Competition and locomotion in a free-living fungiid coral

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Abstract: Some fungiid corals asexually produce unconnected polyps that lie loose on the substratum between coral colonies. These free-living corals cannot build large three-dimensional structures and thus risk overgrowth during competition for space or light with colonial neighbors on coral reefs. This study examined the ecological importance and mechanisms of interspecific competitive damage and movement by the free-living fungiid coral *Fungia scutaria* (Lamarck). Over 40% of a population of *F. scutaria* on Hawaiian patch reefs was observed to contact other species of corals and macroalgae. *F. scutaria* caused unilateral damage to colonial corals in > 94% of natural contacts. In contrast, macroalgae overgrew and smothered *F. scutaria* in all observed cases. During experimental field contacts, small polyps of *F. scutaria* moved away from resident coral colonies, while larger individuals remained in contact and induced tissue damage to residents. *F. scutaria* move over short distances by nocturnal expansion of tissues that push against adjacent surfaces. Laboratory and field experiments suggest that long-distance movement may be via passive transport by water motion. The mechanism of interspecific damage is unique among corals thus far studied; nocturnally expanded polyps deposit a thick layer of mucus 5-15 mm wide onto neighboring corals. The tissue of corals beneath this mucus layer becomes necrotic and sloughs off within 4 days. The abundant mucus secreted by *F. scutaria* contains numerous nematocysts, unlike that of all other Hawaiian corals examined to date. The ability of some free-living corals to actively damage or move away from encroaching corals may be important to their survival on reefs dominated by colonial species.

Key words: Competition; Free-living coral; *Fungia scutaria*; Life-history strategy; Locomotion; Mucus secretion

INTRODUCTION

Free-living corals of the family Fungiidae are common on coral reefs throughout much of the tropical Indo-Pacific (Wells, 1966). Some members of this family, the mushroom corals, exhibit an unusual life history in that they begin life attached to the substratum, break off and then reproduce asexually to form unconnected free-living polyps (Wells, 1966). Individuals may reach 30 cm or more in length (Bosch, 1967), but are small in relation to colonial corals, many of which through asexual growth form branching or massive colonies several meters wide (Connell, 1973). Members of these colonial species can successfully monopolize much of the limited substratum space available to benthic reef organisms (Connell, 1973; Glynn, 1973; Porter, 1974; Benayahu & Loya, 1981). Given the lack of connection between individual polyps and
the relatively small size of the mushroom corals, how do they prevent themselves from being overgrown by large colonial corals on tropical reefs?

Members of the genus *Fungia*, a type of mushroom coral, appear to interact with the environment and with other organisms in ways that allow them to coexist with colonial species. First, they appear to survive storm-generated abrasion better than do co-occurring colonial corals (Jokiel & Cowdin, 1976). Second, members of the more mobile *Fungia* species also actively locomote (Abe, 1939), and thus could avoid overgrowth by moving away from other corals and into unoccupied areas of the reef (Maragos, 1974). Third, some corallivorous sea stars reject *Fungia* spp. and prey selectively upon some species of colonial corals (Ormond et al., 1976; Glynn & Krupp, 1986). In addition, many fungiid polyps form aggregations (Abe, 1939; Wells, 1966) that, through their feeding or other activities, may retard settlement and encroachment by benthic organisms (Jackson, 1977). Storms or other disturbances that create high turbulence can disperse aggregations of unattached corals, however, and *Fungia* often exist as single polyps surrounded by colonial corals. Members of some fungiid species thus may contact massive or branching corals for long periods, and risk being partially or completely overgrown between disturbance events. An important feature that may counteract this process is the ability of some fungiids to actively damage the growing edges of adjacent coral colonies (Hildemann et al., 1975a,b, 1977).

