Control of bleaching in mushroom coral populations (Scleractinia: Fungiidae) in the Java Sea: stress tolerance and interference by life history strategy

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ABSTRACT· Bleaching was studied in populations of phylogenetically closely related species (n = 21) of mushroom corals (Scleractinia: Fungiidae) around Pari Island (Java Sea) during a period of excessive seawater warming in 1983. The interspecific variation in the proportions of affected individuals was significant. Spatial variation in the degree of bleaching among fungiid assemblages depended much on relative species abundances. Mushroom corals in relatively stagnant water of lagoons and on the inner reef flat showed little bleaching. Many of the outer reef mushroom corals at ≤ 9 m depth were affected, but only a few at greater depths (≥ 15 m). In most affected fungiids, the bleached part was pale (associated with pigment loss) instead of white (assumedly caused by zooxanthellae expulsion). The difference between the proportions of paled and whitened corals was not clearly depth-related, but most probably species-related. Most bleached fungiids were affected over their whole upper surface, whereas others showed a mosaic pattern. Entire bleaching was most common at depths <6 m and partial bleaching at 9 m. One species with a predominantly shallow distribution (mainly ≤ 9 m) showed a significant majority of entirely bleached individuals. The smallest mushroom corals ($\varnothing_{max} \leq 5$ cm) on the outer reef, usually in sheltered positions, and the largest ones ($\varnothing_{max} > 20$ cm), usually occurring deep, were the least affected. The latter may have escaped bleaching by recurrent downward migration.

INTRODUCTION

During the last decade, bleaching and subsequent mortality in zooxanthellate corals has occurred as a circumtropical series of events (Brown 1987, Glynn 1990, Williams & Bunkley-Williams 1990). Bleaching may result from expulsion of symbiotic algae known as zooxanthellae, usually visible as complete discoloration (whitening) of the corals, whereas it has also been attributed to a degeneration of zooxanthellar chloroplasts with a subsequent pigmentation decrease, which may be observed as paling (Jaap 1985, Gladfelter 1988, Hoegh-Guldberg & Smith 1989, Kleppel et al. 1989, Jokiel & Coles 1990, Szmant & Gassman 1990). On a local scale, besides interspecific variation in bleaching

patterns, there are also intraspecific differences in coral bleaching, which appear partially related to spatial, bathymetric and size distributions (Faure et al. 1984, Fisk & Done 1985, Harriott 1985, Lang et al. 1988). However, detailed information on bathymetric patterns in bleaching has not been available, and it is not precisely known how these patterns interact with the size distributions within coral populations.

It has been proposed that bleaching is caused by stress, such as excessive light and UV irradiance, prolonged darkness, anomalously high or low temperatures, abnormal salinities, increased suspended sediment load or a synergistic effect of these (Bak 1978, Dustan 1982, Rogers 1983, Oliver 1985, Peters & Pilson 1985, Acevedo & Goenaga 1986, Steen & Muscatine 1987, Jokiel 1988, Jokiel & Coles 1990), but sometimes no presumable cause can be found (Ghiold & Smith 1990, Goreau & Macfarlane 1990). In studies on the occurrence of bleaching it is important to consider how

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such stresses relate to the tolerances within local populations (Brown & Howard 1985). Accurate records of species distribution patterns and demographic constitutions of the populations are basic requirements for such assessments.

In the present study, mushroom corals (Fungiidae) have been selected for a comparison of bleaching among phylogenetically closely related species (Hoeksema 1989). Their bleaching patterns were studied off Jakarta, in the western part of the shallow Java Sea, Indonesia. Bleaching also occurred in the central Java Sea (Suharsono & Kiswara 1984), but not more eastward, in the southern Makassar Strait (W. Moka pers. comm.). Although the reefs off Jakarta are affected by increasing siltation and urban pollution (Robinson et al. 1981, Moll & Suharsono 1986, Soemodihardjo 1986, Purwanto 1987, Sukarno 1987), the 1983 bleaching event was thought to be mainly associated with anomalously high seawater temperatures (Suharsono & Kiswara 1984, Harger 1986, Brown 1987, Brown & Suharsono 1990).

Compared to other reef-dwelling scleractinians, mushroom corals have an important practical advantage in quantitative ecological surveys: as distinct individuals they can easily be counted in the field (Hoeksema 1990). This enabled the study to concentrate on interspecific variation in the kinds and patterns of bleaching, the proportions of affected individuals (especially with regard to their sizes), and how these are related to their spatial and bathymetric distributions.

STUDY SITE AND METHODS

Fieldwork was performed from April to June 1983, around the Pari Island group, which is a reef in the southernmost part of the Thousand Islands ('Kepulauan Seribu'), an island chain extending NNW off Jakarta (Umbgrove 1929, Ongkosongo & Sukarno 1986). The reef is located 17 km off Java's mainland (5° 52' S, 107° 37' E). Pari Island and some smaller islets are arranged around a series of lagoons, which are connected with the surrounding sea by shallow tidal channels (Fig. 1). The monsoon-driven surf (Umbgrove 1929) has caused the emergence of prominent shingle ramparts at the E and SE sides of the reef flat and smaller ones at the W and NW sides (Fig. 2). The small ramparts may not always be discernable, since they were not noticed in 1979 during the study by Brown et al. (1983).

Coral bleaching at Pari Island was first noticed in April 1983 during a period of excessive seawater warming that lasted until the end of July (Brown & Suharsono 1990). To assess the occurrence of bleaching among mushroom corals, 7 transect sites were selected around the reef (Fig. 1): W (2 to 4 June), NW (26 to 29 May), N (23 to 24 May), E (16 to 18 May), SE (5 to 6 June), SW1 (7 to 10 June) and SW2 (19 to 21 May). Sites SW1 and SW2 are located close to a tidal channel where strong currents occur (own obs.).

