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MOBILITY OF FREE-LIVING FUNGIID CORALS (SCLERACTINIA), A DISPERSION MECHANISM AND SURVIVAL STRATEGY IN DYNAMIC REEF HABITATS

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ABSTRACT

The transportation of some solitary, free-living mushroom corals (Fungiidae) was measured at the exposed side of a small cay-supporting coral reef off SW Sulawesi, Indonesia. Corals living on the shallow reef flat are transported away from the seaward edge, towards the cay, while those on the slope and on the base are transported in the opposite direction. Corals on the reef flat are in general the least dynamic, whereas those on the base move faster than corals in the other zones.

Wave action is probably the main driving force on the reef flat and on the reef slope, whereas on the reef base bioturbation may act as a destabilizing agent. The position of the animals alters frequently from upright to upside-down and vice versa. Bottom inclination, bottom relief and substratum type are abiotic factors which affect the mobility rate, which otherwise depends on coral shape and coral weight.

The free-living mode of life is important for the dispersion and survival of fungiid coral populations. During the wet monsoon, when much sand and rubble is transported over the reef, it may prevent burial and suffocation. Although the free-living mode of life is obvious for most Fungiidae, examination of sedentary non-fungiid corals reveals that these may be less strongly attached to their substratum than they appear at first sight.

INTRODUCTION

Corals are generally supposed to be sedentary animals, but most mushroom corals (Fungiidae) are exceptions because they have a free-living phase in their life cycle (Wells 1966). To improve mobility the polyp of some species is able to regulate its buoyancy (Abe 1939); in others it grows a hydromechanically adapted coral shape (Jokiel & Cowdin 1976). Animals of some species are even reported to creep over the soft bottom they inhabit (Catala 1964, Coreau & Yonge 1968, Hubbard 1972, Pichon 1974, Fisk 1983).

As juveniles, mushroom corals live attached and usually well hidden on shaded limestone substrata (Dinesen 1983, Hoeksema in prep.). By becoming free-living, the adults may become scattered over the reef and meanwhile leave space for new recruitment.

No information has been collected on how fast and in which directions fungiids are able to migrate in natural reef environments. Also little is known about what happens to unattached corals during periods of much water turbulence. The present paper aims to give quantitative data on coral mobility and to discuss its advantages further.

METHODS

At the western, most exposed, side of the reef Kudingareng Keke (figure 1) off SW Sulawesi (Indonesia), eight fungiid species were selected for a migration experiment: Fungia fungites (L.), F. granulosa Klunzinger, F. gravis Nemenzo, F. horrida Dana, F. moluccensis Van der Horst, F. scruposa Klunzinger, F. scutaria Lamarck and Ctenactis echinata (Pallas). These species differ in shape, in maximum size or in fineness of their undersurface ornamentation. (For illustrations, see Hoeksema in press). In each of the three investigated reef zones, i.e. flat, slope and base (figure 2), fungiids are abundant, but not on the reef edge. The shallow flat and the strongly inclining slope contain large patches of dense coral coverage, whereas the base shows a gradually declining bottom with little coral growth. The species used for the experiment are each common in one or two of these zones.

In each zone, 10 specimens of each species, varying in size, were marked with small letter tape labels, attached by nylon filament tied tightly around the corals. The underwater weight (W) and undersurface area (A) of the corals were measured to calculate the pressure (W/A) which they could exert on the bottom. For the measurement of underwater weight, a series of four Pessola precision spring scales was mounted in transparent plastic tubes which were closed at the top. The undersurface area of each coral was

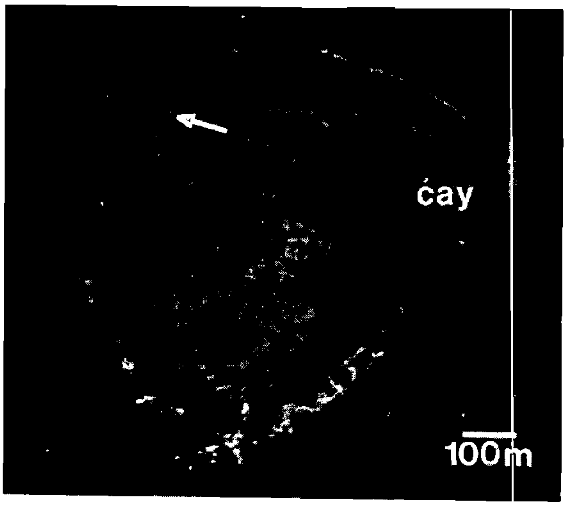

Figure 1. Aerial photograph of Kudingareng Keke, a reef in the Spermonde Archipelago, SW Sulawesi. It has a mobile sand cay on the least exposed side of its reef flat. The site of the experiments is located on the western part of the reef (←).