Investigation of the interspecific damage reaction of fungiids has thus far been limited to laboratory experiments and anecdotal field observations (Hildemann et al., 1975a,b, 1977; Sheppard, 1979). Little is known about competitive interactions in natural populations of *Fungia*, or of the behavioral mechanisms involved. It is important to examine this type of interaction quantitatively in the field, where ecological processes such as predation (Cox, 1986) and interference by epifauna (Bak et al., 1982) can affect the intensity and outcome of competition occurring naturally between corals.

In the present study I assessed the frequency and outcome of natural contacts between polyps of the fungiid *Fungia scutaria* (Lamarck) and other species of corals and macroalgae on Hawaiian reefs. I then conducted field experiments to determine the effects of introduced contacts on rates of interspecific damage and movement by *F. scutaria*. Finally, in the laboratory I observed the behavioral mechanisms of competition and locomotion employed by members of this species.

**MATERIALS AND METHODS**

**STUDY SITE**

This study was conducted during the summer of 1983 at the Hawaii Institute of Marine Biology in Kaneohe Bay, Oahu, Hawaii. Field investigations were carried out on patch reefs in the bay (see Holthus, 1986, for map and description of reefs in Kaneohe Bay).
FIELD OBSERVATIONS

The proportion of individuals of *F. scutaria* that naturally contacted other species of sedentary organisms was estimated by snorkeling over each of eight patch reefs in Kaneohe Bay during daylight hours, and noting whether each observed polyp contacted other scleractinian corals or macroalgae (species given in Table I). Polyps of *F. scutaria* were scored as contacting other organisms if their contracted tissues were within 10 mm of the live tissue of the latter. Individuals of this coral expand their tissues nocturnally to ≈ 10 mm above the skeletal surface (pers. obs.), and thus periodically should contact all sessile organisms within this distance. Polyps that were isolated on sand flats or occurred in the midst of conspecific aggregations were scored as not in interspecific contact.

The outcome of natural contacts between *F. scutaria* and other sedentary organisms was determined by observation at the above eight sites. The outcome of each interaction was categorized as: damage to neither individual, damage only to *F. scutaria*, damage only to the other species, or damage to both. Localized coral injuries were clearly visible as a zone of necrotic tissue or exposed skeleton along the region of interspecific contact (after Wellington, 1980).

FIELD EXPERIMENTS

In order to examine the effects of introduced contact between *F. scutaria* and colonial corals, an experiment was performed along the eastern edge of a patch reef adjacent to the Hawaii Institute of Marine Biology (see Jokiel et al., 1983, for description and map of this reef). The margin of this patch reef contained a large population of *F. scutaria* interspersed among several species of colonial corals. To experimentally introduce *F. scutaria* into contact with resident coral colonies at this reef, I first collected nine *F. scutaria* in each of three size classes from reefs throughout the bay. In the laboratory, the length of each coral was measured as the distance across the longest part of the oblong oral disk. The three size classes were (range of lengths): small (49–62 mm), medium (83–120 mm), and large (142–180 mm). Sizes in the three groups were significantly different (nonparametric multiple comparisons test, \( P < 0.01 \)). Each specimen was marked by engraving a numeral into the calcareous skeleton through live tissue on its aboral surface with an electric engraver. This label caused no apparent long-term damage to the corals, and was visible for the duration of the experiment.

Each labelled *F. scutaria* was then transported to the field and placed adjacent to a haphazardly-chosen undamaged colony of one of the two most common corals, *Montipora verrucosa* (Lamarck) or *Porites compressa* Dana (within 1 mm but tissues not touching), at 1–2 m depth along the reef edge. Each colonial coral was marked by tying a section of numbered plastic line around one branch. I also marked nine coral colonies that were intermingled among the treatment colonies but did not contact *F. scutaria*, as controls for damage to corals not associated with interspecific contact. Once a week for 4 wk, I assessed the condition of each coral colony and its introduced polyp of *F. scutaria*, and measured the distance separating the specimens.
LABORATORY EXPERIMENTS

