Pergamon

117859

PII: S0025-326X(00)00200-9

Marine Pollution Bulletin Vol. 42, No. 1, pp. 7–15, 2001

Printed in Great Britain
0025-326X/01 $ - see front matter

REPORTS

Coral Bleaching and Mortality on Artificial and Natural Reefs in Maldives in 1998, Sea Surface Temperature Anomalies and Initial Recovery

ALASDAIR J. EDWARDS†*, SUSAN CLARK†, HUSSEIN ZAHIR‡, ARJAN RAJASURIYA§, ABDULLA NASEER‡ and JASON RUBENS††

†Department of Marine Sciences and Coastal Management, University of Newcastle, Newcastle Upon Tyne NE1 7RU, UK

‡Marine Research Centre, Ministry of Fisheries, Agriculture and Marine Resources, Male', Maldives

§Coral Reef Research Programme, National Aquatic Resources Research & Development Agency, Crow Island, Mattakkuliya, Colombo 15, Sri Lanka

††GCRMN Regional Co-ordinator, South Asia, 48 Vajira Road, Colombo 5, Sri Lanka

The bleaching and subsequent mortality of branching and massive corals on artificial and natural reefs in the central atolls of Maldives in 1998 are examined with respect to sea surface temperature (SST) anomalies. SST normally peaks in April–May in Maldives. The UK Meteorological Office's Global sea-Ice and SST data set version 2.3b shows that in 1998 monthly mean SST was 1.2–4 S.D. above the 1950–1999 average during the warmest months (March–June), with the greatest anomaly in May of +2.1°C. Bleaching was first reported in mid-April and was severe from late April to mid-May with some recovery evident by late-May. At least 98% of branching corals (Acroporidae, Pocilloporidae) on artificial structures deployed on a reef flat in 1990 died whereas the majority of massive corals (Poritidae, Faviidae, Agariciidae) survived the bleaching. The pre-bleaching coral community on the artificial reefs in 1994 was 95% branching corals and 5% massives ($n = 1589$); the post-bleaching community was 3% branching corals and 97% massives ($n = 248$). Significant reductions in live coral cover were seen at all natural reefs surveyed in the central atolls, with average live coral cover decreasing from about 42% to 2%, a 20-fold reduction from pre-bleaching levels. A survey of recruitment of juvenile corals to the artificial structures 10 months after the bleaching event showed that 67% of recruits (≥0.5 cm diameter) were acroporids and pocilloporids and 33% were from massive families ($n = 202$) compared to 94% and 6%, respectively, in 1990–1994 ($n = 3136$). Similar post-bleaching dominance of recruitment by branching corals was seen on nearby natural reef (78% acroporids and pocilloporids; 22% massives). A linear regression of April mean monthly SST against year was highly significant ($p < 0.001$) and suggests a rise of 0.16°C per decade. If this trend continues, by 2030 mean April SST in the central atolls will normally exceed the anomaly level at which corals appear there are susceptible to mass bleaching.

Keywords: bleaching; community structure; coral recruitment; sea surface temperatures.

Introduction

In 1997–1998 there was unprecedented bleaching and subsequent mortality of corals reported from many areas around the world (e.g., Wilkinson, 1998; Berkelmans and Oliver, 1999; Hoegh-Guldberg, 1999) with particularly severe bleaching and high mortality reported from the Indian Ocean (Lindén and Sporrong, 1999; McClanahan, 2000; Sheppard, 1999; Wilkinson *et al.*, 1999). The Maldives were among sites severely impacted in the Indian Ocean (Rajasuriya *et al.*, 1999) and, being composed entirely of low-lying coral cays, are particularly vulnerable to loss of the protection afforded by healthy,

*Corresponding author. Tel.: +44-191-222-6663; fax: +44-191-222-7891.

E-mail address: a.j.edwards@ncl.ac.uk (A.J. Edwards).

accreting coral reef flats in the face of predicted sea-level rise. Four and a half years of pre-bleaching monitoring of artificial reefs in Maldives (Clark and Edwards, 1994, 1995; Edwards and Clark, 1992a) allowed detailed comparisons of pre- and post-bleaching coral communities as well as a comparison of the taxonomic composition of coral recruits that settled on the artificial reef structures before and after the 1998 bleaching event. In this note we examine in detail the anomalous rise of sea surface temperatures (SST) associated with coral bleaching in the central atolls of the Maldives in April–May 1998 and report on the impact of the bleaching on coral communities on both artificial and natural reefs and the initial progress of recovery from the bleaching event.

Methods

Artificial reef study site

In late 1990 various artificial reef structures, including concrete Sheppard Hill Energy Dissipator (SHED) blocks and Armorflex concrete mattresses (Edwards and Clark, 1992a), were deployed at 0.8–1.5 m depth on the reef flat of a severely degraded faro (ring-shaped reef rising to the sea surface with its own lagoon) 2.4 km north-west of the Maldives capital Malé in the central atolls (Edwards and Clark, 1992b). Recruitment and subsequent growth and mortality of corals on the structures were monitored in detail over 4 yr (Clark and Edwards, 1994, 1995) with progress checked during subsequent sporadic visits. In 1998 the site was visited in the middle of the bleaching event on 12 May, photographs were taken and estimates of the extent of bleaching made. Subsequently, the site was re-visited on 31 July (photographing the impacts of the bleaching) and a survey of the status of the bleached corals was made on 7 August, about 3 months after bleaching was prevalent. A detailed study of survivors and new recruits was made in February–March 1999 about 10 months post-bleaching.

