These observations are yet to be correlated with other geochemical data, but the study certainly indicates a relationship between nickel isotopic ratio, geological history and type of organic matter.

- Ellrich, J., Hirner, A. and Stark, H., Chem. Geol., 1985, 48, 313–323.
- Manning, L. K., Frost, C. D. and Branthaver, J. F., Chem. Geol., 1991, 91, 125–138.
- Alberdi, M. and Lafargue, E., Org. Geochem., 1993, 20, 425– 436.
- Lopez, L., Lo Monaco, S., Galarraga, F., Lira, A. and Cruz, C., Chem. Geol., 1995, 119, 255–262.
- 5. Yen, T. F., in *The Role of Trace Metals in Petroleum*, Ann Arbor Science Publishers Inc., Michigan, 1975, p. 221.
- 6. Saxby, J. D., Chem. Geol., 1976, 6, 173-184.
- Lewan, M. D. and Maynard, J. B., Geochem. Cosmochim Acta, 1982, 46, 2547–2560.

Received 14 August 2000; revised accepted 7 November 2000

Coral bleaching and mortality in three Indian reef regions during an El Niño southern oscillation event

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The 1997–1998 El Niño Southern Oscillation (ENSO) event, which elevated Sea Surface Temperatures (SSTs) of tropical oceans by more than 3°C, was one of the most extreme ENSO events in recent history. Such increases in SSTs above the seasonal average can trigger widespread bleaching in coral reefs. This study examined bleaching in three Indian coral reef regions in relation to SSTs using quantitative rapid assessment methods between April and July, 1998. The Gulf of Kutch reefs showed an average of 11% bleached coral with no apparent bleaching-related mortality. In contrast, bleached coral comprised 82% of the coral cover in lagoon reefs of Lakshadweep and 89% of the coral cover in the Gulf of Mannar reefs. Bleaching-related mortality was high -26% in Lakshadweep and 23% in Mannar. The coral mass mortality may have profound ecological and socio-economic implications and highlights the need for sustained monitoring for coral reef conservation in India.

ECOLOGISTS have long been concerned and fascinated with large-scale disturbances that affect coral reefs. Storms and unusually prolonged low tide events, crown-of-thorns starfish (*Acanthaster planci*) outbreaks, coral

disease epidemics, and elevated seawater temperatures often cause dramatic reductions in coral populations and have far-reaching consequences for their coral reef environments^{1,2}.

The El Niño Southern Oscillation (ENSO) warm water ocean current system of 1997–1998 created a nearly pan-tropical band of warm water and brought in its wake a spate of global climatic and ecological changes. The magnitude of the ENSO event, perhaps the most severe on record³, is implicated as the primary cause of mortality of coral in reef ecosystems across the world⁴.

Elevated Sea Surface Temperatures (SSTs) caused by ENSO are known to cause coral stress and mortality through a phenomenon known as bleaching^{1,5}. Bleaching is a rapid loss of pigmentation of coral, leading to a whitening of the colony. This is a generalized stress response of scleractinian coral, caused by the expulsion of photosynthetic symbiont zooxanthallae by the polyp, or by a severe reduction in the photosynthetic activity of resident zooxanthallae⁶. Bleaching is often a normal, non-lethal response to seasonal variation in water temperatures⁷, and coral regain photosynthetic algae when conditions improve. If bleaching is severe and prolonged, however, the coral may die, often due to secondary stresses⁸. While elevated SSTs have been implicated as the main agent of coral bleaching, increased irradiance, reduced salinity, bacterial infection, and decreased water temperatures have also been known to induce similar responses in coral^{5,9}.

Mass bleaching was first recorded on Pacific coral reefs in 1984 (ref. 10) and has since also been noticed in other tropical reefs. It appears to be well correlated with changes in SSTs and, in El Niño years, the frequency of bleaching events in coral reefs increases dramatically 11,12. The 1998 ENSO resulted in varying degrees of coral bleaching and mortality in reefs throughout the Indo-Pacific tropics and several programmes have been set up to monitor reef degradation and recovery processes.

