Halford, Andrew Robert (2010) ***Disturbance effects on tropical reef fish assemblages at large spatial and temporal scales.*** **PhD thesis, James Cook University.**

Disturbance effects on tropical reef fish assemblages at large spatial and temporal scales

Thesis submitted by

Andrew Robert Halford (B.Sc.) JCU, Qld.

In February 2010

For the degree of Doctor of Philosophy

In the School of Marine and Tropical Biology

James Cook University

Statement of Access

I, the undersigned, author of this work, understand that James Cook University will make this thesis available for use within the University library and via the Australian Digital Thesis Network, for use elsewhere.

I understand that as an unpublished work, a thesis has significant protection under the Copyright Act and I do not wish to place any further restrictions on access to this work.

	16th Feb. 2010
Signature	Date

Statement of Sources

I declare that this thesis is my own work and has not been submitted in any form for another degree or diploma at any university or other institute of tertiary education. Information derived from the published or unpublished work of others has been acknowledged in the text and a list of references is given.

	16th Feb. 2010
Signature	Date

Statement on the Contribution of Others

This thesis was supported and funded in its entirety by the Australian Institute of Marine Science. The work done at Scott Reef was also supported financially by Woodside Energy Limited as operator of the Browse LNG Development Limited. The contributions of my colleagues and numerous volunteers during the collection of the data are all acknowledged. I acknowledge the contributing authors on those manuscripts that have been published from chapters herein. I specifically acknowledge the modeling work done by Dan Ryan during the analysis of Chapter 2. I was supported by a James Cook University fees exemption scholarship for the duration of my thesis. I thank my supervisor Julian Caley for his significant editorial contributions to this thesis.

Acknowledgements

This thesis represents an incredible amount of data, collected as it was over 15 years. Amazingly, I was responsible for almost all the fish surveys during this period. However, my thesis could not have been done without all those colleagues and volunteers, who collected fish data when I was not available, collected the benthic data I used in this thesis and who were my dive buddies. To all of you my heartfelt thanks. I would like to mention specifically my colleagues during the formative years of the AIMS Long Term Monitoring Program. Angus Thompson, Caroline Christie, Debbie Bass, Ian “Bluey” Miller, Steve Neill and Will Oxley. Those years were some of the most enjoyable of my life and I have never worked with a more professional crew.

To the west coast monitoring team I also extend heartfelt thanks, especially to my colleagues, Andrew “Smiley’ Heyward, Luke Smith, Max Rees and Stuey Field. I hope you guys realize how much we accomplished during our 6 years in Dampier. Thankyou to all those boat captains and crew who made it possible to get to so many reefs and conduct our research in a safe and secure manner. I especially acknowledge the help of the Australian Maritime Customs Office out of Broome. It is highly unlikely that my dataset would have been so complete without their involvement, as they provided a boat and crew, *gratis*, for many field trips to Scott Reef.

I thank the Australian Institute of Marine Science for providing me with the opportunity to conduct research in such amazing places. I especially thank the organization for their recognition of the importance of monitoring programs in the process of scientific endeavor. It is only in the fullness of time that the value of their long-term monitoring programs is coming to light – long may they continue.

I would like to thank John Keesing, Peter Doherty and Andrew Heyward for their mentorship during my time at AIMS. All of you represent what I think is good about science and importantly were very supportive of me during my time at AIMS. Thankyou to my supervisors Julian Caley and Geoff Jones but especially Julian for his insightful yet insistent editorial style which is slowly curing me of my tendency to use flowery language. I look forward to more collaboration in the future.

My route to a PhD was a very tortuous one which could have been derailed before I had even completed high school. I thank mum and dad for instilling in me the virtues of an education and insisting that I get one. I especially thank dad for his unfailing financial support during my university days and his continual encouragement to go as far as I could with my education.

I have saved the best for last. To my beautiful wife and mother of our two equally beautiful boys Ethan and Finn, I can only say, “Jenny, you are a saint”. It was your early support that finally gave me the courage to embrace the PhD process and it is your continuing support since then that has allowed me to finally complete the process. I could not have done this without you.

General Abstract

Since the early eighties, when non-equilibrium dynamics became accepted as an intrinsic part of ecological systems, considerable research effort has been invested towards understanding the effects of disturbance on community dynamics. Coral reefs, being one of the most diverse environments on the planet and subject to many varied disturbances are a particularly appropriate system for investigating disturbance effects. Current models of community dynamics incorporate emergent properties of ecosystems, with smaller-scale, non-equilibrium dynamics fitting into a larger framework of hierarchical patch dynamics, metapopulation dynamics, landscape ecology and macroecology. To more fully understand how meta-communities function however, requires a combination of empirical and theoretical studies that bridge the gap between smaller scale field experiments and larger scale phenomena that are presently explored mostly by theory. The need to fill the knowledge gaps at these "in-between" scales was highlighted by the extent of the circum-global bleaching in 1998. A renewed focus on landscape scale dynamics is required to try and understand how, and ultimately whether, entire reef systems are likely to survive such large scale disturbances. This thesis is one of the first examples to use such an approach on coral reefs.

Using a consistent protocol I monitored fixed sites annually, for a period of 10 years, on three reef systems that were fundamentally different from each other in size, location and structure. What these systems did have in common however, was that they all suffered an extreme disturbance event at some time during their monitoring. Reefs in the Capricorn Bunker Sector of the southern Great Barrier Reef suffered extreme storm damage to their north-east flanks which effectively removed the benthic communities back to bedrock. Scott Reef off the north-west shelf of Australia suffered catastrophic levels of coral mortality from the bleaching event of 1998; while Coral Bay,

part of a fringing reef system on the mid-west coast of Australia, suffered severe mortality of many organisms as a result of coral spawn induced anoxia.

The coral and fish assemblages of the Capricorn Bunkers recovered to their pre-impact levels after a period of approximately 10 years. Their recovery was coherent among numerous reefs spread over 80 km, providing evidence of stability at large scales of space and time. This result was one of the first empirical tests of the resilience of meta-reef systems to natural disturbance. In comparison, given its relative isolation it was predicted that the Scott Reef system would struggle to recover from the bleaching event of 1998. It has however, displayed a similar level of resilience to catastrophic disturbance as the reefs in the southern GBR. These results are some of the first to provide evidence of the efficacy of the metapopulation model to explain dynamics on isolated reef systems. Moreover, these results also provide a comprehensive set of baseline conditions with which to compare other such isolated reef systems in the future. In contrast to the other two systems the recovery at Coral Bay has been somewhat slower with the coral and fish assemblages remaining considerably changed from their pre-impact structure some 13 years after the disturbance.

The resilience displayed by reefs in the southern GBR and Scott Reef off the northwest coast was underpinned by the availability of healthy coral and fish assemblages adjacent to the disturbed areas. The availability of these healthy areas was a consequence of firstly, the inherent patchiness of disturbance effects and secondly, the presence of significant reef areas below those depths usually subject to disturbance. This contrasts strongly with other reef systems like the Seychelles which lack significant reef areas at depth and have not recovered from the 1998 bleaching event. On the other hand, the coral reef community at Coral Bay had not recovered over the same time frame despite the availability of healthy reef communities in adjacent areas. This delayed recovery was the result of a recruitment bottleneck to the affected areas which is, in turn, the result of a raised ridge of live and dead coral running across the middle of the bay which impedes water flow.

The lack of recovery in Coral Bay highlights the significance of 'local' conditions in the population dynamics of coral reef communities. These local conditions are prevalent at all reef systems and are not just confined to physical differences in the shape and structure of reefs but may also include differences in the population dynamics of individual species. Localised upwelling effects at Scott Reef played a significant part in conferring resilience to the 1998 bleaching, allowing cooler water to moderate the effects of the warm water mass sitting over the reef. There were also a number of species that responded to the bleaching in the opposite direction to what had been recorded from other reef systems. For example, the territorial, herbivorous damselfish *Plectroglyphidodon lacrymatus* responded positively to the bleaching at Scott Reef whereas it was found to have declined across numerous other similarly disturbed systems. While the reasons for these differences are not clear they nevertheless highlight the fact that there is no single set of predictions applicable to the response of coral reef communities to disturbance with species-, reef-, region- and ocean-specific patterns prevalent. In the search for general principles of coral reef dynamics this can often be overlooked.

The work contained within this thesis reinforces the role of monitoring programs as an essential tool for gathering the long-term and large-scale datasets required to validate current models of community dynamics. Such programs provide a level of detail that periodic assessments can not and in doing so offer considerable insights into the processes driving the observed patterns. The 1998 bleaching event and the scale of predicted disturbance scenarios have highlighted the significant knowledge gaps that exist at intermediate scales. These gaps need to be filled to enable more rigorous testing and validation of metapopulation models. Such models will be vital for troubleshooting and understanding future climate change effects on entire reef systems

Chapter 1: General Introduction 1

Thesis Structure **4**

Chapter 2: Resilience to large-scale disturbance in coral and fish assemblages on the Great Barrier Reef 7

Abstract **7**

Introduction **8**

Methods **12**

Results **16**

Discussion **27**

Chapter 3: Towards an understanding of resilience in isolated coral reefs 34

Abstract **34**

Introduction **35**

Methods **38**

Results **44**

Discussion **54**

Chapter 4: Shedding light on the detail: Species-specific responses to large-scale bleaching at Scott Reef 65

Abstract **65**

Introduction **66**

Methods **69**

Results **71**

Discussion **90**

Chapter 5: Patterns of recovery in catastrophically disturbed reef fish assemblages 97

Abstract **97**

Introduction **98**

Methods **101**

Results **105**

Discussion **114**

Chapter 6: General Discussion 123

List of Tables

Table 2.1 Methods used to collect benthic and fish data over the 14-year time span of this study. *Benthos*: LI - line intercept, MT- manta tow, VT- video transects *Fish*: Log$_5$-timed swims using an abundance scale, LTM – absolute transect counts. See text for references on each method……………………………………………………………14

Table 2.2 Comparisons between pre- and post-impact fish abundance levels for the Capricorn Bunker reefs (impact) and the Swains reefs (reference). Significance is at p ≤ 0.05. ns: not significant, —: no data available, ↓↑: direction of significant change…21

Table 2.3 Relative abundance of those species accounting for 90% of total abundance of chaetodontids and pomacentrids for 1984 (pre-impact), 1992 (immediate post-impact) and 1998 (9 years post-impact). Data is for Lady Musgrave (LM) and One Tree (OT) Island reefs. — : no individuals counted…………………………………………….25

Table 2.4 Percentage of variation in the abundances of dominant families and genera of reef fishes, accounted for by benthic cover and temporal trends in the multiple regression model. ns: not significant……………………………………………………..26

Table 3.1 Correlations (Spearmans Rho) between fish and benthic assemblages at various taxonomic, temporal, and spatial scales of resolution. Benthic matrices were sqrt transformed and fish matrices were ln (x+1) transformed prior to any calculations. NB. 97-97 denotes the 1997 fish assemblage matrix correlated with the 1997 benthic matrix, 98-97 denotes the 1998 fish assemblage matrix correlated with the 1997 benthic matrix, etc. ns – non-significant Acan – Acanthuridae, Chaet – Chaetodontidae, Scar – Scaridae, Poma – Pomacentridae……………………………..51

Table 3.2. Index of Multivariate Dispersion (IMD) between pre-and post-bleaching surveys, for benthic, and fish assemblages at various taxonomic and spatial scales...53

Table 4.1 Results of the Linear Mixed Model analysis for species within the families Acanthuridae, Chaetodontidae, Scaridae and Pomacentridae. Planned contrasts for each post-impact year were against the mean and variance of all pre-impact years combined. The complete model contains 4 lagoon locations and 3 slope locations. L – Lagoon, S – Slope, WR – Whole Reef. Significance Levels - p<0.05 (*), p<0.001 (**), p< 0.0001 (***). NS – non-significant…………………………………………………...75

Table 4.2 The first 3 eigenvectors (components) extracted from the Factor analysis of 15 Benthic variables, and the amount of variance they explain. These components were subsequently used as independent variables in hierarchical regressions with individual fish species abundance. Only vectors with an eigenvalue of >1 were chosen……………………………………………………………………………………79

Table 4.3 Loadings of individual benthic variables on the 3 extracted Factors. Only loadings > 0.6 were tabulated…………………………………………………………….80

Table 4.4 Results of Hierarchical Multiple Regressions of individual species abundance against the first 3 extracted factors from a PCA of 15 benthic variables. Results are interpreted in the context of loadings in Table 6. The amount of variance accounted for by each individual factor is expressed as an absolute percentage of the total explained variance, not a proportion. Negative percentages refer to the direction of the relationship between that factor and the dependent species. NS – No significant relationship at the p<0.05 level of significance……………………………………………81

Table 5.1 Relative abundance (%), by Treatment and Year, for all species within the families Acanthuridae, Chaetodontidae, Scaridae and Pomacentridae………………109

Table 5.2 Results of the Linear Mixed Modelling for the dependent variables of Hard Coral, Species Richness and Abundance of the 4 main fish families, and Abundance of selected species. Significant results are indicated by ***** p<0.05, ****** p<0.001, ******* p<0.0001 Planned comparisons were made between years for each Treatment x Location combination with significant results annotated to the relevant graphics………………115

List of Figures

Fig. 2.1 Location of the seven reefs surveyed at the southern end of the Great Barrier Reef, Australia....13

Fig. 2.2 (a) Percentage cover of hard coral, soft coral and turf algae on 5 reefs in the Capricorn Bunker sector. Values are estimated means and 95% CI's calculated from the mixed linear models. (b) The relative contribution of the main hard coral morphologies to total coral cover in the Capricorn Bunker sector. Coral codes: M – massive, AT – *Acropora* tabulates, AS – *Acropora* submassives, B – branching, E – corals encrusting. (c) Percentage cover of hard coral from 3 reefs in the central Great Barrier Reef subject to a crown-of-thorns outbreak in 1983-84 (Williams D. McB, unpublished). Arrows indicate the timing of the disturbance....17

Fig. 2.3 Video frames of the beginning of Site 1 at One Tree Reef in the Capricorn Bunker sector from (a) 1992 (b) 1996 and (c) 1998. This reef was one of the most badly damaged during the disturbance and this sequence illustrates the rapid regrowth of corals. 18

Fig. 2.4 Species richness of Acanthuridae, Chaetodontidae, Scaridae and Pomacentridae in the Capricorn Bunker and Swains sectors between 1983 and 1998. No data were available between 1984-91. Values are estimated means and standard errors calculated from the mixed linear models. Arrows indicate the timing of the disturbance. 19

Fig. 2.5 Abundance of selected fish species from reefs in the Capricorn Bunker and Swains sectors between 1983 and 1998. No data were available during 1984-91. Values are estimated means and standard errors as calculated by the mixed linear models. Horizontal lines along the X-axis link years where the rate of change was significantly > 0 (at p< 0.05), in the Capricorn Bunker sector. Arrows indicate the timing of the disturbance...23

Fig. 3.1 Location of Scott and Seringapatam Reefs off the NW coast of Australia and the position of the fixed monitoring sites at those reefs. The dashed line represents the edge of the continental shelf. 39

Fig. 3.2 Dendrogram of the benthic assemblages for all location x year combinations sampled at Scott Reef. Clustering was hierarchical using group-average linking and based on Bray-Curtis derived similarity matrices. Sites are coded in the cluster analysis according to their habitat (L = lagoon, S = slope), followed by the location number nested within habitat (first digit), and sampling year (last two digits). The symbols represent the two habitat types and are individually shaded for each location within habitats (△ - Lagoon locations, ○ - Slope Locations) 44

Fig. 3.3 Percentage cover of a) Hard Corals and b) Turfing Algae between 1994 and 2003, within the lagoon and slope habitats. Vertical dashed line indicates time of bleaching. Error bars are one standard error of the mean 46

Fig. 3.4 Non-metric MDS ordinations of the benthic assemblages at Scott Reef, from all location x year combinations. The ordinations used the same similarity matrices used for the clustering. The ordinations are plotted separately for lagoon (a) and slope (b) habitats for easier interpretation. Symbols and color coding pattern are as outlined in the dendrogram of Fig. 3.2. Arrows indicate the direction of change of these communities in multi-dimensional space……………………………………………….47

Fig. 3.5 Rugosity of the benthic communities at Scott Reef. Data presented are from (a) 1997, immediately before the bleaching event, and (b) 2003, five years after the bleaching event (∗∗∗; p<0.0001). Groups of locations not sharing an overscore differed with the indicated probability. Location S3 was not surveyed in 2003 due to bad weather. See text for further details of methods used. 48

Fig. 3.6 Cluster analysis of the fish assemblages from all location by year combinations sampled at Scott Reef. Clustering was hierarchical using group-average linking and based on Bray-Curtis derived similarity matrices. Sites are coded in the cluster analysis according to their habitat (L = lagoon, S = slope), followed by the location number nested within habitat (first digit), and sampling year (last two digits). The symbols are the same as for Fig. 3.2…………………………….……………………………….49

Fig. 3.7 Non-metric MDS ordinations of the fish assemblages at Scott Reef from (a) all location by year combinations, (b) the inner lagoon location L2 only, and (c) all location by year combinations except L2. Sizes of bubbles are proportional to the amount of hard coral cover in each location by year combination. The percentage coral cover present at each location in 1997, just prior to bleaching, is noted in the bubble for that year. L2 is presented separately to aid interpretation of relationships of the fish communities at the other locations. Arrows indicate the temporal progression of sampling, with the full sequence of sampling years depicted for L1. 50

Fig. 3.8 (i) Relative abundance per species, (ii) Total family abundance and (iii) Species richness, for the Acanthuridae, Chaetodontidae Scaridae, and Pomacentridae in (a) lagoon and (b) slope habitats. (i) Relative Abundance: the shaded area delineates the ± 95% confidence interval of the pre-bleaching abundances. Immediate ● - 1998 and longer-term ○ - 2003. post-bleaching abundances are overlaid on this confidence interval. (ii) Total Abundance: Abundance summed across species. The horizontal dashed lines delineate the 95% CI of pre-impact abundance. (iii) Species

Richness: a rarefaction curve with 95% CI, based on the mean abundance of species over the four years pre-impact is presented with the observed total abundance and species richness values for the 1998 and 2003 censuses plotted. Species abbreviations – see Appendix …………………………………………………………..55-58

Fig. 4.1 Change in coral cover between 1997, 1998 and 2003, at all seven surveyed locations at Scott Reef 71

Fig. 4.2 Pie charts indicating the percentage cover of 6 composite benthic categories, for the Lagoon (a) and Slope (b) habitats, immediately before the bleaching event (1997), 6 months after (1998) and 5 years after (2003). NB. CB – Branching corals, CE/CS – Encrusting and sub-massive corals, CM – Massive corals, CF – Foliose corals, TA – Turfing algae, SC – Soft corals. Percentage cover values have been rounded to the nearest whole percent...72

Fig. 4.3 Three screen shots taken from video footage of the inner lagoon site of L2 from the years 1997, 1998 and 2001. The gradual breakdown in structure can clearly be seen. 73

Fig. 4.4 Changes in abundance from pre- to post-bleaching for those species from the (a) Acanthuridae (b) Chaetodontidae (c) Scaridae and (d) Pomacentridae, identified as significant by the Linear Mixed Models. Abundance values are square root transformed estimated means (± 1 S.E.) as calculated by the linear mixed models.........................89

Fig. 5.1 (a) Location map of Coral Bay, Western Australia (b) Decomposing remains of fish and other organisms from the March 1989 coral spawning event in Bill's Bay. (c) Recently killed fish from the April 2002 coral spawning event in the inner Control Bay.

