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Comparison of reproductive patterns among 7 Caribbean sponge species does not reveal a resource trade-off with chemical defenses

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ABSTRACT

Among sponge species on Caribbean coral reefs, some have defensive metabolites in their tissues that deter fish predators, while others tolerate predation. Assuming that resources are limited and chemical defenses are costly, sponge species that produce defensive metabolites should have less energy to allocate toward growth or reproduction. In a previous study, we documented a resource trade-off between chemical defenses and growth among 7 branching sponge species from shallow coral reefs off Key Largo, Florida. In the present companion study, we investigated the relationship between chemical defenses and reproduction among 7 sponge species (6 branching species from the previous study and 1 vase-shaped species) from the same location. From November 2007 to October 2008, monthly tissue samples were collected from the undefended species *Iotrochota birotulata*, *Niphates erecta*, *Callyspongia armigera* and *Callyspongia vaginalis*, and the defended species *Aplysina cauliformis*, *Aplysina fulva* and *Amphimedon compressa*. Using a standardized procedure, tissue samples were fixed, processed for histology, sectioned, stained, and photographed for the presence of reproductive propagules (oocytes, embryos or larvae). A reproductive output index (ROI: % area of propagules/total area of tissue scanned) was calculated for each sponge species. The ROI was highly variable across species and there were no significant differences in ROI between undefended and chemically defended species. Unlike the relationship for growth and chemical defenses, the absence of a clear trade-off between reproduction and chemical defenses is probably due to the additional confounding trade-offs between propagule formation and asexual reproduction by growth and fragmentation, which was previously demonstrated for *C. vaginalis* and *C. armigera*. In combination with our past studies, we provide a 3-dimensional graph of the relative investment in growth, reproduction and defense by the 7 sponge species and discuss how resource allocation has influenced the evolution of sponge communities on Caribbean coral reefs.

1. Introduction

Sponges are dominant members of the benthic sessile community on Caribbean coral reefs (Targett and Schmahl, 1984; Aronson et al., 2002; Maliao et al., 2008). Like all living organisms, sponges allocate available resources to physiological functions such as somatic growth and reproduction. In addition, some sponge species allocate resources to synthesize, store or release secondary metabolites that deter predation (Paul, 1992; Pawlik, 1993). Yet, other species that lack deterrent secondary metabolites co-exist on the reef despite predation (Pawlik et al., 1995; Pawlik, 1998).

The variability in deterrent activity among sponge species can be likened to that in terrestrial plants, for which many hypotheses have been advanced to explain the physiological and geographical patterns of chemical and physical defenses (Stamp, 2003; Agrawal, 2007). According to the resource availability hypothesis, organisms allocate available resources to defense, growth or reproduction (Coley et al., 1985; Bazzaz et al., 1987). Assuming resources are limited, a trade-off occurs. Hence, organisms can either invest in defense in order to resist predation, or tolerate predation by allocating resources to somatic growth or the production of reproductive propagules (Stowe et al., 2000). Resource trade-offs are well-documented in terrestrial plants (Koricheva, 2002; Stamp, 2003; Agrawal, 2007).

The primary predators of sponges on Caribbean coral reefs are angelfishes, parrotfishes, and turtles (Randall and Hartman, 1968; Dunlap and Pawlik, 1996; 1998; Leon and Bjorndal, 2002), all of which feed on a variety of sponge species that lack chemical defenses (Pawlik et al., 1995). Predation on Caribbean reef sponges is generally not affected by physical defenses (glass spicules, collagen fibers) or nutritional quality (Chanas and Pawlik, 1995; Jones et al., 2005); rather, secondary metabolites are primarily responsible for sponge defenses. Pawlik et al. (1995) tested the crude organic extracts of 73 Caribbean sponge species for palatability in feeding assays using the bluehead wrasse (*Thalassoma bifasciatum*). From the results of lab and

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subsequent field assays (e.g., Wilson et al., 1999; Pawlik et al., 2002), Caribbean reef sponge species were grouped into three categories: *preferred* species that are rapidly grazed from apparent locations on the reef and only survive in cryptic refugia, and *palatable* and *defended* species that both co-exist on the reef (Pawlik, 1998). The palatable species do not produce deterrent compounds, but instead tolerate predation by fishes, whereas defended sponge species produce a range of secondary metabolites that deter predation, some of which have been isolated and identified (e.g., Albrizio et al., 1995; Puyana et al., 2003; Grube et al., 2007; Morinaka et al., 2009).

