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Corals and reefs of Cosmoledo and Aldabra atolls: Extent of damage, assemblage shifts and recovery following the severe mortality of 1998

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Abstract
An updated list of over 200 species of corals from Cosmoledo and Aldabra atolls is presented, which more than doubles previously known species diversity, and establishes these atolls as amongst the most species-rich in the Western Indian Ocean. However, partly this is an artefact of a new method of recording with digital cameras, described here, which greatly improves recording efficiency. This is the first underwater study of Cosmoledo, and the first for Aldabra outside the expedition reports cited. The survey extended to >30 m depth, and comes after the 1998 massive coral mortality. Coral cover was virtually eliminated at that time to about 8–10 m depth in Cosmoledo on seaward slopes, below which coral mortality was only about 50%. Mortality was selective regarding different species, genera and families. Cosmoledo's lagoon of >150 km^2 is shallower than the 'critical depth' of 8–10 m, resulting in an almost complete elimination of corals. To compare these atolls with other reefs in the region, critical depths are summarized for over 25 Indian Ocean locations. New coral recruits are abundant in the shallows of Cosmoledo and Aldabra 4 years later, though cover remains very low. Much bare rock remains (with turf algae) and some genera such as *Acropora*, previously apparently abundant, remain relatively very scarce. Apart from *Porites*, whose higher survival is now well documented, the best survivors from the 1998 mortality, and the most successful recruitment of new corals, are of faviids. Soft corals remain extremely scarce in all locations examined above the 'critical depth'. It is predicted that there may be a shift in the identity of the main species of corals in these atolls for many years.

Keywords: *Corals, atolls, Indian Ocean, diversity, warming*

Introduction

The Aldabra group of islands and atolls includes Cosmoledo, Assumption, Astove and Aldabra itself (Figure 1). Three of these are atolls with extremely shallow lagoons (<8 m depth), and steep seaward slopes; Assumption has no lagoon, being a single island with deep water all around. In November 2002, we visited Cosmoledo and, to a lesser extent Aldabra, along with 10 other scientists to examine terrestrial and marine conditions in support of future management and possible development. Cosmoledo and Aldabra are the two largest atolls of the group. This reports the condition, cover and identities of the coral
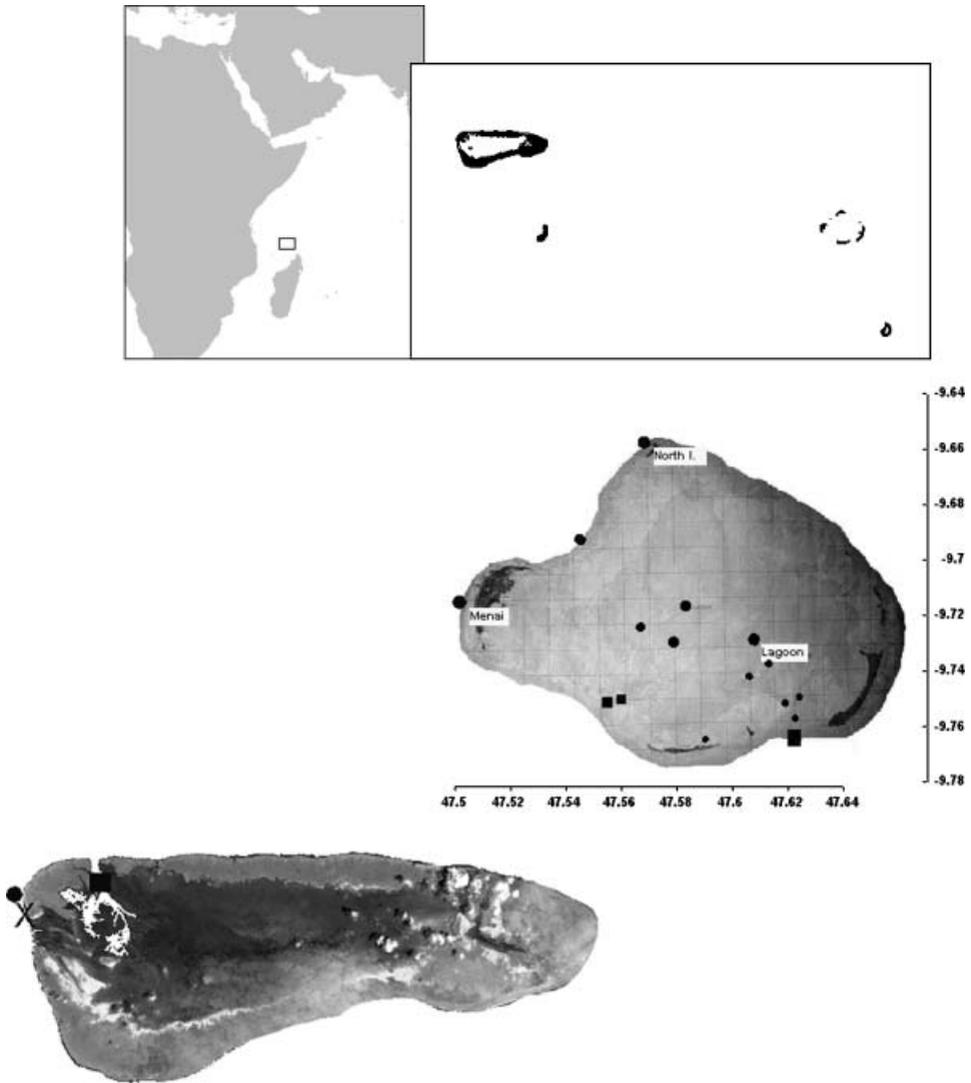
Figure 1. The Aldabra group of atolls, showing survey sites. Top left: location map, rectangle shows location of the four components of the Aldabra group; top right: World Vector Shoreline outline of the four groups; lower right: Cosmoledo Atoll (scanned image from map); lower left: Aldabra (from a Landsat MSS). On lower maps, dots indicate sample sites in lagoon and seaward sites, rectangles indicate sample sites in main channels. In Cosmoledo, lagoon sites are pooled. On seaward side of Cosmoledo, sites were West (Menai Island), North (North Island) and North-West (midway between the two). Seaward site in Aldabra was 300–500 m north of the field station (marked by ×). All sites in Cosmoledo lagoon had radii of at least 100 m, or, on seaward sites, along at least 200 m of reef between 0 and 30 m depth.

fauna of these two atolls, with special reference to coral recovery and new recruitment following the severe mortalities which affected these and most other western Indian Ocean reefs in 1998 (Sheppard 2001; Wilkinson 2000).