Indian coral reefs have not received the same attention because of the lack of field research in coral reefs of the country. Major reef areas exist in India in the Gulf of Kutch, the Lakshadweep, Gulf of Mannar, and the Andaman and Nicobar islands 13,14. Ravindran and others¹⁵ surveyed some of these reef areas and report heavy bleaching of coral in the Andamans (in July 1998), but their surveys of Lakshadweep reefs (between April 1996 and February 1998), did not record high bleaching. This survey, conducted when abnormal sea surface temperatures had begun to affect Indian reef areas, was specifically geared towards rapidly assessing the impact of the 1998 El Niño event on the Gulf of Kutch, Lakshadweep, and Gulf of Mannar. I looked for differences in the effects of bleaching on various benthic components and different lifeforms of coral. In situ studies of coral communities are sorely lacking in Indian reefs and this study is an attempt to provide a minimum baseline from which further monitoring can be done.

Some 42 islands dot the southern lip of the Gulf of Kutch (Figure 1). The reefs that fringe these islands are atypical fringing reef formations, found primarily in the intertidal region of Kutch. Coral survives in shallow tidal pools within the vast intertidal flats that characterize this coastline. Coral cover and diversity is low and patchy¹⁶. Several of these reefs are recovering from large-scale coral mining practised in the past. This region forms part of the Gulf of Kutch Marine Park and Sanctuary, but the anthropogenic pressures on the islands continue to be high¹⁷. Several polluting industries fringe the coastline and development continues unabated, sometimes directly affecting reef areas, as in the case of oil refineries building their receiving pipelines through the reef. The survey was conducted in the reefs of Pirotan, Meetha Chusna, Ajad, and Betu, a submerged reef close to Ajad. The islands were sampled between 28 April 1998 and 9 May 1998.

In the Western Indian Ocean, the Lakshadweep archipelago of coral atolls (Figure 1) comprises about 27

islands, ten of which are inhabited. The total land area of these islands is 32 km^2 , with among the highest population densities in the country (1922 people/km²)¹⁸. The reefs enclose the islands in extensive lagoons and protect them from storm damage and other ravages of the sea. Coral diversity is high and the islands share much of their fauna with the reefs of the Maldives, with some faunal affinity to the reefs of mainland India¹⁹. The survey was conducted in the lagoons of Kavaratti and Kadmat during 9–19 June 1998. Due to the monsoon and inclement weather in the open sea, only lagoon reefs could be sampled.

The Gulf of Mannar and Palk Bay islands are a series of shallow fringing uninhabited islands (Figure 1). The reef fauna is closely allied to Sri Lankan coral reefs. The southeast coast of India is densely populated, and local communities depend heavily on marine resources. A high density of trawlers and boats ply these waters and the seas appear to have a high nutrient influx. Shells, algae, and sea cucumber are extensively collected from the reefs. Corals are also mined illegally from many areas, adding to the anthropogenic pressures 13,14. Bleaching surveys were conducted on the is-

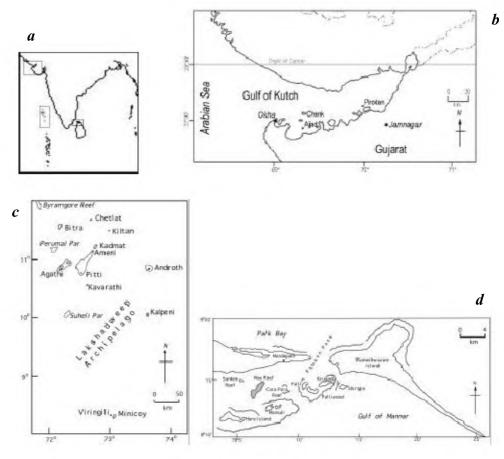


Figure 1. Maps of study areas. *a*, Indian subcontinental and surrounding waters, with study areas marked; *b*, Gulf of Kutch; *c*, Lakshadweep islands; *d*, Gulf of Mannar and Palk Bay.

lands of Manauli Putti, Shingle, and Pumarichan in the Gulf of Mannar during 7–11 July 1998.