The fish are parrotfishes and damselfishes. The reddish scum is coral spawn, with its colour indicative of how recent the mortality event was at the time the picture was taken. (d) The position of the survey sites within Bill’s Bay and the Control Bay - the dashed lines indicate the outer extent of mortality caused by the two disturbances. The numbering of the survey sites in the Control Bay is the same as shown for Bill’s Bay100

Fig. 5.2 (a) Hard coral cover by Treatment and Location, as estimated by the Linear Mixed Effects model. If transformation was necessary for the LME model analysis then transformed data was plotted. Significant differences between years for any given Treatment x Location are indicated thus * p<0.05, ** p<0.001, *** p<0.0001; ● 1995; ○ 2002 (b) Spatial contour plots of hard coral cover within the Control bay and BILL’s bay, for 1995 and 2002. The shading scale represents the percentage cover of hard coral. The dots indicate the positions of the survey sites within each bay. 106

Fig. 5.3 Change in hard coral cover between 1995 and 2002, on the nine transects constituting the INNER Location within the Control bay (see methods for more details). The spatially patchy mortality effects of the 2002 coral spawn disturbance are evident… 107

Fig. 5.4 Dendrogram illustrating the spatio-temporal relationships between the fish assemblages recorded at each site in 1995 and 2002. The abundance data matrix of 44 fish species was ln (x+1) transformed prior to calculation of Bray-Curtis similarities. Clustering was performed using UPGMA. The horizontal dashed line indicates four main groupings at 55% similarity. Colored symbols allow for easier comparison with the ordination of Fig. 5.5 111

Fig. 5.5 Non-metric Multidimensional Scaling ordination of all Site x Year combinations. The similarity matrix underlying the analysis was the same one used for clustering. The four main groupings identified from the dendrogram are encircled. Biplots of the eight fish species most responsible for the observed patterns are superimposed – species were identified through the SIMPER routine in PRIMER (see methods for more detail). Das.arua – *Dascyllus aruanus*, Pgy.lacr – *Plectroglyphidodon lacrymatus*, Pom.molu – *Pomacentrus moluccensis*, Sca.micr – *Scarus microrhinos*, Sca.schl – *Scarus schlegeli*, Sca.sord – *Scarus sordidus*, Ste.livi – *Stegastes lividus*, Ste.obre – *Stegastes obreptus*. Symbol colours follow that of Fig.5.4. Numbers 1-9 represent site locations as identified in Fig. 5.1b 112

Fig. 5.6 Species richness of the families Acanthuridae, Chaetodontidae, Scaridae and Pomacentridae by Treatment and Location, as estimated by the Linear Mixed Effects Model. Legend is same as described in Fig. 5.2a 113

Fig. 5.7 (a) Abundance of fish species by Treatment and Location, as estimated by the Linear Mixed Effects model. Legend is the same as described in Fig. 2a. Only those species showing significant disturbance effects were plotted. 117

Chapter 1: General Introduction

This thesis addresses several core issues throughout its chapters. It is firstly an examination of the roles of scale in the observation of patterns and processes in coral reef environments. It is also an investigation of the effects of disturbances of varying types and intensities on the dynamics of coral reef assemblages. This includes by definition an examination of the role of habitat in mediating disturbance effects. Lastly, it is an endorsement of the utility and effectiveness of monitoring programs as the only effective way to collect the data on which studies like the one presented here can be based.

While there is no single ‘correct’ scale on which to observe patterns and processes within communities and ecosystems, most ecological studies still focus on relatively small scales. However, many of the processes that structure communities operate on spatial and temporal scales many orders of magnitude greater (Levin 1992). Current models of community structure now recognize the emergent properties of ecosystems and incorporate local or small-scale dynamics into a larger framework of hierarchical patch dynamics (Wu & Loucks 1995), metapopulation dynamics (Hanski 1998), landscape ecology (Hobbs 1994), and macroecology (Blackburn & Gaston 2004; Brown & Maurer 1989) .

There remains a paucity of studies at sufficiently large scales of space and time that can provide empirical tests of current models of community structure. Such studies are needed to understand how small-scale, local dynamics, which can be highly variable e.g. Sale et al*.* (1994) and Sale & Steele (1989), are related to stability and/or resilience at larger scales e.g. Cheal et al*.* (2007), Hughes et al*.* (1999) and Ninio et al*.* (2000). There have been, however, a number of recent studies that have addressed larger spatial scales, but these have been either snapshots e.g. Graham et al*.* (2006) or meta-analyses e.g. Wilson et al*.* (2006) but c.f. Wilson et al*.* (2008b). While such studies represent landmark publications, providing broad-scale synthesis of major disturbance effects, my thesis provides the combination of large-scale and long-term observations which are largely missing from the published literature. Moreover, the vast majority of the data presented here was collected by the same observer (myself), using identical methods at all locations providing a level of consistency that is seldom achieved in such studies.

There is an extensive literature on disturbance effects on coral reefs. Moreover, since Connell's (1978) seminal paper, disturbances have become recognized as significant drivers of community structure and an integral part of the dynamics of most communities. The most commonly reported natural disturbances on coral reefs have included storms (Harmelin-Vivien 1994; Lassig 1983; Walsh 1983; Williams 1984) and *Acanthaster planci* (Crown-of-thorns) infestations (Chesser 1969; Colgan 1987; Lourey et al. 2000; Sano et al. 1984; Williams 1986). While such disturbances can cause extensive damage, they have been overshadowed – especially in the last 15 years - by the emergence of coral bleaching as the most damaging perturbation to affect coral reefs in modern times (Hoegh-Guldberg 1999).

There is now a sense of urgency associated with bleaching events as a result of the unprecedented magnitude of the 1998 circum-global bleaching event (Wilkinson et al. 1999). Bleaching of corals is unequivocally tied to warm water anomalies (see review by Brown (1997)) and because current climate change scenarios predict continued atmospheric warming (and subsequent warming of the oceans) (IPCC 2007), it is likely that bleaching events on the scale of 1998 will become more frequent. The 1998 event clearly illustrated the increased scale at which disturbance effects need to be assessed on coral reefs. A renewed focus on metapopulation or landscape scale dynamics is required to try and understand how, and ultimately whether, entire reef systems are likely to survive such large scale disturbances.

Because disturbances directly alter benthic community structure on coral reefs they are also indirectly affecting the associated fish assemblages. Habitat effects on reef fish assemblages can be separated into the effects mediated by live coral and the effects mediated by habitat structure, independent of the presence of live coral (Syms & Jones (2000), Pratchett et al*.* (2008), Wilson et al*.* (2006), Munday (2004), Jones & Syms (1998), Lewis (1997; 1998)). However, while separate processes these effects can be difficult to tease apart. This thesis investigates three different disturbance types each of which affects coral reefs in different ways. These differences between disturbance types and the different reef systems they affected (i.e. barrier reef, isolated reef and fringing reef) provided opportunities to further advance our understanding of fish-habitat relationships. Moreover, the research contained within not only covers spatial scales ranging from an entire bay to individual reefs spread out over 10's of kilometers but the sites contained within these spatial scales have all been monitored over periods of 10 years or more. This extensive spatio-temporal combination provides a new opportunity to understand the responses of coral reefs to disturbance at larger scales.

Metapopulation dynamics provides an appropriate framework for understanding large-scale dynamics of ecosystems, as it is most applicable to spatially heterogeneous and patchy environments - a common description of coral reef environments. An important aspect of metapopulation dynamics is the degree of connectivity between sub-populations. To understand the contribution of connectivity to metapopulation stability and/or resilience of tropical reef communities it is necessary to study reef systems with varying levels of connectivity (~ isolation) between the populations acting as part of a metapopulation. Here I compare disturbance effects in a highly interconnected archipelagic system (Great Barrier Reef), a highly isolated reef system (Scott Reef) and a reef system with intermediate levels of connectivity (Ningaloo Reef). In each case a different disturbance agent has operated. While, ideally, the disturbance agent should have been the same throughout, we nevertheless gain further insight into the roles of habitat as a mediator of disturbance effects on coral reefs.

The studies I present here would not have been possible without the implementation of the long-term monitoring programs established and run by the Australian Institute of Marine Science (AIMS). Monitoring is often criticized as being unscientific, expensive and wasteful (Lovett et al. 2007). If done properly, however, such programs can provide key information about the ecology of complicated ecosystems at spatial and temporal scales that are not amenable to study by small scale manipulative experiments. Indeed, monitoring programs can be very cost effective for resource management and scientific exploration Lovett et al. (2007). The use of well-trained observers utilizing standardized and robust methodologies can result in very high quality data that can be used to evaluate responses to disturbances (as I have done here), and provide baselines against which change and management effectiveness can be evaluated (Lindenmayer & Likens 2009).

Thesis Structure

Chapter 1 is the general introduction which outlines the core elements of this thesis.

Chapter 2 examines resilience to a large-scale storm disturbance in the southern Great Barrier Reef (GBR). The GBR is a highly interconnected reef system that conforms well to contemporary models of meta-population dynamics. Many individual reefs exist in a complex maze with varying degrees of connectivity (Doherty 1991). It is expected that such an arrangement would confer considerable resilience to disturbance on the reef system as a whole. My results quantify this resilience. This study is also one of the first to provide evidence - at long temporal (i.e.14 years) and large spatial (tens of kilometers) scales - that concurs with much of the current theory on how marine communities are structured.

This chapter also provides time frames for community and species specific responses to disturbance within this highly resilient reef system. As such, it provides a baseline against which to measure the resilience of the other reef systems studied here. Theory would suggest that, for example, more isolated reefs would take longer to recover from a similar scale disturbance, and that that extra time would reflect the reduced connectivity inherent in more isolated reef systems.

Chapters 3 and 4 examine community and species level responses, respectively, to the bleaching event of 1998, at Scott and Seringapatam reefs off the northwest shelf of Australia. These reefs are very remote, located some 350km off the coast with their nearest reef neighbours located a similar distance to the north and south. Much of what we know about coral reefs in the southern hemisphere has come from the study of highly interconnected reef systems like the GBR. So monitoring the dynamics of such a large and remote reef community has provided an exceptional opportunity to learn how such systems cope with large disturbances given their isolation and reduced access to external input of propagules. Clearly, they have resilience given their long-term existence, but their ecological dynamics and ability to recover from disturbances of such magnitude are poorly understood, particularly in the face of increasing disturbances.

Chapter 5 describes the response of coral and fish communities to an unusual type of disturbance that occurred within two adjacent bays at Ningaloo reef in Western Australian. Coral spawn trapped inside the bays for an extended period caused extensive mortality of many organisms (including fish and corals), through acute anoxia of the water column. A monitoring program (which covered the entirety of both bays) was implemented to follow the response of the coral and fish communities to the disturbance. The results of this study are compared and contrasted with those of the other studies to provide additional insights into how different reef systems respond to disturbance. For example, although part of a contiguous reef system, the bays studied here face reduced water flow. I ask whether this has had any obvious effects on the response of the resident fish and coral communities to the disturbance.

Chapter 2: Resilience to large-scale disturbance in coral and fish assemblages on the Great Barrier Reef

Halford, A. R., Cheal, A. J., Ryan, D., & Williams, D. McB. (2004) Resilience to large-scale disturbance in coral and fish assemblages on the Great Barrier Reef. *Ecology* 85 (7): 1892-1905

Abstract

Recognition of the complex spatial and temporal variability of abundance and diversity found in many populations has led to a greater focus on the roles of heterogeneity, stochasticity and disturbance in the structure and persistence of communities. This focus is directly relevant to coral reef communities that are characterized by very high species diversity in a spatially heterogeneous environment, display stochastic variability in community structure at small spatial and temporal scales, and are subject to major disturbances. We monitored coral and fish assemblages over 14 years, on fixed sites spread over 80 kilometres of the southern Great Barrier Reef (GBR), Australia, and found evidence of large-scale resilience and predictable recovery of these assemblages. Sometime between November 1987 and October 1989, live coral cover on the shallow northeast flanks of some reefs in the southern GBR decreased from > 80% to < 10%, probably as a result of storm damage. We compared the fish and benthic communities present in these areas prior to the disturbance (1983-84) with those present in 1992 and the subsequent changes through to 1998. Hard coral cover increased slowly from 1992 –1994, then accelerated to be indistinguishable from pre-impact levels by 1998. The response of the coral assemblages was largely due to the predominance of tabulate *Acropora* species and their characteristics of rapid growth and competitive dominance. Patterns of species richness of the fish families Acanthuridae, Chaetodontidae, Scaridae and Pomacentridae mirrored that of hard coral, except the Pomacentridae had not recovered to pre-impact levels by 1998. Of

the 26 fish species analysed for changes in abundance, 88% decreased after the disturbance, then subsequently increased, with all but two recovering to pre-impact levels by 1998. Although processes such as settlement and immigration are ultimately responsible for replenishment of local populations, our data suggested that habitat plays a strong role in modifying fish assemblages. Thus, both coral and fish assemblages demonstrated resilience to large-scale natural disturbance and predictability in the structure of the assemblages, with most taxa approaching the asymptote of abundance and species richness that existed prior to the disturbance.

Introduction

As recently as the 1970's, there was still a view among community ecologists that biological systems tended towards equilibrium conditions (see Pimm 1991 for discussion). Although physical disturbances were recognised as having some role in the development of communities, they were considered transient phenomena, not significant enough to disturb an ecosystem's intrinsic march towards a climax community (Odum 1969). However, an increasing number of studies were unable to reconcile the complex spatial and temporal variability of abundance and diversity found in many communities using the prevailing equilibrium theories (e.g., Doherty (1987)). From this awareness came the rapid development of non-equilibrial theory, and a greater focus on the role of heterogeneity, stochasticity and disturbance in structuring communities (e.g., Holling (1973); Paine and Levin (1981); Chesson et al. (1986)).

It is now well established that disturbance is a major source of temporal and spatial heterogeneity in the structure and dynamics of natural communities, and an agent of natural selection in the evolution of life histories (Pickett & White 1985). Most research however, has focused on terrestrial systems, most notably forests (e.g., Borman and Likens (1979); Heinselman (1981)). It was not until Connell's seminal review that non-equilibrial theory was explicitly applied to coral reefs. While there is still some debate over the general validity of the "intermediate disturbance hypothesis" as espoused by Connell (1978), it nevertheless served to highlight the importance of spatial heterogeneity and the significance of extrinsic factors like disturbance in modifying coral reef community structure (Karlson & Hurd 1993). Current models of community structure now incorporate aspects of patch dynamics, hierarchy theory and metapopulation stability (see Wu & Loucks 1995) thereby incorporating a wide range of spatial and temporal scales explicitly linked to heterogeneity, of which disturbance plays a major role. However, empirical studies at large ecological scales are rare, with most studies constrained to small spatial and temporal scales.

A system can be considered stable in the face of a disturbance if (a) it retains a similar structure (*resistance*), or (b) it returns to a similar pre-disturbance structure after an initial deviation (*resilience*) (Connell & Sousa 1983). Disturbances occur over a range of spatial and temporal scales and with varying intensity. Investigations conducted at small spatial scales have generally concluded that the community is unstable (Sale 1978; Sale & Williams 1982), while studies conducted at larger scales generally consider that communities are stable (Williams & Hatcher 1983). However, the spatial scale at which a reef fish assemblage displays stability will also vary according to the level of larval connectivity in the regional system of assemblages. As reef fish have a highly dispersive larval phase lasting from 10-60 days (Brothers et. al. 1983) the minimum areas under which assemblages will display stability are likely to be large (Connell & Sousa 1983). This is especially likely in an archipelagic system such as the Great Barrier Reef.

In general, studies of the effects of disturbance on coral reefs have been biased towards sessile organisms, most likely because they are easier to observe and quantify. Most large-scale disturbances (> 1km) affecting coral reefs are due to natural events such as large storms (Lassig 1983; Walsh 1983), crown-of-thorns starfish

(COTS) outbreaks (Hart et al. 1996; Hart & Klumpp 1996; Hart & Russ 1996; Williams 1986) and coral bleaching (Wellington & Victor 1985). Their effects on benthic communities can be extensive (e.g., Colgan (1987); van Woesik et al. (1991); Brown (1997); Connell (1997); Connell et al. (1997)). In the case of storms, damage is generally most severe on the windward side of reefs, with corals in the lee often remaining unaffected (Cheal et al. 2002; Connell et al. 1997; Woodley et al. 1981). Damage can vary from removal of entire coral outcrops (over 10's to 100's of meters) in the direct path of the storm, to individual colony damage within more sheltered areas (Done 1993; Van Woesik et al. 1991). In contrast, COTS outbreaks and bleaching events kill only the living veneer of hard corals, leaving the skeletal structures intact. Irrespective of the disturbance type, effects are always patchy, with partial survival of corals even in areas subject to the most intense disturbance (Connell et al. (1997); Done (1992a)). Recovery of benthic communities from such disturbances is highly variable and dependent on the interplay of many factors, e.g., the scale of the disturbance, availability of larval propagules from undamaged areas, and the type of coral community that existed at the time of the disturbance (see Hughes & Connell 1999). However, in general, recovery is usually slower after acute disturbances that alter not only the coral but also the underlying physical environment than after disturbances that kill or damage only the coral (Connell 1997).

In contrast to coral communities, the role of disturbance in shaping reef fish assemblages is still unclear. Current models of fish assemblage dynamics vary widely, encompassing fish populations as stable and resistant to change at one end of a scale, to unstable and highly variable at the other (see review by Jones & Syms (1998)). Evidence of direct disturbance effects on fish assemblages is limited (Bohnsack 1983; Lassig 1983; Walsh 1983), with most of the literature implicating indirect effects through modification of habitat. However, the effects of habitat modification are difficult to predict. Some investigators have found positive correlations between habitat and the abundance and/or diversity of fish (Bell & Galzin 1984; Chabanet et al. 1997; Luckhurst & Luckhurst 1978) while others have found no significant correlations between these variables (Fowler 1990; Green 1996; Roberts & Ormond 1987). More recently, the influence of underlying habitat heterogeneity, rather than coral cover *per se*, has been implicated as a major determinant of reef fish community structure (Lewis 1997; Syms 1998; Syms & Jones 2000). All three of these cited studies demonstrated that removal of substantial proportions of biogenic habitat (e.g., hard corals) at small scales did not necessarily result in altered fish communities.

Given the increasing evidence that recovery of many hard coral assemblages occurs over decades (Ninio et al. 2000; Williams 1986) and that many reef fish species are long-lived (Choat & Axe 1996; Meekan et al. 1999), there is a need for long term studies of fish assemblage dynamics at appropriate scales, analogous to recent works on corals (e.g., Done (1992a); Hughes (1994); Connell et al. (1997)). A dramatic decline in hard coral cover on some reefs of the Capricorn Bunkers region (southern Great Barrier Reef, Australia) between November 1987 and October 1989 provided an opportunity to examine the effects of a large scale disturbance on adult, reef fish assemblages. During this period, benthic cover on the northeast flanks of the most exposed reefs was reduced from > 80% to < 8% (Doherty et al. 1997; Miller et al. 1991). An earlier study investigating the effects of this same disturbance on fish recruitment was unable to unequivocally assign any individual event as causing the damage (see Doherty et al. 1997). After consulting weather records from numerous sources Doherty et al. (1997) concluded that a combination of storms over the period in question was the most likely cause of the damage.

In 1992, when hard coral cover was still very low (site mean of 8.2%, n = 4 reefs x 3 sites; Oliver et al. 1995) a long-term program was implemented to monitor annual changes in adult fish assemblages and benthic assemblage structure on five reefs in the Capricorn Bunker sector. These same reefs had been the focus of two other studies of fish and benthic structure in the 1980’s (Doherty et al. 1997). By combining the results of these pre- and post-impact studies, we were able to gain some historical perspective on the effects of the disturbance and the subsequent patterns of recovery. We focused on four questions: (1) What quantifiable changes occurred in the benthos and fish assemblages immediately after the disturbance? (2) In the years following the disturbance (i.e., between 1992 and 1998), how did the taxa respond? (3) Nine years after the disturbance, how similar were the benthic and fish assemblages to their pre-impact levels? (4) To what extent were changes in the abundance and/or species richness of selected fish taxa correlated with changes in the benthos?

