ABUNDANCE AND DISTRIBUTION OF MUSHROOM CORALS (SCLERACTINIA: FUNGIIDAE) ON A CORAL REEF AT EILAT, NORTHERN RED SEA

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ABSTRACT

Mushroom corals (Scleractinia: Fungiidae) are important components of Indo-Pacific coral reefs, yet little is known about their patterns of abundance and distribution in the Red Sea. On a fringing reef at Eilat, northern Red Sea, mushroom corals were found to be common on the reef flat and shallow slope at <10 m depth, where they occurred at densities of up to 15 individuals m^{-2}, but were rare on the mid to deep reef slope at 10–50 m depth. Eleven species were observed, a 27% increase in the recorded species diversity of this coral family at Eilat. Individuals of two species were limited to the reef flat and shallow reef slope, and members of five other species also occurred mainly on the shallow slope, but had wide depth ranges. Individuals of an additional four mushroom coral species were found mainly on the lower reef slope at low densities. In shallow water, most fungiids occurred in shaded reef habitats such as caves or holes, while at >20 m depth, they mainly occupied open, unshaded habitats. This study documents differences in habitat use between species of mushroom corals on a fringing reef, and substantial migration by the adult free-living polyps of some species out of shaded reef habitats, down the reef slope, and onto soft substratum.

Mushroom corals comprise one of the more diverse families of reef-building corals in the tropical Indo-Pacific region, with 41 known species in the family Fungiidae (Hoeksema 1992, 1993a,b). They are unique among scleractinians in that the individuals of most species are able to move from one habitat to another during their benthic phase. Juvenile mushroom corals (= the anthocaulus stage) grow attached to hard substratum, but after reaching a few cm diameter, the cap-shaped polyps of most species actively dissolve their skeletal attachment to the stalk-like base (Yamashiro and Yamazato, 1996, and references therein), detach from the reef, and become free-living polyps (= the anthocyathus stage) that may migrate onto soft substratum or down the reef slope (Chadwick-Furman and Loya, 1992). The adults of most species form solitary, mobile disks that are among the largest known scleractinian coral polyps (Hoeksema, 1989). The free-living adults sexually produce planktonic planula larvae that settle and metamorphose into attached anthocaulus polyps, which in turn may successively bud off a limited number of anthocyathi (Yamashiro, 1992), thus forming small clones of unconnected, mobile adults (Wells, 1966; Hoeksema, 1989). In addition, the members of some species reproduce asexually from adult polyps after injury (Krupp et al., 1992; Kramarsky-Winter and Loya, 1998). Members of a single clone may disperse over the reef or, if the source anthocaulus is inside a hole or reef depression, may remain aggregated (Hoeksema, 1988; Chadwick-Furman and Loya, 1992). Young fungiid corals suffer high mortality immediately after detachment from the stalk, so that only a small percentage of all anthocyathi that originally detach eventually reach sexual maturity and maximal adult size (Chadwick-Furman et al., 1999). Members of some fungiid genera (*Cantharellus*, *Lithophyllon* and *Podabacia*) have not developed the mobile anthocyathus stage, and remain in the sessile phase during their entire lifespan (Hoeksema, 1989).

Fungiid corals are conspicuous and common members of many Indo-Pacific coral reefs. They contribute to reef-building, and have recently been discovered to construct large patch reefs (Littler et al., 1997). The mobile adults are important colonizers of sandy substratum, in contrast to most other scleractinians which are confined to hard substratum (Chadwick-Furman and Loya, 1992). When fungiid corals die, their calcareous skeletons may remain on the sandy bottom and serve as a base for the adherence of the larvae of other corals, thus becoming nuclei for the formation of new patch reefs and for the extension of coral reefs over sandy areas (Sheppard, 1981).

Little is known about patterns of abundance and distribution on coral reefs by members of this family. Evidence of segregation among species by depth has been found on reefs in Indonesia (Hoeksema, 1990) and at Fanning Island in the central Pacific (Maragos, 1974). However, almost no quantitative information is available concerning their abundance or spatial distribution in the Red Sea. A diverse assemblage of 21 mushroom coral species occurs on Red Sea coral reefs (Sheppard and Sheppard, 1991), and they are conspicuous members of the reef-building coral fauna of Eilat (Loya and Slobodkin, 1971; Chadwick-Furman and Loya, 1992). Twenty of these species also occur at the center of scleractinian coral diversity in Indonesia, and one (*Cantharellus doederleini*) is endemic to the Gulf of Aqaba in the northern Red Sea (Hoeksema, 1989).

We present here information on the abundance, distribution, and habitat use of mushroom corals on a fringing reef at Eilat, northern Red Sea. We increase the number of fungiid species recorded at Eilat to 11, and extend the range of one species (*Fungia paumotensis*) approximately 700 km north from its previously known limit in the central Red Sea (Hoeksema, 1989, 1993b). Our observations document that the detached polyps of some mushroom corals migrate down the reef slope, onto sand and out of reef caves, probably due in part to low light levels in caves at depth.

This study presents the first comprehensive description of distributional patterns and habitat use of mushroom corals on a Red Sea coral reef. As such, it contributes important new information to understanding the biology of solitary reef-building corals.

