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Migration, habitat use, and competition among mobile corals (Scleractinia: Fungiidae) in the Gulf of Eilat, Red Sea

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Abstract. We examined the impact of seven species of mobile mushroom corals (Fungiidae) on the community structure of sheltered reef slopes in terms of their patterns of migration, habitat use and competition with other benthic organisms. On fringing reefs at Eilat, Red Sea, polyps detached at 1 to 6 cm length, and grew to 11–55 cm length. Attached mushroom corals were oriented vertically in reef cavities. Detached corals migrated downward on the reef slope and onto rubble or soft substratum at the reef base, at 29 to 71 $\mathrm{cm\,yr^{-1}}$. Mobility decreased with corallum size and extent of undersurface ornamentation. In aquaria, small corals righted themselves and migrated up to 6 $\mathrm{cm\,d^{-1}}$ by nocturnally inflating and pushing their tissues against the substratum. Autonomous coral behavior and storm-generated water motion appeared to account for most fungiid mobility at Eilat. Mushroom corals did not damage each other upon contact, even in multi-species aggregations, but unilaterally damaged non-fungiid scleractinian corals. Their dominance during contact interactions retards overgrowth by larger attached scleractinians, and mobility allows them to colonize soft substrata not accessible to most other reef corals.

Introduction

Most reef corals remain attached to hard substratum, but some are dislodged by storms, bioerosion or disturbance by foraging organisms (Highsmith 1982). Dislodgement and fragmentation may be important for the survival and spread of coral genotypes following tropical storms (Highsmith 1982, Tunnicliffe 1983). Some scleractinians actively dissolve part of their skeletons and detach as an integral part of development (Yamashiro and Yamazato 1987). Mobility is particularly highly developed in the family Fungiidae (mushroom corals), in which free-living adults occur in 36 out of 41 species (Hoeksema 1989, Hoeksema and Dai 1991) and occupy a wide variety of habitats on Indo-Pacific reefs (Pichon 1974, Hoeksema and Moka 1989).

Mobility represents an alternate life history strategy among corals and exerts unique impacts on reef community structure. Free-living corals may retreat from competitive contact with large colonial corals (Maragos 1974, Chadwick 1988) and avoid bleaching by migrating downslope (Hoeksema 1991 a). They risk burial due to migration onto soft substratum (Yonge 1935, Schuhmacher 1979, Nishihira and Poung-In 1989) and may be overturned by water motion and bioturbation (Hoeksema 1988). Mobile corals extend reefs onto sand and serve as nuclei for the establishment of new reefs (Sheppard 1981).

Little is known concerning the degree of habitat segregation between attached juvenile and mobile adult corals or about their dispersal patterns on sheltered reefs. In addition, the outcome of competitive interactions between fungiid corals and other sessile reef organisms has been examined in only a few localities (Cope 1980, 1981, Chadwick 1988 and references therein).

The northern Red Sea is an area of relatively calm water (Mergner 1971, Head 1987) about which little is known concerning the mobile coral fauna (Schuhmacher 1979, Chadwick and Loya 1990, Dullo and Hecht 1990). We describe here the impact of mobile fungiid corals on Red Sea fringing reefs in terms of habitat use, migration and competition.

Materials and methods

All studies were conducted near the Steinitz Marine Biology Laboratory, Eilat, Israel, in the Gulf of Eilat (Aqaba), Red Sea (habitat description in Loya and Slobodkin 1971). Members of the scleractinian family Fungiidae were identified using Hoeksema (1989) (see also for species authors). Individuals of two species were excluded from mobility analyses on the reef slope; *Fungia* (*Lobactis*) *scutaria* was confined to the reef flat, and *Cantharellus doederleini* occurred only in the attached form. In January 1989, 117 corals in the five remaining species were selected randomly at 5 to 25 m depth. Individuals of *Fungia* (*Danafungia*) *horrida* and *F.* (*D.*) *scruposa* were separable only by perforations in the corallum wall, difficult to distinguish in live corals, and so were grouped under *F.* (*Danafungia*) spp.

