Proceedings of the 11th International Coral Reef Symposium, Ft. Lauderdale, Florida, 7-11 July 2008
Session number 18

Was the 1998 Coral Bleaching in the Southern Seychelles a Catastrophic Disturbance? - 1999-2006 Reef Fish Responses to Coral Substrate Changes

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Abstract. The southern Seychelles Islands suffered extensive bleaching-related losses of live coral habitat in 1998. The Aldabra Marine Programme investigated coral-bleaching-related responses in reef fish communities at the UNESCO-protected Aldabra Atoll and neighboring unprotected Assomption, Astove and St Pierre. These were all coral-rich systems before up to 50% loss of live corals. Hard coral recovery has been minimal except at St. Pierre. Habitat phase shifts have occurred only at Aldabra (soft coral, *Rhytisma*) and at Assomption (macroalgae, *Halimeda*). Fish abundances by species at Aldabra were different between sites and years, but there was no directional change within sites. Multivariate comparisons of fish assemblages at 10m and 20m depths showed no directional changes over time at Aldabra (1999-2006), Assomption (2002-2006), Astove (2002-2005), and St Pierre (2002-2005). At Aldabra, pre-bleaching reef fish community structure persists, and abundance changes appear to represent the "natural" system. Similar patterns at neighboring unprotected islands suggest any anthropogenic impacts are below the thresholds affecting local reef-resident species. Losses of live coral in these coral-rich communities apparently were not catastrophic disturbances that pushed these ecosystems beyond their "tipping point" which would reduce resilience and lead to changes in the basic structure of the reef fish assemblages.

Key Words: Words: bleaching, fish assemblages, catastrophic disturbance, tipping point

Introduction

The 1998 El Niño-related warm water event resulted in mass losses of corals due to bleaching that altered reef habitats on a historically unprecedented global scale (Hoegh-Guldberg 1999, Wilkinson 2004). The western Indian Ocean suffered some of the most severe bleaching-related coral mortality during this 1998 event, with up to 90% of the live corals in the region affected by bleaching (Wilkinson et al. 1999). In the southern Seychelles Islands there were extensive bleaching-related losses of live coral habitat on the outer reefs, with coral mortality ranging from 60-75% and losses of live coral cover as high as 60% (Teleki et al. 1999, Spencer et al. 2000, Spalding and Jarvis 2002, McClanahan et al. 2007). Aldabra Atoll and the neighboring southern Seychelles islands of Assomption, Astove and St Pierre were coral-rich systems prior to losses of up to 50% of live coral in the 1998 bleaching-event (Spalding and Jarvis 2002, Stobart et al. 2005, Downing et al. 2006). A 1998 survey of the outer reef scleratinians at Aldabra Atoll during the late stages of the bleaching event found 36-100% recently bleached or dead depending on depth (Spencer et al. 2000).

Losses of live coral of this magnitude often result in decreased structural heterogeneity of the reef habitat through erosion of the dead coral framework. The associations between reef fishes and coral habitat complexity (review in Wilson et al. 2006) support the conclusion that reef fishes should be affected by mass losses of corals. However, studies of the responses of fishes on different reefs from 1-6 years after the 1998 mass bleaching have yielded mixed and differing results (Spalding and Jarvis 2002, Bellwood et al. 2006, Garpe et al. 2006, McClanahan 2006).

In a controlled experiment Holbrook et al. (2006) found that the amount of live coral habitat can influence fish assemblages, including fishes that have generalized habitat requirements (i.e., non-coral-obligate species). Further, this experiment suggested that on coral-rich reef habitats there must be an almost catastrophic loss of live coral cover to substantially change the basic structure of the fish assemblage.

Here we use results of long term monitoring of the coral reef communities at Aldabra Atoll and the neighboring islands of Assomption, Astove and St. Pierre to assess responses of the associated fishes to the extensive and massive 1998 bleaching-event losses of live coral. These four locations were coral-rich systems prior to 1998. We investigate if changes in the coral habitat in 1998 represented catastrophic disturbances for local fish assemblages. The surveys at one protected and three unprotected locations provide information on responses of local fish populations to any synergy between bleaching and direct anthropogenic or fishing impacts.