Post-bleaching surveys of the artificial reefs

Post-bleaching survivorship and recruitment of corals were assessed in February–March 1999 by carrying out in situ surveys of three 50 m^2 SHED artificial reef structures. Based on locally measured juvenile coral growth rates (unpublished data), branching corals (Acroporidae, Pocilloporidae) with a mean colony diameter of less than 7 cm were deemed to have settled since the 1998 bleaching event and were classified as post-bleaching recruits. For slower growing massive species (Poritidae, Faviidae, Merulinidae, Agariciidae, Siderastreidae), colonies with a mean diameter of 3 cm or less were considered to have settled since the bleaching. Live corals in each category with mean colony diameters greater than 7 or 3 cm, respectively, were deemed to be survivors of the 1998 bleaching event. All visible live corals (> ca. 0.5 cm diameter) were identified as far as possible (at least to genus), their greatest and least diameters measured and their positions on the SHED blocks noted. Detailed pre-bleaching data on recruitment, growth and mortality of corals on the SHED structures were available for 1990–94.

Surveys of natural reefs

Pre- and post-bleaching surveys of live coral cover were conducted using standard Reef Check (Hodgson, 1999) and Global Coral Reef Monitoring Network (GCRMN) procedures using line–intercept transect methods (English *et al.*, 1997). Reef Check surveys were carried out in August 1997 (pre-bleaching) and August 1998 (post-bleaching) and GCRMN post-bleaching surveys in August–October 1998. An estimate of post-bleaching recruitment of corals on natural reefs was obtained in March 1999 using 10 0.25 m^2 quadrats randomly deployed on undegraded reef flat areas near the artificial reef structures. Visible recruits (> ca. 0.5 cm diameter) within the quadrats were identified as far as possible and their greatest and least diameters measured.

SST data set

The Global sea-Ice and SST data set version 2.3b (GISST2.3b) for 1° latitude x longitude areas (Rayner *et al.*, 1996) for January 1950 to May 2000 was used to examine the 1998 warming anomaly in the central Maldives (1–5°N 72–74°E). This uses an empirical orthogonal function to interpolate data-voids and provide global coverage (Smith *et al.*, 1996). Since 1982 this is a blend of bias-corrected advanced very high resolution radiometer (AVHRR) satellite-derived SST data and in situ data and requires little interpolation (Parker *et al.*, 1995; Rayner *et al.*, 1996). The bias-correction adjusts for differences between oceanic skin temperature as measured by the satellite and in situ bulk SST (Reynolds, 1988). The 1950–99 monthly SST data for the eight 1° grid squares covering the central atolls were used to calculate long-term monthly means ('normals') and standard deviations against which anomalies could be assessed.

Results

Firstly, we examine the nature of the SST anomaly that was associated with bleaching and subsequent mortality. Secondly, we report on the differential impact of bleaching on branching and massive corals on both artificial and natural reefs. Thirdly, we report on initial evidence of recovery.

SSTs in Maldives

Maldives weather is dominated by two monsoons. The NE monsoon lasts from January to April and is relatively calm and dry. The SW monsoon is windier and wetter, developing in May and lasting until November/December. During the NE monsoon mean monthly SST rises from a low in December/January to a

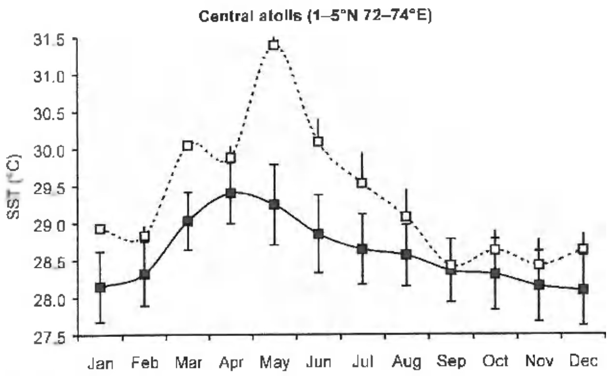


Fig. 1 SSTs for the central atolls of the Maldives. Solid squares show the 1950–99 mean monthly SST (± S.D). Open squares show the GISST2.3b monthly mean SSTs for 1998 (average of values for eight 1° latitude × 1° longitude squares in the area specified) with lines extending upward to show highest mean monthly SST recorded in the area.

high usually in April (Fig. 1) but sometimes in May. In the central atolls, the average seasonal rise is about 1.3°C and mean monthly SSTs rarely exceed 30°C. During the SW monsoon mean monthly SST slowly declines. In the central atolls in 1998, GISST2.3b data show that monthly mean SST was 1.2–4.0 S.D. above average during the warmest months (March–June) with the greatest anomaly in May of +2.1°C (Fig. 1). This May anomaly was 1.1°C above the highest mean monthly SST (30.3°C) expected in any 20 yr period. The GISST2.3b data suggest that abnormally elevated sea temperatures were experienced by corals in May (Fig. 1).

To put the 1998 anomaly in a long-term context, Fig. 2 shows the April and May (when SSTs reach their annual peak) mean and maximum SSTs for the central Maldives for 1950–2000 with an 11 yr moving average for April SST overlaid to show decadal-scale trends. The

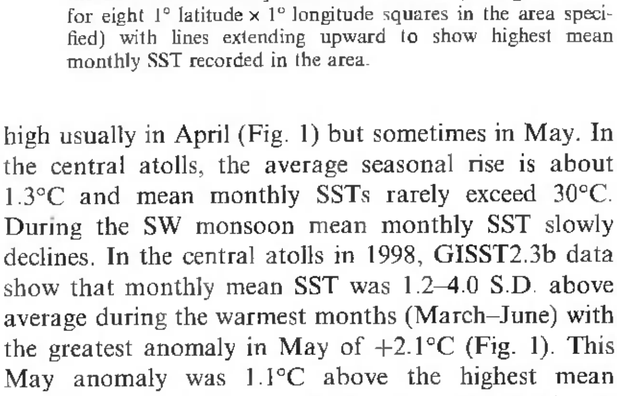


Fig. 2 The long-term context of the 1998 warming event. In Maldives SSTs normally peak in April but occasionally in May. Mean monthly SSTs for the central Maldives, for April and May from 1950 to 2000, are shown together with the least-squares best-fit linear regression line ($p < 0.001$) and 11 yr running average for April SST to show decadal-scale trends. Lines extending upwards from columns indicate the highest SST recorded among the eight 1° squares comprising the study area. Major coral bleaching was recorded in 1987 and 1998. Mean monthly SST in May 1998 was a full degree warmer than anytime in the previous half-century.