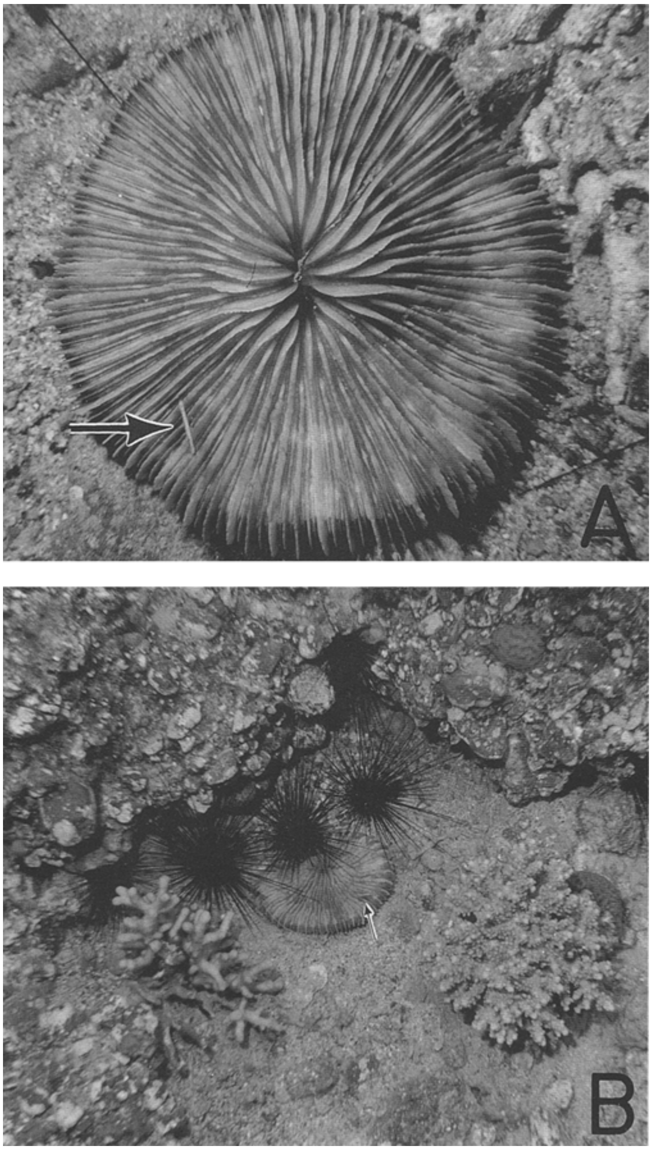

Fig. 1. *Fungia* (*Danafungia*) spp., free-living tagged individuals on coral reefs at Eilat, Red Sea. (A) Closeup showing tag location at coral periphery. (B) Polyp on soft substratum at 5 m depth, with sea urchins (*Diadema* spp.) on coral surface. Arrows indicate tags, each 1 cm length

The location of each coral was marked by a buoy tied to the reef framework <3 m distant, and compass direction (to the nearest 5°) and distance (to the nearest cm) from each buoy to its coral was determined. The following observations were recorded *in situ*: fungiid species, length (largest dimension across the corallum), substratum type (hard vs soft), substratum relief (cavity vs open substratum), orientation (degrees inclination of corallum from horizontal), depth below sea surface, types of sessile organisms contacted, and subsequent outcomes of contact.

Each coral was then transported in seawater to the laboratory and live wet mass determined (after Chadwick and Loya 1990). A small hole (2 mm diameter) was drilled at the corallum edge using an electric hand drill, and a numbered plastic tag inserted (Fig. 1). Less than 1 g of skeletal mass was removed per coral due to drilling. All corals were returned to seawater within 5 min and reexpanded within a few hours. They were maintained in outdoor tanks supplied with flowing seawater at ambient sea temperature for 1 to 7 d, then returned to their original positions on the reef. The corals appeared to recover rapidly from tagging: within 1 wk they covered the exposed skeleton at the drill hole with tissue and in 4 mo deposited skeleton that narrowed or completely closed the drill hole around each tag. Because the tags were small and located at the coral peripheries (Fig. 1), they did not appear to affect coral behavior.

At 4, 8, and 12 mo, the *in situ* observations above were repeated. Very small or very large (<3 or >30 cm length) or attached corals were not tagged; these were relocated by their distinctive morphologies and positions on the reef. Corals that detached during the year were identified by fresh detachment scars and proximity to marked stalks. The sample size decreased during the year due to the inability to relocate some corals.

Additional *in situ* observations on habitat use and competition (described above) were made on randomly-chosen, unmarked *Fungia scutaria* on the reef flat (1 to 2 m depth) and on other fungiids on the reef slope (5 to 25 m depth). Laboratory observations on behavioral mechanisms and short-term rates of movement were conducted on fungiids maintained for <2 wk in aquaria supplied with flowing seawater.