Methods

Quantified digital videography surveys of the benthic habitats, and quantified visual surveys of species and size-groups of fishes, were conducted by the Aldabra Marine Programme (AMP) on the outer reefs at Aldabra Atoll, and Assomption, Astove and St. Pierre Islands (Fig. 1). Surveys were along permanently marked transects on the 10 m and 20 m depth contours (for protocols see Teleki et al. 1999). Surveys at Aldabra Atoll conducted at Sites 1-4, 6 and 8 (Stobart et al. 2001) along the northern shore were used for this study. Site 5 had atypical coral rubble habitat, and Site 7 transect depths were 5m and 15m. Surveys at Aldabra were during November 1999, February 2001 and 2002, May 2003, March 2004 (incomplete surveys), April 2005 and December 2006. Surveys were conducted at one site each at Assomption, Astove and St. Pierre during February 2002, May 2003, March 2004 (incomplete surveys), and April 2005, and at Assomption during December 2006 (Stobart et al. 2002).

The habitat video imagery was analyzed using the

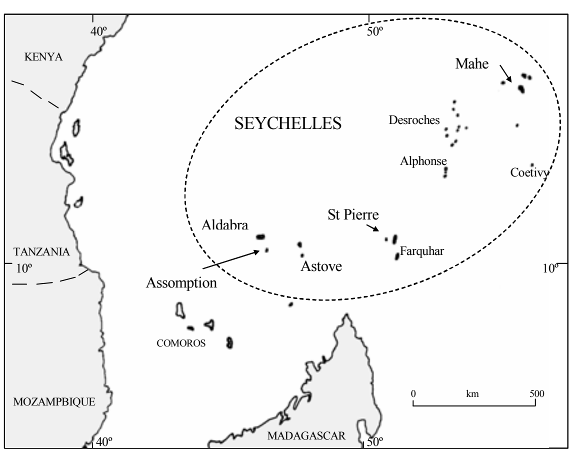

Figure 1: Location of AMP sites in the Seychelles, western Indian Ocean.

AIMS 5-dot method (Osborne and Oxley 1997) and used to compare the annual percentage change in corals, algae and other habitat categories. PRIMER multivariate comparisons (MDS) were made of the abundance of fishes between years, tested for linear sequence (RELATE), and at Aldabra Atoll tested for differences between sites (ANOSIM; Clarke and Warwick 2001).

Results

Benthic habitats

At Aldabra Atoll the increases in live coral cover since the post-bleaching survey in 1999 were driven by extensive growth of the soft coral *Rhytisma* at both 10m and 20m (Fig. 2). There was little change in the growth of other soft corals at either depth. Recovery of hard corals was minimal at 10m and 20m. Macroalgal cover declined at both 10m and 20m to the lowest levels recorded in the eight years following the bleaching event. Erect dead coral habitat continued to decrease at both 10m and 20m (see AMP reports available at http://aldabra.org).

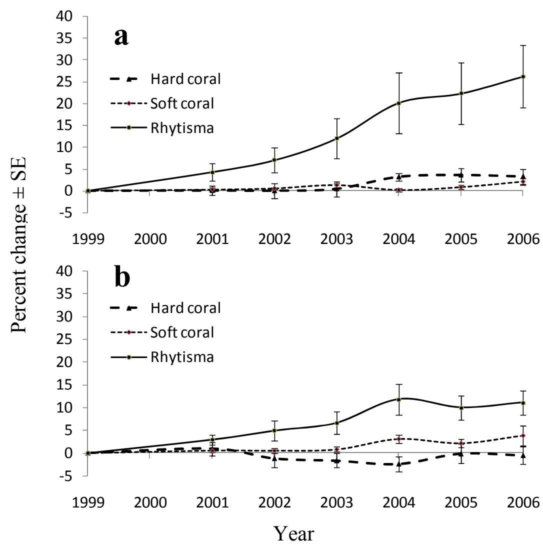

Figure 2. Change in hard coral, soft coral and *Rhytisma* at Aldabra atoll (see legend) at a) 10m and b) 20m depth between 1999 and 2006.