The purpose of this study was to rapidly assess reef responses to seawater temperature elevation. It was important to gather information rapidly because determining causes of mortality becomes increasingly difficult with time.

The core of the sampling strategy was the Point Intercept Transect²⁰. A ten-metre line with 100 points spaced 10 cm apart was laid out along the substratum. I snorkelled directly over the line and counted the number of points intercepted by the following benthic components: (1) live coral, (2) turfed coral (dead coral rock covered with algal turf), (3) coralline and calcareous algae, (4) fleshy macroalgae, (5) other benthic invertebrates such as soft coral, (6) seagrass, (7) sand and (8) rubble, composed of broken and dead coral pieces. Each transect took between 10 to 15 minutes to complete. A total of 34 transects in Lakshadweep and 30 transects in Gulf of Mannar were sampled during the survey.

Data were collected on coral at the genus and lifeform level. For a detailed description of the lifeform classification method see English *et al.*²⁰. Coral affected by bleaching were classified in three ways:

Pale: The colony shows pale pigmentation. This is caused either by a partial loss of zooxanthallae or the lowering of photosynthetic content in available zooxanthallae. The snapshot nature of the sampling made it impossible to determine whether the coral was recovering from a more severe bleaching episode, or had just begun bleaching. In either case though, it is a sign of significant stress.

Bleached: Bleached coral are easy to distinguish in the field from dead coral. The colony shows a bright white appearance, though living polyps can still be clearly seen. The living polyps of bleached coral have severely reduced densities of zooxanthallae. If conditions remain stressful, these bleached coral often die.

Dead: Coral exposed to extensive bleaching eventually die because of bacterial infections and other stresses. Sediment rejection rates decrease, and an ac-

cumulation of sediment on corals prompts the growth of turf algae, forming a thin mat over the colony. Since this turf grows quickly, it is often difficult to separate old coral death from post-bleaching mortality. To be conservative, I classified coral in this category only if the layer of sediment and algae was visibly thin, and traces of the bleached coral could be seen beneath. If other organisms showed signs of bleaching stress, this was also recorded.

The waters of the intertidal reefs of the Gulf of Kutch were too turbid to sample with transect methods because the waters clouded up within a few minutes of sampling. In these reefs, I estimated benthic cover in 15 quadrats of 1 m² placed at every alternate metre along a 30 m line. The size and condition of each coral colony within the quadrat were estimated. Data were pooled for each 30 m line for analysis. A total of seven reefs were sampled with one transect (15 quadrats) per reef. This method is similar to methods I had used in 1995 while intensively sampling these reefs16 and can be used for temporal comparisons. Though the data are not strictly comparable with the Lakshadweep and Mannar data, I present the results together because it represents the field condition fairly accurately. Proportions (arcsine transformed) of different benthic components along the transect line were compared among reef areas using analysis of variance (ANOVA)²¹.

SSTs greater than 1°C above the seasonal average are sufficient to cause significant bleaching of most coral⁸. Using satellite data, it is possible to record changes in regional waters of 0.25°C and above²². I used twiceweekly SST maps of the Indian Ocean (accessed from the NOAA website http://www.noaa.gov) to determine anomalous temperatures in Indian reef waters. I considered anomalous temperatures of 1°C or higher to be potential conditions for bleaching to occur⁸, and calculated the approximate number of days the reefs in the region had been subjected to anomalous temperatures.

There were clear differences among the three reef regions in benthic components. Single factor ANOVA carried out on substrate cover show significant differ-

Table 1. Composition of reef benthic substrate in the Gulf of Kutch, Lakshadweep, and Gulf of Mannar. The Gulf of Kutch data were collected using multiple 1 m² quadrats. The Lakshadweep and Mannar data were collected along 10 m point intercept transects. F-values are for single-factor ANOVAs