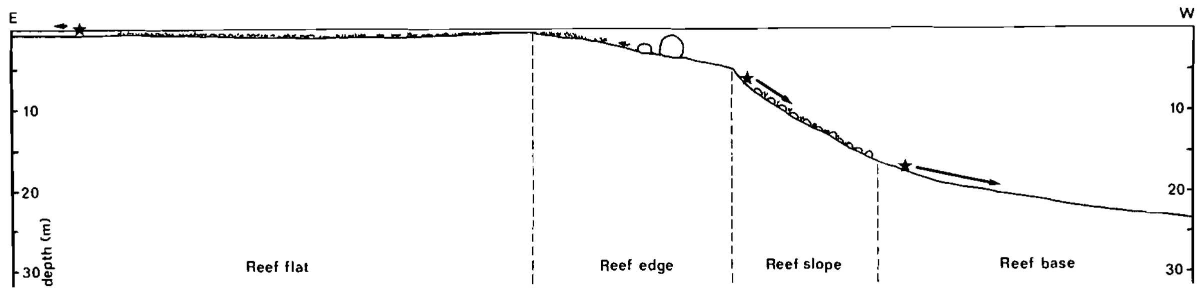

Figure 2. A schematic cross-section of the reef part indicated in figure 1 with the locations shown (★) where labelled corals were placed. The arrows symbolize the direction and the distance of coral movement.

Table 1. Migration of solitary fungiid corals in three reef zones at the west side of Kudingareng Keke in a half year period. The corals belong to species of the genera Fungia and Ctenactis. The corallum outline of the species is either round [o] or elongate [|]; their undersurface is either smooth [=] or coarse [^]. Of the 10 specimens per species inspected in each zone, the mean underwater weight, $\bar{W}$ in kg, the mean pressure on the substratum, $\overline{W/A}$ in kg/m^2 (A is the projected area of the corallum undersurface), the minimum and maximum distance migrated, (D) in m, and the mean distance, $\bar{D}$ in m, is indicated.

Reef zone:		Reef flat				Reef slope				Reef base			
Depth (m):		1				7				17			
Substratum:		Hard rock / rubble				Rubble				Muddy sand			
Slope (°):		< 5				15 - 30				5 - 15			
Species		$\bar{W}$	$\overline{W/A}$	(D)	$\bar{D}$	$\bar{W}$	$\overline{W/A}$	(D)	$\bar{D}$	$\bar{W}$	$\overline{W/A}$	(D)	$\bar{D}$
F. fungites	[o ^]	.10	12	(.0 - .4)	.2	.10	12	(.3 - 2.1)	1.2				
C. echinata	[| ^]	.22	15	(.0 - .4)	.2	.18	13	(.5 - 1.5)	1.0				
F. scutaria	[| =]	.07	13	(.2 - .7)	.3	.06	12	(.8 - 2.9)	1.8				
F. scruposa	[o ^]					.20	11	(.5 - 5.1)	1.5				
F. horrida	[o ^]					.13	12	(1.6 - 4.2)	2.9	.12	12	(1.9 - 5.7)	3.6
F. granulosa	[o =]					.03	8	(.9 - 1.8)	1.2	.03	8	(4.7 - 9.7)	7.2
F. moluccensis	[| ^]									.04	10	(1.6 - 9.6)	6.2
F. gravis	[| =]									.09	13	(4.7 - 11.2)	8.4

estimated by drawing its projected outline on a sheet of paper, cutting around the perimeter and weighing the cut piece of paper; its weight related to that of the complete sheet was multiplied by the sheet's area to obtain the coral's projected undersurface area.