'unprecedented' (Wilkinson *et al.*, 1999) nature of the May 1998 anomaly is clear. The 11 yr moving average of April mean SST for the central Maldives increased by 0.64°C between 1955 and 1995. Linear regression of April mean monthly SST against year is highly significant ($p < 0.001$) and suggests a rise of 0.16°C per decade. If this trend continues, by 2030 mean April SST in the central Maldives will normally exceed that which would be expected to occur once in 20 yr based on 1950–2000 data.

Local reports of the timing and progress of the 1998 bleaching event in Maldives

Table 1 summarizes reports sent to the US National Oceanographic and Atmospheric Administration (NOAA) coral bleaching 'hotspots' (Goreau and Hayes, 1994; Gleeson and Strong, 1995; Strong *et al.*, 1997; Goreau *et al.*, 2000) web site. They suggest that in the central atolls bleaching began in mid-April with sea temperatures measured by divers rising about 2–3°C above the mean monthly bulk SSTs (April = 29.40°C, May = 29.25°C for 1950–99) in late April and the first half of May. Significant warming continued until around the end of May when temperatures had declined to about 1°C above mean monthly bulk SST and some recovery was evident.

Impact of bleaching on coral communities on artificial reefs

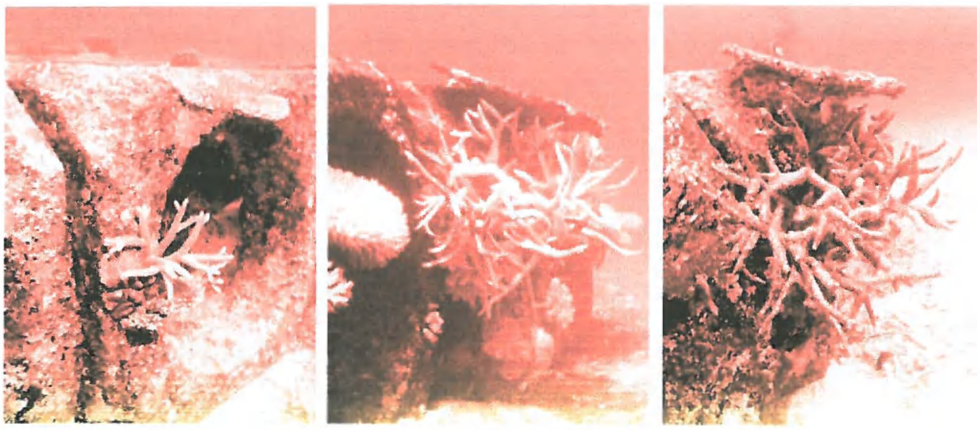
By mid–late 1994 approximately 500 live coral colonies were recorded on each of three 50 m^2 artificial reefs made of 1 m cube SHED blocks, with 20% of colonies over 10 cm in diameter and the largest colonies on each structure reaching 25–30 cm in diameter (Fig. 3(a)). Approximately 5% of these corals ($n = 70$) were massive species, with the majority of recruits being *Acropora* spp. (46%) and *Pocillopora* spp. (49%). On similar sized Armorflex concrete mattress structures *Acropora* colonies (<3 yr old) were approaching 20 cm in diameter by late 1994.

Sporadic visits from 1994 to 1998 indicated continued growth and recruitment on the artificial structures. Post-bleaching measurements of a sample of the largest recently dead *Acropora* colonies ($n = 15$) and the largest *Pocillopora* colonies ($n = 15$) on the SHEDs were made in early August 1998 and compared to comparable samples ($n = 15$) from 1994. These indicated growth in mean maximum diameter from 20 to 37 cm for *Pocillopora* and from 21 to 67 cm for *Acropora* colonies in the *circa* 4 yr prior to bleaching. The largest *Porites* colonies had reached maximum diameters of 20–24 cm from 10–13.5 cm in 1994. The greatest and least diameters of the 15 largest *Acropora* colonies (then <7-yr old) recruited to the Armorflex mattresses were also measured. The largest colony was 135 × 102 cm^2 across when killed by bleaching and the colonies had an average geometric mean diameter of 86.8 cm (S.E. 3.6). Extension rates

TABLE 1
Summary of in situ reports of bleaching in Maldives in 1998 posted to NOAA coral bleaching 'hotspots'.[a]

Date	Location	Report	Source
Mid-April	Central atolls	First signs of bleaching. Some bleached *Acropora* and sea temperatures of 33°C on the reef flat and 31°C at 3 m depth inside the atolls.	W. Allison (locally based marine scientist)
Early May	Central atolls	Major bleaching with water temperatures of 32.5°C on the reef flat near the reef edge.	W. Allison
Mid-May	North Male'atoll	90% bleaching of scleractinian corals, sea anemones, soft corals and giant clams to 20 m depth. Sea temperatures of 32°C reported to 15 m depth. Very low wind speeds and consequent lack of surface mixing noted.	D. Elder (locally based UNDP consultant)
	Central atolls (Felidhu, Ari, N. Nilandhe)	Widespread bleaching; worst on the east side of Felidhu atoll where water clarity was greatest and less in Ari and N. Nilandhe atolls where water clarity was poorer. Noted that *A. hyacinthus, Pocillopora* and *Millepora dichotoma* were particularly hit as well as anemones. Sea temperatures of up to 31°C at 30 m depth (compared to the usual 27°C at that depth).	N. Schmidt (diving instructor; 15 yr local experience)
End of May (24–27 May)	Central atolls	(i) Sea temperatures declining to 30.0–30.5°C on the reef flat with some evidence of reduced bleaching (returning colour), (ii) temperatures of 30.8°C to 10 m depth and heavy cloud and strong winds, (iii) temperatures of 30.5°C over the reef flat but down to 29.5°C away from reef on south and west sides of atolls.	W. Allison

[a] Web page http://psbsgi1.nesdis.noaa.gov:8080/PSB/EPS/SST/climohot.html.