To observe the behavioral mechanisms of locomotion and competition in *F. scutaria*, I collected specimens from patch reefs throughout Kaneohe Bay. Eight corals were collected in each of two size classes, measured as above (range of lengths): small (43–58 mm) and large (108–168 mm). The sizes of corals in the two groups were significantly different (Mann–Whitney *U* test, *P* < 0.01). Corals were maintained in large, shaded outdoor aquaria supplied with running seawater at ambient sea temperature (25 °C). The substratum in these tanks was smooth plastic. Each polyp of *F. scutaria* was placed within 1 mm of a live fragment of the colonial coral *Montipora verrucosa*, also collected from Kaneohe Bay. Each pair of corals was observed once every 2 h for 24 h, then intermittently for several days, and the distance between the individuals of each pair was recorded each week for 3 wk.

The copious mucus secreted by *Fungia scutaria* was collected to examine its nematocyst content. A small pipette was used to gently suction mucus from the surface of a polyp while it remained submerged in seawater, care being taken not to touch the surface of the coral. This mucus sample was observed at 400 × under a phase-contrast microscope and the types (according to Mariscal, 1974) of nematocysts noted.

RESULTS

FREQUENCY OF NATURAL INTERSPECIFIC CONTACTS

Of 819 individual *F. scutaria* that were observed, 307 or 34.93% were in contact with other scleractinian corals (species given in Table I). An additional 52 corals, or 5.92%, contacted macroalgae (species, Table I). The remaining 59.17% were surrounded by aggregated conspecific polyps, or occurred singly on sand flats or rubble, out of contact with other organisms.

OUTCOME OF NATURAL CONTACTS

Of the *F. scutaria* polyps that naturally contacted corals, over 94% (289/307) unilaterally damaged members of other species of scleractinian corals (Table I). The proportion of *F. scutaria* that damaged other corals was independent of the type of coral contacted (*R × C* test of independence using *G* test, *P* > 0.10). Polyps of other coral species often appeared expanded and healthy except in the immediate vicinity of the fungiids. The tips of coral branches adjacent to *F. scutaria* usually bore encrusting algae or a layer of mucus. Small fragments of colonial corals which had fallen into the midst of aggregations of *F. scutaria* were completely dead if < 2 cm in length.

In contrast, macroalgae showed no deleterious effects of contact with *F. scutaria*; they appeared instead to overgrow and damage the corals they encountered (Table I).

*F. scutaria* occurring in the midst of conspecific aggregations appeared undamaged, although no quantitative data were collected on these interactions.
Coral Competition and Locomotion

Table I

Occurrence of tissue damage in natural contacts between the coral *Fungia scutaria* and other benthic macroorganisms on patch reefs in Kanehoe Bay, Oahu, Hawaii. Each observation represents a different individual of *F. scutaria*.

<table>
<thead>
<tr>
<th>Type of organism contacting <em>Fungia scutaria</em></th>
<th>Number of observed contacts with damage to:</th>
<th>Total contacts</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td><em>Fungia scutaria</em> only</td>
<td>Other species only</td>
</tr>
<tr>
<td>Scleractinian corals</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Porites compressa</em> Dana</td>
<td>3</td>
<td>178</td>
</tr>
<tr>
<td><em>Montipora verrucosa</em> (Lamarck)</td>
<td>1</td>
<td>68</td>
</tr>
<tr>
<td><em>Pocillopora damicornis</em> (L.)</td>
<td>0</td>
<td>39</td>
</tr>
<tr>
<td>Other coral species</td>
<td>0</td>
<td>4</td>
</tr>
<tr>
<td>All corals</td>
<td>4</td>
<td>289</td>
</tr>
<tr>
<td>Macroalgae</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Dictyosphaeria cavernosa</em> (green bubble alga)</td>
<td>10</td>
<td>0</td>
</tr>
<tr>
<td>Crustose coralline algae</td>
<td>42</td>
<td>0</td>
</tr>
<tr>
<td>All algae</td>
<td>52</td>
<td>0</td>
</tr>
</tbody>
</table>

Outcome of Introduced Contacts in the Field

The distances moved by corals in experimental field contacts differed significantly among the three size classes of *F. scutaria* (Kruskal–Wallis test, *P* < 0.01) (Fig. 1A). During the 4 wk of observation, small individuals of *F. scutaria* moved significantly farther away from resident colonial corals than did the medium and large polyps (nonparametric multiple comparisons test, *P* < 0.05). One very small coral (49 mm polyp width), which became caught under the overhanging edge of an adjacent colonial coral, apparently was unable to move and remained there for the duration of the experiment.