After these measurements, the corals were placed 0.5 m apart from each other at labelled locations along nylon lines which were attached to the bottom. From June 1985 until the start of the wet season in December, the direction and the distance (D) travelled by the corals and their position (upright or inverted) were recorded at monthly intervals. By counting each time how many corals per species had their position switched from upright to upside-down, or vice versa, an overturning index (O) was obtained.

At the same site the bottom of the reef slope was investigated to study the coverage of unattached corals compared to that of all corals. Only the reef slope, the zone with the highest coverage (Moll 1983: figure 1B), was investigated. For the measurements a 1 x 1 m quadrat was used, divided in 25 smaller quadrats. It could only be used where the bottom relief was fairly regular, making selection inevitable. From 7 to 12 m depth, 22 quadrats were searched for the proportions of fungiids and other unattached corals.

RESULTS

Shortly after the start of the migration experiment, the labelled corals could easily be found again, but later on this became more difficult because of the increased size of the dispersal areas. Nevertheless, all animals remained traceable. Corals placed on the reef flat almost all moved slightly away from the seaward reef edge, with the prevailing wind direction, whereas those on the slope and on the base migrated over longer distances in the opposite direction, down the reef (figure 2).

Some corals on the reef flat, especially the heavier specimens of Fungia fungites and Ctenctis echinata, did not move at all. The elongate and lightweight corals of F. scutaria migrated on average more than the animals of the other two species investigated in the same zone (table 1). They each remained within 1 m of their starting point. On the reef slope, the round corals of F. horrida and F. scruposa migrated over the longest distances (table 1). On average F. horrida travelled more here than the other species. The elongate, coarsely ornamented specimens of C. echinata (having a relative high W/A ratio) migrated the least distance. On the reef base, animals of F. gravis and F. granulosa, which have a relatively smooth undersurface, moved over the longest distances (table 1). The heavyweight corals of F. horrida were distinctly less mobile, probably because their long costal spines offered greater resistance to the bottom. One individual of F. horrida died in the fourth month of the experiment; it reached the maximum distance migrated for the species (figure 3: open triangle).

For most species the position of the corals on the reef flat was more stable than that in the other reef zones. The relatively lightweight and elongate specimens of F. scutaria were overturned most frequently here (table 2). On the reef slope, there was no distinct relation between weight and the number of turn-overs. It is striking though, that the round and flat specimens of F. scruposa overturned very little. When comparing species on the reef base there is also no clear connection between weight (see table 1) and position (table 2). Specimens of species with an elongate shape were less frequently observed in an inverted position than those with a discoidal form.

After the wet monsoon, the labelled specimens were scattered over too large an area for proper dispersion measurements to be made. On some parts of the slope big avalanches of coral debris had passed over the corals. Many sedentary corals and large fungiids on the upper part of the slope had been covered and consequently killed by a 20 to 30 cm layer of rubble. In contrast, many smaller mushroom corals had survived, partly sticking out or lying on top of the heavy debris.

Coral cover in 1 x 1 m quadrats on the reef slope varied from 28 to 100 % (table 3). The portion of unfixed corals ranged between 0 and 100 %. Large parts of the coral cover that seemed to be attached, could actually be easily removed (figure 6). Some of these corals were actually loose fragments. Other ones had settled on rubble or were loosely cemented to the limestone substratum by sponges and by fine sediments that accumulated in the remaining crevices. Large portions of the unstable coral assemblage consisted of free-living fungiids (table 3), which sometimes lived on top of other corals and damaged them. The mushroom corals found together in a mixture of species, often one on another, did not do each other any visible harm.

Table 2. The position of free-living mushroom corals during migration. Ten specimens per species were inspected five times, at monthly intervals. The total number of times a coral was observed in an inverted position (I) was noted and also how frequently it had overturned (O). I and O each range theoretically from 0 to 50.