Results

Sizes and habitats

Attached individuals ranged in size from 0.5 to 6.0 cm length, while free-living (detached) corals became much larger (1.5 to 55.0 cm length) (Fig. 2). Detachment scars or remnants of stalks were visible on 22% of small free polyps (<5.0 cm length, $n=54$), but not on larger free corals ($n=177$). All individuals of *Cantharellus doederleini* remained attached and small (Fig. 2). Some large specimens (>7 cm length) of *Fungia* (*Danafungia*) spp. adhered to calcareous algae and sessile tunicates that were attached to the reef. No attached juveniles of *Herpolitha limax* were found, despite extensive searching.

Attached individuals of the four most common species were oriented significantly more vertically than detached (free) individuals (Fig. 3) [Mann-Whitney *U*-tests, $U=1153$ for *Fungia fungites*, $U=1694$ for *F.* (*Danafungia*) spp., $U=871$ for *F. scutaria*, and $U=623$ for *F. granulosa*, $p<0.001$ for all]. The permanently attached polyps of *Cantharellus doederleini* also occurred at an incline (Fig. 3).

Most attached fungiids (65.5%, $n=55$) occurred in reef cavities, while the rest were attached on open reef. In contrast, 51.5% of free-living corals occurred in cavities, 16.5% on open reef, and 32% on soft substratum at the reef base ($n=163$). Cavities occupied by free corals included depressions in rubble, spaces under other live fungiids, and spaces among colonial coral branches.

Almost half (9/20) of attached marked corals detached from the reef during the year: seven individuals of *Fungia* (*Danafungia*) spp., one of *F. granulosa* and one of *F. fungites*. Four detaching corals fell onto soft substratum, and seven out of the nine landed horizontally. One stalk of *F. fungites* and one of *F.* (*Danafungia*) spp. regenerated new polyps during the study period.

Migration

Migratory rate varied with species. Solitary corals with smooth undersurfaces (*Fungia granulosa*) moved faster than those with coarse undersurface ornamentation [*F. fungities* and *F.* (*Danafungia*) spp.]. Elongate colonial corals (*Ctenactis echinata* and *Herpolitha limax*), which attained the largest sizes, moved at the slowest rates (Table 1). Some individuals of *F. granulosa* were transported >300 cm during a winter storm, then remained stationary for the remainder of the year. In contrast, the fastest polyps of *F. fungites* moved <100 cm yr^{-1} (Table 1).

Migratory rate decreased significantly with body size in unobstructed individuals of all species combined (product-moment correlation test, $r=-0.41$, $p<0.01$) (Fig. 4). Small corals (1 to 100 g wet mass, 1.0 to 9.0 cm length) moved up to 343 cm yr^{-1}, while medium-sized corals (101 to 200 g, 9.1 to 12.0 cm) moved up to only 160 cm yr^{-1}, and large individuals (>200 g, >12.0 cm) moved <20 cm yr^{-1}.

Free corals that occurred in cavities ($n=21$) were obstructed, and thus moved significantly more slowly than unobstructed individuals in the same size range ($n=47$) (Mann-Whitney *U*-test, $U=734.5, p<0.01$) (Fig. 4). Substratum type also affected migratory rate; unobstructed corals on sand ($n=30$) moved at significantly faster rates (10 to 343 cm yr^{-1}) than those on reef rock ($n=26$, 0 to 190 cm yr^{-1}) (Mann-Whitney *U*-test, $U=567.5, p<0.01$).

The corals migrated down-slope and off-reef, as indicated by the changing proportions of marked individuals in each habitat. At the start of the experiment, 20% ($n=98$) were attached to the reef, 45% were free on the reef, and the remaining 35% free on sand. After 1 yr, only 11% remained attached to the reef, 46% were free on the reef, and 43% were now on sand. Thus, movement was

