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Maintenance of Living Space by Sweeper Tentacles of *Montastrea cavernosa*, a Caribbean Reef Coral

C.A. Richardson[1], **P. Dustan**[1] **and J.C. Lang**[2]

[1]Scripps Institution of Oceanography, Marine Biology Research Division, P-003; La Jolla, California, 92093, USA and
[2]Department of Marine Studies, University of Texas; Austin, Texas 78712, USA

Abstract

The reef-building coral *Montastrea cavernosa* Linnaeus possesses sweeper tentacles which have enlarged nematocyst batteries. Sweeper tentacles appear to be used in defense of the coral's living space and may successfully deter mesenterial filament attacks from the more aggressive coral *M. annularis*. *M. cavernosa* therefore possesses a specialized defensive strategy that has not been taken into account by present models describing spatial competition in coral reef ecosystems.

Introduction

The reef-building coral *Montastrea cavernosa* Linnaeus possesses a variable number of specialized, long tentacles known as sweeper tentacles, so named because of their distinctive waving action. In comparison to normal tentacles, the sweepers are approximately three to five times longer, are more opaque and have a much larger acrosphere (Den Hartog, 1977). Lewis and Price (1975) observed that *M. cavernosa* could catch brine shrimp at any point along the length of its sweeper tentacle, and thus suggested that the greater length was a specially evolved food-trapping organ. Den Hartog (1977) also suggested that sweeper tentacles may be involved in competitive interactions due to: (1) the histological resemblance of the cnidom of sweeper tentacles to other known aggressive organs such as actinarian catch tentacles, and (2) the location of sweepers along the periphery of a colony.

Montastrea cavernosa is a mildly aggressive coral, capable of destroying the tissues of a variety of subordinate coral species with its mesenterial filaments (Lang, 1973). In turn, the tissues of *M. cavernosa* are destroyed by the mesenterial filaments of its congener, *M. annularis* Ellis and Solander when the two are placed in contact. However, evidence of such interactions is rarely seen in nature. On Jamaican reefs, *M. cavernosa* can often be found surrounded by *M. annularis*, but it appears that *M. cavernosa* is able to prevent overgrowth by *M. annularis* (Fig. 1), even though the latter is a more aggressive West Indian faviid (family Faviidae) coral. Paradoxically, the intercolony distance between *M. cavernosa* and *M. annularis* is considerably greater than between *M. annularis* and other corals that are subordinate to it and lack sweeper tentacles (Dustan, 1975). Intercolony distance is defined as the narrowest gap between the bordering tissues of two coral colonies providing this narrowest gap is less than 5 cm, as this is the furthest extension of mesenterial filaments observed (Dustan, 1975). Although sweeper tentacles are presumably polyfunctional, our preliminary observations indicated that one of the more conspicuous and unique functions is regulation of intercolony distance between *M. cavernosa* and *M. annularis*. The present investigation presents further evidence that sweeper tentacles function as competitive organs.

Materials and Methods

Although specifically looked for during several dives, we observed sweeper tentacles expanded only once during the day, and in this instance they were not fully expanded nor displaying their "waving-action". Therefore, night dives were made on three areas of the reef at the Discovery Bay Marine Laboratory, Jamaica: (1) the moat at 20 to 25 m on Dancing Lady Reef (Dustan, 1975); (2) the

