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Benthic recovery four years after an El Niño-induced coral mass mortality in the Lakshadweep atolls

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The reefs of the Lakshadweep suffered a mass mortality of coral in 1998, in the wake of an El Niño event of unprecedented severity. In 2002, we conducted a broad-scale benthic survey of six atolls in this group to check if there were geographic trends in recovery patterns across the archipelago. Four years after the mass mortality, live coral cover was relatively low on most atolls, and thin algal turfs dominated the benthos. Clear benthic differences were apparent between eastern and western aspects of reefs, pointing to the importance of local hydrodynamic conditions in determining recovery rates. Where recovery was the most apparent, it was dominated by fast-growing and bleaching-resistant coral genera. Despite the apparent lack of recovery at many sites, the reef system did not show signs of having suffered a 'phase shift' to a macroalgal state. High herbivorous fish abundance was likely responsible in controlling macrophyte levels, and may be crucial for further benthic recovery in these reefs.

Keywords: Benthic recovery, coral bleaching, El Niño, Lakshadweep, mass mortality.

THE El Niño event of 1997–98 raised sea surface temperatures (SSTs) significantly above seasonal averages, causing large-scale coral mortality in tropical reefs[1]. Under stress, the chemical pathways that sustain the symbiotic relationship between algal zooxanthellae and their coral hosts are seriously compromised, and corals expel zooxanthellae, turning pale and then bleaching white[2]. While bleaching may be a routine response to minor stresses, when unfavourable conditions are protracted, corals may bleach en masse, and eventually die[3]. The effect of the 1997–98 ENSO on reefs was unprecedented in intensity, duration and extent; anomalous temperatures rose to previously unrecorded levels, causing mass bleaching of coral in reefs across the tropics at scales never encountered before. Many reefs recovered relatively quickly from this disturbance, but at several locations, corals were not able to recover and sustained considerable reductions to their populations[1,4–7].

Forecasts of climate data suggest that the 1997–98 El Niño presages an environment where SST anomalies will increase in intensity and frequency, resulting in recurrent and widespread coral bleaching and mortality events, possibly every year[8,9]. It is unclear how long reefs will continue to be able to maintain ecological function under such sustained pressure. As the dominant structural element in reefs, the loss of coral could result in major changes in benthic topography and flow-on consequences for other species, including fish. Additionally, the loss of coral could benefit opportunistic species like fleshy macroalgae, which often rapidly overtake benthic substrate, radically altering functional states, and potentially precluding the re-establishment of corals in these areas[10–12]. Once precipitated, these changes in functional state, called phase shifts, can be remarkably difficult to reverse[13,14]. Human communities in the developing tropics depend heavily on reefs for food security as well as a range of other ecosystem services[15], and the reduced function of reefs could potentially have a large impact on these economies[16].

Many reefs in the Indian Ocean were severely affected by the anomalous SST event of 1997–98. Coral mass bleaching and mortality were reported in various locations, including the East African coast, the reefs of continental India, Sri Lanka, and from several oceanic islands[1,17–20]. Reefs in the northern Indian Ocean atoll chain were particularly badly affected: for instance, reefs in Chagos and Maldives experienced large-scale bleaching of coral, with as much as 90% post-bleaching mortality in many of them[21–23].

As part of a broader assessment of bleaching impacts on Indian coral reefs, the first author (R.A.) surveyed shallow-

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water sites in the Lakshadweep in mid-1998, at the peak of the SST anomaly[18]. Bleaching was widespread, and much coral had already succumbed to temperature-related mortality. By December of 1998, surveys of deeper reefs indicated extensive bleaching mortality, with live coral reduced to less than 5% of benthic cover at many sites[18] (Jason Rubens, pers. commun.).

The chain of archipelagos along the Lakshadweep–Chagos submarine ridge is relatively isolated from other major reef areas, and probably functions as a closed metapopulation with rare inputs from more distant reefs. Consequently, a short- to medium-term failure in coral recruitment may have resulted in a protracted period of benthic recovery in the aftermath of the 1998 coral bleaching event. Our initial surveys were restricted to a few accessible islands, and it was unclear if reefs in other atolls in the chain were similarly affected. Here, we present the results of an assessment of reefs in 2002, four years after the 1998 bleaching event. The purpose was to survey reefs in Lakshadweep, extensively rather than intensively. We assessed benthic substrate at reefs sites on six atolls across the chain to ascertain reef status at broad spatial scales. This formed part of an intensive study of temporal patterns in coral populations and other benthic elements after the 1998 mass bleaching[24].