MATERIALS AND METHODS

The present study was conducted during January to April 1996, at Eilat, Gulf of Aqaba, northern Red Sea. We examined fungiid corals at a fringing coral reef site known locally as the Japanese Gardens. The depth profile and overall coral community structure at this site have been described by Loya and Slobodkin (1971). We quantified the abundance of fungiid corals within a series of 1-m^2 quadrats (n = 25) in a band parallel to shore at each of 12 depths on this reef: on the inner edge of the reef flat, on the outer edge of the reef flat (both at 1 m depth), and at 2, 3, 6, 9, 12, 15, 21, 27, 33, and 40 m depth on the reef slope (after Hoeksema, 1990, 1991). We also made qualitative observations on the presence of mushroom corals outside of the quadrats at all depths, especially on the deep reef slope at 41–55 m depth where quadrats were not examined.

Within each quadrat, we identified all mushroom corals to species after Hoeksema (1989). Individuals of *Fungia (Danafungia) horrida* and *F. (Danafungia) scruposa* have both been found to occur at Eilat, and differ only in the presence of perforations in the corallum wall (Chadwick-Furman and Loya, 1992). We were unable to distinguish this trait on live polyps in the field, so the corals of these two species were grouped as *F. (Danafungia)* spp. (after Chadwick-Furman and Loya, 1992). For each mushroom coral observed, we determined the type of substratum occupied (hard vs soft), life history phase (attached anthocaulus vs detached anthocyathus stage), and microhabitat (shaded vs open habitat). Shaded habitats were quantified as those exposed to <10% (range

= 2.0–9.8%) of the light level measured in adjacent open reef habitats, using a submersible light meter (LiCor Instruments, San Diego, California). We also estimated the percent cover of hard substratum within each quadrat, and the percent coveroccupied by fungiid corals, to the nearest 5%.

Results

We observed 11 species of mushroom corals at our study site in Eilat, northern Red Sea (Figs. 1,2). They varied widely in both their overall abundance and in depth distribution, with the members of most species occurring over a wide depth range on the reef slope (Fig. 2). As a group, mushroom corals were most common on the reef flat and shallow slope to 6 m depth, where they reached a maximal abundance of approximately 15 ind m^{-2} and covered up to 5% of the substratum (Fig. 3). They were rare on the mid to deep slope, even though % cover of hard substratum on the deep slope was high (Fig. 3).

Examination of the depth distribution of attached versus free-living phases revealed that attached juveniles occurred almost entirely on the shallow reef slope at <10 m depth, while the adult free-living individuals of some species also were found deeper on the reef (Fig. 4). In most fungiids, free-living adults were more common than the attached juveniles (Fig. 4B–E), except in *Fungia scutaria* (Fig. 4A). Both phases of *F. scutaria* occurred almost entirely on the reef flat at this site, with a median recorded depth of only 1 m (Figs. 1A, 2). On the outer reef flat, they reached abundances of up to eight attached plus four free-living ind m^{-2} (Fig. 4A). Of 469 *F. scutaria* individuals, only 1.1% were found at >3 m depth on the reef (Fig. 4A). Individuals of the elongate fungiid *Ctenactis echinata* (Fig. 1B) also were limited to shallow water at this site, and were not found at >8 m depth even during extensive qualitative surveys down to 55 m depth on the reef slope (Fig. 2). They were common at 2–6 m depth, where they occurred at an abundance of up to two ind m^{-2} (Fig. 4B). Members of five additional species of mushroom corals (*F. fungites*, *F. granulosa*, two species of *F. (Danafungia)*, and *Herpolitha limax*) all had wide depth ranges, but also were most common on the shallow slope, with median depths at 2–9 m (Fig. 2). Of these, members of the two species grouped together under *F. (Danafungia)* spp. were the most abundant (Fig. 2), with up to four ind m^{-2} at 2–3 m depth (Fig. 4E). Both *F. fungites* and *F. granulosa* also were common (Fig. 2), occurring at approximately three and one individual m^{-2} respectively on the shallow reef slope (Fig. 4C,D). The elongate, polystomatous fungiid *Herpolitha limax* was rare at our study site, with only six individuals observed at shallow depths inside the quadrats, and other individuals found scattered deeper on the reef slope (Figs. 1H and 2). Members of the four final species of mushroom corals (*Cantharellus doederleini*, *Fungia costulata*, *F. paumotensis* and *Podabacia crustacea*) were relatively rare, and occurred mainly on the deep reef slope (Figs. 1E,G,2). Only *Cantharellus doederleini* occurred in high enough numbers to assess depth-abundance patterns (Fig. 2). Individuals of this permanently-attached, endemic fungiid were most common at >15 m depth, occurring at approximately 0.3 ind m^{-2} on the deep reef slope (Fig. 4F).