In the transects, 2×10 m^2 sample quadrats were surveyed on the inner reef flat (≤ 1 m depth) and on the outer reef flat (1, 2 and 3 m) using snorkel equipment, and on the reef slope and base (6, 9, 15 and 21 m) with the use of SCUBA (Fig. 2). A 10 m long fiberglass measuring tape was placed along the respective isobaths and a 1 m long PVC tube was guided alongside to demarcate the width of the quadrats. The depths of the quadrats were chosen to obtain an approximately even distribution of the quadrats over the reef profile, down to the maximum depth of mushroom coral occurrence (Fig. 2). The number of selected depths and the size of the quadrats were both limited by the available underwater time. Quadrats that did not contain fungiids usually also did not show any fungiids around them. Each mushroom coral was identified and its length ($\varnothing_{max} \pm 0.5$ cm) was measured along the aboral surface. Furthermore, numbers of paled and whitened, and partially and entirely affected corals were noted. The number of recently killed corals (those not yet covered by filamentous algae) was low and since their cause of death was uncertain, they were not counted in the assessment. In addition, 2 lagoon
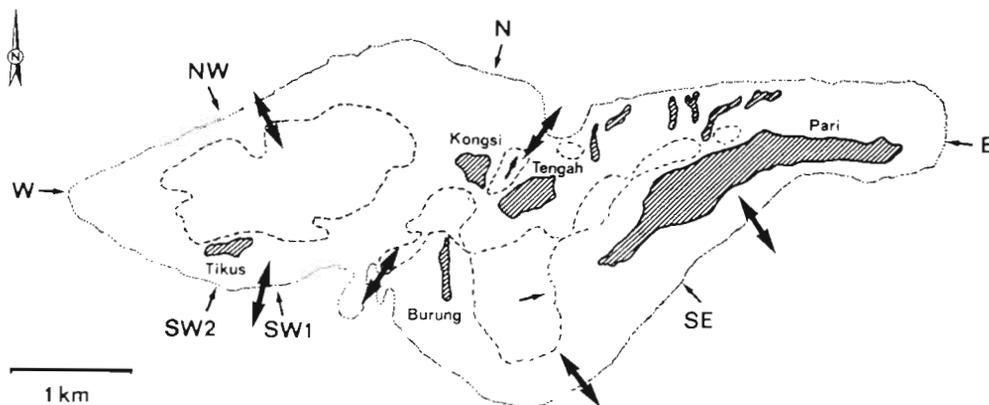
Fig. 1. Pari Island group with indication of study sites (small arrows), islets (hatched), lagoons (dotted) and tidal channels (large double-sided arrows)
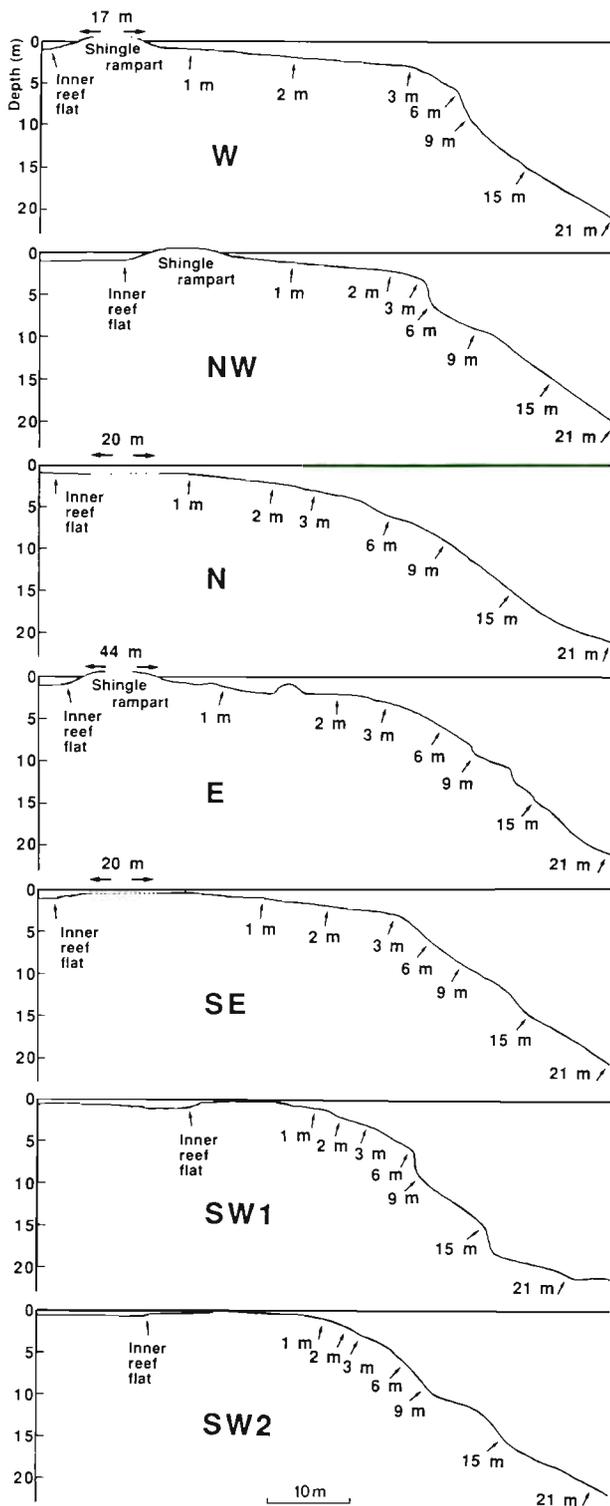
Fig. 2. Reef profiles of the 7 transect sites

the lagoons, fungiid assemblages were only checked for the occurrence of bleaching.

In the outer reef zone, per transect the largest populations (n > 50 corals) were studied to investigate whether bleaching was size-dependent. Since mushroom corals are known to migrate (Hoeksema 1988), coral sizes may differ among the investigated depths. Therefore, variation of mean length among the quadrats was tested with a 1-way ANOVA. Regression analyses were used to find out whether positive correlations between size and depth could be detected. All statistics were calculated with computer programs by Glantz (1988).

Subgenera of *Fungia* (see Hoeksema 1989) are hereafter abbreviated as: *C.*, *Cycloseris*; *V.*, *Verrillo-fungia*; *D.*, *Danafungia*; *F.*, *Fungia*; *W.*, *Wellsofungia*; *L.*, *Lobactis*; *P.*, *Pleuractis*.