Methods

The reefs included in this study were situated in the southern Great Barrier Reef (GBR). Five reefs were in the Capricorn Bunker sector (Broomfield, Wreck, One Tree Is., Fitzroy and Lady Musgrave Is.) and two reefs were in the Swains sector (East Cay and Turner Cay) (Fig. 2.1). Although not ideal as controls, the Swains reefs were the closest reefs to the disturbed area that also contained similar fish and benthic assemblages (Williams 1991). Moreover, given the absence of any large-scale coral decline, they were most likely not subject to the same major disturbance.

Data collection and survey methods

All study sites were located on the shallow northeast flanks of reefs, between the six and twelve metre depth contours. Sites, and transects within sites, were all fixed, with transects running consecutively approximately 5-10 metres apart. Annual reef surveys were conducted using a variety of comparable, established methods (Table 2.1). Benthic data on percentage cover of corals and algae were collected using

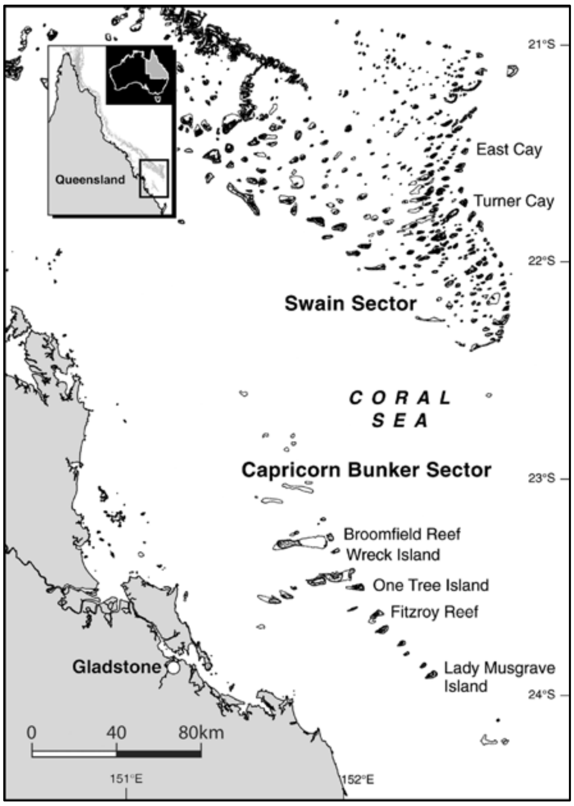


Fig. 2.1 Location of the seven reefs surveyed at the southern end of the Great Barrier Reef, Australia.

manta-tow surveys, video-transect surveys and line intercept surveys (Oliver et al. 1995; Doherty et al. 1997; Sweatman et al. 2000) during 1985-87 and 1989-98. Data on adult fish abundances and species richness from the families Acanthuridae (surgeonfishes), Chaetodontidae (butterflyfishes), Labridae (wrasses), Pomacentridae (damselfishes) and Scaridae (parrotfishes) were collected using two methods. Pre-disturbance data (1983-84) were collected during 45 minute timed swims using a $\log_5$ abundance scale (Williams 1982) while post-disturbance data (1991-98) were collected using absolute abundance counts of selected species within transects of fixed size (see Thompson & Mapstone (2002) for a detailed description)

Table 2.1 Methods used to collect benthic and fish data over the 14-year time span of this study. *Benthos*: LI - line intercept, MT- manta tow, VT- video transects *Fish*: Log_5- timed swims using an abundance scale, LTM – absolute transect counts. See text for references on each method.

Year	1984	1985-87	1988	1989	1990	1991	1992	1993	1994-98
Benthos		LI, MT		MT		MT	MT, VT	LI, MT, VT	MT, VT
Fish	Log_5						LTM	LTM	LTM

LI - 3 sites, 5 x 40m transects per site; VT – 3 sites, 5 x 50m transects per site; MT – 2 minute tows along northeast perimeter.

Log5 – 3 x 45 minute swims with abundance categories: 1 = 1, 2 = 2-5, 3 = 6-25, 4 = 26-125, up to 7.
LTM – 3 sites, 5 x 50m transects. Pomacentridae counted along 1meter wide strip, all other species counted along a 5 meter wide strip.

By assuming that estimates of benthic cover were spatially and temporally consistent for each of the methods, overlap between the three different benthic survey methods provided the necessary comparative information for inter-calibration. However, unlike the benthic data collections, there was no overlap between the fish census methods used, so a dedicated calibration study was undertaken to enable direct comparison of the two methods. Fixed sites at four reefs within the central GBR were initially surveyed using absolute abundance counts and then resurveyed within 24 hours using the log_5 abundance scale. The absolute abundance estimates were then converted to the log_5 abundance scale to correspond with the timed swims. Both data sets were then averaged to reef level (i.e., northeast flanks). This calibration data set was then included in the analysis of the fish data from the Capricorn Bunker sector in order to interpret differences between the two counting methods.

Several additional criteria were used to determine which fish species were included in the analyses of changes in abundance: (1) Comparison of the two methods of data collection was conducted in the central GBR, and some of the species found in the Capricorn Bunker and Swains sectors in the southern GBR were not present. Therefore, only those species that existed in both regions could be part of the full analysis (i.e., pre- and post- impact) of the disturbance data sets. (2) For the remaining species present only in the southern GBR, those that occurred on at least two of the Capricorn Bunker reefs were included. These species could only be analysed for post-impact effects. (3) The caveat for inclusion in either of the first two criteria was sufficient abundance and replication through time to make any analysis worthwhile. In practice, this meant occurrence over at least three consecutive years in the study and relative consistency in abundance between years. Borderline inclusions were checked for normality and where residuals were highly non-normal they were excluded from further investigation.

Statistical analyses

Mixed linear models were fitted independently to the benthic and fish data. Estimates of cover, species richness and abundance were obtained using restricted maximum likelihood as implemented in the SAS MIXED procedure (Littell et al. 1998). The models included (a) the fixed effects of method and the polynomial for the change of benthic cover, species richness and fish abundance over time, for the periods before and after the disturbance, and (b) the random effects for the polynomial over time for each reef (details are presented in the Appendix). The adjusted means for benthic cover were estimated by averaging across reefs for the video transects methodology. Adjusted means for fish abundance and species richness were calculated by combining the parameter estimates from the model to reflect the mean for a given year using the 45-minute timed swim.

Besides examining changes in the benthos and fish independently, we also tested for significant relationships between the amount of benthic cover and fish abundance, using only data from the post-impact period (i.e., collected with one method). Prior to any analysis, estimates of fish abundance were summed to site, and benthic cover averaged to site. Fish abundance was then transformed using log (x +1) and benthic cover transformed using the empirical logit of McCullagh & Nelder (1989). Fish abundance was modelled using a mixed linear model incorporating sampling design effects such as reef and site differences. The remaining variability in fish abundance was then partitioned between the benthic categories of hard coral, soft coral, turf algae, and a residual. The residual was then partitioned into a temporal trend and random error. This approach removed variability from the response due to known factors such as design effects and benthic cover. Any remaining variability that could be related to temporal trends indicated that fish abundance reacted to some other cue not accounted for by the benthic categories. If no significant temporal trend remained, we concluded that the trends in the benthic categories accounted for the trends in fish abundance. Although this conclusion implies that benthic abundance and fish abundance were related, it does not necessarily indicate that a given benthic category caused the observed changes.

Results

Changes in benthic assemblages

In the years immediately preceding the disturbance, the benthic assemblages on the northeast flanks of reefs in the Capricorn Bunkers sector were characterized by very high cover of hard corals (>80% in 1987), especially tabulate *Acropora* (Fig. 2.2a, b). As a result of the disturbance the benthic assemblages were altered dramatically, with mean hard coral cover reduced to less than 10%. The only hard

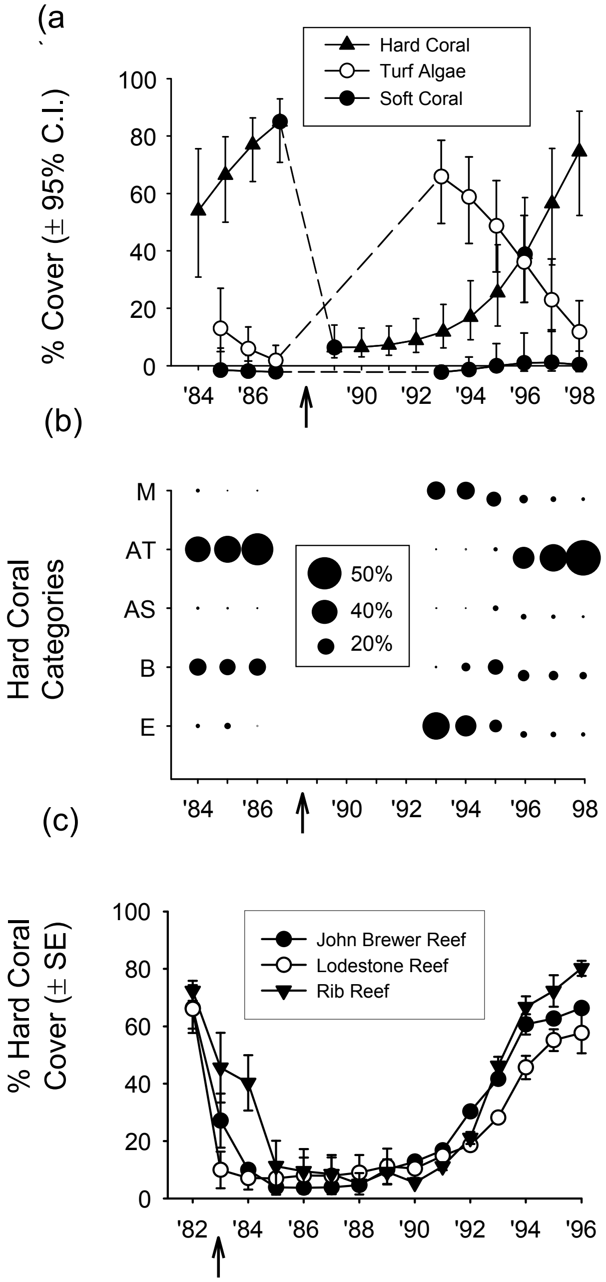


Fig. 2.2 (a) Percentage cover of hard coral, soft coral and turf algae on 5 reefs in the Capricorn Bunker sector. Values are estimated means and 95% CI's calculated from the mixed linear models. (b) The relative contribution of the main hard coral morphologies to total coral cover in the Capricorn Bunker sector. Coral codes: M – massive, AT – *Acropora* tabulates, AS – *Acropora* submassives, B – branching, E – corals encrusting. (c) Percentage cover of hard coral from 3 reefs in the central Great Barrier Reef subject to a crown-of-thorns outbreak in 1983-84 (Williams D. McB, unpublished). Arrows indicate the timing of the disturbance.

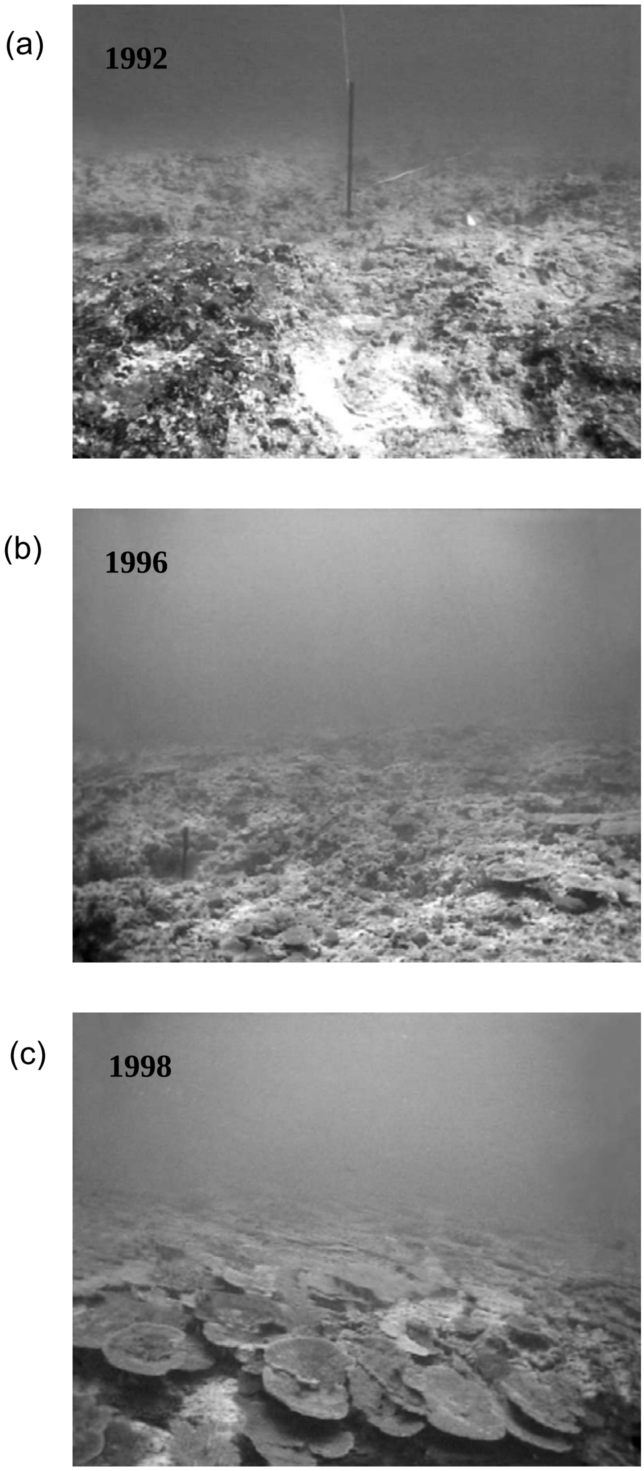


Fig. 2.3 Video frames of the beginning of Site 1 at One Tree Reef in the Capricorn Bunker sector from (a) 1992 (b) 1996 and (c) 1998. This reef was one of the most badly damaged during the disturbance and this sequence illustrates the rapid regrowth of corals.

corals remaining were the more robust and encrusting types. On the most affected reefs at One Tree Is. and Lady Musgrave Is., the benthos was reduced to scoured pavement (Fig. 2.3a). For five years following the disturbance, hard coral cover remained low and turf algae dominated the benthos. However, between 1992 and 1996 hard coral cover began to increase exponentially (Fig. 2.2a, 2.3b), returning to pre-disturbance levels by 1998 (1987 vs 1998, p = 0.135; Figure 2.3c), with tabulate *Acropora* again dominant. Soft corals also declined after the disturbance, but had returned to their low yet stable pre-impact levels by 1995 (Figure 2.2a). By way of comparison, coral cover data collected prior to and following a major crown-of-thorns-starfish outbreak in the central GBR, showed a similar pattern of decline and recovery to this study (Figures 2.2a,c).

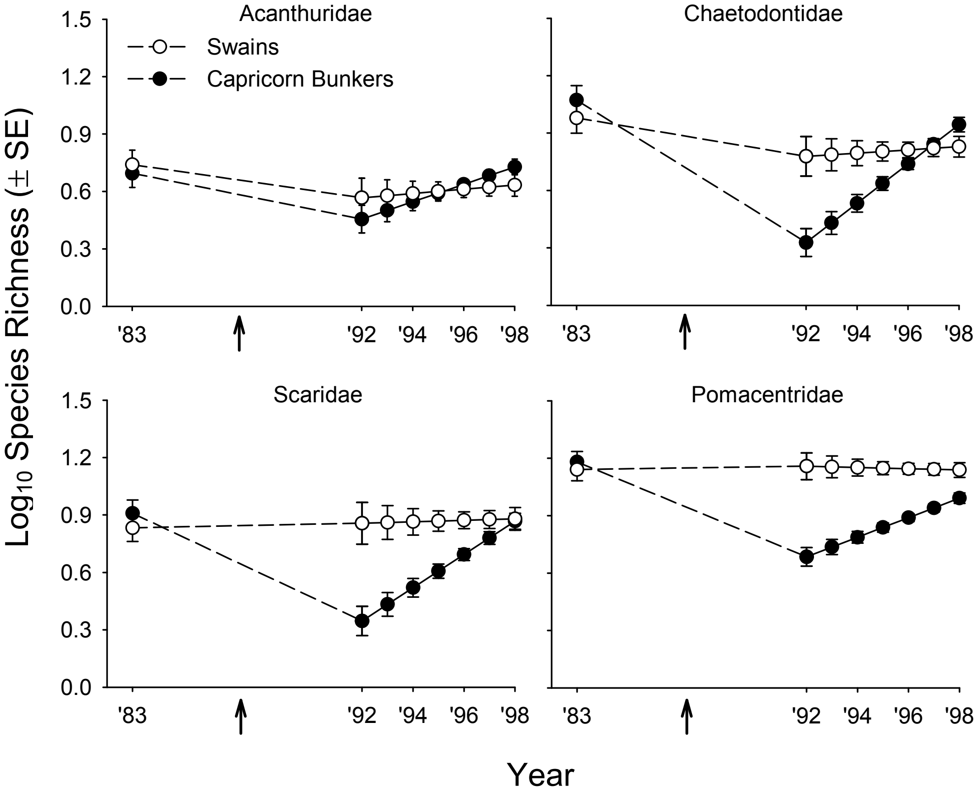


Fig. 2.4 Species richness of Acanthuridae, Chaetodontidae, Scaridae and Pomacentridae in the Capricorn Bunker and Swains sectors between 1983 and 1998. No data were available between 1984-91. Values are estimated means and standard errors calculated from the mixed linear models. Arrows indicate the timing of the disturbance.

Changes in fish assemblages

Species richness

In 1983, approximately five years prior to the disturbance, species richness of the fish families Acanthuridae, Chaetodontidae, Scaridae and Pomacentridae was similar between the Capricorn Bunker and Swains sectors. By 1992, three years after the disturbance, the species richness of all four families had fallen significantly within the Capricorn Bunker sector (Fig. 2.4). This decrease was not mirrored in the Swains reefs, where species richness values remained stable over the entire period of this study (Fig. 2.4). The Chaetodontidae suffered the greatest decrease, with species richness falling by 83 % from an estimated mean of 12 species in 1983 to 2 species in 1992 ($p = 0.0001$). Also strongly affected were the Scaridae and Pomacentridae, with a 75 % and 67 % drop, respectively ($p = 0.0001$ for both). The Acanthuridae did not fare as badly, with a 40 % drop ($p = 0.0075$) in species richness over the same period. Seven years later, recovery was complete for three of the four families, with species richness levels in 1998 not significantly different from pre-disturbance levels. The Acanthuridae had actually recovered their pre-impact levels by 1995, while the Chaetodontidae and Scaridae did not recover their pre-impact richness until 1998. The Pomacentridae were slow to recover, with species richness levels in 1998 still significantly less (~ 35 %) than before the disturbance.

Abundance

While the abundance of fishes on the disturbed Capricorn Bunker reefs varied markedly over the study period, only two species showed significant changes on the reference (Swains) reefs (Table 2.2). One species of herbivorous damselfish (*Chrysiptera rex*) decreased in abundance during 1992-98 and one species of planktivorous damselfish (*Pomacentrus coelestis*) was significantly lower in abundance at the beginning than the end of the study. Importantly, no species differed in abundance on the reference reefs, between the pre-disturbance count in 1983 and the first count post-disturbance in 1992.

Table 2.2 Comparisons between pre- and post-impact fish abundance levels for the Capricorn Bunker reefs (impact) and the Swains reefs (reference). Significance is at $p \leq 0.05$. ns: not significant, —: no data available, ↓↑: direction of significant change.

