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Allelochemical Interactions Between Sponges and Corals

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Abstract. The existence of chemical-biological interactions is routinely invoked to explain patterns of coexistence between neighboring organisms. This study characterizes the consequences of these interactions in interspecific space competition between the neighboring species *Plakortis halichondroides,* the liver sponge, and *Agaricia lamarcki,* the sheet coral. This sponge/coral association was studied *in situ* both at points of natural contact and following manipulations that artificially brought the sponge and coral together. *Plakortis* kills *Agaricia* upon direct contact and upon indirect contact (*i.e.,* waterborne metabolites only). *Plakortis* creates a dead zone of coral around its base as it overgrows the coral. The effect of either direct or indirect contact by *Plakortis* is to reduce: (1) the number of zooxanthellae in *Agaricia,* (2) the weight of chlorophyll *a* per unit area of the coral, and (3) the weight of tissue nitrogen per unit area of the coral.

The necrotic effect also evidences itself as changes in oxygen flux characteristics such as significant increases in the compensation point and the nocturnal respiration rate, and significant reductions in the maximum net and gross photosynthetic rates. As a consequence, the diel integrated production to respiration ratio falls below unity for *Agaricia* colonies in contact with *Plakortis;* this does not occur for coral without neighboring sponges.

Because direct contact between *Plakortis* and *Agaricia* is not necessary to effect stress in the coral, the presence of active chemical metabolites from *Plakortis* is suggested. Thus, mechanical abrasion is excluded as the sole mechanism of dominance by the sponge.

Introduction

Sessile and sedentary coral reef organisms frequently compete for space and food, adopting mechanisms to minimize fouling or overgrowth by epibionts and maximize their own space-capture abilities. Several biological mechanisms that mediate ecologically significant interactions among coral reef organisms have been described. For example, scleractinian corals effect extracoelenteric damage to neighbors via extended mesenterial filaments and long sweeper tentacles (Francis, 1973; Lang, 1973; Richardson *et al.,* 1979; Wellington, 1980; Sheppard, 1982). Likewise, hydrocorals and octocorals can move onto and spread across scleractinians, and thereby compete successfully for space with reef-building corals (Wahle, 1980; La Barre and Coll, 1982; Tursch and Tursch, 1982). Bryozoans employ sweeper appendages which are effective in competition and in prevention of fouling (Jackson, 1977). These structures are used in specific behaviors that involve the recognition of potential competitors and the direction of interference mechanisms against them.

Chemical defense mechanisms have also been suggested. These mechanisms have demonstrable effects on species distributions and individual survivorship in terrestrial plant communities (Fraenkel, 1969; Whittaker and Feeny, 1971; Rosenthal and Janzen, 1979; Meinwald, 1982; Targett and Isman, 1986), and have recently been reviewed in ecological contexts for marine communities (Barbier, 1981; Bak *et al.,* 1982; Fenical, 1982; Norris and Fenical, 1982; Palumbi and Jackson, 1982; Colwell, 1983; Faulkner and Ghiselin, 1983; Steinberg, 1984; Scheuer, 1985; Bakus *et al.,* 1986).

Unusual secondary metabolites have been isolated from numerous sessile solitary and colonial coral reef organisms (Tursch *et al.,* 1978; Cimino *et al.,* 1983; Sullivan *et al.,* 1983; Coval *et al.,* 1984; Bandurraga and Fenical, 1985; Kashman *et al.,* 1985; and Coll *et al.,* 1985). Animals that contain unusual secondary metabolites of-

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ten prove to be toxic in bioassay examinations (Bakus and Thun, 1979; Bakus, 1981; Coll *et al.*, 1982a, 1983; Targett *et al.*, 1983; Gerhart, 1984; McCaffrey and Endean, 1985; Thompson, 1985; Thompson *et al.*, 1985; LaBarre *et al.*, 1986a, b). In addition to their role in organism defense, secondary metabolites are also implicated in the maintenance living space (Jackson and Buss, 1975; Green, 1977; Jackson, 1977; Sheppard, 1979, 1982; Sammarco *et al.*, 1983).