RESULTS

Mushroom coral abundances

Mushroom corals were irregularly distributed over the study sites (Table 1). This uneven distribution cannot be directly attributed to wind-energy exposure. Among the shallowest quadrats (≤2 m deep), the least exposed transects (SW1 and SW2) showed generally higher mushroom coral densities than the other sites (Table 1). Because of the mobility during the free-living stage in their life history (Hoeksema 1988), the distribution of fungiids is probably influenced by bottom relief (Fig. 2). The highest densities of fungiids were usually encountered at 3 to 9 m depth, whereas the inner reef flat also showed some high concentrations of mushroom corals (Table 1).

A total of 21 species was recorded, 8 of which were observed at each of the 7 sites; some were found in high densities and in wide bathymetric ranges (Fig. 3). The highest species richness was encountered at Site W, whereas Site E showed the lowest (Table 2). The highest numbers of species within the transects usually occurred at either 6, 9, or 15 m depth, and the lowest on the inner reef flat, or on the outer reef at 1 or 21 m (Table 2). Inside the lagoons, clusters of mushroom corals were usually found down to 2 m deep.

Bleaching in mushroom coral populations

During the 1983 bleaching event in the Java Sea, the upper surfaces of many fungiid corals occurred in various stages of discoloration. The usual brown was partly or completely replaced by a pale brown or yellow (like lemon or ocher), or by a translucent white. The undersides, which were usually in contact with the bottom,

sites were investigated (down to 4 m depth): one NW off Tengah I. (5 June), and one SW off Pari I. (27 April). Since mushroom corals showed a patchy distribution in
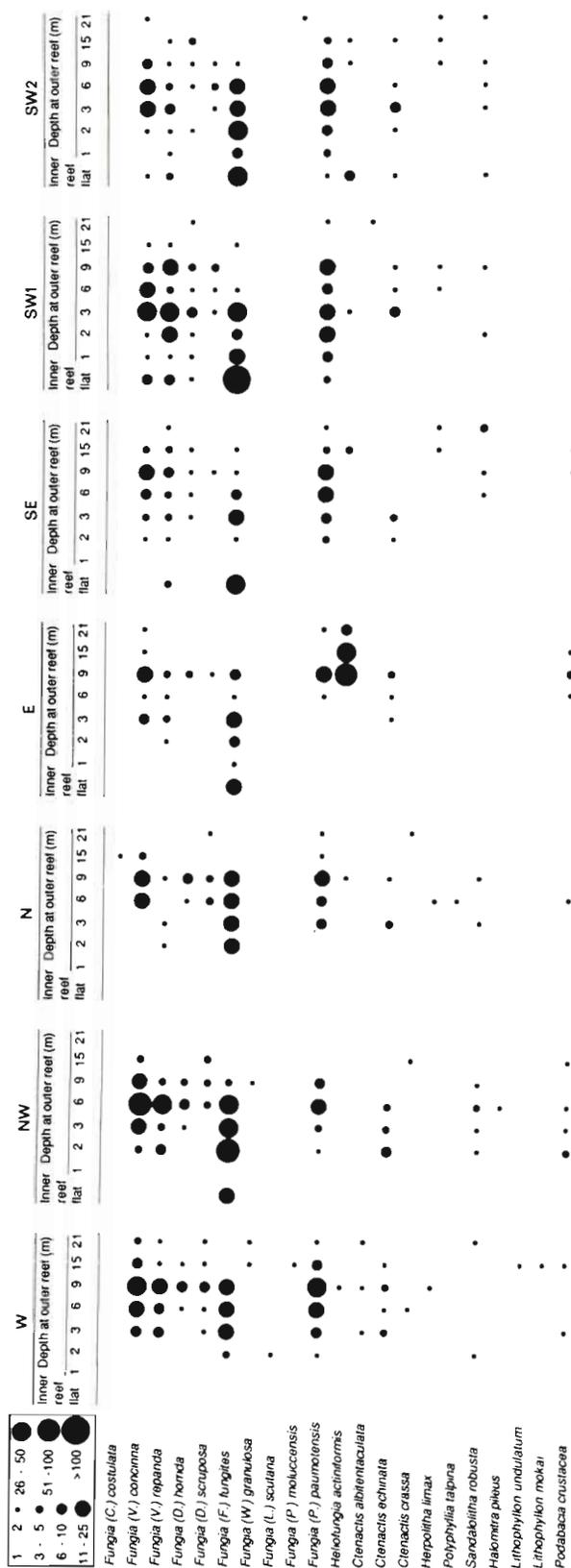
Fig. 3. Abundances of mushroom coral species in 2 × 10 m² quadrats at several depths in each of the transects

were light-colored in bleached individuals and in unbleached ones as well. Some corals appeared to pale or whiten over their whole upper surface at once, whereas others started either in a patchy pattern, around the mouth or at the polyp periphery (Fig. 4). At the lagoon sites, no mushroom coral bleaching was observed. In the transects, 44 % of all studied specimens (n = 2064) were bleached. Quadrats with more than 50 % affected corals were found on the outer reef from 1 to 9 m deep (Table 3). On the inner reef flat, 14 % of the fungiids were affected, whereas overall bleaching on the outer reef was 48 % (Table 4). The proportions of affected mushroom corals on the inner reef flat varied significantly (χ^2 = 9.22, p < 0.05). They were most concentrated at Sites SW1 and SW2 (Table 3; Fig. 5), each at a side of a tidal channel (Fig. 1), with 19 % of the observed fungiids bleached, whereas in the other transects (NW, E, and SE) only 2 % appeared affected.

Bleaching varied significantly among the investigated depths on the outer reef, most specifically with regard to paling and entire bleaching (Table 4). Mushroom corals at 2 to 6 m depth showed the highest percentages, whereas at 15 to 21 m only few individuals were affected. On the entire outer reef, significantly more paled than whitened fungiids were counted, but at no particular depth could such a significant difference be detected (Table 4). At shallow depths, completely bleached mushroom corals were usually more abundant than partially affected ones (significant at 2 and 3 m), whereas at 6 m they were equally abundant. At 9 m depth, partially bleached fungiids were significantly more abundant than completely affected ones (Table 4).

The degree of bleaching among outer reef mushroom coral populations varied significantly with regard to all distinguished categories (Table 5). For example, the percentage of affected *Fungia (V.) repanda* was much higher than that of all other species (χ^2 = 15.59, p < 0.001), whereas populations of *Heliofungia actiniformis* and *Ctenactis echinata* each displayed significantly lower percentages than the rest of the species (χ^2 = 58.67, p < 0.001 and χ^2 = 5.53, p < 0.05, respectively). Significantly more mushroom corals, individuals of *F. (V.) repanda* in particular, were paled than whitened (Table 5). Entirely bleached fungiids, especially *F. (F.) fungites*, were significantly more abundant than partially affected ones.

