DISTRIBUTION OF SWEEPER TENTACLES ON *MONTASTRAEA CAVERNOSA*

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ABSTRACT

In direct competition among reef corals for limited substrate space, some species utilize elongate tentacles with specialized cnidae, or sweeper tentacles, to damage opponents. On species described thus far, these tentacles are not generally present, but develop as competitive interactions progress. Colonies of the Caribbean reef coral *Montastraea cavernosa* frequently have sweeper tentacles distributed over colony surfaces in patterns which do not necessarily correspond to ongoing competitive encounters. Nevertheless, we found that, when injured by the congeneric species *M. annularis*, colonies of *M. cavernosa* increase both the number of polyps with sweeper tentacles and the number of sweeper tentacles per polyp on colony regions close to the encounter.

INTRODUCTION

Reef corals are known to use a variety of mechanisms to compete for limited substrate space in crowded reef environments. Two of the best described are the use of mesenterial filaments (Lang, 1971, 1973; Sheppard, 1979) or of "sweeper tentacles" (Richardson, *et al*., 1979; Wellington, 1980; Bak, *et al*., 1982; Chornesky, 1983) by some corals to damage the tissues of neighboring corals.

Mesenterial filaments are normally present in all polyps of every coral. When corals of different species are placed into direct contact, these digestive filaments are deployed rapidly and extracoelenteric digestion of opponent tissues may take place within hours (Lang, 1971, 1973; Sheppard, 1979). The immediate "winner" (i.e., the animal remaining undamaged) in such interactions is generally predictable among various species pairs. Unlike mesenterial filaments, sweeper tentacles (elongate tentacles with specialized cnidae) are found only on certain species of coral (see Lewis and Price, 1975; Bak and Elgershuizen, 1976). Moreover, within these species, sweepers may not be present on all colonies, and, when present, may be erratically distributed over the colony surface. On some corals, sweeper tentacles develop specifically after damage by mesenterial filaments (Wellington, 1980; Bak, *et al*., 1982; Chornesky, 1983) or after contact with recognition (Chornesky, 1983) of other corals. In natural interactions, this delayed development, and thus the ability of the coral to utilize sweepers against a neighbor, occurs some time after the interaction has begun (on the order of a month--Wellington, 1980; Bak, *et al*., 1982; Chornesky, 1983). However, on at least one species of coral, sweeper tentacles are routinely present and are therefore "ready" to participate in competitive interactions with neighboring corals which grow too close (depending, of course, on their location on the colony relative to that of nearby competitors).

Sweeper tentacles commonly are seen on colonies of the Caribbean coral Montastraea cavernosa (Linnaeus). Descriptive patterns of the location of sweeper tentacles on M. cavernosa variously include: concentration around colony perimeters (den Hartog, 1977; Richardson, et al., 1979); maximal expansion in response to water currents (Price, 1973, in den Hartog, 1977); or a less predictable pattern of distribution over colony surfaces (J.C. Lang, unpub. data). Perhaps in part because they are usually present, sweepers on M. cavernosa have been described as feeding appendages (Lewis and Price, 1975), defensive structures to deter close growth of adjacent competitors (Richardson, et al., 1979), and "polyfunctional" structures which might serve both functions (Lang, 1979). Here we present preliminary data on the behavior and development of sweeper tentacles on M. cavernosa in artificial competitive interactions with the congeneric species M. annularis (Ellis and Solander).

MATERIALS AND METHODS

These experiments were conducted at a depth of 60 feet in Salt River Canyon, St. Croix. They were initiated during a saturation dive in the NOAA NULS II Underwater Habitat in March of 1982. Colonies of M. annularis and M. cavernosa (N=8) were cemented to cinder blocks using underwater epoxy-putty (see Chornesky, 1983, for methods). Corals were arranged so that a gap of about 1 cm remained between paired colonies of M. annularis and M. cavernosa when their polyps and tissues were contracted during the day.

Our initial intent was to examine whether introduction of other corals close to colonies of M. cavernosa would affect the expansion patterns of its sweepers. Thus, prior to introducing colonies of M. annularis, locations of existing sweeper tentacles on the M. cavernosa colonies were carefully mapped. The first night after corals were cemented into place, all colonies of M. annularis digested nearby expanded polyps of M. cavernosa in contact with their tissues. Subsequently, polyps of the digested M. cavernosa remained contracted in the area surrounding the resulting wounds. This unpredicted behavioral response made it impossible to observe the behavior of their sweeper tentacles during the remainder of the saturation dive.

