The 1997/1998 Mass Mortality of Corals: Effects on Fish Communities on a Tanzanian Coral Reef

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The abnormally high surface temperatures in the world's oceans during 1997/1998 resulted in widespread coral bleaching and subsequent coral mortality. An experiment was performed to study the effects of this coral mortality as well as the influence of the structural complexity on fish communities on a Tanzanian coral reef. Changes in fish communities were investigated on plots of transplanted corals after 88% of these corals had died. A distinct shift in fish community composition was found, although diversity was not affected. Fish abundance rose by 39% mostly due to an increase in herbivores, which seemed to benefit from enhanced algal growth on the dead corals. Fish abundance, species diversity and community composition were also strongly influenced by the structural complexity provided by the live and dead corals. This suggests that a coral reef can support abundant and diverse fish populations also after the corals have died as long as the reef structure is sustained. © 2001 Elsevier Science Ltd. All rights reserved.

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Introduction

In 1997 and 1998 coral reefs around the world suffered the most extensive and severe bleaching, and subsequent coral mortality, known to date (ISRS, 1998; Strong *et al.*, 1998; Wilkinson, 1998). This event was correlated with elevated sea surface temperatures often reaching 3–5°C above normal. Due to the disturbance corals lost their symbiotic algae, which give them their colour and supply them with nutrients. Some corals recovered from the bleaching, but in many regions, especially in the Indian Ocean, there were reefs that had a coral mortality up to 90% (Wilkinson, 1998). Such losses would be expected to have profound effects on the coral reef

ecosystem. Fish associated with reefs depend on corals for food and shelter (Bouchon-Navaro, 1986; Caley and St. John, 1996; Hixon and Beets, 1993; Munday *et al.*, 1997); hence corals affect important processes such as recruitment, competition and predation (Buchheim and Hixon, 1992; Hixon and Carr, 1997; Öhman *et al.*, 1998a). However, given the range of factors that regulate fish populations (Caley *et al.*, 1996; Doherty and Fowler, 1994; Jones, 1991; Williams, 1991) it is difficult to predict the outcome of a coral-bleaching event. Most studies on the effects of disturbance on reef-fish communities are opportunistic and non-manipulative field observations where pre-disturbance data or undisturbed controls are missing (Jones and Syms, 1998). Interpretation of these studies may also be confounded by the natural variation among reef-fish communities at different spatial scales. Thus, information on how coral reef-fish communities are affected by habitat degradation is limited, particularly with respect to coral bleaching. Global warming may increase the frequency and severity of temperature related coral bleaching (ISRS, 1998). Therefore, the ability of the reef-fish communities to survive and adapt to events of coral mortality pending the recovery of the disturbed reefs will have far reaching ecological and economic consequences.

The aim of this study was to investigate the effect of coral mortality following a severe bleaching event, on reef-fish assemblages. In addition, we examined how reef-fish communities were influenced by the structural complexity provided by the corals.

Methods

The study site

The study was carried out on plots of transplanted corals at Tutia Reef in the Mafia Island Marine Park, Tanzania (7°40′S, 40°40′E). The plots were situated on the protected side of the reef, at a depth of 3 m at low tide. The seabed at the study site was flat and covered by

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sand, coral rubble and rhodolites. The coral cover was patchy, ranging between 10% and 20% (including standing dead corals), and mainly made up of thickets of branching species of the genus *Acropora*.