Reef zone:	Reef flat		Reef slope		Reef base	
Species	I	O	I	O	I	O
F. fungites	8	9	10	11		
C. echinata	6	7	10	11		
F. scutaria	12	12	3	5		
F. scruposa			1	2		
F. horrida			8	8	16	12
F. granulosa			4	5	16	19
F. moluccensis					5	7
F. gravis					10	15

DISCUSSION

The results of the experiments on fungiid coral movements suggest that free-living mushroom corals are able to migrate over a distance of more than 10 m during a period of six months. Abiotic factors which influence the migration rate are bottom inclination, bottom relief, substratum type and water turbulence. Waves may sweep the free-living corals on the exposed sides of shallow reef flats away from the reef edge and wave action may also be responsible for destabilizing unattached corals living on the reef slope. Further, it causes large quantities of coral debris to slide down the reef taking many loose corals with them.

On the reef flat and on the slope the corals have a higher chance of colliding with obstacles than on the sandy base. On a declining sandy bottom, corals may start to slide downward if the pressure which they exert on the bottom (W/A in table 1) is not causing too much resistance. That they do not just slide on the reef base is shown by the fact, that they have frequently been overturned here (table 2, figures 3-5).

Besides water turbulence, the foraging activity of fishes and other animals may also cause corals to move (Glynn 1974). The reef base is too deep for wave action to transport the corals and currents are minimal here. In this zone fishes, such as rays and goatfishes, and large invertebrates, such as lobsters and sea cucumbers, are perhaps

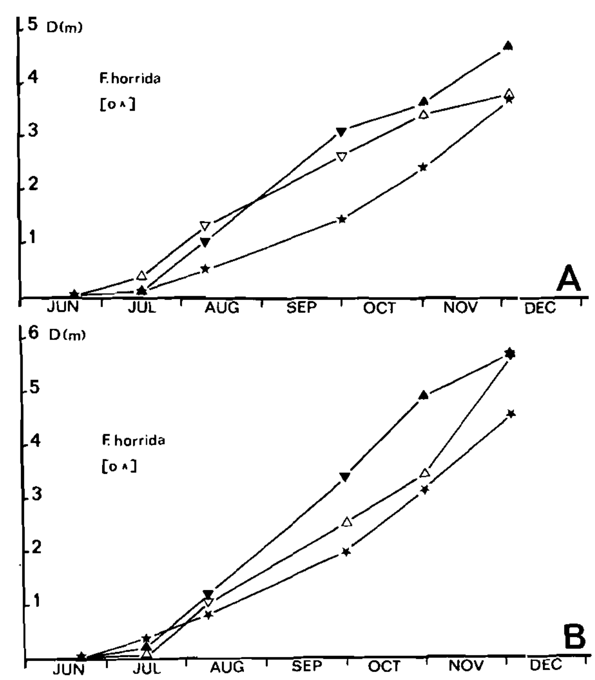

Figure 3. The migrated distance of F. horrida, a large species with a round corallum outline and a coarse underside, is shown for a period of six months. The three fastest specimens (▲, △ and ★) on the reef slope (A) and on the reef base (B) are compared. Downward pointing symbols (▼, ▽ or ★) indicate that a coral was observed upside-down.

responsible for turning over the corals or pushing them around. Jokiel & Cowdin (1976) reported mushroom corals being overturned by crabs. When the weighing took place, before the start of the experiment, it was noticed that small invertebrates, such as ophiurids, had sought refuge from predators on the underside of the corals. Exposure of the lower surface of the corals attracted the attention of fishes, which picked the prey off the corals while they were still being manipulated.

Overturning of mushroom corals in natural reef environments appears to be a common phenomenon. The mouth of solitary mushroom corals in inverted position is usually blocked, which hinders their food intake. Two fungiid species are known to perform righting reactions (Abe 1939, Hubbard 1972). Many corals of F. scutaria in cross-section resemble an airfoil, which may help them to right themselves in a water flow (Jokiel & Cowdin 1976). On the reef flat, however, this species was observed to have the highest inversion rate, which was probably caused by its elongate shape and its lower average weight. Round corals with a large, flat surface were observed to be less easily overturned than those with elongate forms. Specimens of F. moluccensis and F. gravis have a convex upper surface with a consequently high centre of gravity, making it more difficult for them to remain upright. On the other hand, when a coral is overturned, the hump may destabilize its inverted position and cause it to right itself again.