The Lakshadweep group of islands, in the northern Indian Ocean, comprises 27 coral islands occupying a total land area of approximately 32 km^2, between 8–12°N, and 71–74°E (Figure 1). The region is strongly influenced by strong wave and current conditions during the southwest monsoonal system between mid-May and mid-September[25]. The atolls have a distinct windward (west) and a leeward (east) aspect in relation to the monsoon.

Few reliable *in situ* estimates of reef benthic communities existed for Lakshadweep reefs prior to 1998. Anecdotal accounts and the first author's casual observation confirm that scleractinian coral dominated the benthic substrate at most sites in the Lakshadweep, with estimates of 60–90% coral cover in reefs at a depth of 20 m. Benthic surveys in the Maldives and Chagos concur with these estimates, reflecting similar high coral cover communities across the region[21,23].

Six atolls were surveyed in the Amindivi and Laccadive group of islands between March and May 2002: Agatti, Bitra, Chetlat, Kadmat, Kavaratti and Kiltan (Figure 2). A brief profile of each atoll is provided in Table 1. All field data were collected by the first author. We sampled three randomly located sites on the east and west aspects of each atoll. At each sampling location, a tape measure was used to mark a 5×5 m quadrat area. Within the quadrat, visual cover estimates were made of benthic components, including live coral, dead standing coral, algal turf, coralline algae, fleshy macroalgae, calcareous algae, soft coral and other sessile organisms. A timed search was conducted to estimate the relative abundance of coral genera in each quadrat: all coral genera encountered in a 5 min survey were recorded, along with the minute interval in which they were first seen. This technique assumes that, on average, the most abundant genera are more easily visible and are therefore encountered before rarer genera in a timed search. A period of 5 min was determined to be adequate to sample an area of 5×5 m, as the number of new genera recorded after the third minute declined to less than one on average. After sampling for genera, a new sampling location was established by choosing a random direction and swimming along the depth contour for 50 m (measured with a tape measure). Six quadrats were sampled at each location at a depth range of 8 to 14 m, along the slope of the outer reef.

Average per cent cover estimates were compared among islands to determine trends in benthic substrate. Sites on the east and the west were compared for differences between aspects. Coral genera recorded in each quadrat were assigned abundance values based on the minute interval in which they were first sighted in the timed count. This resulted in a scale of relative abundance that ranged from 1 (genera recorded in the fifth minute: least abundant) to 5 (genera recorded in the first minute: most abundant). Relative abundance was averaged across all quadrats at sampled reefs on the east and west. We performed a hierarchical cluster analysis based on square-root transformed Bray–Curtis similarities of coral communities among sites, to compare patterns of composition across the Lakshadweep[26]. We used the software program PRIMER 5 for cluster analysis[27,28], and Microsoft Excel for Windows for all other analysis.

Live coral varied considerably in reefs across the Lakshadweep and there were few noticeable geographical trends in cover between atolls (Figure 3). While northern atolls such as Chetlat and Bitra had relatively high live coral cover, this trend was not consistent: the northern atolls of Kiltan and Kadmat had the lowest recorded cover of live coral. However, there was a distinct difference in live coral cover between aspects. Reefs on the east had considerably lower coral cover than western reefs at most atolls (Figure 4). The exceptions to this pattern were Kavaratti and Chetlat; there were little observable differences in cover between aspects. By contrast, the cover of dead standing coral was considerably higher on eastern reefs in 2002, except at Kavaratti, where there were no noticeable differences (Figure 5).

Algal turf was a dominant benthic component in most reefs in the Lakshadweep, occupying 19 to 30% of the substrate (Figure 6). There were considerable differences in the cover of turf algae among atolls, but it did not differ much between aspects for most reefs. Coralline algae were also abundant at most sites, but there were few clear trends among atolls or aspects (Figure 7). By comparison, fleshy algal cover was never dominant in outer reefs and generally occupied less than 3% of the substrate, except for the western reefs of Agatti, where fleshy macroalgae accounted for 8.1% of benthic cover (Figure 8).