On the outer reef, the transects showed a significant variation (χ^2 = 38.56, p < 0.001) in mushroom coral bleaching (Table 3). There was no significant relation between the time order of measurement and the percentage of bleached animals for the sites (Spearman rank order r_s = 0.64, p = 0.11); there was also no significant relation with the density per site (r_s = 0.39,

Table 1 Density of fungiids (m^{-2}) at various depths (measured in 2×10 m^2 quadrats) and their total number (n) per site around Pari Island

Site	Inner reef flat	Depth at outer reef (m)							Total (n)
		1	2	3	6	9	15	21	
W	0.00	0.00	0.30	2.75	3.45	6.70	1.25	0.70	303
NW	1.10	0.00	3.85	3.75	9.25	2.65	0.55	0.00	423
N	0.00	0.00	0.85	1.35	2.30	4.30	0.30	0.15	185
E	1.15	0.10	0.35	1.55	0.45	5.60	1.85	0.45	230
SE	1.80	0.00	0.50	2.05	1.55	2.25	1.00	0.30	189
SW1	6.75	1.35	1.70	8.10	1.60	2.20	0.30	0.15	443
SW2	2.55	0.65	2.35	3.95	2.85	1.50	0.50	0.20	291

Table 2. Number of mushroom coral species (m^{-2}) at various depths (measured in 2×10 m^2 quadrats) and their total number per site (n) around Pari Island

Site	Inner reef flat	Depth at outer reef (m)							Total (n)
		1	2	3	6	9	15	21	
W	0.00	0.00	0.20	0.40	0.40	0.50	0.55	0.35	18
NW	0.05	0.00	0.35	0.40	0.50	0.40	0.20	0.00	12
N	0.00	0.00	0.10	0.25	0.25	0.40	0.45	0.15	14
E	0.05	0.05	0.10	0.20	0.30	0.45	0.15	0.15	9
SE	0.10	0.00	0.25	0.30	0.30	0.40	0.40	0.20	11
SW1	0.25	0.30	0.30	0.40	0.45	0.40	0.15	0.15	12
SW2	0.35	0.15	0.30	0.40	0.40	0.45	0.35	0.20	12

Table 3. Percentages of mushroom corals affected by bleaching in 2×10 m^2 quadrats at various depths per site around Pari Island (>50 % in boldface)

Site	Inner reef flat	Depth at outer reef (m)							Total outer reef
		1	2	3	6	9	15	21	
W			50	**58**	**75**	**54**	12	7	**54**
NW	5		**52**	**65**	**65**	**53**	0		**59**
N			**71**	**52**	50	33	17	0	42
E	0	50	29	**65**	**67**	6	0	0	17
SE	3		**70**	**63**	**61**	**58**	0	17	**55**
SW1	13	30	47	**68**	25	45	0	0	**53**
SW2	35	**54**	**74**	44	44	20	0	0	45

p = 0.35), nor with the numbers of species ($r_s = 0.18$, p = 0.66). Therefore, the observed spatial variation was not time-, density-, or diversity-dependent. Fungiids on the outer reef of Site E were significantly less affected than those at other sites ($\chi^2 = 32.19$, p < 0.001), whereas those at Site NW were significantly more affected ($\chi^2 = 5.94$, p < 0.05). If the unaffected *Heliofungia actiniformis* would not be considered, there would be no significant variation in bleaching among the sites ($\chi^2 = 7.21$, p > 0.05), Site E would not show a significantly lower percentage of bleached fungiids ($\chi^2 = 2.59$, p > 0.05), and Site NW not a higher one ($\chi^2 = 2.78$, p > 0.05).

On the inner reef flat, where mushroom coral bleach-

ing was relatively rare (Table 3), no significant variation in bleaching among different size classes (Fig. 5) of mushroom corals could be detected ($\chi^2 = 1.30$, p > 0.05). In the analysis of the outer reef corals, those belonging to *Fungia (F.) fungites*, the most dominant species, and the rest of the species, pooled for sufficient representation in all size classes, are considered separately. *F. (F.) fungites* has a prevalent shallow distribution (Fig. 3), whereas the other species are represented more abundantly at greater depths.