All fungiids in the attached phase were observed to occur on hard substratum. Similarly, most free-living individuals also remained on hard substratum (= 99.5% of *Fungia scutaria* (n = 186), 93.7% of *F. fungites* (n = 190), 88.0% of two species of *F. (Danafungia)* (n = 333), and 93.1% of *C. echinata* (n = 102)). Only in *F. granulosa*, a substantial proportion of free-living polyps (=35.6%, n = 118) moved off the reef and onto the surrounding soft substratum (Fig. 1C).
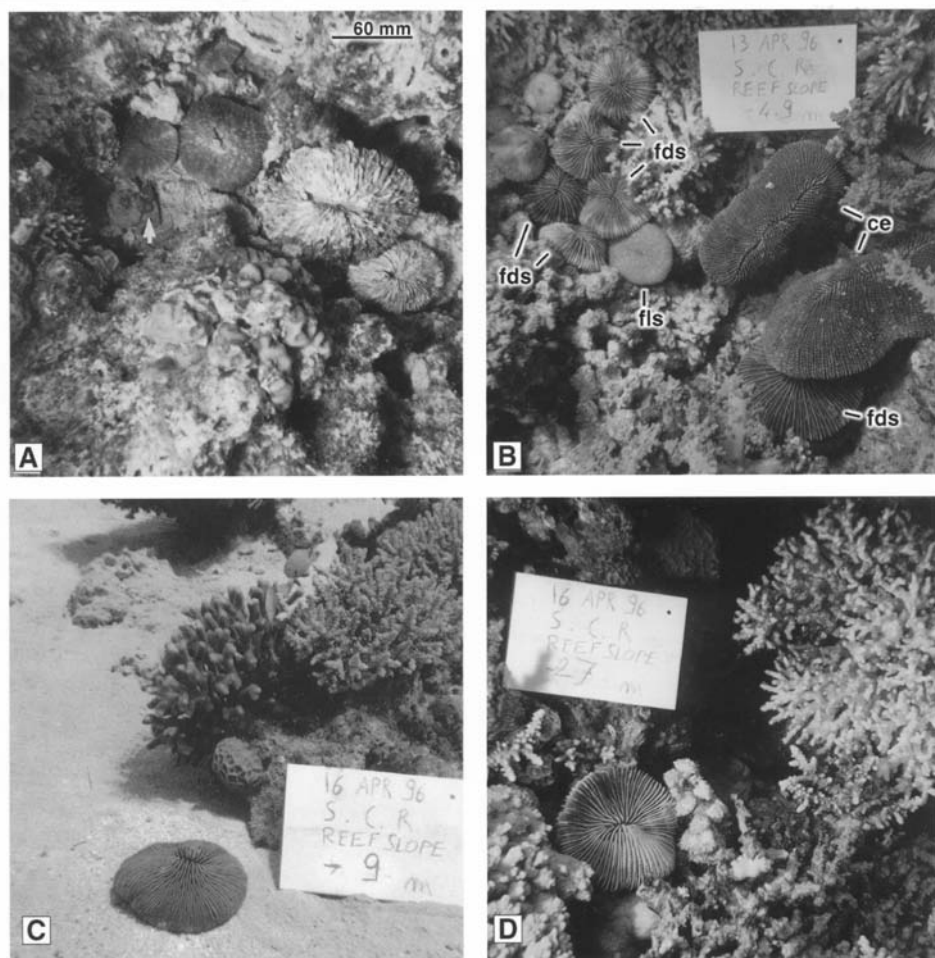
Figure 1. Mushroom corals and typical habitats on a fringing reef at Eilat, northern Red Sea. Scale is indicated by a white slate (15 cm long × 10 cm wide) or a scale bar (6 cm long). (A) Solitary polyps of *Fungia scutaria* in a depression on the reef flat at 1 m depth. Note small attached polyps (arrow) and dead adult corals. (B) Mixed aggregation on hard substratum on the shallow reef slope at 4.9 m depth (fds = *F. (Danafungia)* spp., fls = *F. scutaria*, ce = *Ctenactis echinata*). (C) Patch reef and free-living polyp of *Fungia granulosa* on soft substratum on the mid reef slope at 9 m depth. (D) Free-living polyp of *F. (Danafungia)* sp. on hard substratum on the deep reef slope at 27 m depth. *(opposite page)* (E) Large, permanently-attached individual of *Podabacia crustacea* on the deep reef slope at 40 m depth. Colony = 60 cm diameter. (F) Mixed aggregation on the deep reef slope at 50 m depth (fds = *Fungia (Danafungia)* spp.; fff = *F. fungites*, fsp = *Fungia* sp.). (G) Two free-living polyps of *F. paumotensis* on the deep reef slope at 45 m depth. (H) A free-living polystomatous individual of *Herpolitha limax* (hl) and a polyp of *Fungia fungites* (fff) on coral rubble on the deep reef slope at 55 m depth.