Field methods and coral mortality

Colonies of the branching staghorn coral *Acropora formosa* were transplanted in 1995 to 32 quadrate plots measuring 2.5×2.5 m^2 each (Lindahl, 1998), which were evenly distributed between two sites (A and B), separated by 200 m. The corals were transplanted as an experiment on rehabilitation of degraded coral reefs, aiming at developing methods for re-establishment of coral cover in areas where the unstability of the sub-strate precludes natural re-colonization. Branches of staghorn corals were collected from naturally growing thickets in an area adjacent to the study site. They were placed in the plots either loosely or connected to each other and to anchoring stones with strings for increased stability. Each plot was planted with corals from only one distinct thicket, believed to be a clone, and each thicket was used for only one plot. The density of live corals in the plots at the time of the first fish census ranged between 10% and 84% area cover, with an av-erage of $33 \pm 3.3\%$ (SE). During the 1998 coral bleach-ing event, which was most severe in March–April, all corals died in 28 plots whilst those in the four remaining plots were less affected. The average live coral cover in these four plots changed from $28 \pm 8.7\%$ (SE) in 1997 to $25 \pm 7.0\%$ (SE) in 1998. Most of the corals in the sur-rounding coral community were killed as well. In Oc-tober 1998 we assessed the average relief in each plot by measuring the height of the coral branches above the substratum. This was done in ten 10 cm sections of two parallel line transects laid across the plot. Two consec-utive fish censuses were made on all plots of trans-planted corals. The first census was carried out in October 1997, six months before the coral mortality, and the second census was conducted 1 year later, six months after the coral mortality. The fishes were counted by a stationary SCUBA diver using a method modified from Bohnsack and Bannerot (1986). A list of all fish taxa encountered in the study area was prepared before the census. To avoid any miss-identifications, fishes were grouped into easily identifiable species, or species groups, using a set list of 84 taxa. During the census the diver rested at the seabed approximately 1 m from the edge of the plot. Both transient and stationary fishes were counted for a period of 10 min at each oc-casion. For the purpose of accuracy, and to reduce the problems encountered when fishes were swimming in and out of the plot, the fish count was limited to one half (i.e. 3.1 m^2) of each plot. Identification of the plot was facilitated by reinforcement bars marking the corners and a string marking half of the plot. Only fishes oc-curring up to 1.5 m above the seabed were counted. The counts were replicated three times on different days.

Data analysis

The Wilcoxon Signed Rank Test was used to inves-tigate changes in the total fish abundance as well as the abundance in each of the major feeding categories (co-rallivores, herbivores, invertebrate and fish feeders, omnivores and planktivores). Fishes were classified into feeding categories based on published material (Allen, 1985, 1991; Lieske and Myers, 1994; Randall *et al.*, 1990). In order to detect changes in fish community composition between the two censuses a non-parametric rank similarity matrix was produced, based on Bray–Curtis similarities among the fish communities in the plots. The similarity matrix was converted into a mul-tidimensional scaling (MDS) ordination, (Clarke, 1993) where the distances between the data points (Figs. 1 and 3) display the relative similarities of the fish assemblages among the plots. The similarity percentage procedure (SIMPER) is based on the same Bray–Curtis similarity matrix as the MDS plot, and ranks the contribution of each taxon to the total dissimilarity between the two censuses (Clarke, 1993). This method was used to identify the fish taxa whose abundance change had the most significant effect on the composition of the fish community. The relation between the structural com-plexity in the plots and the fish abundance as well as the number of taxa was investigated with linear regression.

Results

A distinct shift in fish community composition oc-curred between the two censuses (Fig. 1). This was most pronounced in the 28 plots where the corals did not survive the disturbance. Fish assemblages in the plots containing surviving corals were grouped with the pre-disturbance communities in the MDS configuration. Site A had a similar variability in community composition
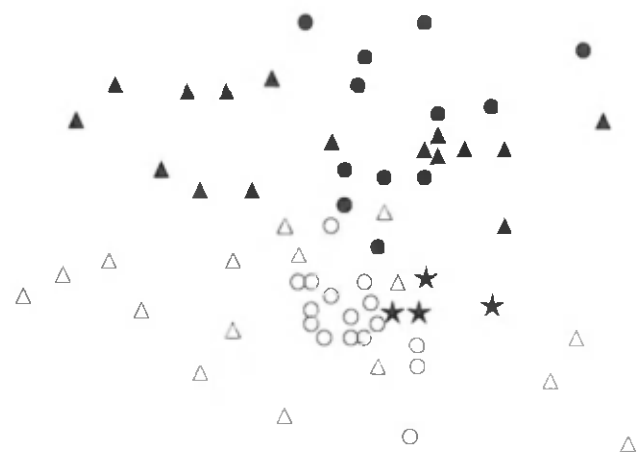