The proportion of colonial corals damaged depended on the size class of *F. scutaria* they contacted (*R* × *C* test of independence, *P* < 0.01). Most medium and large *F. scutaria* remained within tissue contact of resident colonial corals, and by the end of 4 wk had caused damage to a significantly greater proportion of residents than did the small polyps (test of homogeneity of replicates, *P* < 0.01) (Fig. 1B). Localized damage to colonial corals occurred within 4 days of initiation of contact, and persisted throughout the experiment. The transplanted polyps of *F. scutaria* did not show any tissue damage. The control coral colonies that did not contact *F. scutaria* exhibited significantly less damage (0/9 colonies damaged) than did the treatment colonies (15/27 damaged) (*G* test of independence, *P* < 0.01).
LABORATORY OBSERVATIONS ON LOCOMOTION

When placed adjacent to fragments of the colonial coral *Montipora verrucosa* in the laboratory, most polyps of *Fungia scutaria* moved very little. After 3 wk, small corals had moved only $7.12 \pm 1.10$ mm (mean $\pm$ SD), and large corals had moved $3.12 \pm 2.42$ mm (not significantly different, Mann–Whitney U test, $P > 0.10$). One small coral (52 mm length) moved 34 mm, and was the only polyp to move $> 10$ mm during the course of the experiment. These results contrast sharply with the large distances moved by small corals in the field (Fig. 1A).

Polyps of *F. scutaria* appeared to locomote in the laboratory via nocturnal expansion of their soft tissues to 5–15 mm above their calcareous skeletons. The expanded tissues pushed the polyps away from adjacent coral skeletons and other surfaces. Using this mechanism, most polyps moved an average of only a few mm each week (see above), and remained in intermittent tissue contact with adjacent corals during nightly expansions.
LABORATORY OBSERVATIONS ON AGGRESSION

Specimens of both *Montipora verrucosa* and *Fungia scutaria* appeared to maintain their health in aquaria during the 3-wk observation period. Portions of the colonial coral *Montipora verrucosa* that occurred within contact of the expanded tissues of *Fungia scutaria* were covered by these tissues for 10–12 h each night. Upon contraction of *F. scutaria* in the morning, a layer of mucus was observed on the adjacent corals. During the 1st day following contact, polyps under this layer were still intact. Within 2 days, coral tissue underneath the mucus began to decay, and microorganisms invaded the mucus. By 4 days, the mucus had sloughed off and exposed bare coral skeleton (Fig. 2; see also photographs in Hildemann et al., 1975a,b, 1977). After 2–3 week, a layer of encrusting algae often colonized this area and remained on the coral for the duration of the experiment. Corals were capable of complete regeneration of tissues within 3 wk after separation from *F. scutaria*.

The copious mucus secreted by *F. scutaria* contained many nematocysts. The types observed were microbasic p-mastigophores, holotrichous isorhizas, and spirocysts. Nematocysts were only a minor component of the mucus by volume.

DISCUSSION

FREQUENCY AND OUTCOME OF NATURAL CONTACTS

This study demonstrates that a substantial proportion (>40%) of specimens of *F. scutaria* in Kaneohe Bay are in soft-tissue contact with other species of sedentary macroorganisms. Contact with colonial corals was over three times as frequent as contact with algae.

