Competitive strategies of soft corals (Coelenterata: Octocorallia): III. Spacing and aggressive interactions between alcyonaceans*

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ABSTRACT: Interactions were observed in the field between neighboring colonies of the alcyonacean octocoral *Sinularia flexibilis* (Quoy & Gaimard) and *Sinularia* sp., as well as between *Sarcophyton glaucum* (Quoy & Gaimard) and *Sinularia* sp. Visible effects observed included growth modification, stunting, scarring, and bleaching. Allelopathy was suspected as the cause. An experiment was performed to examine the responses of certain alcyonaceans to each other in competition for space and possible causes of the observed effects. Specimens of 3 species of erect soft corals (*Sinularia flexibilis*, *Nephthea* sp., and *Alcyonium molle* Dean) were collected and relocated in pairs under both contact and non-contact (close proximity) conditions at a depth of 3 to 5 m in Pioneer Bay, Orpheus Island, Queensland (18° 40' S, 145° 30' E). Initial effects observed included tissue necrosis and destruction of polyps, especially in contact situations, followed by colony reorientation. Long-term visible damage was minimal because, in all cases, the colonies subsequently moved apart. These sessile organisms exhibit a spacing behaviour allowing them to maintain an 'individual distance' in the same manner as many sedentary or vagile organisms. This decreases the incidence of aggression and potentially destructive interactions. Alcyonacean corals possess numerous adaptations which allow them to survive both predation and competition for space.

INTRODUCTION

The acquisition and maintenance of living space is critical to the survival of sessile organisms, and intense competition for space among such organisms has been documented extensively. This competition tends to be of the interference rather than the exploitative type, i.e. access to a limiting resource, in this case space, is reduced by the presence of a competitor (Miller 1967, Case & Gilpin 1974, Davies 1978, McNaughton & Wolf 1979). This living space may be acquired:

- (1) via growth interactions (e.g. Jackson 1977, Karlson 1980, Sammarco 1980, 1982, Inose 1982, Sammarco & Carleton 1982);
- (2) via aggressive or cannibalistic interactions (e.g.

Johnson 1959, Lang 1973, Woodin 1974, Richardson et al. 1979, Levin 1981, Sheppard 1982);

- (3) via feeding interactions (e.g. Buss 1980); or
- (4) via allelopathy.

Allelopathy may be defined as the 'direct inhibition of one species by another using noxious or toxic chemicals' (Ricklefs 1979, see also Muller 1966, Muller et al. 1968, Whittaker & Feeny 1971). Allelopathy has only been documented in 3 groups of sessile marine organisms – sponges (Porifera; Jackson & Buss 1975, Jackson 1977, Sullivan et al. 1983), anemones (Bak & Borsboom 1984), and soft corals (Coelenterata: Alcyonacea), which are abundant on many Indo-Pacific coral reefs (Benayahu & Loya 1977, Nishihira 1981, Dinesen 1983). Approximately one-half of the soft coral species on the Great Barrier Reef are known to contain toxic compounds (Coll et al. 1982b, Coll & Sammarco 1983). Although the toxins may play an anti-predatory role

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(Bakus 1971, 1976, 1981, Cameron 1976), they may also serve as an adaptation for use in competition for space against scleractinian corals. Some species of soft corals release toxic terpenes into the seawater, causing mortality in certain scleractinian corals in the absence of contact (Sammarco et al. 1983).

Laboratory experiments have demonstrated that some soft coral terpenes affect photosynthesis and respiration in certain scleractinian corals (Webb & Coll 1983). Mortality can also be induced in scleractinian corals in the laboratory with soft coral terpenes at concentrations as low as 5 to 10 ppm (Coll & Sammarco 1983). The same scleractinian corals, however, are also capable of causing local mortality in a different set of soft corals, namely *Nephthea brassica* Kukenthal and *Capnella lacertiliensis* MacFayden (Sammarco et al. 1985).

Another adaptation of selective advantage to soft corals in competition for space is their ability to change their orientation and growth patterns. They can actually move across live tabulate scleractinian corals, leaving elaborate trails as evidence of this movement (La Barre & Coll 1983).

Few studies have concentrated on competitive interactions between corals within the Octocorallia. Theodor (1966, 1971) performed a number of experiments on interspecific interactions between gorgonian octocorals, demonstrating clear dominance of some species over others. Tissue necrosis and disintegration were induced in the subordinate species at or near the zone of contact.

Here we demonstrate experimentally the occurrence of interspecific interference competition between alcyonacean corals. We also examine the processes involved in the interactions between these colonial organisms and the mechanisms by which they space themselves. The results of these experiments provide a possible explanation for the infrequent observation of such interactions in the field.