Fig. 1 MDS ordination plot based on Bray–Curtis similarities showing the fish community composition in the 32 plots in 1997 and 1998. Stress = 0.19. Each symbol represents the fish community in one plot at one time. ($\triangle$) = site A 1997 ($n = 16$); ($\blacktriangle$) = site A 1998 ($n = 16$); ($\bigcirc$) = site B 1997 ($n = 16$); ($\bullet$) = site B 1998 (only plots with dead corals, $n = 12$); ($\star$) = Site B 1998 (plots with surviving corals, $n = 4$).

among plots before and after the coral mortality, whereas in site B the fish communities became more variable after the disturbance.

The average abundance of fish increased significantly ($p = 0.002$) between 1997 and 1998 from 23 ± 3.3 (SE) to 32 ± 4.0 fishes per count, while the species richness and diversity remained fairly constant. In the different trophic groups the herbivores increased significantly ($p < 0.001$) from an average of 3.5 ± 0.4 to 13.7 ± 2.6 fishes per count and the omnivores were reduced ($p = 0.024$) from 4.1 ± 0.5 to 2.8 ± 0.5 fishes per count (Fig. 2). The other trophic groups did not change significantly in abundance ($p > 0.05$). Schools of herbivorous parrot fishes (Scaridae) and surgeonfishes (Acanthuridae) (Table 1) gave the most significant contribution to the increase in fish abundance. Also the territorial herbivorous damselfish *Plectroglyphidodon lacrymatus* increased in numbers, whereas the abundance of two other damselfishes, *P. dickii* and *Dascyllus carneus*, that are commonly associated with live corals was reduced aft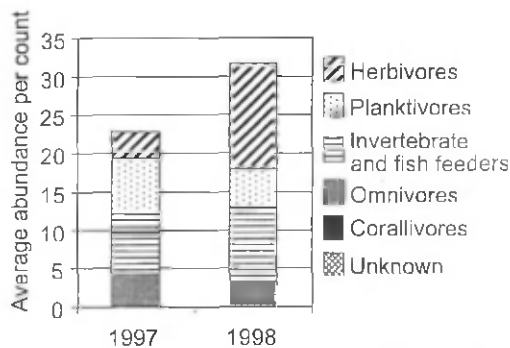er the coral mortality. The significance of these changes in abundances for the fish community structure was confirmed by the SIMPER procedure which ranks all species according to their contribution to the overall community shift (Table 1).

The average relief (= cm above substrate) provided by the corals in each of the 32 plots ranged from 3 to 27 cm after the coral mortality. This relief was the result of two years of steady growth terminated by the 1998-bleaching event. The dead corals were mostly intact, standing in the same position as they had before the bleaching event. There was a highly significant relation between the relief and fish abundance ($p < 0.001$) as well as between the relief and the number of fish taxa ($p < 0.001$) (Fig. 3). The strong relationship did not change if the four plots with surviving corals were excluded from the analysis.