Family	†Trophic	Capricorn Bunkers			Swains		
	Group	‘83-‘92	‘83-‘98	‘92-‘98	‘83-‘92	‘83-‘98	‘92-‘98
Species							
Acanthuridae							
Acanthurus dussumieri	*su*	ns	ns	0.0034↓	ns	ns	ns
A. nigrofuscus	*lc*	—	—	0.0019↑	—	—	ns
Ctenochaetus spp.	*su*	0.0001↓	0.0017↓	0.0418↑	ns	ns	ns
Naso unicornis	*lc*	ns	ns	ns	ns	ns	ns
Zebrasoma scopas	*lc*	ns	ns	0.0101↑	ns	ns	ns
Chaetodontidae							
Chaetodon citrinellus	*si*	ns	ns	0.0041↑	ns	ns	ns
C. flavirostris	*si*	—	—	ns	—	—	ns
C. kleini	*si*	—	—	0.0001↑	—	—	ns
C. plebius	*cf*	—	—	0.004 ↑	—	—	ns
C. rainfordi	*si*	0.0001↓	0.0498↓	0.0001↑	ns	ns	ns
C. trifascialis	*cf*	0.0009↓	ns	0.0001↑	ns	ns	ns
Scaridae							
Scarus chameleon	*sp*	0.0071↓	ns	0.008 ↑	ns	ns	ns
S. globiceps	*sp*	0.0012↓	ns	0.041 ↑	ns	ns	ns
S. psittacus	*sp*	0.0054↓	ns	0.0028↑	ns	ns	ns
S. sordidus	*sp*	—	—	ns	—	—	ns
Labridae							
Gomphosus varius	*mi*	0.0001↓	ns	0.0001↑	ns	ns	ns
Halochoeres hortulanus	*si*	0.0172↓	ns	ns	ns	ns	ns
Hemigymnus fasciatus	*si*	0.0017↓	ns	0.0091↑	ns	ns	ns
H. melapterus	*si*	0.0011↓	ns	0.0015↑	ns	ns	ns
Pomacentridae							
Chromis nitida	*zp*	—	—	ns	—	—	ns
Chrysiptera rex	*sc*	ns	ns	ns	ns	ns	0.0245↓
Neopomacentrus azysron	*zp*	ns	ns	ns	ns	ns	ns
Pomacentrus bankanensis	*sc*	—	—	0.0015↑	—	—	ns
P. coelestis	*zp*	0.0075↑	ns	0.0733↓	ns	0.0001↓	ns
P. lepidogenys	*om*	0.0016↓	ns	0.0084↑	ns	ns	ns
P. wardi	*sc*	ns	ns	ns	ns	ns	ns

† Trophic codes (after Williams 1983): cf = hard coral feeder, mi = motile invertebrate feeder, lc = large cropper (algae) om = small omnivore, sc = small cropper (algae), sp = scraper (algae), zp = small zooplankton feeder, su = sucker (algae), si = sessile invertebrate feeder.

On the impact (Capricorn Bunker) sites, 11 of 19 species analyzed for pre- and post-impact changes decreased significantly in abundance following the disturbance: 1/4 acanthurids (*Ctenochaetus* spp.); 2/3 chaetodontids (*Chaetodon rainfordii*, *C. trifascialis*); 3/3 scarids (*Scarus chameleon*, *S. globiceps*, *S. psittacus*); 4/4 labrids (*Gomphosus varius*, *Halichoeres hortulanus, Hemigymnus fasciatus*, *H. melapterus*); and 1/5 pomacentrids (*Pomacentrus lepidogenys*). Only one species, *Pomacentrus coelestis*, increased in abundance following the loss of live coral (Table 2.2).

Over the “recovery” period from 1992 to 1998, 59% of fish taxa increased in abundance as coral cover increased from less than 10% to over 70%. This increase included all but one (*Halichoeres hortulanus*) of the eleven species that decreased following the disturbance, plus four species whose abundance prior to the disturbance was unknown (*Acanthurus nigrofuscus*, *Chaetodon kleinii*, *C. plebius*, and *Pomacentrus bankanensis*). Four species showed no significant change in abundance during the entire study (*Naso unicornis*, *Pomacentrus wardi*, *Chrysiptera rex* and *Neopomacentrus azysron*). Another four species whose abundance prior to the disturbance was also unknown showed no change in the recovery phase (*Chaetodon flavirostris*, *Scarus sordidus*, *Chromis nitida* and *Pomacentrus australis*). Only two species declined in abundance during the period 1992-98 (*Acanthurus dussumieri* and *Pomacentrus coelestis*).

By 1998, the abundance of only one species and one species group (*Chaetodon rainfordi* and *Ctenochaetus* spp.) differed significantly from their pre-disturbance levels (Fig. 2.5). While the *Ctenochaetus* group appeared to be some way from complete recovery, the pre-disturbance abundance counts were inflated by the inclusion of *Acanthurus nigrofuscus* among the *Ctenochaetus* spp. While it was not possible to separate *A. nigrofuscus* from the pre-impact counts the naturally high

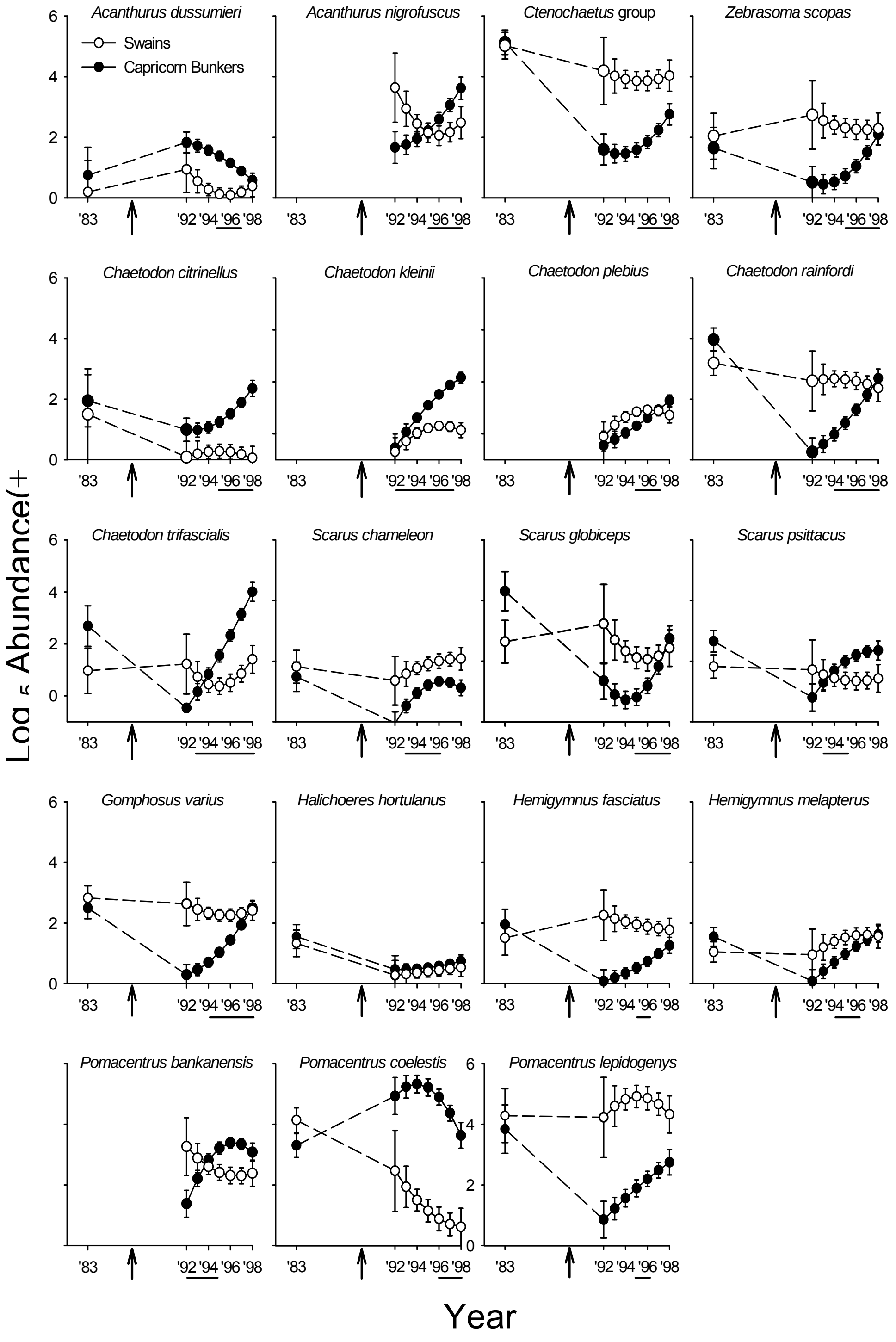


Fig. 2.5 Abundance of selected fish species from reefs in the Capricorn Bunker and Swains sectors between 1983 and 1998. No data were available during 1984-91. Values are estimated means and standard errors as calculated by the mixed linear models. Horizontal lines along the X-axis link years where the rate of change was significantly > 0 (at p< 0.05), in the Capricorn Bunker sector. Arrows indicate the timing of the disturbance.

abundance of this species implies that recovery would have been nearly complete by 1998, for the *Ctenochaetus* spp.

Rates of recovery

The first post-disturbance counts began 3-4 years after the loss of coral, when coral cover was still very low. The timing of increases in fish abundance post-disturbance varied among species, with little or no consistent patterns within families or genera (Fig. 2.5). A few species maintained significant increases in rates of change over an extended period of five or more years (*Chaetodon kleinii*, *C. trifascialis*, *C. rainfordi* and *Gomphosus varius*), while other species showed significant increases only over a relatively brief period (*Chaetodon plebius*, *Scarus psittacus*, *Hemigymnus melapterus*, *H. fasciatus* and *Pomacentrus lepidogenys*). By the end of the study in 1998, 50% of species were still increasing significantly. The one exception to the consistently positive rate of recovery was *P. coelestis*, which declined significantly in abundance from 1996-97.

Changes in community structure

The butterflyfishes (Chaetodontidae) and damselfishes (Pomacentridae) underwent changes in community structure as a result of the severe loss of coral cover. The pre-disturbance communities of butterflyfish on Lady Musgrave Is. and One Tree Is. reefs (the two most heavily impacted reefs) were dominated by *Chaetodon rainfordi* and *C. trifascialis* (Table 2.3). Both species were absent in the first surveys post-disturbance, but by 1998, *C. trifascialis* was again numerically dominant on both reefs while *C. rainfordi* had recovered its numerical dominance on One Tree Is., but not Lady Musgrave Is. In 1992, when coral cover was very low, *C. citrinellus* was the numerically dominant butterflyfish on both reefs while *C. auriga* and *C. kleinii* were also dominant at One Tree Is. This dominance of a different suite of butterflyfish species during the years immediately following the disturbance was due to the absence of previously dominant species rather than any positive numerical response by the remaining species. Nevertheless, both *C. citrinellus* and *C. kleinii* increased in abundance from 1992 to 1998 (Fig. 2.5) as live coral cover increased, but their relative dominance in the butterflyfish assemblage decreased (Table 2.3).

Table 2.3 Relative abundance of those species accounting for 90% of total abundance of chaetodontids and pomacentrids for 1984 (pre-impact), 1992 (immediate post-impact) and 1998 (9 years post-impact). Data is for Lady Musgrave (LM) and One Tree (OT) Island reefs. — : no individuals counted.

	Relative Abundance (%)					
	Pre-disturbance		Post-disturbance			
Family	’84		‘92		‘98	
Species	LM	OT	LM	OT	LM	OT
Chaetodontidae						
Chaetodon auriga	—	—	3.7	28.57	—	—
C. baronessa	—	1.87	—	—	—	—
C. citrinellus	4.95	1.87	29.63	28.57	8.76	—
C. flavirostris	3.2	4.1	7.41	14.29	—	8.26
C. kleinii	3.49	4.1	14.81	28.57	13.92	7.8
C. lineolatus	—	—	3.7	—	—	—
C. melannotus	—	11.94	—	—	—	6.42
C. ornatissimus	—	—	—	—	4.12	—
C. pelewensis	5.82	—	18.52	—	—	—
C. plebeius	4.08	6.34	—	—	—	5.96
C. rainfordi	27.66	35.45	—	—	6.19	27.52
C. trifascialis	27.66	18.66	—	—	46.91	37.16
C. trifasciatus	5.82	5.22	—	—	4.64	—
C. unimaculatus	2.33	—	—	—	—	—
C. vagabundus	—	—	7.41	—	—	—
Forcipiger spp.	4.95	—	14.81	—	4.64	—
Pomacentridae						
Chromis atripectoralis	46.85	19.18	—	—	—	—
Neopomacentrus azysron	25.55	17.97	3.18	—	3.47	—
Pomacentrus coelestis	14.85	25.52	77.57	98.77	75.07	80.92
P. moluccensis	4.92	—	—	—	—	—
P. lepidogenys	3.73	—	6.54	—	9.07	—
C. nitida	—	35.56	—	—	—	8.78
C. margaritifer	—	—	2.06	—	—	—
P. bankanensis	Not included in census		5.42	—	4.13	6.03

Prior to the disturbance, the most numerically abundant damselfishes on Lady Musgrave Is. and One Tree Is. reefs were *Chromis atripectoralis, Neopomacentrus azysron*, *Pomacentrus coelestis* and *Chromis nitida*, although the latter species was only present on One Tree Is. (Table 2.3). By 1992, these species had either disappeared completely or been reduced to a minor proportion of the surviving assemblage. At the end of this study in 1998, the situation remained mostly unchanged from 1992, with minor recovery of these species or none at all. The one exception to this pattern was *P. coelestis*, which actually increased in abundance after the disturbance and remained the overwhelmingly abundant damselfish for the remainder of this study.

Table 2.4 Percentage of variation in the abundances of dominant families and genera of reef fishes, accounted for by benthic cover and temporal trends in the multiple regression model. ns: not significant.

	Overall effects		Within benthic/temporal effects			
	Blocking	Benthic/Temporal	Hard coral	Soft coral	Turf algae	Temporal trend
Acanthuridae	94.7	2.9	ns	ns	ns	ns
Chaetodontidae	63.6	36.4	86.5	ns	ns	ns
Scaridae	75.6	24.4	84.2	1.7	10.7	4.1
Labridae	74	26	81	5	8	ns
Chromis	64	36	76	ns	10.6	ns
Pomacentrus (minus *P.coelestis*)	83.7	16.3	ns	45.9	25.2	ns

Fish – habitat correlations

For those families and genera investigated, the majority of variation in the data was due to sampling-design effects, although there were considerable family differences in the strength of this relationship (Table 2.4). Benthic variables and/or temporal trends explained very little of the variation in abundance of the Acanthuridae, with > 90% of the variation attributable to sampling-design effects. For the Chaetodontidae, Labridae and Scaridae, 36%, 26% and 24% of the variation in abundance respectively, could be explained by benthic/temporal trends, with most of the variation (> 80%) directly attributable to changes in hard coral cover alone. For the Chaetodontidae, changes in hard coral cover explained virtually all the variation

(86.5%), whereas for the Labridae and Scaridae, a small but significant correlation was also present with soft coral and turf algae. Furthermore, the temporal trends for the Scaridae were significant, suggesting a trend in abundance over time divorced from the effects of the benthic variables investigated. Of the two damselfish genera examined, benthic/temporal trends explained over twice as much of the variation in abundance of *Chromis* compared with *Pomacentrus*. For *Chromis*, 76% of this variation was explained by hard coral cover and 10% by turf algae. *Pomacentrus* showed no correlation with hard coral cover but rather an association with soft coral and turf algae.

Discussion

Benthic and fish assemblages in the southern GBR displayed a high degree of resilience to major storm activity. Despite catastrophic habitat losses, within 10 years hard coral cover and the species richness and abundance of most fish taxa had recovered to be virtually indistinguishable from pre-impact values. Given that these assemblages were situated on various reefs spread over 80 kilometres, the coherency in response to the disturbance event at this scale provides supporting evidence of stability at large scales of space and time and suggests substantial resilience of meta-reef systems to natural disturbance (see also Bythell et al (2000) and Ninio & Meekan (2002)). The decadal time frame of this response was similar to benthic and fish community recovery periods in other studies (Connell 1997; Ninio et al. 2000; Sano 2000).

Resiliency in coral assemblages

The loss of live coral cover on the northeast reef slopes of the Capricorn Bunker reefs in the late 1980’s was extreme; from more than 80% cover to less than 10%. Although damage was recorded to other reef zones, it was minimal in more protected areas (see Miller et al. 1991). This “patchiness” in storm damage is common and results in undamaged areas remaining as sources for future renewal of the damaged areas (Bythell et al. 2000; Ninio et al. 2000). The extent of the damage was most likely due to the vulnerable state of the reefs immediately prior to the disturbance: a combination of high percentage cover of coral and the dominance of relatively fragile tabulate acroporid corals. The proportion of cover lost during a severe storm is usually greater the higher the cover just before the storm (Connell et al. 1997), and the morphological form of tabulate corals makes them especially susceptible to the shearing forces generated by wave action from such storms (Massel & Done 1993).

Recovery of hard corals was negligible until 1995, when cover increased rapidly, reaching pre-impact levels by 1998. The recovery of the hard coral community was precipitated by two factors. First, large areas of undamaged reef (i.e., northern flanks and back reef zones) with high coral cover provided a substantial source of new recruits for recolonisation. Second, the regenerating assemblages were dominated by tabulate *Acropora* species. The characteristics of rapid growth and competitive dominance in these species ensured that, once started, coral recovery was relatively quick (Baird & Hughes 2000; Stimson 1985). However, despite overall hard coral cover recovering to pre-impact levels by the end of the study, branching corals were still under-represented compared to the late 1980's. Hence overall structural heterogeneity in 1998 remained below pre-impact levels.

In the absence of anthropogenic effects, coral assemblages subject to acute “natural” disturbances have been found to recover to previous levels of cover within a decade (Connell 1997). One of us (D. McB. Williams) monitored fish and coral assemblages on reef slopes dominated by tabulate *Acropora* species in the central section of the Great Barrier Reef, following a crown-of-thorns outbreak in 1982/83. Recovery of coral cover to pre-impact levels took 12 years and, similar to our observations, initial recovery was slow but accelerated greatly after seven years. Hard corals also recovered from an extensive COTS outbreak at Iriomote Island in Japan over a similar period of time (Sano 2000).

The rate and maximum extent of recovery from disturbance is usually a function of the history of previous damage and recovery (Connell et al. 1997; Hughes & Connell 1999). Large-scale disturbance may therefore be a regular feature on the northeast flanks of the Capricorn Bunker reefs. Drilling and monitoring studies have shown that there is little windward accretion on reefs within the Capricorn Bunkers, indicative of a high-energy environment (Davies & Marshall 1979; Davies & Marshall 1980). Moreover, recent examination of detrital ridges on a series of sites spanning the length of the Great Barrier Reef has also indicated that highly destructive storms are much more common than was previously thought (Nott & Hayne 2001).

Resiliency in fish assemblages

Given the removal of such a large amount of coral from the northeast reef flanks, it is not surprising there was such a significant impact on the fish assemblages. Recent studies have indicated that habitat structure exerts significant influence on reef fish assemblage composition, rather than coral cover *per se* (see Lewis 1997; Syms 1998; Syms & Jones 2000). However, these studies did not encounter a situation where live coral cover was providing most of the habitat. They found the underlying reef matrix was more influential in determining fish assemblage structure and as such moderated disturbance effects to live coral. However, as hard corals provided most of the structure on the northeast flanks of the Capricorn Bunker reefs (see Fig. 2.3), their removal should have had much greater effects on the fish assemblage than if underlying substrate was providing most of the complexity. Our results support this conclusion, but unfortunately, the lack of underlying structural heterogeneity also means that the role of habitat vs coral *per se* was confounded and the relative roles of these two factors could not be separated.

Although our results clearly showed the extent of the response by the fish community to the disturbance, observational studies cannot easily separate the relative influences of processes such as recruitment, competition, predation and migration, in the recovery process. Nevertheless, inferences can still be made. A separate study of the same disturbance and its effects on fish recruitment, to the same reef areas as in our study, found that by 1995-96 recruitment of most fish was neither lower, nor less diverse, than during the pre-impact period (Doherty et al. 1997). However our results indicated that a large part of the changes we observed occurred after 1996, hence recruitment alone would not have been sufficient to generate a full recovery of the fish assemblages.