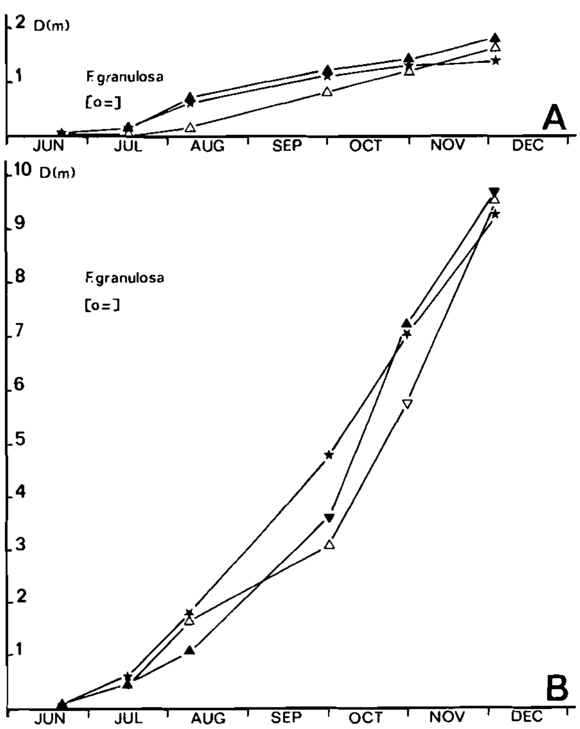

Figure 4. The three fastest specimens of F. granulosa on the reef slope (A) and on the reef base (B). The species remains relatively small, it has a round corallum outline and a smooth under-surface. Symbols as in figure 3.

The long distances that free-living fungiids are able to migrate may help them to colonize substrata that are unsuitable for larval settlement, such as soft bottoms. In this way they may avoid competition for space with sedentary animals. Soft substrata are commonly observed at the reef base; they are inhabited by several fungiid species which are rarely encountered in the shallower zones (Hoeksema in prep.). Mushroom corals with a smooth undersurface move faster and probably reach the deeper zones more easily than those with a coarsely ornamented underside; the latter may prevent a continued downward migration.

The free-living mode of life may help corals of opportunistic species to reach a variety of reef environments, ranging from shallow to deep and varying from stable to dynamic. The importance of dispersal depends on the pattern of variation in the environment (Horn 1984). The malleable shape of the corals may help them to survive under various abiotic conditions (Hoeksema & Moka in

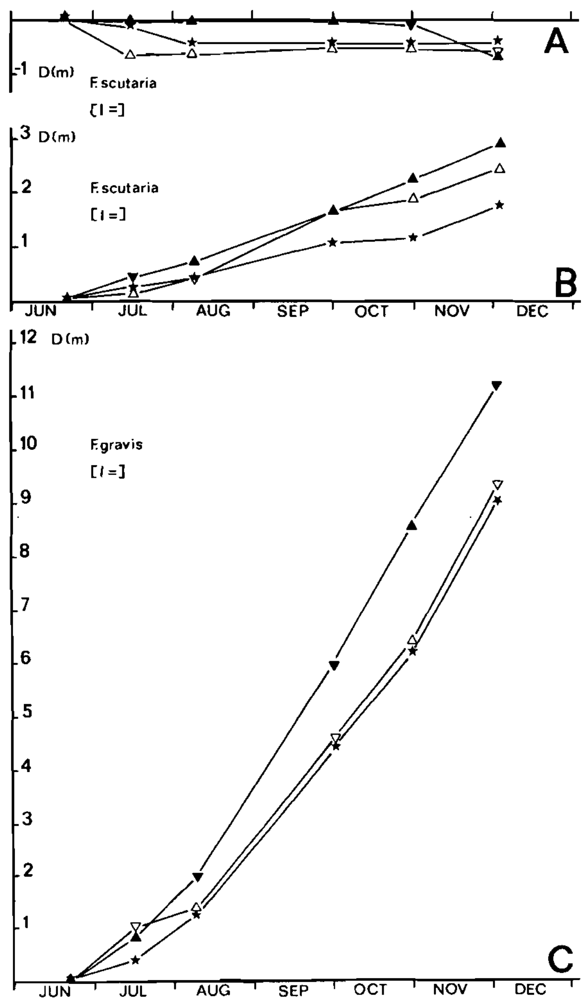

Figure 5. F. scutaria on the reef flat (A) and on the reef slope (B), and F. gravis on the reef base (C). Both species have an intermediate maximum size; their corallum outline is elongate and their under-surface is smooth. Symbols as in figure 3.

press). However, if they dwell on hard substrata, they may have to compete for space with sedentary corals. Therefore mushroom corals behave aggressively towards non-fungiid corals when they accidently come into contact with them (Sheppard 1979, Chadwick 1986).