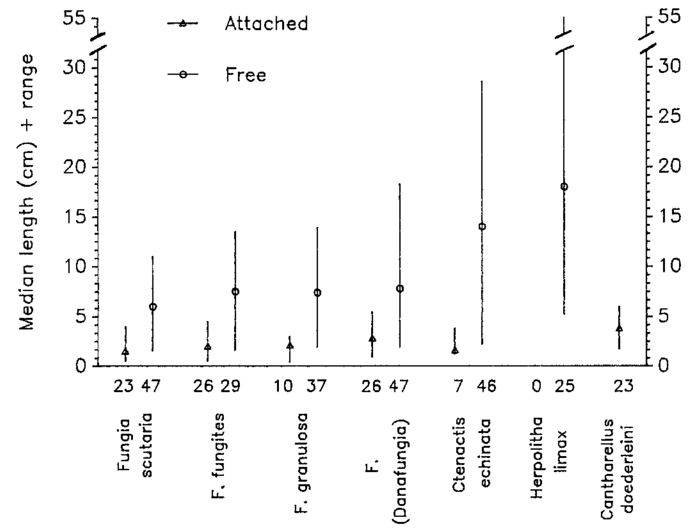

Fig. 2. Sizes of attached and free mushroom corals on reefs at Eilat, Red Sea. Numbers at bottom indicate sample sizes

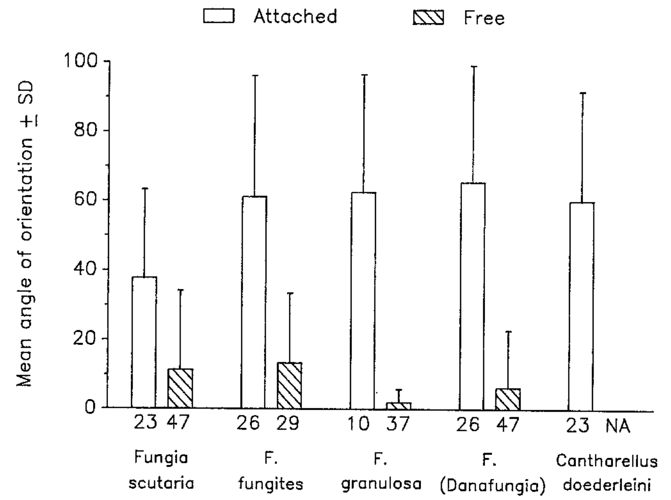

Fig. 3. Orientation (degrees inclination of corallum from horizontal) of attached vs free mushroom corals on reefs at Eilat. Numbers at bottom indicate sample sizes

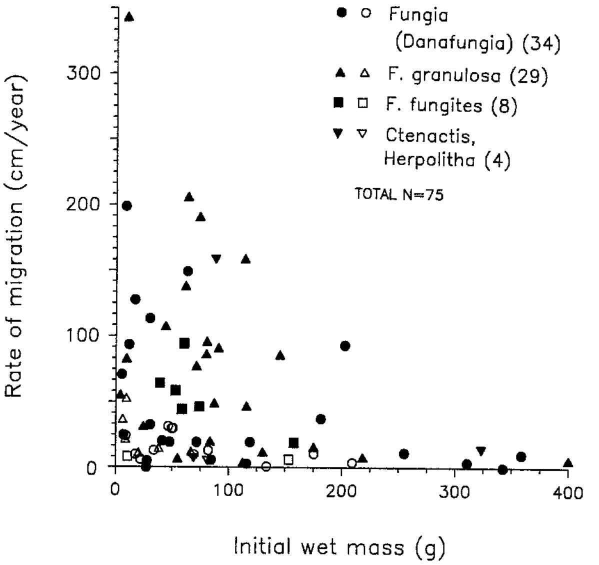

Fig. 4. Variation in mobility with corallum size, in five species of fungiid corals during 1 yr at Eilat, Red Sea. Filled symbols: unobstructed corals; open symbols: obstructed corals. Numbers in parentheses indicate sample sizes

Table 1. Migration of scleractinian corals in the family Fungiidae on coral reefs at Eilat, Red Sea, during 1 yr. The corallum outline of each species is either round (o) or elongate (|), and the undersurface is either smooth (=) or coarse (^) (after Hoeksema 1988). n = sample size

n	Species	Corallum outline and undersurface type	Mean wet mass at start (g)	Distance migrated (cm yr^{-1})	
				Mean (SD)	Range
29	*Fungia granulosa*	(o=)	83	71 (77)	4–343
38	*Fungia* (*Danafungia*) spp.	(o^)	128	40 (52)	0–199
10	*Fungia fungites*	(o^)	64	40 (27)	6– 94
8	*Ctenactis echinata, Herpolitha limax*	(|^)	343	29 (53)	5–158