Post–recruitment processes also have great potential to significantly influence patterns established at settlement (see Jones (1991) and Hixon (1991) for a review). From 1996 onwards, the recovering benthic assemblages (principally hard coral cover) were increasing biogenic habitat at an exponential rate. This growth in turn provided an increasingly greater diversity and abundance of refuges for fish. As the strength of ecological interactions can be mediated by habitat (Caley & St John 1996; Friedlander & Parrish 1998; Hixon & Beets 1993), reduced post-recruitment mortality rates via competition and predation may have allowed for the co-existence of more individuals and species, subsequently enhancing the recovery process. This situation would also encourage immigration by juveniles and adults of those species that were able to do so (Ault & Johnson 1998; Walsh 1983).

Regardless of the relative roles of settlement and immigration post-settlement, our data suggest a strong role of habitat in the recolonisation process. Although the majority of variation in fish abundances was due to sampling design effects, between 20 and 40% of the variance was explainable by changes in the benthos. This is comparable to the amount of variation explained by experimental factors in similar studies conducted at much smaller scales (e.g., Lewis 1997; Syms & Jones 2000). Live coral acts as shelter and/or provides a food source, either directly, or indirectly by creating favorable conditions for other prey items to flourish. Scarids (parrotfishes), for example, use live coral principally as shelter (Randall et al. 1990). The increased coral cover after 1996 would have allowed species within this family to take advantage of the substantial feeding grounds still remaining by providing them with the necessary shelter from predation (Hart & Klumpp 1996). Chaetodontids (butterflyfishes) are foremost among those species with strong affinities to coral, with some species recruiting, feeding and sheltering in live coral (Allen et al., 1998). Because of their affiliations these taxa could also be expected to be very sensitive to gross changes in coral cover, as was the case in this study.

Of the families investigated, the Pomacentridae (damselfishes) demonstrated the most varied responses. They were also the only family that had not recovered to pre-impact levels by the end of this study. This lagged recovery may be due, in part, to the small-scale site attachment typical of most of the family (Randall et al. 1990). Between 1995 and 2000 overall species richness of fish assemblages on the disturbed areas in the Capricorn Bunkers increased from 76 to 92 (Sweatman et al. 2001) with approximately 40% of this increase within the Pomacentridae alone. Some species, such as *Chromis atripectoralis*, which were abundant prior to the disturbance, require branching corals for shelter as adults (Randall et al. 1990). Although total hard coral cover had recovered by 1998, branching corals were still only present in small amounts. These results are consistent with the idea of finer-scale habitat changes happening more slowly through time, to provide the diversity of microhabitats necessary for the reestablishment and survival of a highly diverse family.

Conclusions

Although the evolving view of coral reefs is about large-scale patterns and processes, these concepts are still mostly derived from the assembly and integration of smaller-scale observations (Buddemeier & Fautin 2002). This study is one of the first to provide evidence, on a relatively large scale (14 years and 10's of kilometres), of parity with much of the current theory on how marine communities are structured. The essentially stochastic nature of the disturbance, its variable effects in space and time and the ultimate recovery of the benthic and fish assemblages to a documented, relatively stable state could all be accommodated under the theories of hierarchical patch dynamics (Wu & Loucks 1995), landscape ecology (Hobbs 1994) or metapopulation dynamics (Hanski 1998). Local devastation of parts of reefs is buffered at a metapopulation level by the connectivity within and between individual reefs (Doherty 1991; Fowler et al. 1992). These local populations and assemblages are at differing stages in a temporal continuum, the sum of which confers stability at larger scales. The asymptotic recovery trajectories of the coral and fish assemblages imply a ceiling beyond which increases will not continue. While this asymptote will vary within stochastically defined bounds (Connell & Sousa 1983), it is most likely set by processes operating at regional spatial scales and evolutionary temporal scales (Caley & Schluter 1997; Cornell & Karlson 1996). While caution must be applied to extrapolating the results of this study beyond the system studied, we believe that similar results to studies from other systems and studies conducted at smaller scales, offers evidence for generality of these results.

On a precautionary note, while similar resilience to large natural disturbances might be expected in other relatively healthy archipelagic reef systems, this outcome may not necessarily be the case in more isolated systems or those impacted by anthropogenic disturbances. The poor health of many of the world's coral reefs, due to a combination of overfishing, destructive fishing practices, and large-scale natural disturbance events like bleaching, storms and disease (Wilkinson 1999), raises questions about the long-term resilience of coral reefs. Studies investigating the interplay of natural and anthropogenic factors over appropriately large scales of space and time (e.g., Hughes 1994) are necessary to understand and prevent future degradation of reefs.

Chapter 3: Towards an understanding of resilience in isolated coral reefs

Halford, Andrew R. & Caley, M. Julian (2009) Towards an understanding of resilience in isolated coral reefs. *Global Change Biology* 15 (12): 3031-3045

Abstract

In 1998, seawater temperature anomalies led to unprecedented levels of coral bleaching on reefs worldwide. We studied the direct effects of this thermal event on benthic communities and its indirect effects on their associated coral reef fish communities at a group of remote reefs off NW Australia. Long-term monitoring of benthic and fish assemblages on these reefs allowed us to compare the responses of these communities to coral bleaching using a data series that included 4 years prior to, and 6 years following, this bleaching event. While bleaching mortality was evident to >30 m depth, it was patchy among the shallower survey sites with decreases in live coral cover ranging from 30 - 90% across seven surveyed locations Within two years of the bleaching, hard coral recovery had begun at all sites and by 2003 reef-wide coral cover had increased to ~ 39 % of its pre-impact levels. We exploited this pattern of differential survival of corals among sites, the associated changes in these benthic communities, and their patterns of recovery, to better understand links between benthic community dynamics and their associated fish communities. Temporal changes in the resident fish communities strongly reflected the differential shifts in the benthic communities, but were lagged by 12 - 18 months. Five years after the bleaching event, the fish communities on five of the seven surveyed locations showed evidence of recovery, however, none had regained their pre-impact structures. Analyses of these communities by taxonomic family revealed a range of responses to the disturbance reflective of their life-histories and trophic and habitat affiliations. The slow but recognizable recovery of this isolated reef system has parallels with other relatively

isolated systems that displayed resilience to the 1998 bleaching event, e.g. the Chagos archipelago, but it also contrasts sharply with low levels of resilience documented in other isolated reef systems subject to the same disturbance, e.g. the Seychelles. In this context, our results highlight the significant knowledge gaps remaining in understanding the resilience of these ecosystems to disturbance.

Introduction

Ecosystems worldwide are under threat from anthropogenic disturbances and coral reef ecosystems have suffered particularly badly (Wilkinson 2004). While natural disturbances like storms (Harmelin-Vivien, 1994) and Crown-of-Thorns starfish (COTS) outbreaks (Chesser 1969; Lourey et al. 2000; Sano et al. 1984) have caused considerable damage to coral reefs, anthropogenic effects such as increased sedimentation, pollution and the unsustainable exploitation of reef resources pose the greatest threats (Wilkinson, 2004). Such disturbances, while global phenomena, have largely been local in their effects (Wilkinson, 1999). In 1998, however, unprecedented levels of coral bleaching indicated that global warming was likely to impact coral reefs at global scales, with the potential for nearly simultaneous, truly large-scale impacts on coral reefs (Hoegh-Guldberg, 1999). With the latest global climate change models predicting continued warming (IPCC, 2007), it is becoming increasingly important to understand the resilience of coral reef ecosystems, and the extent to which such resilience depends on connectivity among reefs (Bellwood et al. 2006; Halford et al. 2004; Hughes et al. 2003; West & Salm 2003; Wilson et al. 2006).

Many coral reefs, such as Australia’s Great Barrier Reef, or the archipelagos of the Maldives and Indonesia, exist as parts of highly interconnected systems (Spalding et al. 2001). Hence, much of what we understand about the dynamics of coral reefs and their potential for recovery from disturbance has come from these types of systems. In such systems, evidence suggests that demographic connectivity among individual reefs confers a level of persistence at large spatial and temporal scales (Halford et al. 2004, Ninio and Meekan 2002). Under such conditions, reef communities can be quite resilient, with recovery from disturbance possible within 1-2 decades (Bohnsack, 1983; Connell, 1997; Halford et al. 2004; Sano, 2000). At the other end of the spectrum though, are reefs that are spatially very isolated. Because of their isolation, these reefs must persist with less external input of propagules. Such reefs, their ecological dynamics, and their abilities to recover are much more poorly understood, particularly in the face of increasing disturbance. What is clear though, is that under some sets of circumstances, spatially isolated reefs can show low resilience to catastrophic bleaching (Graham et al. 2006). What is also clear is that as reefs are degraded there is the potential for connectivity to decrease e.g. because of damage to source reefs (Jones et al. 2007; Pineda et al. 2007), and under predicted climate change regimes, ocean circulation patterns may change (Vecchi & Soden 2007) thereby affecting connectivity. Under such scenarios, it will become increasingly important to understand the relationship between connectivity and resilience for the management and conservation of these systems. One way to begin to understand how reefs might function under conditions of reduced connectivity is to focus on reefs currently functioning under different levels of spatial isolation, particularly those that are more isolated.

While the supply of new recruits, whether locally produced or arriving from elsewhere, will ultimately drive the recovery of fish communities that have been degraded as a direct or indirect effect of some disturbance (Caley et al. 1996), the rate and extent of recovery is likely to be mediated by habitat (Caley & St John 1996). In general, complex habitats provide more refuges than simple ones and moderate post-settlement mortality from predation and competition, which ultimately supports more diverse reef fish communities (Carr and Hixon, 1995, Hixon and Beets, 1993, Syms and Jones, 2000). Coral reefs are subject to a range of disturbances all of which can affect habitat differently. Physical disturbances like cyclones damage hard corals and the underlying reef structure (Van Woesik et al. 1991) causing rapid loss of habitat complexity. In contrast, bleaching events and COTS infestations affect only the living coral veneer, leaving the habitat structure initially intact, but which then erodes through time (Aronson et al. 2000a; Colgan 1987). These different disturbances create differing habitat mosaics which may elicit different responses from the associated fish communities. In more isolated reef systems, the recovery of fish communities may be further impeded if the rate at which the habitat recovers is decreased by a reduction of the input of propagules of habitat forming species such as corals. Loss of coral cover in response to disturbance is also typically associated with changes in other habitat characteristics, such as the proportion of algae in the benthic community (Halford et al. 2004). Such changes are likely to favor some fish species over others (Wilson et al. 2006).

In 1998, the persistence of anomalously high sea surface temperatures caused a circum-tropical bleaching event of unprecedented magnitude and severity (Hoegh-Guldberg, 1999; Wilkinson et al. 1999). Reefs in the Indian Ocean were particularly badly affected with coral mortality of 90% common in depths less than 20m (Wilkinson et al. 1999). While devastating to many reefs, this bleaching event has nevertheless provided a number of valuable opportunities to study the resilience of tropical reefs. One of the coral reef areas badly affected was Scott Reef, a remote reef complex off the NW coast of Australia. At these reefs, a long-term monitoring program of fish and benthic communities had been in place for 4 years prior to bleaching. The continuation of this monitoring program for 6 years following the 1998 bleaching event, coupled with the comparative isolation of these reefs, provided one of the first opportunities to track changes in the benthic communities of an isolated reef system and any associated indirect effects of the bleaching on the fish communities for an extended period of time, from before bleaching through to the initial stages of their recovery.

Here we report on relationships between the benthic communities at Scott Reef and their associated fish communities, and how these relationships changed in response to coral bleaching. We focus on three major aspects of these relationships. Because of the nature of the disturbance to these communities, whereby corals died followed by the collapse of the habitat structure they provided, we tested for lag effects of bleaching on fish community structure by examining changes in the correlation between fish and benthic community structure with the expectation that any pre-existing correlation between the two would diminish through time as the indirect effects of habitat loss became manifest. Exploiting spatial variation in the impact of the bleaching event on the benthic communities of these reefs, we also tested for changes in the dispersion of reef fish community structure that would be expected if benthic community structure influences the structure of these fish communities and the benthic communities were differentially impacted. Finally, because of the relative conservatism of how families of reef fish species use reef resources, and the expectation that these resources would be affected differently at different times following coral bleaching, we also compared the dynamics of the numerically dominant reef fish families monitored at Scott Reef.

Methods

Study Area

The Scott and Seringapatam reefs complex, referred to hereafter as Scott Reef, is an isolated group of coral reefs surrounded by 400-700 m deep water, and is situated on the edge of Australia’s North West Shelf (Lat. 14.050^0S, Long. 121.800^0E), approximately 260 km from the mainland (Fig. 3.1). Scott Reef is a complex of two very large reefs - North Scott (16.3 x 14.4 km) and South Scott (27.4 x 17 km), while

Seringapatam is slightly smaller (8 x 10 km) and situated 25 km to the north east of North Scott Reef (Berry, 1986). These three reefs form part of a widely dispersed chain with the nearest reefs lying hundreds of kilometres to the northeast and southwest (Fig. 3.1).

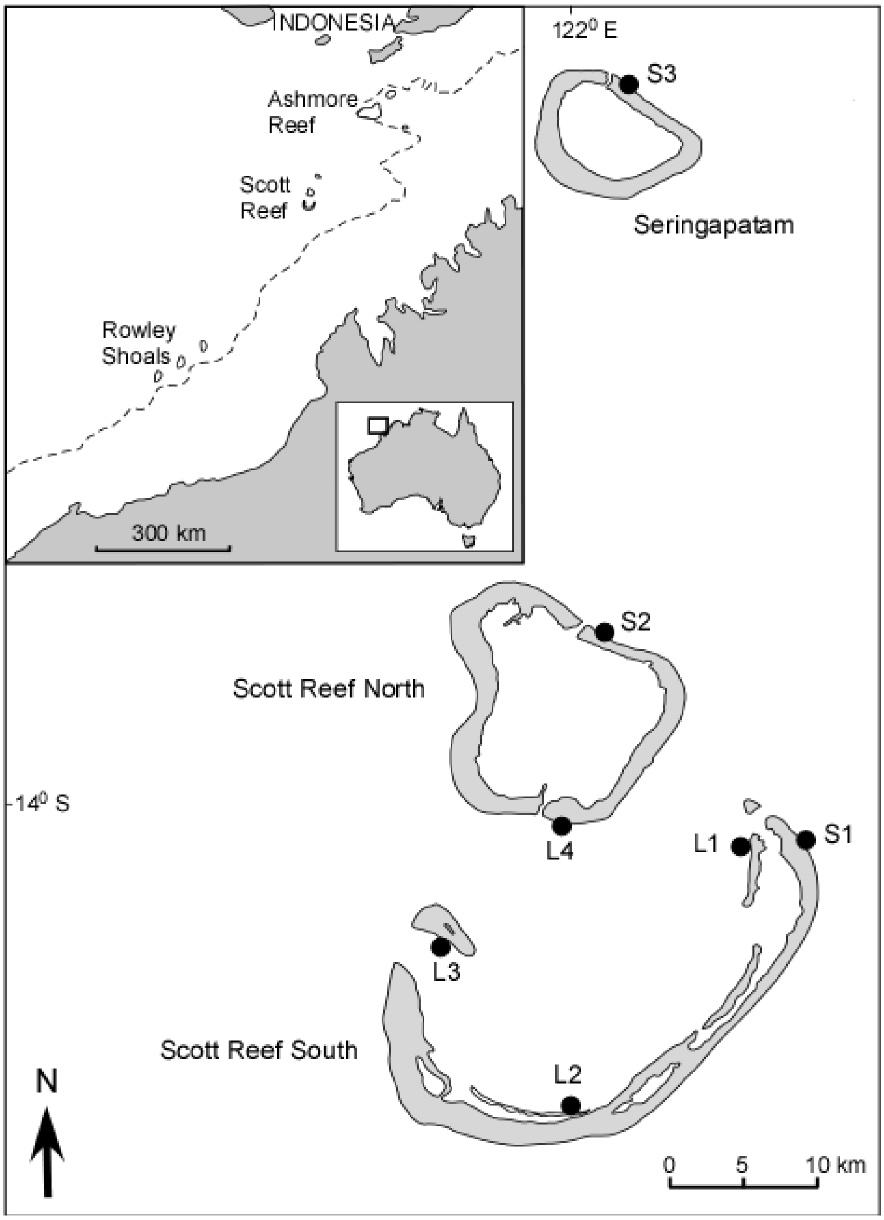


Fig. 3.1 Location of Scott and Seringapatam Reefs off the NW coast of Australia and the position of the fixed monitoring sites at those reefs. The dashed line represents the edge of the continental shelf.

Survey Methods

Seven permanent study locations, dispersed among the three reefs, were established in October 1994 (Heyward et al. 1998). These locations include the major habitat types found within the 3 - 20 m depth contours of these reefs and are broadly categorised here as either lagoonal (L) or slope (S) (Fig. 3.1). Three sites, approximately 250 m apart, were established within each location. Within each site, five, 50 m permanent transects were situated between the 6-10 m depth contour. These transects were arrayed consecutively with approximately a 10 m gap between each. Each transect was marked with a steel picket at each end and sections of steel rod every 10 m. This arrangement facilitated the laying of fibreglass measuring tapes along the transects during each survey to act as a reference line. These transects were sampled for benthos and fish annually from 1994-1999, inclusively, and again in 2001 and 2003. Each survey was done between October and December. Some surveys were missed because of bad weather, but these represent less than six percent of the total possible combinations of year by location.

Benthic cover on transects was recorded using a diver-held video camera. The footage generated was converted to percentage cover estimates using a point sampling technique after Page et al. (2001). Cover was estimated for five broad categories; hard coral, soft coral, turf algae, sponges and sand. The category, hard coral, was further separated into the following morphological categories: Acropora branching, caespitose and corymbose combined; Acropora digitate; Acropora encrusting and sub-massive combined; Acropora tabulate, Acropora bottlebrush, non-Acropora branching; non-Acropora encrusting; non-Acropora foliose, non-Acropora massive; Fungiids; non-Acropora sub-massive and Millepora. Benthic rugosity along these transects was also estimated in 1997 and 2003, using the chain and tape method as outlined by (McCormick 1994). Different chain link sizes were used in different years, hence rugosity estimates could only be compared within years.

Abundances of 121 species of fish were estimated along transects of fixed width following the protocols of Halford and Thompson (1994) and Cheal and Thompson (1997). Two transect widths were used, with relatively large and mobile fish species from the Acanthuridae (Surgeonfishes), Chaetodontidae (Butterflyfishes), Labridae (Wrasses), Lethrinidae (Emperors), Lutjanidae (Snappers), Serranidae (Groupers), Scaridae (Parrotfishes), Siganidae (Rabbitfishes), and Zanclidae (the Moorish Idol), surveyed along a 50 m x 5 m corridor. Smaller and more site-attached species from the family Pomacentridae (Damselfishes), were sampled on a return pass along the same transects but using a 50 m x 1 m corridor. Only fish considered to be > 1 yr old were counted.

Data Analysis

Prior to any analyses, the benthic data were square root transformed to accommodate proportional data, and the fish data ln (x+1) transformed to weight less abundant species more heavily, thereby emphasising community dynamics over the dynamics of the one or two most abundant species. For the fish data, counts on transects were summed within sites to reduce the number of zero counts for individual species. To standardize for the different areas surveyed for large mobile versus small sedentary fish species, counts were converted to densities (i.e. # per 250m^2).

Clustering and non-metric multidimensional scaling (NMDS) were used to describe the spatial and temporal dynamics of the benthic and fish communities. These methods make few assumptions about the form of the data and hence alleviate many of the problems associated with analyses of data matrices containing many zeroes (i.e. highly multivariate non-normal) (Clarke & Warwick 2005). The similarity matrices underlying these analyses were calculated using the Bray-Curtis measure of association between samples (Bray & Curtis 1957). This measure performs consistently well in analyses of ecological data sets (Faith et al. 1987; Minchin 1987). Hierarchical clustering was performed on the similarity matrices using group-average linking.

