

Archipelago-wide coral recovery patterns since 1998 in the Chagos Archipelago, central Indian Ocean

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ABSTRACT: Patterns of coral recovery are analysed across reefs of the Chagos Archipelago, which spans 400 × 250 km in the central Indian Ocean. This archipelago mostly lacks direct human impacts and is subject only to global changes such as a rise in sea surface temperature. Following very heavy coral mortality (mostly >90%) caused by the 1998 warming event, and despite 2 further sub-lethal bleaching events, the recovery of coral cover, colony numbers and juvenile recruitment has been good in many parts of the archipelago. There was little discrimination between atolls and depths, with a notable exception of 1 atoll where a repeat of heavy mortality had occurred in 2005. In 2006, coral cover was almost restored to pre-1998 values at most shallow sites, but had recovered much less in deeper waters. However, in shallow water, coral cover values alone are a poor indication of recovery, because present, shallow cover mainly comes from *Acropora palifera* and other corals that are largely encrusting in juvenile form, in contrast to their mature condition, in which they provide a 3-dimensional 'forest' structure. Recruitment of juvenile colonies in 2006 ranged from 6 to 28 m⁻². Total juvenile density showed no significant pattern with atolls or with depth, but, taking each genus of juveniles in turn, many genera showed a marked depth preference. No shift was observed towards algal domination, or to assemblages dominated by *Porites* or faviids, as has been reported elsewhere. Recovery in Chagos 8 yr after massive coral and soft coral mortality is discussed in relation to an absence of other, locally manageable factors such as pollution, over-fishing and sedimentation.

KEY WORDS: Coral reef · Coral bleaching · Recovery · Sea surface temperature

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INTRODUCTION

Much has been written about the substantial loss of corals and reefs following the 1998 seawater warming (see Wilkinson 2004 for summary). Estimations of amounts and rates of subsequent recovery are important both to predictions of future reef condition and to management of protected areas (McClanahan 2007), but so far there is much less information on recovery, particularly at the scale of whole reef systems.

Deterioration of most reefs clearly began decades ago from over-fishing, disease, crown-of-thorns starfish *Acanthaster planci* outbreaks, pollution and other natural reasons such as hurricanes (e.g. Jackson 1997, Jackson et al. 2001, Pandolfi et al. 2003, Roberts 2007).

Even so, only a decade ago, Connell (1997) could say that of 65 sets of coral data examined, 58% had stable communities, and, of those which had suffered decline, many had subsequently recovered. Since the 1998 mass mortality, more attention has been focussed on long-term, global changes. Declines reported more recently (Gardner et al. 2003, Bruno & Selig 2007) have led to debate concerning the ability of reefs to recover, whether many settle into some form of 'alternative stable state' (Knowlton 1992), or where, exactly, along any particular declining trajectory, there may be a point beyond which recovery is irreversible.

The Indian Ocean was the worst affected by the 1998 warming episode (Wilkinson 2004). Remote islands and archipelagos were especially vulnerable, contrary

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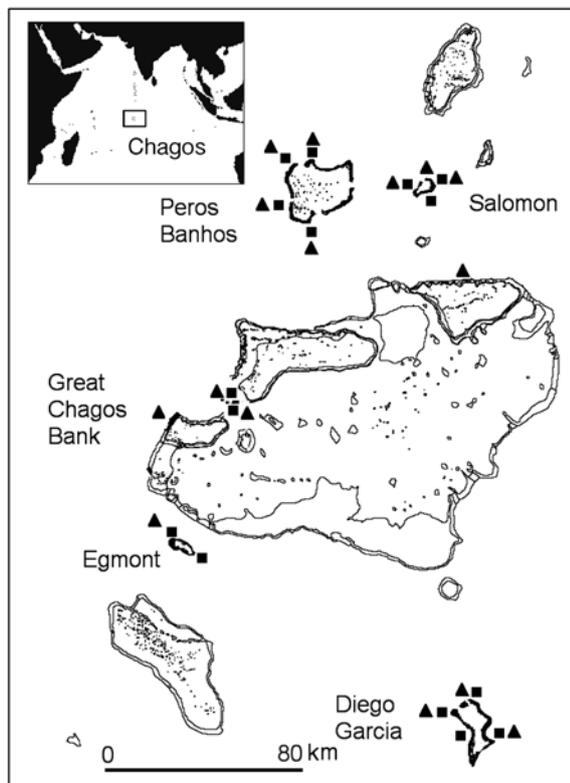


Fig. 1. Location and map of the Chagos Archipelago. ■: sites sampled for N and percent cover; ▲: sites of juvenile coral counts

to previous predictions which had assumed that remoteness from direct human impacts afforded protection (Bryant et al. 1998). The very remote Chagos Archipelago (Fig. 1) was particularly badly affected, suffering total or very heavy coral mortality on seaward slopes to >30 m depth (depending on the atoll), with species-specific mortality extending deeper still (Sheppard et al. 2002). Cover values of coral and soft coral on seaward slopes before 1998 totalled 50 to 95%, which declined in 1998 to an average of 12%, and even to zero between 0 and 5 m depth in some shallow areas (Sheppard 1999a). Such massive impact, and forecast trends of further water warming and acidification, have led to several very gloomy prognoses for the future of reefs (Hoegh-Guldberg 1999, Sheppard 2003, Hoegh-Guldberg et al. 2007).