The high proportion of *F. scutaria* that caused unilateral damage in natural contacts with other species of corals (>90%, Table I) is consistent with anecdotal field observations and laboratory studies on other members of this genus. Sheppard (1979) reported that *Fungia* spp. were dominant over all six species of colonial corals that they contacted on reefs in the Chagos Archipelago, Indian Ocean. Hildemann et al. (1975a,b) observed that *F. fungites* at Enewetak Atoll, Pacific Ocean, caused unilateral damage to at least five species of colonial corals in both field and laboratory contacts. In Hilo, Hawaii, Hildemann et al. (1977) also found that *F. scutaria* damaged six of the most common Hawaiian corals during laboratory pairings. The quantitative observations reported here show a strong, one-way effect of field interactions (Table I). This lack of observed reversals supports the suggestion that this competitive outcome is rarely reversed by other ecological factors such as fish predation (Cox, 1986) or growth of epifauna (Bak et al., 1982).

The dominance of algae over *F. scutaria* is similar to their effect on other Hawaiian corals (Banner & Bailey, 1970). Macroalgae are known also to damage corals in other tropical reef systems (Glynn, 1973; Potts, 1977).
Fig. 2. The free-living coral *Fungia scutaria* (right) and the colonial coral *Montipora verrucosa* after 7 wk in the laboratory. (A) At 5 mm inter-skeletal distance. Note that *F. scutaria* has deposited a small patch of mucus (arrow) on the colonial coral during nocturnal expansions, but that the latter’s tissue remains uninjured. (B) Less than 1 mm inter-skeletal distance. Note the 5–10 mm wide margin on *M. verrucosa* that has been injured by the expansion of tissues and deposition of mucus by *F. scutaria*. Note also the strand of mucus retained between the two corals. Nylon restraining bands visible in the photographs were not used on corals during quantitative behavioral observation. Ruler lines = 1 mm.
OUTCOME OF INTRODUCED CONTACTS

The experiment performed in this study demonstrates that *F. scutaria* can actively damage colonial corals in the field. The results suggest that corals of this species benefit from alternate competitive strategies at different life-history stages. Small specimens (<70 mm polyp length), unless restrained, tended to avoid competition by moving away from adjacent coral colonies. In contrast, larger specimens (>90 mm polyp length) moved little during the course of a month, and instead damaged the growing edges of neighboring corals. The effect of this size-related variation is to disperse small *F. scutaria* to other, possibly less-crowded areas of the reef, while the more sedentary large individuals, which may be too heavy to move much, defend space for growth by damaging encroaching neighbors.

This study measured the movement rates of only transplanted individuals placed in contact with colonial corals. Specimens of *F. scutaria* that have not been transplanted, or do not contact coral colonies, may exhibit different rates of movement in the field.

MECHANISM OF MOVEMENT

The mechanisms of movement employed by these unattached corals appear to be two-fold. *F. scutaria* actively locomote over short distances (<10 mm) by expanding their tissues and pushing against adjacent hard surfaces. Long-distance movement (10 mm to several m) may be primarily passive, via water motion. This interpretation is suggested by the observation that small corals, which weigh little (≈40 g wet weight), move large distances in the field (Figure 1A) where turbulence is high. In laboratory aquaria where water motion is relatively low, small corals do not move significantly farther than do the larger, heavier corals (≈300 g wet weight) (see Results). However, small corals may also move less in the laboratory because they are unable to gain traction on the smooth substratum, or due to other factors that differ between laboratory and field. For example, in natural habitats, some unattached corals (*Heteropsammia michelinii*) are transported by symbiotic sipunculid worms (Goreau & Yonge, 1968). In the present study, mobile invertebrates were not observed to associate with *Fungia scutaria*. Even on sandy substratum in the laboratory, members of this species move little in comparison with other, more "acrobatic" species of free-living corals (Hubbard, 1972; Hubbard & Pocock, 1972). Current evidence is consistent with the hypothesis that movement of *F. scutaria* over distances greater than a few millimeters occurs mainly through water motion. Further evidence is needed to directly test this hypothesis.