	Gulf of Kutch $(n = 7)$		Lakshadweep $(n = 34)$		Gulf of Mannar $(n = 30)$		ANOVA	
	Mean	SE	Mean	SE	Mean	SE	\overline{F}	P
Coral cover	11.7	3.22	37.2	1.99	33.6	3.21	10.00	< 0.01
Turfed coral	41.4	4.55	21.4	2.16	32.0	2.73	5.81	< 0.01
Coralline & calcerous algae	5.1	1.76	14.9	1.02	10.3	1.02	2.43	0.09
Fleshy algae	15.5	3.31	0.0	0.00	5.7	1.91	11.94	< 0.01
Seagrass	0.0	0.01	0.2	0.21	0.0	0.00	2.25	0.11
Other invertebrates	7.6	3.07	0.4	0.15	0.5	0.19	4.11	0.02
Sand	18.8	2.97	18.9	2.55	11.0	2.89	1.43	0.25
Rubble	0.0	0.00	7.0	1.23	6.9	1.77	3.04	0.05

ences in the coral cover, turfed coral, coralline and filamentous algae, macroalgae, and sedentary invertebrates (Table 1). These differences are largely due to the substrate cover values encountered in the Gulf of Kutch. The Gulf of Kutch is characterized by sparse, patchy coral cover of around 11.7% and old dead coral covered with turf and mud dominate the substrate. Several species of macrolagae, including *Ulva*, *Sargassum*, *Caulerpa*, and *Padina*, are common in the Kutch reefs. The reefs of Lakshadweep and Mannar are more similar in their substrate composition, reflecting the basic structural differences between the reefs of the Kutch (shallow intertidal) and the reefs of Lakshadweep and Mannar (deeper lagoonal and fringing structures).

Coral genera are limited in the Kutch; this study recorded 11 genera of coral, restricted to massive and encrusting forms, dominated by *Favites*, *Porites*, and *Platygyra*. In contrast, the lagoon reefs of the Lakshadweep had a much higher coral cover and nearly 15% coralline algal cover. Eighteen genera of coral were recorded in Kavaratti and Kadmat lagoons, *Porites*, branching *Acropora*, and *Pavona* being the most abundant (Table 2). The shallow reefs of the Gulf of Mannar had 33.6% coral cover, and a large proportion of old dead and turfed coral (32%). *Montipora*, tabular *Acropora* and *Porites* were the most dominant of the 12 genera recorded in Mannar reefs.

Bleached coral were encountered in all reefs surveyed. The Lakshadweep and Mannar reefs were most severely affected by the bleaching; more than 80% of the coral cover in the Lakshadweep, and nearly 90% of the coral cover in the Gulf of Mannar showed signs of bleaching stress (Table 3). Between 30% and 40% of the coral cover in these reefs was severely bleached, and more than 20% dead in both reef areas because of bleaching-related stress. The reefs of the Gulf of Kutch in contrast, seemed to be less severely affected than the other reef areas. No obvious bleaching-related death was observed in the seven reefs surveyed, and only 1.92% of the coral was bleached severely.

The differences in bleaching correlate well with the number of SST anomaly days recorded on satellite imagery before the survey dates (Table 3). The Gulf of Kutch was sampled before abnormal mean SSTs were noticed in the gulf. In contrast, the reefs of Lakshadweep had already experienced at least 78 days of elevated temperatures before this sampling, and the Gulf of Mannar at least 99 days, temperatures rising to as much as 3°C above seasonal averages.

Coral lifeforms showed a differential response to coral bleaching in Lakshadweep and the Gulf of Mannar (Figure 2). While solitary Fungiids appeared indifferent to the rise in temperatures, tabular, branching, and massive corals were significantly affected by the bleaching in both reef areas. Encrusting coral show conflicting responses in both reef areas, being largely unaffected in

the Lakshadweep (71.1% healthy coral), but severely bleached in the Gulf of Mannar (6.5% healthy coral). Part of the reason for this difference is that the encrusting coral in the Gulf of Mannar was monogenerically *Montipora*, which appeared to be badly affected by the bleaching in both reef areas. In the Lakshadweep islands, several genera, dominated by *Pavona*, showed encrusting lifeforms and appeared largely unaffected by the anomalous temperatures.

