

## ***Reef shark declines in remote atolls highlight the need for multi-faceted conservation action***

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### ABSTRACT

1. The decline of large-bodied predatory species in the oceans is a concern both from a sustainability perspective and because such species can have important ecological roles. Sharks are particularly vulnerable to fishing as their life histories are characterized by late age at maturity, large body size, and low fecundity.

2. Substantial shark population declines have been documented for a number of coastal and pelagic systems, with high population abundance limited to a few remote locations. The relative abundance and composition of reef shark populations are assessed from 1975 to 2006 at a remote, largely uninhabited, group of atolls in the central Indian Ocean; the Chagos Archipelago.

3. Number of sharks observed per scientific dive declined from a mean of 4.2 in the 1970s to 0.4 in 2006, representing a decline of over 90%. Silvertip sharks displayed an increase in abundance from 1996, whereas blacktip and whitetip reef sharks were rarely encountered in 2006.

4. Poaching in the archipelago, is the most likely cause of these declines, highlighted by a number of illegal vessels containing large numbers of sharks arrested since 1996. The data highlight that shark populations, even in remote, otherwise pristine, marine areas, are vulnerable to distant fishing fleets, and a range of strategies will need to be used in concert for their conservation. Copyright © 2010 John Wiley & Sons, Ltd.

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### INTRODUCTION

Fishing typically targets larger individuals first, which often results in large and rapid declines in top predators (Jennings and Kaiser, 1998; Friedlander and DeMartini, 2002; Myers and Worm, 2003; Sibert *et al.*, 2006). Documenting such information is not only important to monitor declines in fishery target stocks, but also because loss of top predators can have ramifications for the rest of the ecosystem, including trophic cascades (Worm and Myers, 2003; Bascompte *et al.*, 2005; Daskalov *et al.*, 2007; Myers *et al.*, 2007; Heithaus *et al.*, 2008), changes in the timing of prey life history parameters (DeMartini *et al.*, 2005), and a reduction of key ecosystem functions (Worm *et al.*, 2002). Elasmobranchs (sharks and rays) are among the apex predators of marine food webs. Unfortunately, many species of elasmobranchs are vulnerable to over-exploitation owing to particularities of their life

histories, including late age at maturity, large body size, and low fecundity with a long gestation period (Reynolds *et al.*, 2001).

The decline of sharks has increased in the past two decades, linked to increases in the shark fin trade (Fong and Anderson, 2002; Schindler *et al.*, 2002; Clarke *et al.*, 2007), with fins selling for as much as US\$700/kg (Verlecar *et al.*, 2007). Direct targeting of sharks has become more widespread, but even when taken as bycatch, common in some longline and trawl fisheries, sharks are often more accurately considered as secondary targets rather than waste (Dulvy *et al.*, 2008). Indeed, the sale of shark fins is an important supplementary income to crews on some longline vessels. Large declines in pelagic shark species have been reported (Baum *et al.*, 2003; Baum and Myers, 2004; Ferretti *et al.*, 2008), linked to commercial or industrial scale fisheries. Similar declines in coral reef associated sharks have also been reported, even

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occurring in well managed marine protected area networks (Robbins *et al.*, 2006). Based on spatial comparisons, some remote coral reef locations and no-go preservation areas still host large populations of reef associated sharks (Robbins *et al.*, 2006; Stevenson *et al.*, 2007; DeMartini *et al.*, 2008; Sandin *et al.*, 2008). However, such studies of reef shark populations come under scrutiny as they do not have a historical baseline (Jackson *et al.*, 2001) and other factors may be driving trends. For example, spatial comparisons using underwater visual census data may be influenced by increased inquisitive behaviour displayed by sharks where divers are not common or where fishing pressure is very low. Many studies of reef shark population status are based on spatial comparisons as few long-term records of reef shark population status are available. This is unfortunate, as there is a clear need to document how populations are changing in the long term to understand which management strategies are working and to prioritize conservation efforts.

Here, relative reef shark population size data from a remote atoll system in the central Indian Ocean, the Chagos Archipelago, are presented. Such information is particularly important as little fisheries and ecological information exists for sharks in the Indian Ocean (Dulvy *et al.*, 2008). Shark sightings by scientific divers are documented from 1975 to 2006, representing the longest temporal dataset of shark numbers reported for coral reefs. The results are discussed in terms of shark conservation, identifying a need for multiple strategies from fishery enforcement through to consumer education.

The Chagos Archipelago, 500 km south of the Maldives, and roughly 1700 km south-west of Sri Lanka, comprises seven atoll structures, with a total area of over 15 000 km<sup>2</sup>, and an exclusive economic zone of over 650 000 km<sup>2</sup>. In total, 55 islands comprise the archipelago. Diego Garcia in the south-east of the archipelago, which covers 1% of the total area of the archipelago but which contains 50% of the land area, hosts a US Navy base and the British administration for the territory. The remaining atolls and associated islands have been uninhabited since the early 1970s. A small seasonal (June–August) Mauritian fishery has operated in the archipelago since the early 1970s, which has been under licence since 1991 (Mees, 1996). The fishery, which largely targets grouper and deep water snappers, is very small, with no uptake of licences in some years (Mees, 1996, C. Mees, personal communication). In addition to this inshore fishery, there is a licensed blue-water fishery largely for tuna, and a limited recreational fishery around Diego Garcia (Anon., 2007). Since 2006 all licensed fishing vessels in Chagos have to declare the quantities of shark fin bycatch and other products on board upon inspection by the Chagos fishery patrol vessel and in log books. Furthermore, shark finning was banned in 2006 and use of wire trace on longlines has been banned in the consolidated fisheries ordinance since 1999, with an associated penalty of £100 000 (Anon., 2007). A British Indian Ocean Territory Patrol Vessel, whose main activities are fisheries patrols and border protection, has actively patrolled the archipelago since 1996, charged with managing the Mauritian inshore fishery and offshore tuna fishery and detecting illegal fishing vessels. Illegal vessels come principally from Sri Lanka, which visit the archipelago to target sharks (Anderson *et al.*, 1998) and Beche de Mer (Spalding, 2006; Price *et al.*, 2009).

## METHODS

### Data collection

Data were collected on the number of reef sharks seen per dive by scientific divers during each of five scientific expeditions to the Chagos Archipelago (for a map showing the location of Chagos and lay out of the atolls; see Sheppard *et al.*, 2008). Data were collected by one of the authors in each of the following years: 1975, 1978–9, 1996, 2001 and 2006. In each year three atolls were surveyed; Salomon, Peros Banhos and the Eagle and Brothers group in the western area of the Great Chagos Bank. Furthermore, the same locations in each atoll were consistently visited among years for comparison through time. All observations were made between 9am and 4pm while the authors were undertaking surveys of reefs and fishes, but scanning the surrounding waters to record sharks every few minutes. Specific features, such as direction of movement and size of animal were mentally noted to avoid double counting of individuals. Dives were of 1 h duration and were restricted to the reef front between 5 m and 25 m. Water clarity is very high in the Chagos Archipelago, with horizontal visibility typically >30 m. From 1996 onwards the species of shark was also recorded. Although such data do not provide density of sharks, as no specific unit area of reef surveyed was recorded, it does provide reliable data on the relative abundance of sharks among years. Dives were quite static (~50–100 m), with little active or unidirectional swimming, so relatively small areas of reef were covered. There has never been any recreational diving activity in the Chagos Archipelago, and diving occurs only during scientific expeditions, the five represented here being all such expeditions since 1975. Therefore, any behavioural response of sharks to divers in the water is deemed consistent among years. In 2006, along with N.A.J.G. whose data are used here, three additional scientists recorded sharks during dives, including C.R.C.S. who collected data in 1975 and 1979. These data were used to assess inter-observer error in observing sharks.