For Cosmoledo atoll, 140 km east of Aldabra, there are almost no records of corals or reports of the reef communities at all. What corals existed in shallow waters before the 1998

massive mortality cannot be known for certain, but inferences can be made from present condition and from the probable identity of the vast expanses of recently killed coral in the shallows. In deeper water (10–30 m) the position is clearer, as survival of corals at these depths was much better, though in both atolls, as discussed later, substantial components, such as the Acroporidae, are mostly missing throughout their depth range.

In Aldabra, the coral fauna was listed by Rosen (1971, 1979) who collated records from the Sladen expedition and from the 1960s, totalling about 90 species (possibly fewer given modern synonymies), focusing on the very shallow fauna. Otherwise corals, and especially their ecology, were never studied to the degree which might have been expected given that atoll's subsequent extensive terrestrial programmes following its World Heritage Site status, its attendant renown and good land-based research facilities. Below snorkelling depth, information is sparse. Barnes et al. (1970, 1971) determined that Aldabra's sheltered reefs grew better than exposed reefs, while from photo-transects Drew (1977) described a simple coral zonation in which branching and columnar forms dominated to 6 m depth, soft corals with faviids and massive corals from 6 to 14 m depth, followed by encrusting corals and gorgonids deeper to 42 m. Even with this paucity of ecological information, Rosen (1971) was able to use coral records from Aldabra with other sites to produce his influential account of Indian Ocean coral biogeography, highlighting regional patterns of coral occurrences. Then, despite the above-mentioned facilities and opportunities, little was done for the next quarter of a century. This has turned out to have been unfortunate given the massive mortality which affected most areas of the Indian Ocean in the 1990s, especially 1998. After the latter event, expeditions which used scuba diving for more substantive observations indicated that coral cover previously probably had exceeded 50%, but was now massively reduced in shallow water and possibly halved in deeper water (Teleki et al. 2000; Stobart et al. 2002). An unpublished report recorded 57 species of corals in Aldabra (Stobart et al. 2001).

The present study of November 2002 examined ecological aspects of reefs of Cosmoledo and Aldabra, the relation of present reef condition to climate change and fish community structure, as well as aspects of atoll management (Linden et al., in preparation; Obura et al., in preparation). The present paper details the present condition of corals of these two atolls. We note which species are abundant today in the form of new recruits, and which species can be regarded as having been good 'survivors' of the 1998 mortality. The issue of survivorship is recognized as being increasingly important. While substantial evidence of mass mortality exists for many parts of the western Indian Ocean region (Linden and Sporong 1999; Souter et al. 2000; Wilkinson 2000), evidence is also emerging of a change in the type of coral assemblages that now occupy Indian Ocean reefs which were heavily affected, due both to differential susceptibility by corals to the temperature rise which caused the mortality (Obura 2001), and to their different recruitment rates, which do not necessarily correlate well with abundance of surviving adults (Sheppard and Loughland 2002). This differential survival may be locally significant to any future recovery, and appears to be changing the nature of the coral assemblage in affected regions.

An additional important point addressed here is the depth to which mass coral mortality extended in these atolls. In many parts of this ocean, severe mortality affected reefs to a fairly specific depth, beneath which coral survival was commonly much greater, the transition usually occurring across a fairly sharp depth boundary (McClanahan 2000; Spencer et al. 2000; Wilkinson 2000; Sheppard et al. 2002). This 'critical depth' varies between reefs or regions, and may depend on the position of a local thermocline during the warm period. However, this critical depth does not apply equally to all coral families. Most

species in families such as Acroporidae and Fungiidae were very severely affected, indeed virtually eliminated, at all depths accessible to scuba survey. A second group may be distinguished, notably the Faviidae, which remain sparse above the critical depth, and which have a high diversity below it, but only with low or moderate cover because they exist today mainly as many small, young colonies (Sheppard et al. 2002). For some families, notably the Poritidae and some Mussidae, survival of adults below the critical depth was appreciable, where their large surviving colonies provide conspicuous cover today.

The present much extended list of coral fauna places these atolls together as perhaps the most species-diverse of the Indian Ocean. The relationship, if any, of a species count with abundance, cover or ecological condition is discussed later. An important consideration is the method used in this work (next section) which clearly is substantially more efficient than has been available to date. For this reason, comparisons across the Indian Ocean generally should be cautious until similar methods are deployed in other regions.

Methods

In Cosmoledo, several lagoon sites and the two major lagoon passes, both of which lie on the southern side, were examined, along with several seaward sites on the west, north-west and north (Figure 1). In Aldabra, one site on the west and the lagoon pass were examined. No eastern-facing seaward sites were visited due to weather conditions.

Species recording was mainly done with scuba and underwater digital cameras during 30 hours (Cosmoledo) and 6 hours (Aldabra) underwater. Over 2500 high resolution images (approximately 2000×1500 pixels each, medium compression jpeg size approximately 0.5–1 Mb each) were taken to 30 m depth, from which nearly 1000 were retained after discarding duplicate or inadequate images. A CD-rom of images is available on request to the first author. Identification was done *in situ* for several additional common and easily identified species but, for the most part, identification was by later use of photographs in conjunction with Veron (2000), Wallace (1999) and other more modest sources (e.g. Sheppard and Sheppard 1991). Initially, photography was undertaken in straight lines, photographing all species passed over. However, the scarcity of corals in shallow water and rapid duplication of common ones led us then to simply search for all colonies which possibly differed from those already captured. This was conditioned partly by the fact (see Results) that there was only between 0 and 5% coral cover down to about 8 m depth, slightly greater coral cover between 8 and 15 m and a greater but still clearly reduced coral cover deeper than 15 m. A 'running tally' from images downloaded to computer each day allowed us increasingly to focus on genera which were not yet well recorded, and thus avoid much duplication.