Initial mortality of benthic coelenterates was followed by a collapse of the reefs' architectural structure, which brought with it, firstly, some selective losses of obligate corallivores (Spalding & Jarvis 2002) followed after a few years by substantial changes in many fish populations (Graham et al. 2006). On many reefs, algal abundance increased substantially too (Rogers & Miller 2006).

In Chagos, no algal increase followed the coral mortality, so that substantial areas of rocky substrate remained essentially uncolonised by macro-organisms for at least 3 yr (Sheppard et al. 2002). By 2001, new coral recruitment on old rock, newly dead coral colonies and unconsolidated rubble was substantial to a depth of 30 m.

In the present study, we measure the degree of coral recovery on seaward reefs across the Chagos Archipelago. This location mostly lacks reef fishing, shoreline construction, sediment disturbance, or local pollution (Guitart et al. 2007), which therefore do not confound recovery from the warming-induced mortality. However, repeated, though less severe, bleaching and associated mortality events have been observed throughout the archipelago in intervening years (C. R. C. Sheppard unpubl. data), in common with similar repeats of warming episodes in adjacent regions such as the central Maldives (C. Anderson pers. comm.), Oman and the Straits of Hormuz in both 2002 and 2004 (Wilson et al. 2002), Rodrigues in 2002 and later (Hardman et al. 2004), the Seychelles (Sheppard et al. 2005) and Mauritius in 2003 (Turner & Klaus 2005). Several further instances of moderate bleaching in this ocean are reported in Wilkinson (2004), who notes varying degrees of severity from India to Africa, with some island groups being apparently more affected than several mainland areas. Thus, any recovery must be examined in the context of repeated but lesser warming events rather than as a simple succession from a single severe impact.

METHODS

Sampling sites. Seaward slopes of all 5 islanded atolls of the Chagos Archipelago (Fig. 1) were investigated from February to March 2006. We used a nested sampling design of 5 atolls, studying a total of 18 sites around the atolls, and up to 5 depths at each site (at 5, 10, 15, 20 and 25 m), with a varying number of replicates at each depth. Coral cover and numbers of colonies >5 mm diameter were estimated in quadrats at all 5 depths, with additional counts of new recruits at 5, 15 and 25 m depth.

As many sites as possible needed to be studied across all 5 atolls. Thus, 440 quadrats (0.5 × 0.5 m) were examined on transects placed along depth contours on seaward slopes. In each quadrat, the number (N) of all coral colonies >5 mm were counted. Secondly, an estimate was made by eye of total coral cover in each quadrat. Eye estimation followed AIMS protocols, with the differences that estimates were made in the quadrats rather than across large reef areas, as is common, for example, with manta tows, and, secondly,

finer divisions of percent cover were made than specified for values <10% or >75% coral cover. Quadrats were laid randomly along the depth contours. Colonies counted included those which partly extended outside the quadrats.

Data on the number of colonies and percent cover were strongly non-normal after all common transformations, precluding ANOVA. Therefore, nonparametric methods were used (Primer v6; Clarke & Gorley 2006), mainly the ANOSIM (analysis of similarity) routines. Simple standardisation procedures were used to account for different numbers of quadrats at different sites, and Primer's 'normalisation' procedure was used to give equal weight to N and cover values prior to creating Bray-Curtis similarity matrices.

A second set of measurements of juvenile colonies at 5, 15 and 25 m depth recorded size and genus of colonies within an additional 1159 randomly placed 0.11 m² (33 × 33 cm) quadrats. Up to 46 replicates were recorded at each site. Juveniles were recorded in 10 mm size categories from 0 to 100 mm, measured as total distance across the surface of each colony along the longest axis. A further 2603 hard coral juveniles from 35 genera were recorded in a total sampling area of 129 m². ANOSIM and χ^2 were used to test for distribution patterns with depth.

Sea temperature data. HadISST1 sea surface temperature (SST) data were used to obtain SST patterns for Chagos (Rayner et al. 2003); this is monthly, with a spatial resolution of 1° latitude and longitude. Chagos is covered by a 3 × 3 grid, so the average of the 9 cells was used to illustrate the broad temperature pattern in the region as a whole.