Sponges are remarkable because they lack specialized organs and behaviors, and yet are successful in an environment where such adaptations are common. However, sponges do contain a variety of bioactive secondary metabolites. More than three dozen compounds with lethal or growth inhibitory properties are described from tropical sponges in reviews by Russell and Saunders (1967), Sigel *et al.* (1969), Martin and Padilla (1973), Baker and Murphy (1976), Hollenbeak *et al.* (1976), Faulkner (1977), Cimino (1977), Minale (1978), Kaul and Sinderman (1978), and Hashimoto (1979). These researchers characterize the compounds chemically and occasionally list effects on organisms of direct interest to man, but rarely include data on the ecological importance of the compound or demonstrate effects on other marine organisms likely to have frequent encounters with the species. Recent work continues to identify unusual secondary metabolites from sponges (*e.g.*, Fusetani *et al.*, 1981; Tachibana *et al.*, 1981; Carmely *et al.*, 1983; Cimino *et al.*, 1983; Gonzalez *et al.*, 1984; Nakatsu *et al.*, 1983, 1984; Manes *et al.*, 1985; Braekman *et al.*, 1985; Walker *et al.*, 1985; Nakamura *et al.*, 1986; Mayol *et al.*, 1986) and also identifies several ecological contexts in which the metabolites might function (Thompson *et al.*, 1982; Cimino *et al.*, 1982).

Sullivan *et al.* (1983) demonstrate that the burrowing sponge *Siphonodictyon* sp. secretes a guanidine-containing sesquiterpene, siphonodictidine, in its mucus. This compound kills adjacent coral tissue, thereby preventing the coral from overgrowing the sponge's oscular chimneys. The compound stimulates coral respiration and it has been speculated that increased respiration rate and decreased photosynthetic rate would probably result in death for the coral. However, Sullivan *et al.* (1983) point out that because so many factors can affect hard corals under aquarium conditions, one must be cautious in extrapolating to the long-term effects of siphonodictidine at subacute concentrations. Environmental information on the effects of these kinds of compounds *in situ* is needed.

In this paper, we characterize the consequences of chemical-biological interactions in interspecific space competition between the coral *Agaricia lamarcki* (Milne Edwards & Haime, 1848) and the sponge *Plakortis halichondroides* (Wilson, 1902). Interactions between *Plakortis* and *Agaricia* are common in St. Croix, U. S. Virgin Islands, and in Jamaica where *Plakortis* overgrows living coral, utilizing the newly dead coral skeletons as a primary point of attachment and growth (N. Targett, J. Neigel, J. Porter, unpub. data). Upon physical contact or proximity of less than five centimeters to the sponge, *Agaricia* bleaches and shows a marked necrosis in the region of contact (Fig. 1).

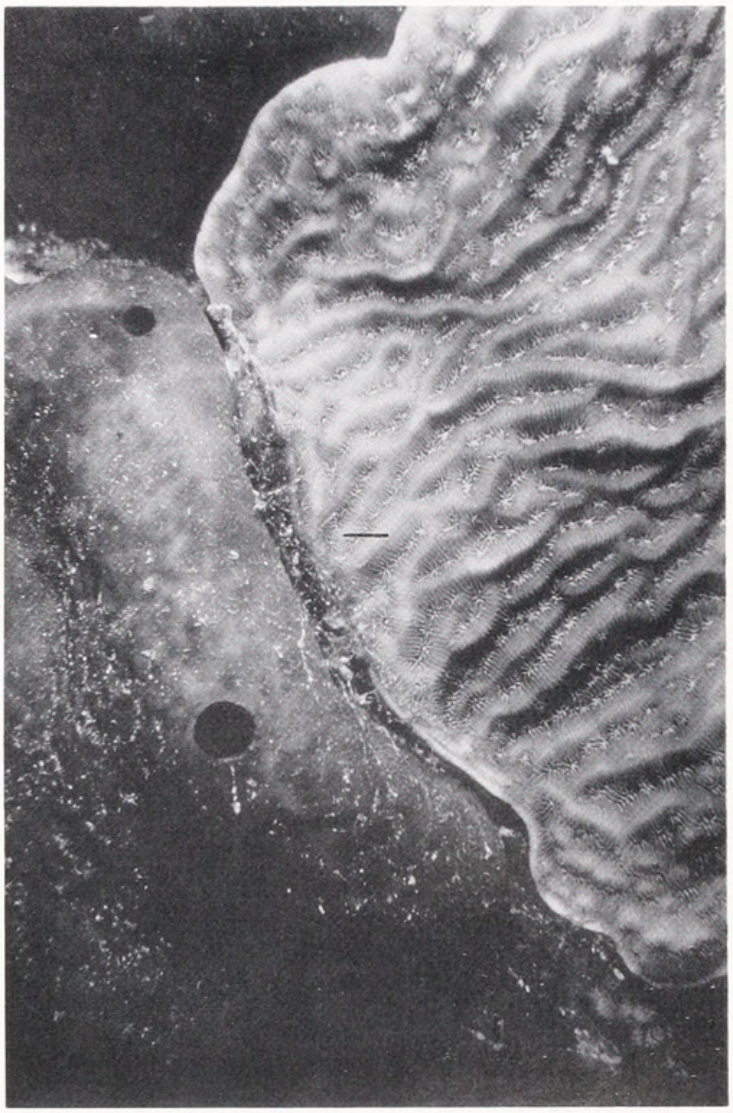

Figure 1. Natural associations of the sponge *Plakortis halichondroides* and the coral *Agaricia lamarcki* show a bleached area at the zone of contact. The necrotic area is evident in this photograph on the left side of the coral along the region adjacent to the sponge and above the 1.0 cm scale bar in the center. (Salt River Canyon, St. Croix, 25 m depth; photograph by R. S. Smith).

