in the field, the degree of deterrence clearly varied within the pairs of tropical and temperate sponges, as indicated by the lack of correlation between the GD of the two members of each pair and also by the significant differences in feeding inhibition detected in up to 86% of the sponge comparisons. Although closely related from a phylogenetic perspective, tropical and temperate relatives have evolved under different evolutionary regimes, resulting in differences in their degree of deterrence against predators (Targett and Arnold 1998). These evolutionary forces seem dissociated from the particular traits associated with tropical and temperate environments since there is no dominance of one geographic area over the other one, i.e., for each geographic location there are sponges that are either more or less deterrent than their counterparts. Our results suggest that one or several evolutionary forces act in a species-specific manner irrespective of the geographic area investigated. Similarly, the lack of a latitudinal trend in marine algal polyphenolics and the variability within species at both tropical and temperate regions suggest that other factors may play a more critical role within each geographic area (Targett et al. 1992; Van Alstyne et al. 1999).

Our results apparently contradict those obtained from tropical and temperate seaweeds (Bolser and Hay 1996). To test the hypothesis that chemical defenses are more powerful in tropical than in temperate algae, these authors conducted feeding experiments involving extracts from seven genera of algae from North Carolina and the Bahamas. They concluded that tropical seaweeds have stronger chemical defenses than temperate seaweeds, although they found the genus *Dictyota* to be an exception to the overall pattern (Bolser and Hay 1996). The feeding deterrent properties of lipophilic extracts from tropical and temperate algae differed significantly in 53% (8 of 15) of the algal comparisons (Fig. 5A in Bolser and Hay 1996). Tropical algae were significantly more deterrent than their temperate counterparts in half of these comparisons (4 of 8), but the opposite was true for the other half. Excluding the genus *Dictyota*, there are five species comparisons left, and only two of them differed significantly between counterpart species (Bolser and Hay 1996). Thus, these results are in agreement, rather than in contradiction, with our findings for tropical and temperate sponges. In addition, Cetrulo and Hay (2000) found no difference in the frequency of activated chemical defenses in tropical and temperate algae.

We used two different natural assemblages of generalist fish predators in each geographic area in an attempt to provide a broader idea of how effectively chemical defenses deter predators, without limiting the output of our experiments to the specific behavior of a single species (Pennings et al. 2001). Large fish predators had lower tolerance than small fish predators to the same sponge extracts, supporting the idea that predators can respond to chemical defenses in a species-specific manner. Some of the small fish predators seem unlikely to include sponges in their natural diets, while large fish predators include species that are benthic grazers and microcarnivores, which may be consistent with the apparent selection of large fish against treated food. Thus, species composition rather than size itself might explain the differences between small and large predators. Tropical and temperate fish predators had the same tolerance and behaved similarly to the presence of the same sponge extracts, as indicated by the similarity of acceptance ratios between regions and by the strong correlation in deterrence obtained against tropical and temperate predators. Likewise, the feeding behaviors of the tropical and temperate sea urchins *Lytechinus variegatus* and *Arbacia punctulata* also are positively correlated (Bolser and Hay 1996). True sponge specialists might respond differently than generalist fish predators to the presence of sponge chemical defenses; i.e., they might actually be attracted to their food source. Quantitative data on site-specific differences in opisthobranch predation and other field-based, quantitative data on sponge predation are lacking and would provide valuable information on the effectiveness of chemical defenses against specialist sponge feeders across geographic regions.

The similarity of sympatric and allopatric deterrence suggests that the origin of a sponge (whether it was from a sympatric or allopatric habitat) did not affect predator behavior. Since most comparisons involved sponges belonging to the same genus, the possibility that the same (or structurally related) secondary metabolites may be responsible for the deterrent properties of the two species in each pair cannot be rejected. However, it is unlikely that these compounds occur at the same concentrations in each of the counterpart species due to the high variability in the production of secondary metabolites in sponges. For example, avarol, a sesquiterpenoid hydroquinone, is present in both the temperate *Dysidea avara* and in the tropical *Dysidea* sp. at concentrations ranging from 5% to 6% of dry mass in Spain (Uriz et al. 1996) and from 2% to 4% of dry mass in Guam (Davidson 1993). *Cacospongia* spp. produce a wide variety of scalarane sesterterpenes, including scalaradial and desacetylscalaradial, with the concentrations of individual compounds ranging from 0.004% to 1% dry mass (Rueda et al. 1997; Becerro et al. 1998; Cambie et al. 1998; Thacker et al. 1998). Although we have no evidence to support variation in the number of secondary metabolites and the concentrations at which they occur in each counterpart species, we did find a higher percent yield of crude organic extract in tropical than in temperate sponges. Whether secondary metabolites or other compounds, such as membrane lipids, account for these differences remains unknown; however, variation in the concentrations of secondary metabolites, as well as possible additive or synergistic effects, could explain differences in deterrence between counterpart species.