There is accumulating evidence for resource trade-offs between chemical defenses and other life functions among Caribbean reef sponges, confirming that chemical defenses are costly to the sponges that have them. Walters and Pawlik (2005) demonstrated that common palatable species of tube sponges have faster rates of wound healing than similarly common defended species. Sponge colonization patterns on new benthic substrata also provided compelling evidence for resource allocation trade-offs. Surveys conducted on a 4-year-old shipwreck revealed that palatable sponge species dominated the wreck surface, unlike the surface of the adjacent coral reef, suggesting that undefended palatable species have higher rates of propagule production leading to faster recruitment, or more rapid growth, each of which would account for faster colonization (Pawlik et al., 2008). More recently, field experiments were conducted to directly test for trade-offs between growth and chemical defenses among 7 species of branching sponges (Leong and Pawlik, 2010a). When placed in cages that protected them from predatory fishes, chemically undefended, palatable sponge species grew faster than defended species, and palatable sponges outside of cages grew more slowly because of grazing by fish predators (Leong and Pawlik, 2010a).

Complicating matters of assessing resource trade-offs between chemical defenses and reproduction in sponges are the alternative strategies employed by sponges to reproduce, which are also subject to resource trade-offs. We recently examined trade-offs between growth and reproduction between two congeneric palatable sponges, the branched species *Callyspongia armigera* and the tube-forming *C. vaginalis,* and found that the former relies primarily on growth and fragmentation for reproduction, while the latter relies on the production of propagules (Leong and Pawlik, 2010b). Therefore, resource trade-offs between modes of reproduction may obscure trade-offs between chemical defenses and reproduction or growth.

Despite the foregoing, the objective of the study reported herein was to assess the resource trade-offs between chemical defense and reproduction as a companion investigation to our previous multispecies investigation of chemical defense and growth (Leong and Pawlik, 2010a). With the exception of *Callyspongia vaginalis*, all of the species used in the present study have a branching morphology, which made them more appropriate for previous comparisons of growth in field caging experiments (Leong and Pawlik, 2010a). In order to fully appreciate trade-offs in resource allocation, all the significant components to which resources may be allocated must be considered (Mole, 1994). However, because resources could be variably split at least 3 ways for any given species (growth, reproduction, and defense), patterns may be obscured in multispecies experiments designed to tease apart trade-offs between chemical defense and either growth or reproduction for palatable and defended species (Leong and Pawlik, 2010a,b). To address this concern, we focused on the same common sponge species as before: the palatable sponges *Iotrochota birotulata*, *Niphates erecta*, *C. armigera*, and *C. vaginalis,* and the defended species *Aplysina cauliformis*, *Aplysina fulva* and *Amphimedon compressa*. Of the defended sponge species, *Aplysina* spp. contain brominated tyrosine alkaloids common to all verongiid sponges (Puyana et al., 2003) and *A. compressa* produces pyridinium alkaloids that are highly deterrent to predators (Albrizio et al., 1995). Faced with the costs of synthesizing, storing or releasing these complex metabolites, we predicted that chemically defended sponge species would produce fewer propagules than undefended species. We used a histological approach to compare reproductive effort among species as a function of the surface area of propagules in sections of sponge tissue over the course of a year.

2. Materials and methods

Sponges were collected from Conch Wall in Key Largo, Florida, USA (N24°56'44 W80°27'23) and from shallow patch reefs shoreward of Conch Wall in Hawk Channel at 5–12 m depth. Monthly samplings were carried out between November 2007 and October 2008 on the following dates: 30 November, 18 December, 21 January, 24 February, 28 March, 19 April, 1 June, 27 June, 1 August, 28 August, 26 September, 25 October. For each species, three cubes of tissue, 1 cm on a side, were collected from mid-branch of each of five individual sponges and immediately fixed in 10% formalin buffered in seawater. Individuals were haphazardly selected, after ensuring a distance of at least 5 m between individuals to avoid the collection of clones.