At shallow depths of <20 m, most attached individuals occurred in shaded reef habitats such as reef caves or holes (Table 1). In contrast, the proportion of free-living individuals that remained in shaded habitats varied widely between species (Table 1). In both *Ctenactis echinata* and *F. granulosa*, a substantial proportion of the individuals (approx 65 and 45%, respectively) moved out into open, unshaded reef areas once they became free-living (Table 1). Individuals of only *F. (Danafungia)* spp. and *C. doederleini* occurred at
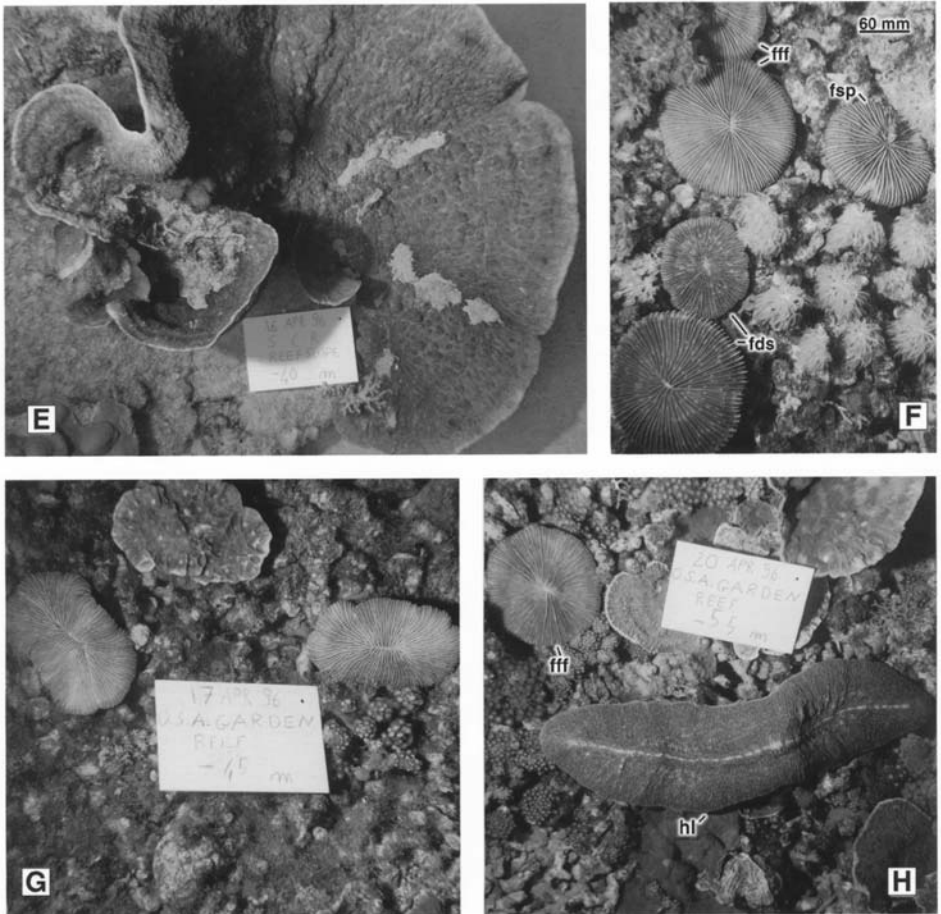
sufficient abundance on the deep reef slope to assess changes in the use of shaded habitat with depth (Fig. 4E,F). In these corals, significantly lower proportions of polyps were found in shaded habitats in deep than in shallow areas of the reef (Table 1) (G test of independence, G = 21.77, 17.31 and 37.97 for *C. doederleini*, attached and free-living *Fungia (Danafungia)* spp., respectively, P < 0.01 for all). Fungiids did not abruptly change their habitat use at a given depth, but appeared to gradually decrease the proportion of polyps occurring in shaded habitats with depth on the reef (Fig. 5). As a group, mushroom corals in shaded habitats decreased from 74.6% of individuals at <10 m depth to only 17.2% of individuals at >30m depth (Fig. 5).