Correlations between the benthic and fish communities were estimated using comparative (Mantel-type) tests between the benthic and fish similarity matrices used in the clustering and ordination procedures described above. These matrices were converted into ranks before calculation of Spearman's coefficient of correlation (ρ) for which $\rho = 1$ denotes a perfect match. The statistical significance of the correlation between the fish and benthic matrices was estimated by re-randomising one of the matrices 999 times and recalculating ρ each time to estimate the distribution of ρ to which the observed value of ρ was compared (see Clarke and Warwick (2005) for more detail). Correlations between the benthic and fish communities were estimated separately for the lagoon and slope habitats. Correlations between the benthic assemblage and the whole fish community and between the benthic community and the Acanthuridae, Chaetodontidae, Scaridae and Pomacentridae were estimated separately. This set of correlations was calculated for the censuses conducted five months prior to, and seven months after, bleaching in order to examine change in the associations between the benthic and fish communities.

Biological communities that are perturbed tend to exhibit greater variability in structure among replicate sites than equivalent sites that are not perturbed (Warwick & Clarke 1993). Therefore, the benthic communities studied here should have exhibited greater variability following bleaching than before. If the fish communities associated with these benthic sites were affected indirectly by changes in their habitat in response to bleaching, such indirect effects should have also been reflected in greater variability of the fish communities following bleaching. Similarly, any differences in the average responses of the benthic communities between habitats (i.e. lagoons vs. slopes) should also have been manifest in different community responses of the associated fish communities. We tested these predictions using an Index of Multivariate Dispersion (IMD) (Warwick & Clarke, 1993) for the benthic and fish communities within the lagoon and slope habitats. This index contrasts the average rank of the Bray-Curtis dissimilarities among pre-bleaching samples with the average rank among the post-bleaching samples. The IMD will have a maximum value of + 1 if all dissimilarities among the post–bleaching samples are greater than any dissimilarities among the pre-bleaching samples. In contrast, IMD will assume a value of -1 if all dissimilarities among the pre-bleaching samples are greater than any dissimilarities among the post-bleaching samples. Values of IMD near zero indicate no difference between treatment groups.

To test for differential responses among taxonomic families of reef fishes, we explored the dynamics of the Acanthuridae, Chaetodontidae, Scaridae and Pomacentridae in more detail. For each family, changes in species relative abundance, species richness, and total family abundance were evaluated. Pre-bleaching rank abundance curves were generated based on the mean abundances of each species at each site over the 4 year pre-bleaching period. The 95% Confidence Limits of the relative abundances of these species were also calculated as a measure of pre-disturbance temporal variability. To examine how these species' relative abundance relationships were affected by bleaching, we compared these pre-bleaching rank-abundance curves to the curves generated from the survey immediately following bleaching in 1998 and the curves from the final census in 2003. In order to compare the post-bleaching curves with the pre-bleaching ones, we used the pre-bleaching species abundance rank orders throughout. Expected species richness for each of the families was calculated for 1998 and 2003 using rarefaction based on pre-bleaching species abundances relationships. Changes in total family abundance in 1998 and 2003 were measured against the mean pre-impact abundance and 95% confidence limits.

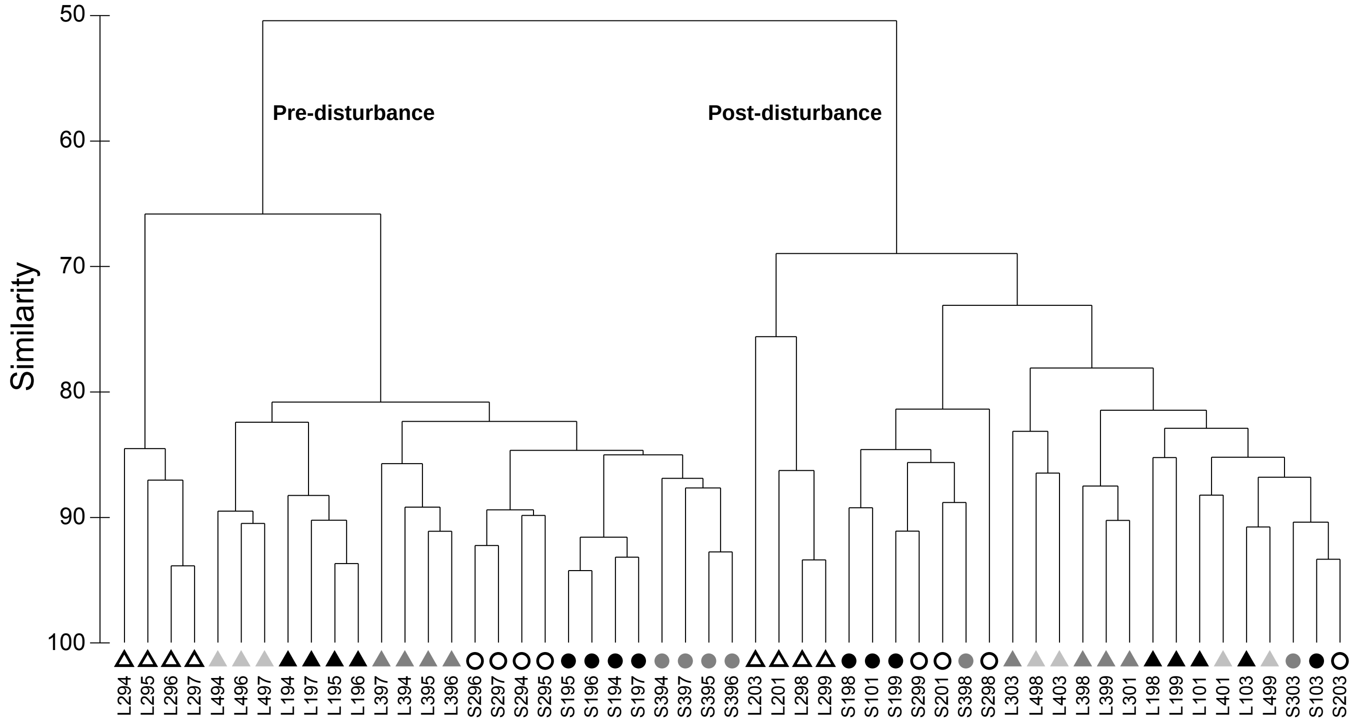


Fig. 3.2 Dendrogram of the benthic assemblages for all location x year combinations sampled at Scott Reef. Clustering was hierarchical using group-average linking and based on Bray-Curtis derived similarity matrices. Sites are coded in the cluster analysis according to their habitat (L = lagoon, S = slope), followed by the location number nested within habitat (first digit), and sampling year (last two digits). The symbols represent the two habitat types and are individually shaded for each location within habitats (△ - Lagoon locations, ○ - Slope Locations).

Results

Benthic Communities

Spatio-Temporal Patterns

Prior to bleaching, benthic communities at lagoon locations clustered separately from slope locations, and all years for a particular site clustered together (Fig. 3.2). Following bleaching, this consistent spatial structure broke down, with the benthic communities no longer clustering consistently according to habitat (Fig. 3.2). Just prior to bleaching in Oct/Nov 1997, percentage live coral cover ranged between 35 - 66 %

for lagoon locations ($\overline{X}$ = 45.1 %) and 49 – 60 % for outer slope locations ($\overline{X}$ = 53.5 %) (Fig. 3.3a). However, by November 1998, eight months after bleaching, hard coral cover had decreased precipitously in both lagoon and slope locations (Fig. 3.3a), with a 90 % reduction at location L2. Where pre-bleaching coral cover was greatest, bleaching resulted in greater mortality both in absolute and relative terms and irrespective of the spatial scale examined. Prior to bleaching, turfing algae comprised < 7 % of total benthic cover, increasing to >75 % within two years following the bleaching. By 2003, the cover of turfing algae had decreased to ~ 45 % within the lagoon locations, but remained above 60 % on the slopes (Fig. 3.3b).

Hard coral abundance was beginning to recover at all locations by 2003 although it was more pronounced within the lagoon (n = 4 locations; $\overline{X}$ = 23.4 %) than on the slopes (n = 3 locations; $\overline{X}$ = 12.7 %; Fig.3). Ordinations also indicated that benthic community structure was beginning to move in the direction of its pre-impact structure with the 2003 communities of L3 and L4 showing the greatest movement (Fig. 3.4). Despite these indications of recovery, the benthic communities nevertheless remained considerably changed from their pre-bleaching structure six years after bleaching.

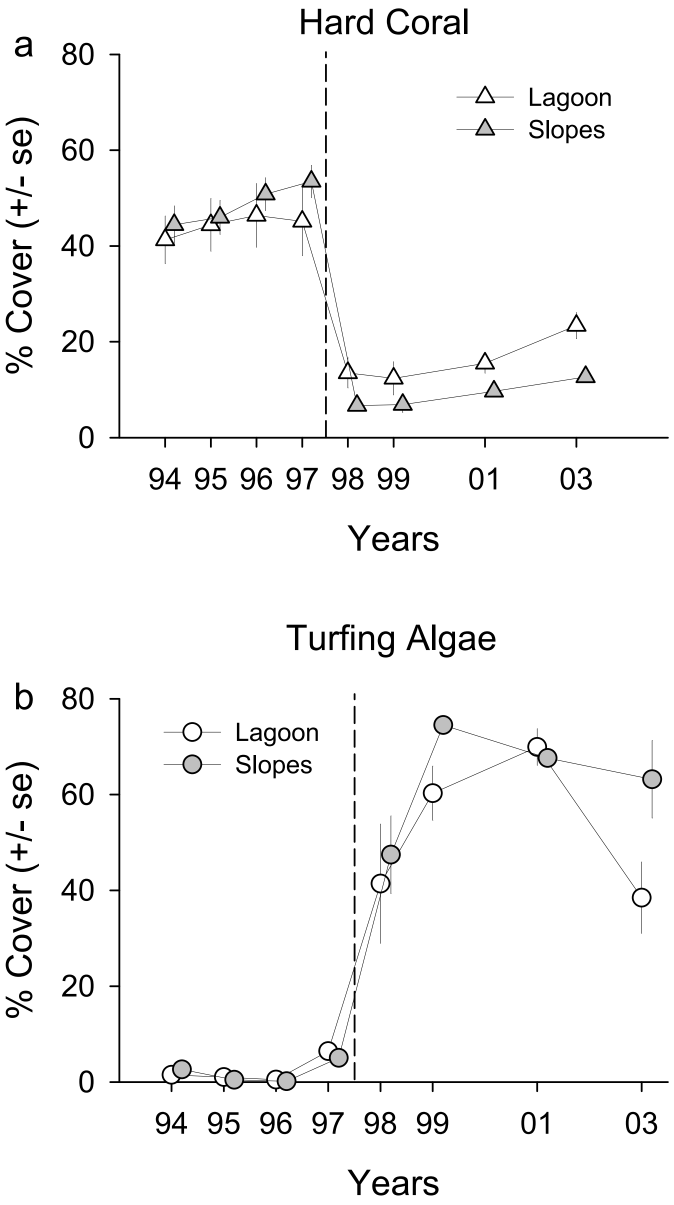


Fig. 3.3 Percentage cover of a) Hard Corals and b) Turfing Algae between 1994 and 2003, within the lagoon and slope habitats. Vertical dashed line indicates time of bleaching. Error bars are one standard error of the mean

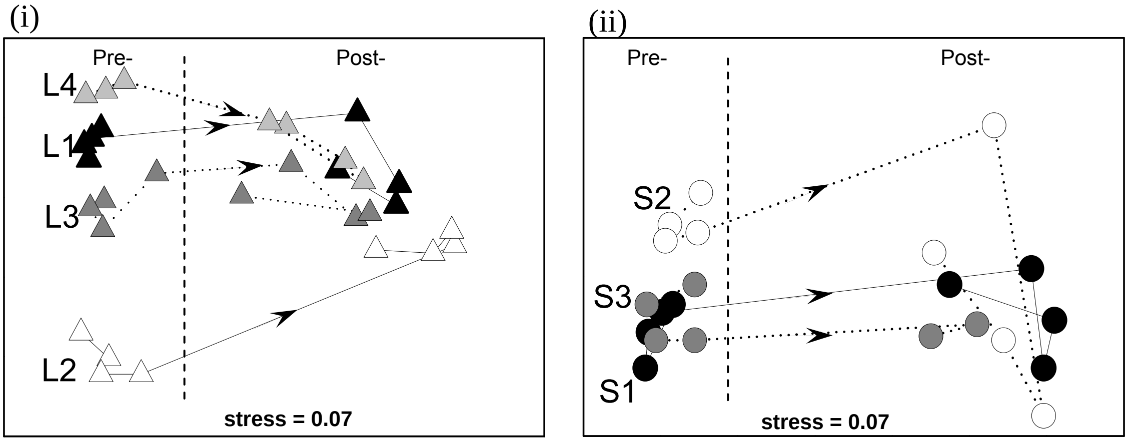


Fig. 3.4 Non-metric MDS ordinations of the benthic assemblages at Scott Reef, from all location x year combinations. The ordinations used the same similarity matrices used for the clustering. The ordinations are plotted separately for lagoon (i) and slope (ii) habitats for easier interpretation. Symbols and color coding pattern are as outlined in the dendrogram of Fig. 2. Arrows indicate the direction of change of these communities in multi-dimensional space.

Rugosity

Although hard coral cover was greater on the slope sites immediately prior to bleaching (Fig 3.3a), the rugosity of the slope communities was significantly less than those at the lagoon sites (Fig. 3.5). This difference resulted from the dominance of the outer slope coral communities by *Acropora bruegmanni*, which forms densely branching, but relatively homogenous ‘meadows’. Rugosity of this habitat is low even when live coral cover is high, hence high mortality of the monospecific coral community had little effect on rugosity. In 2003, five years after the bleaching event, the relative differences in rugosity between the lagoon and slope areas remained, with the exception of the lagoon location L2, which suffered a disproportionately greater fall in rugosity than any of the other sites (Fig. 3.5).

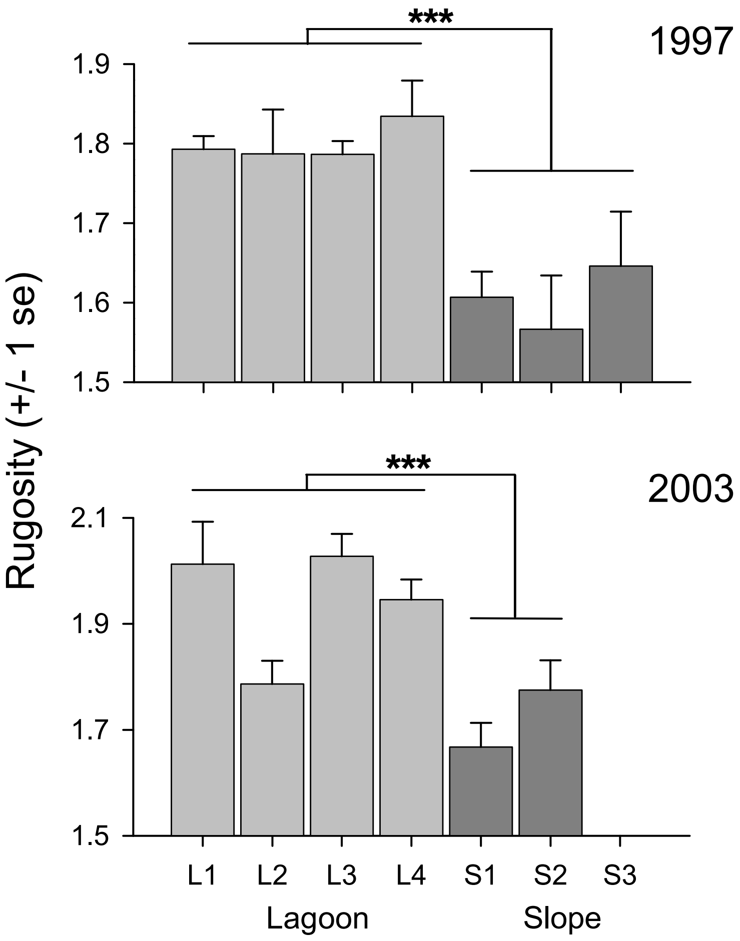


Fig. 3.5 Rugosity of the benthic communities at Scott Reef. Data presented are from (a) 1997, immediately before the bleaching event, and (b) 2003, five years after the bleaching event (∗∗∗; p<0.0001). Groups of locations not sharing an overscore differed with the indicated probability. Location S3 was not surveyed in 2003 due to bad weather. See text for further details of methods used.

Fish Communities

Spatio-Temporal Patterns

The fish communities clustered consistently with respect to location, and habitat, with the exception of L2 which showed no clear affinity for either Lagoon or Slope locations (Fig. 3.6). In contrast to the benthic communities, however, these spatial differences persisted following bleaching. Within all sampling locations, 1998 fish communities clustered with the pre-impact communities, while the 2001 and 2003 communities clustered together, indicating that immediately following bleaching the reef fish communities at Scott Reef were more similar to the pre-impact communities than they were to subsequent post-impact ones.

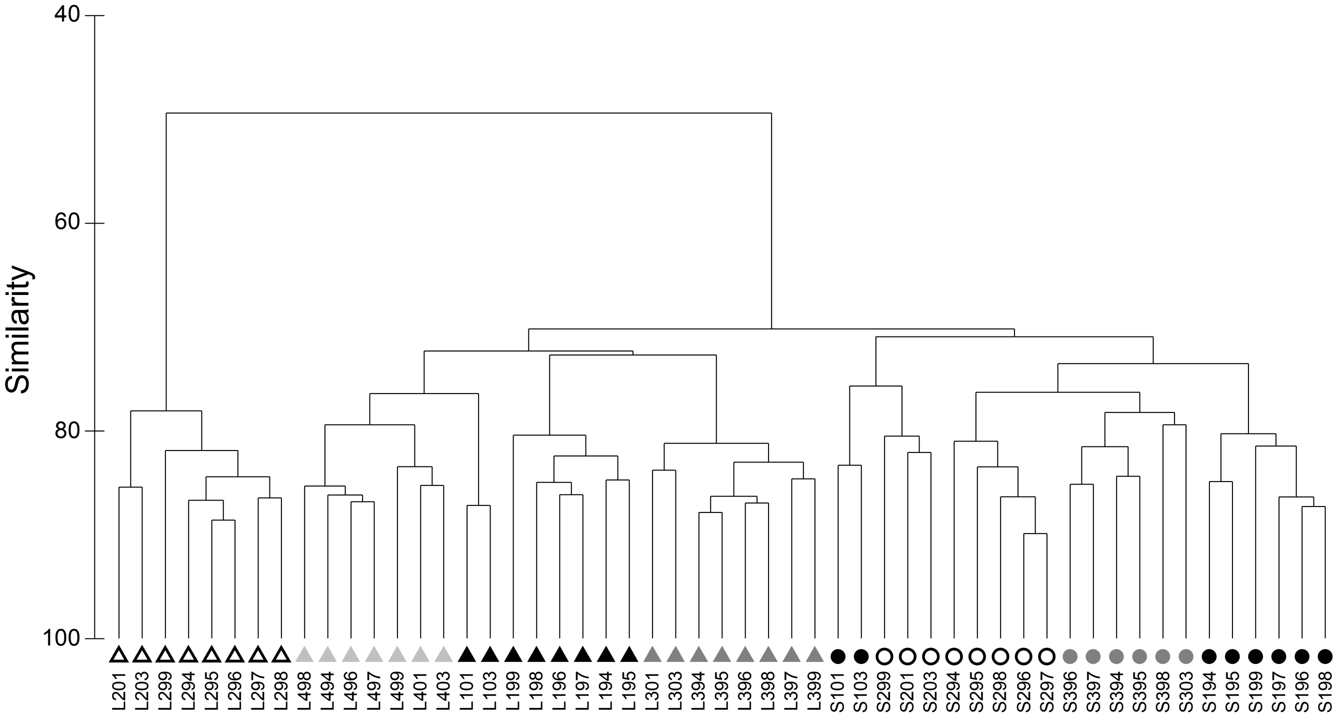


Fig. 3.6 Cluster analysis of the fish assemblages from all location by year combinations sampled at Scott Reef. Clustering was hierarchical using group-average linking and based on Bray-Curtis derived similarity matrices. Sites are coded in the cluster analysis according to their habitat (L = lagoon, S = slope), followed by the location number nested within habitat (first digit), and sampling year (last two digits). The symbols are the same as for Fig, 3.2.