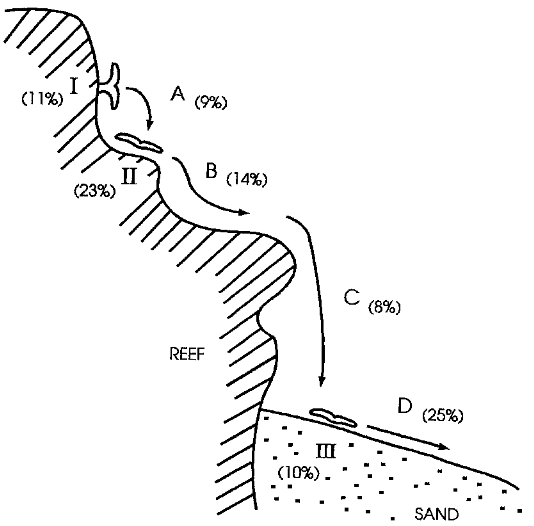

Fig. 5. Migratory patterns of mushroom corals ($n = 98$) on shallow coral reefs at Eilat, Red Sea. Roman numerals designate corals that remained stationary during 1 yr. Letters designate corals that changed position. Numbers in parentheses refer to the percent of corals that exhibited each behavior pattern. See "Results – Migration" for details

from the attached to free phase, and from the reef to sand habitat. No corals were observed to move from sand back onto reef, or from deeper to shallower depths. The corals that were transported during a storm moved down-slope, away from the shoreline. Less than half (44%) of all corals remained stationary throughout the year (Fig. 5).

Most free corals remained upright (oral side up) throughout the year. However, 10.3% of *Fungia granulosa* individuals ($n = 29$) and 18.4% of *F.* (*Danafungia*) spp. polyps ($n = 38$) became inverted. Some righted themselves in <4 d in the field.

In the laboratory, some fungiids actively moved fast enough to account for rates of field mobility at Eilat. Small (10 to 100 g, 4 to 9 cm length) upright individuals *Fungia* (*Danafungia*) spp. and *F. granulosa* ($n = 14$ each) moved up to 6 cm d^{-1} on both sand and rock. Inverted individuals ($n = 12$ each) righted themselves in 1 to 3 d, and continued to migrate while inverted. The corals moved by nocturnally inflating and pushing their soft tissues against the substratum.

Competitive interactions

The fungiids did not suffer tissue damage during contact with each other (Table 2). Polyps often occurred in aggregations, sometimes partially or completely underneath fungiids of other species, with no visible damage. In contrast, members of the six species on the reef slope unilaterally damaged non-fungiid scleractinian corals (Table 2). Damage was visible as an area of exposed skeleton on neighboring corals along the region of contact. Soft corals (Octocorallia) appeared to interact benignly with fungiids (Table 2). In two cases, unidentified corallimorpharians grew over and killed attached polyps of *Cantharellus doederleini*. No fungiids were observed to contact macroalgae.

Table 2. Outcome of natural competitive interactions between fungiid scleractinian corals and other sessile organisms on reef slopes at Eilat, Red Sea. →: coral in the horizontal column injured organism in the vertical column. 0: no injury. ( ): number of cases observed

Fungiid species	Sessile organisms contacted:			Total
	Fungiids	Non-fungiid scleractinia	Octo-corals	
Fungia granulosa	0 (25)	→ (18) 0 (1)	0 (19)	63
F. (*Danafungia*) spp.	0 (30)	→ (24)	0 (23)	77
F. fungites	0 (21)	→ (13)	0 (6)	40
Ctenactis echinata	0 (21)	→ (23) 0 (2)	0 (6)	52
Herpolitha limax	0 (1)	→ (2)	0 (2)	5
Cantharellus doederleini	0 (1)	→ (4)	0 (2)	7[a]
All	0 (99)	→ (84) 0 (3)	0 (58)	244

[a] In addition, two individuals of *C. doederleini* were overgrown and killed by unidentified corallimorpharians

Table 3. Persistence of contacts between fungiid corals and non-fungiid sessile macro-organisms on coral reef slopes at Eilat, Red Sea

Species	Number in contact:			Total
	During entire year	During part of year	Not at all	
Fungia granulosa	3	5	21	29
Fungia (*Danafungia*) spp.	7	10	32	49
Fungia fungites	0	2	7	9
Ctenactis echinata	1	2	0	3
Herpolitha limax	1	0	5	6
Cantharellus doederleini	1	0	7	8
All species	13	19	72	104
Percentages	12.5%	18.3%	69.2%	100%

Due to their mobility, only 12.5% of fungiids ($n = 104$) maintained persistent contact with non-fungiid benthic organisms during the entire year. Most (69.2%) did not contact other benthic organisms at all, and 18.3% moved into or out of contact during the year (Table 3). Thus, most contacts between mobile fungiid corals and other sedentary organisms on Eilat reef slopes were benign to the fungiids and did not persist for long periods.