Sponge tissue samples were processed for histology using standard techniques. Dehydration was carried out in graduated steps using ethanol (50%, 70%, 95%, 95%, 100%, 100%), then samples were cleared using toluene before being embedded in Paraplast Plus (Fisher Scientific) embedding medium. Sections were cut from embedded samples with a rotary microtome at 10 μm thickness and stained using haemotoxylin and eosin.

Photographs of sections were obtained using a SPOT camera connected to an Olympus BX60 microscope at 4x magnification. An area of 130 mm^2 was photographed haphazardly for each sponge (~40 mm^2 per cube), corresponding to 20 views among the sections. With 5 sponge samples per species, a total area of 650 mm^2 was photographed for each species per month. The area of reproductive propagules (comprising oocytes, embryos, or larvae, depending on the species) and the total area of the slides were quantified using ImageJ (Rasband, 1997). The reproductive output index (ROI = % area of propagules/total area of tissue scanned) was calculated for each individual sponge (after Whalan et al., 2007). The primary advantage of using ROI over counts or other common measures of reproduction is that it enables comparisons of reproductive output to be made among species.

Non-parametric statistical tests were used to determine whether total annual reproductive output (sum of monthly average ROI) was different among species, because the ROI data contained a large number of zeroes and did not have a normal distribution. The Kruskal–Wallis test was used to analyze the data, and followed by pair-wise comparisons using the Wilcoxon rank-sum test with a Bonferroni correction.

3. Results

Results for *C. armigera* and *C. vaginalis* were reported previously in a study comparing growth, fragmentation and propagule formation in two congeneric undefended sponge species with different growth morphologies (Leong and Pawlik, 2010b) and are repeated in this multispecies comparison of chemically defended and undefended sponge species that were previously examined for trade-offs between chemical defenses and growth (Leong and Pawlik, 2010a).

Aplysina cauliformis and *A. fulva* were oviparous, and produced small (20–30 μm) oocytes. The remaining species were viviparous and produced multicellular propagules, assumed to be sexual products (embryos and larvae), although no sperm were observed in sections of any species of sponge throughout this study (see Leong and Pawlik, 2010b). *Callyspongia vaginalis*, *C. armigera* and *N. erecta* had larvae of ~830 μm, 670 μm and 950 μm, respectively, consolidated in brood chambers, whereas *A. compressa* and *I. birotulata* had larvae of ~560 μm and 650 μm, respectively dispersed throughout the mesohyl (Table 1).

Table 1

Reproductive characteristics of 7 Caribbean sponge species sampled near Key Largo, Florida, USA. Bold species names indicate chemically defended species. Mean Reproductive Output Index (ROI) and standard deviation (SD) were calculated from 60 samples for each species (5 samples monthly) over a 1-year period. Post-hoc comparisons were carried out using Wilcoxon's test with a Bonferroni correction. Statistical differences in ROI between species are shown in different letter groups. "% repro" indicates percentage of reproductive samples out of 60. Propagule type is "O" for oocyte, "E" for embryo, or "L" for larvae. Size indicates the longest dimension of propagules observed in the samples.

	ROI	SD	Sig	Duration	% repro	Mode	Brood chambers	Propagules	Shape	Size (μm)
Amphimedon compressa	0.434	1.166	A	Mar–Sep	25	Viviparous	N	E, L	Round	560
Aplysina cauliformis	0.001	0.008	B	–	3	Oviparous	–	O	Round	20
Aplysina fulva	0.001	0.010	B	–	2	Oviparous	–	O	Round	30
Callyspongia armigera	0.041	0.222	B	–	3	Viviparous	Y	E, L	Elongated	830
Callyspongia vaginalis	0.535	1.082	A	May–Sep, Dec	30	Viviparous	Y	O, E, L	Elongated	670
Iotrochota birotulata	0.391	0.983	A	Mar–Oct	28	Viviparous	N	O, E, L	Round	650
Niphates erecta	0.096	0.427	B	May–Jul	5	Viviparous	Y	E, L	Elongated	950