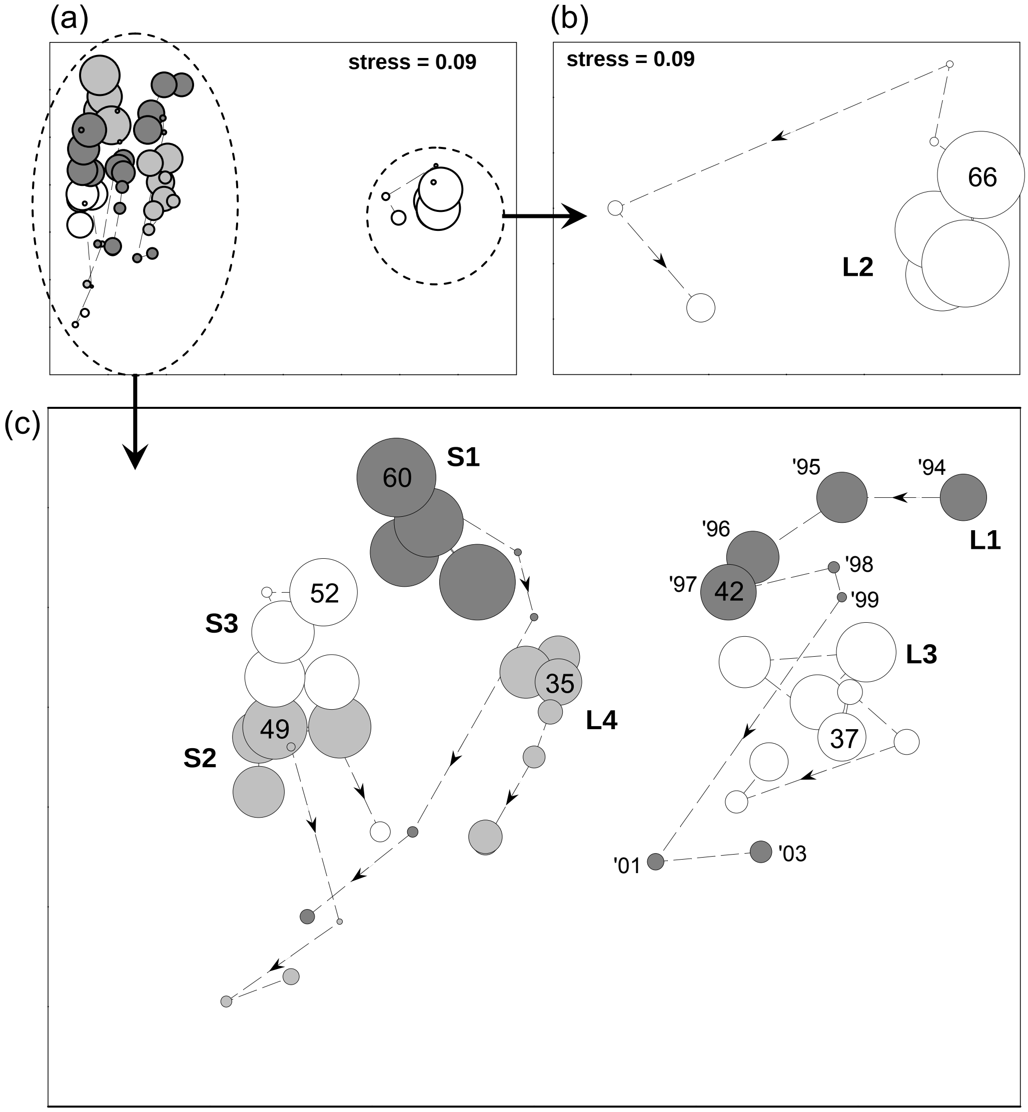


Fig. 3.7 Non-metric MDS ordinations of the fish assemblages at Scott Reef from (a) all location by year combinations, (b) the inner lagoon location L2 only, and (c) all location by year combinations except L2. Sizes of bubbles are proportional to the amount of hard coral cover in each location by year combination. The percentage coral cover present at each location in 1997, just prior to bleaching, is noted in the bubble for that year. L2 is presented separately to aid interpretation of relationships of the fish communities at the other locations. Arrows indicate the temporal progression of sampling, with the full sequence of sampling years depicted for L1.

Following bleaching, the structure of the fish communities at Scott Reef changed to a degree not seen during the four years of pre- bleaching surveys. These changes were slow to manifest, however, with no significant changes in fish community structure seen until the 1999 survey, 18 months after bleaching had occurred (Fig. 3.7). The first post-bleaching survey (i.e. Nov. 1998) was conducted before the main recruitment period for reef fish at Scott Reef, hence the lack of change immediately following bleaching reflects the short-term responses of the established adult communities only. In 2003, the fish communities remained considerably changed from their pre-bleaching structure (Fig. 3.7), although there was evidence of recovery with the multivariate trajectories of 5 of the 7 locations all moving back towards their pre-impact structure.

Table 3.1 Correlations (Spearmans Rho) between fish and benthic assemblages at various taxonomic, temporal, and spatial scales of resolution. Benthic matrices were sqrt transformed and fish matrices were ln (x+1) transformed prior to any calculations. NB. 97-97 denotes the 1997 fish assemblage matrix correlated with the 1997 benthic matrix, 98-97 denotes the 1998 fish assemblage matrix correlated with the 1997 benthic matrix, etc. ns – non-significant Acan – Acanthuridae, Chaet – Chaetodontidae, Scar – Scaridae, Poma - Pomacentridae

Fish-Benthos	Whole Assemblage	Acan	Chaet	Scar	Poma
Lagoon					
97-97	0.890	0.354	0.700	0.148^{ns}	0.896
98-98	0.762	0.112^{ns}	0.687	0.443	0.760
98-97	0.892	0.250	0.674	0.511	0.891
Slopes					
97-97	0.711	0.337	0.490	-0.144^{ns}	0.695
98-98	0.489	0.430	0.329	0.386	0.269^{ns}
98-97	0.662	0.388	0.368	0.239^{ns}	0.543

Correlations between Fish and Benthic Communities

Lags between the timing of the bleaching event and the responses of the fish communities at Scott Reef were evident from the strength of correlations between the matrices representing the benthic and fish assemblage structure. Between 1997 and 1998 (i.e. 97-97 vs 98-98) there was a decline in the correlation coefficient between the fish and benthic communities for seven of ten correlations examined (i.e. 5 fish groupings x 2 locations; Table 3.1). Moreover, in seven cases the correlation coefficient between the fish communities in 1998 and benthic communities in 1997 were greater than between fish communities in 1998 and benthic communities in the same year. Correlations were also consistently greater at the lagoon sites than on the slopes, both before and after the bleaching. At lagoon sites, the pomacentrids and chaetodontids had consistently higher correlations with the benthos than either the acanthurids or scarids. However, this was not the case on the slopes where the Acanthuridae and Scaridae both had higher correlations with the benthos in 1998.

Multivarate Dispersion in Benthic and Fish Communities

The fish and benthic communities within the lagoon exhibited little or no differences in dispersion between the pre- and post-bleaching periods. This was in direct contrast to the slope communities where post-bleaching assemblages exhibited much greater dispersion through time than the pre-bleaching assemblages (Table 3.2). At the taxonomic level of families within the fish communities, the Acanthurids in the lagoon and the Chaetodontids and Pomacentrids on the slopes all displayed greater dispersion through time post-bleaching (Table 3.2).

Table 3.2. Index of Multivariate Dispersion (IMD)* between pre-and post-bleaching surveys, for benthic, and fish assemblages at various taxonomic and spatial scales

Habitat	Benthic Assemblage	Whole Assemblage	Acan	Chaet	Scar	Poma
Lagoon	0.025	-0.025	0.164	-0.036	-0.155	0.023
Slopes	0.389	0.317	-0.048	0.315	-0.055	0.380

*IMD values range between +1, where all dissimilarities among the post–bleaching samples are greater than any dissimilarities among the pre-bleaching samples and -1, where all dissimilarities among the pre-bleaching samples are greater than any dissimilarities among the post-bleaching samples. Values of IMD near zero indicate no difference between treatment groups. See Warwick and Clarke (1993) for further details of the calculation of IMD. Acan – Acanthuridae; Chaet – Chaetodontidae; Scar – Scaridae; Poma - Pomacentridae

Family-level Dynamics

Temporal dynamics of these fish communities in response to bleaching differed among families and habitats (Fig. 3.8). Acanthurid and Scarid species changed little in relative abundance through time with most species remaining within the 95% CI of their pre-bleaching levels (Fig. 3.8i). This response was consistent between the lagoon and slope habitats. Total abundance for the Acanthuridae increased through to the completion of this study in 2003 while Scaridae abundances returned to pre-impact levels after an initial spike in 1998. Species richness for Acanthurids in the lagoon had largely recovered from the losses seen in 1998 while on the slopes, species richness of the surgeonfishes was largely unchanged. Species richness patterns for the Scaridae were similar to the Acanthuridae with recovery in the lagoons and little change on the slopes. In contrast, relative abundances of individual species in both the Chaetodontidae and Pomacentridae changed considerably from pre-bleaching levels.

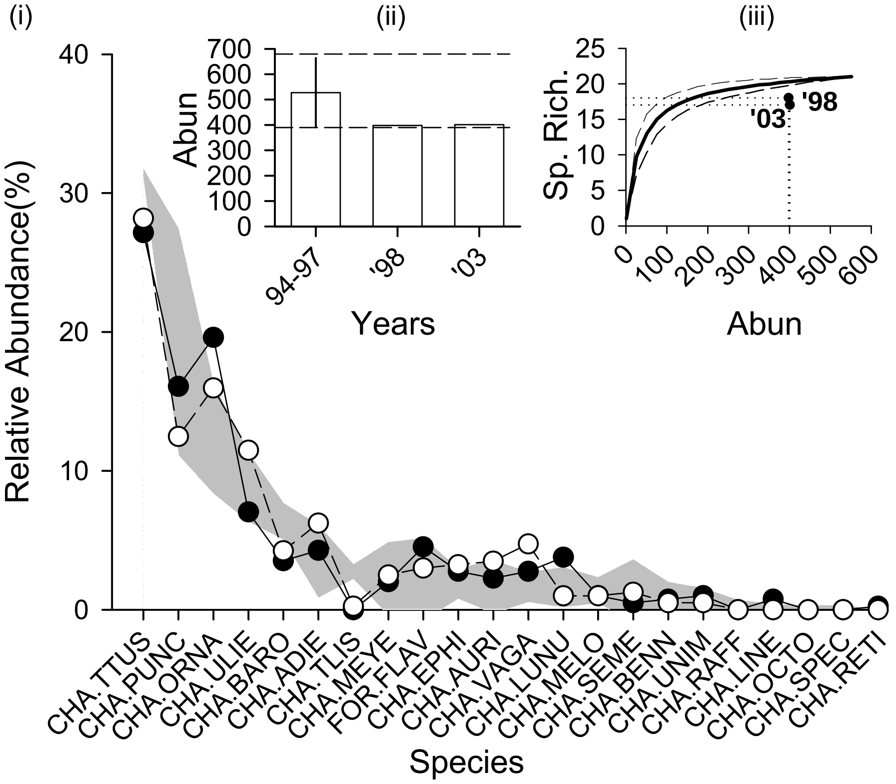
For both families, these changes were greatest on the slopes. Changes in abundance for the Chaetodontidae were rapid, being evident by the first post-bleaching survey in 1998. By 2003, relative abundances of species in this family were returning to the pre-impact levels. This return to the pre-impact situation was evident in both habitats, although the total number of species remaining outside the 95% CI was greater on the slopes. Total abundance and species richness declined immediately after bleaching and was still lower than before bleaching at the 2003 survey. For Pomacentridae, no changes in abundances of individual species were evident in 1998, but by 2003 the abundances of many species had changed, and more so on the slopes. Species richness of this family had decreased by 1998 and in 2003 remained so, in both habitats. Total family abundance was also significantly reduced on the slopes, but not in the lagoons.

Discussion

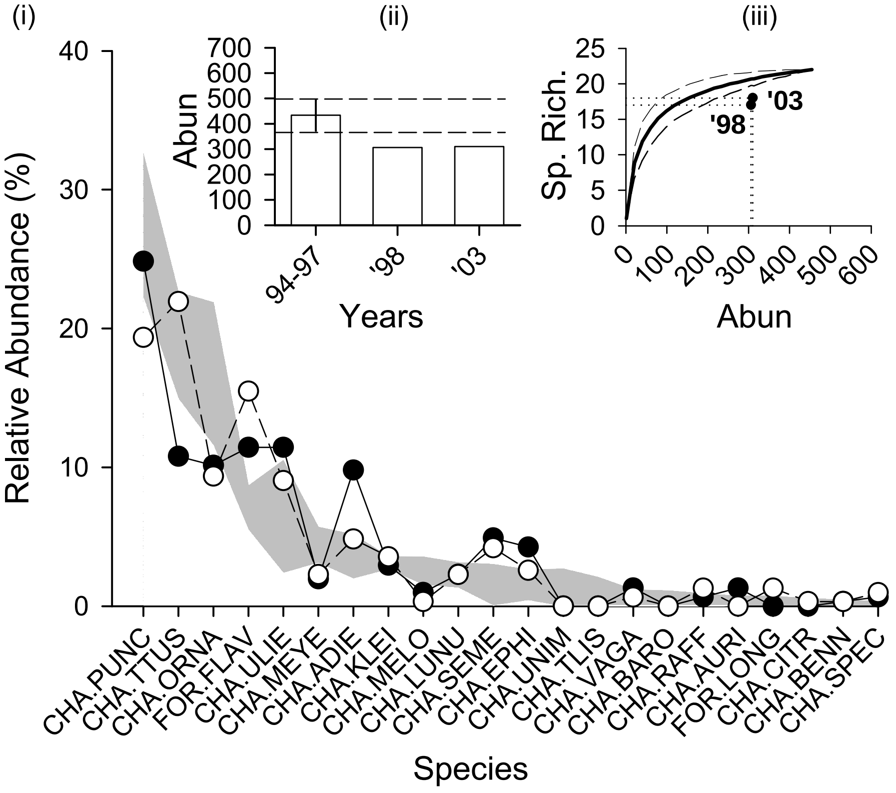
The coral bleaching at Scott Reef was extensive though patchy, with two of the seven surveyed locations (L3 & L4) suffering considerably less coral mortality. Within eight months of the disturbance the previously consistent spatial structure of the benthic communities had disappeared, as turfing algae began to dominate. By 2003, however, the benthic communities were showing signs of recovery with their trajectories in multivariate space moving in the direction of their pre-impact structure and hard coral cover reaching ~ 40% of pre-impact levels (Smith et al. 2008). The structure of the benthic communities, however, remained very different to what existed prior to bleaching, although the once dominant coral families of Acroporidae and Pocilloporidae recovered significantly over the last few post-bleaching surveys (Smith et al. 2008).