By displaying the fish community from 1998 in an MDS, with the size of each data point proportional to the relief in the plot we demonstrate that the fish community changed in relation to reef structure (Fig. 4). It is also noticeable that the plots with live corals were

Fig. 2 Average abundance per 10 min count of fishes with different feeding habits.
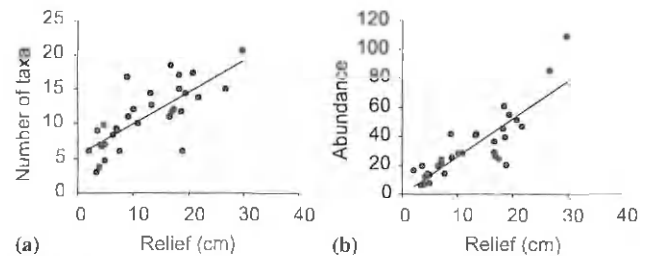

Fig. 3 Linear regressions for the average number of fish taxa (a) and abundance (b) per count versus the average height of the coral cover (relief) in each plot. $n = 32$ in both graphs. (a): $r^2 = 0.59$; $y = 0.46x + 5.29$; $p < 0.001$. (b): $r^2 = 0.73$; $y = 2.60x - 0.14$; $p < 0.001$.

TABLE 1

Average abundance per 10 min count of the 20 fish taxa giving the most significant contribution to the community shift between 1997 and 1998[a,b].

Taxon	Abundance 1997	Abundance 1998	Contribution to dissimilarity (%)	Feeding habits
Scaridae	0.71	5.89	11.99	H
Plectroglyphiododon dickii	3.08	1.04	9.42	O
Acanthuridae	1.22	3.80	8.60	H
Plectroglyphiododon lacrymatus	1.40	2.89	7.45	H
Dascyllus carneus	2.08	0.99	6.60	P
Chromis viridis	3.66	0.07	4.74	P
Pseudocheilinus hexataenia	2.19	2.11	4.68	I/F
Labridae spp	0.98	1.56	4.23	I/F
Chromis weberi	0.72	0.90	3.03	P
Centropyge multifasciatus	0.40	1.12	2.86	O
Thalassoma hebraicum	1.28	0.74	2.86	I/F
Chromis ternatensis	0.31	1.29	2.55	P
Halichoeres hortulanus	0.93	0.68	2.35	I/F
Parupeneus barberinus	0.49	0.73	2.07	I/F
Dascyllus aruatus	0.33	0.44	1.93	P
Dascyllus trimaculatus	0.18	0.42	1.67	P
Stethojulis bandanensis	0.31	0.56	1.51	I/F
Halichoeres cosmeticus	0.34	0.24	1.25	I/F
Gomphosus caerulus	0.36	0.31	1.24	I/F
Stegastes spp	0.04	0.44	1.03	H

[a] The contribution to the dissimilarity was given by the SIMPER procedure comparing the fish communities between the two censuses.
[b] H: herbivores; O: omnivores; P: planktivores; I/F: invertebrate and fish feeders; C: corallivores.
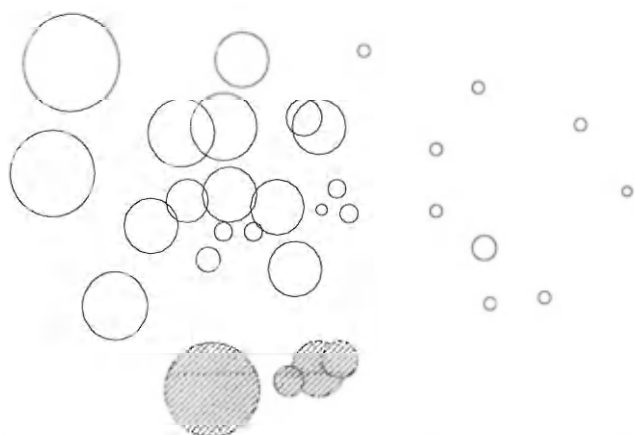
Fig. 4 MDS ordination plot based on Bray–Curtis similarities showing the fish community composition in the 32 plots in 1998. Stress = 0.18. Each circle represents the fish community in one plot, and the size of the circles is proportional to the average height of the coral cover (relief) in the plot. The shaded circles represent the plots with surviving corals.

separated from the rest. Hence, the relief did not only influence fish densities and species diversity there was also a gradual shift in fish community composition with increasing relief.

