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Abstract. Alphonse Atoll, southern Seychelles (7°01’S; 52°44’E), a small (11.28 km²) atoll with minimal anthropogenic influences, was severely impacted by the Indian Ocean warming event of 1997-1998. Quantitative measurements of benthic cover commenced at this location at the peak of the warming (April 1998). Underwater videography surveys of fixed transect lines were made 2001-2007, providing quantitative information on the changing benthic cover. Immediately post-bleaching, the scleractinian community was dominated by few genera, which rapidly re-colonised bare surfaces, including dead coral skeletons. Lagoon corals and many shallow water corals, presumably acclimatized to warmer water conditions, were resilient to the 1998 thermal stress and may have seeded local coral recovery. In December 2006, wave fields associated with the passage of Cyclone Bondo resulted in transport of *Porites* colonies and large blocks of reef framework onto reef-flats, loss of post-bleaching coral recruits and increased macro algal cover on the fore-reef slope. This location provides one of the most detailed long-term (> 9 yrs) records of post-bleaching reef dynamics in the Western Indian Ocean. It demonstrates i) the interaction between, and subsequent recovery from, both physiological and physical disturbances and ii) varying resilience by atoll environment (fore-reef slope, reef crest, lagoon).

Key words: Western Indian Ocean, coral bleaching, reef recovery, cyclone impact.

Introduction

The major El Niño which started in early 1997, and lasted for 12 months until a rapid switch to La Niña conditions in mid 1998, resulted in severe coral bleaching and bleaching-related mortality world-wide (Wilkinson 2000). The Indian Ocean in particular was severely affected with ‘probably the most extensive bleaching ever witnessed’ occurring in the central and northern Indian Ocean during the first six months of 1998 (Wilkinson 2000:23), although there were considerable regional differences in the intensity and duration of ocean warming and related bleaching (Spencer et al. 2000; Turner 1999). Individual reefs in the Seychelles suffered between 40-90% coral mortality as a consequence of this bleaching event (Bigot et al. 2000).

From July 1997 to July 1998, mean monthly sea surface temperature for the Seychelles showed a marked divergence from the long-term trend (1961-1997) (Spencer et al. 2000). Sea surface temperature remained above 30°C for three months, until April 1998, and an anomaly of nearly 2°C was recorded during February 1998, the peak of the warming event in this region (Spencer et al. 2000). An immediate post-bleaching change in the benthic community composition of the fore-reef slope of Alphonse Atoll, southern Seychelles (Fig. 1) from 1998-2003 has been previously reported (Hagan and Spencer, 2006). Here, we report new findings from 2005 and 2007, focusing on the recovery and resilience of this reef system in terms of its scleractinian community, 9 years after a major bleaching event and following interaction with physical disturbance in the form of reef aspect-controlled wave damage.
Material and Methods

Alphonse Atoll (7°01’S; 52°44’E) lies at the southern extremity of the Amirantes Ridge, 415 km southeast of Mahé in the granitic Seychelles. It is a small (6 x 4 km; total area 11.28 km²) symmetrical atoll, with peripheral reefs 640-1,900 m wide, covering an area of 4.02 km² (Stoddart 1984; Fig. 2). It has a 5.4 km² central lagoon which reaches a maximum depth of ~10m (Spencer et al. 2000).

The topography of the outer reefs at Alphonse can be separated into 3 distinct sections. Immediately seaward of the reef-flats, in less than 5 m water depth is a shallow rocky pavement characterized in places by distinct spur and groove formations. Spur and groove topography is particularly well developed on the north-west, leeward side of the atoll, where the U-shaped grooves are approximately 2 m deep. From -5 m to -15 m, a 50-150 m wide gently sloping rock surface extends down to a drop-off (Spencer et al. 2000), at -17 m to -20 m. The drop-off may either be a sheer vertical reef wall, as observed on both sides of the north-east tip of the atoll, or it may be a steep slope, as in the south-west.

In 2001 and 2002, 30 permanent transect sites (29 fore-reef slope, 1 lagoon), encompassing a wide range of depths (-3.5 m to -18 m) and geographical aspects were selected. 15 m long transects were established parallel to the reef crest, marked with steel rods to aid re-location of the survey sites. Quantitative surveys were undertaken using standard video transect techniques. Video survey data was also obtained from 1998 (Hi8 format; Spencer et al. 2000) and 1999 (digital video; Teleki et al. 1999). A re-survey of all permanent transects was undertaken in 2003 and re-surveys of selected sites were carried out in 2005 and 2007.

Video data was analyzed using the AIMS 5-dot method (Osborne and Oxley 1997) to show changes in percentage cover for 7 benthic categories (sand, rubble, bare substrate, calcareous algae, Scleractinia, non-Scleractinia and macroalgae). Corals and algae were identified to genus level. Two datasets were generated; ‘benthic categories data’, from which percentage cover was calculated for each benthic category, and ‘coral genera data’. Multivariate and univariate statistics were conducted, and dominance curves plotted, using PRIMER (Plymouth Routines In Multivariate Ecological Research) (Clarke and Warwick 2001).