(a) (b) (c)

Fig. 3 (a) *Acropora cytherea* (foreground, top), *A. valenciennesi*, *Pocillopora verrucosa* and *A. divaricata* (left-hand side) colonies on a SHED block in September 1994, (b) the same and adjacent bleached colonies on 12 May 1998 at the height of the bleaching event, (c) the same corals on 31 July 1998, now dead and covered in algae (photographs: (a) A. Edwards, (b) A. Rajasuriya, (d) H. Zahir).

indicate continued good conditions for growth at the site prior to bleaching.

On 12 May 1998 close to 100% bleaching of both branching and massive corals (Fig. 3(b)) was observed. Photographs show almost all live corals to have been bleached and indicate that 10–15% of sizeable branching colonies (>5 cm diameter) had died prior to the bleaching event (already algal covered/eroded). Photographs from 31 July and a survey of the site on 7 August showed that almost all the branching corals were dead and coated in filamentous algae (Fig. 3(c)) but that the majority of massive corals appeared to have recovered from the bleaching event.

The loss of branching coral colonies evident from Table 2 suggests at least 98% mortality of these corals on the artificial reefs following bleaching (with conservative assumptions of no recruitment since 1994 and 50% pre-bleaching mortality of colonies then established). All five surviving *Pocillopora* colonies were still alive 10 months after bleaching as were three of the *Acropora* survivors (one *A. nasuta*, one *A. tenuis* and one colony whose species could not be determined in the field), but two of the partially dead *Acropora* colonies had died by late February 1999. Prior to bleaching, the species composition of the *Acropora* community on the artificial structures was: *A. hyacinthus* (41%), *A. cythe-*

TABLE 2

Comparison of numbers of live coral colonies in dominant branching taxa on the three SHED structures in 1994 with numbers recorded 3 months after bleaching in August 1998.[a]

Branching taxon	Number of live colonies	
	Late 1994	3 months after bleaching
Pocillopora damicornis	241	2
Pocillopora verrucosa	526	3
Acropora spp.	728	5

[a] Of the five live *Acropora* three were partially dead.

rea (14%), *A. divaricata* (12%), *A. humilis* (9%), *A. gemmifera* (8%), *A. digitata* (7%), *A. nasuta* (7%), *A. tenuis* (1%) and *A. valenciennesi* (1%).

By contrast to the branching corals, the majority of massives on the SHEDs, including almost all *Porites* spp. (mainly *P. lutea* and *P. lobata*) and *Pavona*, appeared to have survived or already recovered from the bleaching event by August. In 1994 there were 70 massive colonies established on the SHED blocks, whereas post-bleaching there were 240 surviving in February 1999 (not including post-bleaching recruits). 28 *Porites* colonies and 13 *Pavona* were established on the SHED blocks in 1994; this had risen to 87 and 102 colonies, respectively, by 1999, indicating continued slow recruitment prior to the bleaching. Other massives that survived the bleaching included *Cyphastrea*, *Favia*, *Favites*, *Goniastrea*, *Hydnophora*, *Leptastrea*, *Leptoria*, *Platygyra* and *Psammocora*. Although it was clear that some *Favites* and *Platygyra* died as a result of the bleaching, the small numbers present do not allow useful estimates of mortality rates to be made. However, it was clear that they suffered considerably less than the branching corals. Of nine *Goniastrea* surviving, eight had suffered partial mortality and of six *Leptoria* survivors, four were partly dead. By contrast, only seven of the 87 surviving *Porites* on the SHEDs had suffered partial mortality. The taxonomic composition by family of the pre- (late 1994) and post-bleaching coral communities on the SHED structures are compared in Fig. 4.

Three months after bleaching, among 34 *Porites* on an Armorflex structure, 26 (76%) seemed to have recovered, six appeared to be recovering but were still partially bleached, and only two remained almost totally bleached. Proportions were similar on nearby natural reef flat. Among other common coral species on the reef flat, the majority of *Goniastrea* were still bleached after 3 months but with coral tissue still largely intact and some signs of recovery.

Impact of bleaching on coral communities on natural reefs

Monitoring of transects showed significant reductions in live coral cover at all sites studied (Table 3) with average live coral cover decreasing from about 42% to 2% on the transects surveyed. Several sites had sufficient surveys carried out to allow direct statistical comparisons of % live coral cover pre- and post-bleaching and all showed significant declines (Table 3). These included Bandos island (N. Malé) and three sites monitored as part of Reef Check (a patch reef north of Kuda Anbaraa in Felidhu atoll and Thuvaru and Maduvvari islands in Mulakatholu atoll). A number of other sites provided additional information on pre- and post-bleaching live coral cover. The surveys show that mean live coral cover was reduced to about 5% of pre-bleaching levels in shallow water ($\leqslant 10$ m deep) in the central atolls.