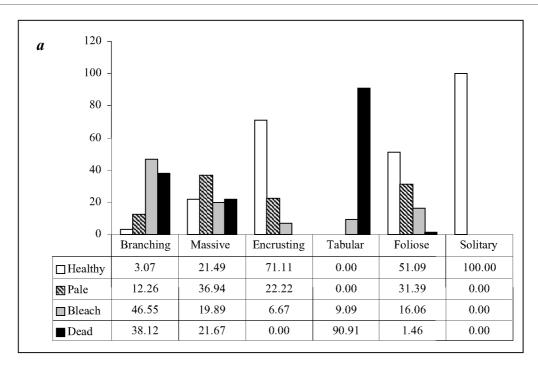
After two months of elevated SSTs, bleaching appeared to have resulted in large-scale mortality in the Lakshadweep and Mannar reefs. Viewed in isolation, this may be a misleading snapshot of reef health. What is apparent, however, is that at the time of the survey, large-scale coral stress and death was occurring, coincident with an anomalous rise in ocean temperatures.

Table 2. Cover of stressed and dead coral recorded in the reefs of Kutch, Lakshadweep, and Mannar. Only coral where the cause of death could unambiguously be assigned to bleaching were included in the Dead Coral category, so as not to overestimate the impact of the bleaching. The anomaly days represent the approximate number of days the studied reef had been exposed to SSTs of higher than 1°C, prior to the dates of sampling

	Anomaly days	Pale (%)	Bleached (%)	Dead (%)	Total affected
Kutch	0	8.81	1.92	0	10.73
Lakshadweep	78	26.0	30.09	25.71	81.80
Mannar	99	24.98	41.26	23.00	89.24

Table 3. Per cent composition of coral genera in the Lakshadweep,
Gulf of Mannar and Gulf of Kutch

Genus	Lakshadweep	Gulf of Mannar	Gulf of Kutch
Branching Acropora	12.41	6.82	
Tabular Acropora	0.90	22.02	_
Astreopora	1.15	_	1.77
Cyphastrea	2.71	0.31	2.04
Favia	_	5.03	4.74
Favites	1.45	0.91	24.59
Fungia	0.24	-	
Galaxea	0.46	_	_
Gardinerorseris	0.76	_	_
Goniastrea	0.41	0.42	
Goniopora	0.15	_	12.77
Hydnophora	_	0.84	1.23
Leptastrea	0.71	_	_
Millepora	1.48	_	_
Montipora	4.31	35.77	2.64
Mycedium	0.08	_	_
Pavona	10.94	_	_
Platygyra	0.46	_	18.03
Pocillopora	1.44	3.55	_
Porites	57.95	14.51	23.91
Stylophora	1.99	_	
Symphyllia	_	0.33	5.27
Turbinaria	=	9.47	3.02



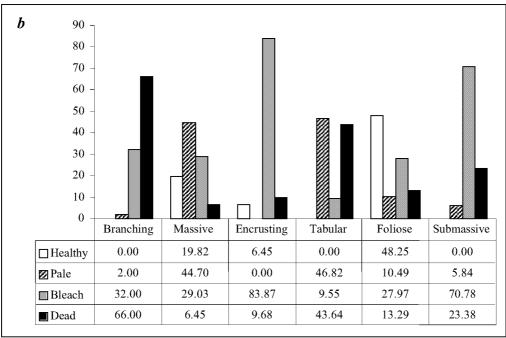


Figure 2. Coral lifeforms, showing differential stress responses to bleaching. a, Lakshadweep Islands; b, Gulf of Mannar.

Within three months of the anomaly, between 80 and 90% of the coral was bleached or dead in the Lakshadweep and Mannar. It is difficult to determine from a rapid study whether coral mortality was a direct result of bleaching or because of secondary stresses. Synergistically acting disturbances such as nutrient enrichment and sedimentation could likely account for the high coral mortality observed – heavy bleaching reducing the coral's ability to reject reef sediments and turfing algae^{1,8}. The southwest monsoon could also have played a

role in making waters more turbid, increasing suspended sediment levels in the water, and exposing the shallow reef areas to lowered salinity.