The limiting factor of 'underwater time' in searching was substantially overcome by this method, though identification to species from all the images then required several more weeks. Photographs of almost all species are available from the authors. Veron (e.g. 2000) has emphatically and correctly pointed out that traditional use of skeletons alone in taxonomy of corals, as was used for over a century, is not satisfactory and has led to many problems, and probably the same can be said of the use of photographs on their own, without collected and cleaned specimens. Collection of specimens was not possible or permitted in this study. Both authors, however, have fairly extensive collections of both photographs and cleaned specimens from many parts of the western and central Indian Ocean, including mainland coasts and atolls, such that, based on this past dual collection of photographs and matched specimens, we believe that we have achieved reliability in the

present study. A conservative approach was taken in this paper of omitting or noting species where there is uncertainty.

For many coral species, probably *all* observed specimens were photographed. This illustrates the extreme rarity of many at the present time, at least of colonies sufficiently large to be recognised following recruitment after 1998. Conversely, some formerly abundant species such as *Acropora palifera* are recovering in the shallows, and of these only a small selection was photographed. Other than in the case of the latter species, and one or two others which were common in the lagoon, most *Acropora* colonies seen on seaward slopes were photographed. For most faviids, and *Porites*, selectivity was used after the first few dives. For most other families (except some Pocilloporidae which were fairly common) there was a mixture of rare and relatively common species, and again, selectivity was progressively used in photographing them.

Results

The Appendix lists all the corals found, followed by a summary of the totals. A total of about 201 species indicates a high diversity in western Indian Ocean terms, about 177 for Cosmoledo and 118 for Aldabra, which reflects the much shorter time spent in the latter. Equally significant might be those species which were apparently missing but which might have been expected to have been seen, even abundantly, according to distribution maps in Veron (2000). Assumption was visited very briefly during departure (by snorkel only), when remarkably, 10 more species were observed in the sheltered anchorage.

Coral cover was most severely reduced in shallow waters both in the lagoon and on seaward slopes of the two atolls (Figure 2a, b). In less than 10 m of water, it was evident from the abundance of dead coral colonies and bare substratum that mortality had been severe, exceeding 90% and even >99% in some areas. Coral cover improved with depth (Figure 3) with a transition to improved survival between 8 and 10 m, where coral cover was variable, with evidence of moderate to high mortality. Deeper than this, cover was higher, though selective mortality was evident at least to 30 m depth. In the lagoon, coral cover was predominantly <5%, though there was new growth of *Acropora*. This pattern is consistent with that reported in other southern Seychelles atolls (Teleki and Spencer 2000). This indicates a severe reduction of corals in these atolls at present compared with what might have once been expected (see Discussion). Importantly, most of the species recorded were small colonies, clearly younger than about 4 years. Exceptions were *Porites*, and some faviids and mussids, some of which existed as remnants of older, mature colonies.

In several cases, identification is difficult with young colonies: the most obvious examples are table *Acropora* where colony shape does not develop until a few years old, and likewise many columnar or leafy species are encrusting or small-massive in shape while young. Thus many clues from colony shape have not yet developed amongst new recruits, and juveniles were overwhelmingly the most numerous colonies in shallow waters, greatly exceeding the numbers of larger 'survivors'.

Sites shallower than 10 m depth

In all sites in both atolls, the very low cover to 10 m depth suggests that the mortality was very high in 1998 and in many sites was nearly total (Figure 3). In Cosmoledo, the lagoon of approximately 25 km diameter is only 6–8 m deep, and dominated by sand and seagrass expanses, with scattered hard substratum or patch reefs in channels penetrating the lagoon.

Figure 2. (a) Seaward reef slope of West Cosmoledo. This is typical of shallow seaward slopes of south, through west to the north, showing very limited coral growth, but presence of algae. (b) Dead *Millepora* colonies in the lagoon are extensive, without sign of live growth and few new recruits. (c) *Acropora palifera*, showing recovery on shallow seaward slopes. It is growing on the side of a large dead colony of the same species. (d) Dead *Acropora cytherea*, eroded but still standing. Most examples in November 2002 were remnants of stumps. A new *Acropora* has since settled on the table. The yellow device is a newly installed temperature logger.

On most patch reefs we observed close to 99% mortality of corals. One relatively deep patch reef in the centre of the lagoon was seen with 15% coral cover, dominated by *Acropora* species (*palifera*, *digitata*, *millepora* and *pharaonis*), and by *Seriatopora hystrix*. Cosmoledo lagoon was evidently once rich with corals: vast areas of stagshorn *Acropora* rubble, dead faviids and *Porites* attest to a previous, much better condition. Dead *Millepora* was especially conspicuous in inner channel locations (Figure 2b); its abundance and size of up to 2 m tall suggest that this had been a dominant group. Mostly, the corals listed in the Appendix are new recruits; colonies were small and most were clearly less than 4 years old. Indeed many were probably only half that age, suggesting a delay of a year or two in recruitment following 1998, as has been noted from other atolls (Englehardt et al. 2002; Sheppard et al. 2002).

On western seaward slopes, a broad zone of dead *Acropora palifera* dominated to about 5 m depth in two out of four sites visited. This coral, however, is showing much new recruitment, seen both as juveniles as well as apparently recovered branches of much older and larger colonies (Figure 2c). Even so, its live cover was still only between 1 and 5%, compared to its previously obviously dominant condition of up to 50%, based on remaining dead colonies. On Cosmoledo's seaward slopes from 5 to 10 m depth, very few live table corals of over 1 m diameter were seen (*A. cytherea* and *A. clathrata*). There were, however, countless apparent 'stumps' of table corals (Figure 2d), suggesting that tabular *Acropora*
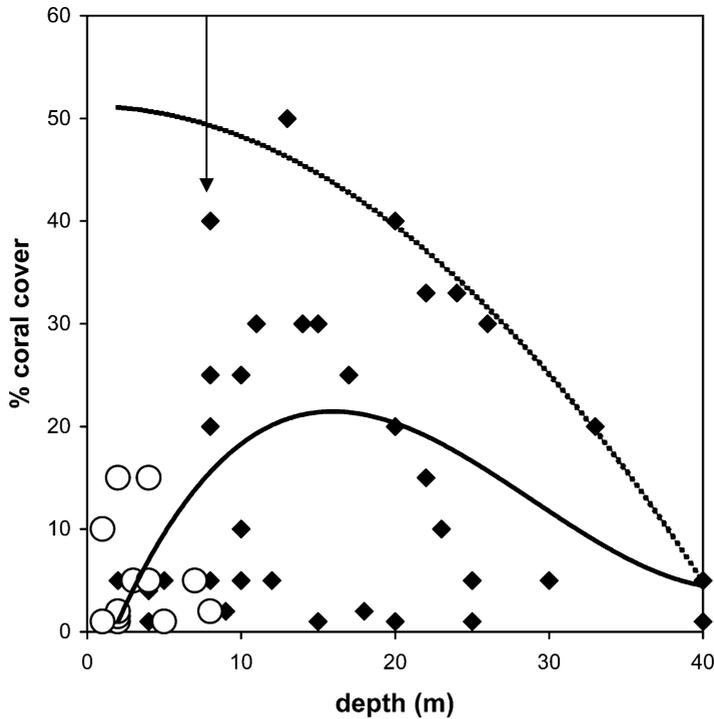
Figure 3. Visual estimates of coral cover at various depths on seaward slopes (diamonds) and lagoon patch reefs (open circles). The dotted curve indicates hypothetical or possible approximate maximum pre-bleaching coral cover with depth, based on maximum values found in patches here at shallow and intermediate depths. The solid curve is a third-order polynomial fit of the seaward reef cover values. Average seaward reef mortality is suggested by the gap between the two curves. The arrow marks the approximate transition depth.