### Data Analysis

The mean number of sharks per dive was calculated for each year and 95% confidence intervals calculated to compare the relative abundances among years. Insufficient resolution in the data in earlier years prevented breaking down the data by individual atoll or using more sophisticated statistical tests. However, the interest was in large differences that may have occurred through time and across the three atolls surveyed. Where 95% confidence intervals overlap, there is no significant difference in relative abundance of sharks between those years. The numerical and percentage contribution of different species of shark to the total in 1996, 2001 and 2006 was also calculated. Variation in sharks per dive among the three atolls and across 1996–2001–2006 was assessed using two-way crossed ANOVA. This enabled one to assess if there were aggregations of sharks on certain atolls. Furthermore, using the data collected by additional observers in 2006, inter-observer bias in recording sharks seen per dive was assessed using one-way ANOVA. For both sets of data, homogeneity of variances was confirmed using Levene's test and normality of the data with Q–Q plots.

**RESULTS**

The relative abundance of reef sharks in Chagos was stable at 4.2 per dive between 1975 and 1979 (Figure 1). However, this abundance was greatly reduced by 1996, to a mean of 0.7 sharks per dive. A small increase in 2001 (1.4 sharks per dive) was not sustained in 2006, with a mean abundance per dive of 0.4 (Figure 1). The data represent a decline of over 90% in the number of sharks observed in the Chagos Archipelago between 1975 and 2006.

The composition of reef sharks changed between 1996 and 2006. A greater proportion of the silvertip shark, *Carcharhinus albimarginatus*, was observed in 2001 and 2006 (Figure 2), and this was also evident in the mean abundance reported (Table 1). The proportion and abundance of the grey reef shark, *Carcharhinus amblyrhynchos*, increased between 1996 and 2001, and decreased again by 2006 (Figure 2, Table 1). The proportional representation of the tawny nurse shark, *Nebrius ferrugineus*, declined across the three sampling years (Figure 2), despite a small increase in actual abundance in 2001 (Table 1). This decline in nurse sharks was similar for blacktip reef sharks, *Carcharhinus melanopterus*, which did not feature in the 2006 data (Figure 2, Table 1). The whitetip reef shark, *Triaenodon obesus*, was recorded in very low abundance in all three years.

Variation in sharks seen across the three atolls and through time for the post-1996 data was small, with no significant difference detected among the atolls ( $F_{2,36} = 0.47, P = 0.63$ ) or among years ( $F_{2,36} = 2.76, P = 0.08$ ). Furthermore, there was no significant difference in sharks observed per dive between

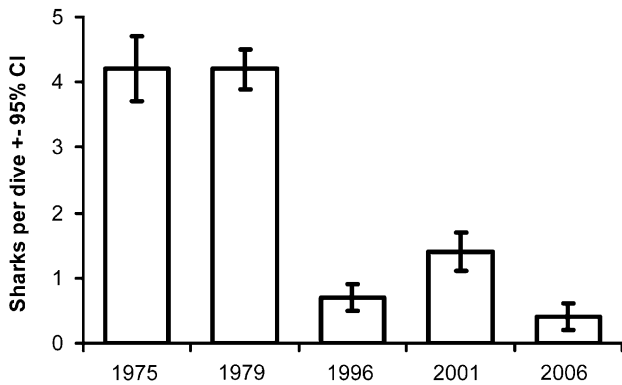


Figure 1. Change in relative abundance of reef-associated sharks seen per scientific research dive in the Chagos Archipelago, 1975–2006. Number of dives per year: 1975–67, 1979–140, 1996–68, 2001–20, 2006–46.

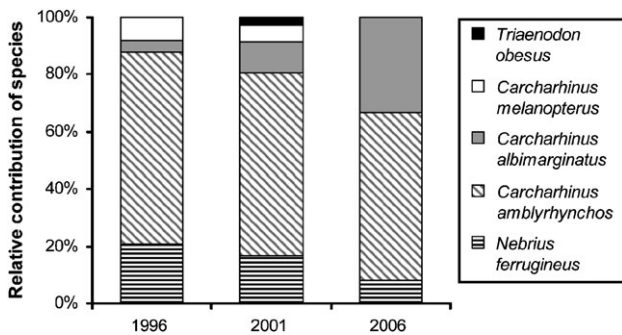


Figure 2. Relative contribution of species-level sharks seen per scientific research dive in the Chagos Archipelago, 1996–2006.

the four observers in 2006 ( $F_{3,16} = 0.33, P = 0.81$ ), with mean values ranging from 0.37 to 0.59.

Data were available on the number of fishing vessels detected in the archipelago and the number of vessel arrests made since 2002. Vessels found not fishing, and with no evidence of fish on board, were not arrested. It should be noted that patrolling for illegal vessels is only one of a number of activities undertaken by the fisheries patrol vessel, and hence patrolling effort may not be consistent among years. A small apparent decline in the number of vessels detected and arrests made since 2003 was broken with the arrest of six vessels in 2009 (Table 2). It is not clear if this variation corresponds to changes in poaching activity in the territory or simply reflects reduced search effort or better avoidance on the part of poachers. It was estimated that the fishery patrol vessel had a success rate of ~10% several years ago, with the actual number of poaching vessels, taking sharks and holothurians, working in the archipelago being 30–60 per year (Price *et al.*, 2009). Vessels that are caught fishing often have a large quantity of shark carcasses in their hold (Figure 3).

**DISCUSSION**

We have observed very large declines in reef shark abundance in a remote area over a 30 year period. The declines of 90% are comparable with long-term declines of pelagic species in the

Table 1. Species level sharks seen per scientific research dive in the Chagos Archipelago, 1996–2006

	1996		2001		2006	
	Sharks/dive	SE	Sharks/dive	SE	Sharks/dive	SE
Whitetip reef shark ( <i>Triaenodon obesus</i> )	0.00	0.00	0.04	0.02	0.00	0.00
Blacktip reef shark ( <i>Carcharhinus melanopterus</i> )	0.06	0.03	0.08	0.03	0.00	0.00
Silvertip shark ( <i>Carcharhinus albimarginatus</i> )	0.03	0.01	0.16	0.05	0.12	0.05
Grey reef shark ( <i>Carcharhinus amblyrhynchos</i> )	0.49	0.14	0.92	0.28	0.21	0.10
Tawny nurse shark ( <i>Nebrius ferrugineus</i> )	0.15	0.15	0.24	0.09	0.03	0.03

Table 2. Number of Sri Lankan fishing vessels detected by the BIOT fishery patrol vessel 2002–2009. Vessels passing through the territory legally did not receive a warning

Year	Inspections	Arrests	Warnings
2002	12	3	7
2003	26	8	9
2004	17	5	0
2005	11	6 <sup>a</sup>	6
2006	3	2	0
2007	3	1	0
2008	7	2	0
2009	12	6	0

<sup>a</sup>In 2005 five of the arrests involved fishing camps set up on islands, where the principal target was Beche de Mer.



Figure 3. Arrested illegal Sri Lankan fishing vessels in the territorial waters of Chagos frequently have large quantities of sharks in their holds. These sharks were confiscated from the small vessel adjacent to the pier in 2008. Photo taken by Rob Gater and provided courtesy of the MRAG Ltd, London.

north-west Atlantic (Baum *et al.*, 2003; Baum and Myers, 2004). In contrast, however, spatial surveys of reef shark populations have indicated remote locations such as the Cocos (Keeling) Islands and the northern Line Islands, and no-go areas on the Great Barrier Reef, still host very high abundances compared with locations closer to larger human population densities (Robbins *et al.*, 2006; DeMartini *et al.*, 2008; Sandin *et al.*, 2008). However, this study highlights that even remote areas are not immune to the pressures of fishing, with fishers increasingly exploiting most marine realms of the world (Berkes *et al.*, 2006). Indeed, even the remote northern Line Islands have not escaped shark finning, although shark extraction appears to have been more prevalent at Kiribati-owned Tabuaeran (Fanning) and Kiritimati (Christmas) atolls (E. DeMartini, personal communication). With shark fins receiving up to US\$700 kg<sup>-1</sup> (Verlecar *et al.*, 2007), the reward from these fisheries often outweighs the risks.