At 7°S in the Western Indian Ocean, tropical cyclones are rare; frequencies for the area 0-10°S; 50-60°E are 2.1 per decade (Walsh 1984). However, in December 2006, Cyclone Bondo formed southwest of Diego Garcia and moved west across the Indian Ocean. It was a small but intense system (radius of hurricane force winds ~20 km) and category 2 strength (154-177 km h⁻¹) winds hit the Seychelles. The cyclone passed 330 km south of Alphonse Atoll, and although no terrestrial damage was observed, the associated wave field resulted in coral block detachment and transport on the northwestern side of the atoll, leaving a coral boulder debris field on the reef-flat (Plates 1 and 2). Coral blocks and dead Porites colonies, some measuring over 1 m in diameter, were observed in October 2007 on the reef-flat. Underwater surveys showed that these reef-flat deposits originated from depths of 7-12 m on the fore-reef slope and had been transported a horizontal distance of approximately 500 m.

Results


1998 data were only available for 5 transect lines, all of which were on the western fore-reef slope of the atoll. With such a small, localized dataset, these data cannot be assumed to be representative for the entire atoll. However, the 1998 surveys showed that live scleractinian cover ranged from 11.9-19.8% and bleached scleractinian cover values range from 8.9-19.4%. The combination of these values suggests that pre-bleaching, scleractinian cover represented between 20% and 40% of the benthos. In 1999, scleractinian cover represented between 8.8-13.7% of the benthic community, and in subsequent years, fore-reef slope scleractinian cover increased by over 5% in a 1-1.5 year period, from an average of 17.2% cover in 2001/02 to an average of 22.7% cover in 2003. However, between 2003 and 2007, there was no increase in average scleractinian cover (Table 1).

<table>
<thead>
<tr>
<th></th>
<th>Scleractinian Cover % ± 1 s.d.</th>
<th>Macroalgal Cover %</th>
</tr>
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<tbody>
<tr>
<td>1998</td>
<td>14.8% ± 3.0</td>
<td>0.3</td>
</tr>
<tr>
<td>1999</td>
<td>10.3% ± 1.8</td>
<td>8.0</td>
</tr>
<tr>
<td>2001/02</td>
<td>17.5% ± 7.8</td>
<td>3.3</td>
</tr>
<tr>
<td>2003</td>
<td>22.6% ± 7.4</td>
<td>2.0</td>
</tr>
<tr>
<td>2005</td>
<td>22.2% ± 7.1</td>
<td>1.0</td>
</tr>
<tr>
<td>2007</td>
<td>21.2% ± 9.1</td>
<td>3.5</td>
</tr>
</tbody>
</table>

Table 1: Average scleractinian and macroalgal percentage cover 1998-2007 from video transect data.

Statistical tests between 1999 and 2001/02 on benthic percentage cover data showed no significant difference between these communities (ANOSIM; P=0.05) but there was a significant difference (ANOSIM; P<0.01) between 1999 and 2003.

Partitioning of these island-wide statistics shows marked differences in the time course of live coral cover changes between eastern and western survey sites. At eastern sites, a clear trend of increasing coral cover was shown 2001/02-2007 except for at the 5 m depth transect (Fig. 3). By 2007, scleractinian cover ranged between 24% and 38%. Conversely, the western sites showed a downward trend in scleractinian cover over this time period. Although scleractinian cover started off at a higher level in 2001/02 compared to eastern sites, there was a clear drop in cover in later years. By 2007, western sites displayed a maximum of 16% live scleractinian cover (Fig. 4).


$k$-dominance curves (Fig. 5) for each of the survey years show the change in the scleractinian community composition 1998-2007. Curves for 2001/02 and 2003 cross those of 1998 and 1999, so it is inappropriate to comment on the comparison between all four curves (Lambshead et al. 1983). However, the curve for 1999 lies below that of 1998, indicating increased biodiversity in the 1999 coral genera dataset compared to the 1998 dataset. The curve of 2001/02 lies below that of 2003, indicating that the coral community of 2001/02 was more diverse than that of 2003. There appears to have been a small increase in diversity between 2003 and 2005 but this decreased again by 2007.
Coral genera diversity has decreased over time, with the lowest diversity (i.e. the highest \( k \)-dominance curve) being seen in 2007 (Fig. 5). The point at which the curves cross the y-axis becomes increasingly higher in later years, and by 2007, 60% of the scleractinian community was accounted for by just one genus.

Pielou’s Evenness (\( J' \)) (how evenly the individuals are distributed among different genera) was seen to increase between 2003 and 2005, but decrease between 2005 and 2007, supporting the findings of the \( k \)-dominance curves. The difference between mean Evenness values over the time series is statistically significant (ANOVA; \( F = 3.53, P<0.01 \)).

Figure 5: \( k \)-dominance curves for 1998 (red), 1999 (pink), 2001/02 (green), 2003 (purple), 2005 (yellow) and 2007 (turquoise) using coral genera data from video surveys.