A total of 41 genera were recorded in timed counts from the Lakshadweep. The most common genera across all sites

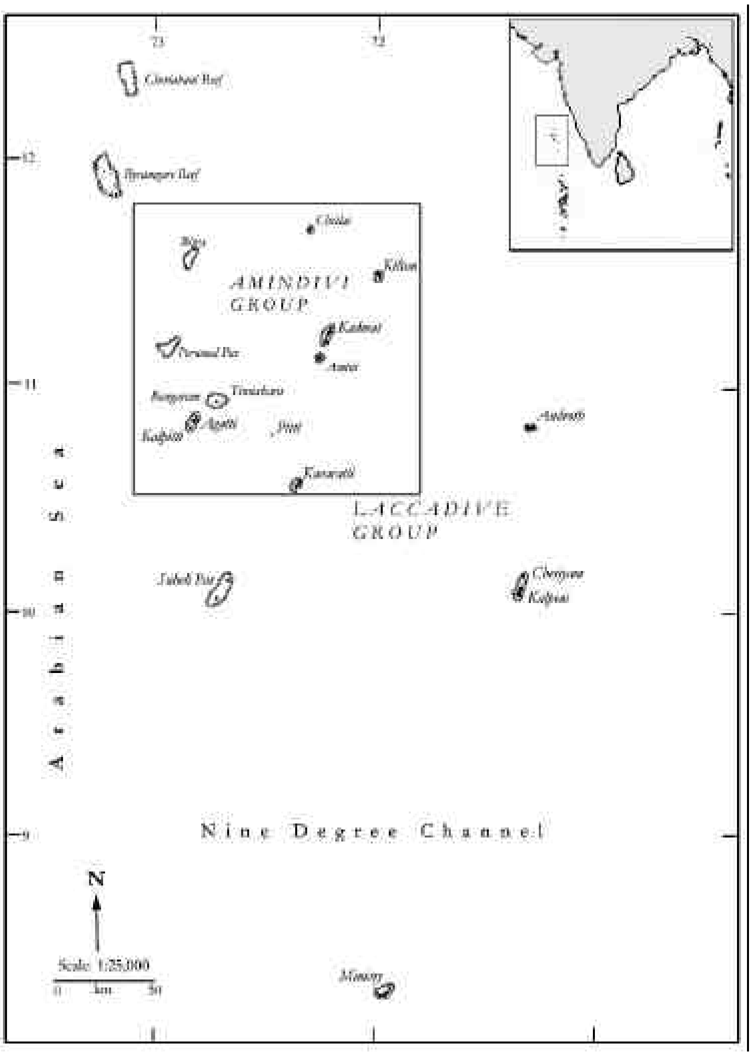

Figure 1. Atoll reefs of Lakshadweep Arcipelago in northern Indian Ocean. Boxed region shows area enlarged in Figure 2.

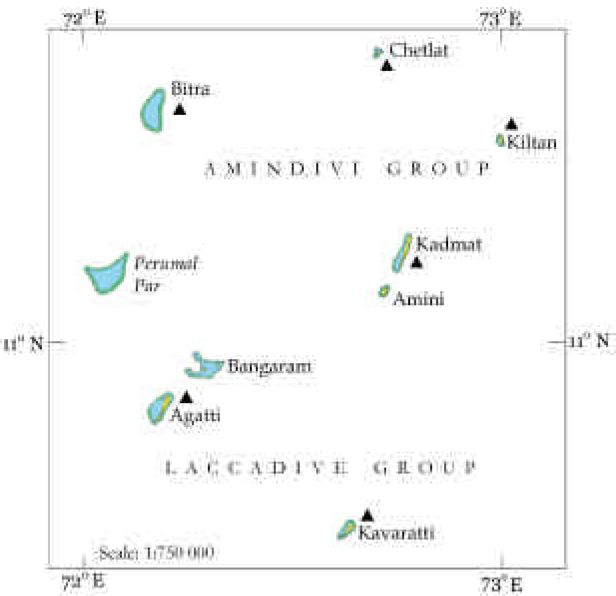

Figure 2. Map of Amindivi and Laccadive atolls. Triangles show atolls chosen for rapid assessment.

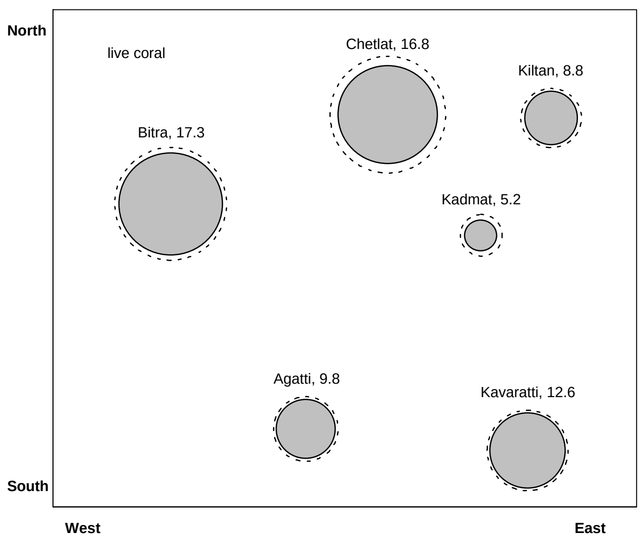

Figure 3. Live coral cover at Lakshadweep reefs in 2002. Bubble size represents relative per cent cover of coral at each location. Dotted lines are positive standard errors.