Despite the potential knock-on effects of a reduction in top predators (Worm and Myers, 2003; Bascompte *et al.*, 2005; Daskalov *et al.*, 2007; Myers *et al.*, 2007; Heithaus *et al.*, 2008), the Chagos Archipelago appears to be a near pristine environment. No permanent residents inhabit the islands outside Diego Garcia. The resilience of the system has been highlighted by the rapid recovery of the coral reefs from the 1998 bleaching event (Sheppard *et al.*, 2008). Reef fish and coral cover have recovered well since the ocean-wide coral mortality of 1998, highlighting Chagos as a pillar of stability in an otherwise heavily exploited and increasingly degraded region (Graham *et al.*, 2008; MacNeil and Graham, 2010). Indeed the diversity of reef fish assemblages in Chagos are far less affected than those of the Seychelles (Spalding, 1999). It appears that the only serious poaching in the archipelago is for sharks and Beche de Mer; both high value commodities. A recent study found that poaching has reduced shark populations in the no-take zones of the Great Barrier Reef (Robbins *et al.*, 2006), despite effective management of other reef fish species (Russ *et al.*, 2008). Vessels caught poaching sharks in the waters of Chagos are impounded in Diego Garcia, and the vessel owner can be fined up to a maximum of £100 000 (Anon., 2007), although often a smaller

fine is imposed (Spalding, 2006). In reality such fines are often not paid and the owner (usually not on the vessel) forfeits his boat, which is later destroyed, and the crew repatriated. The haul of sharks which these vessels are taking (Figure 3), and the amount that shark fins sell for on the market, highlights why fishers may be willing to risk such large fines, or sacrifice their vessels. It is possible that the more stringent rules in the British Indian Ocean Territory consolidated fisheries ordinance (Anon., 2007) and if the general trend of a reduction in the number of Sri Lankan poaching vessels arrested since 2003 represents reduced effort, there may be some chance of recovery of shark populations. However, any recovery would probably be slow, poaching may increase again if numbers increase, and continued monitoring of shark populations in Chagos will be required to quantify any such recoveries.

Because all the species assessed were reef associated, the observed decline is probably due to inshore poaching, rather than incidental bycatch from the tuna longline fishery or the small and monitored Mauritian inshore fishery, both of which fish in areas off the reef where pelagic sharks, and species such as silvertip sharks are more common. Baum and Myers (2004) showed that coastal species of shark did not change in abundance (based on longline catches) greatly between the 1950s and 1990s in the Gulf of Mexico, in sharp contrast to pelagic species, which seem much more prone to this kind of exploitation. In Chagos between 1996 and 2006 there has been an increased dominance of silvertip sharks. These sharks are more active and voracious than some of the other species, and thus may be expected to be vulnerable to fishing. It is possible that the small increase is in response to the wire trace and finning regulations introduced to the licensed fishery. In contrast, there has been a reduction in more tightly reef-associated species such as the tawny nurse and blacktip reef sharks, which further suggests that the fishery is highly reef associated. Data from the tuna long-line fishery in Chagos were not available to estimate impacts that this may be having on pelagic shark species. The recent ban on finning and wire trace in the territory should be beneficial to such species, although policing of such bans is extremely difficult as finning must be observed directly. Longline vessels are transient and fish across the Indian Ocean, so will typically already have a haul of shark fins on board before entering Chagos waters. It must be noted that the small increase in silvertip sharks in recent years is likely insignificant compared with the baseline abundance of these sharks before exploitation.

Although the data collection protocol was standardized as best as possible, and the three authors were the sole data collectors, observational data of this nature is not without its problems. Targeted and quantitative underwater surveys of reef sharks is a labour-intensive undertaking, requiring long and wide transects, with very few examples worldwide (Robbins *et al.*, 2006). The data presented here represents relative abundance, but cannot be used to estimate standing density or biomass. As few observers were involved, Chagos is not disturbed by other divers, water clarity is very high, and the differences in relative abundance between the 1970s and 1996 onwards were so great, we feel the data presented here do reflect the trends that have occurred in shark numbers in Chagos. Data post-1996 indicated that abundances of sharks among the three atolls were similar, and thus any slight variations in time spent at each atoll should not bias the results. Furthermore, a comparison of four observers in 2006 indicated that observer bias was not a problem.

These data beg the question as to whether the abundance of sharks in Chagos in the 1970s is a rational baseline. Baum and Myers (2004) assess baselines in shark populations in the Gulf of Mexico from 1950, as industrial long-line fishing in that region commenced in 1957. Given that, (1) Chagossian people who inhabited the islands until the early 1970s were copra plantation workers, rather than fishing communities, (2) coastal species of shark are not greatly affected by long-line fishing fleets (Baum and Myers, 2004), and (3) the shark fin trade really took off in the 1980s and 1990s (Fong and Anderson, 2002; Schindler *et al.*, 2002), it seems possible that the 4.2 reef sharks observed per dive in the 1970s is a realistic baseline for Chagos. Such numbers correspond to numbers of sharks seen in some remote locations that are thought to have escaped poaching (JH Choat, personal communication). Furthermore the stability between 1975 and 1979 would suggest declines in reef shark numbers did not occur during that decade. It should be noted, however, that fishery exploitation, at least to some extent, may have occurred well before the 1970s, and the true baseline is very hard to ascertain (Jackson *et al.*, 2001).

With the huge declines in shark stocks reported here and from numerous other locations (Anderson *et al.*, 1998; Stevens *et al.*, 2000; Baum *et al.*, 2003; Baum and Myers, 2004; Robbins *et al.*, 2006; Ferretti *et al.*, 2008; Sandin *et al.*, 2008), a critique of conservation and management strategies is clearly necessary. Marine protected areas, or fisheries closures, have been proposed for shark conservation by numerous authors (Bonfil, 1999; Baum *et al.*, 2003; Robbins *et al.*, 2006; Watson *et al.*, 2009). However, even reef sharks are fairly mobile species (Chapman *et al.*, 2005), and the success of small closures can be limited (Robbins *et al.*, 2006). Furthermore, the highly lucrative shark fin industry is likely to encourage poaching (Berkes *et al.*, 2006; Robbins *et al.*, 2006) as is evident in Chagos. It is clear from these data, and those of other studies (Robbins *et al.*, 2006), that if enforcement and/or compliance are weak, substantial depletions of stocks can occur. However, closures do have an important role, with carefully positioned long-line closures predicted to produce large benefits for shark bycatch species (Baum *et al.*, 2003; Watson *et al.*, 2009), and well enforced no-go reef closures and remote locations are likely to maintain reef shark abundance (Robbins *et al.*, 2006; Sandin *et al.*, 2008).

Shark fisheries are generally poorly monitored and regulated in many countries. Poor data quality and high variance make accurate stock assessments difficult (Dulvy *et al.*, 2008). Greater efforts to monitor fisheries are necessary, with the implementation of species specific size limits, and the use of total allowable catches and individual transferable quotas (Fong and Anderson, 2002). However, as many reef shark populations are exploited in countries where fisheries enforcement and monitoring is not strong, such fisheries tools will be difficult to implement. Bans on finning are expected to reduce catch and waste and to promote more ethical fishing practices. Again, although such bans are likely useful, they will be hard to enforce in many locations and will have little effect where the carcass was already utilized (as appears to be the case in Sri Lankan shark fisheries, as exemplified by whole carcass sharks commonly retrieved from poaching vessels in Chagos (Figure 3)).