Fungia (F.) fungites and all other fungiid species showed significant variations in bleaching among the 5 distinguished size classes (Fig. 5; Table 6). This
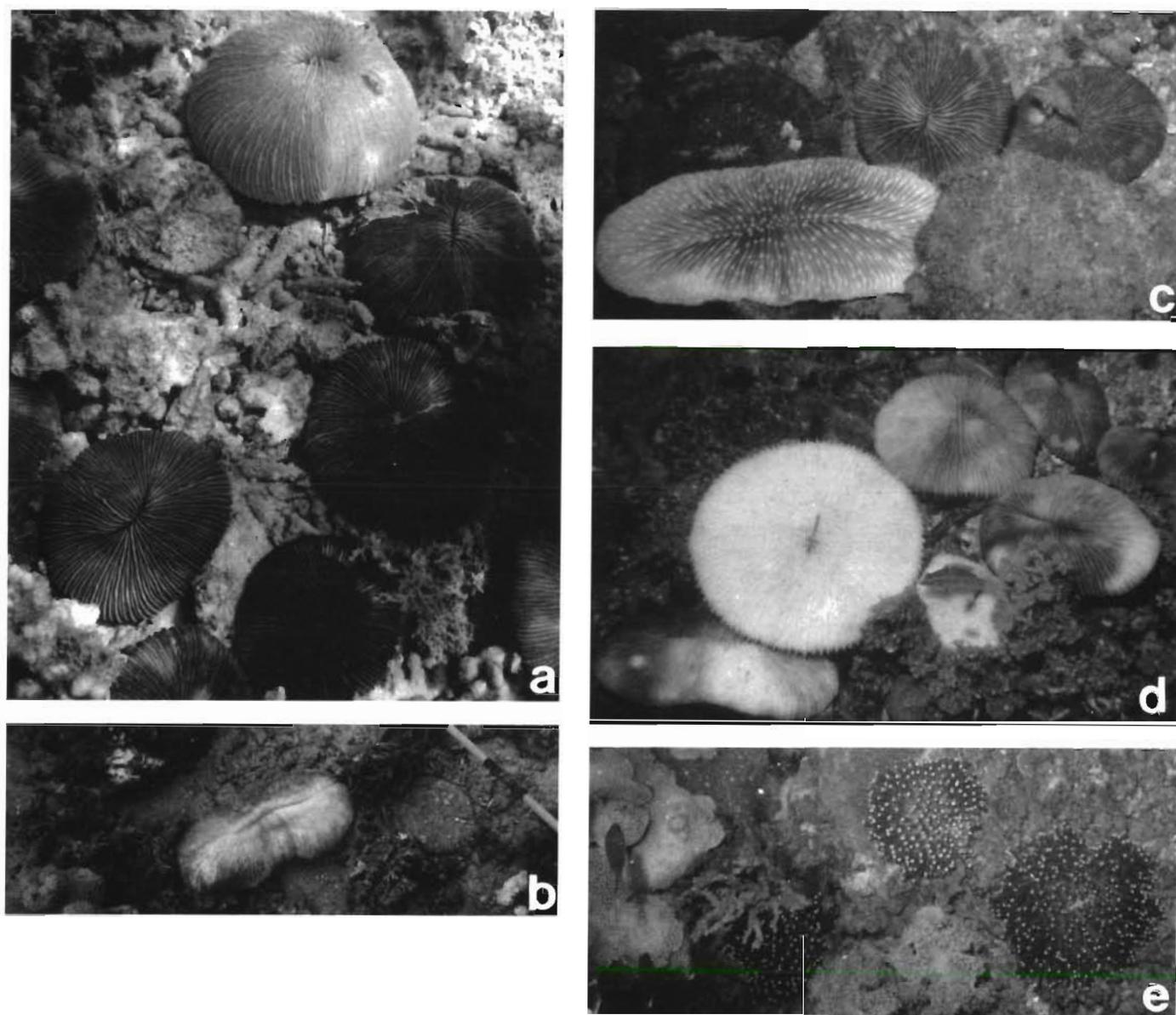
Fig. 4. Mushroom corals showing various degrees of bleaching: (a) *Fungia (F.) fungites* (Linnaeus), one coral completely pale, some showing white patches and the others brown (inner reef flat at Site SW2); (b) *Ctenactis echinata* (Pallas), whitened around the mouth (9 m at Site SW2); (c) *C. albitentaculata* Hoeksema paratype (RMNH 16103), whitened at periphery, and 3 individuals of *F. (V.) concinna* Verrill displaying white spotting (21 m at Site W); (d) *F (V.) repanda* Dana, circular corals completely white or pale and *F. (P.) paumotensis* Stutchbury, elongate corals showing patchy bleaching (6 m at Site SW2); (e) *Heliofungia actiniformis* (Quoy & Gaimard), 3 unaffected corals showing fleshy polyps (12 m at Site E)

variation was also apparent for the different categories of bleaching, especially with regard to paled corals and those that were completely affected. In size class 10.5 to 15.0 cm, it was most clearly shown that paled corals were significantly more abundant than whitened ones, and entirely affected individuals more than partially bleached ones (Table 6). In *F. (F.) fungites*, the smallest individuals ($\varnothing_{max} \leq 5$ cm) were the least affected, whereas the largest ones ($\varnothing_{max} > 20$ cm) showed the highest degree of bleaching. The other species also displayed a relatively low proportion of affected small corals

but in contrast to *F. (F.) fungites*, they showed a small percentage of affected large corals as well (Table 6).

Since the low bleaching in large corals on the outer reef might have been depth-dependent, and partial bleaching in particular (Table 4), 1-way ANOVAs and regression analyses were performed for the largest outer reef populations (Fig. 5) to analyse whether the coral length varied and even corresponded with depth. In most populations the mean coral length varied significantly (Table 7). Exceptions are populations of *Fungia (F.) fungites* at Sites W, E and SE, and of *F (P.) paumotensis* at Site SW1.

Table 4. Percentages of mushroom corals affected by different categories of bleaching (paled or whitened, partial or entire) and their totals at various depths (measured in 2 × 10 m² quadrats) at 7 sites around Pari Island. Statistics (χ^2) are given on differences between bleaching categories per depth and on variations in the degrees of bleaching among outer reef depths; n = number of corals per depth

| Degree | Inner reef flat | Depth at outer reef (m) | | | | | | | Total outer reef | χ^2 outer reef |
		1	2	3	6	9	15	21		
Pale	10	25	27	36	34	20	0	2.5	27	51.07***
White	4	13	31	25	26	18	3	2.5	21	29.13***
χ^2 pale-white	3.21	0.31	0.23	3.48	1.75	0.58	0.67	0.00	6.57	
Significance	ns	ns	ns	ns	ns	ns	ns	ns	*	
Part	5	10	15	19	30	25	1.5	5	21	36.72***
Whole	9	28	43	42	30	13	1.5	0	27	60.08***
χ^2 part-whole	1.12	0.88	12.95	19.24	0.00	8.62	0.00	0.00	5.62	
Significance	ns	ns	***	***	ns	**	ns	ns	*	
Total	14	38	58	61	60	38	3	5	48	80.54**
n	267	42	198	470	429	504	115	39	1797	

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; ns = non-significant

Table 5. Mushroom coral populations ($n_{tot} > 5$ individuals) and their assemblage on the outer reef of Pari Island. Percentages of individuals affected by different categories of bleaching (paled or whitened, partial or entire) and their totals are presented. Statistics (χ^2) are given on differences between bleaching categories per species, and on variations in the degree of bleaching among the species