At Assomption, Astove and St. Pierre, the growth of *Rhytisma* and other soft corals was minimal, although relatively more pronounced at Assomption. The soft corals were not important factors in any increases in live coral cover at either 10m or 20m. Increases in hard coral cover were minimal at Assomption and Astove, but relatively large and steady at St. Pierre at 10m and 20m, driven by recruitment of *Pocillopora eydouxi* (Fig. 3). Macroalgal cover was a minor part of the reef habitat at Astove and St. Pierre, but at Assomption there was a rapid increase in macroalgal cover (primarily *Halimeda*) at 10m, and a steady, but less dramatic, increase at 20m following a major decrease in macroalgae at this depth in 2003. Erect dead coral

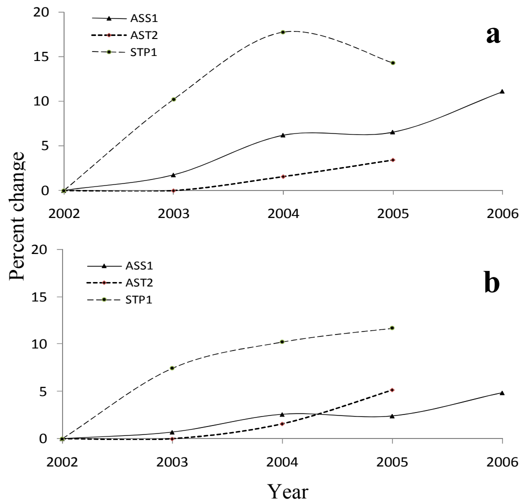

Figure 3. Change in hard coral at Assomption, Astove and St. Pierre (see legend) at a) 10m and b) 20m depth between 2002 and 2006.

formed minimal habitat at Assomption, Astove and St. Pierre at both 10m and 20m, and is generally decreasing.

Fish surveys

The number of species in the annual fish surveys were as follows: Aldabra Atoll – avg. 178, ra. 138-191; Assomption – avg. 90, ra. 88-92; Astove – avg. 88, ra. 83-94; St. Pierre avg. 108, ra. 107-110. At Aldabra the annual means of fish abundances by species, taking into account site differences, showed there were significant differences between sites and years at both 10m and 20m (ANOSIM: Year – 10m P = 0.02, Rho = 0.425; 20m P = 0.03, Rho = 0.316; Sites – 10m P = 0.01, Rho = 0468). However, there were no directional changes following a linear sequence within sites (multiple Figures not shown), with the exception of Site 4 (20m) where there was high annual variability in ten species of schooling, reef-resident planktivores. Site 4 (20m) was no longer significant when these species were removed from the analyses. MDS plots of fish abundances between years at all 10m and 20m sites at Aldabra Atoll (Fig. 4)and single sites at Assomption (Fig. 5), Astove (Fig.

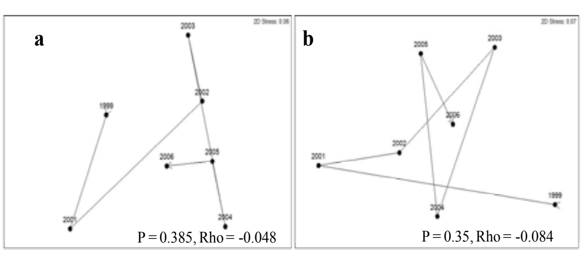

Figure 4. MDS of fish abundance between years for Aldabra atoll (all sites) at a) 10m and b) 20m depth. Line represents trajectory between years and P and Rho are for RELATE seriation analysis.

6) and St Pierre (Fig 7) showed no linear sequence or directional changes over time at either depth (significance levels and stress values shown on graphs; Clarke and Warwick 2001).