RESULTS

Seawater temperature

Monthly SST values for the Chagos region from 1980 to 2006 (Fig. 2) show the large warming spike in 1998, as well as more recent spikes, which, in Chagos, also caused extensive bleaching (C. R. C. Sheppard unpubl. data), though subsequent mortality was minor at all observed sites except at Egmont atoll (see 'Egmont atoll repeat mortality'). Warming is neither smooth nor continuous; however, it shows a 3 to 5 yr cycle, which may result from a combined influence of the Indian Ocean Dipole and the El Niño-Southern Oscillation

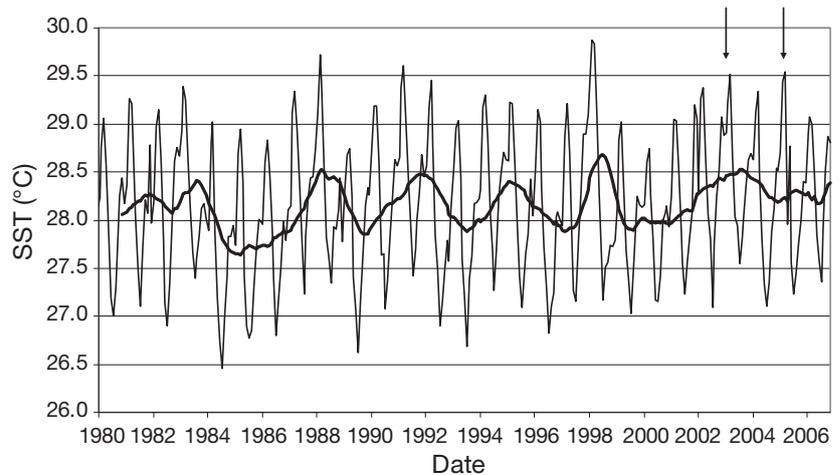


Fig. 2. Monthly sea surface temperature (SST) data for Chagos Archipelago, 1980 to 2006 inclusive. HadISST1 data for the 9 cells covering the archipelago are averaged. Arrows mark the temperature peaks in 2003 and 2005, both of which caused a repeat of bleaching, but no observed subsequent mortality in most places. Heavy line: 12 mo centred running mean showing 3 to 5 yr cycles

(ENSO) (Purkis & Riegl 2005). The 12 mo monthly running mean of the SST data (see Fig. 2) similarly shows that this cycle in Chagos is about 0.4 to 0.8°C, enough to trigger bleaching (Hoegh-Guldberg 1999). Coral recovery must therefore be considered against the background of a repeat in high temperature events sufficient to cause physiological stress to corals.

Coral recovery

Eight years after the very heavy mortality, overall recovery patterns were variable over the archipelago (Fig. 3). There was no significant correlation between N and percent cover ($r = 0.041$, $p = 0.390$), with quadrats containing 100% cover by 1 or 2 colonies (usually *Acropora* tables), to a maximum of 36 colonies in 1 quadrat at 10 m depth. Most conspicuous was the recovery of cover of *A. palifera* in the shallowest zone (0 to 5 m depth) and of tabular *A. cytherea* at some sites between 4 and 10 m depth; both species had been virtually eliminated in 1998. Patchiness within this average is marked, and, overall, there was no marked pattern of change in either cover or total colony density with depth. The one exception was the continued very low cover at several sites on the Egmont atoll (see 'Egmont atoll repeat mortality'). Much evidence remained of old, dead colonies, especially in shallow water, which may reflect further interruptions to recovery in the earlier 2000s as well as being a legacy from 1998.

Frequency diagrams (Fig. 4) show the variability (across atolls and depths) in the frequencies of values

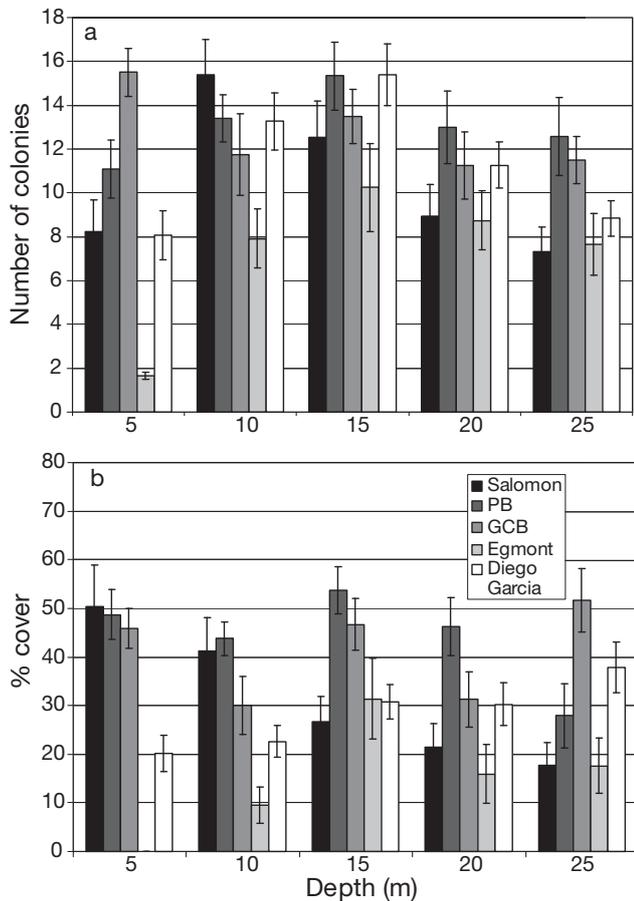


Fig. 3. (a) Number of colonies per quadrat and (b) percent coral cover, measured in the quadrats, at each depth on each atoll. Error bars show mean \pm SE. PB: Peros Banhos; GCB: Great Chagos Bank