Reproduction was highest between May and October, peaking in July and August (Fig. 1). *Amphimedon compressa* contained propagules throughout May to October. *Callyspongia vaginalis* also contained propagules throughout the summer, but had an additional reproductive peak in December. *Niphates erecta* contained propagules between May to July. *Iotrochota birotulata* contained propagules in the latter half of the summer, between July and October. It was difficult to determine seasonality in *A. cauliformis*, *A. fulva* and *C. armigera* because reproduction occurred at very low levels. Two samples of *A. cauliformis* contained oocytes in June, one sample of *A. fulva* was reproductive in January, and one sample of *C. armigera* from each of March and October contained propagules.

Annual reproduction was significantly different among species (Kruskal–Wallis; $\chi^2 = 53.244$, df = 6, $p < 0.0001$), and was highly variable within each species. The highest levels of reproduction occurred in *C. vaginalis*, the undefended tube sponge, which had an annual ROI of 0.54 ± 1.08% (mean ± sd; n = 60; Table 1). However, this was not significantly different from the defended rope sponge *A. compressa* (0.43 ± 1.17%) or the undefended rope sponge *I. birotulata* (0.39 ± 0.98%). Significantly lower levels of reproduction were found in the undefended rope sponges *N. erecta* (0.10 ± 0.43%) and *C. armigera* (0.04 ± 0.22%), followed by the defended rope sponges *Apysina cauliformis* (0.00 ± 0.01%) and *A. fulva* (0.00 ± 0.01%).

The species with the highest ROI also had the highest number of reproductive individuals: 18 out of 60 for *C. vaginalis*, 15 out of 60 for *A. compressa*, 17 out of 60 for *I. birotulata*, compared with 3 out of 60 for *N. erecta*, 2 out of 60 for *C. armigera* and *A. cauliformis*, and 1 out of 60 for *A. fulva*. When calculated using only the sponges where propagules were found, mean ROI per individual was comparable (0.012–0.019%) for all the viviparous sponges, and much lower for the oviparous sponges (0.0003–0.0007%).

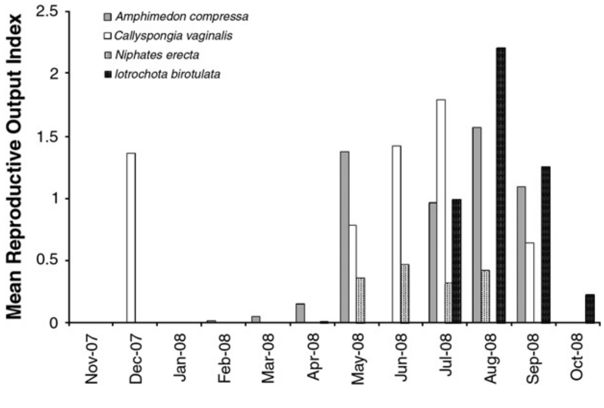

Fig. 1. Mean monthly reproductive output index (ROI) for samples of tissue from 4 coral reef sponge species sampled near Key Largo, Florida (n = 5). Data not shown for the remaining 3 species because ROI was very low (see Table 1). Variance for each mean is shown in Table 1. *Amphimedon compressa* is chemically defended, while the other 3 species shown are not.

4. Discussion

A resource trade-off between chemical defenses and reproduction among the sponge species compared in this study was not evident, unlike that seen between chemical defenses and somatic growth for the same species in a previous companion study (Leong and Pawlik, 2010a). On average, chemically defended sponge species did not produce fewer propagules than the undefended palatable species, suggesting that competing resource allocation to chemical defenses is not a major factor determining allocation to reproduction in these sponge species. If there was a trade-off between chemical defenses and reproduction, it was likely too weak to stand out from confounding factors in this multispecies comparison, particularly the compounded trade-off between fragmentation and propagule formation for branching sponge species (Leong and Pawlik, 2010b; see below). Resource trade-offs between defense and reproduction are documented for plants, but only in comparisons among conspecifics (Bergelson and Purrington, 1996; Koricheva, 2002). Similar comparisons among Caribbean reef sponges are not possible, because conspecifics are either chemically defended or not (Pawlik et al., 1995).