Table 1. Characteristics of atolls surveyed. Population figures are provisional data from the Directorate of Census Operations[39]

	Agatti	Bitra	Chetlat	Kadmat	Kavaratti	Kiltan
Latitude	10°51′N	11°36′N	11°41′N	11°13′N	10°33′N	11°29′N
Longitude	72°11′E	72°10′E	72°43′E	72°48′E	72°38′E	72°00′E
Total land area (km^2)	3.84	0.1	1.40	3.20	4.22	2.20
Population (2001 census)	7007	264	2289	5319	10113	3664
Population density (individuals/km^2)	1841	1430	2239	1705	2786	2248
Total lagoon area (km^2)	17.5	45.61	1.6	37.5	4.96	1.76
Reef circumference (km)	22.1	32.3	7.9	26.2	15.4	7.3

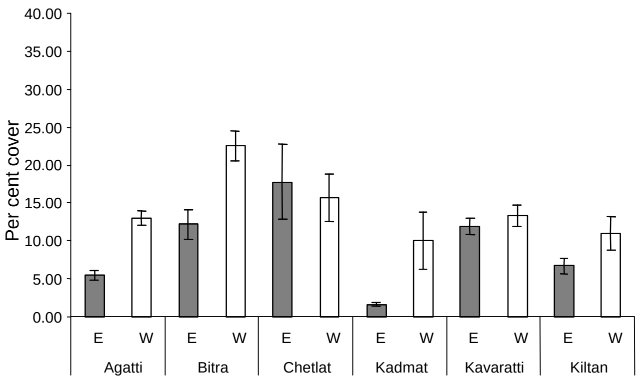

Figure 4. Per cent cover of live coral in Lakshadweep reefs in 2002. Bars represent average live coral cover on the east (E) and west (W) aspects of sampled atolls. Error bars are standard errors.

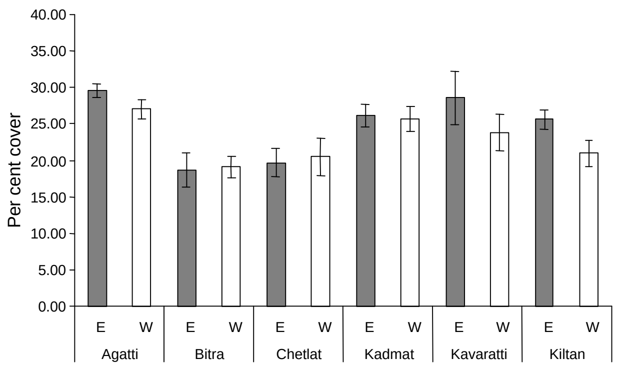

Figure 6. Per cent cover of algal turfs in Lakshadweep reefs in 2002. Bars represent average algal turf cover on the east (E) and west (W) aspects of sampled atolls. Error bars are standard errors.

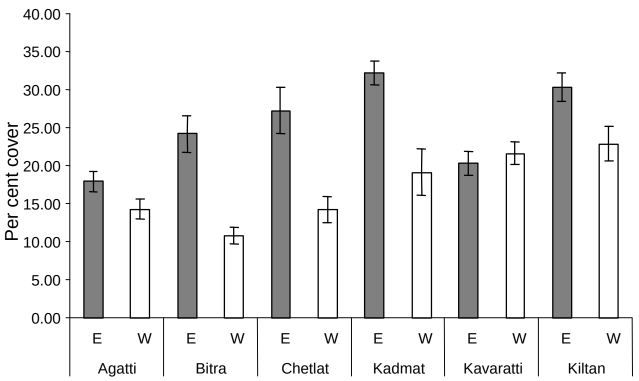

Figure 5. Per cent cover of dead standing coral in Lakshadweep reefs in 2002. Bars represent average dead standing cover on the east (E) and west (W) aspects of sampled atolls. Error bars are standard errors.