Using the *Plakortis/Agaricia* interaction as a basis for study, we: (1) describe the *in situ* effect of *Plakortis halicondroides* on *Agaricia lamarcki* both at points of natural contact and following manipulations that artificially bring together the sponge and coral, (2) quantify the *in situ* effects of direct sponge contact and indirect sponge contact (*i.e.*, exposure to whole sponge exudates only)

on photosynthetic and respiratory oxygen fluxes in the coral, and (3) suggest the long-term effects on tissue biomass, growth rate, and survival of *Agaricia* colonies growing in association with *Plakortis* sponges.

Materials and Methods

Site description

This research was conducted utilizing the NOAA underwater habitat, Hydrolab, located at a depth of 17 m on the north coast of St. Croix, U. S. Virgin Islands. Experimental material and line transect data were collected from the east coral reef slope of the Salt River Canyon within the research area available from the habitat.

Field studies

Transects ten meters in length and two meters wide (for a total of 20 m^2 in each transect area) were layed parallel to depth contours at 20 and 30 m. The number of *Plakortis halichondroides* colonies within one meter of the line were counted. The number of times *P. halichondroides* grew within five centimeters of living tissue of *Agaricia lamarcki* was also noted. Additionally, a swimming census covering 1000 m^2 was conducted between the 20 and 30 m depth contours to record all species of scleractinian corals adjacent to *P. halichondroides* colonies.

Biomass determinations

Coral tissue was removed from the surface of the coral skeleton using a Water Pik (Johannes and Wiebe, 1970) with filtered seawater. The tissue slurry was homogenized for one minute in a blender and triplicate aliquots were removed for analysis of nitrogen content, zooxanthellae cell density, and chlorophyll *a* concentration. Standard protocols for sample preparation and analysis were used for fluorometric determination of chlorophyll *a* (Holm-Hansen *et al.,* 1965), hemocytometric counts of zooxanthellae (Muscatine *et al.,* 1984), and micro-Kjeldahl nitrogen digestions (Parsons *et al.,* 1984) as described for coral tissue analysis in Porter *et al.* (1984). Coral surface area was determined for *Agaricia lamarcki* using Marsh's (1970) aluminum foil overlay technique.

Oxygen flux determinations

Oxygen flux in three experimental chambers and ambient PAR light flux on a 4-π quantum sensor were recorded on a Datel magnetic tape data logger at four minute intervals during the 24-hour experimental incubations. Tapes from each experiment were read into a Tektronics 4054 microcomputer where consecutive readings were subtracted from one another. The result was then multiplied by the volume of water in the incubation chambers to give net rates of oxygen production or consumption. These oxygen flux values were normalized to biomass units of surface area, and mass of nitrogen and chlorophyll *a*.

Coral pieces were cut from larger colony rosettes and were used in physiological experiments after they had acclimated for 24 hours. Experimental corals were monitored prior to treatment as well as after treatment, and therefore each served as its own pre-treatment control.

Photosynthesis *versus* irradiance curves were constructed for each control or experimental condition by computing average fluxes over small intervals of irradiance (maximum interval 50 $\mu Em^{-2}\ s^{-1}$). These points were fitted to a hyperbolic tangent function (Jassby and Platt, 1976) which represented the best-fit for patterns of coral productivity (Porter, 1980; Chalker, 1980). The program derived from this function allowed accurate statistical determinations of (1) α the initial slope of the photosynthesis-irradiance curve, (2) I_c, the light compensation point, (3) I_k, the break point, where the P:I curve approached p max, (4) p_c net max and p_c gross max, the maximum net and gross coral head production, (5) r_c, coral nocturnal respiration rate, and (6) an integrated, diel P/R ratio. We have fully described the interpretive model for coral photosynthesis/respiration ratios elsewhere (Muscatine *et al.,* 1981; Muscatine *et al.,* 1984; Porter, 1985).