Discussion

Results from this study showed that there was an increase of fish densities within a reef area following massive coral mortality. This may seem remarkable as coral mortality would be expected to reduce habitat quality for reef fishes. However, with the diversity of feeding strategies characterizing reef fishes, certain assemblages could benefit from the coral mortality. Filamentous algae, which are the preferred food for many herbivorous fish species, will grow rapidly on bare coral substratum. Fish numbers may have increased either by recruitment or by migration. Since corals in the whole area were influenced by mortality to the same extent as the corals at the experimental site, migration seems less likely. A more probable explanation is that recruits that settled in an area with favourable conditions caused the increase. Young fishes are more able to avoid predators, and have a rapid growth rate if they associate with habitats with good quality (Kerrigan, 1994; van Rooij et al., 1995; Booth and Hixon, 1999).

A similar increase in abundance of herbivorous reef fish was found after the die-off of the grazing sea urchin *Diadema antillarum* in the Caribbean (Carpenter, 1990; Robertson, 1991) and after coral mortality following an infestation of the crown-of-thorns starfish *Acanthaster planci* in the American Samoa (Wass, 1987). The reduced abundance of omnivorous fishes, in this study, was mainly caused by a decline in the damselfish *P. dickii*, which is commonly associated with live corals. Wass (1987) also observed a similar shift from *P. dickii*

to *P. lacrymatus*. The mass mortality of *D. antillarum* and the *A. planci* infestation led to either reduced competition among grazers or increased substrate for algae, and the increase in herbivorous fish was regarded as evidence of food limitation prior to the impact. In contrast, little or no effects were detected on herbivores after corals were killed by *A. planci* on the Great Barrier Reef (Hart et al., 1996; Williams, 1986). Reef-fish communities are structured by a variety of processes (Caley et al., 1996). The relative importance of factors such as migratory patterns, competition, predation, disturbance and recruitment dynamics could vary from one reef to another. Thus, the effect of coral mortality on the reef-fish communities in this study could be unique for the conditions at Tutia Reef.

It has been shown that disturbances may lead to increased variability in the composition of marine communities (Dawson Shepherd et al., 1992; Warwick et al., 1990). In this study, the variability in the fish communities increased after the El Niño event in site B, whereas the variability in site A was large before the coral mortality as well. The situation at site A could be caused by another source of disturbance, a large spawning population of the triggerfish *Pseudoballistes flavimarginatus*. This large, aggressive fish which disturbed the fish assemblages at site A typically excavates and defends spawning pits and chases away fishes in the surrounding area.

The importance of the reef structure in determining fish community composition has been suggested in numerous studies (Carpenter et al., 1981; Lewis, 1997; Luckhurst and Luckhurst, 1978; McCormick, 1994; Öhman and Rajasuriya, 1998; Öhman et al., 1998b; Syms, 1998). However, it is usually difficult to separate between live coral and the structure it gives. There are reasons to believe that the architectural structure in itself is a more important factor influencing fish numbers than the live coral cover. In this study we were able to separate between live coral and coral structure. Apparently there was a strong relationship between fish numbers and structural complexity without living corals. This suggests that an abundant fish community can be facilitated by any reef structure with or without living coral. In fact, there are other tropical reef formations that are not biogenic but still have abundant fish populations such as rocky reefs (Jennings et al., 1996; Öhman et al., 1998b), or reefs made by lava (Godwin and Kosaki, 1989). However, corals provide the limestone framework of coral reefs through active calcium carbonate accretion. Thus, if the corals die chances are that the reef and the structure it carries will be degraded and with that, the associated fish fauna. A dead coral skeleton is more susceptible to bioeroders and other disturbances than a living coral colony. After an infestation of *A. planci* in the Ryukyu Islands, Japan, the dead corals were degraded into rubble within 2 years and the fish abundance and diversity were drastically reduced (Sano et al., 1987).

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