Nevertheless, we were provided with the opportunity to follow the longer-term consequences of such interactions for colonies of M. cavernosa on which the location of sweeper tentacles was already well documented. These interactions subsequently were observed on six nights over the following two months. During each observation, the positions of sweepers on the M. cavernosa colonies were carefully mapped and the behavior and condition of both corals were recorded. For data analysis, each colony of M. cavernosa was divided into regions adjacent to and not adjacent to the M. annularis. Boundaries of these "adjacent" and "non-adjacent" regions were designated arbitrarily on maps resulting from the first set of observations, and then held constant for all subsequent observations. Data were analyzed by contrasting changes in the relative proportion of polyps with sweeper tentacles on adjacent and non-adjacent regions of colonies. Adjacent regions were consistently smaller than non-adjacent regions on the same colonies (approximately a third of the size). Therefore, comparison of the absolute number of polyps with sweepers between adjacent and non-adjacent regions yields a conservative estimate of their density on adjacent regions (i.e., when adjacent and non-adjacent regions have equal numbers of polyps with sweeper tentacles, adjacent regions actually would have greater densities of sweeper tentacles than non-adjacent regions).

RESULTS

Figure 1 compares the number of polyps with sweeper tentacles on: A) tissues adjacent to the M. annularis, and B) tissues not adjacent to the M. annularis. The median and a quarter of the range is plotted on this graph since these data were clearly non-normal and sample sizes were small (7-8). There is a significant correlation between the number of polyps with sweeper tentacles on adjacent tissues and time after initiation of the experiment

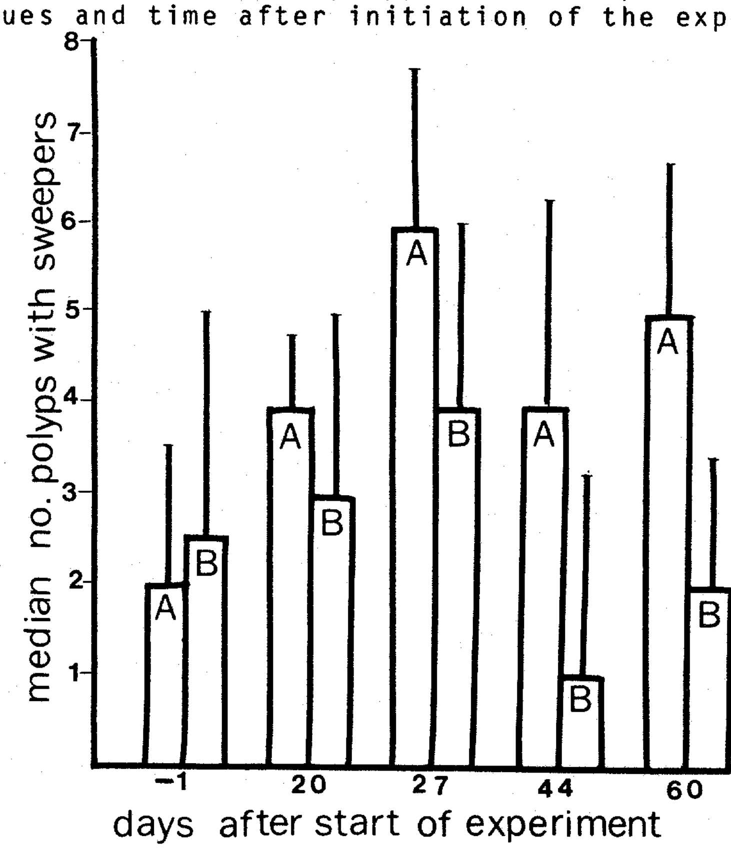

FIGURE 1. For M. cavernosa, change in number of polyps with sweepers on regions that are adjacent (A) or non-adjacent (B) to opponents (M. cavernosa). Vertical bars indicate quartile ranges.

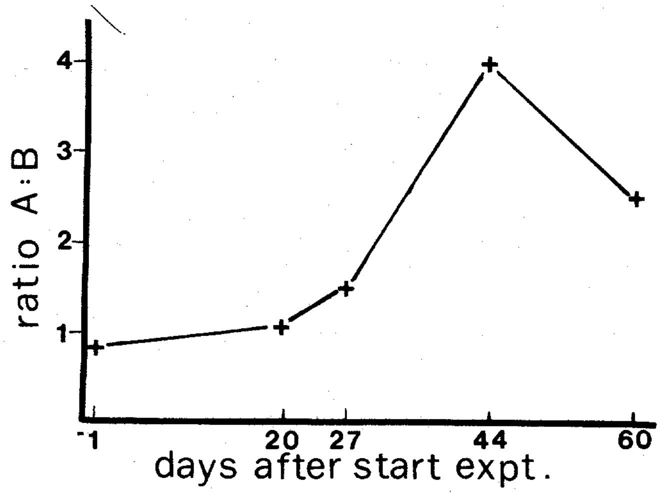

FIGURE 2. Increase in relative proportions of sweepers on adjacent regions over time.