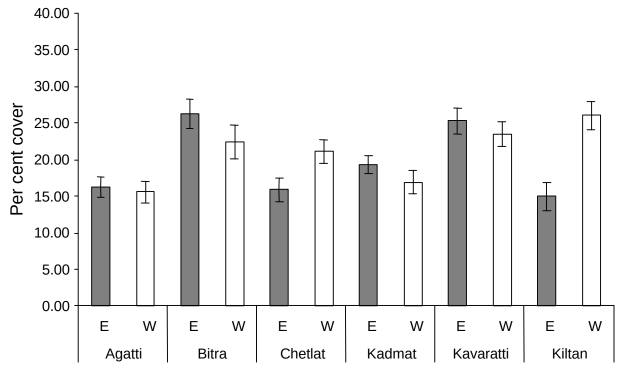

Figure 7. Per cent cover of coralline algae in Lakshadweep reefs in 2002. Bars represent average coralline algae cover on the east (E) and west (W) aspects of sampled atolls. Error bars are standard errors.

included *Porites*, *Favites*, *Acropora*, *Pavona* and *Galaxea*. There were weak geographical trends in the composition of coral across the archipelago. The atolls of the Amindivi group in the north (Bitra, Chetlat, Kiltan and Kadmat), were more similar in generic composition than the more southern atolls of the Laccadive group, Agatti and Kavaratti (Figure 9). The composition of reefs in Kadmat West was an exception to this trend, and was different from all other sites. Aspect appeared to play an important part in determining coral composition, particularly in the northern reefs, where there were closer affinities between aspects than between atolls. For instance, the western reefs of Chetlat, Bitra and Kiltan clustered together, while the eastern reefs formed two separate clusters (Kiltan and Chetlat, and Kadmat and Bitra). By contrast, at Kavaratti and Agatti, sites were more similar within atolls than between aspects (Figure 9).

It is often difficult to predict how reefs will respond to catastrophic disturbances such as coral mass bleaching events[29]. The recovery of corals in reefs after such incidents is likely dependent on the interaction of several factors, including the scale of disturbance, availability, settlement success and growth of coral recruits, mediation of competitive exclusion by other species, and the presence of anthropogenic stressors[30]. Due to the complexity of these interactions, recovery of reefs is highly variable. While in some instances, reefs may show few signs of recovery, and others take decades or more to begin returning to coral dominance, others may regain their full complement of coral cover in as little as five years[30–32]. In a long-term study of Heron Island reefs in the Great Barrier Reef, Connell *et al.*[33] found that recovery of coral species diversity and richness after catastrophic cyclones can vary from 3 to 25 years. This study was made at small spatial scales (1 m^2 quadrats), but variation in recovery after disturbance has been recorded at entire reef scales as well[34]. The current survey was designed to establish the broader geographical response of Lakshadweep reefs to the 1998 coral mortality. Temporal trends in benthic recovery in the Lakshadweep after the 1998 mass mortality are reported elsewhere[24].

Without a comparative baseline, this rapid survey can only provide a snapshot of reef condition four years after the 1998 anomalous SST event. However, there is a strong indication that coral mortality was high throughout the atoll chain. Much of the live coral cover recorded was evidently from new growth, particularly at many western sites, where relatively small-sized colonies (~ 10 to 50 cm maximum diameter) of fast-growing genera like *Acropora* were seen[24]. Despite this, coral cover was still less than 25% of the benthic cover at most reefs, and the substrate was conspicuously dominated by thin algal turfs that grew on the dead skeletons of coral. The fact that there were no discernable geographical trends in coral cover, points to the importance of local environmental conditions in determining the recovery of these reefs. Variability in the initial response of reefs to increased ocean temperatures may have resulted in patchy mortality across the archipelago. The subsequent regrowth of remnant populations and settlement success of post-1998 coral recruits could also vary considerably among atolls, creating a response mosaic, with some atolls like Bitra recovering well, while others like Kadmat and Kiltan considerably slower in their recovery. This geographical patchiness is probably characteristic of disturbances like bleaching, where the response of coral may be influenced by a complex interaction of large scale and local-scale processes[35,36].