Levels of bleaching stress encountered correlate well with the number of days reefs were exposed to abnormal high temperatures. This perhaps explains why, while Ravindran and others¹⁵ found high levels of bleaching during their survey of the Andamans in July 1998, their survey of the Lakshadweep Islands earlier that year did not capture the intensive bleaching re-

corded in the course of this survey. Both the duration and the intensity of temperature change determine the severity of bleaching. Satellite imagery gives a reliable overview of temperature conditions over a large area of the ocean, and helps track temperature changes over time. Ground truthing has shown that satellites can record 0.25°C change in temperature, with a maximum error of 0.5°C (ref. 22). In the absence of continuous and reliable field data from Indian reefs, the NOAA/NESDIS images are still the most useful and accurate means of gaining a comprehensive picture of the El Niño anomaly in Indian seas.

It is important to note that abnormal temperatures continued to persist for at least four weeks after the survey dates. This survey, carried out while anomalous temperature conditions were still active, does not reflect the full extent of the damage caused by the bleaching event. Subsequent observations of Lakshadweep reefs, for instance, showed that coral mortality increased significantly after the survey (J. Rubens, pers. commun.). After the 1998 monsoon, I recorded live coral cover to be as low as 8% in Kavaratti and Kadmat, with some areas along the eastern front having less than 5% live coral cover (unpublished data).

The causal mechanisms of coral bleaching are not fully understood, nor conclusively proven¹. The evidence for seawater temperature rise being chiefly responsible for bleaching is largely circumstantial, and it is not possible to discount the influence of other stressing agents in Indian reefs. Both the Gulf of Mannar and Lakshadweep are exposed to nutrient inflows from the land, among a host of other anthropogenic disturbances 13,14. High levels of nutrients and bacterial infections have been implicated as causal agents in coral bleaching^{1,9}, and may facilitate the proliferation of fleshy algae and coral bioeroders^{23–26}. These being chronic stresses, they are not likely to cause sudden intense mass bleaching, as reported here. They are nevertheless important agents of coral stress, and may lower the disease-resistance of coral, exacerbating postbleaching mortality.

The Gulf of Kutch, in contrast with the other reef areas surveyed, did not seem to be as badly affected, with 10.7% of the coral showing signs of bleaching. Temperatures in the intertidal reefs of the Gulf of Kutch commonly reach 36°C and higher in reef areas during summer 16, and the bleaching observed could well be attributable to normal summer bleaching related to seasonal temperature rise. It is conceivable that coral species in these intertidal reefs are adapted to such seasonal temperature fluctuations 7. SST anomalies may not be as significant a disturbance because wide temperature variations are common at these latitudes 27. However, SST anomalies were not recorded in Kutch waters till after the present survey was conducted, and it is possible that the sampling picked up only the start of a more

extensive bleaching event in the Gulf of Kutch. A study conducted in 1995, estimating benthic cover in the Gulf of Kutch, reported between 1.2% and 1.4% bleached coral in the summer months before the monsoons 16. This suggests that bleaching levels reported in this survey are considerably higher than normal summer bleaching. Elevated temperatures, even below bleaching threshold may have significant impacts on coral health, retarding growth and reproduction 28. More detailed post-bleaching surveys of the Kutch reefs will be required to establish the significance of the ENSO on the Kutch reefs.

In the absence of sustained reef monitoring and a reliable baseline, it is difficult to predict how Indian reefs will respond to coral mass mortality. It is vital to understand the dynamics of reefs subjected to such large infrequent disturbances before any ameliorative conservation action can be taken. Although bleaching of this intensity is unprecedented, it is possible to outline likely paths of decline and recovery that reefs may take after such disturbances.

Bleached coral suffer from lowered growth rates and reproductive potential^{29,30} and individual colonies may take up to five months to recover³¹. The reef itself may take 5–10 years to recover^{2,5} and several species may go locally extinct in the process³². For instance, Brown and Suharsono⁵ demonstrate that the reef had recovered only 50% of its original composition five years after a major bleaching event.