Experimental design

Eleven null hypotheses were formulated to investigate the consequences to *Agaricia lamarcki* of association with *Plakortis halichondroides.* These null hypotheses included information on biomass patterns (9–11), physiological rates (1–6), and carbon budget totals (7–8) for corals before and after contact with sponges (direct contact) or with sponge exudates (indirect contact). The following null hypotheses were advanced:

1. α Before = α After Exposure
2. I_k Before = I_k After Exposure
3. I_c Before = I_c After Exposure
4. p_c net max Before = p_c net max After
5. p_c gross max Before = p_c gross max After
6. r_c night Before = r_c night After
7. P/R Ratio Before = P/R Ratio After
8. P/R Ratio Exceeds 1.0 Before; Less Than 1.0 After
9. [Zooxanthellae] Before = [Zooxanthellae] After
10. [Pigment] Before = [Pigment] After
11. [Nitrogen] Before = [Nitrogen] After

The four experimental treatments listed below were designed to test these hypotheses, *i.e.,* they were designed to reject the contention that there were no significant

effects on coral biomass or oxygen flux patterns after contact with sponges. The *in situ* manipulations included:

1. Control, no contact or history of contact between *Plakortis halichondroides* and the examined *Agaricia lamarcki* colonies.
2. Indirect contact, *A. lamarcki* colonies in contact with seawater containing exudates from coarsely mashed *P. halichondroides.*
3. Direct contact, *A. lamarcki* colonies in physical contact with pieces of *P. halichondroides* cut from the reef and tied to the coral colonies for 24 hours prior to the oxygen flux measurements.
4. Direct contact, *A. lamarcki* colonies naturally occurring adjacent to uninjured *P. halichondroides* colonies on the reef.

Experimental condition (4) was of greatest ecological interest since, of the three experimental treatments, it most closely recorded conditions of natural contact on the reef.

Oxygen consumption by the electrodes (all experiments) and the injected sponge water (Experiment 2 only) were determined just prior to the experimental incubations. These chemical oxygen demands were added to oxygen fluxes inside the chambers to give the metabolic activity of the coral alone.

The injured and uninjured sponges used in the last two treatments (3 and 4, respectively) were removed from the coral's surface prior to oxygen flux measurements on the coral colony. Since sponge metabolic rates *per se* were not of direct interest in the experimental design, and since Reiswig (1971) has shown that small chambers are unsuitable for the determination of oxygen flux characteristics for sponges like *Plakortis* with high pumping rates, the metabolic activity of *Plakortis* was not determined.

As a control on the experimental method employed, the effects of contact with sponges such as *Agelas, Haliclona,* and *Verongula,* which did not cause bleaching and necrosis, were also monitored. Finally, to examine metabolites released from *P. halichondroides,* an *in situ* chemical sampling pump concentrated organic compounds from the water surrounding uninjured colonies of this species.

Results

Field studies

All coral species found in the transect area are overgrown and killed by *Plakortis halichondroides* (Table I). These fourteen species are from eight of the nine Caribbean coral families (the remaining family, the Acroporidae, was not found in this reef zone). The overgrown corals are more similar morphologically than taxonomically; they are all horizontally flattened, and as such, provide a level substratum on which *Plakortis* can grow. The only exception to this pattern is the finger coral, *Madracis mirabilis,* which is killed at the base of its branches in contact with the sponge.

Table I

Hermatypic scleractinian corals killed in situ *by* Plakortis halichondroides *(Wilson, 1902)*

I.	Family Astrocoeniidae Koby, 1890
	1. *Stephanocoenia michelinii* Milne Edwards & Haime, 1848
II.	Family Pocilloporidae Gray, 1842
	2. *Madracis decactis* (Lyman, 1859)
III.	Family Agariciidae Gray, 1847
	3. *Agaricia agaricites* (Linnaeus, 1758)
	4. *Agaricia lamarcki* Milne Edwards & Haime, 1851
IV.	Family Siderastreidae Vaughan & Wells, 1943
	5. *Siderastrea siderea* (Ellis & Solander, 1786)
V.	Family Poritidae Gray, 1842
	6. *Porites astreoides* Lamarck, 1816
VI.	Family Faviidae Gregory, 1900
	7. *Diploria labyrinthiformis* (Linnaeus, 1758)
	8. *Diploria strigosa* (Dana, 1846)
	9. *Colpophyllia natans* (Houttuyn, 1772)
	10. *Montastraea annularis* (Ellis & Solander, 1786)
	11. *Montastraea cavernosa* (Linnaeus, 1766)
VII.	Family Meandrinidae Gray, 1847
	12. *Meandrina meandrites* (Linnaeus, 1758)
VIII.	Family Mussidae Ortmann, 1890
	13. *Mycetophyllia lamarckiana* Milne Edwards & Haime, 1848–1849
	14. *Mycetophyllia ferox* Wells, 1973

Approximately one-third (34.0 ± 6.8%) of all *Plakortis* colonies occur on or directly adjacent to living coral (Table II). The remaining members of the population grow on stable substrata, many of which are recently dead coral plates. Almost half of the corals with sponges on or near them show signs of bleaching and necrosis (40.8 ± 3.4%, Table II), but all coral specimens show tissue death in the area directly underneath the sponge.