Data on reproduction for sponges are rare, and this study represents the first systematic analysis of reproductive output for several reef sponge species over a full year. Reproductive output of viviparous species in this study ranged from 0.01 to 0.54%, falling in the same range as ROI reported for other sponge species (Whalan et al., 2007). No sperm were observed in any histological sections, a finding that has been reported for other studies of reproduction in sponges and attributed to sampling bias due to the transient nature of sperm in the mesohyl compared to the longer brooding times of larvae (Fell, 1989; Corriero et al., 1996; Tsurumi and Reiswig, 1997). Whalan et al. (2007) measured an ROI of 0.02–1.03% for propagules in *Rhopaloeides odorabile*, and calculated an ROI of <1–12% for other sponge species in the literature. Low levels of reproduction for *Aplysina* spp. reported in the present study is in agreement with an earlier study of *A. cauliformis*, in which only 9 sponges out of 208 were found to contain propagules (Tsurumi and Reiswig, 1997).

Despite the reproductive differences among the species in this study, we believe that the ROI was valid for making comparisons of trade-offs in resource allocation. While it could be argued that investment in oocytes may be lower than in embryos or larvae, either because the energy content or developmental time of these propagules may be different, the oviparous species had the lowest ROI values and among the lowest percentage of reproductive individuals in the population (Table 1), removing this potential complication. While a resource allocation trade-off was not evident between reproduction and chemical defense for these sponge species, a trade-off was documented between growth and chemical defense (Leong and Pawlik, 2010a).

Patterns of reproductive seasonality were consistent with examples in the literature in that most sponges were observed to contain or release propagules in the warmer months of the year (Elvin, 1976;

Fromont, 1994; Fromont and Bergquist, 1994; Mercurio et al., 2007; Whalan et al., 2007; McMurray et al., 2008). In the present study, the highest levels of reproduction during the warmer months between May and October also coincided with the season of highest growth (Leong and Pawlik, 2010a). Higher light levels during the summer may benefit sponges that gain nutrition from algal symbionts in their tissues (e.g., Cheshire and Wilkinson, 1991), but photosynthetic symbionts were not present in the tissues of 5 of the 7 species used in this investigation (all but *Aplysina* spp.; Steindler et al., 2002). It has been proposed that sponge growth rates may be tied to picoplankton concentrations, which increase during summer months (Trussell et al., 2006). Food availability may be higher in the warmer months, enabling sponges to obtain a higher amount of resources to invest in both growth and reproduction.

The most problematical issue when investigating resource trade-offs between chemical defenses and reproduction among multiple sponge species is likely the obscuring effect of trade-offs between different modes of reproduction. Organisms that reproduce clonally allocate fewer resources to propagule formation (Tunnicliffe, 1981; Highsmith, 1982; Lasker, 1984; Thomsen and Hakansson, 1995; Barrat-Segretain et al., 1998). Branching sponges can disperse and rapidly colonize new substrata by fragmentation (Wulff, 1991, 1995), and therefore allocate more resources to growth, producing fewer propagules (Tsurumi and Reiswig, 1997; Leong and Pawlik, 2010b). For example, the palatable species *Callyspongia armigera* has the lowest ROI, but the highest growth rate (Leong and Pawlik, 2010a,b). Its congener, *C. vaginalis*, has high ROI but lower growth rates (Leong and Pawlik, 2010b). Simultaneous trade-offs between chemical defense, propagule formation and growth, the last of which also plays a role in reproduction, complicates any attempt to specifically examine the relationship between propagule formation and chemical defense across multiple sponge species.