Like colonial sedentary organisms (see Buss 1979), populations of free-living (solitary) fungiids are capable of finding spatially unpredictable refuges on marine substrata. After resettlement of a mushroom coral, colonization can take place by (asexual) reproduction and lead to succesful occupation of a refuge. Populations of some fragmenting species can reach densities of more than thousand individuals per square metre (Goreau & Yonge 1968). Although mobility of fungiids supposedly is advantageous for their populations, it involves an increased mortality risk for the pioneering individuals. This risk may be compared with that of the exploring portions of colonial sedentary animals which accidentally come into hazardous spatial positions (Buss 1979).

Fungiids may overcome mortality by their high regenerative capacity of clonopary (term from Rosen 1986), in which buds or fragments survive after the parent animal dies. As for colonial corals, which may undergo partial colony mortality, colony fission and colony fusion (Hughes & Jackson 1980), it may be hard to estimate how old a solitary mushroom coral is. Through asexual reproduction, corals may achieve virtual immortality (Highsmith 1982), making their dispersion strategy even more succesful. Mobility of buds and fragments may prevent them having to compete among themselves for limited space; the latter may be the case in crowded populations of sedentary adults with non-dispersive offspring (Horn 1984).

The mobility of mushroom corals may act as a survival strategy. When severe storms cause waves to transport large quantities of rubble over the reef slope, many corals become covered. The most mobile specimens, however, can become integrated with the moving sediment, which lessens their risk of burial. On soft substrata mobility may help to unbury fungiids after too much sedimentation (Gill & Coates 1977).

The unstable position occupied by many corals on the reef slope at the exposed side of Kudingareng keke indicates that this slope is a more dynamic and variable environment than it superficially appears to be. Several sessile corals here consist of loose fragments or have settled on rubble which eventually may slide downward. The reef slopes are maintained by a dynamic equilibrium, temporarily consolidated by sponges and other, mainly encrusting, organisms. Substratum shifting downwards over the slope is replaced by new substratum from above and by local coral growth. Mobile Fungiidae appear to be perfectly adapted to live in such a dynamic and variable environment.