Monitoring and limiting the trade in shark products is another possible management and conservation strategy. Assessments of the trade in shark fins have identified that the biomass of sharks passing through the trade exceeds global catch statistics 3–4-fold, highlighting the limitations of relying

on fishery statistics (Clarke *et al.*, 2006a). Under-reporting and mis-reporting of species in the shark fin trade is a problem (Clarke, 2004), but DNA techniques are providing the means to more accurately monitor species specific biomass (Clarke *et al.*, 2006b; Verlecar *et al.*, 2007). More accurate monitoring of the species specific trade of reef sharks should enable key exploited locations to be identified and permit identification of where a large proportion of juvenile individuals are being exploited. The use of shark fin products is deeply engrained in Chinese culture (Clarke *et al.*, 2007). Movement of the trade from Hong Kong to mainland China has made the trade harder to monitor and that country's increased consumer spending power suggests demand may increase. Tackling shark conservation from the consumer end may therefore be an appropriate policy to reduce demand (Clarke *et al.*, 2007).

The substantial decline in reef shark populations documented here for a remote and pristine location in the Indian Ocean highlights the need for a re-assessment of shark conservation and management strategies. The return received for shark fin products suggests that even remote and protected locations are at risk of depletion. The conservation and management strategies outlined above are all likely to fail in isolation. Rather, a multi-faceted and integrated conservation policy, incorporating protection, fisheries regulations and monitoring, finning bans, monitoring of the trade and consumer education will be necessary to effectively manage shark stocks.

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# Seabird populations of the Chagos Archipelago, Indian Ocean: an evaluation of IBA sites

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**Abstract** Indian Ocean seabirds are subject to numerous threats, and populations are thought to be at a fraction of historical levels. We carried out a rapid assessment of the seabird breeding populations of the Chagos Archipelago, a UK Overseas Territory, during early March 2006. We surveyed 26 islands covering the four island groups of the Archipelago. A total of 17 species of breeding seabird were recorded. Since the last survey in 1996, nine species showed reductions in the number of breeding pairs, with brown noddy *Anous stolidus* and lesser noddy *Anous tenuirostris* showing reductions of *c.* 22,000 and *c.* 27,000 pairs, respectively. These reductions, coupled with apparent sooty tern *Sterna fuscata* colony relocations, are central to our suggested changes to the Important Bird Areas (IBAs) criteria in the Archipelago and we propose two new sites for IBA status. We discuss our findings within a regional conservation context and provide recommendations for the implementation of an annual monitoring scheme of Chagos seabird populations to allow appropriate conservation management.

**Keywords** Chagos, conservation, IBAs, Indian Ocean, monitoring, seabirds.

This paper contains supplementary material that can be found online at <http://journals.cambridge.org>

## Introduction

The islands of the Indian Ocean are among the most biologically diverse regions on earth and provide a haven for the region's breeding seabird species (Conservation International, 2006). There are still many data deficiencies for seabird populations in the Indian Ocean. Populations are thought to be at a fraction of their historical levels and subject to widespread and numerous terrestrial (Feare, 1976, 1978; Courchamp *et al.*, 2003; Baker *et al.*, 2004) and marine threats (Klaer & Polacheck, 1997; Willmann, 2001; Ramos *et al.*, 2002; van der Elst *et al.*, 2005).

Biogeographically, the Chagos Archipelago lies at the southern end of the Laccadives-Maldives-Chagos ridge, covers an area of 60,000 km<sup>2</sup> and consists of a series of islanded atolls, several drowned atolls, and submerged banks (Sheppard &

Seaward, 1999). All islands within the archipelago have been uninhabited since the late 1960s with the exception of Diego Garcia, which supports a US military facility of *c.* 3,000 personnel (Sheppard & Seaward, 1999). The last extensive survey of the breeding seabirds in Chagos was in 1996 (Symens, 1999) and since then only the birds of Diego Garcia have been surveyed (Carr, 1998, 2004, 2005). Ten Important Bird Areas (IBAs) are currently designated on Chagos (BirdLife International, 2004), all of which support significant seabird/waterbird congregations (Symens, 1999; Carr, 2004).

The lack of up-to-date information for seabirds in the Chagos Archipelago is a fundamental barrier to the detection of threats, construction of management plans, and implementation of conservation actions. Here we present the results of a survey of the Chagos Archipelago and synthesize the best current information on the breeding seabird populations in the Archipelago and interpret these within both a regional and global conservation context.

## Methods

The seabirds of the Chagos Archipelago were surveyed over 1–15 March 2006 by AMcG. In total, breeding seabirds were counted on 26 islands covering most island groups (Appendix). Rapid assessment surveys were conducted between 08.00 and 18.00 and the amount of time spent on each island was 0.75–4 h, dependent on the size of the island and the number of seabirds present. During the course of a survey the perimeter of the island was mapped using a global positioning system (GPS) for calculation of perimeter distance and island surface area. As birds were not marked, we endeavoured to survey islands that were in close proximity to one another on the same day to reduce the potential problem of double counting.

For all islands we estimated the number of breeding pairs of each seabird species present by using apparently occupied nest-sites (AONs; Bibby *et al.*, 1992) and followed the criteria for an AON for each species from Symens (1999). For the smallest islands only, direct counts of all AONs were made for each seabird species present but for the majority of islands a different approach was required and the survey techniques employed are detailed below.

Boobies (Sulidae), frigatebirds (Fregatidae) and tree-nesting terns (Sternidae)

As the vast majority of boobies, frigatebirds and tree-nesting terns nest in the vegetation in close proximity to the sea's

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edge a series of plot counts was conducted around the entire coastline of each island. All plots were at the interface between the vegetation line and either the open sand, rocky substratum or sea's edge depending upon the nature of each island. At each plot we counted the number of AONs of each seabird species in a 10 m (along the coastline)  $\times$  5 m (inland) plot and repeated counts every 100 m around the entire coastline of each island. We derived individual island population estimates for each species by dividing the total circumference of each island by 10 and then multiplying this value by the mean number of AONs per plot. Any major seabird colonies, mainly lesser noddy *Anous tenuirostris*, that had been identified as occurring outside the area surveyed, were visited and direct counts of AONs made and added to island totals. The areas occupied by these colonies were subtracted from the island circumference estimate for that species. Colonies that had been identified as occurring in the interior of an island, mainly frigatebirds and some lesser noddies, were also visited and direct counts of AONs made and added to island totals.

#### Ground-nesting terns (Sternidae)

We endeavoured to minimize disturbance at ground-nesting tern colonies. Sooty tern *Sterna fuscata* colonies were generally large and expansive, with a high density of birds, and therefore we adopted a species-specific approach. Firstly, the perimeter of the colony was walked and mapped using a GPS. Next, the number of visible AONs in a 5 m radius circle were counted at five or six points on a transect line through the colony (mean distance between plot counts =  $105.1 \pm \text{SE } 12.4$  m; range 17–292 m;  $n = 40$  inter-point distances from three colonies) because the density of nests is known to vary throughout a colony (Feare *et al.*, 1997). The number of plot counts was dependent on the size and shape of the colony. Mean number of AONs per  $\text{m}^2$  was calculated for each colony and this value was multiplied by colony surface area to give an overall estimate of breeding pairs. Colony surface area was calculated from GPS mapping data using the software *MatLab* (Mathworks, Cambridge, UK). We did not conduct plot counts in the sooty tern colony on Grande de Coquillage because the risk to eggs and chicks was deemed too great. To attain an estimate for this sooty tern colony we mapped the colony as above and then used an average AON per  $\text{m}^2$  from the other three colonies. For all other ground-nesting tern species colonies were small and direct counts of AONs were made.

#### Shearwaters (Procellariidae)

In Chagos two species of shearwater, Audubon's shearwater *Puffinus lherminieri* and wedge-tailed shearwater *Puffinus pacificus*, nest in mixed colonies (Symens, 1999). To derive estimates for the number of breeding pairs of each, we used

a similar approach to that used for sooty terns. Firstly, we visually estimated the percentage of the surface area of the island that had burrows present and then conducted a series of plot counts (range 4–9 points) within the colony. All plot counts took place along the fringes of the colony because of the dangers from collapsing burrows. At each plot we counted the number of burrows of each species in a  $10 \times 5$  m plot and used an occupancy rate of 45% (Symens, 1999) to derive an estimate of AONs per  $\text{m}^2$  for each point. Burrows were assigned to a species on the presence of large pre-fledging chicks. The mean number of AONs per  $\text{m}^2$  for each species, for all plots, was multiplied by colony surface area to derive an island population estimate.