Species	Pale	White	χ^2	Part	Whole	χ^2	Total	n_{tot}
Fungia (V.) concinna	28	18	3.66 ns	25	21	0.60 ns	46	408
Fungia (V.) repanda	50	25	8.20**	32	43	1.63 ns	75	224
Fungia (D.) horrida	31	17	0.81 ns	31	17	0.81 ns	48	67
Fungia (D.) scruposa	10	41	3.28 ns	30	21	0.08 ns	51	47
Fungia (F.) fungites	29	25	0.51 ns	17	37	15.27***	54	458
Fungia (P.) paumotensis	26	26	0.00 ns	22	30	1.96 ns	52	328
Heliofungia actiniformis	1	0	0.67 ns	0	1	0.67 ns	1	121
Ctenactis echinata	2	19	3.80 ns	10	11	0.04 ns	21	61
Herpolitha limax	9	0	3.63 ns	9	0	3.63 ns	9	11
Sandalolitha robusta	23	23	0.00 ns	30	16	0.15 ns	46	30
Podabacia crustacea	0	24	1.20 ns	14	10	0.75 ns	24	21
All fungiids	**27**	**21**	**6.57***	**21**	**27**	**5.62***	**48**	**1797**
χ^2	68.41	35.31		39.49	56.70		76.77	
Significance level	***	***		***	***		***	

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; ns = non-significant

Furthermore, in most of the populations, coral length appeared to have a significant positive correlation with depth, especially in those that were most abundantly represented at the greatest depths (Fig. 5). This was usually not so for F. (F.) fungites with only a total of 3 (unaffected) specimens at 15 m, at Sites SE and SW1 (Fig. 5i, l).

DISCUSSION

During the 1983 coral bleaching around Pari Island, many coral species, such as those belonging to the branching genera Acropora, Pocillopora and Monti-

pora, suffered from high mortality rates (Brown & Suharsono 1990). For most Fungiidae, however, it was little more than a sublethal incident. Mushroom corals may be relatively heat-tolerant as evidenced by experiments (Edmondson 1928, Coles et al. 1976, Jokiel & Coles 1977, Yang et al. 1980).

Without the occurrence of the unaffected Heliofungia actiniformis, the investigated sites around Pari Island would not have shown a significant variation in the degree of bleaching. The high coral density of this species at Site E may be related to its migratory capability (Abe 1939) and to its high number of recruits (Fig. 5h: $\varnothing_{max} \leq 5$ cm), which could have been asexu-
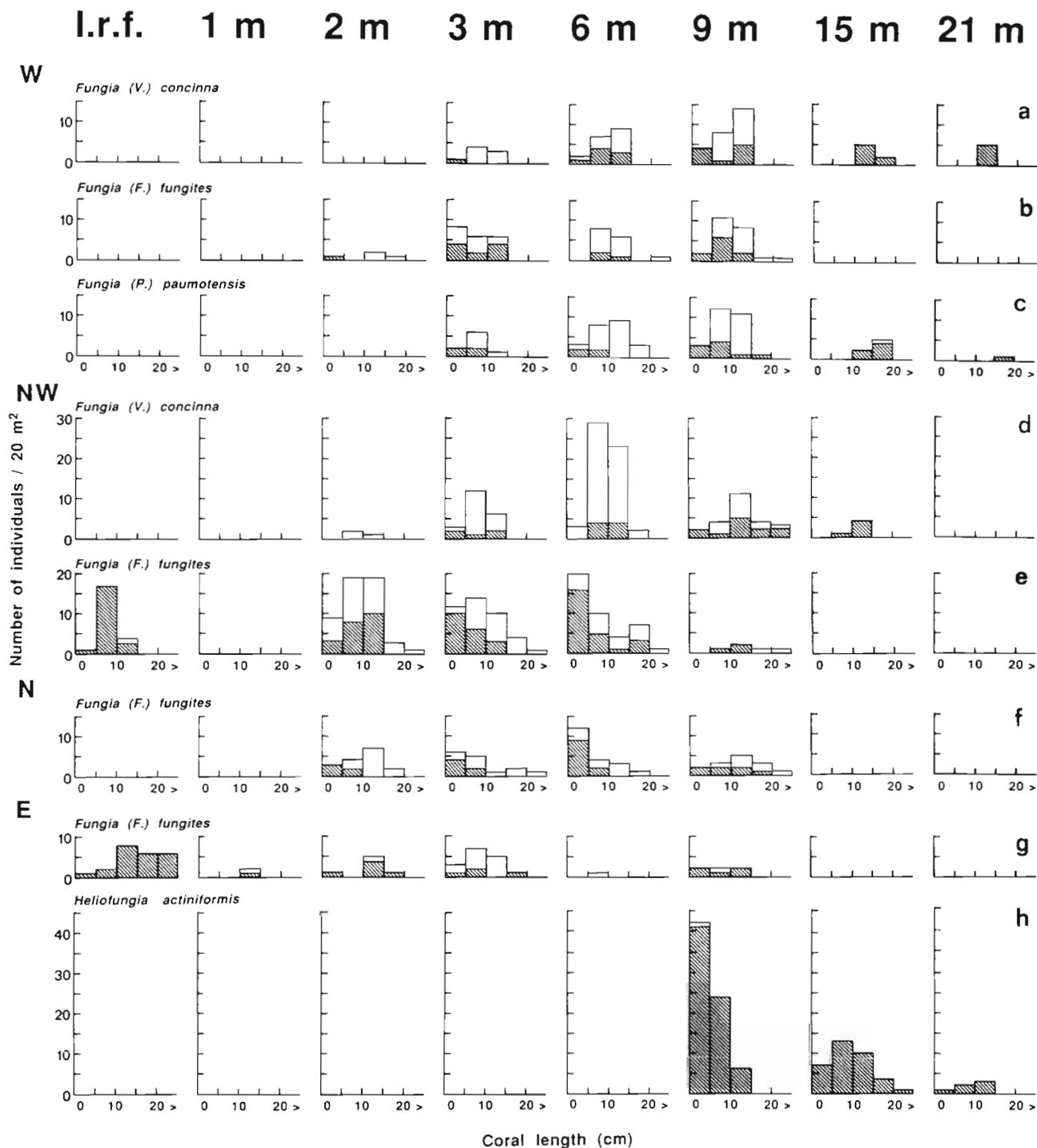
Fig. 5. Transects with mushroom coral populations (n > 50) divided into size classes and the numbers of bleached (open bars) and unaffected corals (hatched) in the investigated 2 × 10 m² quadrats (depths indicated above)

ally derived by regeneration from previously empty stalks (Hoeksema 1989, 1990). That corals of this species remained unaffected (Fig. 4e) may be due to the thick layer of gastrodermis in which their zooxanthellae are embedded, or its green fluorescent pigment in the epidermis (Kawaguti 1944); both may provide protection against intense sunlight.