Post-bleaching recruitment

Within 10 months of the bleaching event, 202 live coral recruits were recorded in situ on the SHED structures. Of these 67% were acroporids and

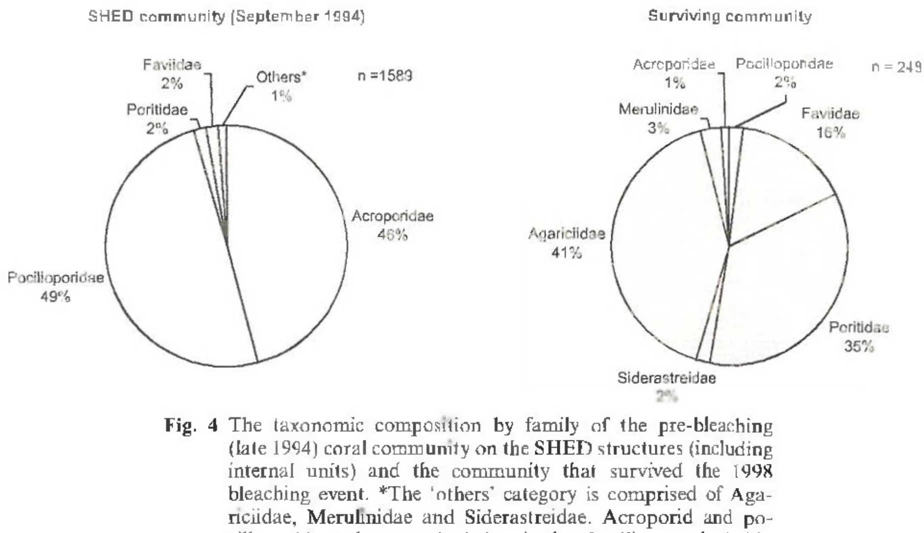


Fig. 4 The taxonomic composition by family of the pre-bleaching (late 1994) coral community on the SHED structures (including internal units) and the community that survived the 1998 bleaching event. *The 'others' category is comprised of Agariciidae, Merulinidae and Siderastreidae. Acroporid and pocilloporid corals are unshaded and other families are shaded in grey to emphasize the community shift.

TABLE 3

Mean percentage live coral cover ±95% confidence limits recorded at sites in the central atolls of the Maldives before and after the 1998 bleaching event.[a]

Survey sites/atolls	% live coral cover			
	Pre-bleaching		Post-bleaching	
	MRS/ERU (various reports)	MRS Reef Check August 1997	GCRMN August–October 1998	MRS Reef Check August 1998
Bandos (Malé)	37.3 ± 11.0 ($n = 4$)	–	4.1 ± 5.7 ($n = 4$)*	–
Other sites (Malé)	40.2 ± 8.0 ($n = 8$)	–	1.3 ± 0.7 ($n = 8$)**	–
Patch reef (Felidhu)			1.3 ± 1.0 ($n = 3$)	
3 m depth		57.5 ± 11.7 ($n = 4$)		0.0 ± 0.0 ($n = 4$)*
10 m depth	–	47.5 ± 11.3 ($n = 4$)		2.5 ± 3.2 ($n = 4$)*
Foththeyo (Felidhu)	–	–	4.6 ± 2.4 ($n = 4$)	–
Vattaru	–	–	2.7 ± 2.2 ($n = 3$)	–
Various sites (Ari)	–	–	1.1 ± 0.8 ($n = 15$)	–
Thuvaru (Mulakatholu)				
3 m depth	–	28.1 ± 17.9 ($n = 4$)	–	0.0 ± 0.0 ($n = 4$)*
10 m depth	–	40.0 ± 8.6 ($n = 4$)	–	1.3 ± 4.0 ($n = 4$)*
Maduvvari (Mulakatholu)				
3 m depth	–	53.8 ± 17.6 ($n = 4$)	–	5.0 ± 7.3 ($n = 4$)*
10 m depth	–	33.8 ± 9.5 ($n = 4$)	–	3.8 ± 2.3 ($n = 4$)*
Central atolls	42.0 ± 4.0 ($n = 36$)		2.0 ± 0.6 ($n = 61$)**	

[a] The number of transects surveyed are recorded in parentheses. The patch reef surveyed in Felidhu was north of Kuda Anbaraa. Sources of data are various reports to the Marine Research Section (MRS) of the Ministry of Fisheries and Agriculture and Environment Research Unit (ERU), Ministry of Planning, Human Resources and Environment, surveys carried out under the auspices of the Global Coral Reef Monitoring Network (GCRMN) South Asia, and Reef Check surveys carried out by the Marine Research Section (Allison, 1999; Zahir *et al.*, 1998; Naeem *et al.*, 1998). *Reduction in live coral cover significant at $p < 0.05$, **Reduction in live coral cover significant at $p < 0.001$ (Mann–Whitney U-tests except where all post-bleaching transects have 0% live coral cover when Wilcoxon signed rank tests were used).

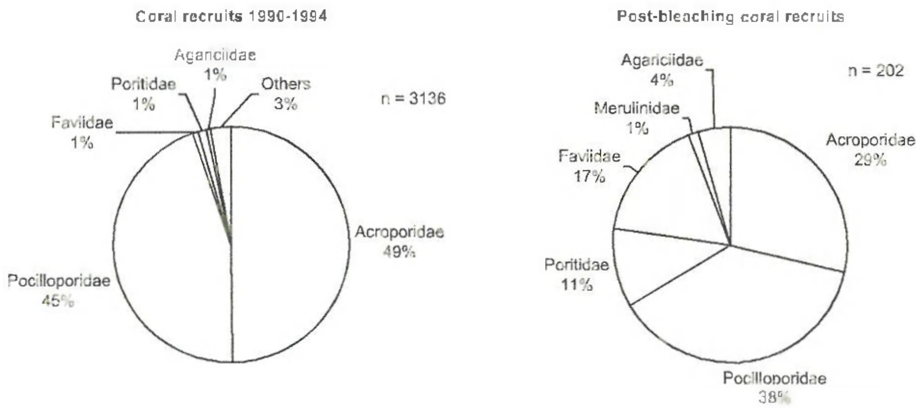


Fig. 5 Comparison of the taxonomic composition by family of coral recruits recorded on the SHED structures during 1990-94 and in the 10 months post-bleaching. Despite 98% mortality of branching corals (Acroporidae and Pocilloporidae) on the structures, recruitment is still dominated by these families. Recruits are 'visible' recruits, i.e., those which have survived to at least *c.* 0.5 cm diameter post-settlement. Acroporid and pocilloporid corals are unshaded and other families are shaded in grey to emphasize the community shift.