DISCUSSION

We demonstrate here that mushroom corals varied widely among species in their patterns of depth distribution, abundance and habitat use on a coral reef in the Red Sea. These differences may relate to variation between the species in their morphologies and life history strategies. The observed patterns of space use also indicate that the free-living
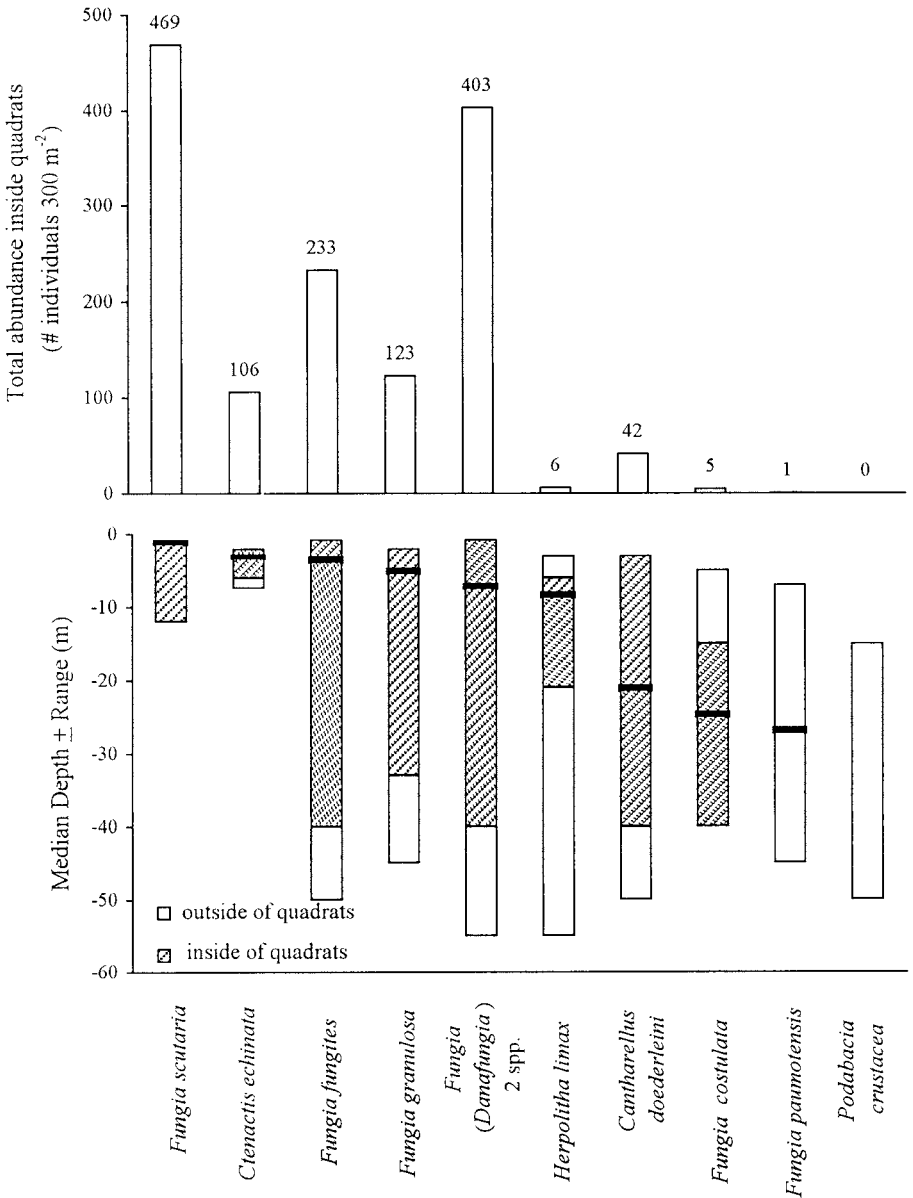
Figure 2. Depth ranges and relative abundances of members of 11 species of mushroom corals on a fringing reef at Eilat, northern Red Sea. Coral abundance was quantified at 0–40 m depth inside quadrats, and the presence of each species also was recorded outside of quadrats at 0–55 m depth. A total area of 300 m^2 was examined inside quadrats (= 1-m^2 quadrats [n = 25] per depth × 12 depths examined).
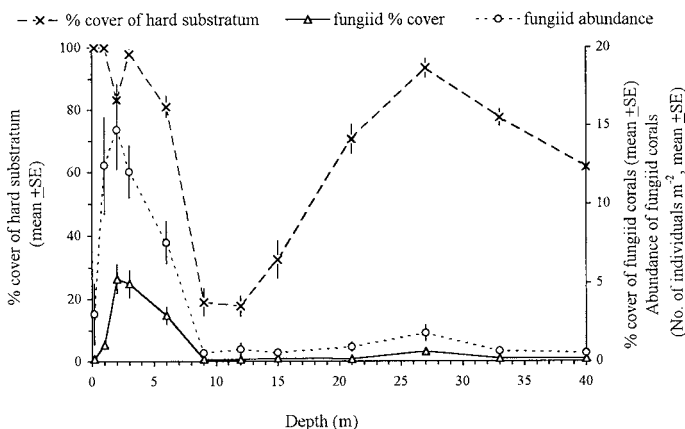
Figure 3. Variation in the percent cover of hard substratum, and the percent cover and abundance of mushroom corals with depth on a fringing coral reef at Eilat, northern Red Sea. n = 25 quadrats of 1-m² each were examined at each depth. For clarity, the inner reef flat is presented as 0 m depth and the outer reef flat as 1 m depth.

individuals of some species migrated down the reef slope, onto soft substratum, and out of shaded areas on the reef slope (Figs. 4,5, Table 1). The ability of fungiid corals to actively and passively migrate on the reef has been documented previously (Hoeksema, 1988; Chadwick-Furman and Loya, 1992). Several species of fungiids also are known to move actively toward light (Yamashiro and Nishihira, 1995), a form of positive photo-taxis that may explain in part their increased occurrence in open rather than shaded habi-tats following the end of the attached phase during their life history (Table 1). The present study is the first detailed analysis of abundance and distributional patterns of mushroom corals on a Red Sea coral reef, and substantially increases the recorded species diversity for this group at Eilat.

We found 11 species of mushroom corals at Eilat, in contrast to only six species re-corded by Loya and Slobodkin (1971), and eight by Chadwick-Furman and Loya (1992). This increase in observed diversity is due in part to a recent taxonomic revision of the family Fungiidae (Hoeksema, 1989), and also likely due to deep water research on the members of rare species (Fig. 2). Our observation of *F. paumotensis* is the first confirmed record of this species in the Gulf of Aqaba, and extends its range from Yambu, Saudi Arabia in the central Red Sea, a northward extension of 700 km (Hoeksema, 1989, 1993b). The total diversity of fungiid corals in the Gulf of Aqaba, now 15 species, is remarkably high, given the position of this area at the northwestern edge of the Indo-Pacific region, far from the center of scleractinian coral diversity in southeast Asia, where 39 fungiid species occur (Hoeksema, 1992). The relatively high number of fungiid corals at Eilat corresponds to a high diversity of scleractinian corals in general at this site (Loya, 1972).