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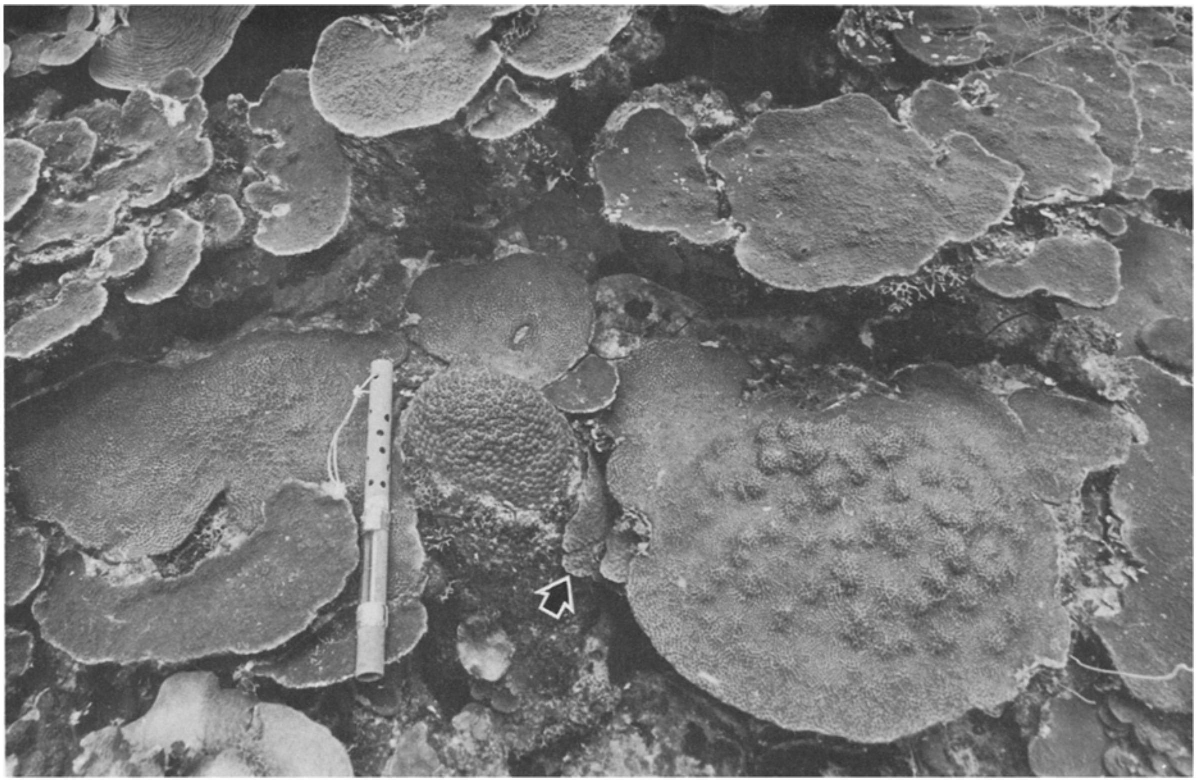

Fig. 1. *Montastrea cavernosa* colony surrounded by colonies of *M. annularis*. Arrow points to encrusting colony of *Helioseris cucullata* growing below tissue line of *M. cavernosa*. (Pressure-proof thermometer is approximately 50 cm long, for scale). 35 m Buoy Reef, Discovery Bay, Jamaica

fore-reef terrace at 12 m on Dancing Lady Reef; (3) the east fore-reef terrace at 12 m just east of the Kaiser Bauxite Channel (Woodley and Robinson, 1977). These studies were carried out from March through June 1978.

Photographs were taken with a Nikonos camera, 28 mm lens, strobe, and various combinations of extension tubes. The intercolony distance between *Montastrea cavernosa* Linnaeus and other scleractinian species was measured to the nearest millimeter with a plastic ruler and recorded underwater on a slate.

Small pieces of *Montastrea annularis* were broken off and its living, epidermal surface presented to the sweeper tentacles of *M. cavernosa*; interactions were noted and photographed. A second interaction experiment (after Lang, 1970) was arranged between the two species; the tissues of *M. cavernosa* were placed in contact with the tissue of *M. annularis*. Finally, colonies of the two species in close proximity *in situ* were searched for and subsequently photographed.

Results

At night, colonies of *Montastrea cavernosa* with expanded sweeper tentacles were observed in abundance in the study area. Because of the great numbers of sweepers, it was not possible at this time to quantify and pinpoint their location on a given colony. However, we did observe that in colonies of *M. cavernosa* growing in the moat and on the fore-reef terrace on Dancing Lady Reef, polyps having sweeper tentacles seemed to be located mostly on the periphery of the colonies. On the east fore-reef terrace no obvious tendency existed; sweepers were seen in all polyps on all areas of the colony. In all study areas, hemispherical colonies of *M. cavernosa* predominated (see Fig. 1). These included both large- and small-polyped growth forms (Lasker, 1977). The sweepers in all locations ranged in length from 1 to 5 cm. Several polyps had single expanded sweepers and many other individual polyps had several (as many as 6 were counted) expanded sweeper tentacles. In most polyps with more than one sweeper,

