Bleaching Damage and Recovery Potential of Maldivian Coral Reefs

T. R. McCLANAHAN*

Coral Reef Conservation Project, The Wildlife Conservation Society, P.O. Box 99470, Mombasa, Kenya

Same-site comparisons of Maldive–Chagos reefs in the 1990s with studies before 1980 have found large losses in coral cover that were probably associated with warm El Niño events. To determine the spatial extent of this damage and potential for recovery I surveyed benthic cover, hard coral communities, and coral recruitment in previously unsurveyed sites in three reef atolls of the central Maldives in 1999, one year after the warmest recorded El Niño event of 1997–1998. Coral cover was the lowest recorded for this region, at 8%, and evidence for the local extirpation of species was found. Most reefs are presently dominated by coralline and turf algae (68%) with erect fleshy algae and sponge being higher than previously reported on Maldivian reefs. Branching coral species appeared most affected and the dominant coral genera in 1998 were massive *Porites* and *Astreopora*, whereas the original community was dominated by *Acropora*. Coral recruits were sufficiently abundant, at 29 ind/m^2, to insure recovery of coral cover, but the most common recruits were in genera previously reported as subordinate genera, such as *Pavona* (11.7 ind/m^2) and *Coscinarea* (4.4 ind/m^2), whereas the previously dominant branching and encrusting species (*Acropora*, *Montipora* and *Pocillopora*) had recruit densities less than 0.65 ind/m^2. Unless there is significant compensation in growth and mortality there may be future changes in coral species composition and benthic cover of these reefs. © 2000 Elsevier Science Ltd. All rights reserved.

Keywords: atolls; bleaching; coral recruitment and mortality; disturbance; El Niño; Maldives.

Introduction

During the last two decades coral reefs have experienced an increase in the number of environmental disturbances associated with global-level changes in temperature and light (Glynn, 1991; Goreau and Hayes, 1994; Brown, 1997a,b; Goreau *et al.*, 2000). Many recent changes in reefs have been associated with localized phenomenon of nutrification (Tomascik and Sanders, 1987; LaPointe *et al.*, 1997; LaPointe 1997; Green *et al.*, 1997), diseases (Aronson and Precht, 1997), and heavy fishing (Hughes, 1994; McClanahan *et al.*, 1999), but investigators have also reported large ecological changes from remote areas or areas with low levels of human influence, such as remote islands and reef atolls (Glynn, 1994; Allison, 1996; McClanahan and Muthiga, 1998; Sheppard, 1999a,b, 2000a). Ecological changes in these remote areas are more likely to have a global rather than local cause, and are, therefore, instructive in distinguishing local from global factors that influence reef ecology. Coral reefs of the Maldive-Chagos ridge are one of the areas with the lowest human influences in the western Indian Ocean (McClanahan *et al.*, 2000) and, therefore, changes in these reefs are a likely indicator of global change.

One of the most recent global-level disturbances to coral reefs was the 1997–1998 El Niño event (Strong *et al.*, 1998; McPhaden, 1999; Wilkinson *et al.*, 1999; Goreau *et al.*, 2000). The Maldive–Chagos region is historically the warmest region of the Indian Ocean (Rosen, 1971), and satellite records also indicate that the warmest temperature anomalies in 1997–1998 were in this area of the north-western Indian Ocean, with temperatures exceeding 31°C, and anomalies of +1–3°C sustained over two years (Wilkinson *et al.*, 1999; Goreau *et al.*, 2000). This warm water was associated with widespread bleaching of scleractinian corals and mortality between May and September 1998 (Allison, W., Clarke, S., Sluka, R., pers. comm.). This large-scale warming probably represents one of the biggest large-scale disturbances to coral reefs in recent history (Strong *et al.*, 1998; Goreau *et al.*, 2000; ISRS Statement on Bleaching). The outcome of these temperature fluctuations is of concern to the future of coral reefs as they may be indicative of future climate patterns associated with global warming (Glynn, 1991, 1993; Brown and Ogden, 1993).

This study examines the status of Maldivian coral reefs by comparing their current state with earlier surveys of Maldivian reefs undertaken by Scheer (1971) in 1958, Davies *et al.* (1971), in 1964, and Allison (1995) in the early 1992. In 1992, Allison (1995) repeated surveys of some sites studied by Scheer (1971) and Davies *et al.*

*Tel.: + 254-11-486549.
  E-mail address: crcp@africaonline.co.ke (T.R. McClanahan).
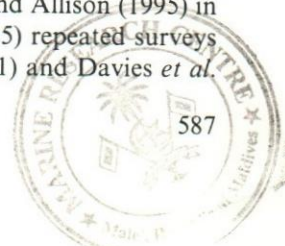
(1971), and found a large reduction in coral cover, particularly the branching species. Allison (1995) attributes these changes to coral bleaching associated with elevated temperature in the late 1980s and early 1990s. This study reports on the status of a larger and more dispersed sampling of sites, in the middle atolls of the Maldives, to determine the possible spatial extent of Allison's (1995) reported changes and to determine the status of these reefs after the 1997–1998 El Niño.

Methods

Study sites

The Maldives is a ~700 km long chain of 26 atolls, having ~1200 coral reef islands (only ~200 are inhabited). The islands have one of the lowest levels of human influence on coral reefs in the western Indian Ocean due to the oceanic location (having a total land area of only 186 km^2 of which 80% is <1 m above sea level) and the Maldivian cultural habits of eating pelagic tunas rather than reef fishes (Sheppard and Wells, 1988; McClanahan et al., 2000; Risk and Sluka, 2000). This unique environment has produced a highly successful beach and dive tourism industry over the past three decades that has largely reduced fishing as the main economic resource for these islands (Price and Firaq, 1996). The reefs are, therefore, relatively undisturbed by resource extraction and nutrification, with the exception of resort diver and snorkeler influences (Allison, 1996; Price and Firaq, 1996), coral mining (Brown and Dunne, 1988; Dawson-Sheppard, 1992; Clark and Edwards, 1995), shark fishing, money cowry, aquarium fish and sea cucumber collection (Adam et al., 1997), the live grouper trade (Sluka, 1998), and nutrification from the capital city, Malè (Risk et al., 1994). A survey of divers employed by resorts (Price and Firaq, 1996) suggested that reef condition was good, but decreases with the age of the tourist resort and increased with distance from the densely populated capital, Malè.

Maldivian reefs, along with the Chagos, are among the warmest and most species-rich reefs in the western Indian Ocean (Rosen, 1971; Sheppard, 2000b). Sheppard (2000b) lists 187 species among 57 genera of hard corals for the Maldives which is only second to neighboring Chagos. Nine hundred species of shallow-water fishes have been recorded (Randall and Anderson, 1993). Coral bleaching has been reported on these reefs during the late 1980s and early 1990s (Allison, 1995; Price and Firaq, 1996), with a large bleaching event in 1997–1998 (Allison, W., Clarke, S., Sluka, R., pers. comm.).