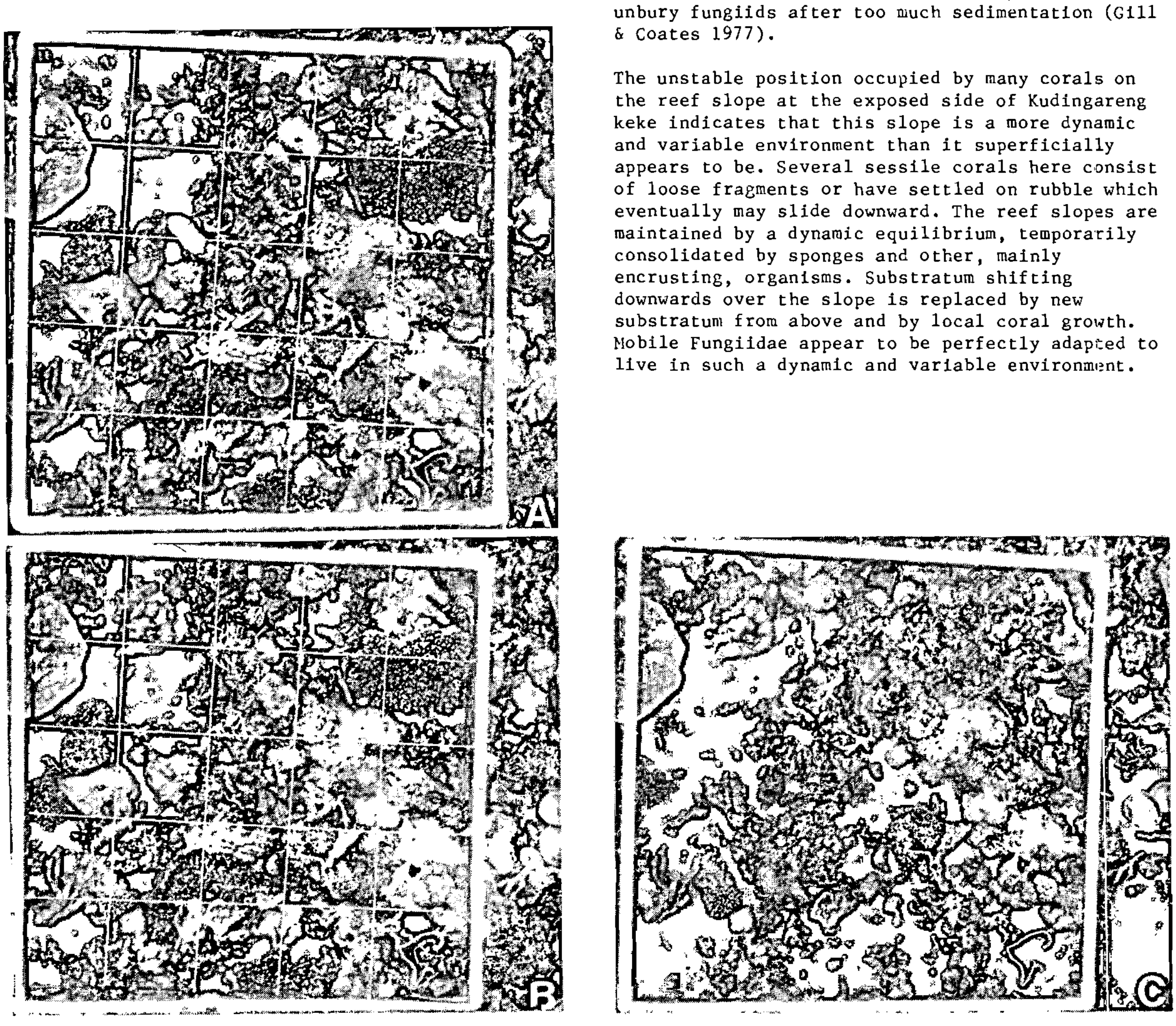

Figure 6. The western reef slope of Kudingareng Keke at a depth of 11 m. In a 1 x 1 m quadrat the living coral coverage is shown still complete: 50 % (A), after the removal of all free-living fungiids: 30 % (B) and after all other loose corals are taken away, leaving the attached ones remain: 18 % (C).

Table 3. The components in the total living coral coverage of all unstable corals and that of free-living fungiids only, measured in 1 x 1 m quadrats at the western reef slope of Kudingareng Keke.

Coral coverage (%)	Unstable part (%)	Fungiids (%)	Depth (m)
100	1	1	7
100	0	0	11
100	0	0	10
80	2	1	9
76	100	84	11
60	5	2	10
56	100	54	12
56	98	86	10
56	98	71	8
56	93	43	9
56	68	50	10
56	56	28	10
54	96	52	12
54	78	26	11
52	90	61	7
50	64	40	8
48	98	42	8
44	82	64	8
34	97	82	12
34	94	76	10
28	100	79	7
28	100	64	7

CONCLUSIONS

Particularly on a reef slope, the percentage cover of unattached corals may be higher than it appears at first sight. Usually, a large and conspicuous part of the unattached coral assemblages consists of free-living Fungiidae, which are very mobile.

There are two disadvantages of mobility for mushroom corals: (1) they may accidently reach reef areas with hazardous conditions; (2) they may become overturned, remain too long in an inverted position and die.

There are four possible advantages of mobility for fungiids, in which it may act as either a dispersion mechanism or a survival strategy: (1) it enables fungiids to occupy habitats that are unsuitable for larval settlement; (2) it gives them the potential for continuous dispersal over a variety of habitats, ranging from stable to dynamic and from variable to invariable; (3) after too much sedimentation it may help them to unbury themselves; (4) in avalanches of coral rubble, it may prevent burial.

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