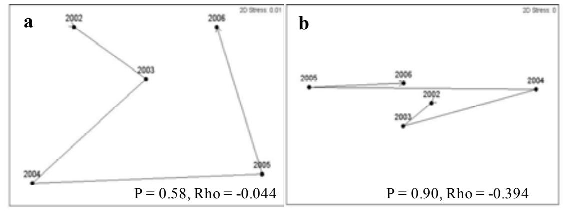

Figure 5. MDS of fish abundance between years for Assomption

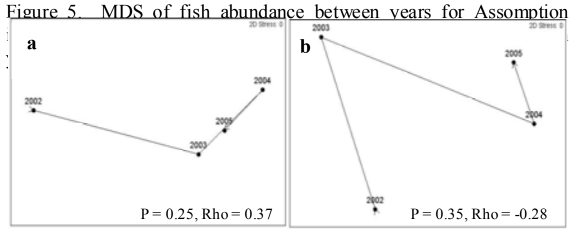

Figure 6. MDS of fish abundance between years for Astove island at a) 10m and b) 20m depth. Line represents trajectory between years and P and Rho are for RELATE seriation analysis.

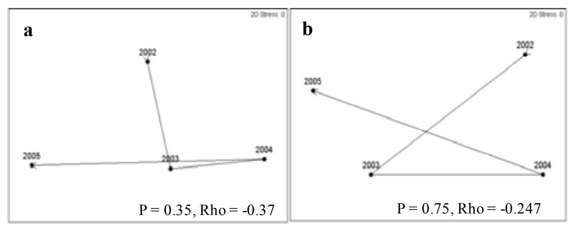

Figure 7. MDS of fish abundance between years for St. Pierre island at a) 10m and b) 20m depth. Line represents trajectory between years and P and Rho are for RELATE seriation analysis.

Discussion

Aldabra Atoll and Assomption, Astove and St. Pierre Islands all suffered massive and extensive bleaching-related losses of live coral habitat in 1998. However, the pre-bleaching reef fish communities at these four locations seem to persist long-term post-bleaching, as demonstrated by the lack of directional changes between years in the MDS plots. Many studies have documented the strong associations between live coral habitat and reef fishes (review in Wilson et al. 2006), as well as the high variability in reef fish communities (review in Holbrook et al. 2006). The responses of reef fishes found in this study leads to an intriguing question of why directional changes in these fish communities have not occurred during eight years following the bleaching event in which there were two location-specific habitat phase-shifts. Change is used here with the caveat of “detectable within the bounds of the methodology used by AMP”. There are likely many factors contributing to the lack of change in the assessed reef fish assemblages. We discuss some here in relation to the concept of pushing the ecosystems to their “tipping point”, beyond which reduced resilience can lead to change and undesirable phase shifts (Littler and Littler 2007).

The four systems under study were rich in corals and fishes prior to the 1998 bleaching impacts and coral richness could have influenced the apparent continued-stability responses of the reef fish communities to the single-event loss of up to 50% of the live coral habitat. That is, the 1998 event was not a catastrophic-enough level of decline in live coral in these rich systems to trigger change in the basic reef fish assemblages (after Holbrook et al. 2006).

At Aldabra Atoll the rapid habitat phase shift to *Rhytisma* could have ameliorated the loss of hard coral habitat by providing the modest recovery of the living coral on the reef that could enhance stability of the fish assemblage as noted by Holbrook et al. (2006). For *Rhytisma* to be a factor, it would have to provide an ecologically acceptable alternative to important habitat functions affecting the fish community structure that were likely reduced with the loss of hard coral. There is limited information on any direct habitat functions of soft corals for reef fishes, but there is the potential for indirect effects on the composition of reef fish assemblages through biotic interactions between soft corals and other organisms, including hard corals (Syms and Jones 2001). However, *Rhytisma* habitat was a factor only on Aldabra Atoll and not on the three islands that also had no directional changes in their post-bleaching fish communities. Determining if *Rhytisma* habitat had a positive or neutral, or maybe negative, affect on reef fish communities is beyond the scope of this study, leaving the habitat-function role of *Rhytisma* in this situation open for continued speculation.