The most complete study of Maldivian corals was completed by Scheer (1971) in 1957–1958 who described corals in 5 m×5 m quadrats in 25 Maldivian sites, most of them on the southern most Addu atoll, but also on Ari and Fadiffolu Atolls (Fig. 1). He also recorded the number of genera found on these and Rasdu and Gaha Faro atolls. Davies et al. (1971) report some supplementary data collected in 1964 on coral cover and species distributions based on two transects off the island of Gan on Addu Atoll. Allison (1995) repeated some of the same study sites as Scheer (1971) and Davies et al. (1971) in 1992. This study adds additional study sites in the central Maldives to determine if the loss or low coral cover reported by Allison (1995) was widespread.

The CEDAM/WCS expedition study presented here reports on benthic cover and generic diversity from three atolls in the central Maldives. Felidu (also spelled Felidhoo), Mulaku and South Malè (Fig. 1). Studies were undertaken between 1 and 30 m depths on a variety of windward, leeward and lagoonal reef sites (Table 1; Fig. 1). Most sites were steeply sloping outer-edge carbonate atoll reefs dropping into waters in excess of 50 m, but a few inner-atoll farces and pinnacle sites were also studied (Table 1). Many sites were near channels or breaks in the reef leading from the outer-edge to the inner lagoon. We did our transects on the outer exposed edges of these channels and these channels are, therefore, comparable to outer reef sites. The condition of the substratum, scleractinian coral abundance, diversity of genera, and coral recruitment patterns were examined. Twenty six sites were visited, and benthic cover transects were completed on 19 sites and coral recruitment abundance on 11 reefs within the three coral reef atolls.

Field methods and analyses

Benthic cover, coral generic composition and coral recruitment were studied in April 1999, or approximately one-year after the reported bleaching. Benthic cover was determined by 131 10 in line transects laid parallel to the depth contour, but otherwise haphazardly placed between depths of one and 30 m in each of the 19 study sites. Between four and nine transects were completed per site. For each line, the point-intercept method was used with 30 randomly located points on each line. Points under the line were categorized into nine groups that included live hard coral, recently dead coral (a white skeleton with no live coral tissue on it), coralline and turf algae, sand, soft coral, sea squirts (ascidians of which virtually all were *Didemnun molle*), sponge, erect algae (i.e. *Turbinaria*, *Sargassum*, *Dictyota*, *Halimeda*), and an 'others group' for those observations not fitting the above categories. The percentage cover of each of the nine groups on each transect was calculated from the total of 30 points. Raw and transformed data (arcsin and log) were not normally distributed so nonparametric rank statistics (Kruskal–Wallis tests) were used for comparisons (Sall and Lehman, 1996). Cover data were pooled into 1 m depth categories and mean values were tested for relationships between average percent cover and water depth by either straight-line or quadratic equations (Sall and Lehman, 1996).

Analysis of generic community composition of corals involved a time-sampling procedure which records the first time genera (individual size >5 cm; Veron 1986; Sheppard and Sheppard, 1991) was observed during a
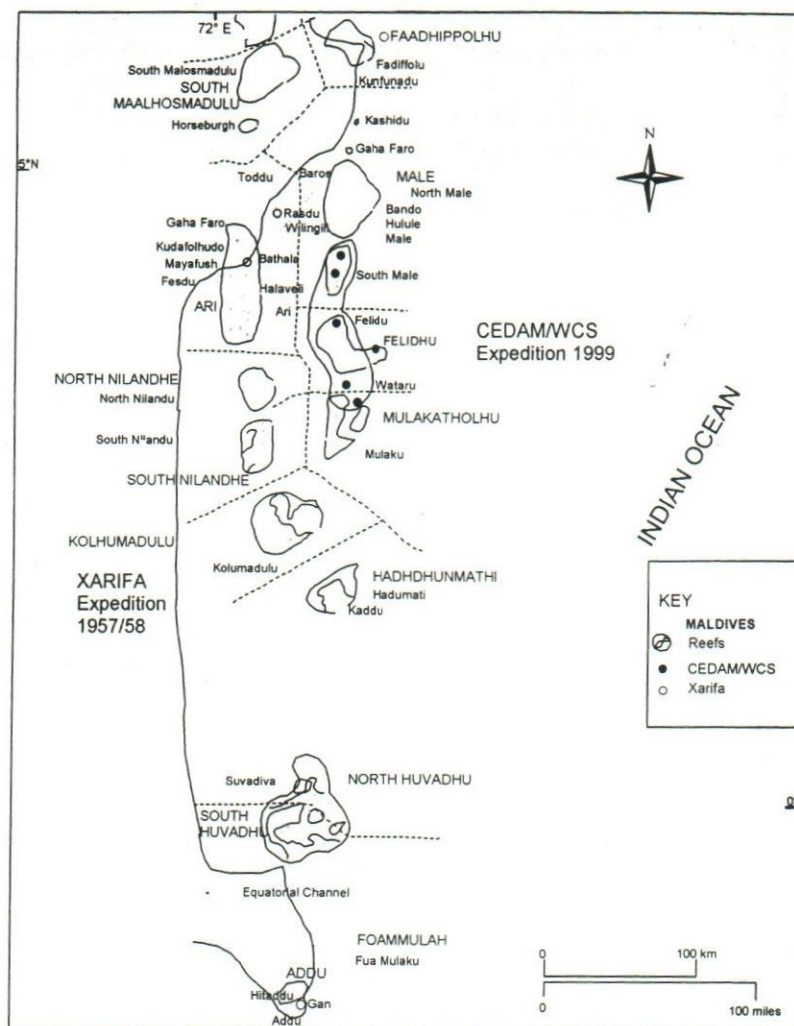
Fig. 1 Map of the central and southern Maldives showing the route and study sites of the Xarifa (Scheer, 1971) and this expedition.

30-min sampling interval. Coral relative abundance is calculated and assumed to be inversely related to the time taken to observe the first individual of this genus. This method was used because the low density of corals in this study made it difficult to describe the community or the number of genera at each site with either the point-intercept transects or the 5 m × 5 m quadrats used by Scheer (1971). The search method was also useful for comparing the number of genera per atoll presented by Scheer (1971). In the calculation of relative abundance, the search method underestimates dominance and, therefore, relative abundance measures are not directly comparable with quadrats or point or line-intercept methods. Ranks are comparable, however, so I relied on ranks and rank-order statistics for comparisons. Consequently, I compared coral communities in the study of Scheer (1971) using coral genera ranks for cluster analysis and for rank correlation statistics (Sall and Lehman, 1996). We tested for differences among atolls to determine the extent of spatial variability and to test the ability to objectively compare different atolls or study sites.

Hard coral recruits were sampled at 5 and 10 m depth intervals in 10–20 30 cm × 30 cm haphazardly tossed quadrats. Recruits were categorized as individual isolated corals less than 5 cm in diameter. Recruits lying within the quadrats were counted, identified to the genus (Veron, 1986; Sheppard and Sheppard, 1991), measured and placed into two size categories, 0.5–2 and 2–5 cm.