Biomass

Our results clearly demonstrate a marked effect on algal densities, algal pigment concentration, and coral tissue mass for all of the experimental conditions relative to the control condition (Table III). The number of zooxanthellae per unit area, and as a consequence, the chlorophyll *a* per unit area of coral, decreases by a factor of three after contact with injured sponges, uninjured sponges, and sponge water (Table III). The amount of chlorophyll *a* per algal cell does not follow a consistent pattern under the experimental treatments; only after exposure to sponge water does the mass of chlorophyll *a* per algal cell decline significantly (Table III).

Table II

Plakortis halichondroides *population density and interactions with scleractinian corals ($\bar{x} \pm$ one S.D.; n = 4)*

Station name	Total number of sponge colonies per 20 m^2	Total number of sponge colonies within 5 cm of coral	% of sponge population in contact with coral	Number of coral colonies within 5 cm of sponges	Number of coral colonies showing visible signs of stress	% of contacted corals showing signs of stress
20m Right	62	18	29	16	6	38
30m Left	39	13	33	13	5	38
30m Right	105	32	30	33	15	45
20m Left	90	40	44	36	15	42
	74 ± 29	26 ± 12	34.0 ± 6.9	24 ± 12	10 ± 5	40.8 ± 3.4

Nitrogen mass per unit area of coral tissue decreases by a factor of two (Table III). This effect cannot be explained solely by the loss of zooxanthellae since they constitute only 7% of the coral tissue biomass (Porter and Muscatine, in prep.). Coral tissue lysis also occurs (Fig. 2). The effect of these combined plant and animal tissue responses is to create a bleached zone, or necrotic halo, on the coral in the vicinity of the sponge that is visually obvious from a meter away (Fig. 1).

Oxygen flux

Contact with *Plakortis* effects both oxygen production and oxygen consumption (Fig. 3). Oxygen consumption more than doubles for corals in direct contact with injured or uninjured sponges, rising from approximately 6 to 12 $\mu gO_2 cm^{-2}\ h^{-1}$ (Table IV). Coral respiration rate stays the same during injection of sponge water in the short-term indirect contact experiments. However, the maximum net photosynthetic rate drops by almost half for both direct contact with injured or uninjured sponges and for indirect contact with sponge water. These lowered photosynthetic rates occur within eight minutes of injecting sponge water, suggesting that sponge metabolites rapidly diminish this coral species' photosynthetic capacity. Rising respiration rates and diminishing production rates tend to offset one another mathematically. And hence, only for indirect contact with sponge water, where production falls but respiration does not rise concomitantly, does the maximum gross production show a significant decline.

The compensation light intensity is significantly higher under all experimental treatments relative to the control (Fig. 3; Table IV). This demonstrates that more light is needed for corals near or adjacent to sponges to meet their basal metabolic demands through photosynthesis than for corals at a distance from sponges. Further, it suggests that coral production balances coral respiration later in the morning and stops earlier in the afternoon for corals near sponges (Fig. 3).

Given the lowered production rates and increased respiration rates observed under the experimental treatments, it is not surprising that coral P/R ratios are also substantially lower among corals in contact with sponges (Table IV). The overall effect is that while the integrated P/R ratio is always at or above unity in control corals, it is always below 1.0 in corals exposed to injured or uninjured sponges under field conditions (Table IV). P/R ratios below 1.0 are never found for this species in Jamaica,

Table III

Biomass variation ($\bar{x} \pm$ one S.D.; N = 3) for colonies of the sheet-coral, Agaricia lamarcki *under different exposures to the liver sponge,* Plakortis halichondroides *(see Figs. 1 & 2)*

Characteristic	Units	Experimental treatment: No contact (Control)	Contact with sponge water	Contact with injured sponge	Contact with uninjured sponge
Zooxanthellae	10^6 cells cm^{-2}	1.04 ± 0.08	0.36 ± 0.08*	0.38 ± 0.06*	0.40 ± 0.14*
Pigments	pg Chl *a* $cell^{-1}$	10.02 ± 0.10	5.82 ± 0.93*	9.81 ± 4.05	10.57 ± 1.88
Pigments	μg Chl *a* cm^{-2}	10.39 ± 0.86	2.08 ± 0.13*	3.79 ± 1.61*	2.84 ± 1.00*
Nitrogen	mg TKN cm^{-2}	0.57 ± 0.06	0.25 ± 0.03*	0.25 ± 0.16	0.25 ± 0.10*

* Means significantly different from the Control ($P \leq 0.05$, ANOVA).