Discussion

Habitats

We document a shift in habitat use between juvenile and adult fungiid corals due to adult mobility. Such developmental segregation is rare among scleractinian corals and occurs only when early benthic stages are attached and subsequent stages fragment or become free-living (Highsmith 1982). A few cases have been described: adult Indonesian *Fungia* (*Pleuractis*) *moluccensis* occur deeper than juveniles due to their migration onto soft substratum at the reef base (Hoeksema 1990). In 14 Great Barrier Reef fungiids, cavity-dwelling is limited to attached juveniles <3 cm diameter (Dinesen 1983), while adults presumably move out onto open reef and sand. By moving from one area to another as they mature, mobile corals may impact a greater diversity of reef habitats than do permanently attached corals.

The sloping corallum orientation of attached fungiids (Fig. 3) may assist them in avoiding burial, which is a major source of mortality among newly settled corals (Bak and Engel 1979). Vertically-oriented coral polyps remove sediment more effectively than do horizontal polyps of the same species (Logan 1988). Free-living fungiids appear to use their larger size, mobility and well-developed mechanisms of sediment rejection to resist burial (Schuhmacher 1979).

We demonstrate a high rate of detachment among juvenile mushroom corals (almost 50% in 1 yr, see "Results"). Additional data on rapid juvenile growth (Chadwick-Furman and Loya in preparation) suggest that the attached phase may extend <2 yr in some species. The present study is the first to document in nature the complete cycle of anthocaulus growth, detachment of the anthocyathus, and regeneration of new anthocauli from the same stalk.

Sizes of free-living corals

Free-living fungiid corals reach small maximum sizes (Fig. 2) relative to those of attached ones, which may grow to >1 m diameter (review in Hoeksema 1991 b). Convergence in the size limitation of free corals from different scleractinian families (maximum diameters all <20 cm) (Yonge 1935, Glynn 1974, Scoffin et al. 1985, Lewis 1989) appears to be due to the physical constraints of large size on mobility. Large free corals may become immobile, the tissue on their undersurfaces may die, and eventually they may sink into the substratum (Glynn 1974, Sheppard 1981, Hoeksema 1991 b).

Mobile corals also become free-living at very small minimum sizes, <3 cm length in most species (Yonge 1935, Glynn 1974, Scoffin et al. 1985, Lewis 1989, our Fig. 2). Detachment from the substratum when small may be advantageous, because dispersive and righting abilities are greatest when small (Hubbard 1972, Glynn 1974, Hoeksema 1988, our Fig. 4). If corals detach at larger sizes, they consequently exhibit lower mobility at the beginning of the free phase, and thus have less time to disperse and move away from competitors before they grow into relatively large and sedentary individuals.

Patterns of migration

The migratory rates of fungiids on relatively sheltered reef slopes at Eilat (Table 1) were lower than those of the same species on an exposed reef slope in Indonesia (Hoeksema 1988). In both localities, dispersal rate generally was higher for species with smooth undersurfaces than for those with coarse undersurface ornamentation. The lower mobility of ornamented species may be due to their highly dentate costae which stabilize them by increasing friction with the substratum (Hoeksema 1988).

Decreasing mobility with size (Fig. 4) has also been demonstrated for mobile coralliths in Panama (Glynn 1974). Due to partial mortality, fission and fusion, coral size does not necessarily reflect age (Hughes and Jackson 1980). However, because free-living corals are disconnected from the substratum and each other, these processes are detectable via regeneration scars and irregularities in corallum outline (Hoeksema 1989, Lewis 1989). In the present study, evidence of the above processes were observed in only 4.3% of individuals ($n=117$). Thus, for most Eilat fungiids, corallum size appears to vary directly with age; they migrate relatively rapidly when young and newly detached from the reef, decrease dispersal rate with age, and become essentially immobile upon reaching >200 g wet mass (approximately 11 to 13 cm length) (Fig. 4).