We did not survey the main island of Diego Garcia and used breeding pair estimates for this island from Carr (2005). To assess the regional and global significance of the island populations and IBA criteria we used data from the literature on biogeographical and global population sizes. Terns are classified as waterbirds, rather than seabirds, for the purposes of the Ramsar Convention (Delaney & Scott, 2002) and therefore Asian and global estimates of the number of breeding pairs of each tern species were taken from published literature on the number of estimated individuals (BirdLife International, 2004) and halving this value. Global estimates of the number of breeding pairs of each seabird species, excluding terns, were also taken from BirdLife International (2004). As far as we are aware there are no Asian population estimates currently available for any seabird species. Species' names and classification follows BirdLife International (2004).

## Results

All 17 species recorded breeding in 1996 (Symens, 1999) were recorded in 2006 (see full data set by island in Appendix). We directly compared the breeding numbers of each seabird species for islands that were surveyed in both 1996 and 2006. In 2006 nine species showed a decrease in the number of breeding pairs (mean relative reduction in population = 57.6%, range 13.3–90.1%) compared to 1996 (Table 1). The largest absolute decreases occurred in both species of noddy, with brown noddy *Anous stolidus* c. 22,000 pairs fewer (78%) and lesser noddy c. 27,000 pairs fewer (91%). There were also large relative decreases in the number of pairs of masked booby *Sula dactylatra* (354 pairs, 67.4%) and Audubon's shearwater (399 pairs, 68.6%). Three of the species (bridled tern *Sterna anaethetus*, roseate tern *Sterna dougallii*, and white-tailed tropicbird *Phaethon lepturus*) that showed large relative decreases (46–80%) have very small ( $\leq 20$  pairs) population estimates.

Eight species showed an increase in the number of breeding pairs since 1996 (Table 1), with a mean relative increase in population size of  $492.5 \pm \text{SE } 293.9\%$  (range 12.6–2,262.1%).

TABLE 1 Estimated number of breeding pairs of each of nine waterbird and eight seabird species occurring within the Chagos Archipelago in 1996 (from Symens, 1999) and 2006 (with % population change from 1996 to 2006), and in Asia and globally. For full 2006 data set and species' Latin names, see Appendix.

Species	No. of breeding pairs		Population change (%)	Asian population <sup>1</sup> (% of Asian population occurring on Chagos Islands)	Global population <sup>1</sup> (% of global population occurring on Chagos Islands)
	1996	2006			
<b>Waterbirds</b>					
Great crested tern	60	52	-13.3	20,000 (0.52)	
Roseate tern	20	4	-80.0	5,000 (0.16)	82,000 (0.01)
Black-naped tern	29	69	137.9	15,000 (0.92)	
Little tern	4	6	50.0	25,000 (0.05)	410,000 (<0.01)
Bridled tern	15	6	-60.0	500,000 (<0.01)	
Sooty tern	73,000	82,208	12.6	2,000,000 (8.22)	22,000,000 (0.75)
Brown noddy	28,533	6,433	-77.5	750,000 (1.72)	
Lesser noddy	29,505	2,682	-90.9	1,000,000 (0.54)	1,200,000 (0.45)
White tern	521	603 <sup>2</sup>	15.7	500,000 (0.24)	1,100,000 (0.11)
<b>Seabirds</b>					
Audubon's shearwater	582	183	-68.6		30,000 (0.61)
Wedge-tailed shearwater	3,400	2,863	-15.8		1,500,000 (0.19)
White-tailed tropicbird	13	7	-46.2		25,000 (0.03)
Brown booby	29	685	2,262.1		100,000 (0.69)
Masked booby	525	171	-67.4		100,000 (0.17)
Red-footed booby	7,165	8,156 <sup>2</sup>	13.8		300,000 (2.72)
Great frigatebird	12	164	1,266.7		170,000 (0.10)
Lesser frigatebird	85	239	181.2		100,000 (0.24)

<sup>1</sup>From BirdLife International (2004)

<sup>2</sup>Estimates include values for main island of Diego Garcia from Carr (2005)

Both frigatebird species showed large relative increases (lesser frigatebird *Fregata aerial* 154 pairs, 181%; great frigatebird *Fregata minor* 152 pairs, 1,267%), although the largest relative increase was of brown booby *Sula leucogaster* (656 pairs, 2,262%). Sooty terns increased by *c.* 9,000 pairs (12.6%).

In a direct comparison of the islands surveyed in 1996 and 2006, all the island groups experienced decreases in species richness of breeding seabirds. Lesser noddy was lost from the Salomon island groups along with roseate tern, which was also lost from Diego Garcia. Peros Banhos lost four breeding species (Audubon's shearwater, wedge-tailed shearwater, white-tailed tropicbird and brown booby), and the Great Chagos Bank lost bridled tern and great crested tern *Sterna bergii*. Despite experiencing species losses, all island groups, with the exception of the Great Chagos Bank, gained new breeding species. The Peros Banhos group gained lesser frigatebird and bridled tern, which was also new for the Diego Garcia group. The Salomon Islands have been colonized by red-footed booby *Sula sula* since 1996. In terms of the absolute number of breeding pairs only the Peros Banhos island group showed an increase (7,867 pairs, 9%), whereas the other island groups all showed declines ranging from 4% (181 pairs, Diego Garcia) to 81% (45,278 pairs, Great Chagos Bank; Fig. 1). The large apparent decreases are predominately being driven by two species, lesser noddy and brown noddy, from three islands in the

Great Chagos Bank (North Brother, Sea Cow and South Brother).

We surveyed eight of the 10 IBAs (the islands of Danger and Nelson in the Great Chagos Bank were not visited). Of the IBAs surveyed, four islands (Sea Cow, South Brother, Middle Brother and Ile Longue) failed to meet the requirements for IBA status (Table 2). The remaining four islands met the IBA status objectives but with alterations to their current criteria. Barton Point Nature Reserve on Diego

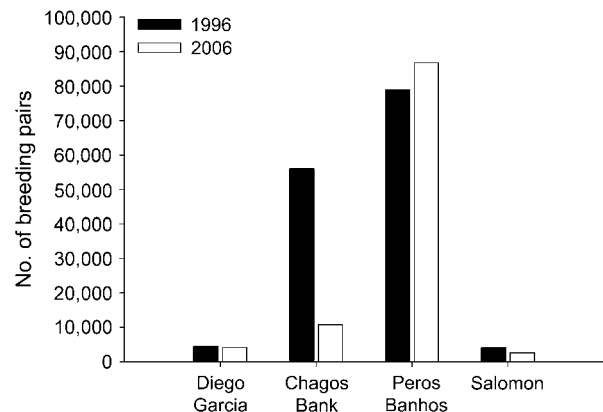


FIG. 1 Total number of breeding pairs of seabirds on the four main island groups (see Appendix for full dataset) in 1996 (from Symens, 1999) and 2006 (this study).

TABLE 2 Current and proposed criteria for the Important Bird Areas of the Chagos Archipelago. Numbers in brackets refer to the estimated number of breeding pairs.