once formed a conspicuous zone on the shallow platform just shallower than the 'drop-off', a condition also seen in several other Indian Ocean atolls (Sheppard et al. 2002). In both Cosmoledo and Aldabra, several west-facing seaward slopes had considerable stands of the seagrass *Thalassondendron ciliatum*, indicating that a large part of the shallow platform was not coral dominated before 1998, similar to coral reefs on the East African coast (Hamilton and Brakel 1984). Cosmoledo lagoon similarly contained large stands of *T. ciliatum* and other seagrasses, as well as of *Halimeda* and other green algae. Aldabra lagoon was not examined for corals, other than in its main western pass.

Passes into the atolls

In Cosmoledo there are two main passes, both to the south, with maximum depths of 8 m in the lagoon to 10–12 m at the seaward side, which contained much *Halimeda* and other green algae, but very few corals (<1% cover). The brightly fluorescent red *Micromussa amakusensis* was a rare but notable sight here, its first record from Indian Ocean atolls. In Aldabra, there is one major lagoon pass with an outer depth of >30 m, which experiences very strong tidal currents. Inwards from the atoll rim this pass is lined with abundant, ahermatypic *Tubastraea micrantha* (recorded by Barnes et al. 1971 as *Dendrophyllia*). About 5 km into the lagoon and on the shallow edges of the channels, there remain rich patches of large *Acropora*, including *A. cytherea* and *A. abrotanoides*, clearly survivors older than 5

years, as well as many new recruits. The comparative richness of *Acropora* in this region contrasted markedly with all other locations (to a degree that raised comments from several that the area was 'just like things used to be'). It may be speculated that the strong currents, including perhaps exchange of cooler water, have enabled these patches to survive.

Sites 10–30 m depth

Deeper than 10 m in all sites visited on seaward slopes in Cosmoledo and Aldabra, coral cover averaged about 20–25% (Figure 3), which supports cover values presented by Spencer et al. (2000) at their western Aldabra site. This suggests approximately a halving of total coral cover at these depths since the 1998 event (Teleki et al. 2000). Visually, the contrast in coral abundance at these depths made them appear rich compared with shallower sites on the same slopes.

Notable absences were again the *Acropora* species. It is likely that table *Acropora* were once abundant in a zone close to the 'drop-off' on seaward reefs, as is the case elsewhere in the Indian Ocean, evidence for which comes from the many bioeroded 'stumps' noted above, and a few still-standing tables (Figure 2d). Everywhere (including in lagoons) free fungiids were very sparse in both diversity and abundance. Agariciids were also a severely affected group, and were relatively scarce even in their usual depth range of 20–30 m. Amongst siderastreids, several genera were recorded, though most were very uncommon, and *Siderastrea* itself, usually a hardy genus, was not seen at all.

Porites species were the main survivors. A failing of the photographic method is its inability to discriminate many species of this genus (usually difficult with collected, cleaned specimens in this genus too). *Porites lutea* and *P. solida* were two notable members of this group, along with the branching forms *P. cylindrica*, *P. nigrescens* and *P. profundus*. *Goniopora* was uncommon even in sheltered locations where it might have been expected.

Faviids were the most common in terms of numbers of colonies between 10 and 30 m depth on seaward slopes of both atolls. Most colonies were small and younger than 4 years. Mussids had low diversity, but *Lobophyllia hemprichii* was clearly a good survivor with very large colonies, as was *Symphyllia radians* and *S. agaricia*, whose large colonies were fairly abundant below 15 m. No live *L. corymbosa* was seen, though this is generally a common species in the Indian Ocean.

Discussion

The genus *Acropora* has been transformed from being the most speciose and abundant coral genus in the Indian Ocean to one of relative scarcity and low diversity. This situation applies to Cosmoledo and Aldabra atolls at present. *Acropora* was among the genera most susceptible to mortality in 1998 (Obura 2001) and had low recruitment for the first 2 years after that for several areas in the Indian Ocean, for example in the Maldives (McClanahan 2000), other parts of South Asia (Rajasuriya et al. 2000) and East Africa (Obura et al. 2000a, b). From 2000 onwards, however, juvenile *Acropora* became abundant among newly recruiting species in Chagos (Sheppard et al. 2002). Interestingly, in one region of northern Kenya, the proportion of *Acropora* in the recruit population has decreased progressively each year, decreasing from 70% in 1999 (when only 18 recruits were recorded in over 200 quadrats), to 3%, 0.8% and 0% in 2002 (Obura 2002). The genus *Acropora* may suffer, in years following mass mortality events, from reproduction and dispersal failure, ultimately leading to contracted distributions and species loss.

In the same family, *Montipora* species were moderately diverse, but all colonies were small, and no large foliose colonies or ramose colonies had survived at any site. Comments made in the past, regarding the massive reduction of the conspicuous *Acropora*, apply also to *Montipora*. Amongst the faviids, few of large size were seen. *Diploastrea heliopora* was an exception, one colony over 1 m in diameter was noted on Aldabra's western seaward slope, but otherwise this species was not seen at all. Most faviids which are capable of reaching large sizes were seen as colonies comprising only a few dozen corallites each. From the estimated ages of most of these corals, the mass mortality occurred <5 years ago, presumably during the warming of 1998 as is the case in much of this ocean (Linden and Sporong 1999).