The framework of erect dead coral provides reef habitat heterogeneity after bleaching disturbance, which is a major factor in reducing changes in the reef fish community (review in Wilson et al. 2006). However, erect dead coral has not registered as a major habitat at Aldabra Atoll or the other three locations, after showing initial decreases and then minimal percentage changes between years. This is more an artifact of the habitat surveys than a true measure of the presence or rate of deterioration of the dead coral framework. The increases in other biotic habitats, such as the growth of *Rhytisma* at Aldabra Atoll, *Halimeda* at Assomption, and encrusting algae at all four locations, have both covered the surface of coral framework and likely added to its' stability and durability. Complex dead coral habitats can provide the habitat functions required by reef fishes with facultative or no relationships with live coral (Bellwood et al. 2006, Holbrook et al. 2006, Graham et al. 2007). Only those fishes with specific dependence on live hard corals will show marked responses to loss of this habitat (Pratchett et al. 2006, Feary et al. 2007) and there were few of these species in the systems surveyed in this study (Buckley et al. 2005).

The trophic plasticity of the fishes on these post-bleaching habitats would be an important factor in the resilience of the fish assemblages over time. If all but the few coral obligate fishes had the ecological versatility to adapt to any changes in prey resource availability caused by the reductions in live hard coral, then these trophic-functional groups of reef fishes would persist even though there was some variability at the species level (see Spalding and Jarvis 2002).

Direct anthropogenic disturbances to reef fishes can have a greater influence on fish assemblages than bleaching-related losses of live coral habitat (McClanahan 2006). Also, these two processes acting in synergy can confound determinations of the natural responses of the reef fishes to coral habitat impacts. Aldabra Atoll was protected from all but minimal anthropogenic disturbances primarily from local subsistence fishing (Pistorius and Taylor 2009) and the pre-bleaching fish assemblage persisted over time. Similar patterns at neighboring unprotected islands suggest any anthropogenic impacts at these locations were below the thresholds affecting local reef-resident species.

The coral habitat in the huge lagoon at Aldabra Atoll received minimal impacts from the 1998 bleaching event (Stobart et al. 2002). This physically protected area is thought to function as a sanctuary for reproductive-age adults and as a nursery area for many reef fishes (AMP, unpublished data). This reproductive potential could provide a steady supply of larval and juvenile fishes for the outer reefs at Aldabra, as well as to islands in the surrounding region. Even at moderate levels, this output could possibly override any bleaching-related loss of local and regional reproductive potential. This is an area of future research by AMP.

The findings here support earlier assessments that the reef fishes at Aldabra Atoll continue to reflect pre-bleaching reef fish community structure, and abundance changes appear to represent the ecology of the "natural" system (Downing et al. 2005, Downing et al. 2006). The pre-bleaching reef fish communities also appear to persist at Assomption, Astove and St. Pierre Islands. It is apparent that the 1998 bleaching impact was not a catastrophic disturbance to these systems. If there was any synergy between the loss of live coral and other post-bleaching biotic or habitat factors, it does not appear to have pushed the ecosystems past their tipping points, initiating directional changes in the associated reef fish assemblages.

Acknowledgement
We thank the Fondation d'Enterprise Total for their part in funding this project. Funding in early years was also provided by CORDIO. The Seychelles Islands Foundation has offered essential support to the AMP since its foundation, and we particularly thank Executive Director Lindsay Chong-Seng, Executive Officer Ronny Renaud, Chief Executive Officer Dr Frauke Fleischer-Dogley and SIF chairman M. Lostau Lalanne for their support. We also thank Rolph Payet, Seychelles Ministry of Environment and Transport and Patrick Lablache, Ministry of Land Use and Habitat. The TUI AG group, British Airways Assisting Conservation, Dahm International, PADI Project Aware, Profitability Business Simulations, S.Y. Thalassi, Borg Warner and many anonymous donors have also given their kind support. Finally, Tom Spencer is thanked for his encouragement and advice at the inception of AMP. Finally thanks to the Save Our Seas Foundation for funding attendance of the 11th ICRS.

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