Results

Benthic cover in April–May 1999 was dominated by coralline and turf algae, being 68% of the total cover, followed by erect algae (9%), hard coral (8%), sand (7%), and other invertebrate groups being less than 3.5% of the cover (Table 1). The sea squirt, *Didemnum molle*, was around 3%, but reached nearly 12% of the benthic cover at one site, Dhon Faru. Erect algae was seldom above 15% of the cover, but two sites had cover in excess of 20%, and one visited but unsampled lagoonal pinnacle site had a cover of the erect algae *Padina* that exceeded 20%. Although live hard coral cover was

589

TABLE 1

Study sites, reef types, geographic location and percent benthic cover summary statistics (x ± sem) in the 19 study sites arranged by reef atoll.[a]

Atoll	Site name	Reef type	Geographic position	Transects n	Hard coral Mean	Sem	Recent dead Mean	Sem	Coralline/Turf Mean	Sem	Soft coral Mean	Sem	Sea squirts Mean	Sem	Sponge Mean	Sem	Erect algae Mean	Sem	Sand Mean	Sem	Other Mean	Sem
Felidu	Bomas Pass	Channel	E73°23' N3°41'	7	6.1	2.1	0.5	0.5	68.2	6.7	0.5	0.5	6.5	2.7	1.4	1.4	8.4	5.0	8.0	1.7	0.5	0.5
Felidu	Cherry Caves	Channel	E73°42' N3°29'	6	7.2	1.8	0.0	0.0	80.0	2.3	0.0	0.0	2.8	1.0	1.7	1.1	2.8	1.0	5.6	2.5	0.0	0.0
Felidu	Dhon Faru	Barrier reef slope	E73°33' N3°28'	6	4.4	1.6	0.0	0.0	70.6	7.5	1.1	0.7	11.7	4.8	1.7	1.1	5.0	2.1	5.0	3.2	0.6	0.6
Felidu	Ethere Faru	Barrier reef slope	E73°25' N3°29'	7	1.9	1.0	0.5	0.5	70.7	8.2	0.5	0.5	9.6	2.7	0.5	0.5	9.1	6.0	6.7	2.2	0.5	0.5
Felidu	Fehuri Haa	Channel	E73°30' N3°33'	6	6.7	1.2	1.7	1.7	84.4	5.1	1.1	1.1	0.6	0.6	0.0	0.0	3.9	3.3	1.7	0.7	0.0	0.0
Felidu	Felido Muli	Inner reef	E73°32' N3°32'	8	10.8	2.1	0.0	0.0	82.5	3.7	0.0	0.0	1.7	0.6	0.4	0.4	2.9	1.9	1.3	0.9	0.4	0.4
Felidu	Felido Wall	Channel	E73°24' N3°40'	9	5.2	1.6	0.4	0.4	47.8	5.6	0.0	0.0	1.1	0.6	4.4	1.2	32.2	4.6	8.1	3.2	0.0	0.5
Felidu	Kahumbu Tila	Channel	E73°27' N3°41'	7	8.1	1.8	0.0	0.0	75.2	3.0	1.9	1.0	2.4	1.0	1.9	1.0	7.1	3.2	3.3	1.5	0.0	0.0
Felidu	Mathi Kandu	Channel	E73°23' N3°40'	5	5.4	1.7	0.8	0.5	58.2	7.8	2.7	1.9	2.0	2.0	4.0	1.6	5.3	2.7	22.4	10.4	0.4	0.4
Felidu	Rakido Steps	Channel	E73°27' N3°18'	8	5.4	1.8	3.4	2.3	72.1	6.3	1.3	0.9	2.5	1.0	2.1	0.9	12.5	6.4	2.9	1.6	0.4	0.4
Felidu	Razak Giri	Pinnacle	E73°25' N3°34'	9	3.0	1.2	0.7	0.5	64.3	8.3	0.0	0.0	0.0	0.0	5.5	1.6	12.4	4.6	11.1	4.6	0.4	0.4
Mulaku	Digaru Outer	Barrier reef slope	E73°35' N3°6'	9	9.3	1.7	0.7	0.7	64.4	3.5	0.7	0.5	1.5	0.8	1.1	0.6	8.5	3.0	13.3	3.2	0.4	0.4
Mulaku	Digaru Kandu	Channel	E73°35' N3°6'	6	15.6	4.4	0.0	0.0	62.2	2.9	2.2	0.7	2.2	1.6	1.1	0.7	4.4	2.8	11.7	3.6	0.6	0.6
Mulaku	Vataru Wall	Channel	E73°26' N3°12'	5	14.5	5.0	0.0	0.0	55.7	6.4	0.0	0.0	3.3	2.1	0.7	0.7	20.1	5.5	5.2	1.7	0.6	0.6
South Malè	Biya giri	Pinnacle	E73°26' N3°51'	4	3.3	1.4	0.0	0.0	69.2	9.3	0.0	0.0	0.8	0.8	1.7	1.7	5.0	2.2	20.0	8.7	0.0	0.0
South Malè	Bodu Muli	Barrier reef slope	E73°30' N3°59'	8	9.5	2.0	0.0	0.0	69.2	5.6	1.6	0.9	1.7	0.9	3.3	1.2	7.7	3.3	5.0	1.4	2.0	1.0
South Malè	Cocoa Corner	Channel	E73°29' N3°59'	7	6.6	2.7	0.0	0.0	79.3	6.6	1.9	0.7	0.0	0.0	0.9	0.9	2.8	1.3	7.6	3.9	1.0	1.0
South Malè	Fushi Diga	Barrier reef slope	E73°32' N4°30'	6	19.6	6.0	0.6	0.6	71.8	6.6	0.6	0.6	2.3	1.1	2.3	2.3	1.7	0.8	0.0	0.0	1.1	0.7
South Malè	Guli channel	Channel	n.d.	7	18.1	2.0	0.0	0.0	52.0	8.0	6.3	2.0	7.2	2.0	1.9	1.3	9.2	3.8	5.3	3.0	0.0	0.0
Site summary				130	8.3	0.7	0.5	0.2	68.2	1.6	1.2	0.2	3.1	0.4	2.0	0.3	9.0	1.1	7.2	0.9	0.5	0.1
Atoll summary																						
Felidu				78	5.8	0.1	0.7	0.2	70.4	0.6	0.8	0.2	3.7	0.4	2.2	0.2	9.2	0.5	6.9	0.8	0.3	0.1
Mulaku				20	13.1	1.0	0.2	0.2	60.8	1.1	1.0	0.2	2.3	0.4	1.0	0.0	11.0	0.9	10.1	0.6	0.5	0.1
South Malè				32	11.4	0.8	0.1	0.1	68.3	0.6	2.1	0.3	2.4	0.3	2.0	0.2	5.3	0.6	7.6	1.5	0.8	0.2

Rank Statistics-Kruskal–Wallis test

Atoll variation

	Hard coral	Recent dead	Coralline/Turf	Soft coral	Sea squirts	Sponge	Erect algae	Sand	Other
chi-squared	15.6	1.5	6.7	8.5	0.9	1.7	1.2	7.0	2.0
p< (d.f.=2)	0.0004	NS	0.035	0.014	NS	NS	NS	0.03	NS

Site variation

	Hard coral	Recent dead	Coralline/Turf	Soft coral	Sea squirts	Sponge	Erect algae	Sand	Other
chi-squared	44.4	15.3	41.6	36.8	42.3	29.3	33.5	35.8	13.5
p< (d.f.=18)	0.0005	NS	0.0013	0.006	0.001	0.045	0.015	0.0074	NS

[a] Rank order statistics (Kruskal–Wallis test) for comparisons between sites and atolls are given.

low, recently dead coral was on average <1% and never exceeded 4% of the substratum. Comparisons between sites and atolls suggest statistically significant site differences for hard coral, coralline and turf algae, soft coral, sea squarts, sponge, erect algae and sand (Table 1). There was about an order of magnitude difference among sites in hard coral cover, ranging from around 2% to 20% at the study sites, but varied by only a factor of 2, from 6% to 13%, based on atolls. Comparisons between atolls suggest lower variation and few significant differences for these comparisons, but significant differences were found for hard coral, coralline and turf algae, soft coral and sand. Scheer's (1971) data from Addu, Ari and Fadiffolu atolls produced a coral cover ranging from 50% to 80% cover based on sites pooled into atolls.