of colonies and of percent cover in the 440 quadrats. There is considerable variability in lower frequencies, at which different values of N occurred (Fig. 4a,c), across both atolls and depths. Coral cover (Fig. 4b,d) was much more consistent across both atolls and depths. Low cover values of <20% were frequent at 3 atolls and all depths. The patterns suggest that some depths (shallow) and atolls (Egmont and Peros Banhos to a lesser extent) show greater variability or different patterns to the others, emphasising the patchiness in the extent to which sites recover considering these 2 measures.

A 2-way crossed ANOSIM (Clarke & Gorley 2006) on colony count (N) and coral cover (factors are 5 atolls and 5 depths) showed that differences between atolls (across all depths) and between depths (across all atolls) (Table 1) were strongly significant globally ($R = 0.057$, $p = 0.001$; $R = 0.06$, $p = 0.001$, respectively). Pair-wise results showed that all pairings involving Egmont atoll had consistently much higher global R-values than pairings without Egmont atoll. Global differences

Table 1. ANOSIM crossed, 2-way probability values of percent coral cover, using the 5 atolls and 5 depth zones on each. Atoll and depth are factors. Every atoll and every depth in turn was then excluded from ANOSIM runs. Values in bold show the only omission of all of the combinations (Egmont atoll) that produced $p > 0.01$

	All sites	Without Egmont atoll
Between atoll groups (across all depths)	$R = 0.057$ $p = 0.001$	$R = 0.003$ $p = 0.42$
Between depths (across all atolls)	$R = 0.06$ $p = 0.001$	$R = 0.059$ $p = 0.001$

were re-examined after removing data for each depth and then each atoll in turn: differences remained strongly significant after removing data for each depth in turn, but when data for each atoll were removed, the removal of Egmont atoll (and only Egmont) from the ANOSIM test showed no difference between the remaining atolls ($R = 0.003$, $p = 0.42$) (Table 1, right-hand column). Egmont atoll as a whole, therefore, was strikingly different, and, from Fig. 4, this can be seen to apply to both cover and N. Interestingly, the partially militarised atoll of Diego Garcia had a pattern of N and cover that was not different from the uninhabited atolls, except Egmont.

Coral cover with depth in 2006 can be compared with mean values collected from quadrats or line transects from both 1978 and shortly after mortality in 2001. Data from the 2 northern atolls (Fig. 5) are used, as these are the locations examined on all 3 dates. Recovery of coral cover was greatest in shallow water, where it appeared to be approaching values seen 30 yr ago. In deeper water, recovery was substantially less and, deeper than approximately 20 to 25 m, it still resembled immediate post-mortality values. Below 25 m, coral cover in 2004 appeared considerably greater (but was not measured).

Juvenile colonies

The number of juveniles was counted in 2006 (Table 2) and compared with numbers counted in 2001. Overall juvenile density in 2006 averaged 23.3 m^{-2} , with a range of 6 juveniles m^{-2} at Egmont (5 m) to 28 juveniles m^{-2} at Salomon atoll (15 m). The 2006 density is lower than in 2001, but numbers must be qualified by 2 factors. Firstly, the defined size of 'juvenile' was larger in 2001. Secondly, only 2 yr after the mass mortality, cover by coelenterates was only about a quarter of that seen in 2006, leaving much more unoccupied substrate available to planulae. If this greater available