The initial, near-total mortality of all corals down to depths of about 8 m (including most of the lagoon of Cosmoledo atoll) raises questions about future recovery of corals, decay of reef structure and of architectural topography, leading to erosion on shorelines, a point important to several groups of atolls in this ocean (Teleki and Spencer 2000; Sheppard 2002). In all shallow (<10 m) sites visited there were insufficient corals to describe an 'assemblage'. Prior to the mass mortality, in Cosmoledo an *Acropora* zone was once described for the shallows (unpublished report in Seychelles Ministry of Environment), while in Aldabra, Drew (1977) remarked that soft corals once favoured this zone. The few measurements that have been made suggest that bioerosion and wave erosion continue to be important on coral rock not covered with live corals; they have resulted in removal of a coral 'breakwater' 1.5 m high on reefs seaward of some reef crests in Chagos in only 3 years (Sheppard et al. 2002), while in the Maldives bioerosion alone removed between 4 and 14% of experimental coral blocks in only 14 months (Zahir 2002). No shoreline data exist for estimating shore erosion in Cosmoledo, though in Aldabra, concern has been expressed about markedly increased erosion of the shore and even of the raised reefs beside the field station (Guy Esperon, Manager, Aldabra Research Station, personal communication).

In deeper water, there has been a distortion of the coral assemblage, towards a condition currently dominated by *Porites* and faviids, as has been the case elsewhere in the Indian Ocean (Obura 2001; Riegl 2002; Sheppard and Loughland 2002), due to the removal of more sensitive groups. Based on the condition in severely affected sites in the Arabian Gulf, it was predicted (Sheppard and Loughland 2002) that those reefs would in future become 'faviid and *Porites* reefs' rather than *Acropora* reefs, not only because of differential survival but because of the larger numbers of recruits from these groups compared with others. It was further predicted that this may come to be seen as the condition in many Indian Ocean reefs in future and, for the present at least, this appears to be what is occurring in Cosmoledo and Aldabra.

How long this situation may persist remains unknown. Presumably even a low and currently undetected survival of many species, including some not identified in the present study, could result in at least a partial restoration to the assemblage which existed prior to the 1998 mortality. The large list of living species recorded here suggests this is clearly possible. It may take many decades or even centuries, given the growth rate of most corals, but recruitment is occurring, even though the locations of sufficient sources of many large, adult colonies are not obvious. Recovery of some species may be especially important. For example, in shallow water on seaward slopes, *Acropora palifera* is already recovering in the sense that many new colonies and many surviving patches on old and largely dead colonies now provide perhaps 1–5% cover, which is especially important given the wave-breaking location and character of this large species (Sheppard 2002). Given its growth rate of

several centimetres each year, its previous cover of over 50% in shallow water may be regained in another decade or less. In Cosmoledo lagoon, in contrast, restoration to a previous condition is likely to be very slow indeed: the previously abundant *Millepora* shows almost no recovery at all to date (Figure 2b). Similarly, large expanses of *Acropora* 'stagshorn' rubble in the lagoon indicate the importance of this group here previously, but none of the typical 'stagshorn' *Acropora* species (e.g. *formosa*, *grandis*, *nobilis*) were seen live in Cosmoledo lagoon in this survey.

Soft corals were not surveyed, beyond noting that they were generally very scarce, providing cover of <1%. Exceptions were some large patches of the carpeting genera *Sinularia* and *Sarcophyton* at mid-depths on fore reef slope, and conspicuous gorgonian fans up to 2 m across below 30 m on the deep walls. Like the scleractinian corals, these were heavily affected in 1998 but, without persistent skeletons, their decline has left large bare expanses (see Wilkinson 2000; Sheppard et al. 2002). The observation by Drew (1977) that soft corals used to dominate in some parts of Aldabra at 6–14 m depth may explain the extreme scarcity of attached cnidarians of any kind seen now in shallow water in the sites studied.

Recovery may occur if there is no recurrence of lethally warm water. The probability of this given rising temperatures is discussed for Cosmoledo in Obura et al. (in preparation), but it is likely that recurrences of warming will occur (Hoegh-Guldberg 1999; Pittock 1999; Sheppard 2003). Spencer et al. (2000) discuss the past sea-surface temperature regimes of several Seychelles atolls, and noted that Aldabra's maximum sea temperature in 1998 was 30.65°C and noted that temperatures of over 30°C (but less than the 1998 value) also occurred in 1969, 1983 and 1987. Unfortunately, no survey work determined whether any of the earlier warming episodes caused bleaching. A slightly lower 29.8°C is the maximum temperature stated for the Aldabra region in the newest HadISST1 data set (Rayner et al., in press). In November 2002, a few live colonies were seen to be bleached, but bleaching was uncommon, and occasional bleaching of a few colonies is not itself indicative of a current problem.

In the Indian Ocean generally, the depths to which severe mortality occurred may be locally important to both coral recovery and to future reef condition and erosion. In this sense, Cosmoledo and Aldabra appear to have an advantage over some locations. The 'critical depth' in these atolls of 8–10 m is fairly shallow compared with many atolls and other reefs in the region (Table I), where the transition from extremely heavy to partial mortality may be equally sharp but considerably deeper at 30–40 m in some cases, leaving little unaffected reef in the well-illuminated zone. On mainland coasts of East Africa, the transition depth was usually greater than 10 m (Obura et al. 2000a, b) and appears to have been between 15 and 20 m. Unfortunately, in many post-1998 studies on coral cover, the depths of surveys is not always clear, or may include a considerable range whose cover values are presented as an average, or they may have used measurements taken at widely spaced depths such that any 'transition zone' cannot now be deduced. The number of examples listed in Table I, however, suggests that a transition depth is a common occurrence.

The reasons for such varied 'transition depths' remains unknown, but may be due to the presence of local thermoclines during the critical periods. The importance of having a relatively shallow transition zone, such as in Cosmoledo and Aldabra, is that this leaves a much greater expanse of seaward reef within the photic zone which still has appreciable coral diversity and cover. The 8–10 m transition depths on the western sides of Cosmoledo and Aldabra is similar to that recorded in other southern Seychelles atolls as well (Teleki

Table I. Depths in Indian Ocean atolls where severely reduced coral cover transitions to much higher cover of many genera.