Plots of benthic cover components as a function of water depth up to 30 m found that depth was a significant factor for all cover categories except recently dead coral which was uncommon (Fig. 2). Hard coral was lowest in the shallowest and deepest sites, but never exceeded 10% of the cover in intermediate depths. Turf and coralline algae were most abundant in shallow water, being 90% of the cover, but reduced to 60% at depths >20 m. Sand, soft corals, and sponges increased with depth, but were also patchily distributed. Sea squirts and erect algae were most abundant at intermediate depths of around 15 m.
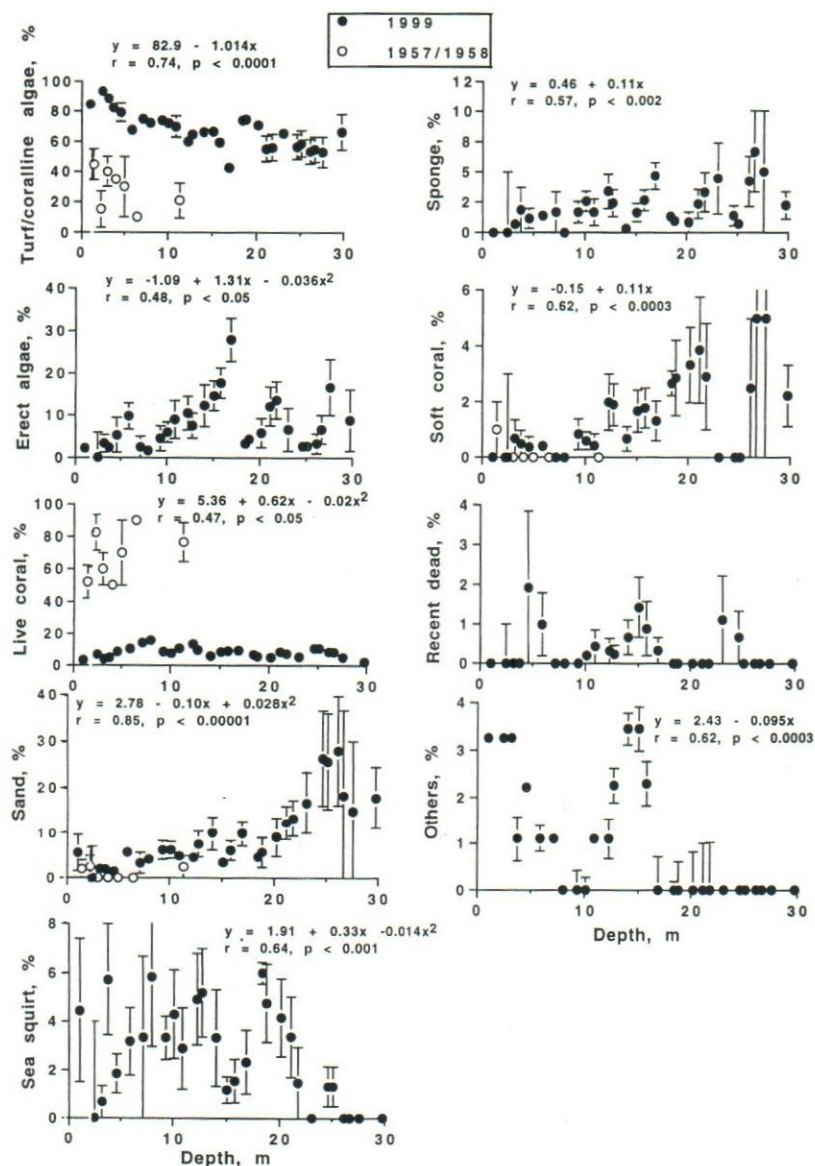

Fig. 2 Plots and regression analysis of the 1999 benthic cover category data with depth up to 30 m. Data pooled into 1 m intervals and means and sem are plotted. Open circles are data from Scheer (1971) collected in 1958 in Addu, Ari and Fadiffolu atolls, closed circles are the data from this study collected in April–May 1999 in Felidu, Mulaku and South Malè atolls.

Recruit densities at the 11 study sites had an average of 2.6 ± 0.3 recruits per quadrat which is equivalent to 29 ind/m^2 (Table 2). There were statistically significant differences in recruit densities between sites and atolls, but not with depth. Variation between sites ranged from 1 to 4.2 but atoll variation was only between 2 and 3.5 recruits per quadrat. The dominant subgenera of recruits were *Pavona*, *Coscinarea*, *Porites* and *Synarea* (Table 3). There was a moderate level of correlation (0.76) between the two size classes of coral recruits, and with large corals in 1999 (0.76 and 0.69), but a weak relationship (0.28) between 1958 adults in Scheer's (1971) study sites and the smallest recruits in the 1999 study sites (Table 4).

Comparison of the 1958, 1964, 1992 and 1999 Maldivian benthic cover surveys suggest that hard coral cover has decreased from ~60% to 8% of the substrate, with the change occurring after 1964 (Table 5). Earlier studies did not note, record or measure sea squirt, sponge or erect algae abundance. Comparisons of the number of genera found in the studied atolls suggest that there has been no overall change in the number of genera per atoll (*t*-test, NS), being around 33 genera, but some differences were observed in the recorded genera (Table 6). The total number of genera found in 1958 was 53 while 46 were found in 1998. Five genera recorded in 1998 were not recorded in 1958 and 12 genera recorded in 1958 were not recorded in 1998. Most missing genera in 1998 are not typically abundant species with the exception of *Stylophora* and *Seriatopora* in 1999 which were ranked eighth and thirteenth, respectively in Scheer's (1971) 1958 benthic cover studies (Table 3). Only two colonies of plating *Millepora* were seen in the 1999 survey whereas this genus was the fifth most common genera in 1958.

Comparing the coral community generic composition of Scheer's (1971) study with our study indicates significant differences between 1958 and 1999 studies (Tables 3 and 4; Fig. 3). A Kruskal–Wallis test comparison of genera composition for the four categories (1958, 1999 adults, 1999 2–5 cm, 1999 0.5–2 cm) produced a highly significant differences (Chi-squared = 16.7, $p < 0.0008$). In 1958 the reefs were largely dominated by *Acropora* but in 1999 *Porites* was the dominant genus (Table 3). *Astreopora* was the second most common genus in 1999 but was ranked last in 1958. Cluster analysis of the ranked coral genera suggest that sites override atolls in terms of coral rank associations and that the 1958 and 1999 relative coral generic compositions were entirely distinct (Fig. 3). There was also greater generic similarity among sites in the 1958 than in 1999 survey, largely attributable to greater dominance of *Acropora* in 1958.