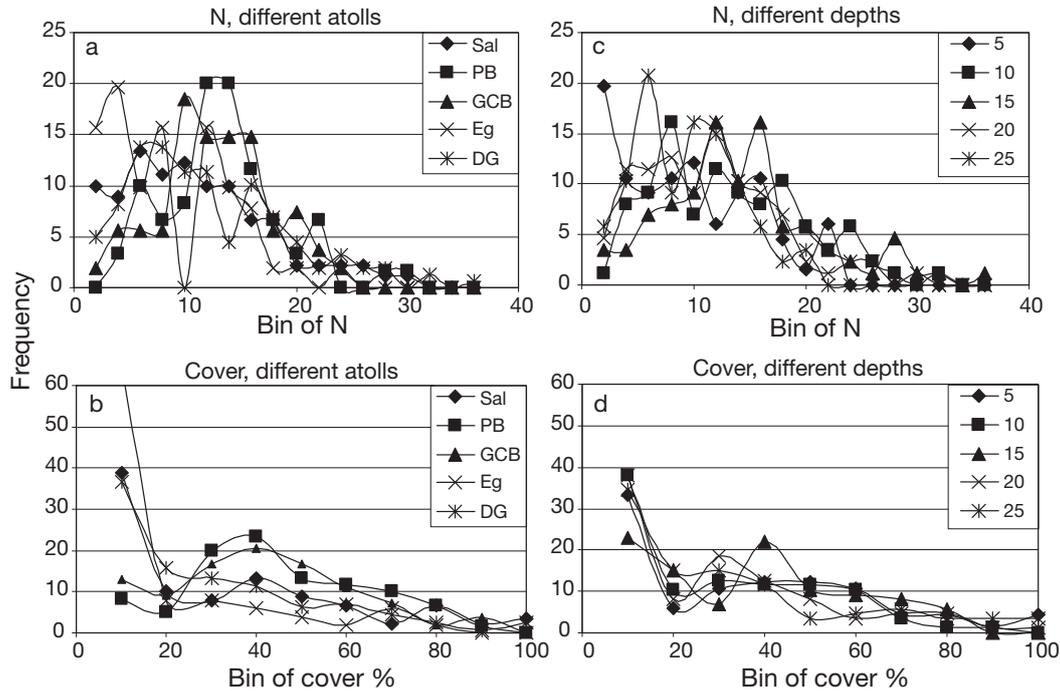


Fig. 4 (a,c) Number of colonies (N) and (b,d) coral cover for the different atolls and different depths. Bins for N in each quadrat are in intervals of 2. Bins for percent cover in the quadrats are in intervals of 10%. Sal: Salomon; PB: Peros Banhos; GCB: Great Chagos Bank; Eg: Egmont; DG: Diego Garcia

space is taken into account, then juvenile density in the 2 yr is more similar (Table 2). There are no data on juveniles from before the 1998 mortality.

Total juvenile numbers are abundant. The main difference noted in 2001 was that Great Chagos Bank had only about half the number of juveniles than all other atolls (Sheppard et al. 2002), but, by 2006, this difference had disappeared.

The generic identity of juveniles was distinguished in both 2001 and 2006. The most abundant are shown

Table 2. Density of juveniles and percent of bare substrate potentially available for juveniles in 2001 and 2006 (data for 2001 from Sheppard et al. 2002 and S. Wilson unpubl. data). The mean value of 23.2 m⁻² in 2006 is the average for the 36 atoll/depth combinations. 'Adjusted' mean number takes into account the greater potential space for settlement in the earlier year

	2001	2006
Size of juvenile	2–160 mm	0–100 mm
Mean juveniles m ⁻²	65.8 (SD 52)	23.2 (range 6–28)
% coral cover	12.3 (SD 10.9)	31.7 (SD 25)
% soft coral cover	Trace	13.6 (SD 15)
% coral + soft coral	~13	45.4
% not covered by coral and soft coral	87	54.6
'Adjusted' mean number of juveniles	75	42

in Table 3. In 2001, *Acropora* juveniles were dominant, which in 2006 is reflected in the high cover at some sites of adult *A. cytherea* and *A. palifera*. This was followed by *Montipora*, *Pavona* and several faviids, mainly *Favia* and *Favites*. The same groups dominated again in 2006, but *Acropora* was proportionately less prevalent because of a marked increase of *Pavona* var-

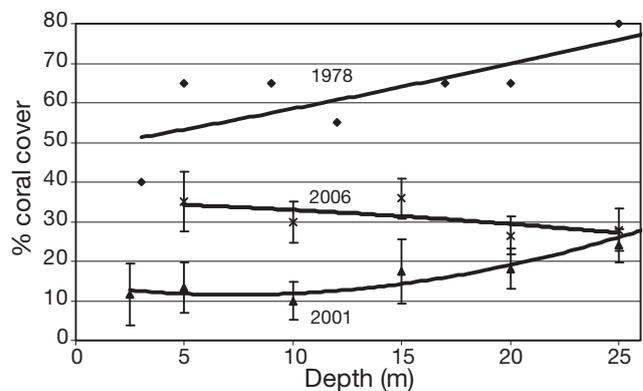


Fig. 5. Coral cover with depth (second-order polynomial lines of best fit) at the 2 northern Chagos atolls where data exist for 1978, 2001 and 2006. Measurements for each year were taken from the same locations and depths. Error bars on the 2001 and 2006 curves are 95% CI limits. Data to obtain CI or error bars for 1978 were lost; ◆: mean values for the different depths in 1978. Data for 1978 and 2001 are from Sheppard (1980), Sheppard et al. (2002) and C. R. C. Sheppard (unpubl. data)

ians juveniles. *Montipora*, which had been second in numerical importance 3 yr after the mortality event, was considerably reduced in 2006. Densities of faviids and *Porites* were similar on both dates.

The number of total recruits showed no differences in average density between depths or atolls. However, when generic information is included, a 2-way crossed ANOSIM testing (unreplicated) for differences in coral juvenile genera (pooled data for each depth at each atoll) shows significant differences between depths ($R = 0.75$, $p = 0.049$), but not between atolls ($R = 0.122$, $p = 0.31$).