More subtle community changes are also likely to occur in bleached reefs. Eakin²⁵ reports increases in urchin densities in mass-bleached reefs, leading to the potential of further coral death through spine abrasion and erosion. Fleshy algae, potential competitors of coral, also benefit by coral death, and, presumably by shading coral, can retard coral growth³³. The effects of bleaching on other reef organisms, such as fish have not been well studied. Species of fish and invertebrates dependent on coral for shelter, camouflage, and food will be the most badly affected, whereas herbivorous fish populations may increase after large-scale coral death³⁴. Omnivorous fish numbers have been known to rise opportunistically with coral bleaching, as previously cryptic invertebrates are exposed. Whether this translates into more permanent changes in reef communities has not yet been demonstrated. Lowered coral resistance could also increase coral bioeroder numbers, considered one of the primary factors controlling post-bleach recovery in coral³⁵. Increased bioerosion, along with lowered coral growth rates in post-disturbance reefs could result in lowered topographic complexity, a reduction of spatial niches and the consequent reduction in faunal diversity.

Mass bleaching may portend a global disaster for coral reefs, but it will most profoundly affect local people. Local communities depend on these reefs for their artisanal and bait fishery, and as a source of ornamental products and cheap construction material. Mass bleaching and its fallouts could affect reef-based cottage industries and fishery. Large-scale reef erosion could be disastrous for tiny atoll islands like the Lakshadweep, significantly changing beach dynamics, and leaving them unprotected from storms and cyclones. Tourism is also likely to suffer as aesthetic value of the reef declines and is replaced by remnant reefscapes of rubble.

This survey suffers naturally from the lack of a reliable baseline in time, with which to compare cover values for coral and other benthic components. It is imperative that a sustained monitoring of the reefs be initiated in the wake of this bleaching event to track changes in coral reef health. This is also important to monitor the effects of chronic stresses on reef community structure. Several easily applicable techniques for reef monitoring have been developed, which require moderate amounts of training²⁰. The Lakshadweep Island administration, for instance, has begun a programme of instituting posts of Honorary Environment Wardens, engaging local youth in environmental awareness programmes. Working in tandem with a local dive operation, some wardens are trained as SCUBA divers so that they can effectively participate in monitoring programmes. Initiatives like this that involve local communities and sustained monitoring are extremely promising, and could point to a new approach for marine conservation in India.

- 1. Glynn, P. W., Coral Reefs, 1993, 12, 1-17.
- Connell, J. H., Proceedings of the VIII International Coral Reef Symposium (eds Lessios, H. A. and Macintyre, I. G.), Smithsonian Tropical Research Institute, Balboa, Panama, 1997, pp. 9-22.
- 3. Hoegh-Guldberg, O., Mar. Freshwater Res., 1999, 50, 839–866.
- Wilkinson, C. R. and Buddemeier, R. W., Report of the UNEP-IOC-ASPEI-IUCN Global Task Team on Coral Reefs. IUCN, Gland, p. 124.
- 5. Brown, B. and Suharsono, E., Coral Reefs, 1990, 8, 163–170.
- 6. Kleppel, G. S., Dodge, R. E. and Reese, C. J., *Limnol. Oceaonogr.*, 1989, **34**, 1331–1335.
- 7. Gates, R. D., Coral Reefs, 1990, 8, 193-197.
- Brown, B., Proceedings of the VIII International Coral Reef Symposium (eds Lessios, H. A. and Macintyre, I. G.), Smithsonian Tropical Research Institute, Balboa, Panama, 1997, pp. 65-74.
- Kushmaro, A., Loyola, Y., Fine, M. and Rosenberg, E., *Nature*, 1996, 380, 396.
- 10. Glynn, P. W., Trends Ecol. Evol., 1991, 6, 175-179.
- 11. Glynn, P. W. and D'Croz, L., Coral Reefs, 1990, 12, 1-17.
- 12. Williams, E. J. J. and Bunkley Williams, L., *Atoll Res. Bull.*, 1990, 335, 1-72.
- Bakus, G. J. (ed.), Coral Reef Ecosystems, Oxford and IBH, New Delhi, 1994.
- Pillai, C. S. G., in Marine Biodiversity Conservation and Management (eds Menon, N. G. and Pillai, C. S. G.), CMFRI, Cochin, 1996, pp. 16-31.