Discussion
The 1997-98 bleaching event had a considerable impact on the community composition of the fore-reef slope of Alphonse Atoll. In 1998, at the height of the bleaching event, live scleractinian cover was reduced to an average of 14.8%, and this value had further decreased one year after the bleaching event (Table 1). By 2003, scleractinian cover had more than doubled from 1999 levels. Taking 1999 as the first year that gives a true indication of actual mortality suffered at Alphonse (1998 surveys were taken at time of ongoing bleaching), this implies that a period of at least 4 years (1999-2003) was required after this major disturbance before any statistically significant recovery in scleractinian community cover could be observed.

Coral genera diversity increased between 1998 and 1999, as illustrated by the 1999 curve being lower than that of 1998 on the \( k \)-dominance plot (Fig. 5). However, between these two years, a decrease in live scleractinian percentage cover was calculated. The increase in biodiversity but decrease in total coral cover that was observed at Alphonse between 1998 and 1999 may imply that the bleaching event quickly removed certain genera from the 1998 dataset. However, some of these genera may have made a rapid return to the reef in 1999, increasing biodiversity levels, although their small size would not have increased the percentage cover values for that year. There was a further decrease in scleractinian diversity between 2001/02 and 2003, and again between 2005 and 2007. The \( k \)-dominance curves (Fig. 5) and Pielou’s Evenness values indicate that in later years, there has been a reduction in diversity in the scleractinian community present and increased dominance by a few (or even just one) coral genera.

The dominant (in terms of percentage cover) scleractinian genus on the fore-reef slope of Alphonse in 2007 was *Porites*. Due to the size of many of the *Porites* colonies observed (some measured over 2 m across), it is clear that these massive, slow-growing colonies must have survived the 1998 thermal stress. In addition, lagoon corals and many shallow water corals also survived, presumably by being acclimatized to warmer water conditions (Spencer et al., 2000). The survival of these pockets of corals is likely to have improved reef resilience on the fore-reef slope at Alphonse, with these colonies acting as larval sources to re-seed degraded areas.

The second most dominant genus in 2007 was *Pocillopora*, which was widespread on all reefs at Alphonse. *Pocillopora damicornis* has been described as an opportunistic species, due to its rapid reproductive cycle and fast growth rate, enabling it to quickly occupy any newly available space (Endean and Cameron, 1990).

The granitic Seychelles islands in the north suffered over 90% coral mortality during the 1997-98 ocean warming (Wilkinson, 2000) but the southern islands were less severely affected, with an average mortality of around 60% (Spencer et al. 2000). It is suggested that this difference was due to the moderating influence of the South Equatorial Current at the southerly locations, in contrast to the heating of shallow waters, and long water residence times, on the Seychelles Plateau. As more of the corals at Alphonse survived the bleaching event compared to reefs of the granitic Seychelles islands, it can be suggested that reef resilience at Alphonse has been aided by the interaction of geographical location with regional oceanographic processes.

Another of the main factors driving reef resilience at Alphonse has been the minimal anthropogenic impact, which may have allowed more rapid natural reef regeneration than in areas with high human pressure (as has been demonstrated elsewhere; Sandin et al. 2008). Alphonse has a very small resident population (~60 people) and tourism is small-scale, with only 30 double chalets. Boat traffic at Alphonse is minimal (a maximum of 4 boats over 10
m in length were in operation at time of reef surveys) and anchoring on the reef is prohibited.

Variations in coral cover histories on reefs of differing aspect require further investigation. Cyclone Bondo caused extensive damage in a localised area on the northwest fore-reef slope, but a downward trend in live scleractinian cover was already evident in 2005 (Fig. 4). It is not known what caused this decline. One possibility is wave refraction around the atoll during the December 2004 Asian tsunami and consequent disturbance of coral cover, although general tsunami impacts in the southern Seychelles were low in littoral environments (Hagan et al., 2008).

Despite a rapid increase in macroalgae cover one year after the peak of the bleaching event, the Alphonse reefs have not succumbed to the algal ‘phase shift’ from a ‘hard’ reef community to a ‘soft’ reef community (Done 1999) that has been seen after reef disturbance elsewhere. An altered fore-reef slope coral community appears to exist at Alphonse 9 years after the ocean warming related mortality. Large skeletons (1-3 m diameter) of Porites spp., Lobophyllia spp., and Symphyllia spp. have been colonized by Pocillopora spp. and to a lesser extent Acropora spp., suggesting that the Alphonse fore-reef slope may be in an interim phase of development, through which the coral community must pass before regaining high levels of coral coverage and diversity.

Alphonse provides one of the most detailed long-term (>9 yrs) records of post-bleaching reef dynamics in the Western Indian Ocean and demonstrates not only the general interaction between physiological and physical disturbances (where human impacts can be disregarded) but also the complexities of response by atoll environment (fore-reef slope, reef crest, lagoon) and reef aspect. Continued monitoring may shed more light on the nature of these controls on reef resilience and recovery.

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