The depth distributions of fungiids recorded here may relate to some unique features of our study site. For example, their low abundance on the mid reef slope corresponded to a lack of hard substratum and an abundance of sandy habitat at this depth (Fig. 3). Other reefs that do not display such wide variation in hard substratum availability with depth might have different zonation patterns of fungiid corals. Some mushroom corals are able to colonize sandy substratum, but the abundance of most species is higher on reef slopes
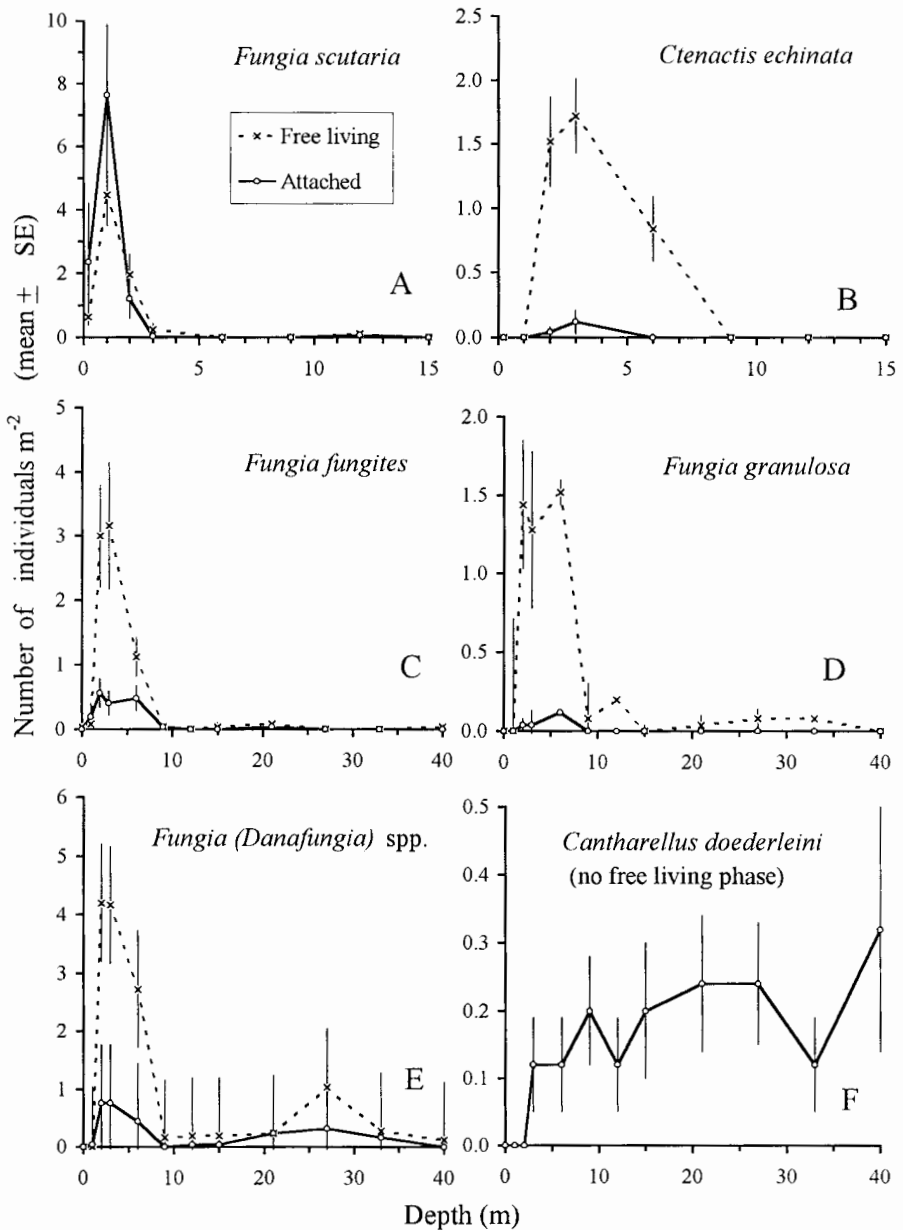
Figure 4. Variation in the abundance of attached versus free-living stages with depth among common species of fungiid corals on a fringing reef at Eilat, northern Red Sea. n = 25 quadrats of 1-m² each were examined at each depth. For clarity, inner reef flat presented as 0 m depth and outer reef flat as 1 m depth. Note the differences in scale between graphs.
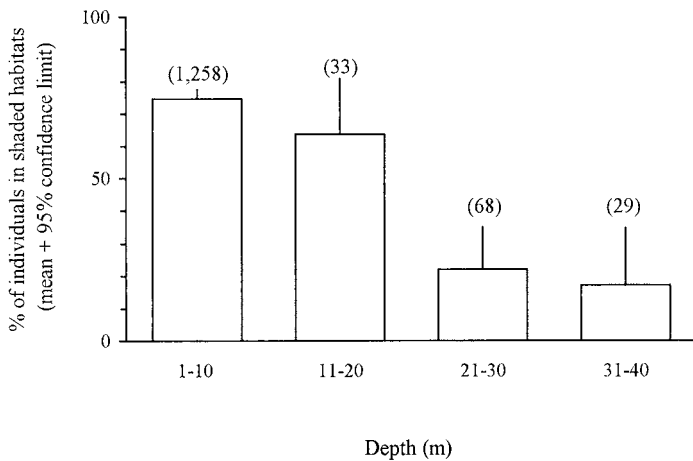
Figure 5. Variation in the occupation of shaded reef habitats with depth by mushroom corals on a fringing reef at Eilat, northern Red Sea. Sample sizes are given in parentheses. Shown are data for all fungiid corals observed inside transects; note that most individuals occurred in shallow water.

with hard substratum than on adjacent slope areas with mainly sediment cover (Hoeksema, 1990). At a nearby site in Eilat that contained only patch reefs and rocky rubble, a similar depth distribution pattern was observed for *F. scutaria* (range = 0.5–5 m depth), but not for *F. granulosa* (range = 5–25 m depth, but maximum abundance at 15–25 m depth) (Kramarsky-Winter and Loya, 1998; compare with Fig. 2). This difference probably is due to between-site variation in substratum characteristics, and to the special ability of *F. granulosa* to invade sandy and rubble habitats (see Results).