The bleaching event at Pari Island was preceded by an unusually protracted cloud-free period (Brown & Suharsono 1990). Since coral species are not equally

Fig. 3 (continued)
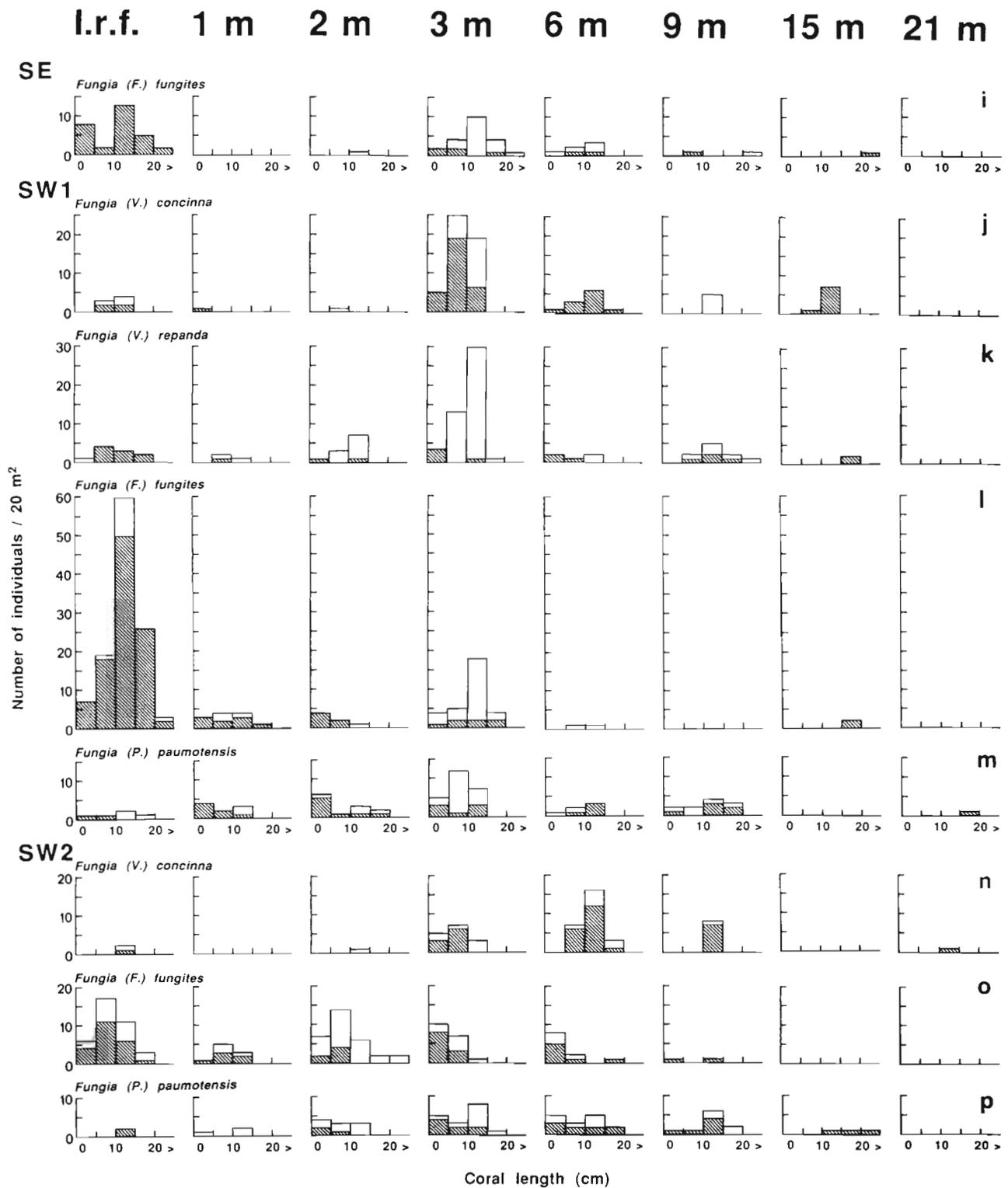
protected by UV-absorbing compounds (Siebeck 1988), a synergistic effect of high seawater temperature and ultraviolet radiation (Harriot 1985) may also lead to different bleaching rates. Furthermore, closely related coral species can contain dissimilar strains or species of zooxanthellae (Trench & Blank 1987, Rowan & Powers 1991a, b), which may show different physiological tolerances. For example, *Fungia (V.) repanda* corals showed a predominantly shallow distribution (Fig. 3), which does not account exclusively for the high bleach-

Table 6. Size classes of *Fungia (F.) fungites* and all other mushroom coral species together on outer reef quadrats around Pari Island. Percentages of individuals affected by various categories of bleaching (paled or whitened, partial or entire, and their totals). Statistics (χ^2) on differences between categories of bleaching are given per size class. Per category, a statistic on variation among size classes is indicated; n = number of corals per size class

Species Bleaching category	Size class (cm)				
	0.5–5.0	5.5–10.0	10.5–15.0	15.5–20.0	>20.0
Fungia (F.) fungites:					
Pale: 29 %; $\chi^2 = 21.58$***	9	27	52	36	31
White: 25 %; $\chi^2 = 4.61$ ns	17	27	21	32	61
χ^2 pale-white	1.26 ns	0.00 ns	4.35*	0.00 ns	0.17 ns
Part: 17 %; $\chi^2 = 7.70$ ns	7	23	24	18	23
Whole: 37 %; $\chi^2 = 14.60$**	19	31	49	50	69
χ^2 part-whole	2.70 ns	0.66 ns	8.03**	2.54 ns	0.71 ns
Total: 54 %; $\chi^2 = 14.60$**	**26**	**54**	**73**	**68**	**92**
n	129	141	131	44	13
Other Fungiidae:					
Pale: 26 %; $\chi^2 = 28.70$***	11	25	37	26	12
White: 20 %; $\chi^2 = 12.07$*	8	23	22	20	21
χ^2 pale-white	0.11 ns	0.13 ns	8.30**	0.46 ns	0.66 ns
Part: 22 %; $\chi^2 = 11.99$*	10	24	24	26	21
Whole: 24 %; $\chi^2 = 29.45$***	9	24	35	20	12
χ^2 part-whole	0.01 ns	0.00 ns	4.87*	0.46 ns	0.66 ns
Total: 46 %; $\chi^2 = 35.29$*	**19**	**48**	**59**	**46**	**33**
n	225	388	490	151	85