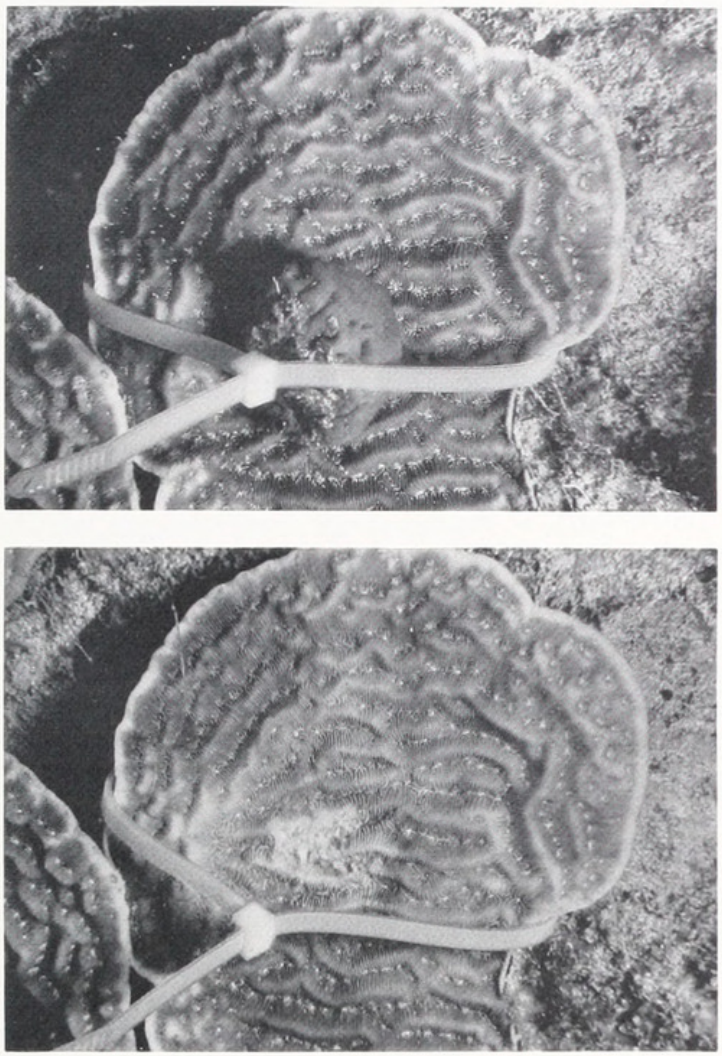

Figure 2. After two hours of experimentally induced contact between *Agaricia lamarcki* and *Plakortis halichondroides* (a, top), a bleached, necrotic area appears on the coral (b, bottom). (Salt River Canyon, St. Croix, 25 m depth; photograph by N. M. Targett).

even over greater depth ranges (Porter and Muscatine, in prep.), and therefore these values for coral colonies in contact with sponges are indicative of unsustainable carbon deficits.

In all cases, the differences observed between control and experimental coral oxygen flux patterns demonstrate significantly reduced photosynthetic capacity in coral colonies in contact with sponges or their metabolites. Therefore, the null hypotheses (no discernable effect) must be rejected for hypotheses (3) compensation point, (4) net production, (5) gross production, (6) nocturnal respiration rate, and (7) integrated P/R ratio under either field conditions or idealized "cloudless day" illumination. Hypothesis (8) P/R ratio > 1.0 is also falsified.

Other species of sponges (*Agelas conifera, Haliclona rubens,* and *Verongula* sp.) were also placed in contact with *Agaricia lamarcki.* They did not bleach the coral, thus indicating that mechanical irritation and pressure are not responsible for the effect observed with *P. halichondroides.*

Crude organic extracts were isolated from *Plakortis halichondroides* and coated onto synthetic cellulose pads, "tuffy sponges." When tied to living coral, these extract-soaked pads caused bleaching within 24 hours. Control pads (uncoated or coated with ether solvent only) produce no effect. While the exact nature of these organic compounds is still unknown, comparative thin layer chromatography of crude extracts from whole *P. halichondroides* and compounds isolated from waters surrounding uninjured *Plakortis* suggests that compounds in the surrounding water are the same as those produced naturally by the sponge.