Atoll	'Transition depth' (m)	Reference
Aldabra, Seychelles	8–12	This paper
Cosmoledo, Seychelles	8–12	This paper
Alphonse, Seychelles[‡]	10–15	Spencer et al. 2000
St Pierre, Seychelles[‡]	10–15?	Spencer et al. 2000
Seychelles, granitic islands	15	Turner et al. 2000
Southern islands, Seychelles	10–20	Teleki and Spencer 2000; Teleki et al. 2000
Mayotte	>30	Quod and Bigot 2000
Masoala, Madagascar	10	Obura, personal observation
Felidu, Maldives	>30	McClanahan 2000
Mulaku, Maldives	>30	McClanahan 2000
North Malé, Maldives	>30	C. Anderson, personal communication
South Malé, Maldives	>30	McClanahan 2000; C. Anderson, personal communication
Ari, Maldives	>30	C. Anderson, personal communication
Vaavu, Maldives	>30	C. Anderson, personal communication
Addu, Maldives	6–10	C. Anderson, personal communication
Salomon, Chagos	8–15	Sheppard et al. 2002
Peros Banhos, Chagos	8–15	Sheppard et al. 2002
Great Chagos Bank (west)	>30	Sheppard et al. 2002
Egmont, Chagos	>30	Sheppard et al. 2002
Diego Garcia, Chagos	>30	Sheppard et al. 2002
Northern Kenya, East Africa	10–15	Obura 2000
Southern Kenya, East Africa	>20	Obura et al. 2000a, b
East Africa mainland	15–20	Obura et al. 2000a, b
Rodriguez	2.5	Turner, personal communication
Socotra	12–15	Turner, personal communication
Abu Dhabi, UAE[†]	3–5	Sheppard and Loughland 2002

[†]In Arabian Gulf, the maximum depth in inshore sites is 12 m. [‡]Measurements only done at 10 and 15 m, so 'transition depth' lies between these two values.

and Spencer 2000), so there may be a regional effect, perhaps caused by a more widespread thermocline during the critical warming period.

Factors additional to simple sea temperature were almost certainly involved in the massive Indian Ocean coral mortality in 1998, and temperature alone may prove to be inadequate as a sole descriptor. UV light is likely to be very important (see examples in Sheppard 1999; Wilkinson 2000), and overall illumination is important, as evidenced by the fact that heavy cloud cover at the critical period 'saved' the reefs of Mauritius (Wilkinson 2000; Turner, personal communication). The physiological and photosynthetic mechanisms involved are becoming clearer (Brown et al. 1995, 2002; Douglas 2003). However, these other factors, where important, also appear to require raised temperatures to impart their harmful, probably synergistic effect, and none appears to have been measured in these (or many other) atolls. Further, there is limited evidence that these factors have changed by a significant amount in recent years. Sea-surface temperature data, in contrast, are now widely available for all areas from remote-sensing methods if not direct measurements, so that they serve as a useful (indeed only) surrogate even if sea-surface temperature is not the only determinant.

For Cosmoledo and Aldabra, the relative shallowness of a transition depth from heavy mortality to significant survival of corals bodes well for their future in terms of coral diversity and possible recovery. Whether or not acclimation to warming will match the predicted continued rise in temperature remains to be seen and, equally important here may be not only the measured sea-surface temperatures but also other aspects of climate change such as wind, which may affect the degree of thermocline stability and the depths at which they become established.

Acknowledgements

Appendix

Corals of Cosmoledo and Aldabra

Key to sites: CW, Cosmoledo West; CNW, Cosmoledo North-West; CN, Cosmoledo North; CL, Cosmoledo lagoon; CWP, Cosmoledo West Pass (south side of atoll); CEP, Cosmoledo East Pass (also south side of atoll); A, Aldabra West; AP, Aldabra Main Pass, As, Assumption. The last was sampled with one casual swim only, and is included because it surprisingly produced new records. In the table, + shows presence at that site; ++ indicates particularly abundant at that site (approximately 20 or more colonies seen in one dive); ⋆ indicates sight record without photograph.

Species	CW	CNW	CN	CL	CWP	CEP	A	AP	As
Acroporidae									
Montipora turgescens Bernard, 1897						+			
Montipora calcarea Bernard, 1897		+	+						
Montipora danae (Milne Edwards and Haime 1851)	+⋆	+					+		
Montipora efflorescens Bernard, 1897	+		+⋆	+					
Montipora grisea Bernard, 1897						+⋆	+		
Montipora lobulata Bernard, 1897				+			+		
Montipora monasteriata (Forskål 1775)	+⋆			+⋆		+⋆			
Montipora orientalis Nemenzo, 1967		+				+			
Montipora peltiformis Bernard, 1897	+	+⋆		+⋆		+⋆	+⋆	+⋆	
Montipora stilosa (Ehrenberg 1834)			+⋆					+⋆	
Montipora tuberculosa (Lamarck 1816)	+		+⋆	+⋆			+⋆		
Montipora turgescens Bernard, 1897	+	+⋆		+					
Montipora undata Bernard, 1897		+	+⋆	+		+⋆	+		
Montipora venosa (Ehrenberg 1834)	+								
Montipora verrucosa (Lamarck 1816)							+		
Montipora sp. 1		+							
Montipora sp. 2	+		+	+			+⋆		
Acropora abrotanoides (Lamarck 1816)								+ ⋆	+
Acropora anthoceris (Brook 1893)			+						

(*Cont.*)