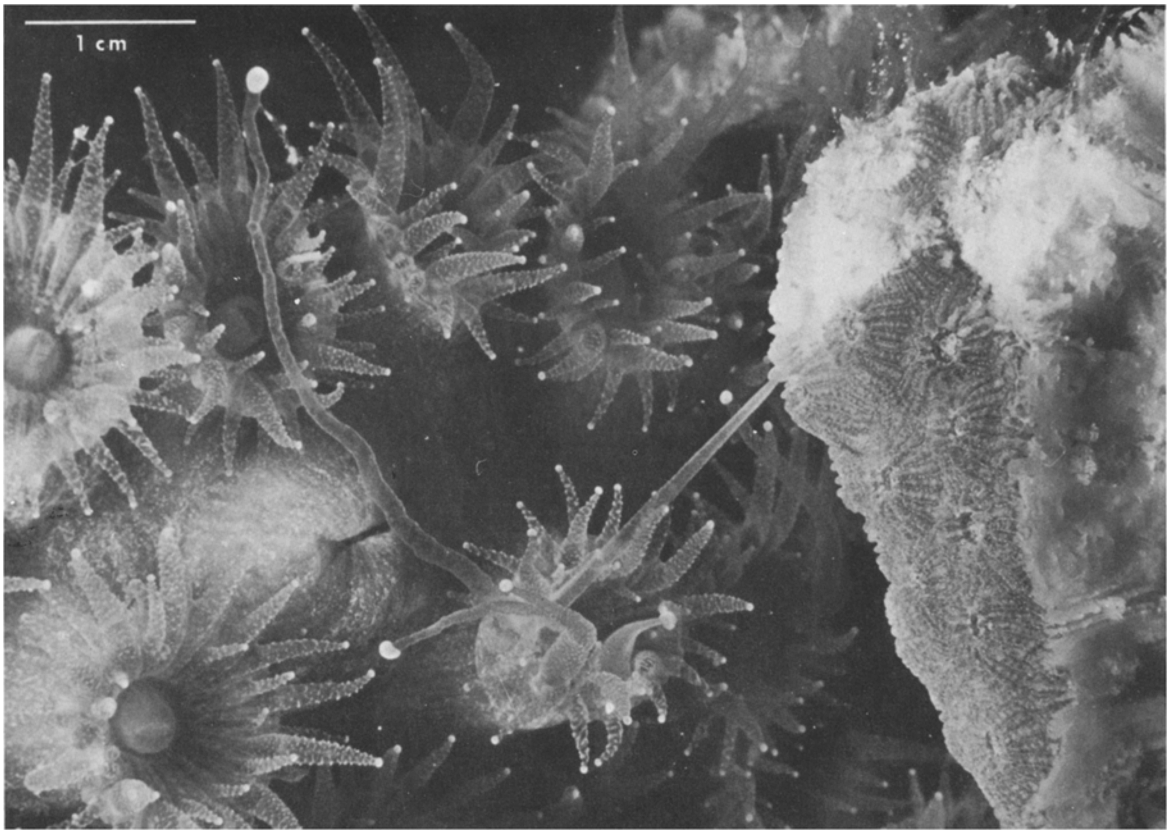

Fig. 2. *Montastrea cavernosa*. Sweeper tentacle adhering to tissue of small colony of *M. annularis* that was presented by a diver. 12 m East Fore Reef, Discovery Bay, Jamaica

the sweepers tended to be clustered in one section of the tentacular ring. However, polyps were also seen with sweepers distributed throughout the tentacular ring.

The waving action of the sweepers was seemingly indiscriminate. Their movement could be described as flailing and, especially at 12 m depth, they waved alternately back and forth, evidently under the influence of the surge. Presentation of a small living colony of *Montastrea annularis* to a sweeper tentacle of *M. cavernosa* often resulted in the sweeper's acrosphere sticking to the tissue of the *M. annularis* colony (Fig. 2). Two other observations made at night (12 m, Dancing Lady Reef) deserve mention. A sweeper tentacle was seen seemingly attached (stinging?) to the arm of a brittle star located on a sponge about 3 cm away from the surface of *M. cavernosa*. A sweeper was also seen adhering to the surface of a sponge for several seconds before releasing itself to resume waving about (Fig. 3). No obvious feeding of sweepers on particulate organic material was observed, although the normal tentacles on colonies where both sweepers and normal tentacles were expanded were seen catching plankton that had been attracted by our underwater lights.

When a piece of *Montastrea cavernosa* was placed in contact with a piece of *M. annularis* in an aquarium with running seawater, no expansion of sweeper or normal tentacles was observed even at night. *M. annularis* extruded its mesenterial filaments approximately 4 h after contact and began destroying the tissue of *M. cavernosa*. No cases of *M. annularis* attacking the tissue of *M. cavernosa* were found in the field, even though many colonies of *M. cavernosa* were almost completely surrounded by *M. annularis*; intercolony distances averaged 3.2 cm. As Table 1 shows, this distance is significantly greater than the distance between the more aggressive *M. annularis* and its other neighbors which are subordinate in the digestion dominance hierarchy (Dustan, 1975), but similar to the distance between *M. cavernosa* and surrounding subordinate species.