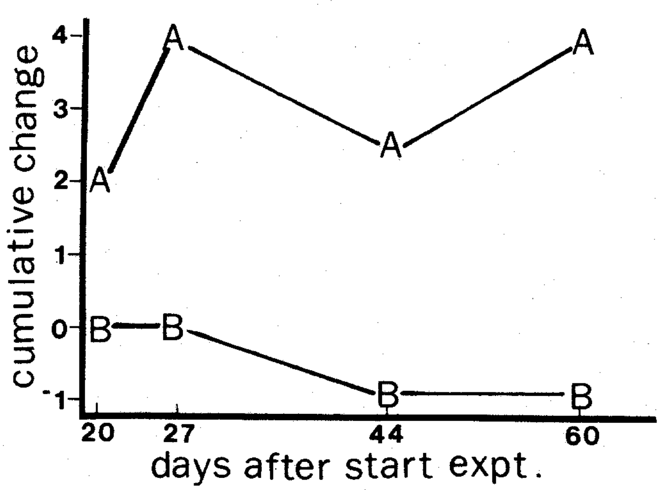

FIGURE 3. Cumulative changes in the number of polyps with sweepers on adjacent (A) and non-adjacent (B) regions. Each value incorporates summed changes from all previous observations.

(Spearman rank correlation r_s = .333, P < .05). The correlation for non-adjacent tissues is not statistically significant (r_s = - .133, P > .05). The ratio of A:B is plotted in figure 2 and demonstrates that the relative proportion of polyps with sweeper tentacles on adjacent regions increased during the observation period. Figure 3 shows the cumulative changes (median) in the number of polyps with sweepers on adjacent (A) and non-adjacent (B) regions at various times after initiation of the experiment. These data suggest a cumulative decrease in the number of sweepers on tissues not adjacent to colonies of *M. annularis*. This was clearly true for at least two colonies of *M. cavernosa* on which sweeper tentacles on non-adjacent tissues disappeared after the experiments were begun (4 and 6 weeks, respectively).

Necrotic wounds appeared on most colonies of *M. annularis* close to the colonies of *M. cavernosa*. Most (5 of 6) wounds formed in intervals between observations, during which time the number of *M. cavernosa* polyps with sweeper tentacles adjacent to the *M. annularis* also increased. Sweeper tentacles of the *M. cavernosa* often were observed touching live *M. annularis* tissues close to necrotic regions.

DISCUSSION

M. cavernosa apparently can increase the number of polyps with sweeper tentacles close to the site of competitive encounters with other corals. Although our data specifically reported the number of polyps having sweeper tentacles, observations by one of us (SLW) suggest that, in addition, the number of sweeper tentacles per polyp and the size of the acrospheres on existing sweeper tentacles may increase close to the site of such encounters.

Moreover, our data suggest that either the number of polyps with sweeper tentacles or expansion of sweeper tentacles on portions of colonies not involved in competitive interactions possibly may decrease as the number of expanded sweepers close to the interaction increases. If so, this might reflect a "cost" incurred by the production and/or expansion of additional sweeper tentacles close to the site of competitive encounters.

Although caution should be exercised in ascribing causes for wounds in coral-coral interactions (see Bak, *et al.*, 1982; Chornesky, 1983), it appears that the sweeper tentacles of *M. cavernosa* were capable of damaging tissues of *M. annularis* within their reach. Whether the course of natural interactions is similar to these experiments (i.e., digestion of *M. cavernosa* by *M. annularis* development of sweeper tentacles by *M. cavernosa* damage to *M. annularis* by *M. cavernosa* sweepers) is less clear. For example, if colonies of *M. annularis* and *M. cavernosa* grow gradually into contact, *M. cavernosa* may be able to develop sweeper tentacles prior to digestion by *M. annularis*. Similarly, at a greater distance than the 1 cm gap in these experiments, *M. cavernosa* sweeper tentacles might efficiently deter close growth by *M. annularis* and/or digestion by *M. annularis* (*sensu* Richardson, *et al.*, 1979; see Chornesky, 1983, for discussion of how natural and experimental interactions sometimes may differ).

Richardson, D. A., P. Dustan, and J. C. Lang. 1979. Maintenance of living space by sweeper tentacles of *Montastrea cavernosa*. Mar. Biol. 55: 181-186.

Sheppard, C. R. C. 1979. Interspecific aggression between reef corals with reference to their distribution. Mar. Ecol. Prog. Ser. 1: 237-247.

Wellington, G. M. 1980. Reversal of digestive interactions between Pacific reef corals: mediation by sweeper tentacles. Oecologia 47: 340-343.