Discussion

Studies of Maldivian coral reefs have been periodic and not always repeated in the same site. Consequently, determining the timing and spatial extent of disturbance is troubled by long periods between sampling and sampling different or few sites. Despite the individual problems of these studies, in composite and conjunction with similar studies, there are some suggestive patterns. Recent studies (Allison, 1995; Sheppard, 1999a,b) and this study suggest large and widespread changes in the benthic cover and coral generic composition of reefs on the Maldivian–Chagos ridge over the past 20 years with the greatest differences occurring between the late 1970s and the 1990s. Allison's (1995) study directly compared sites in terms of gross substrate categories and found a hard coral cover decrease from 60% to 28% between 1964 and 1992. A long-term and same-site study of Chagos also found a decrease in hard coral cover from 60% to 36%, associated with an increase in red algae,

TABLE 2

Population density ($x \pm$ sem per 0.09 m^2) of hard coral recruits (< 5 cm) in the 11 study sites and Kruskal–Wallis test comparisons between depths, sites and atolls.

Atoll	Site		Mean	Sem	N	Chi-squared	p
Felidu	Dhon Faru		2.7	0.5	20		
Felidu	Felido Muli		2.9	0.5	29		
Felidu	Felido Wall		4.2	0.6	25		
Felidu	Mathi Kandu		3.0	0.5	30		
Felidu	Rakido steps		1.1	0.2	40		
Felidu	Razak Giri		1.0	0.2	36		
Mulaku	Digaru Kandu		2.8	0.3	40		
Mulaku	Digaru Out Reef		2.1	0.3	40		
Mulaku	Vitaru Channel		1.7	0.2	40		
South Malè	Bodu Muli		3.4	0.5	29		
South Malè	Guli Channel		3.6	0.5	31		
Site summary			2.6	0.3	11	66.43	0.00001
Atoll summary	Felidu		2.1	0.1	209	14.33	0.0008
	Mulaku		2.5	0.3	91		
	South Malè		3.5	0.3	60		
Depth (m)		5	2.6	0.2	184	2.73	0.099
		10	2.2	0.2	176		

TABLE 3

Relative frequency of coral subgenera in Scheer's (1971) 1958 study of Addu, Ari and Fadiffolu atolls, this 1999 study for adults (>5 cm) and in the recruitment quadrats for the two size classes for Felidu, Mulaka and South Malè atolls.[a]

1958		1999		Recruits			
Genera	All corals	Genera	>5 cm	Genera	2–5 cm	Genera	0.5–2 cm
Acropora	67.92	Porites	4.76	Pavona	45.33	Pavona	40.58
Echinopora	11.24	Astreopora	4.46	Coscinarea	15.51	Coscinarea	17.51
Pocillopora	4.45	Pavona	4.44	Synarea	8.55	Porites	10.88
Porites	3.52	Favites	4.30	Porites	8.35	Synarea	8.22
Millepora	2.29	Fungia	4.22	Favia	3.38	Acropora	3.71
Pavona	1.51	Favia	4.13	Heliopora	1.99	Tubastrea	3.71
Goniastrea	1.36	Leptastrea	4.12	Cyphastrea	1.79	Favia	2.92
Stylophora	1.16	Coscinarea	4.01	Fungia	1.79	Fungia	2.12
Montipora	1.10	Symphyllia	3.84	Gardinoseris	1.59	Leptastrea	1.86
Platygyra	0.98	Montipora	3.56	Acropora	1.39	Montipora	1.86
Leptora	0.90	Goniastrea	3.54	Leptastea	1.39	Favites	1.59
Favia	0.61	Acropora	3.50	Montipora	1.39	Heliopora	1.59
Seriatopora	0.60	Galaxea	3.49	Podabacia	1.19	Galaxea	0.80
Fungia	0.58	Platygyra	3.36	Hydnophora	0.99	Goniastrea	0.53
Lobophyllia	0.38	Hydnophora	3.03	Astreopora	0.80	Montastrea	0.53
Favites	0.33	Pachyseris	2.96	Favites	0.80	Astreopora	0.27
Galaxea	0.24	Cyphastrea	2.93	Montastrea	0.60	Cyphastrea	0.27
Psammacora	0.18	Montastrea	2.80	Pocillopora	0.60	Echinopora	0.27
Heliopora	0.13	Tubastrea	2.59	Tubastrea	0.60	Merulina	0.27
Mycedium	0.11	Halomitra	2.31	Alveopora	0.40	Pocillopora	0.27
Echinophyllia	0.08	Pocillopora	2.19	Echinopora	0.40	Psammacora	0.27
Plerogyra	0.06	Podabacia	2.11	Goniopora	0.40		
Goniopora	0.05	Heliopora	1.99	Symphyllia	0.40		
Halomitra	0.05	Alveopora	1.91	Galaxea	0.20		
Oulnophyllia	0.03	Gardinoseris	1.90	Pachyseris	0.20		
Cyphastrea	0.03	Turbinaria	1.76				
Turbinaria	0.02	Goniopora	1.75				
Euphylia	0.02	Echinopora	1.70				
Merulina	0.02	Diploastrea	1.67				
Oxypora	0.02	Herpolitha	1.57				
Podabacia	0.01	Mycedium	1.52				
Symphyllia	0.01	Merulina	1.12				
Alveopora	0.01	Lobophyllia	1.07				
Astreopora	0.01	Acanthastrea	0.81				
		Plerogyra	0.61				
		Leptoria	0.51				
		Leptoseris	0.41				
		Psammacora	0.36				
		Diaseris	0.13				
		Millepora	0.13				
		Ctenactis	0.11				
		Physogyra	0.06				
		Caulastrea	0.02				

[a] Comparison of the ranks is possible, but not the actual abundance frequency due to different sampling methods used in 1958–1999.

TABLE 4

Spearman rank correlations for comparisons of the four coral communities, 1958 data from Scheer (1971) and juvenile and adult communities form this 1999 study.[a]

Community	1958 Adults	1999 Adults	1999 recruits	
			2–5 cm	0.5–2 cm
1958	1.00			
1999	NS	1.00		
1999 2–5 cm	NS	0.76	1.00	
1999 0.5–2 cm	0.28	0.69	0.76	1.00

[a] Spearman rho given if correlation was statistically significant.

soft corals and sponges between 1978 and 1996 (Sheppard, 1999a,b, 2000a). Some unpublished studies and observations in the mid 1990s indicate some recovery of corals in the mid 1990s (Allison, unpub. data), that was eliminated by the 1997–1998 El Niño warming. It therefore seems likely that the 1997–1998 El Niño was the most destructive bleaching event in this region as it reduced coral cover to the lowest levels recorded in the past 40 years (Sheppard, 1999b).