Overall, our results showed remarkable variation in deterrence among tropical and temperate sponge species, yet no geographic pattern emerged. We found that 6 of 11 tropical species were more deterrent than their temperate counterparts to large predators (Table 2) and to small predators (Table 3), supporting the hypothesis that tropical sponges are chemically better defended than temperate sponges. Supporting the opposite hypothesis, 1 of 11 temperate sponges was more deterrent than tropical sponges to large predators (Table 2) and 3 of 11 to small predators (Table 3). Variation of secondary metabolites occurs at several scales, including intra-specimen, intra-specific, and geographic scales (Uriz et al. 1991; Harvell et al. 1993; Becerro et al. 1995, 1998; Cronin and Hay 1996; Thacker et al. 1998; Van Alstyne et al. 1999). Although we evaluated deterrence rather than concentrations of secondary metabolites, and there is evidence that variation in secondary chemistry may have no consequences in generalist predators (Meyer and Paul 1992; Becerro et al. 1998), we collected multiple specimens from multiple locations in both geographic areas in an attempt to overcome the potential intra-specimen and intra-specific variability in sponge deterrence. However, we exclusively compared one tropical area in the Indo-Pacific region (Guam, western Pacific Ocean) with one temperate area in the Atlantic region (Northeastern Spain, western Mediterranean Sea). Marine organisms from the Indo-Pacific have higher levels of defenses against predators than those from the Caribbean (Palmer 1978; Vermeij 1978; Sammarco et al. 1986). Similarly, brown algae from temperate Australia have higher levels of chemical defenses than those from the temperate Atlantic (Steinberg 1989). Given the variation that occurs within tropical and temperate areas and our lack of replication within areas (Pennings et al. 2001), our results should be interpreted as an example where chemical defenses from temperate sponges can be as efficient as those from tropical sponges. A more general reading of our results is uncertain and should be attempted with caution. Further studies in other geographic areas and with other organisms will confirm whether our results are part of a global pattern or respond to specific traits of the areas we investigated.

Although there may be higher levels of predation in the tropics compared to temperate environments (Paine 1966; Pianka 1966; Bertness et al. 1981; Menge and Lubchenco 1981; Coley and Aide 1991; Warren and Gaston 1992; Coates 1998), other factors may follow a similar pattern. For example, competition can also be more intense in the tropics (Dobzhansky 1950; Williams 1964; Huston 1979). Since sponge secondary metabolites are known to play a role against competitors (Porter and Targett 1988; Thacker et al. 1998), the original inverse relationship between toxicity of sponges and latitude (Bakus and Green 1974) could reflect differences in competitive rather than predatory pressures. Thus, tropical sponges might be as deterrent as temperate sponges but simultaneously be better space competitors than temperate sponges.

Our results provide the first experimental evidence that the chemical defenses of tropical sponges are not more deterrent than those of temperate sponges, suggesting that chemical defenses from temperate and tropical sponges may be equally effective. These findings are consistent with the lack of a latitudinal gradient in the production of chemical defenses in sponges. However, our study does not demonstrate a general lack of latitudinal gradients, especially if we consider the multiple functions that secondary metabolites may play in nature, many of which may co-vary with predation. Because anti-predatory compounds seem to be present in many sponges, irrespective of their habitat or geographic area of origin (McClintock 1987; Van der Vyver et al. 1990; Uriz et al. 1992a; Pawlik et al. 1995), our results also suggest a recurrent selection for chemical defenses in sponges as a general trait of their life history. The ability to chemically deter generalist predators could explain the low levels of predation that many sponge species seem to suffer in the field (Hiatt and Strasburg 1960; Randall and Hartman 1968). Since predation is one of the main sources of mortality in benthic organisms, reducing levels of predation may provide sponges a remarkable advantage that could explain their ecological success in most benthic communities around the globe.

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