The genera driving these global depth differences were determined by χ^2 tests; the number of recruits of each genus was tested against the null hypothesis of no difference with depth (Table 4). Thirteen genera showed clear depth preferences. Many genera were encountered too infrequently to achieve the χ^2 validity requirement of no more than 20% of expected frequencies being <5 , though an additional 5 genera showed >5 -fold differences between depths, and these are also noted in the final column of Table 4. Since recruitment

Table 3. Generic identity of juveniles in both 2001 and 2006 (data for 2001 from Sheppard et al. 2002 and S. Wilson unpubl. data). Numbers as percent of total juveniles counted. Genera are ranked according to dominance in the first year of sampling. All other genera contributed $<1\%$ each to the total

Genus	2001	2006
<i>Acropora</i>	27	11.5
<i>Montipora</i>	17	3.6
<i>Pavona</i>	12	25.6
Faviids	9	10.5
<i>Porites</i>	7	12
<i>Psammocora</i> , <i>Coscinaraea</i>	1.5	17
<i>Pocillopora</i> , <i>Stylophora</i>	1.5	5.3

was onto substrates that largely lacked both coelenterates and significant macroalgae, this suggests strong depth selection at the juvenile stage by many genera. However, there is no way to distinguish whether this is itself caused by depth selection by larvae or by random settlement of larvae followed rapidly by differential post-settlement mortality at different depths.

Depth differences are illustrated further with 'bubble plots' (Fig. 6), which superimpose genus-specific hard coral juvenile density values onto an MDS (multi-dimensional scaling) plot of all sites (Bray-Curtis dissimilarity index after square-root transformation) to illustrate changes in densities of individual genera between depths. The mostly shallow *Acropora* and the deep *Pachyseris* are shown.

Egmont atoll repeat mortality

Several of these results showed Egmont atoll to have anomalously and significantly weaker recovery than other atolls. The western side had clear indications that good recovery of tabular *Acropora cytherea* had taken place between 5 and 10 m depth, but the species then was largely killed again about a year before this survey (Fig. 7). The dead *A. cytherea* tables (with some *A. clathrata*) were up to 120 cm diameter, or approximately 5 to 7 yr old given a radial growth of 10 cm yr^{-1} and an initial year of 'pre-table' development during which colonies develop an encrusting base and then stem (Wallace 1999). The

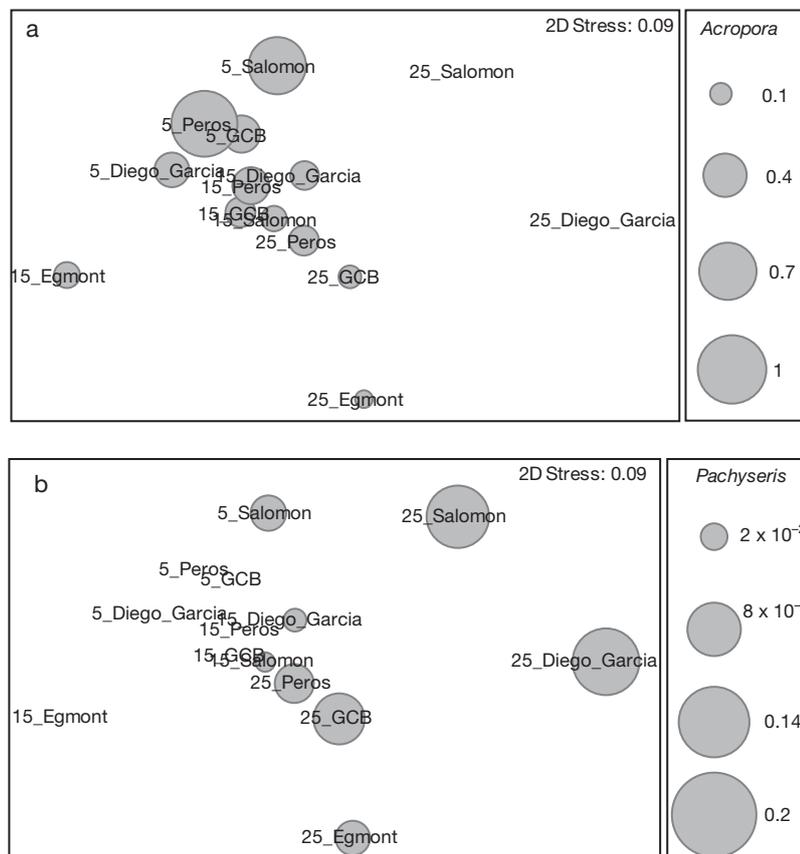


Fig. 6. Multi-dimensional scaling ordination of juveniles. Bubble plots superimposing 2 genera: (a) shallow *Acropora* juveniles and (b) deeper *Pachyseris* juveniles. Scale units are average number of juveniles of the genus per quadrat, from pooled data for each depth at each atoll