MECHANISM OF INTERSPECIFIC DAMAGE

Behavioral observations on the mode of competitive damage by *F. scutaria* support the suggestion that mucus secretion may be involved. The observed polyps did not apply special structures such as the sweeper tentacles (Den Hartog, 1977; Wellington, 1980) or mesenterial filaments (Lang, 1973; Chadwick, 1987) used by some corals and
corallimorpharians during competition. Instead, they simply expanded and deposited a thick layer of mucus onto adjacent corals.

Individuals of *F. scutaria* are known to secrete large quantities of mucus, even when not in contact with other species (Coles & Strathmann, 1973; Glynn & Krupp, 1986). Mucus secretion is thought to serve several functions in corals, including rejection of sediment (Hubbard & Pocock, 1972), food capture (Lewis & Price, 1976), and supply of organic nutrients to symbiotic crabs that protect the corals from predators (Knudsen, 1967; Glynn, 1976). My observations support the idea that *F. scutaria* also uses mucus to competitively damage encroaching species of colonial corals. The secretion of many nematocysts into the mucus may be related to this function. *F. scutaria* is the only coral for which competitive use of mucus has been documented, and it is also the only Hawaiian coral species known to secrete large quantities of nematocysts in its mucus, out of six common Hawaiian species examined by Coles & Strathmann (1973).

Hildemann *et al.* (1977) proposed a mechanism of interspecific damage in *F. scutaria* involving non-dialyzable, xeno-cytotoxic molecules present in secreted mucus. Their evidence, however, is consistent with an alternate hypothesis in which the cytotoxic agents are nematocysts. Either mechanism can be used to explain why algae are resistant to damage by *F. scutaria*; the algae observed in this study have thick cell walls of cellulose or calcium carbonate that may be impermeable to penetration by nematocysts or cytotoxic molecules. The exposed soft tissue of corals, in contrast, appears to be more susceptible to damage from competing cnidarians.

The mucus secreted by *F. scutaria* may serve as a matrix that carries nematocysts which then remain in contact with the target coral for several days. This would explain why damage to adjacent corals is not observed immediately, but occurs only after several days under the mucus layer. It is also possible that after several days of being covered by mucus, the marginal tissues of colonial corals suffocate (are oxygen starved), or are more susceptible to attack by bacteria. It is not clear whether *F. scutaria* directly injures corals or creates a situation in which injuries are likely to occur. In contrast, anthozoans that attack their neighbors by applying specialized structures (acrorhagi, sweeper tentacles) laden with nematocysts appear to cause direct, immediately damage to victims (Bigger, 1982; Hidaka & Miyazaki, 1984). Further experiments to isolate and test different fractions of the mucus of *F. scutaria* would more precisely determine what component of the mucus in this species indirectly or directly causes interspecific injury.

Polyps of *F. scutaria* do not appear to cause competitive damage to conspecifics (Hildemann *et al.*, 1977; pers. obs.). However, in some corals the effects of intraspecific competition are quite subtle (Rinkevich & Loya, 1983) and would not have been detected in this study. The lack of obvious injury during intraspecific contact in free-living corals, even when they are piled several layers deep (Goreau & Yonge, 1968; pers. obs.), may contribute to their survival in shifting aggregations. *F. scutaria* is the only species of *Fungia* to occur in Hawaii. However, it would be interesting to observe the outcome of intra-generic contacts in regions where several species of the genus co-occur. The copious mucus secreted by these unattached corals surrounds them with a protec-
tive sheath that may, in addition to the other functions mentioned above, offer protection from conspecific or congeneric polyps in aggregations.

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REFERENCES

ABE, N., 1939. Migration and righting reaction of the coral, Fungia actiniformis var. palawensis Doderlein. Palao Tropical Biological Station Studies, No. 4, pp. 671–694.


DEN HARTOG, J.C., 1977. The marginal tentacles of Rhodactis sanctithomae (Corallimorpharia) and the sweeper tentacles of Montastrea cavernosa (Scleractinia); their cnidom and possible function. Proc. Third Int. Coral Reef Symp., Vol. 1, pp. 464–469.