Despite localized differences due to reef topography and substratum type, the depth distributions of some of the fungiids measured here were similar to those observed on

Table 1. Variation among mushroom coral species in the percentage of individuals that occurred in shaded habitats on a coral reef at Eilat, northern Red Sea. Sample sizes are given in parentheses. Data are given for both major life history stages within each species.

Species	Percent of individuals that occurred in shaded habitat during:	
	attached stage	free-living stage
Ctenactis echinata	100% (4)	35.3% (102)
Fungia scuriata	96.8% (283)	82.8% (186)
F. fungites	100% (43)	72.1% (190)
F. granulosa	100% (5)	55.1% (118)
F. (Danafungia) (2 species)*		
shallow (0–20 m)	82.9% (52)	60.8% (291)
deep (21–40 m)	27.8% (18)	11.9% (42)
*Cantharellus doederleini**		
shallow (0–20 m)	100% (19)	**
deep (21–40 m)	39.1% (23)	**

* Shallow and deep areas shown separately for these species because they were the only ones common at both deep ranges.
** Does not have a free-living stage during the life cycle.

reefs in Indonesia (Hoeksema, 1990). Most mushroom corals reached maximal abundances at shallower depths at Eilat (Fig. 2) than in Indonesia (Hoeksema, 1990), possibly due to the relatively protected location and low levels of water motion at Eilat, which is located at the northern end of an enclosed sea (Chadwick-Furman and Loya, 1992; Genin et al., 1994). Other possible explanations, such as low light penetration or temperature levels due to the high latitude of reefs in Eilat, do not explain these differences: light penetration is known to be high in the northern Red Sea, and temperatures remain practically constant with depth on reefs in Eilat (Fricke and Schuhmacher, 1983). Three species (*F. scutaria*, *F. fungites* and *C. echinata*) were found to be shallow-water corals at both sites, occurring mainly on the intertidal reef flat and upper reef slope (Hoeksema, 1990; Fig. 4). However, two other species (*F. paumotensis* and *Podabacia crustacea*) were common shallow-water fungiids in Indonesia (Hoeksema, 1990), but were rare and deep at the site examined in Eilat (Fig. 2). Interestingly, the sister species of *Fungia (Danafungia) horrida* and *F. (D.) scruposa* were observed to have almost identical depth distributions in Indonesia (Hoeksema, 1990), so the pattern recorded here for the two species grouped under *F. (Danafungia)* spp. (Figs. 2,4) may accurately reflect the depth distributional pattern for members of the subgenus *Danafungia* at Eilat.

The depth ranges observed here also were shallower than for fungiid corals examined on a reef at Fanning Island in the central Pacific (Maragos, 1974; Fig. 2). At Fanning Island, both *F. fungites* and *F. scutaria* occurred at 6–20 m depth, and were the shallowest of the five fungiid corals recorded there (Maragos, 1974). In contrast, at Eilat, these two species also were among the shallowest, but reached their peak abundances at only 1–3 m depth (Fig. 2). These differences again appear related to levels of water motion. The reef at Fanning Island is exposed to large oceanic swells which generate high levels of water motion at shallow depths (Maragos, 1974), while the sheltered reef examined in Eilat, as noted above, experiences relatively low levels of water motion during most of the year (Chadwick-Furman and Loya, 1992), with a mean current speed of only 5.5 cm s^{-1} (Genin et al., 1994). Due to their free-living life style, shallow water fungiids on exposed reefs are transported downslope by wave action (Hoeksema, 1988), resulting in possibly deeper distributions than for those occurring on protected reefs.

Individuals of *F. scutaria* are unique among mushroom corals in that often they are limited to reef flats in very shallow water, as observed in Papua New Guinea (Claereboudt, 1988), Indonesia (Hoeksema, 1988; 1990), Hawaii (Krupp et al., 1992 and references therein), and Eilat (Chadwick-Furman and Loya, 1992; Kramarsky-Winter and Loya, 1996, 1998; Figs. 2,4). Members of this species possess traits suited for life in shallow turbulent waters and exposure to frequent physical disturbances such as low tides and fresh-water runoff. The polyps have a bowl-like shape that passively rights itself when overturned by water motion, and a dense skeleton that resists abrasion (Jokiel and Cowdin, 1976). The septa of *F. scutaria* have fine, sharp spines that are unable to resist tissue damage due to sedimentation, and thus are not suited for life on soft substratum (Schuhmacher, 1977). The dense skeleton and convex shape of *F. scutaria* may hinder movements by anchoring the corals in crevices on the reef flat instead of allowing them to migrate downslope or onto sand (Hoeksema, 1988). Finally, if adult polyps of *F. scutaria* are partially killed by low-tide events or other disturbances, their remaining tissues rapidly regenerate many small polyps (Krupp et al., 1992; Jokiel et al., 1993). Damaged individuals of *F. scutaria* produce >10× more buds per polyp than do those of other fungiid species (Kramarsky-Winter and Loya, 1996). This high rate of asexual reproduction leads to a proliferation of