IBA location	Criteria of current status <sup>1</sup>	Proposed status criteria
Barton Point Nature Reserve, Diego Garcia	A4ii red-footed booby (16,067); A4iii >10,000 pairs of seabirds	A4ii red-footed booby (4,061) <sup>2</sup> ; retain A4iii
Danger, Chagos Bank	A4i brown noddy (11,100); A4ii red-footed boobies (3,470); A4iii >20,000 waterbirds	Not surveyed in 2006; retain until next survey
Sea Cow, Chagos Bank	A4i brown noddy (11,500); A4iii >20,000 waterbirds	Retain until annual monitoring implemented
North Brother, Chagos Bank	A4ii Audubon's shearwater (420); A4iii >10,000 pairs of seabirds	A4ii Audubon's shearwater (183); retain A4iii
Middle Brother, Chagos Bank	A4i sooty tern 12,500; A4iii >20,000 waterbirds	Retain until annual monitoring implemented
South Brother, Chagos Bank	A4i lesser noddy 7,300; A4i brown noddy 6,100; A4iii >20,000 waterbirds	Retain until annual monitoring implemented
Nelson, Chagos Bank	A4i lesser noddy 13,700; A4i brown noddy 8,300; A4iii >20,000 waterbirds	Not surveyed in 2006; retain until next survey
Petite Ile Bois Mangué, Peros Banhos	A4i lesser noddy 12,000; A4iii >20,000 waterbirds	A4i sooty tern (20,424); A4iii >20,000 waterbirds
Ile Parasol, Peros Banhos	A4i sooty tern 14,000; A4iii >20,000 waterbirds	A4i sooty tern (9,186); A4iii >20,000 waterbirds
Ile Longue, Peros Banhos	A4i sooty tern 32,000; A4iii >20,000 waterbirds	Retain until annual monitoring implemented
Petite de Coquillage, Peros Banhos		A4i sooty tern (34,669); A4iii >20,000 waterbirds
Grande de Coquillage, Peros Banhos		A4i sooty tern (15,429); A4iii >20,000 waterbirds

<sup>1</sup>From Birdlife International (2005)

<sup>2</sup>Estimates include values for main island of Diego Garcia from Carr (2005)

Garcia and North Brother in the Chagos Bank failed to match the A4iii criteria (see Delaney & Scott, 2002, for details of the criteria) although the A4ii criteria for both sites was met with reduced breeding pair estimates (Table 2). The islands of Ile Bois de Mangué and Ile Parasol in Peros Banhos met the A4iii criteria and Ile Parasol also retained the A4i categorization for sooty tern but with a reduced breeding pair estimate (Table 2). Ile Bois de Mangué should be assigned A4i status for sooty tern (20,424 pairs) but it failed to meet the A4i criteria for lesser noddy (Table 2). We propose the islands of Petite de Coquillage and Grande de Coquillage for IBA status based on the A4i and A4ii criteria for the number of breeding pairs of sooty tern (Table 2).

## Discussion

Of the 17 breeding seabird species that were recorded in the Chagos Archipelago nine showed a decrease in breeding numbers since 1996 and eight showed an increase. There were no clear patterns, although both species of frigatebird appear to have increased, whereas both species of noddy appear to have declined. All the island groups within Chagos both gained and lost individual species although the most striking overall losses in breeding numbers occurred on

the Great Chagos Bank. Our assessment of eight IBA sites revealed that 50% failed to meet the necessary criteria, and the remaining IBA sites, although meeting IBA status, require the application of altered species specific criteria compared to that used in the original IBA designation.

It is difficult to interpret data of this type as we have two independent studies conducted 10 years apart and, although some islands were surveyed in both years, spatial coverage was not complete in either survey. We detected profound declines in both noddy species, for which Chagos is important. It would be prudent to interpret the observed changes only as indicators of possible trends. The phenology of all the seabirds in this study is likely to be a contributing factor to the observed differences between the 1996 and 2006 estimates. Unlike most temperate species, which have clearly defined breeding seasons, tropical and subtropical species tend to breed whenever conditions are favourable (Stearns, 1992) and not necessarily on a strictly annual cycle (Chapin, 1954; Chapin & Wing, 1959). Consequently, although both surveys occurred during February and March they may have taken place at different stages of the breeding cycle for some species and hence our estimates may not necessarily reflect true differences in breeding numbers. Our estimates also need to be taken as a minimum because

a single count taken at the best time of year can underestimate the number of pairs of some species by up to 60%, depending on the degree of synchrony in breeding phenology (N. Ratcliffe, pers. comm.).

Our results, in conjunction with those from the 1996 survey, clearly highlight the need for a monitoring programme to be initiated to elucidate trends and potentially identify the causes of changes in populations. Implementation of systematic monitoring was identified as a key component in the Chagos Conservation Management Plan (Sheppard & Spalding, 2003) but no further action has been forthcoming. The lack of basic life history information for seabirds breeding in Chagos makes it difficult to explain the contrasting fortunes of the 17 species surveyed. The implementation of an annual monitoring scheme would allow essential basic information to be gathered and is crucial for the conservation of the Archipelago's seabirds.

Beyond methodological concerns there are many potential causes of changes in the breeding seabird species of the Chagos Archipelago, including predation (Kepler, 1967; Feare, 1979; Warham, 1990; Megyesi & Griffin, 1996; Martin *et al.*, 2000), human exploitation (Feare, 1976, 1978; Symens, 1999) and natural events such as the El Niño Southern Oscillation (N. Dunlop, pers. comm.). However, we believe that at-sea changes in food supply offers the most likely explanation. Food availability now or since 1996 for seabirds in the Indian Ocean is not known. However, sea surface temperatures have been continually rising (Goreau *et al.*, 2000) and corals declined by almost 90% in 1998 in some parts of the Indian Ocean (Goreau *et al.*, 2000). This temperature rise triggered exceptional ecological changes (McClanachan *et al.*, 1999) and has most likely decreased prey availability for some species of seabird. Furthermore, overfishing of a wide variety of marine species has taken place in the Indian Ocean over the last 10 years (Willmann, 2001; van der Elst *et al.*, 2005) and will almost certainly be driving changes in the number and type of prey available to seabirds. Nevertheless, without some form of systematic monitoring in the Chagos Archipelago it will not be possible to distinguish between and identify the likely causes of population changes.

The overall importance of the Chagos seabird populations is already recognized by the 10 designated IBAs (BirdLife International, 2004) and we propose two further sites based on our findings (Table 2). Although four IBAs failed to meet IBA criteria we advocate that all sites retain their IBA status until an annual monitoring scheme has been underway for several years. From a regional perspective the Chagos Archipelago is important for several species, with the number of breeding pairs of six of 17 breeding species reaching the 1% population thresholds that indicate regionally important populations (Table 1). As our findings are only based on breeding pairs, the Chagos populations of sooty tern, red-footed booby and Audubon's

shearwater would be large enough to trigger the 1% global population thresholds if chicks and non-breeding individuals were included. The Asian population of sooty tern is estimated at 1–4 million breeding pairs (Rocamora *et al.*, 2003; BirdLife International, 2004) and Chagos accounts for 2–8% of the regional population. Similarly, based on estimates of the breeding numbers of red-footed booby in the Seychelles and other Indian Ocean island groups (Rocamora, 2003), the entire Chagos population (c. 11,500 pairs, including values from 1996 for islands not surveyed in 2006) would account for c. 20% of the Asian population and 2.7% of the global population. With a global population of 30,000 pairs (BirdLife International, 2004), our estimates of the breeding Audubon's shearwaters in Chagos, and those of Symens (1999), account for 0.6–1.9% of the global population. These three species alone warrant the need for annual monitoring. Coupled to these species, Chagos is also regionally important for black-naped tern, lesser noddy (previously globally important) and brown noddy.

The important regional and global status of breeding seabirds in Chagos and potentially worrying declines of some species mandates further action. The lack of concerted ongoing monitoring is a cause for concern and we strongly recommended that the UK government implement an annual monitoring scheme, particularly on those islands hosting seabird colonies with IBA status, to allow effective conservation management of this important aspect of the UK's biodiversity.