Many reefs in other regions reported losses of hard coral in the 1980s often associated with warm water or diseases (Glynn, 1984, 1991; Aronson and Precht, 1997; Shulman and Robertson, 1997; Doherty et al., 1997) but also nutrification (Green et al., 1997; LaPointe, 1997) and overfishing (Hughes, 1994; McClanahan and Muthiga, 1998) or a combination of these factors (Shulman and Robertson, 1997; LaPointe, 1999). Some reefs were colonized by erect algae (Hughes, 1994; Shulman and Robertson, 1997; McClanahan and

TABLE 5

Substrate cover from Maldivian studies undertaken in 1958 (Scheer 1971, $n = 25$ sites), 1964 (Davies *et al.*, 1971, $n = 2$ sites), 1992 (Allison 1995, $n = 2$ sites) and this study in 1999 ($n = 19$ sites).[a]

	1958		1964		1992			1999		Kruskal–Wallis	
	Mean	Sem	Mean	Sem	Mean	Sem		Mean	Sem	Chi-squared	p
Live coral	64.8	5.4	56.3	3.1	27.5	17.5	Live coral	8.3	0.7	58.1	< 0.00001
Rubble	32.1	5.4					Recently dead coral	0.5	0.2		
Sand	2.3	1.0					Turf/Coralline algae	68.2	1.6	32.0	< 0.00001
Soft coral	0.4	0.4					Sand	7.2	0.9	10.6	< 0.001
							Soft coral	1.2	0.2	4.7	< 0.03
							Sea squirts	3.1	0.4		
							Sponge	2.0	0.3		
							Erect algae	9.0	1.1		
							Other	0.5	0.1		

[a] Rank order comparison (Kruskal–Wallis test) of the 1958–1999 data also given.

TABLE 6

Comparison of (top) the number of genera per atoll found by Scheer (1971) in 1958 and this 1999 study, the total number of genera found, and (bottom) a comparison of the genera not found in each survey.[a]

1958		1999	
Atoll	Genera	Atoll	Genera
Ari	32	Felidu	37
Addu	42	Mulaku	32
Rasdu	39	South Malè	35
Gaha Faro	22		
Fadiffolu	26		
Average/atoll			
Mean	32.2		34.7
S.D.	8.4		2.5
			t-test, NS
Total genera	53		46

Genera not recorded			
1958	Species/genus	1999	Species/genus
Coscinarea	2	Balanophyllia	1
Ctenactis	1	Cynarina	1
Diaseris	1	Dendrophyllia	2
Gardinoseris	1	Euphyllia	1
Montastrea	2	Oxypora	1
		Pectinia	?
		Physophyllia	3
		Polyphyllia	2
		Sandalolitha	1
		Scolymia	2
		Seriatopora	2
		Stylophora	2

[a] Species per genus is the expected number of species per genus for the Maldives.

Muthiga, 1998), others by sea urchins (Eakin, 1996), or previously numerically subordinate coral species (Aronson and Precht, 1997). Maldivian reefs have very low abundance of sea urchins (McClanahan, pers. obs.), but probably experienced increases in sponges and erect algae (*Dictyota, Padina, Turbinaria, Sargassum*, an unidentified red algae) cover at intermediate to deep waters, similar to reports for Chagos reefs (Sheppard, 1999a,b, 2000a).

It is too early to determine if there will be a change in the dominant coral species on these reefs, but the recruitment study found that the dominant recruits in 1999 were different from the original coral community. *Pavona* was the dominant recruiting genus in 1999 but was ranked sixth in abundance in 1958 (Scheer, 1971). Aronson and Precht (1997) found that *Agaricia tenuifolia* replaced *Acropora cervicornis* in their Caribbean study sites during the 1980s. Interestingly, *Pavona* and *Agaricia* are sister genera in the Agaricidae family, *Pavona* being the dominant genera in the Indo-Pacific (Veron, 1986), so there is a possibility for a similar species replacement associated with similar environmental changes and, perhaps, family-specific (i.e. reproductive life histories, temperature tolerance, basal metabolism, zooxanthallae symbionts) species adaptations to these changes. *Pavona* may, however, be a species common to small size classes and, therefore, numerical density, but less dominant for cover (Sheppard, 1980), and the loss of overstory species, such as acroporids, has resulted in a relative increase in this species. It is not uncommon for coral recruits to differ from adult abundance and still be stable (Hughes *et al.*, 1999). Therefore, future studies will be needed to determine if species replacements in dominance are occurring on these reefs.

Changes in generic composition that I recorded may, however, not be stable, but rather a temporary response to warm-water disturbances, that have temporarily eliminated the most temperature-sensitive species. With time, existing differences may fade as the community approaches the typical dominance of *Acropora*, massive *Porites* (*P. lutea*) and other branching and encrusting species (*Pocillopora, Montipora, Millepora* and *Stylophora*). For example, it is clear that branching species were reduced most by recent environmental changes, similar to findings from other studies in the Indo-Pacific (Brown and Suharsono, 1990; Jokiel and Coles, 1990; Glynn, 1993; Hoegh-Guldberg and Salvat, 1995). A compilation of hard coral temperature tolerances (Sheppard *et al.*, 2000) suggests that branching *Acropora, Stylophora* and à branching *Porites* (*P. nodifera*) are the least tolerant of temperature changes among the studied genera and species. Morphology appears to be
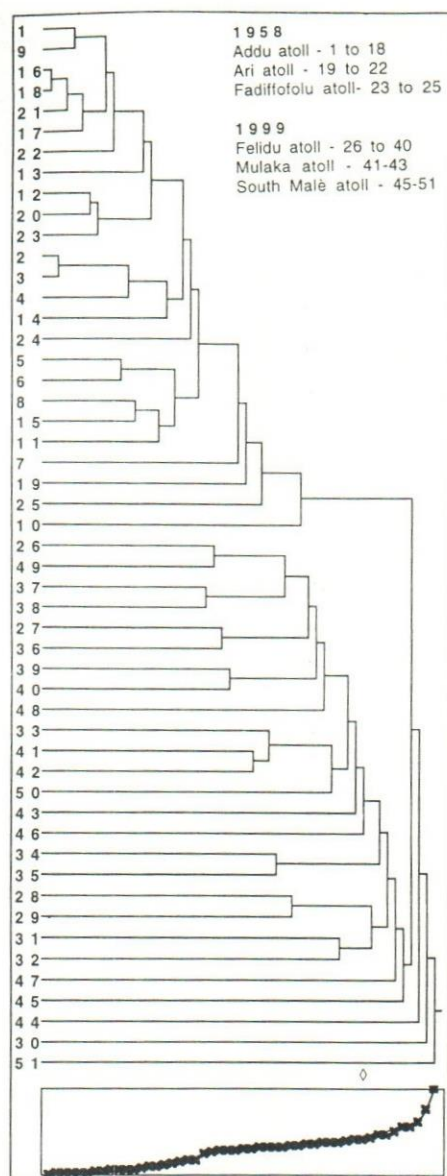
Fig. 3 Cluster analysis based on the ranked generic composition of the 25 sites in Scheer's (1971) 1958 study (sites 1–25 in Addu, Ari and Fadiffolu atolls) and this 1999 study (sites 26–51 in Felidu, Mulaku and South Malè). Clustering uses the Ward Method. Graph at the bottom indicates the percentage of variation contained for each cycle of clustering.

more important than taxonomic affiliation because the present dominants, *P. lutea* and *Astreopora myriophthalma,* are massive forms in the Poritidae and Acroporidae, respectively. Consequently, it may be that branching forms are most affected by temperature disturbances, but potentially have high colonization rates that could eventually compensate for the loss. The recruitment study, again, suggests some caution for this scenario because of the low abundance of recruits of the previously dominant species. For example, *Acropora, Montipora* and *Pocillopora* recruitment densities were, respectively at 0.65, 0.43 and 0.12 per m² considerably lower than 11.7 and 4.4 per m² for *Pavona* and *Coscinarea* recruits.