pocilloporids, with the remaining 33% being recruits of massive species (Fig. 5). 60% of the juveniles recorded as recruits were 2.5 cm or less in mean diameter. The taxonomic composition of the post-bleaching recruitment is compared in Fig. 5 to that in a 3.5 yr period from 1990 to 1994, when some 94% of recruits to the SHED structures were acroporids and pocilloporids, with only 6% contributed by massive families. On a nearby natural reef flat in March 1999 the mean density of recruits was 23.2 m^{-2} (S.E. ± 2.4) with 22% of recruits of massive species (Poritidae, Faviidae, Merulinidae, Agariciidae, Siderastreidae) and 78% branching corals (comprising 47% Acroporidae, 31% Pocilloporidae). The relative numbers of branching as opposed to massive species recruits on the natural reef did not differ significantly from those on the artificial structures (X^2-test, $p > 0.05$).

Discussion

Six major episodes of 'mass bleaching' of corals, coincident with El Niño Southern Oscillation (ENSO) events, have been reported since 1979 (Goreau and Hayes, 1994; Hoegh-Guldberg, 1999). However, only one instance of major bleaching and subsequent coral mortality had been reported for Maldives prior to the 1998 event. This occurred in 1987 and, due to its unprecedented nature, stimulated the government to invite an overseas expert to investigate likely causes (Wood, 1987). The GISST2.3b data indicate that apart from 1998, in the last 50 yr only in 1987, 1991, 1992 and 1997 did mean monthly SST in any 1° grid square in the central Maldives exceed the predicted one in 20 yr anomaly for the warmest month (equivalent to a mean monthly SST approaching 30.5°C). Only in 1987 and 1991 did some areas experience mean monthly SSTs at these anomalous levels in both April and May. Only in 1987 were May SSTs greater than those in April, giving prolonged thermal stress.

The bleaching in 1987 was considerably less than in 1998 but was locally dramatic with effects recorded to 30 m depth and extensive bleaching of scleractinian corals, soft corals (e.g., *Sinularia*, *Sarcophyton*) and anemones (e.g., *Heteractis*) in shallow (<10 m depth) water in all the central atolls (Malé, Ari, Felidhu and Vattaru) surveyed (Wood, 1987; Edwards, pers. obs.). Mortality was estimated to be 'considerable' but monitoring data, which would have allowed quantification, were unavailable (Wood, 1987). Despite the anomalous warming in both April and May 1991, significant bleaching does not appear to have been reported then. The 1987, 1991 and 1998 warming anomalies in Maldives coincided with strong ENSO events but do not appear correlated to strong Indian Ocean dipole events (for details see Webster *et al.*, 1999; Saji *et al.*, 1999). The latter have greatest impacts at the western and eastern margins of the Indian Ocean, whereas the Maldives are centrally situated.

The transects studied by GCRMN and Reef Check teams in the eastern central atolls (Table 3) indicated mean live coral cover of 42% ($n = 36$) before bleaching and 2% ($n = 61$) 3–6 months after bleaching (August–October 1998). McClanahan (2000) reported mean live coral cover of 8% ($n = 130$ transects) for the same eastern central atolls (Malé, Felidhu, Mulakatholu) about 11 months post-bleaching (April 1999). This suggests some recovery (the 1999 lower 95% confidence limit is around 6.9% live coral cover, the 1998 upper 95% confidence limit is 2.6% live coral cover) although individual study sites differed and so are not strictly comparable.

The scarcity of significant bleaching events in Maldives is markedly different to that seen in French Polynesia, where ENSO effects are more marked, and where bleaching events occurred in 1983, 1986, 1991, 1994, 1996 as well as 1998 (Hoegh-Guldberg, 1999). However, the upward trend in Maldives SST during the critical April–May period (1.6°C per 100 yr) is particularly worrying, since, if it continues, conditions that currently appear to make corals susceptible to mass bleaching and mortality will occur in most years by 2030. It is notable that the five warmest years for SST have occurred since 1987.

Unfortunately, the potential role of other factors that may have had a more direct role in the 1998 bleaching in Maldives, such as elevated photosynthetically active radiation (PAR) (Brown, 1997; Brown *et al.*, 1999, 2000) and/or elevated solar ultraviolet radiation (UVR) (Glynn *et al.*, 1992; Lesser *et al.*, 1990; Lesser, 2000), which could have resulted from contemporaneous clear skies and calm weather, could not be assessed from the available meteorological data. Although elevated SST clearly makes corals susceptible to mass bleaching and the sustained (since we are dealing with mean monthly (i.e., 4 week) anomalies) rise in SST was probably the key factor in the high coral mortality rates in Maldives following bleaching, recent work (e.g., Fitt and Warner, 1995; Hoegh-Guldberg, 1999; Jones *et al.*, 1998; Warner *et al.*, 1996) suggests that these other (seldom measured) factors may be primarily responsible for triggering bleaching itself.

The greater susceptibility of 'branching' (pocilloporid and acroporid) corals to bleaching than 'massives' (mainly poritids and agariciids in this case) has also been reported elsewhere (e.g., Glynn, 1983; Brown and Suharsono, 1990; Gleason, 1993; Hoegh-Guldberg and Salvat, 1995; Sheppard, 1999; McClanahan, 2000). Although some of the massive colonies had settled on parts of the SHED blocks relatively shaded from incident PAR, many of the surviving poritid colonies were located on the unshaded tops of the SHED blocks in less than 50 cm of water, so it is unlikely that settlement site preferences were a significant factor in the differential mortality between these groups. The result of the differential susceptibility to the effects of bleaching was a major community shift on the artificial reefs from a 95% pocilloporid/acroporid dominated coral community to a 92% agariciid/poritid/faviid dominated one (Fig. 4). Monitoring is continuing as part of the Coral Reef Degradation in the Indian Ocean (CORDIO) programme (Lindén and Sporrong, 1999) to see how the community structure changes over time.