Table 4. Depth preferences of juveniles in 2006. First 3 columns: juveniles showing preferences for shallow, mid-, or deep sites. Fourth column: juveniles with 5-fold difference in density between depths (most abundant depth/least abundant depth), but not fulfilling the χ^2 requirement of no more than 20% of expected frequencies being <5 . *Porites* was found almost equally at the 2 shallowest sites, but very much less at 25 m

Shallow (5 m) sites	Mid-depth (15 m) sites	Deep (25 m) sites	Non-significant trends
<i>Acropora</i>	<i>Favia</i>	<i>Leptoseris</i>	<i>Acanthastrea</i> ^a
<i>Stylophora</i>	<i>Favites</i>	<i>Lobophyllia</i>	<i>Astreopora</i> ^b
<i>Porites</i>	<i>Leptastrea</i>	<i>Pachyseris</i>	<i>Coscinaraea</i>
	<i>Montipora</i>		<i>Galaxea</i> ^c
	<i>Pavona varians</i>		<i>Stylocoeniella</i> ^b
	<i>Pocillopora</i>		
	<i>Porites</i>		
	<i>Psammocora</i>		

^aPreference for 5 m; ^bPreference for 25 m; ^cPreference for 15 m

mortality affecting these corals probably occurred in 2005 (see Fig. 2). No *A. cytherea* colonies were seen wholly alive, although small live patches ($<5\%$ colony area) persisted on some tables. No evidence of 'band', 'patch', or 'spot' diseases on remaining live portions were found, though swabs are being examined further (R. Jones unpubl. data). Many tables had crumbled and collapsed, and a talus layer was developing on the

steeper reef slope, causing some damage to all genera in the deeper zones.

On Egmont's eastern side, in contrast, there was almost no living coral or soft coral, and no sign of recently dead table corals. The site exhibited less coral cover and fewer colonies than on the western side ($t = 19$, $p \leq 0.001$; $t = 11$, $p \leq 0.001$, respectively), and remained almost totally denuded of living coelenterates. Brief observations made at this site in 1996, 2 yr before the mass mortality, had shown 35 to 50% hard coral cover at both 5 and 10 m depths, with an additional 20% cover of soft coral (C. R. C. Sheppard unpubl. data). The site had no recently dead tables, and indeed no clear coral structure on the increasingly smoothed limestone surface, indicating either that there has been no recruitment to this side of the atoll, or that repeat mortalities have been frequent, preventing even rudimentary regrowth. It is this denuded eastern side more than the western side that separates this atoll from all others with respect to coral cover and colony number.

DISCUSSION

Shallow zone recovery

Patchy but strong recovery is clear, at least in shallow water, in terms of number of colonies, coral cover

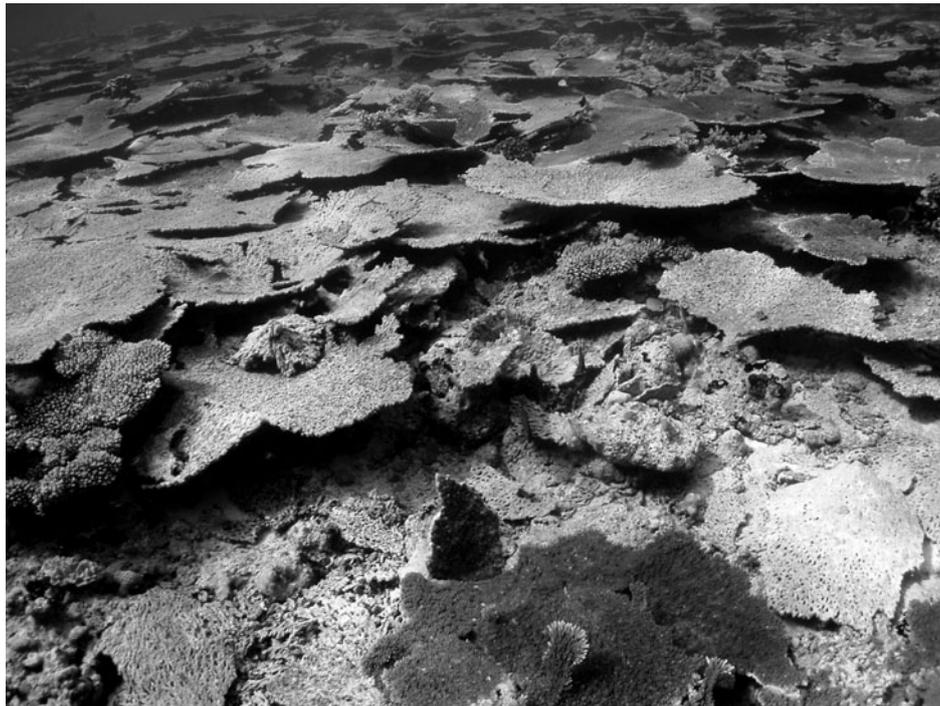


Fig. 7. *Acropora cytherea*. Western Egmont atoll, seaward slope at 8 m depth. Coral tables are mainly dead, some with living parts