Discussion

The sponge *Plakortis halichondroides* actively inhibits the metabolism and tissue survival of adjacent corals. Inhibition results from both direct and indirect contact (waterborne metabolites only) suggest that *Plakortis* uses allelochemicals as one means to secure and occupy space on the reef.

Plakortis halichondroides bleaches *Agaricia lamarcki* and causes marked tissue necrosis. The effects on coral biomass and coloration are sufficiently dramatic that it is possible to survey these interactions visually from some distance above the reef surface. The loss of zooxanthellae from corals following exposure to sponges or sponge exudates parallels the loss of symbiotic algae during other natural stresses such as abnormal temperatures, salinity fluctuations, or high rates of sedimentation (Porter, 1987).

These coral biomass reductions contribute to the profound effects that sponges have on coral oxygen metabolism. Parallelling the loss of zooxanthellae is a significant decline in primary production. Although the algae that remain appear to have normal concentrations of photosynthetic pigments, the few remaining zooxanthellae cannot compensate for the overall loss of algae. Further, despite the fact that there is significantly less coral tissue per unit area on corals adjacent to sponges than on corals without sponge contact, the respiration rate is still significantly higher. This respiratory increase suggests a stress or repair-metabolism response to the active sponge metabolites.

The overall effect on the P/R formula of decreasing the numerator and increasing the denominator is to lower the ratio below one for *Agaricia lamarcki.* These suboptimal values are not found in this photoautotrophic coral species. For example, even to depths of 50 m, *Agaricia* has an annual integrated P/R ratio of 1.13 (Porter and Muscatine, in prep.).

The ecological role of specific secondary metabolites

Table IV

Variation ($\bar{x} \pm 95\%$ confidence limits; n = 6) in photosynthesis-light utilization characteristics for in situ *colonies of* Agaricia lamarcki *under different exposures to* Plakortis halichondroides *(see Fig. 3)*

Characteristic	Units	Experimental treatment			
		No contact (Control)	Contact with sponge water	Contact with injured sponge	Contact with uninjured sponge
α (cm^2)	$\mu gO_2\ cm^{-2}\ h^{-1}\ \mu E^{-1}\ m^{-2}\ s^{-1}$	0.222 ± 0.046	0.140 ± 0.058	0.266 ± 0.141	0.303 ± 0.196
I_k (cm^2)	$\mu Em^{-2}\ s^{-1}$	137.82 ± 9.16	129.64 ± 27.93	109.40 ± 25.10	101.32 ± 36.12
I_c (cm^2)	$\mu Em^{-2}\ s^{-1}$	27.69 ± 1.70	60.54 ± 15.58*	76.90 ± 21.00*	85.84 ± 19.68*
p_c net max	$\mu gO_2\ cm^{-2}\ h^{-1}$	24.88 ± 1.95	10.64 ± 2.22*	17.90 ± 4.19*	15.05 ± 7.12*
p_c gross max	$\mu gO_2\ cm^{-2}\ h^{-1}$	30.66 ± 1.95	14.78 ± 2.22*	29.16 ± 4.19	30.98 ± 7.12
Average r_c night	$\mu gO_2\ cm^{-2}\ h^{-1}$	5.77 ± 0.21	4.14 ± 0.29	11.26 ± 0.80*	15.93 ± 1.09*
P_c gross/R_c 24 h	Ratio (field)	1.98 ± 0.51	1.37 ± 0.31	0.83 ± 0.34*	0.73 ± 0.23*

* Means significantly different from the Control ($P \leq 0.05$).

in marine organisms is known in only a few cases (Webb and Coll, 1983; Sullivan *et al.,* 1983; Morse and Morse, 1984; Targett *et al.,* 1986; Pawlik, 1986). In the boring sponge *Siphonodictyon,* mucus-borne metabolites kill corals (Sullivan *et al.,* 1983). Our study demonstrates that chemical-biological interactions are important in non-boring sponge species and in over-growth, not just anti-fouling, processes.

Several toxic exudates from soft corals appear to be responsible for causing localized mortality in hard corals, since extensive mortality of hard corals can occur even when direct contact is not established with the soft coral (Sammarco *et al.,* 1985). Coll *et al.* (1982b) isolated secondary metabolites from the water surrounding two species of octocorals that were identical to those isolated from the octocorals themselves. Flexibilide, dihydroflexibilide, sarcophine, and sarcophytoxide were isolated from crude extracts of *Sinularia flexibilis* and *Sarcophyton crassocaula,* respectively, and from their surrounding water when sampled *in situ* (Coll *et al.,* 1982b). Flexibilide and sarcophytoxide cause death in scleractinian corals at concentrations > 10 ppm (Webb and Coll, 1983). These compounds are also structurally related to sinulariolide, a potent algal growth inhibitor (Tursch, 1976).