The recruit densities reported by McClanahan (2000) from 11 study sites in the eastern central atolls in April 1999 averaged 29 m^{-2}, a similar density to that (23.2 m^{-2}) recorded by our much more limited study of one site in North Malé atoll in March 1999. Despite the decimation of the shallow water pocilloporid and acroporid communities, these families continued to dominate recruitment, contributing 67% of the post-bleaching juveniles on the artificial structures compared to 94% pre-bleaching. The survey of the artificial reefs 3 months after bleaching did not record recruits. Given uncertainties about precisely how long the time span is between settlement from the plankton to 'visible recruitment' at approximately 0.5 cm, the larger (5–7 cm diameter) presumed post-bleaching recruits of branching corals may have been present at small size (< ca. 1 cm) at the time of the bleaching event. If branching corals were present then as recently settled juveniles, their survival suggests a much greater resilience to the warm water anomaly compared to established *Acropora* and *Pocillopora* colonies. Relative resilience of coral recruits (2–20 mm diameter) to bleaching compared to adult colonies has recently been shown by Mumby (1999), who suggested that bleaching-induced mortality of coral recruits was insignificant during the 1998 bleaching episode at Glovers Atoll, Belize. The relative susceptibility of coral recruits to bleaching and their potentially significant contribution to post-bleaching recovery of coral communities is clearly an area that requires further research.

Despite the severity of mortality, recovery appears to be proceeding much faster in Maldives than in the species poor eastern Pacific after the 1982–1983 ENSO warming event (Glynn, 1993). Fortunately, Hoegh-Guldberg (1999) suggestion that 'recruitment may totally fail in severe bleaching events such as those experienced in the Indian Ocean' has not come about.

We thank Hassan Maizan Maniku, Ahmed Hafiz and Ali Waheed of the Marine Research Centre, Ministry of Fisheries, Agriculture and Marine Resources, Maldives for their help and the Intergovernmental Oceanographic Commission and UK Department for International Development for their support of GCRMN South Asia activities. We thank the Hadley Centre for Climate Prediction and Research, Meteorological Office, Bracknell, UK for use of the GISST2.3b data set, William Allison for his indefatigable reef monitoring work and four reviewers for their helpful comments on an earlier version of the manuscript.

Allison, W. R. (1999) *Maldives GCRMN pilot coral reef monitoring study results and recommendations.* Draft report to Ministry of Fisheries Agriculture and Marine Resources, Republic of Maldives, 33 pp.

Berkelmans, R. and Oliver, J. K. (1999) Large-scale bleaching of corals on the Great Barrier Reef. *Coral Reefs* **18**, 55–60.

Brown, B. E. (1997) Coral bleaching: causes and consequences. *Coral Reefs* **16**, Supplement, S129–S138.

Brown, B. E., Dunne, R. P., Ambasari, I., LeTissier, M. D. A. and Satapoomin, U. (1999) Seasonal fluctuations in environmental factors and variations in symbiotic algae and chlorophyll pigments in four Indo-Pacific coral species. *Marine Ecology Progress Series* **191**, 53–69.

Brown, B. E., Dunne, R. P., Goodson, M. S. and Douglas, A. E. (2000) Bleaching patterns in reef corals. *Nature* **404**, 142–143.

Brown, B. E. and Suharsono (1990) Damage and recovery of coral reefs affected by El Niño related seawater warming in the Thousand Islands, Indonesia. *Coral Reefs* **8**, 163–170.

Clark, S. and Edwards, A. J. (1994) The use of artificial reef structures to rehabilitate reef flats degraded by coral mining in the Maldives. *Bulletin of Marine Science* **55**, 726–746.

Clark, S. and Edwards, A. J. (1995) Coral transplantation as an aid to reef rehabilitation: evaluation of a case study in the Maldive Islands. *Coral Reefs* **14**, 201–213.

Edwards, A. J. and Clark, S. (1992a) Rehabilitation of coral reef flats using precast concrete. *Concrete* **26**, 16–19.

Edwards, A. J. and Clark, S. (1992b) Re-establishment of reef fish populations on a reef flat degraded by coral quarrying in the Maldives. *Proceedings of the Seventh International Coral Reef Symposium* **1**, 593–600.

English, S., Wilkinson, C. and Baker, V. (1997) *Survey manual for tropical marine resources.* 2nd ed. Australian Institute of Marine Science, Townsville.

Fitt, W. K. and Warner, M. E. (1995) Bleaching patterns of four species of Caribbean reef corals. *Biological Bulletin (Woods Hole)* **187**, 298–307.

Gleason, M. G. (1993) Effects of disturbance on coral communities: bleaching in Moorea, French Polynesia. *Coral Reefs* **12**, 193–201.

Gleeson, M. W. and Strong, A. E. (1995) Applying MCSST to coral-reef bleaching. *Advances in Space Research* **6**, 151–154.

Glynn, P. W. (1983) Extensive "bleaching" and death of reef corals on the Pacific coast of Panama. *Environmental Conservation* **10**, 149–154.

Glynn, P. W. (1993) Coral reef bleaching: ecological perspectives. *Coral Reefs* **12**, 1–17.

Glynn, P. W., Imai, R., Sakai, K., Nakano, Y. and Yamazoto, K. (1992) Experimental responses of Okinawan (Ryukyu Islands, Japan) reef corals to high sea temperatures and UV radiation. *Proceedings of the 7th International Coral Reef Symposium* **1**, 27–37.