* p<0.05; ** p<0.01; *** p<0.001; ns = non-significant

Table 7 Summary results of 1-way ANOVA and least squares linear regression analyses with regard to length and depth of mushroom corals of the outer reef populations indicated in Fig. 5. ANOVAs show variation in mean coral length among investigated depths. Slope (S) indicates how much coral growth in a population (length, cm) corresponds with an increase in depth (cm); n = number of outer reef individuals per site

Site	Species	ANOVA F	Linear regression r	S	n
W	*Fungia (V.) concinna*	6.81***	0.477***	0.033	74
	Fungia (F.) fungites	2.34 ns	0.219 ns	0.037	63
	Fungia (P.) paumotensis	7.33***	0.463***	0.052	67
NW	*Fungia (V.) concinna*	5.80***	0.336***	0.043	111
	Fungia (F.) fungites	3.00*	0.024 ns	0.006	137
N	*Fungia (F.) fungites*	3.20*	0.039 ns	0.008	65
E	*Fungia (F.) fungites*	2.60 ns	−0.375*	−0.059	32
	Heliofungia actiniformis	7.36***	0.332***	0.044	110
SE	*Fungia (F.) fungites*	1.47 ns	0.271 ns	0.053	31
SW1	*Fungia (V.) concinna*	4.83**	0.459***	0.043	65
	Fungia (V.) repanda	3.70**	0.413***	0.049	78
	Fungia (F.) fungites	4.78**	0.420**	0.073	54
	Fungia (P.) paumotensis	1.03 ns	0.311*	0.038	64
SW2	*Fungia (V.) concinna*	14.65***	0.529***	0.088	50
	Fungia (F.) fungites	2.52*	−0.116 ns	−0.028	71
	Fungia (P.) paumotensis	3.72**	0.457***	0.064	56

* p<0.05; ** p<0.01; *** p<0.001; ns = non-significant

ing rate of this species. Two times as many of its individuals were paled instead of whitened (Table 5); this is not clearly related to depth (Table 4). Other species, some with nearly similar bathymetric distributions, were significantly less affected. Were pigmentation decrease in zooxanthellae primarily caused by bright light, but zooxanthellae expulsion mainly induced by high temperature (Hoegh-Guldberg & Smith 1989), it would be likely that paling in an assemblage of mushroom corals primarily depended on how much the algae in separate species were photo-adapted (or protected by their host) and whitening

would be mainly related to the bathymetric range of the warmed surface layer. This would explain why interspecific variation in paling is much higher than in whitening (Table 5).

Adjacent individuals of the same species may vary from unaffected to entirely whitened, which may be attributed to differences in their genotypes (Jokiel & Coles 1990). Nevertheless, partial and entire bleaching in mushroom corals could clearly be distinguished as depth-related (Table 4). In the shallow part of the outer reef, most clearly at 2 and 3 m depth, the majority of affected fungiids was completely bleached, whereas downward, especially at 9 m, partial discoloration was more common (Fig. 4d). A similar change in discoloration pattern was also noticed by Jaap (1985), who assumed that entire bleaching in corals occurred mainly in shallow, uniformly hyperthermic water, whereas partial bleaching could have been caused by sunken pockets of hot hypersaline water that penetrated layers of cooler subsurface water. However, Hayes & Bush (1990) believed that homogeneous extrinsic conditions around corals may also cause variable mosaic patterns of bleaching, namely by inducing different responses to stress within the individuals concerned. Partial bleaching may also be due to differences in light exposure, which results in relatively shaded parts being the least affected (Goenaga et al. 1989, Goreau & Macfarlane 1990). However, in mobile mushroom corals it is not necessarily clear which part of the surface was most exposed (Hoeksema 1988); their usually light-colored underside suggests that prolonged darkness may also cause low zooxanthella concentrations (cf. Yonge & Nicholls 1931a, b).

Although a bathymetric relation with regard to coral bleaching has been observed at other localities (Faure et al. 1984, Fisk & Done 1985, Jaap 1985, Oliver 1985, Lang et al. 1988), it was hitherto only little known that individuals living on the shallow inner reef and in lagoons could be less affected than conspecifics on the outer reef, at similar and greater depths (Goreau & Macfarlane 1990). Only inner-reef-flat fungiids at Sites SW1 and SW2, near a tidal channel in which strong currents prevail (Fig. 1), showed noticeable bleaching. Water exchange and consequent temperature fluctuations could have been higher at these sites than at the rest of the inner reef flat and therefore might have prevented a high thermal resistance in the mushroom corals here. Coles & Jokiel (1978) found that pre-exposure of corals to temperatures in the upper sublethal range could increase their tolerance to heat. The present results also agree with observations by Cook et al. (1990), who found more extensive coral bleaching on offshore reefs than in lagoons and on inshore reefs with presumed higher temperatures. Furthermore, Glynn & D'Croz (1990) found that corals from an area with low-

temperature upwelling were more sensitive to experimental high temperatures than those from a neighboring area without upwelling.

The size-dependent bleaching of mushroom corals is probably largely connected to their life histories (Hoeksema 1989: Fig. 42). In juvenile stage, corals of most species live attached and usually well hidden on shaded limestone substrata (Dinesen 1983), whereas later on they become free-living and able to disperse over the reef substratum (Hoeksema 1988). The free-living corals on the reef slope are likely to migrate downward with increasing age and size (Hoeksema 1988); this explains why positive correlations can be found between size and depth of the corals. Accordingly, corals living below the bleaching zone (≥ 15 m depth) have the greatest $\varnothing_{max}$, which explains at least partly why the largest fungiids ($\varnothing_{max} > 20$ cm) on the slope are less affected than smaller ones. *Fungia (F.) fungites* is an exception, since it rarely showed any correlation between size and depth (Table 7). This species is known to display a predominantly shallow recruitment and little downward migration (Hoeksema 1988, 1990); therefore it was rarely found below 15 m (Figs. 3 & 5). Consequently, it showed a disproportionally high number of large affected individuals (Table 7); this was most clearly demonstrated at Sites W, NW, N, SE, and SW2 (Fig. 5b, e, f, i, o).

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