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## Appendix

The appendix for this article is available online at <http://journals.cambridge.org>

## Biographical sketches

ANDY MCGOWAN is active in both fundamental and applied research related to marine turtles, cooperative breeding in avian systems, dispersal, animal migration, and avian roosting behaviour. ANNETTE BRODERICK and BRENDAN GODLEY co-ordinate the work of the Marine Turtle Research Group at University of Exeter, with research into the ecology and conservation of marine turtles in many locations around the globe.

# 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<sup>-2</sup>. 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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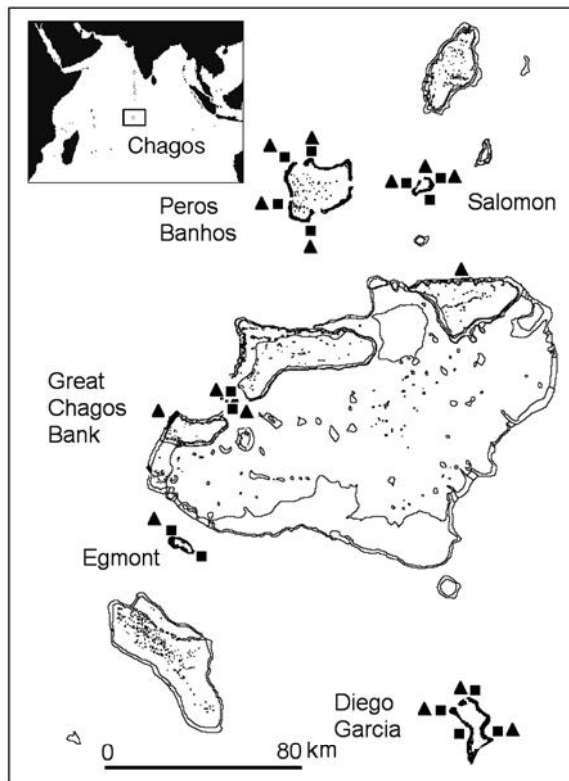


Fig. 1. Location and map of the Chagos Archipelago. ■: sites sampled for N and percent cover; ▲: sites of juvenile coral counts

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 m<sup>2</sup> (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 m<sup>2</sup>. ANOSIM and  $\chi^2$  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

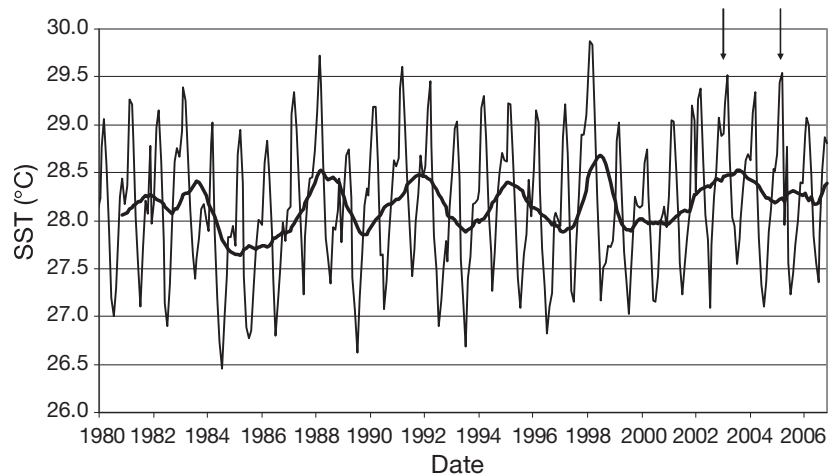


Fig. 2. Monthly sea surface temperature (SST) data for Chagos Archipelago, 1980 to 2006 inclusive. HadISST1 data for the 9 cells covering the archipelago are averaged. Arrows mark the temperature peaks in 2003 and 2005, both of which caused a repeat of bleaching, but no observed subsequent mortality 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

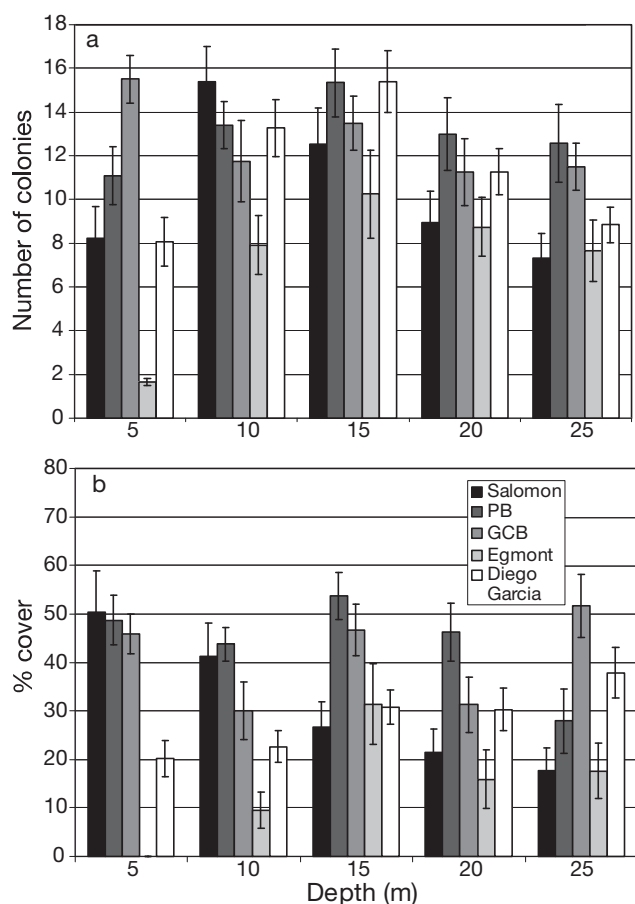


Fig. 3. (a) Number of colonies per quadrat and (b) percent coral cover, measured in the quadrats, at each depth on each atoll. Error bars show mean  $\pm$  SE. PB: Peros Banhos; GCB: Great Chagos Bank

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)	$R = 0.057$ $p = 0.001$	<b><math>R = 0.003</math></b> <b><math>p = 0.42</math></b>
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  $23.3 \text{ m}^{-2}$ , with a range of  $6 \text{ juveniles m}^{-2}$  at Egmont (5 m) to  $28 \text{ juveniles m}^{-2}$  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

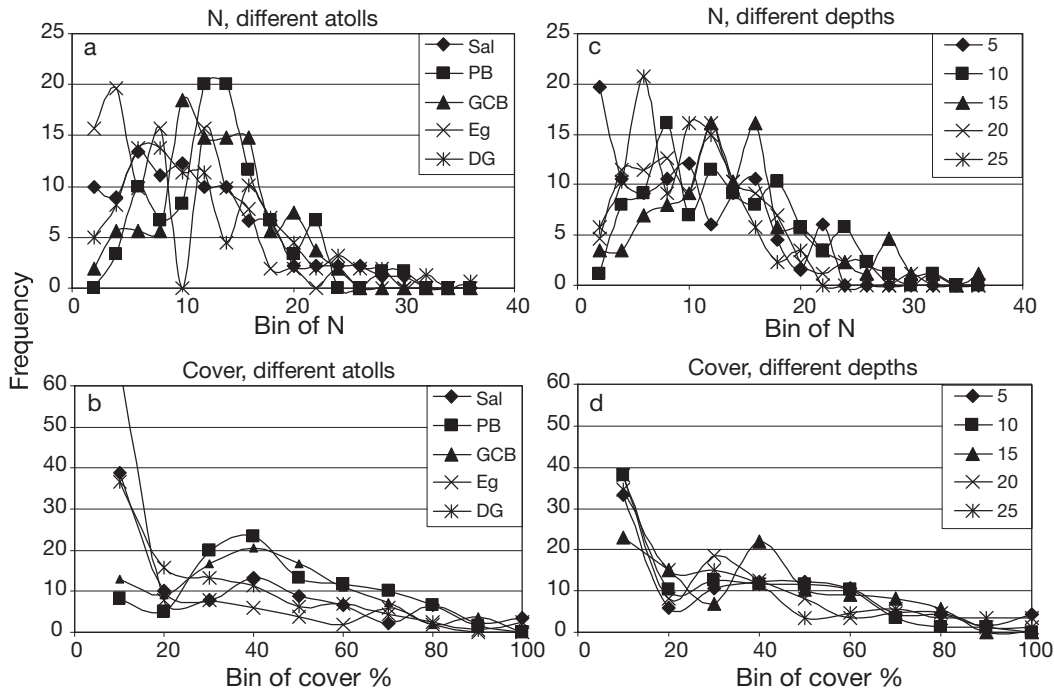


Fig. 4 (a,c) Number of colonies (N) and (b,d) coral cover for the different atolls and different depths. Bins for N in each quadrature are in intervals of 2. Bins for percent cover in the quadrats are in intervals of 10%. Sal: Salomon; PB: Peros Banhos; GCB: Great Chagos Bank; Eg: Egmont; DG: Diego Garcia