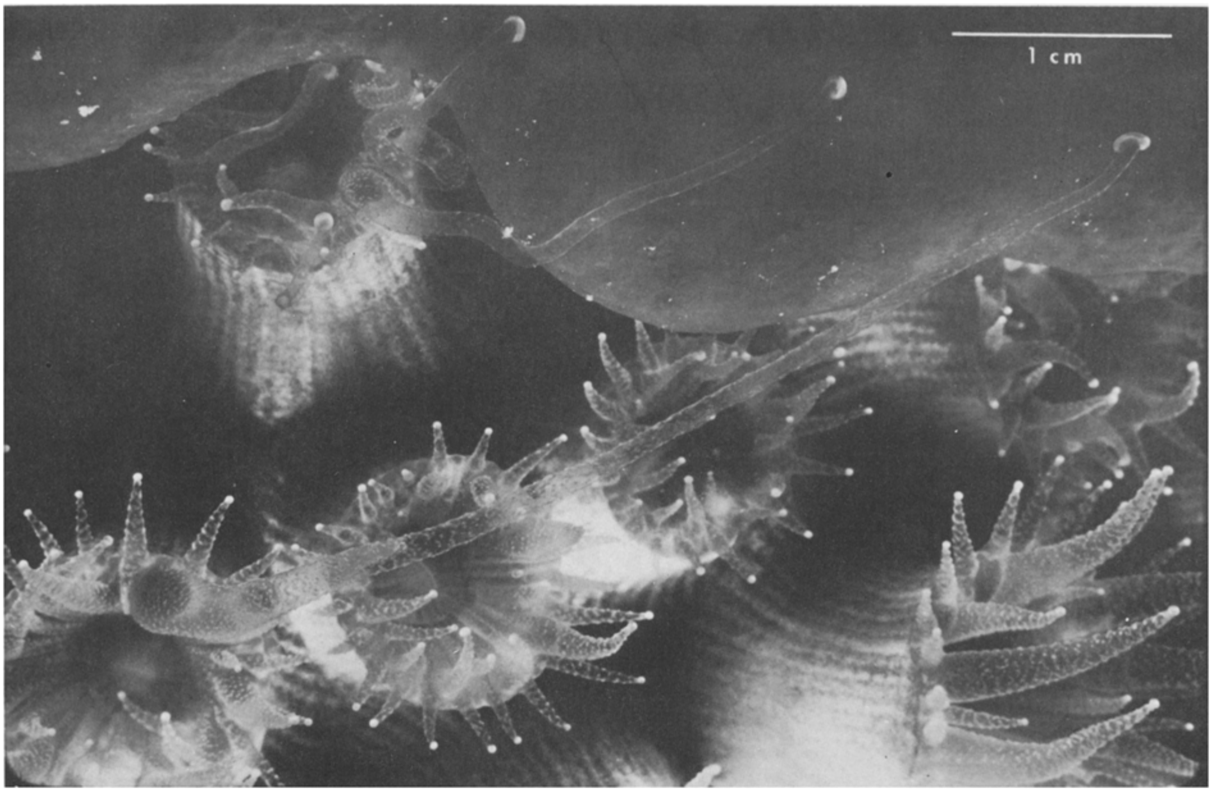

Fig. 3. *Montastrea cavernosa*. Sweeper tentacles attached to surface of a sponge adjacent to the coral colony. Note large acrosphere of the sweepers in comparison to normal tentacles. 12 m Dancing Lady Reef, Discovery Bay, Jamaica

Table 1. *Montastrea cavernosa* and *M. annularis*. Comparison of mean intercolony distance (defined as narrowest gap between two colonies on the reef, providing gap is less than 5 cm). Analysis of variance was used to test the null hypothesis that the *M. cavernosa-M. annularis* distances are significantly different from interactions with other species. *M. annularis* data from Dustan (1975). SD: standard deviation, LS: level of significance, ns: not significant

Species	Inter-colony distance (cm)	SD	*n*	LS
Montastrea cavernosa				
Montastrea annularis	3.2	0.95	25	-
Siderastrea sidera	2.6	0.93	6	ns
Agaricia spp.	2.3	0.90	16	ns
Porites spp.	2.2	0.60	5	ns
Montastrea annularis				
Montastrea cavernosa	3.39	0.50	9	-
Siderastrea sidera	1.27	1.0	12	.001
Agaricia spp.	1.63	0.60	38	.001