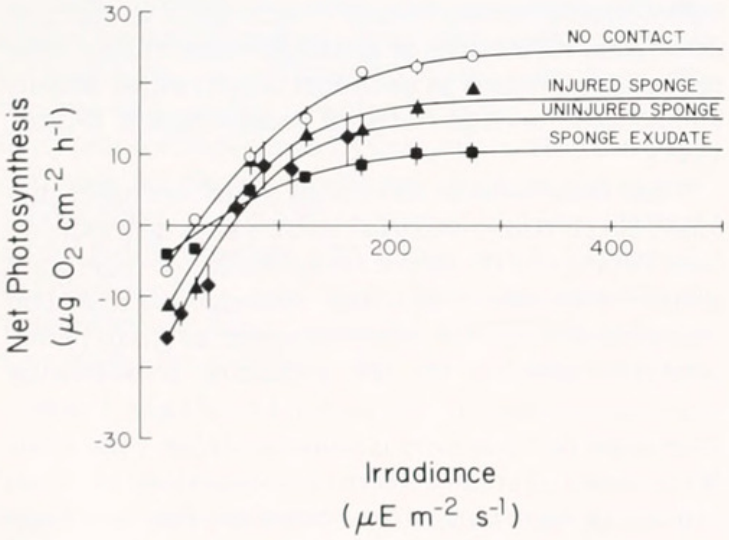

Figure 3. Net photosynthesis-irradiance curves are graphed for *Agaricia lamarcki* colonies (n = 3) from 20 m depth under different levels of contact with *Plakortis halichondroides.* The curves are fitted to a hyperbolic tangent function (see Table IV for the statistical comparisons between curves). Experimental Condition 1: control, no contact with *Plakortis* (open circles). Experimental Condition 2: indirect contact with water containing exudate from coarsely mashed *Plakortis* (solid squares). Experimental Condition 3: direct contact with injured *Plakortis* (solid triangles) (see Fig. 2). Experimental Condition 4: direct contact with uninjured *Plakortis* (solid diamonds) (see Fig. 1). Experimental Condition 4 most closely mimics conditions of natural contact on the reef.

The sponge *Plakortis halichondroides* contains numerous unusual secondary metabolites such as cyclic peroxides and aromatic lactones (Faulkner *et al.,* 1979; Stierle and Faulkner, 1980). It is possible that the cyclic peroxides cause the bleaching response described above and that the phenolic compounds contribute to tissue lysis. The closely related congener, *Plakortis zygompha,* contains (Z)-7-methyl-4-octen-3-one and several derivatives of 3-hydroxy-4-hydroxymethyl-4-pentenoic acid (Faulkner and Ravi, 1980). These may be involved in both the coral biomass changes and the oxygen flux modifications observed for the *Plakortis/Agaricia* association.

Between 30 and 40 percent of all *Plakortis* colonies on the reef are contiguous with scleractinian corals. Of these contacts, half show bleaching and necrosis on the coral tissue near the sponge; all show death of the coral tissue underneath the sponge. More importantly, based on the results of our *in situ* manipulations, the same effect is observable prior to the establishment of direct sponge-

coral contact. This implies that the sponge exudes waterborne metabolites which have a detrimental effect on coral respiration and photosynthesis. If even naturally low concentrations of these waterborne metabolites are effective at suppressing coral photosynthesis, then there is the distinct possibility that sponge exudates may influence ecosystem productivity in the deeper zones of the reef.

Plakortis kills and colonizes the dead skeletons of at least 14 scleractinian coral species. These species are distributed in all 8 Caribbean coral families located in the 20–30 m survey area. Our demonstration that toxins from *Plakortis* are so effective against corals, the otherwise most successful order of benthic invertebrates on the reef, suggests that further investigation of this interaction is warranted. Future research should focus on the mechanisms of action and chemical structure of the compounds that inhibit photosynthesis, stimulate respiration, and reduce coral colony biomass. The range of potency and the half-life of these allelochemicals once released into the water column is also of critical interest. Finally, information on the long-term survival of corals at varying distances from sponges, and the sources of mortality for *Plakortis* would be of great value to our understanding of the chemical ecology of this association. Allelochemistry gives *Plakortis* a measurable advantage in space competition with scleractinian corals, but is only one factor among many other biotic and abiotic factors which determine its population structure and dynamics.

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