and number of recruits. However, most views of shallow (0 to 5 m) seaward slopes in 2006 gave an impression of relatively depauperate coral, which is at odds with the values reported here of essentially restored coral cover at 5 m depth. Before 1998, seaward slopes to about 5 m depth were heavily dominated by mature *Acropora palifera* and by some *A. abrotanoides* that formed dense, branching stands >1.5 m tall (Sheppard 1999b), while, in 2006, these species existed in the form of young colonies that were still encrusting with incipient or rudimentary branches less than about 25 cm tall. This 'maturity discrepancy' is commonly overlooked in many reef surveys, and cannot be accounted for in simple cover values, yet spatial complexity is important to many other species, including fishes (Graham et al. 2006). The growth rate of *A. palifera* is not known, but its very dense skeleton suggests much slower growth than the tabular forms. Thus, recovery of substrate cover in *A. palifera* zones appears to precede recovery to a mature, branching structure by perhaps 10 to 20 yr.

In contrast, at mid-depths on reef slopes (approximately 5 to 10 m) several branching and tabular species have recovered their 3-dimensional complexity, although total substrate cover has recovered more slowly than in shallower water. Coral cover itself is therefore an insufficient measure of ecological condition; this has been stated before (Bellwood et al. 2004, Price et al. 2007), but cover continues to be retained in many surveys of reefs because of its simplicity compared with many alternatives.

These results and observations indicate that despite repeated warming and bleaching events, warming to lethal temperatures has not recurred in most of this archipelago. It is possible that some of the warmer years of the 2000s that caused bleaching did cause a repeat in set backs to juveniles or reproduction, but, although small colonies of 2 to 3 yr may be readily counted, tiny but dead juveniles younger than this are often impossible to detect using visual *in situ* census. Further, it is not known what duration or severity of bleaching is necessary to interrupt reproduction. However, the abundance of juvenile corals at all depths on the rapidly recovering Chagos reefs, including western Egmont where a repeat of mortality of adults was observed, suggests that recruitment has not been a limiting factor across most of this archipelago. As early as 2001, a high number of juveniles was counted, although total coral cover averaged only 12% at that time. While recruitment (notably of previously dominant *Acropora*) has been identified as a limiting factor preventing reef recovery at marginal reef sites in east Africa (Souter & Linden 2000), this has not been limiting here.

A number of authors have documented community shifts in post-1998 coral assemblages, such as relative

increases of faviids and *Porites* at the expense of *Acropora*, notably in the more severely stressed Persian Gulf (e.g. see Riegl 2002). Changes in coral have also been accompanied by changes in associated fish composition (Berumen & Pratchett 2006). However, no such change towards a different coral assemblage can be seen at Chagos.

Much briefer observations in the lagoons showed similarly strongly recovered dominance by *Acropora* (authors' unpubl. data). It has been observed previously (Sheppard 1999a) that corals in all the deep (25 to 60 m) lagoons (all except Egmont, which is extremely shallow) survived considerably better than corals on seaward slopes, and it was supposed that because lagoonal corals were more regularly subjected to elevated water temperatures (Pugh & Rayner 1981), they perhaps acclimated better to it. It can be speculated that these lagoons may be a reservoir of surviving adults that have led to such successful recruitment throughout. Sources of larvae may also include adults that had a refuge in depth on seaward slopes. Non-local recruitment is likely to be much slower. Upcurrent of Chagos in different seasons lies Indonesia or Africa/Seychelles, both several 1000s of kilometres distant, while the Maldives, which are closer, do not lie upcurrent in the major oceanic flows of the Indian Ocean during any season.

Future trends and management

While recovery in Chagos illustrates what is possible in 8 yr following heavy mortality, temperature projections suggest that only about 20 yr are available before temperature peaks will occur too frequently to permit recovery (Sheppard 2003). As well as a rising mean, the 40 and 60 mo SST cycle of up to 0.8°C superimposed on the overall rising temperature trend (see Fig. 2) suggests that further episodes of severe warming are very likely. These cycles may be due to the Indian Ocean Dipole (Abram et al. 2007) coincident with ENSO.

Effects of global warming and local impacts such as nutrification, over-fishing, sedimentation and various forms of pollution may be synergistic, and separating effects from multiple causes is difficult and sometimes contentious (Richmond et al. 2006). Given that examples of reefs without local impacts are rare, these results illustrate the importance of reference sites such as this that lack local, direct impacts. Effective management is considering locations and kinds of reefs that can most effectively be managed (Obura 2002). In the absence of local impacts in Chagos, recovery appears to have progressed steadily at an archipelago scale, so that in the face of rising global changes that

cannot be managed at a local level, management of those issues that can be controlled becomes increasingly important.

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