Species	CW	CNW	CN	CL	CWP	CEP	A	AP	As
Acropora arabensis Hodgson and Carpenter, 1995	+★								
Acropora austera (Dana 1846)									+
Acropora brueggemanni (Brook 1893)	+	+					+		
Acropora cerealis (Dana 1846)			+★			+			
Acropora clathrata (Brook 1891)						+			
Acropora cytherea (Dana 1846)			+	+	+	+		+★	
Acropora digitifera (Dana 1846)				+		+			
Acropora divericata? (Dana 1846)						+			
Acropora florida (Dana 1846)									+
Acropora globiceps (Dana 1846)						+			+
Acropora inernis (Brook 1891)				+			+		
Acropora latistellata (Brook 1891)		+							
Acropora listeri (Brook 1893)			+★						
Acropora lutkeni Crossland, 1952	+★	+★	+★				+★	+★	
Acropora massawensis Maranzeller, 1906							+★		
Acropora microclados (Ehrenberg 1834)		+★	+★						
Acropora monticulosa (Bruggemann 1879)			+						
Acropora nana (Studer 1878)	+★		+★	+	+★				
Acropora nasuta (Dana 1846)				+					
Acropora palifera (Lamarck 1816)	++	+★	++	+			++		
Acropora pharaonis (Milne Edwards and Haime 1860)				+					
Acropora plantaginea (Lamarck 1816)				+					
Acropora retusa (Dana 1846)							+★		
Acropora robusta (Dana 1846)							+		+
Acropora rosaria (Dana 1846)						+			
Acropora samoensis (Brook 1891)							+		
Acropora secale (Studer 1878)							+		
Acropora tenuis (Dana 1846)				++	+				
Acropora valida (Dana 1846)		+★			+				
Astreopora listeri Bernard, 1896					+	+			
Astreopora myriophthalma (Lamarck 1816)	+	+★	+			+	+★	+★	
Astrocoeniidae									
Stylocoeniella armata (Ehrenberg 1834)	+	+	+				+★		
Pocilloporidae									
Pocillopora cf. *capitata/ligulata*				+					
Pocillopora damicornis (Linnaeus 1758)	+★		+★	+★			+★		
Pocillopora elegans Dana, 1846				+		+			
Pocillopora eydouxi Milne Edwards and Haime, 1860	+		+★	+		+	+		
Pocillopora fungiformis? Veron, 2000						+			
Pocillopora indiania Veron, 2000	+			+					
Pocillopora verrucosa (Ellis and Solander 1786)	+	+★	+★	+	+	+	+		
Seriatopora hystrix Dana, 1846				+			+		+★
Stylophora pistillata Esper, 1797	++	++	+★				+		
Euphyllidae									
Plerogyra sinuosa (Dana 1846)		+	+★				+		
Physogyra lichtensteini (Milne Edwards and Haime 1857)	+★		+				+		

(*Cont.*)

Species	CW	CNW	CN	CL	CWP	CEP	A	AP	As
Oculinidae									
Galaxea astreata (Lamarck 1816)									
Galaxea fasicularis (Linnaeus 1767)			+		+		+		
Siderastreidae									
Anomastrea irregularis Marenzeller, 1901				+	+		+		
Psammocora haimeana Milne Edwards and Haime, 1851	+★	+★	+★	+		+	+		
Psammocora nierstraszi Horst, 1921	+	+	+★						
Psammocora obtusangulata (Lamarck 1816)	+★						+	+★	
Coscinaraea columna (Dana 1846)	+★				+		+		+
Coscinaraea crassa Veron and Pichon, 1980	+	+★				+★	+	+★	
Coscinaraea excesa (Dana 1846)	+★	+★	+★	+			+		
Coscinaraea monile (Forskål 1775)	+★	+	+			+★	+		
Agariciidae									
Pavona clavus (Dana 1846)	+★						+		
Pavona explanulata (Lamarck 1816)	+★		+				+		
Pavona varians Verrill, 1864	++	++	++				+★		
Pavona venosa (Ehrenberg 1834)			+★	+★		+★	+★		
Leptoseris explanata Yabe and Sugiyama, 1941	+		+★						
Leptoseris incrustans (Quelch 1886)	+	+★	+				+★		
Leptoseris mycetoceroides Wells, 1954			+						
Gardineroseris planulata (Dana 1846)	+	+	+				+		
Pachyseris speciosa (Dana 1846)	++	+★	+	+			+		
Fungiidae									
Cycloseris costulata (Ortmann 1889)	+		+						
Diaseris distorta (Michelin 1843)							+★		
Fungia corona Döderlein 1901							+		
Fungia danai Milne Edwards and Haime, 1851							+★		
Fungia fungites (Linnaeus 1758)					+				
Fungia klunzingeri Döderlein, 1901							+		
Fungia paumotensis Stuchbury, 1833							+★		
Fungia puishani Veron and DeVantier in Veron, 2000							+		
Fungia repanda Dana, 1846					+		+		
Fungia scabra Döderlein, 1901					+				
Fungia scutaria Lamarck, 1801	+		+★				+		
Fungia seychellensis Hoeksema, 1993	+	+★	+				+		
Podabacia crustacea (Pallas 1766)		+	+						
Podabacia motoporensis Veron, 1990		+					+		
Pectiniidae									
Echinophyllia aspera (Ellis and Solander 1788)	+								
Echinophyllia echinata (Saville-Kent 1871)		+							
Echinophyllia echinoporoides Veron and Pichon, 1980							+		
Echinophyllia orpheensis Veron and Pichon, 1980							+		
Oxypora crassispinosa Nemenzo, 1979	+	+							
Oxypora lacera (Verrill 1864)	+	+	+	+★					
Mycedium elelpantotus (Pallas 1766)	+	+★	+★				+	+★	

(*Cont.*)