Goreau, T. J. and Hayes, R. M. (1994) Coral bleaching and ocean "hot spots". *Ambio* **23**, 176–180.

Goreau, T., McClanahan, T., Hayes, R. and Strong, A. (2000) Conservation of coral reefs after the 1998 global bleaching event. *Conservation Biology* **14**, 5–15.

Hodgson, G. (1999) A global assessment of human effects on coral reefs. *Marine Pollution Bulletin* **38**, 343–355.

Hoegh-Guldberg, O. (1999) Climate change, coral bleaching and the future of the world's coral reefs. *Marine and Freshwater Research* **50**, 839–866.

Hoegh-Guldberg, O. and Salvat, B. (1995) Periodic mass-bleaching and elevated sea temperatures: bleaching of outer reef slope communities in Moorea, French Polynesia. *Marine Ecology Progress Series* **121**, 181–190.

Jones, R., Hoegh-Guldberg, O., Larkum, A. W. L. and Schreiber, U. (1998) Temperature induced bleaching of corals begins with impairment of dark metabolism in zooxanthellae. *Plant Cell and Environment* **21**, 1219–1230.

Lesser, M. P. (2000) Depth-dependent photoacclimatization to solar ultraviolet radiation in the Caribbean coral *Montastraea faveolata*. *Marine Ecology Progress Series* **192**, 137–151.

Lesser, M. P., Stochaj, W. R., Tapley, D. W. and Shick, J. M. (1990) Bleaching in coral reef anthozoans: effects of irradiance, ultraviolet radiation and temperature on the activities of protective enzymes against active oxygen. *Coral Reefs* **8**, 225–232.

Lindén, O. and Sporrong, N. (Eds.) (1999) *Coral Reef Degradation in the Indian Ocean.* CORDIO, Stockholm University. 108 pp.

McClanahan, T. R. (2000) Bleaching damage and recovery potential of Maldivian coral reefs. *Marine Pollution Bulletin* **40**, 587–597.

Mumby, P. J. (1999) Bleaching and hurricane disturbances to populations of coral recruits in Belize. *Marine Ecology Progress Series* **190**, 27–35.

Naeem, I., Rasheed, A., Zuhair, M. and Riyaz, M. (1998) *Coral bleaching in the Maldives – 1998.* Survey carried out in the North and South Malé atolls. Marine Research Section, Ministry of Fisheries and Agriculture and Environment Research Unit, Ministry of Planning, Human Resources and Environment, 14 pp.

Parker, D. E., Folland, C. K. and Jackson, M. (1995) Marine surface temperature: observed variations and data requirements. *Climatic Change* **31**, 559–600.

Rajasuriya, A., Maniku, M. H., Subramanian, B. R. and Rubens, J. (1999) Coral reef ecosystems in South Asia. In *Coral reef degradation in the Indian Ocean*, eds. O. Lindén, N. Sporrong. CORDIO, Stockholm University, pp. 11–24.

Rayner, N. A., Horton, E. B., Parker, D. E., Folland, C. K. and Hackett, R. B. (1996) Version 2.2 of the Global sea-Ice and Sea Surface Temperature data set, 1903–94. *Climate Research Technical Note No. 74.* Hadley Centre for Climate Prediction and Research, Meteorological Office, Bracknell.

Reynolds, R. W. (1988) A real-time global sea surface temperature analysis. *Journal of Climate* **1**, 75–86.

Saji, N. H., Goswami, B. N., Vinayachandran, P. N. and Yamagata, T. (1999) A dipole mode in the tropical Indian Ocean. *Nature* **401**, 360–363.

Sheppard, C. (1999) Coral decline and weather patterns over 20 years in the Chagos Archipelago, Central Indian Ocean. *Ambio* **28**, 472–478.

Smith, T. M., Reynolds, R. W., Livezey, R. E. and Stokes, D. C. (1996) Reconstruction of historical sea surface temperatures using empirical orthogonal functions. *Journal of Climate* **9**, 1403–1420.

Strong, A. E., Barrientos, C. S., Duda, C. and Sapper, J. (1997) Improved satellite techniques for monitoring coral reef bleaching. *Proceedings of the Eighth International Coral Reef Symposium* **2**, 1495–1498.

Warner, M. E., Fitt, W. K. and Schmidt, G. W. (1996) The effects of elevated temperature on the photosynthetic efficiency of zooxanthellae in hospite from four different species of reef coral: a novel approach. *Plant Cell and Environment* **19**, 291–299.

Webster, P. J., Moore, A. M., Loschnigg, J. P. and Leben, R. R. (1999) Coupled ocean-atmosphere dynamics in the Indian Ocean during 1997–98. *Nature* **401**, 356–360.

Wilkinson, C. (1998) The 1997–1998 mass bleaching event around the world. In *Status of Coral Reefs of the World: 1998*, ed. C. Wilkinson. Australian Institute of Marine Science, pp. 15–38.

Wilkinson, C., Lindén, O., Cesar, H., Hodgson, G., Rubens, J. and Strong, A. E. (1999) Ecological and socioeconomic impacts of 1998 coral mortality in the Indian Ocean: an ENSO impact and a warning of future change? *Ambio* **28**, 188–196.

Wood, E. (1987) Recent reef degradation (bleaching). In Engineering Geology Ltd and Tropical Coastal Management Consultants Ltd, *Geological, Geotechnical and Ecological Studies of Selected Atolls of the Republic of Maldives*. Report No. 426/FE/1187B. Department of Public Works and Labour, Maldives, pp. 35–44.

Zahir, H., Naeem, I., Rasheed, A. and Haleem, I. (1998) *Reef Check Maldives: Reef Check 1997 and 1998*. Marine Research Section, Ministry of Fisheries and Agriculture, Republic of Maldives, 30 pp.