- Ravindran, J., Raghukumar, C. and Raghukumar, S., Curr. Sci., 1999, 76, 233-237.
- Arthur, R., M Sc thesis, Wildlife Institute of India, Saurashtra University, Rajkot, 1995.
- 17. Patel, M. I., Proceedings of the Symposium on Endangered Marine Animals and Marine Parks, 1985, vol. 3, p. 41.
- Thangal, A. P. A. (ed.), Basic Statistics 1993–94: Union Territory of Lakshadweep, Department of Planning and Statistics, Kavaratti, 1994.
- 19. Sheppard, C. R. C., Atoll Res. Bull., 1987, 307, 1-32.
- English, S., Wilkinson, C. and Baker, V. (eds.), Survey Manual for Tropical Marine Resources, Australian Institute of Marine Science, Townsville, 1997, 2nd edn.
- 21. Sokal, R. R. and Rohlf, F. G., *Biometry*, W.H. Freeman, San Francisco, 1981, 2nd edn.
- 22. Gleeson, M. W. and Strong, A. E., Adv. Space Res., 1995, 16, 151-154.
- 23. Cuet, P., Naim, O., Faure, G. and Conan, J. Y., Proceedings of the VI International Coral Reef Symposium (eds Choat, J. H., Barnes, D., Borowitzka, M. A., Coll, J. C. and Davies, P. J.), ICRS, Townsville, 1988, vol. 2, pp. 207–212.
- 24. Hallock, P., Paleogeogr., Paleoclimatol., Paleoecol., 1988, 63, 275–291.
- 25. Eakin, C. M., Pac. Sci., 1992, 46, 377.
- Gabric, A. J. and Bell, P. R. F., Aust. J. Mar. Freshwater Res., 1993, 44, 261–283.
- Cook, C. B., Logan, A., Ward, J., Luckhurst, B. and Berg,
 C. J. J., Coral Reefs, 1990, 9, 45-49.
- 28. Jokiel, P. L. and Coles, S. L., *Coral Reefs*, 1990, **8**, 155–162.
- Goreau, T. J. and Macfarlane, A. H., Coral Reefs, 1990, 8, 211– 215.
- Szmant, A. M. and Gassman, N. J., Coral Reefs, 1990, 8, 217– 224
- 31. Bunkley Williams, L., Morelock, J. and Williams, E. J. J., Aquat. Anim. Health, 1991, 3, 242–247.
- 32. Glynn, P. W. and de Weerdt, W. H., Science, 1991, 253, 69-71.
- 33. Sheppard, C. R. C., in Proceedings of the VI International Coral Reef Symposium (eds Choat, J. H., Barnes, D., Borowitzka, M. A., Coll, J. C., Davies, P. J. and Flood, P.), ICRS, Townsville, 1988, vol. 3, pp. 297–302.
- Eakin, C. M., Smith, D. B., Glynn, P. W., D'Croz, L. and Gil, J.,
 22nd Annual Meeting Abstracts, Association of Marine Laboratories of the Caribbean.
- 35. Scott, P. J. B., Risk, M. J. and Carriquiry, J. D., in Proceedings of the VI international Coral Reef symposium (eds Choat, J. H., Barnes, D., Borowitzka, M. A., Coll, J. C., Davies, P. J. and Flood, P.), ICRS, Townsville, 1988, vol. 2, pp. 517–520.

ACKNOWLEDGEMENTS. The study, carried out under difficult conditions, would not have been possible without the help of several people. Invaluable assistance was provided by Dr S. Krishnan, N. Mhatre, K. Condillac, Oomer *bhai* (Kutch), Dr S. I. Koya, M. D. Madhusudan and the Environment Wardens of Kavaratti and Kadmat (Lakshadweep), and D. Mudappa, T. R. Shankar Raman, Dr M. K. Kumaraguru and his students (Mannar). I owe T. R. Shankar Raman an additional debt of gratitude for making the manuscript see the light of day. This survey was funded by the Wildlife Conservation Society, India Programme.

Received 11 May 2000; revised accepted 6 September 2000