Species	CW	CNW	CN	CL	CWP	CEP	A	AP	As
Mycedium umbra Veron, 2000	+								
Pectina africanus Veron, 2000	+	+					++		
Merulinidae									
Hydnophora exesa (Pallas 1766)	+			+★			+		
Hydnophora microconos (Lamarck 1816)	+		+		+	+★		+★	
Merulina ampliata (Ellis and Solander 1786)				+			+		
Dendrophylliidae									
Turbinaria mesenterina (Lamarck 1816)	+								
Turbinaria reniformis Bernard, 1896	+	+★	+						
Turbinaria stellulata (Lamarck 1816)		+		+			+		
Turbinaria irregularis Bernard, 1896				+					
Mussidae									
Micromussa amakusensis (Veron 1990)				+	+	+	+★		
Acanthastrea brevis Milne Edwards and Haime, 1849	+		+★	+	+				
Acanthastrea echinata (Dana 1846)	+	+★	+★			+	+		
Acanthastrea ishigakiensis Veron, 1990							+★		+
Acanthastrea rotundiflora Chevalier, 1975		+					+		
Acanthastrea cf. *hillae* Wells, 1955						+			
Lobophyllia hemprichi (Ehrenberg 1834)	++	++	++				++		
Lobophyllia robusta Yabe and Sugiyama, 1936	+	+					+		
Symphyllia agaricia Milne Edwards and Haime, 1849	++	++	+				+★		
Symphyllia radians Milne Edwards and Haime, 1849	++	++	++					+★	
Symphyllia sp.	+								
Cynarina lachrymalis (Milne Edwards and Haime 1848)			+★						
Faviidae									
Favia favus (Forskål 1775)				+		+★	+		
Favia lacuna Veron et al. in Veron, 2000				+	+				
Favia lizardensis Veron and Pichon, 1977				+					
Favia matthai Vaughan, 1918	+	+	+	+		+★	+		
Favia pallida (Dana 1846)				+		+★	+		
Favia rotumana (Gardiner 1899)					+				
Favia speciosa Dana, 1846	+			+			+		
Favia stelligera (Dana 1846)	++	+	+				+★		
Favia veroni Moll and Borel-Best, 1984	+								
Favites abdita (Ellis and Solander 1786)	+★			+	+★	+★	+		
Favites chinensis (Verrill 1866)						+	+		
Favites complanata (Ehrenberg 1834)	+			+★	+★		+		
Favites flexuosa (Dana 1846)	+	+★	+			+★	+		
Favites halicora (Ehrenberg 1834)		+				+	+		
Favites micropentagona Veron, 2000			+					+★	
Favites paraflexuosa Veron, 2000	++		+						
Favites pentagona (Esper 1794)	+	+	+★	+		+★	+★		
Favites russelli (Wells 1954)	+		+★	+			+★		
Favites spinosa (Klunzinger 1879)						+	+		
Favites stylifera (Yabe and Sugiyama 1937)							+		
Favites vasta (Klunzinger 1879)	+	+	+	+		+			
Goniastrea edwardsi Chevalier, 1971	+	+	+★	+★			+		
Goniastrea minuta Veron, 2000	+			+		+			

(*Cont.*)

Species	CW	CNW	CN	CL	CWP	CEP	A	AP	As
Goniastrea pectinata (Ehrenberg 1834)	+★	+	+★	+	+★		+		
Goniastrea peresi (Faure and Pichon 1978)	+	+★	+★	+★		+	+★		
Goniastrea retiformis (Lamarck 1816)	+	+	+★			+★	+		
Platygyra carnosus Veron, 2000	+								
Platygyra contorta Veron, 1990	+	+★	+	+			+	+★	
Platygyra crosslandi Matthai, 1928	+					+	+★		
Platygyra daedalea (Ellis and Solander 1786)					+		+★		
Platygyra lamellina (Ehrenberg 1834)	+							+★	
Playtgyra pini Chevalier, 1975	+						+		
Platygyra ryukyuensis Yabe and Sugiyama, 1936			+				+		
Platygyra sinensis (Milne Edwards and Haime 1849)	+			+			+		
Leptoria irregularis Veron, 1990	+						+★		
Leptoria phrygia (Ellsi and Solander 1786)				+★			+★		
Oulophyllia crispa (Lamarck 1816)	+★				+				
Leptoria phrygia (Ellis and Solander 1786)	+						+	+★	
Montastrea colemani Veron, 2000	+						+		
Montastrea curta (Dana 1846)	+★	+	+	+			+		
Montastrea magnistellata Chevalier, 1971		+★		+					
Montastrea salebrosa (Nemenzo 1959)		+		+				+★	
Montastrea valenciennesi (MilneEdwards and Haime 1848)	+	+					+		
Plesiastrea versipora (Lamarck 1816)		+★	+	+★	+			+★	
Diploastrea heliopora (Lamarck 1816)							+★		
Leptastrea aequalis Veron, 2000						+	+★		
Leptastrea bottae (Milne Edwards and Haime 1849)							+		
Leptastrea inaequalis Klunzinger, 1879					+	+★	+★		
Leptastrea pruinosa Crossland, 1952	+	+				+			
Leptastrea purpurea (Dana 1846)	+	+	+★			+★	+		
Leptastrea transversa Klunzinger 1879	+	+★	+★				+★		
Cyphastrea chalcidicum (Forskål 1775)	+	+	+★	+★			+★	+★	
Cyphastrea microphthalma (Lamarck 1816)	+		+★	+					
Cyphastrea seralia (Forskål 1775)					+	+★			
Echinopora gemmacea Lamarck, 1816	+	+	+			+	+		
Echinopora hirsutissima Milne Edwards and Haime, 1849	+	+							
Poritidae									
Porites australensis Vaughan, 1918		+★	+★	+			+		
Porites cylindrica Dana, 1846				+			+		
Porites harrisoni Veron, 2000	+		+	+					
Porites lobata Dana, 1846	++	++★	+★						
Porites lutea Milne Edwards and Haime, 1851	++	++	++	+	+	+	+		+★
Porites profundus Rehberg, 1892	+	+★	+				+		
Porites rus (Forskål 1775)							+		
Porites solida (Forskål 1775)	+★		+						
Poritiporella paliformis Veron, 2000	+								
Goniopora columna Dana, 1846			+						

(*Cont.*)

Species	CW	CNW	CN	CL	CWP	CEP	A	AP	As
Goniopora djiboutiensis Vaughan, 1907	+★								
Goniopora lobata Milne Edwards and Haime, 1860				+					
Goniopora minor Crossland, 1952					+				
Goniopora somaliensis Vaughan, 1907						+★			
Goniopora tenuidens (Quelch 1886)				+		+			
Non-scleractinians and ahermatypes									
Heliopora coerulea (Pallas 1766)									+
Millepora complanata Boschma, 1948				+					
Millepora exesa Forskål, 1775	+★		+★	+					
Millepora platyphyllia Hemprich and Ehrenberg, 1834	+			++		+★			
Millepora tenella Bochma, 1948				+					
Tubastraea coccinnea (Ehrenberg 1834)				+★		+			
Tubastraea micranthus (Ehrenberg 1834)				++				++	
Tubastraea aurea (Quoy and Gaimard 1833)				++					
Summary totals									
Cosmoledo	177								
Aldabra	118								
Assumption	10								
Total	201								

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