Despite individual variation among atolls, differences in coral cover between aspects were striking: for most atolls, coral cover was considerably higher on western reefs in comparison with eastern reefs (Figure 4). By contrast, the cover of dead standing coral was almost always higher on eastern reefs (Figure 5). This reflects differences in hydrodynamic influences between aspects, particularly during the summer monsoon. Monsoon currents flow eastward across the Arabian Sea, bringing stormy conditions to the west-facing reefs of the Lakshadweep from May to September[37]. These summer storms potentially perform a vital role in removing dead unstable coral from the western reefs at a much faster rate than the eastern reefs. This could have differentially affected the long-term viability of settlement substrate on the east and west, and possibly drives the difference in live coral between aspects.

Differences in environmental conditions between aspects likely also influenced generic composition of coral on the east and the west. For most of the northern atolls, community composition was more similar between aspects than within atolls (Figure 9), suggesting that differences in conditions between aspects may favour particular groups of genera over others. Northern reefs may share better connectivity than reefs further south: coral communities here have a high similarity, and are clustered tightly together. In contrast, coral composition at Kavaratti and Agatti was distinct within atolls, suggesting that these more southern reefs may be isolated in comparison with other sampled reefs. It will require a detailed knowledge of local currents and patterns of recruitment before these trends can be fully understood.

Despite relatively low live coral cover at most reefs, fleshy macroalgae were not dominant at any of the sampled locations. This was encouraging for the future recovery

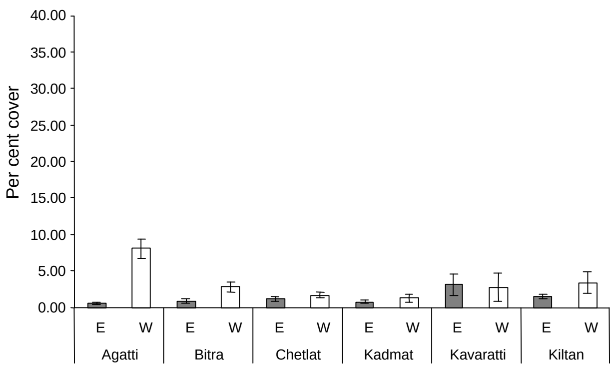

Figure 8. Per cent cover of fleshy macroalgae in Lakshadweep reefs in 2002. Bars represent average fleshy macroalgae cover on the east (E) and west (W) aspects of sampled atolls. Error bars are standard errors.

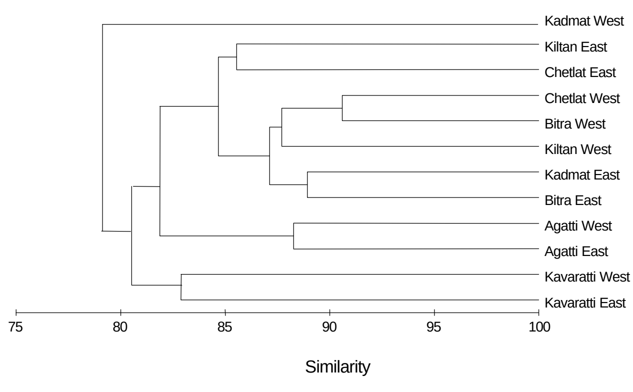

Figure 9. Similarity of coral composition in Lakshadweep islands. Dendrogram is a group means clustering of Bray–Curtis similarity between sampled sites.

of coral in these reefs, as it reduces the potential for competitive exclusion by fast-growing, opportunistic macrophytes. Several factors could have contributed to low levels of fleshy algae. Open ocean atolls are generally nutrient-poor, reducing the growth of algae in these well-flushed systems. Perhaps more important though is the influence of herbivorous surgeonfishes (Acanthuridae) and parrotfishes (Scaridae). They were present in large abundances at all reefs surveyed, and played an extremely important role in controlling algal biomass on Lakshadweep reefs[24].

Overall, although cover was relatively low at most surveyed atolls, coral was growing back well at many sites in the Lakshadweep. Genera that dominated the post-bleached reefs included a mix of hardy, bleaching-resistant taxa like *Porites* and *Favites*, and fast-growing taxa like *Acropora*, representing both remnant populations that survived bleaching as well as cohorts that were possibly recruited after 1998. The availability of new recruitment was important for this recovery to take place, and patchiness of the initial response may have been extremely important to supply recruits to areas with high mortality. The long-term resilience of the Lakshadweep system may be dependent on these refuge sites, and it may be vital to identify, monitor and protect them from other disturbances[36,38]. Global warming and its consequences are perhaps impossible to manage at a local scale, but pre-emptive management may help bolster the natural capacity of coral reef systems to absorb environmental changes and recover from such catastrophic events.

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