In order to evaluate resource allocation patterns among chemical defenses, growth and propagule formation, the values of these metrics for each of the seven sponge species were plotted on a graph with three axes (Fig. 2). The values for chemical defenses were taken from Pawlik et al. (1995) as the mean number of sponge extract-treated food pellets eaten by bluehead wrasses in aquarium assays. Values for growth were taken from Leong and Pawlik (2010a). Values on each axis were standardized to fall between 0 and 1, with the maximum value observed for each factor fixed at 0.9. The points disperse widely across the graph, indicating that sponges employ a range of evolutionary strategies to cope with resource allocation constraints. A theoretical surface plot where all axes sum to 1 was superimposed over Fig. 2 to show the range of expected values of resource allocation on which most species should theoretically lie. Species that lie above the plane should be more efficient and more abundant than species that lie on or below it. There are several assumptions of the model that need to be investigated further. The model does not account for variation in filtration and resource uptake rates among different sponge species, which may explain why defense, reproduction and growth do not sum to 1 for the species shown. Also, resource allocation and phenotypic traits should be constrained by natural selection to be correlated, but only if defensive metabolites have similar costs across species, an assumption that is probably not true. In fact, although the per-unit cost of producing propagules and tissue is constrained across species, the per-unit cost of producing defense probably varies, particularly if symbiotic bacteria are involved to lesser or greater degrees in the synthesis of deterrent metabolites. Defended species therefore have the highest potential to move above the plane, explaining why chemical defenses likely evolved multiple times. The small number of species on the graph is an obvious limitation, but as more information becomes available about growth and reproduction in other species of Caribbean sponges, clear patterns may emerge.

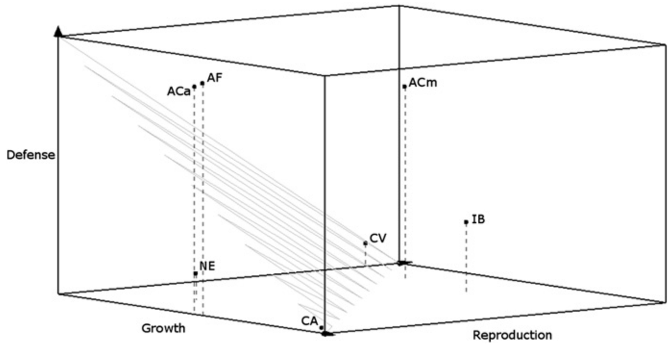

Fig. 2. Plot of relative investment in growth, reproduction and defense for the 7 sponge species included in this study, with each axis scaled between 0 and 1. Theoretical surface plot is overlaid, where the three axes sum to 1 (grey plane). Data taken from this and previous studies (see discussion).

With a better understanding of resource trade-offs between growth, reproduction and chemical defenses among Caribbean sponges, we can revisit and better explain patterns of sponge colonization on a shipwreck off Key Largo, Florida (Pawlik et al., 2008). In addition to documenting sponge abundance on the shipwreck, Pawlik et al. (2008) also measured the volumes of the largest sponges of each species present to infer their growth rates. Sponge species on the shipwreck with the largest biomass corresponded to the most reproductively prolific in the present study: the tube sponge *C. vaginalis* and a closely related congener *Callyspongia fallax*. Considering that branching sponge species have lower rates of propagule formation, it is possible that the growth rates of the branching species are underestimates if recruitment occurred later for these species. Sponge fragments, which are much larger and heavier than propagules, would not have recruited to the deck of the shipwreck because it was >15 m above the sand bottom on which the ship was sunk in an upright position. Interestingly, while *I. birotulata* was the second most abundant sponge on the wreck, *A. compressa* was not present, yet both produced similar high levels of propagules in the present study (Table 1). Information about differences in larval dispersal distances and settlement behavior may help to resolve this issue, but *I. birotulata* grows much faster than *A. compressa* (Leong and Pawlik, 2010a) and may rapidly grow and increase in abundance once a few propagules recruit to the wreck surface. It will be interesting to see how the sponge community continues to change on the shipwreck, and whether future studies of sponge community patterns, and of sponge growth and reproduction, corroborate our conceptual model of resource allocation trade-offs.

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