MATERIALS AND METHODS

All observations and experimentation in this study were performed on the fringing reef at 3 to 5 m depth in Pioneer Bay, Orpheus Island (Palm Island Group), central region of the Great Barrier Reef (18°40'S, 145°30'E). The site was chosen for its high abundance of soft corals (18 % of total live cover; La Barre 1984) and the potential for interactions between them (Fig. 1).

An experiment was initiated in May 1982. Colonies of each of 3 species of alcyonaceans – *Simularia flexibilis*, *Nephthea* sp. (C-2939: Northern Territory

Museum number), and *Alcyonium molle* – were collected with attached substratum and tagged *in situ*. Fifteen pairs were established by cementing 5 colonies of each species with a colony of each of the other 2 species in small plastic flower pots. The pots were wired to a galvanized mesh frame located at ~ 3 m depth. The pairs of alcyonacean colonies were cemented in contact with one another. 'Non-contact' was considered to be a situation where the 2 colonies could not make physical contact, polypal or otherwise, as assessed by visual examination of expanded colonies (distance = ~ 2.5 cm). Three specimens of each species considered in the experiment were cemented into individual flower pots alone as controls and monitored. Three specimens of each species, occurring naturally in the field in a position isolated from potential competitors, were also monitored throughout the study as undisturbed controls.

Responses of the colonies were recorded after 1 d, 3 d, 4 wk, 7 wk, 12 wk, and 20 wk. Visible effects of any interactions were assessed for each pair of colonies under contact and non-contact conditions. Effects were identified as (1) localized tissue necrosis in the region of proximity or contact, (2) avoidance via 'bending away' or growth modification, and (3) movement or displacement of colonies away from one another. Controls were also assessed for these characters.

Two-way (time $\times$ effect) and 3-way (time $\times$ contact $\times$ effect) contingency tests of independence were used to analyze the data (Sokal & Rohlf 1981). Details of the specific results of these analyses may be found in the figure legends. Higher-order interactions will only be discussed if significant.

RESULTS

In overview, a temporal pattern emerged in the responses of all soft corals (Fig. 2). With respect to tissue necrosis, the overall response was rapid, occurring within 1 d and peaking after 4 wk. The avoidance response on the whole lagged behind the necrotic response by at least 2 d and remained high for 4 to 7 wk after initiation of the experiment. In both of these types of responses, non-contact effects were significantly lower than contact effects.

In all pairings of soft corals, the movement response was the same. Although no movement was observed initially, all colonies exhibited movement away from each other after 4 wk, and this response continued for the duration of the experiment. In several cases, soft coral colonies moved to the extreme edge of the experimental containers (Fig. 3). No directed movement was observed in the controls.

Nephthea sp. caused a high degree of necrosis

Fig. 1. (a) *Sarcophyton glaucum*. Three colonies observed exhibiting an avoidance response to *Sinularia flexibilis* under natural field conditions. (b) *Sarcophyton glaucum* exhibiting tissue necrosis in area of colony proximal to *Sinularia* sp. under natural field conditions

Fig. 2. Summary of effects of one species of soft coral upon another when placed in association experimentally in the field. Data shown through time with 95 % confidence limits under (●) contact conditions (with left-hand oriented confidence-limit demarcations where confidence intervals overlap); (○) non-contact conditions (with right-hand demarcations). (▲): overlapping points. Data for necrosis, avoidance, and movement responses pooled, respectively, for all combinations of soft corals examined here

almost immediately when in contact with *Sinularia flexibilis* (Fig. 4). This strong initial reaction declined after 38 d and disappeared after 112 d. Non-contact effects were indistinguishable from controls. By contrast, *S. flexibilis* had virtually no effect on *Nephthea*. Avoidance did not occur within the first few days of the experiment, but was consistently observed in both species under contact and non-contact conditions after 38 d. This response ceased entirely after 112 d.

Alcyonium molle initially induced significant ne-

crosis in *Sinularia flexibilis* when in contact (Fig. 5). The effects increased further after 38 d and subsequently disappeared. Under non-contact conditions, significant necrotic effects were observed initially but quickly subsided. *S. flexibilis* also induced necrosis in *A. molle* under contact conditions, but it only reached significant levels after 38 d. *A. molle* exhibited no necrosis under non-contact conditions. With respect to an avoidance response, *A. molle* and *S. flexibilis* both oriented away from each other in a manner similar to that described above, with the response occurring at the 38 d mark. The avoidance response of *A. molle* was less pronounced than that of *Nephthea* sp. under non-contact conditions.