Species losses, at least on the time and spatial scale or our study, appeared evident. This was most evident for the four species in the genera *Stylophora* and *Seriatopora,* but also for some of the uncommon genera. *Stylophora* and *Seriatopora,* usually very common genera, were never seen in either the adult or recruit surveys. There were also probably more species losses in recorded genera with many species. For example, no species of branching *Porites* or *Millepora* were observed in the adult survey and were not distinguishable in the recruit survey. Consequently, *P. nodifera, P. compressa, M. tenera* and *M. intricata* are among those species likely to be locally extirpated. There were probably even more losses in speciose genera like *Acropora* and *Montipora* as my observations suggest only a few species in these genera were present in the 1999 survey. For example, the easily recognized *A. palifera* was not observed in the adult survey. Consequently, it is likely that many species were reduced to such low levels that they were not detectable by this search. Warm El Niño events in the eastern Pacific also reduced *Millepora* to such low levels that it is nearly locally extinct (Glynn and Weerdt, 1991; Glynn and Feingold, 1992).

The Maldives-Chagos ridge is one the warmest and most specious areas of the Indian Ocean (Rosen, 1971; Sheppard, 2000a). Despite a history of warm and stable water temperatures, the 1998 warm El Niño event caused considerable damage to coral abundance and species diversity. It may be that high diversity is associated with periodic disturbances (Connell, 1978), but by this hypothesis, it is unexpected for both coral cover and diversity to be high, or for species to be lost or reduced to such low levels by disturbance. It would seem more likely that warm conditions between 25°C and 29°C are good for coral growth (Buddemeier and Kinzie, 1976; Jokiel and Coles, 1977; Coles and Jokiel, 1978), survival and species richness (Rosen, 1971; Veron and Minchin, 1992), but that there are also species and environment- or region-specific thresholds somewhere above 30°C (Glynn and D'Croz, 1990; Brown *et al.,* 1996), and that above these temperatures many of the dominant species are lost. Regional patterns of water temperature suggest warming waters since measured more than 50 years ago (Parker *et al.,* 1995; Brown *et al.,* 1996; Charles *et al.,* 1997; Kuhnert *et al.,* 1999; Sheppard, 1999b; Cole *et al.,* 2000), as predicted by global-warming scenarios (Houghton *et al.,* 1990). Continued trends in water temperature are likely to increase the incidence of coral mortality (Hoegh-Guldberg, 1999) unless significant temperature adaptation occurs.

595

Adam, M. S., Anderson, R. C. and Shakeel, H. (1997) Commercial exploitation of reef resources: examples of sustainable and non-sustainable utilization from the Maldives. In *Proceedings of the Eighth International Coral Reef Symposium*, vol. 2, pp. 2015–2020.

Allison, W. R. (1995) Changes in the Maldivian reef system. *Coastal Management in Tropical Asia* 4, 6–8.

Allison, W. R. (1996) Snorkeler damage to reef corals in the Maldive Islands. *Coral Reefs* 15, 215–218.

Aronson, R. B. and Precht, W. F. (1997) Stasis, biological disturbance, and community structure of a Holocene coral reef. *Paleobiology* 23, 336–346.

Brown, B. E. (1997a) Disturbances to reefs in recent times. In *Life and Death of Coral Reefs*, ed. C. Birkelands, pp. 354–379. Chapman & Hall, New York.

Brown, B. E. (1997b) Coral bleaching, cuases and consequences. *Coral Reefs* 16, S129–S138.

Brown, B. E. and Dunne, R. (1988) The environmental impact of coral mining on coral reefs in the Maldives. *Environmental Conservation* 15, 159–166.

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.

Brown, B. E., Dunne, R. P. and Chansang, H. (1996) Coral bleaching relative to elevated seawater temperature in the Andaman Sea (Indian Ocean) over the last 50 years. *Coral Reefs* 15, 151, 152.

Brown, B. E. and Ogden, J. C. (1993) Coral bleaching. *Scientific American* 268, 64–70.

Buddemeier, R. W. and Kinzie, R. A. (1976) Coral growth. *Oceanography and Marine Biology Annual Review* 14, 183–225.

Charles, C. D., Hunter, D. E. and Fairbanks, R. D. (1997) Interaction between the ENSO and the Asian Monsoon in a coral record of tropical climate. *Science* 277, 925–928.

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.

Cole, J., Dunbar, R., McClanahan, T. and Muthiga, N. (2000) Tropical Pacific forcing of decadal variability in SST in the western Indian Ocean. *Science* 287, 617–619.

Coles, S. L. and Jokiel, P. L. (1978) Synergistic effects of temperature, salinity and light on the hermatypic coral *Montipora verrucosa*. *Marine Biology* 49, 187–195.

Connell, J. H. (1978) Diversity in tropical rain forests and coral reefs. *Science* 199, 1302–1310.

Davies, S. P., Stoddart, D. R. and Sigee, D. C. (1971) Reef forms of Addu Atoll, Maldive Islands. *Symposium of the Zoological Society of London* 28, 217–259.

Dawson-Sheppard, A. R. (1992) An analysis of fish community responses to coral mining in the Maldives. *Environmental Biology of Fishes* 33, 367–380.

Doherty, P. J., Meekan, M. G., Miller, I. R., Osborne, K. and Thompson, A. A. (1997) Catastrophic loss of coral cover from reefs in the southern Great Barrier Reef and the impact on fish recruitment. In *Proceedings of the Eighth International Coral Reef Symposium*, vol. 2, pp. 1005–1010.

Eakin, C. M. (1996) Where have all the carbonates gone? A model comparison of calcium carbonate budgets before and after the 1982–1983 El Niño at Uva Island in the eastern Pacific. *Coral Reef* 15, 109–119.

Glynn, P. W. (1984) Widespread coral mortality and the 1982/83 El Niño warming event. *Environmental Conservation* 11, 133–146.

Glynn, P. W. (1991) Coral reef bleaching in the 1980s and possible connections with global warming. *TREE* 6, 175–179.

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

Glynn, P. W. and D'Croz, L. (1990) Experimental evidence for high temperature stress as the cause of El Niño-coincident coral mortality. *Coral Reefs* 8, 181–191.

Glynn, P. W. and Feingold, J. S. (1992) Hydrocoral species not extinct. *Science* 257, 1845.

Glynn, P. W. and Weerdt, W. H. (1991) Elimination of two reef-building hydrocorals following the 1982–83 El Nino warming event. *Science* 253, 69–71.

Glynn, P. W. (1994) State of coral reefs in the Galapagos Island: Natural vs anthropogenic impacts. *Marine Pollution Bulletin* 29, 131–140.

Goreau, T. J. and Hayes, R. L. (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.

Green, A. L., Birkeland, C. E., Randall, R. H., Smith, B. D. and Wilkins, S. (1997) 78 years of coral reef degradation in Pago Pago Harbor, a quantitative record. In *Proceedings of the Eighth International Coral Reef Symposium*, vol. 2, pp. 1883–1888.