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<sup>-2</sup> 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 <sup>-2</sup>	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-

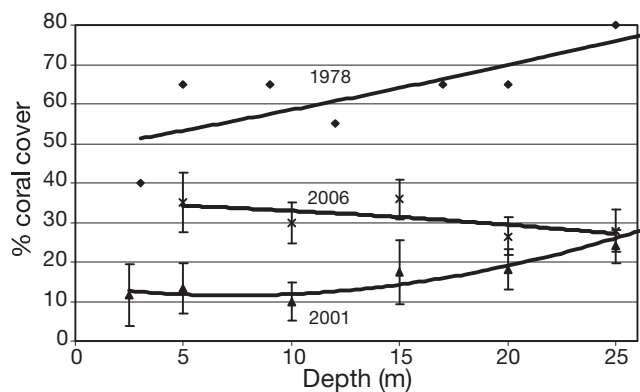


Fig. 5. Coral cover with depth (second-order polynomial lines of best fit) at the 2 northern Chagos atolls where data exist for 1978, 2001 and 2006. Measurements for each year were taken from the same locations and depths. Error bars on the 2001 and 2006 curves are 95 % CI limits. Data to obtain CI or 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  $\chi^2$  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  $\chi^2$  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>Psammodora</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  $10 \text{ cm yr}^{-1}$  and an initial year of 'pre-table' development during which colonies develop an encrusting base and then stem (Wallace 1999). The

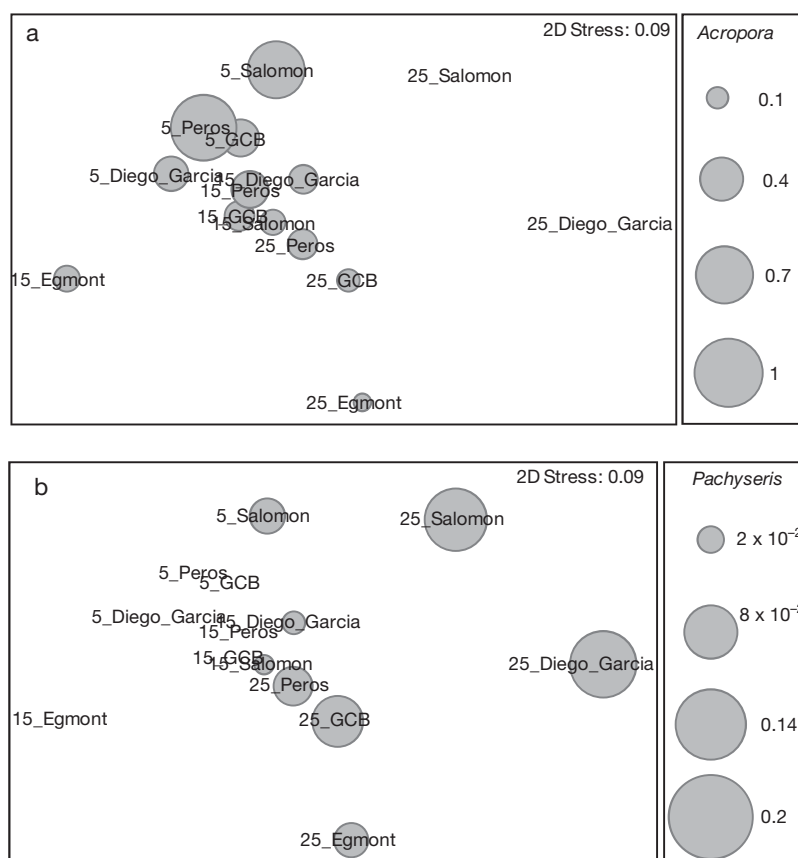


Fig. 6. Multi-dimensional scaling ordination of juveniles. Bubble plots superimposing 2 genera: (a) shallow *Acropora* juveniles and (b) deeper *Pachyseris* juveniles. Scale units are average number of juveniles of the genus per quadrat, from pooled data for each depth at each atoll

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  $\chi^2$  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> <sup>a</sup>
<i>Stylophora</i>	<i>Favites</i>	<i>Lobophyllia</i>	<i>Astreopora</i> <sup>b</sup>
<i>Porites</i>	<i>Leptastrea</i>	<i>Pachyseris</i>	<i>Coscinaraea</i>
	<i>Montipora</i>		<i>Galaxea</i> <sup>c</sup>
	<i>Pavona varians</i>		<i>Stylocoeniella</i> <sup>b</sup>
	<i>Pocillopora</i>		
	<i>Porites</i>		
	<i>Psammocora</i>		

<sup>a</sup>Preference for 5 m; <sup>b</sup>Preference for 25 m; <sup>c</sup>Preference 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

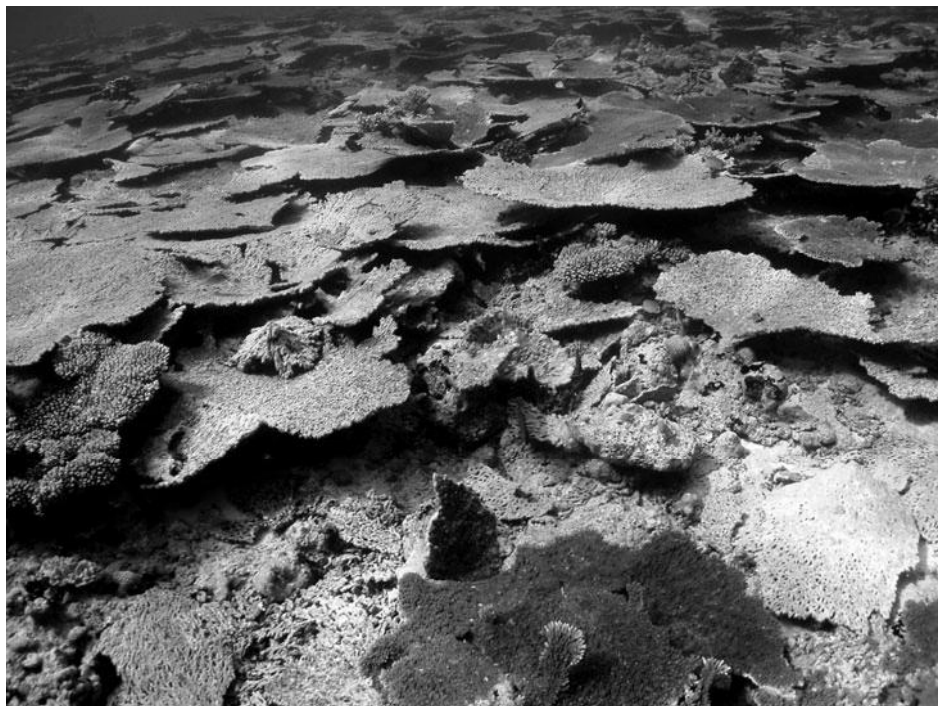


Fig. 7. *Acropora cytherea*. Western Egmont atoll, seaward slope at 8 m depth. Coral tables are mainly dead, some with living parts

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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