Nephthea sp. induced significant necrotic effects in *Alcyonium molle* (Fig. 6). This occurred only under contact conditions. *A. molle* also induced highly significant levels of necrosis in *Nephthea* under both contact and non-contact conditions (Fig. 7). These effects subsided with time (Fig. 6). *A. molle* exhibited a more rapid avoidance response to *Nephthea* than any other combination of soft coral under contact conditions. Once again, this response peaked after 38 d. *Nephthea* exhibited a strong avoidance response to *A. molle* after 38 d, especially under contact conditions.

DISCUSSION

In this experimental study of competitive interactions between alcyonaceans, initial effects on the colonies somewhat paralleled effects previously observed between alcyonaceans and scleractinians (Sammarco et al. 1983). Tissue destruction and local mortality were all observed as a result of contact (and, in 1 case, non-contact) between the alcyonaceans during the first 3 d of the study. Thus, the interactions previously documented to occur between alcyonaceans and scleractinians should not be considered unique to those groups. That is, those same interference mechanisms documented are also effective between species within the Alcyonacea in competition for space. In addition, most interactions between pairings of alcyonacean species were 2-way; no clear hierarchy of dominance could be established. This suggests that a non-transitory competitive network similar to those reported for other benthic marine communities (Jackson & Buss 1975, Connell 1976, Kay & Keough 1981, Russ 1982) is also operating in Great Barrier Reef alcyonaceans.

The necrotic effects observed here are similar to those reported by Theodor (1971) in the gorgonaceans. It seems probable that mucus-borne terpenes, which are known to be present in and released by certain soft corals (Coll et al. 1982a) may be responsible for the

Fig. 3. (a) Movements in *Nephthea* sp. induced by *Sinularia flexibilis* after being placed in association experimentally in the field. (b) Movement response observed in both *Nephthea* sp. and *Alcyonium molle* under similar experimental conditions

Fig. 4. Effects of *Nephthea* sp. on *Sinularia flexibilis* and vice-versa with respect to both necrosis (left-hand set of graphs) and avoidance response (right-hand set). Data shown with 95 % confidence limits for an average of 2 d (t_1), 38 d (t_2), and 112 d (t_3) under both contact and non-contact conditions. Points designated C represent levels of response in soft coral controls. For example, C_{s1} = levels of necrosis in relocated *S. flexibilis* control; C_{s2} = levels of necrosis in undisturbed *S. flexibilis* control; C_{s3} = levels of avoidance in relocated *S. flexibilis* control; and C_{s4} = levels of avoidance in undisturbed *S. flexibilis* control. Significant change in necrosis with time in *S. flexibilis* ($p < 0.01$, 3-way contingency analysis; Sokal & Rohlf 1981) but not in *Nephthea* ($p > 0.05$). Necrosis significantly higher under contact conditions in *S. flexibilis* ($p < 0.001$) but not in *Nephthea* ($p > 0.05$). Significant change in avoidance with time in both *S. flexibilis* ($p < 0.001$) and *Nephthea* ($p < 0.001$). No significant difference between avoidance under contact vs non-contact conditions in either species ($p > 0.05$).

Fig. 5. The effects of *Alcyonium molle* on *Sinularia flexibilis* and vice-versa with respect to both necrosis (left-hand set of graphs) and avoidance (right-hand set). Data shown for 2, 38, and 112 d (t_1 , t_2 , t_3 , respectively) under both contact and non-contact conditions. 95 % confidence limits shown. C = levels of control response; codes similar to those in Fig. 4. Significant change in necrosis with time in both *S. flexibilis* ($p < 0.001$, 3-way contingency analysis) and *A. molle* ($p < 0.05$). Necrosis significantly higher under contact conditions in both *S. flexibilis* ($p < 0.01$) and *A. molle* ($p < 0.01$). Significant change in avoidance with time in both *S. flexibilis* ($p < 0.001$) and *A. molle* ($p < 0.001$). Avoidance significantly higher under contact conditions in *A. molle* ($p < 0.05$) but not in *S. flexibilis* ($p > 0.05$).