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

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

Houghton, J. T., Jenkins, G. J. and Ephraums, J. T. (1990) *Climate Change, The IPCC Scientific Assessment*. Cambridge University Press, Cambridge.

Hughes, T. P. (1994) Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* 265, 1547–1551.

Hughes, T. P., Baird, A. H., Dinsdale, E. A., Moltschaniwskyj, N. A., Pratchett, M. S., Tanner, E. and Willis, B. L. (1999) Patterns of recruitment and abundance of corals along the Great Barrier Reef. *Nature* 397, 59–63.

Jokiel, P. L. and Coles, S. L. (1977) Effects of temperature on the mortality and growth of Hawaiian reef corals. *Marine Biology* 43, 201–208.

Jokiel, P. L. and Coles, S. L. (1990) Response of Hawaiian and other Indo-Pacific Reef corals to elevated temperature. *Coral Reefs* 8, 155–162.

Kuhnert, H., Patzold, J., Hatcher, B., Wyrwoll, K.-H., Eisenhauer, A., Collins, L. B., Zhu, A. R. and Wefer, G. (1999) A 200-year coral stable oxygen isotope record from a high-latitude reef off Western Australia. *Coral Reefs* 18, 1–12.

Lapointe, B. E., Littler, M. M. and Littler, D. S. (1997) Macroalgal overgrowth of fringing coral reefs at discovery Bay, Jamaica, bottom-up versus top-down control. In *Proceedings of the Eighth International Coral Reef Symposium*, vol. 1, pp. 927–932.

Lapointe, B. E. (1997) Nutrient thresholds for bottom-up control of macroalgal blooms on corals reefs in Jamaica and Southeast Florida. *Limnology and Oceanography* 42, 1119–1131.

Lapointe, B. E. (1999) Simultaneous top-down and bottom-up forces control macroalgal blooms on coral reefs (Reply to the comment by Hughes et al.) *Limnology and Oceanography* 44, 1586–1592.

McClanahan, T. R. and Muthiga, N. A. (1998) An ecological shift in a remote coral atoll of Belize over 25 years. *Environmental Conservation* 25, 122–130.

McClanahan, T. R., Muthiga, N. A., Kamukuru, A. T., Machano, H. and Kiambo, R. (1999) The effects of marine parks and fishing on the coral reefs of northern Tanzania. *Biological Conservation* 89, 161–182.

McClanahan, T. R., Sheppard, C. R. C. and Obura, D. O. (2000) *Coral Reefs of the Indian Ocean, Their Ecology and Conservation*, p. 526. Oxford University Press, New York.

McPhaden, M. J. (1999) Genesis and evolution of the 1997–98 El Niño. *Science* 283, 950–954.

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

Price, A. R. G. and Firaq, I. (1996) The environmental status of reefs Maldivian resort islands, a preliminary assessment for tourism planning. *Aquatic Conservation Marine Freshwater Ecosystems* 6, 93–106.

Randall, J. E. and Anderson, R. C. (1993) Annotated checklist of the epipelagic and shore fishes of the Maldive islands. *Ichthyological Bulletin of the J.L.B. Smith Institute of Ichthyology* 59, 1–47.

Risk, M., Dunn, J. J., Allison, W. R. and Horrill, C. (1994) Reef monitoring in Maldives and Zanzibar, Low-tech and high-tech science. In *Proceedings of the Colloquium on Global Aspects of Coral Reefs*, pp. 66–72. Miami, Rosensteil School of Marine and Atmospheric Science.

Risk, M. J. and Sluka, B. (2000) The Maldives. In *Coral Reefs of the Indian Ocean, Their Ecology and Conservation*, eds. T. R. McClanahan, C. R. C. Shepard and D. O. Obura, pp. 325–351. Oxford University Press, New York.

Rosen, R. (1971) The distribution of reef coral genera in the Indian Ocean. *Symposium of the Zoological Society of London* 28, 263–299.

Sall, J. and Lehman, A. (1996) *JMP Start Statistics*. Duxbury Press, Belmont.

Scheer, G. (1971) Coral reefs and coral genera in the Red Sea and Indian Ocean. *Symposium of Zoological Society of London* **28**, 329–367.

Sheppard, C. R. C. (1980) Coral cover, zonation and diversity of reef slopes of Chagos Atolls, and population stuctures of the major species. *Marine Ecology and Progress Series* **2**, 193–205.

Sheppard, C. R. C. (1999a) Changes in corals over 18 years. In *The Chagos Archipelago*, eds. M. Seaward and C. R. C. Sheppard. Linnean Society of London, London.

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

Sheppard, C. R. C (2000a) The Chagos Archipelago. In *Coral Reefs of the Indian Ocean, Their Ecology and Conservation*, eds. T. R. McClanahan, C. R. C. Sheppard and D. O. Obura, pp. 445–470. Oxford University Press, New York.

Sheppard, C. R. C (2000b) Coral reefs of the western Indian Ocean: an overview. In *Coral Reefs of the Indian Ocean, Their Ecology and Conservation*, eds. T. R. McClanahan, C. R. C. Sheppard and D. O. Obura, pp. 3–38. Oxford University Press, New York.

Sheppard, C. and Wells, S. M. (1988) *Coral Reefs of the World*. Gland, Switzerland, UNEP/IUCN, pp. 389.

Sheppard, C. R. C. and Sheppard, A. L. S. (1991) *Corals and Coral Communities of Arabia*. Fauna of Saudi Arabia. 170 p.

Sheppard, C. R. C. Wilson, S. C., Salm, R. V. and Dixon, D. (2000) Reefs and coral communities of the Arabian Gulf and Arabian Seas. In *Coral Reefs of the Indian Ocean, Their Ecology and Conservation*, eds. T. R. McClanahan, C. R. C. Sheppard and D. O. Obura, pp. 257–294. Oxford University Press, New York.

Shulman, M. J. and Robertson, D. R. (1997) Changes in the coral reef of San Blas, Caribbean Panama, 1983–1990. *Coral Reefs* **15**, 231–236.

Sluka, R. D. (1998) The live fish food trade in the Maldives: a study of spawning aggregations and their role in the conservation of Napoleon wrasse (*Cheilinus undulatus*) and grouper (*Epinephelus* spp. and *Plectropomus* spp.) Report to The Wildlife Conservation Society, Bronx, New York.

Strong, A. E., Goreau, T. J. and Hayes, R. L. (1998) Ocean hotspots and coral reef bleaching, January–July 1998. *Reef Encounters* **24**, 20–22.

Tomascik, T. and Sanders, F. (1987) Effects of eutrophication on reef building corals II. Structure of scleractinian coral communities on fringing reefs, Barbados, West Indies. *Marine Biology* **94**, 63–75.

Veron, J. E. N. (1986) *Corals of Australia and the Indo-Pacific*. Angus and Robertson Publishers, London.

Veron, J. E. N. and Minchin, P. R. (1992) Correlations between sea surface temperature, circulation patterns and the distribution of hermatypic corals of Japan. *Continental Shelf Research* **12**, 835–857.

Wilkinson, C., Linden, O., Cesar, H., Hodgson, G. and Strong, A. E. (1999) Ecological and socioeconomic impacts of 1998 coral mortality in the Indian Ocean, An ENSO impact and warming of future changes. *Ambio* **28**, 188–196.