numerous juvenile anthocauli attached to the dead parent coralla of *F. scutaria*, and thus a population structure dominated by young, attached individuals on reef flats at both Eilat (Loya, 1975; Figs. 1A,4A) and Hawaii (Krupp et al., 1992). At Eilat, disturbances in the form of catastrophic low tides and oil pollution in the early 1970s killed most of the stony corals on the reef flat at the Japanese Gardens site (Loya, 1975). These disturbances apparently facilitated the proliferation of many small fungiids by (1) creating open space for colonization, and (2) damaging the tissues of adult mushroom corals, which responded by asexually budding new polyps (Loya, 1975; Krupp et al., 1992; Kramarsky-Winter and Loya, 1996, 1998). The result was a large increase in the abundance of mushroom corals on the reef flat in the mid 1970s (Loya, 1975). We propose that the high abundance of *F. scutaria* polyps today at this site (Fig. 2) is a consequence of severe physical disturbance, followed by a lack of coral recovery during the last 20 yrs (Loya, 1990) and subsequent lack of spatial competition with other corals. Likewise, the proliferation of *F. scutaria* on reef flats in Kaneohe Bay, Hawaii, appears related to catastrophes in the form of freshwater flooding (Krupp et al., 1992; Jokiel et al., 1993).

The four other common mushroom corals on the shallow reef slope at Eilat (*C. echinata*, *F. fungites* and two species of *F. (Danafungia)*) (Fig. 2), all possess morphologies that are well-suited to life on the hard substratum of reef slopes. They all possess large costal spines on their aboral surfaces, that serve to anchor them and reduce downward migration to the deep slope (Hoeksema, 1988). They also have sharp, narrow septa on the oral surface, which do not protect tissues from damage by extensive sedimentation, and thus are not suited to living on fine sand (Schuhmacher, 1977). At Eilat, almost all free-living individuals of these species remained on hard substratum on the shallow reef slope, and did not migrate out onto the surrounding sand (see Results).

In contrast, polyps of *F. granulosa* appear to be adapted for life on soft substratum adjacent to the reef. They have relatively porous, lightweight skeletons with small, granular aboral spines that allow for rapid migration from the reef onto sand (Hoeksema, 1988; Chadwick-Furman and Loya, 1992). They also possess broad granular septa that resist tissue damage during sedimentation and burial in sand, and thus the polyps are able to rapidly unearth themselves if buried (Schuhmacher, 1977). At Eilat, our current and previous studies have shown that polyps of *F. granulosa* migrate faster on the reef (Chadwick-Furman and Loya, 1992) and move more frequently onto sand (see Results, Fig. 1C) than do those of other, co-existing mushroom corals.

The use of shaded habitats by attached mushroom corals (Table 1) also has been documented by Chadwick-Furman and Loya (1992) and Dinesen (1983). Attached fungiids may prefer shaded reef habitats because they provide favorable conditions for juvenile coral survival, due to relatively low levels of competition (Dinesen, 1983), sedimentation, predation (Sammarco, 1991 and references therein), and damaging ultraviolet radiation (Hoeksema, 1991). The disadvantages of cave-dwelling increase with depth for zooxanthellate corals, in part because light levels available for photosynthesis decrease exponentially with depth in open reef habitats at Eilat, to 10% of surface light at 50 m depth, and only 1% of surface light at 100 m depth (Fricke and Schuhmacher, 1983, and references therein). In shaded habitats containing fungiid corals, light levels were >10× lower than on the open reef (see Materials and Methods), resulting in very low light levels available to corals occurring in the shade at depth. The fungiids observed here gradually switched from shaded to open habitats with depth (Fig. 5), a pattern that also has been observed for juvenile stony corals in Australia (Sammarco, 1991). The mechanisms con-

tributing to this pattern may include: (1) preferential settlement by coral larvae on open rather than shaded surfaces on deep reefs, (2) higher coral mortality in shaded areas, and (3) active movement by mushroom corals out of caves once they become free-living, facilitated by their positive phototactic behavior (Yamashiro and Nishihira, 1995). At Eilat, light levels are apparently high enough (10% of surface light at 50 m depth) on the open reef for some free-living fungiids to occur down to 55 m depth (Fig. 2) and even deeper (Fricke and Schuhmacher, 1983).

We conclude that morphological traits (aboral surface smoothness, septal morphology, skeletal density) explain in part the occurrence of some fungiid corals in sandy habitats, while others remain on hard substratum on the reef. In addition, the reproductive traits of at least one species (*F. scutaria*) allow it to survive and proliferate in the unique, frequently-disturbed environment of the shallow reef flat (Kramarsky-Winter and Loya, 1998). Both types of strategies (morphological and reproductive) allow mushroom corals to persist on coral reefs that are dominated by colonial attached corals (Maragos, 1974). Finally, the migratory behavior of mushroom corals reduces competition on the reef, and allows some of them to make use of sandy habitats that are not available to most other corals (Chadwick-Furman and Loya, 1992). Thus, their unique life histories and morphological and behavioral adaptations appear to explain the persistence and diversity of fungiids on reefs dominated by larger, attached colonial corals.

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