Fig. 6. The effects of *Nephthea* sp. on *Alcyonium molle* and vice-versa with respect to necrosis (left-hand graphs) and avoidance (right-hand graphs). Data shown for 2, 38, and 112 d (t_1 , t_2 , t_3 , respectively) under both contact and non-contact conditions with 95 % confidence limits. C = levels of control response; codes similar to those in Fig. 4. Significant change in necrosis with time in both *A. molle* ($p < 0.05$, 3-way contingency analysis) and *Nephthea* ($p < 0.001$). Necrosis significantly higher under contact conditions in both species ($p < 0.001$). Significant change in avoidance with time in both species ($p < 0.001$). Avoidance significantly higher under contact conditions in *Nephthea* ($p < 0.01$) but not in *A. molle* ($p > 0.05$)

Fig. 7. *Nephthea* sp. Tissue necrosis induced by *Alcyonium molle* after being placed in contact under experimental conditions in the field

tissue destruction. In fact, a laboratory study has shown that pure terpenes from *Sinularia flexibilis* and *Lobophytum pauciflorum* kill *Acropora formosa* and *Porites andrewsi* (Scleractinia) at concentrations as low as 5 to 10 ppm (Coll & Sammarco 1983). The coral tissue lyses, presumably following cell death, and the tissue falls away from the scleractinian skeletons after about 8 h. Similar localised tissue destruction was observed in this study. Numerous other examples of tissue lysis appear in the literature relating to inter-specific scleractinian grafts (Hildemann 1974, Hildemann et al. 1977).

In contrast to interactions between scleractinians and alcyonaceans, the alcyonaceans were able to alter their orientation to one another within several weeks by curving their sterile stalks, resulting in lack of contact. Once the soft corals were no longer in contact, a significant reduction in levels of antagonism occurred, allowing affected necrotic areas to heal. This 'bending' and the physiological mechanism responsible for it are probably similar to those reported for *Nephthea brassica* (Alcyonaceae) in its movement across *Acropora hyacinthus* (Scleractinia) (La Barre & Coll 1983).

In all cases, after the soft corals suffered necrosis, they subsequently reoriented and then commenced to move apart. The timing of this movement was virtually identical in all species. In a previous study (La Barre & Coll 1983), it was determined that reorientation consistently preceded movement (also see Benayahu & Loya 1981).

These alcyonaceans seem to straddle the boundary between sessile and sedentary organisms. At first, they exhibited aggressive interaction, causing apparently chemically mediated damage to one another upon contact in much the same way as has been observed in some sessile organisms such as sponges (Jackson & Buss 1975). But, in the longer term, they moved and agonistic interactions subsided, as observed in some sedentary and vagile organisms such as anemones (Francis 1973, Ayre 1982), polychaetes (Woodin 1974, Levin 1981), tube-dwelling amphipods, and fiddler crabs (Connell 1963). This avoidance behaviour resulted in the maintenance of an 'individual distance' (Conder 1949) which is known to promote coexistence among competing species (Davies 1978). This type of interaction is also known to affect the overall pattern of dispersion of both plants and animals in space. In fact, the pattern of dispersion in these animals could easily be a result of past interference and competition for space (Pielou 1960, Crisp 1961, Laessle 1965, Whitaker 1975, Fonteyn & Mahall 1981).

Alcyonacean/alcyonacean interactions are much less commonly observed in the field than scleractinian/alcyonacean interactions. Even at the relatively high

densities observed in Pioneer Bay, Orpheus Island, colonies of certain co-occurring alcyonacean species are not found in contact. The 2 examples of deleterious interactions shown in Fig. 1 thus represent the exception rather than the rule at any one time. This mechanism for avoidance of competition represents one adaptation which may contribute to the continued coexistence of certain soft corals within a community. Each contains potentially toxic terpenes which, at least in *Sinularia flexibilis*, are released into the surrounding seawater (Coll et al. 1982a). This character may also assist them in maintaining space via allelopathic interactions with other sessile organisms.

The combination of avoidance behaviour, movement, and allelopathic capabilities confers considerable adaptive advantage upon the soft corals studied here.

CONCLUSIONS

The major results of this study may be summarised as follows:

- (a) With respect to competition for space between the alcyonacean corals *Sinularia flexibilis*, *Nephthea* sp., and *Alcyonium molle*, significant tissue necrosis was observed in almost all cases within 1 to 3 d where contact between colonies occurred. Necrosis also occurred under non-contact conditions but much less commonly.
- (b) All species exhibited a significant avoidance response ('bending-away' or reorientation) within 3 d of being placed in contact with or mere proximity to each other.
- (c) In all cases, soft corals exhibited movement away from each other (actual displacement of the colony) after the initial avoidance response. This movement was significant after 4 wk and continued thereafter. To the level of temporal resolution examined here, the timing of this response was identical in all cases.
- (d) The combination of allelopathy with avoidance behavior and the ability to move confers an important adaptive advantage on alcyonacean corals in competition for space with other sessile reef organisms.

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