Discussion

Once the tissues of *Montastrea cavernosa* and *M. annularis* contact each other, the former apparently has no means of avoiding the onset of destruction by the mesenterial filaments of the latter. Within a few hours after contact, conspicuous destruction of tissue of *M. cavernosa* invariably resulted. These results are consistent with the experimental work of Lang (1970). Paradoxically, we have never observed this aggressive interaction in nature even though *M. cavernosa* is seen growing close to colonies of *M. annularis* and other coral species. Of special interest are the cases where *M. annularis* almost totally surrounds *M. cavernosa*, indicating that the former has had ample opportunity to interact with the latter.

The sweeper tentacles may protect a colony of *Montastrea cavernosa* by their extended presence around the colony, preventing more aggressive species, such as *M. annularis*, from getting close enough to destroy the tissue of *M. cavernosa*. This may also apply to subordinate species as the intercolony distances in Table 1 indicate. Corals found at the base of *M. cavernosa,* below the line of living tissue, grow closer to the tissue of *M. cavernosa* (Fig. 1). Perhaps the radius of motion of the sweepers is limited downwards, preventing contact with these encroaching coral colonies.

Thus far, two major means by which corals avoid overgrowth and/or destruction have been recognized by reef biologists. Faster growing corals overgrow their neighbors which usually leads to eventual destruction due to shading, sediment build-up, or decrease in available nutrients (Gravier, 1910, 1911; Wells, 1957; Connell, 1973, 1978; Lang, 1973; Porter, 1974; Dustan, 1975; Maguire and Porter, 1977; Dustan and Lang, personal observations). Slower growing corals of the suborder Faviina are known to possess more potent mesenterial filaments than their faster growing counterparts in other suborders and are able to destroy their neighbors by digesting their tissue, as opposed to overgrowing them. Mesenterial filaments do not possess muscles that allow them to stand free above the colony. Thus, their aggressive tactics are limited by gravity to horizontal extension. Sweeper tentacles are able to stand free in the water column and therefore may provide protection against overgrowth and shading to a greater extent than mesenterial filaments. *Agaricia* spp. compete with *Montastrea cavernosa* and *M. annularis* through overgrowth. The intercolony distance between *Agaricia* spp. and *M. cavernosa* is greater than that between *Agaricia* spp. and *M. annularis* (Table 1), lending support to the above argument. Thus, *M. cavernosa* with its special sweeper tentacles may possess a third means of holding its place on the reef. The long, waving sweeper tentacles may act like a boxer with his glove on the opponent's head, keeping the opponent's punching arms (mesenterial filaments) just out of reach of his vital organs.

Competition for space is of prime importance in the coral reef ecosystem. The work of Lang (1970, 1973) demonstrated that, within the scleractinian corals, a complex linear hierarchy of aggressive dominance has evolved (A>B>C>D) as measured by the relative potency of mesenterial filaments. This form of competition is counterbalanced by the greater skeletal growth rate of less aggressive corals. Most of the aggressive species are small and have slow growth rates while the less aggressive corals have faster growth rates and are able to escape through rapid growth. This tradeoff of aggressive dominance versus rapid growth rate explains, in part, why no single species of coral dominates the reef.

Sessile, cryptic organisms, especially bryozoans, sponges, and ascidians, from reef environments compete for space through allelochemical-mediated networks (Jackson and Buss, 1975; Jackson, 1977). No one single species in a network enjoys the total dominance of a simple linear ranked hierarchy (A>B>C>A) (Jackson and Buss, 1975). In the apparent absence of physical disturbance and predation as important ecological factors, the allelochemical competitive network scheme has been suggested as a mechanism for the maintenance of species diversity in space-limited systems.

The sweeper tentacles of *Montastrea cavernosa* demonstrate that, within the corals, intricate defense mechanisms have evolved that enable a less aggressive, slower growing species to maintain itself in the presence of a more highly aggressive, faster growing species (Fig. 1). In contrast to the allelochemical model of competition, where occupation of space results in tissue destruction, the sweeper tentacles appear to be defensive organs. Thus *M. cavernosa* does not fit into present models of coral-reef spatial competition, and the maintenance of its living space is far more complex than first envisaged. An examination of other coral species may further reveal a variety of defensive mechanisms which corals have evolved to maintain their living space in the reef community.

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