Migration from reef to sand and from shallower to deeper habitats, in both sheltered (Fig. 5) and exposed environments (Hoeksema 1988), has important implications for the initiation and extension of coral reefs. Fungiids actively extend the reef onto the surrounding soft substratum (Sheppard 1981), where their skeletons shelter mobile organisms (echinoderms, molluscs, crustaceans) (Hoeksema 1988, N. Chadwick-Furman personal observation) and provide hard substratum for further coral recruitment.

Mechanisms of coral mobility

Fungiids in the present study actively righted themselves following inversion. Members of some species accomplish this via bouts of rocking motion created by periodic expansion and contraction of the coelenteron (Hubbard 1972, Nishihira and Poung-In 1989), while others are righted passively due to the hydraulic response of their skeletons (Jokiel and Cowdin 1976). At Eilat, the skeletons of dead fungiids remained upside down for >1 yr in the field, while live polyps righted themselves, thus supporting the hypothesis that polyp behavior plays a major role in their righting response.

Polyp behavior also appears responsible for coral migration at Eilat of several cm d^{-1}. Fungiids employ diverse mechanisms of benthic mobility, including controlled constriction and relaxation of distended tissue (Goreau and Yonge 1968, Fisk 1983, this paper), the use of long, continuously-expanded tentacles as a ship-sail to facilitate transport by currents (Abe 1939), and secretion of a mucus float to increase buoyancy during locomotion (Hubbard 1972).

Autonomous locomotion has remained undetected in most studies of mobile corals, because they usually move at night when their polyps are expanded (Chadwick 1988) and because most movement is restricted to small individuals (Hubbard 1972, Glynn 1974, Pichon 1974, Chadwick 1988, our Fig. 4).

Other organisms, such as obligate sipunculan symbionts (Goreau and Yonge 1968, Fisk 1983, Hoeksema and Best 1991) and foraging fish (Glynn 1974, Dullo and Hecht 1990) also may relocate free-living corals. At Eilat, the long-shore current (A. Genin personal communication) may enhance the mobility of nocturnally-expanded fungiids. Currents or storm waves also may shift sediment underneath large free corals, causing them to slide downslope (Pichon 1974). Finally, seasonal monsoons (Hoeksema 1988) and other periodic storms (this paper) may carry detached corals over great distances in short time intervals.

We conclude that, at Eilat, fungiids migrate via active locomotion, with infrequent storms causing rapid, short-term transport of some corals. However, the extent of bioturbation has not been quantified and also may play a role in local coral transport (Dullo and Hecht 1990).

Competitive interactions

Fungiid corals are competitively dominant during contacts with non-fungiid scleractinians in the northern Red Sea (Table 2), as well as at sites in the Indian and Pacific Oceans (Chadwick 1988 and references therein, Hoeksema 1988). Active damage of other corals may be important for these relatively small, flat coralla to retard overgrowth by larger branching and massive colonial corals. In contrast, fungiids do not exhibit damage interactions among themselves (Chadwick 1988, Hoeksema 1988, our Table 2). Due to their size and mobility, they do not risk overgrowth or smothering by each other, although they may deprive each other of light and food (Hoeksema 1988). Overall, there does not appear to be great adaptive value in investing energy into damaging other fungiids. In addition, the thick mucus sheath secreted by most fungiids may protect them from damaging each other, as well as having an offensive function (Chadwick 1988).

Fungiids and soft octocorals appear to interact benignly (Table 2) possibly due to rapid healing of octocoral tissue or to the absence of a hard skeleton showing evidence of damage. Alternately, soft corals may be able to protect themselves effectively from noxious fungiid mucus (Chadwick 1988) by virtue of their own toxins (Sammarco et al. 1983), voluminous mucus production and flexible skeletons.

It is significant that the only fungiid corals killed by competitors were permanently-attached individuals (Table 2). Detachment and dispersal away from sessile competitors (Table 3, Fig. 5) may enhance survival in many fungiid species (Maragos 1974, Hoeksema 1988). The percentage of fungiid corals contacting other sessile macro-organisms is similar on coral reefs at Eilat (30.8%, Table 3) and Hawaii (40.8%, Chadwick 1988), and at both localities many contacts do not persist.

Due to their competitive abilities and mobility, fungiid corals are well-equipped to defend space on crowded reefs and also to colonize habitats not available to other corals. These traits allow them to flourish in both highly variable reef environments (Hoeksema 1988) and also on the relatively stable, calm-water reef slopes of the northern Red Sea.

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