CHAETODONTIDAE

a) Lagoon

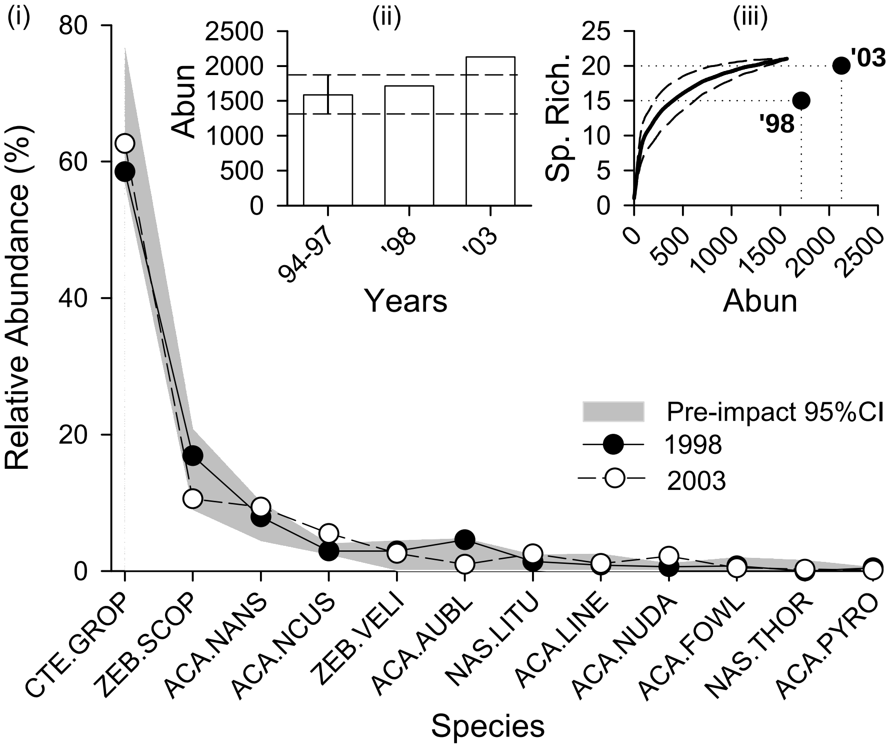


b) Slopes

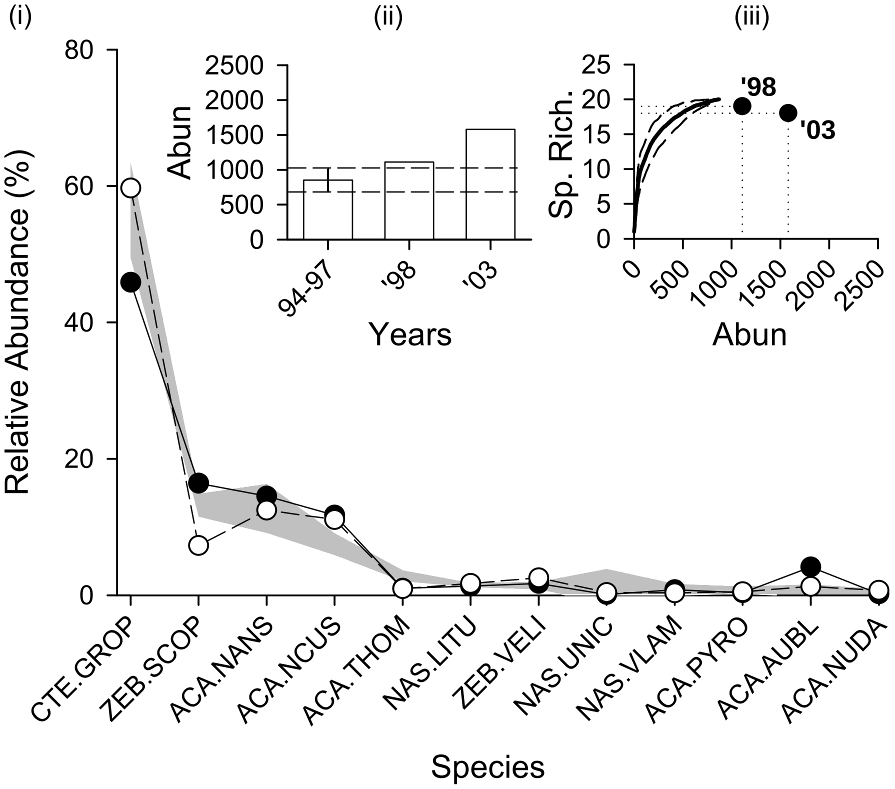


ACANTHURIDAE

Lagoon

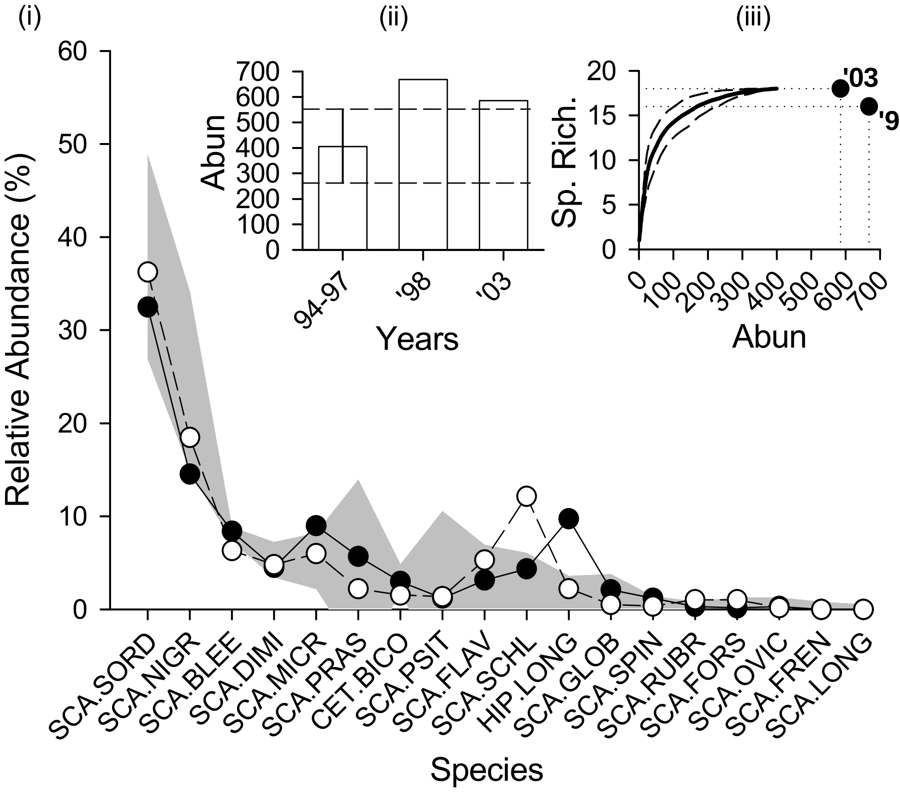


b) Slopes

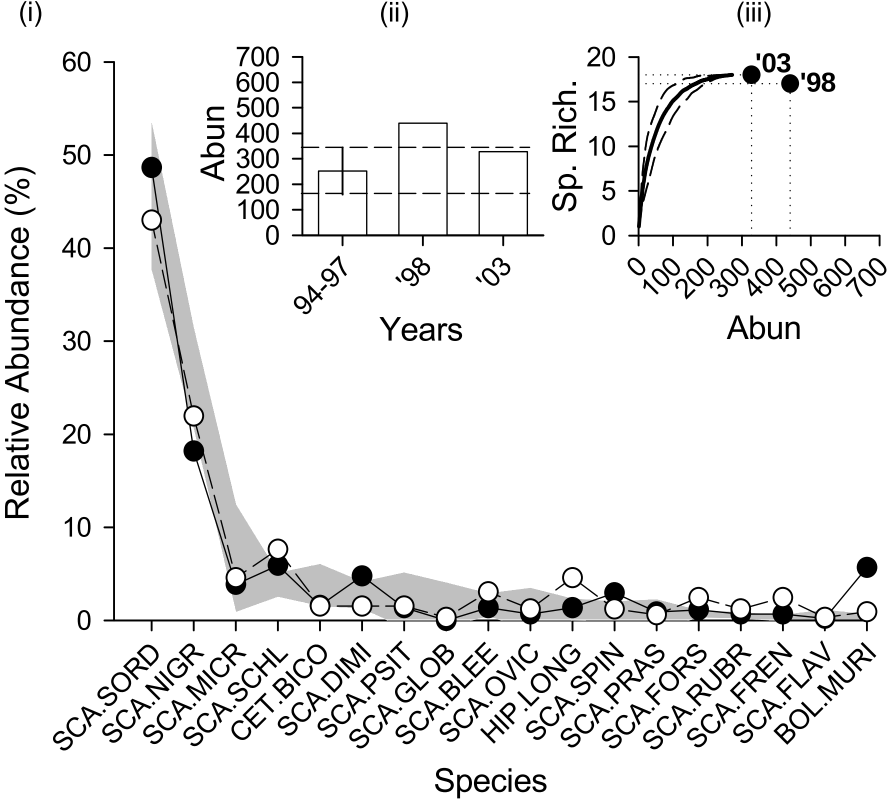


SCARIDAE

a) Lagoon

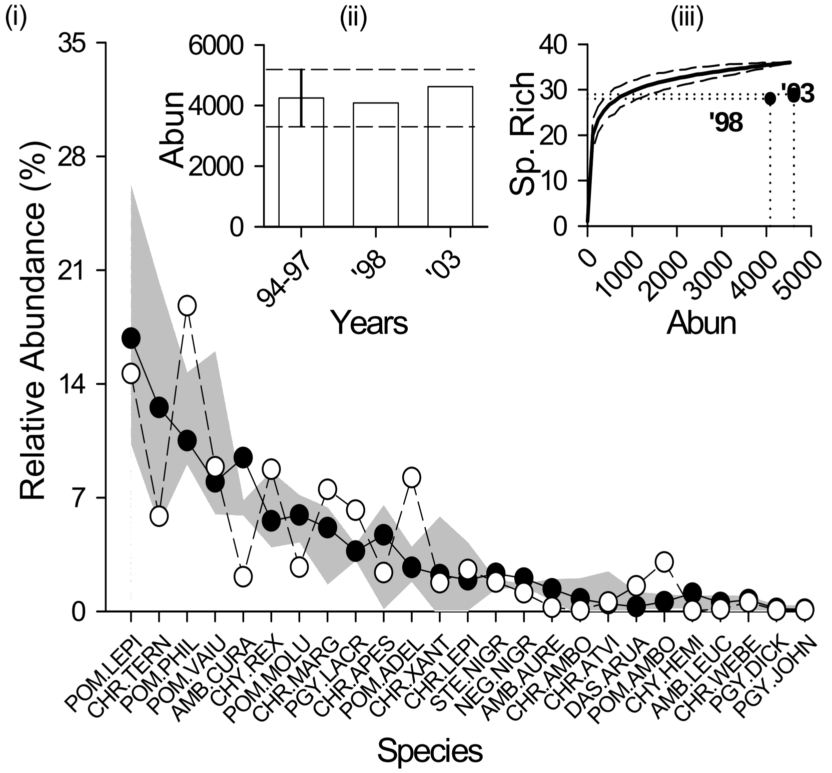


b) Slopes



POMACENTRIDAE

a) Lagoon



b) Slopes

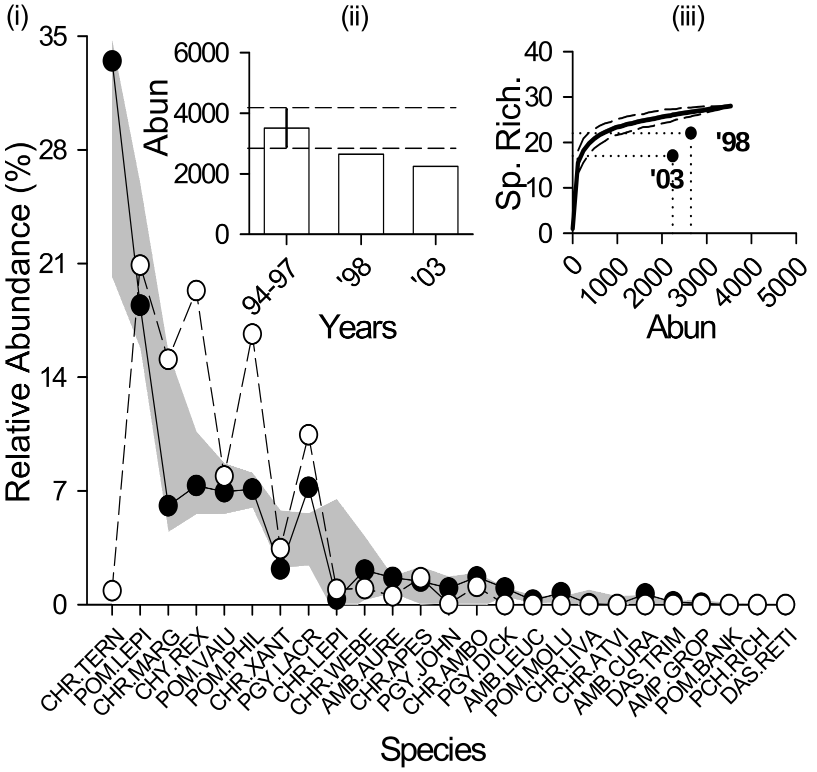


Fig. 3.8 (i) Relative abundance per species, (ii) Total family abundance and (iii) Species richness, for the Acanthuridae, Chaetodontidae Scaridae, and Pomacentridae in (a) lagoon and (b) slope habitats. (i) Relative Abundance: the shaded area delineates the ± 95% confidence interval of the pre-bleaching abundances. Immediate ● - 1998 and longer-term ○ - 2003. post-bleaching abundances are overlaid on this confidence interval. (ii) Total Abundance: Abundance summed across species. The horizontal dashed lines delineate the 95% CI of pre-impact abundance. (iii) Species Richness: a rarefaction curve with 95% CI, based on the mean abundance of species over the four years pre-impact is presented with the observed total abundance and species richness values for the 1998 and 2003 censuses plotted. Species abbreviations – see Appendix 1

Changes in rugosity, however, were more complex and did not simply reflect degradation of the structure of the corals that were killed by bleaching. Prior to the bleaching event, rugosity was greater at the lagoon locations even though hard coral cover was higher on the slopes. This was due to the greater complexity of the consolidated reef matrix that the lagoonal coral communities were growing on. This underlying matrix preserved rugosity within the lagoon, even after significant coral mortality had occurred. The one exception to this was the very sheltered inner lagoon location (L2) where delicate branching corals predominated. Coral mortality was highest at this location and resulted in the complete collapse of the previously live coral matrix, and a subsequently large drop in rugosity. In contrast, the outer slope coral communities were dominated by *Acropora bruegmanni* which forms densely branching, but relatively homogenous, ‘meadows’. Rugosity of this habitat was low even when live coral cover was high; hence coral mortality caused little change in rugosity from its already low values.

The responses of the fish communities to this bleaching event were substantially different from those of the benthic ones. The spatial structure of the fish communities identified during the pre-impact period of this study remained in place throughout the post-bleaching survey period. Bleaching related changes, which were comparable across all locations, were lagged by 12-18 months, with the greatest changes occurring after this period of time. This lag in the responses of these fish communities was evident in the stronger correlation of the immediate post-bleaching fish communities with the pre-bleaching coral communities, rather than with the post-bleaching benthic communities. Such lags in the responses of reef fish communities to disturbance have not been well documented as earlier studies have lacked sufficient time series to do so e.g. Lindahl et al. (2001), Booth and Beretta (2002) and Spalding and Jarvis (2002). A recent study, however, has highlighted the potential importance of lag effects due to bleaching. Seven years after the 1998 bleaching event, there was a reduction in the number of smaller fish in the reef fish communities in the Seychelles (Graham et al. 2007). They interpreted this reduced abundance of small fishes as an indirect effect of the gradual erosion of the structural complexity of their coral reef habitats. Our study supports such an interpretation of the dynamics of tropical reef fish communities in response to coral bleaching.

By November 1999, the fish communities at the seven survey locations were no longer resisting the effects of bleaching and had begun to change to an extent not seen previously during this monitoring program. These fish communities continued changing at least until the 2003 survey, by which time, most of them had begun to show signs of recovery. We did not attempt to assess the causes of these lagged responses directly, but given that erosion over a period of 18 months post-bleaching had gradually reduced the benthos to a highly fragmented landscape dominated by turfing algaes and crumbling corals, some processes are more likely than others to have caused these effects. Habitat complexity is an important determinant of reef fish community structure (Caley and St John, 1996; Hixon and Beets, 1993; Syms and Jones, 2000) and was likely an important cause of the changes observed here. Associated with the structural changes in these benthic habitats was a shift towards dominance by turfing algae. Such shifts in resource availability can cause sub-lethal effects on reef fish (Pratchett et al. 2004) and declines in population size for some species (Jones et al. 2002) but increases in the abundances of others, such as herbivores, through faster growth rates, and potentially higher survivorship of recruits and adults associated with a greater food availability(Hart et al. 1996; Hart & Russ 1996).

Habitat degradation can also affect recruitment by reducing the complexity and diversity of habitat required to support the large number of fish species typically found on coral reefs. Many reef fishes require live coral for settlement and survival and for these species reductions in the availability of live coral at settlement may decrease their numerical abundance (Feary et al. 2007). Such changes in settlement patterns associated with reef degradation could have affected the shifts observed in fish community structure at Scott Reef. Any decrease in abundance of these species may also feedback into lower recruitment as the isolated position of Scott Reef favours self-recruitment as a means of replenishment.

Increased multivariate dispersion in ecological communities is often interpreted as an indication of the impact of disturbance (Garpe et al. 2006; Warwick et al. 2002; Warwick and Clarke, 1993). Our results support such an interpretation. Although the time scales on which these benthic and fish communities responded to this disturbance were very different, their responses in terms of multivariate dispersion were quite similar. Both the benthic and fish communities within the slope habitats at Scott Reef displayed greater dispersion in their structures after the bleaching. In contrast, the fish and benthic communities in the lagoons displayed little or no change in dispersion between the pre- and post-bleaching periods. We interpret these results as an indirect effect of the changes in the benthic communities after 1998 on the structure of these fish communities. These results correlate well with the observed spatio-temporal patterns in rugosity, with fish communities displaying greater change and variation where rugosity was lower; an outcome previously documented experimentally (e.g. Lewis 1997; Syms 1998).

Responses to bleaching by fishes at Scott Reef varied among families. Species richness and abundance of Chaetodontids decreased significantly in both the lagoon and slope habitats during the first eight months following bleaching and remained so for the duration of this study. These results are consistent with previous studies of the effects of the loss of hard coral cover on butterflyfish populations (Bouchon-Navaro et al. 1985; Sano et al. 1984; Williams 1986) and are likely related to reduced food availability. While species richness also declined in the other three families during the first eight months after the disturbance, by 2003 the Acanthurids and Scarids had recovered. These two families had also increased in abundance by the end of this study, most likely in response to increases in the availability of suitable habitat for settlement and increases in their preferred food source, turfing algae (Bellwood 1988; Choat et al. 2002; Green 1998). The responses of the Pomacentrids to the bleaching were initially lagged, but by the end of the study this group had undergone more change than the other three families. Overall, the responses of these four families of reef fishes to the bleaching were consistent with the degree of reliance of their constituent species on live coral for food and shelter and thus was consistent with other studies of the responses of coral reef fishes to disturbance (reviewed by Wilson et al. 2006).

While still exhibiting significantly altered community structure in 2003, these benthic and fish communities nevertheless displayed signs of recovery by 2001. This reef system, therefore, while quite spatially isolated, appears to respond to disturbance like more highly connected reef systems where recovery from disturbance has occurred within 1-2 decades (e.g. Bohnsack 1983, Connell 1997, Sano 2000, Halford et al. 2004). Other relatively isolated reef systems like the Chagos Archipelago and the Maldives have also shown recovery from the 1998 bleaching disturbance (Graham et al. 2008; Sheppard et al. 2008; Wilkinson 2002) but these are geographically more extensive systems than Scott reef. In contrast, the Seychelles, another isolated but also geographically small system has shown little or no recovery from the same bleaching disturbance (Graham et al. 2006). Given that the geographic isolation and extent of Scott Reef is more akin to the Seychelles than the other more highly connected systems why has Scott Reef begun to recover more rapidly than the Seychelles?

There are at least two possibilities worth considering. First, two of the lagoon locations (i.e. L3 and L4) were impacted less by coral bleaching than the others due to local hydrodynamic conditions that provided greater cooling during the 1998 temperature anomaly (Bird, 2005). The benthic communities at these locations survived better, and for at least for one coral species (*Seriatopopa hystrix*) one of these locations acted as a source of new recruits for more heavily impacted locations (Underwood et al. 2007). Second, although bleaching at Scott Reef was spatially extensive and extended below 30 m, a spatial refuge for many of these species appears to exist at this location below this depth. Substantial hard coral communities have been documented within the lagoons at Scott Reef between 40 and 60 m (Heyward et al. 2000) and these coral communities survived the bleaching event intact. Additionally, many of the fish species found on the shallower reef slopes are also found in these deeper water communities. For example, for the Acanthuridae and Chaetodontidae there is almost 100% overlap in the species present at 10 m and 50 m

(M. Cappo, unpublished data). Patchiness in bleaching –induced coral mortality and the existence of deep water refuges has also been implicated in the recovery of the Maldives and Chagos Archipelagoes (Graham et al. 2008; Sheppard et al. 2008). These buffers to disturbance, however, were lacking in the northern reefs of the Seychelles which have comparatively shallow depth profiles (Graham et al. 2006) and hence limited potential to provide similar spatial refuges from bleaching.

The responses of the benthic and fish communities at Scott Reef to the 1998 bleaching compared to the responses of other coral reef systems illustrate that geographic isolation on its own is unlikely to act as an effective and simple proxy for the role of connectivity, or as a predictor of the resilience of these ecological communities. While connectivity was likely key to the resilience of these reef communities, characteristics of the hydrodynamics surrounding Scott Reef, and the spatial structure of the reef whereby a local spatial refuge from which populations and communities could be re-assembled, may have also been associated with resilience at Scott Reef being higher than that which would be predicted based on its geographic isolation alone. Despite the length of this monitoring program at Scott Reef, understanding whether or not the pace of recovery would be sustained was still constrained by its length. Such constraints illustrate how difficult it will be to improve on our ability to predict the resilience of coral reefs to anthropogenic disturbances, particularly in situations where a diversity of processes may interact to confer resilience on these communities and ecosystems. Furthermore, research focused on understanding the resilience of more connected systems of coral reefs has the potential to underestimate the capacity for recovery resulting from the exchange of propagules over quite short distances.

Chapter 4: Shedding light on the detail: Species-specific responses to large-scale bleaching at Scott Reef

Abstract

Bleaching of Scott Reef in 1998 caused extensive mortality of the shallow water corals down to 30 meters. However, because of localised upwelling of deeper, cooler water and patchiness in the distribution of warm water across the reef, mortality was not ubiquitous across the shallows, with areas of coral surviving with significantly less damage. Community level assessment of reef fish showed the greatest changes were in those locations where coral mortality was highest and underlying rugosity was lowest; and this was on the slope sites. By the end of the study in 2003 the fish communities at all locations were recovering and moving towards their previous positions in multivariate space, albeit with some way to go. The individual species within these fish communities responded according to the strength of their affiliations with live coral. The corallivorous butterflyfish which require live coral for food and shelter suffered immediate and large declines, while many herbivorous species whose relationship with live coral is more tenuous actually increased in abundance. Most responses were lagged by up to three years which, in the case of those species that declined in abundance, coincided with a gradual decline in rugosity over the same period. For those herbivorous and non-coral associated species that responded positively after 3 years I interpreted the lag as reflecting the length of time for the positive stimulus to filter through the population and result in increased recruitment and/or survival of adults. While most of the responses I recorded were similar to what had occurred in other reef systems there were differences, which I interpret as local effects. These “local” effects represent the unique combination of tides, reef shape and type, prevailing currents, geographic location etc that exist at Scott Reef. These factors influence reefs worldwide but their relative influence changes from location to location

and must be included in modelling of outcomes from disturbance. My results here show a reef system slowly but surely recovering from a large disturbance. Continuous monitoring through time has shown that even those species that appeared locally extinct have begun to return once benthic cover had started to increase.

Introduction

Natural disturbances are now well accepted as an integral part of the processes helping create the asynchronous or non-equilibrial conditions that are fundamental to community dynamics (Sousa 1984; Wu & Loucks 1995). In tropical marine environments, coral reefs are subject to a wide range of disturbances, including storms (Harmelin-Vivien 1994), *Acanthaster* outbreaks (Lourey et al. 2000; Sano et al. 1987; Williams 1986), coral disease (Harvell et al. 2004), toxic algal blooms (Landsberg 2002) and coral bleaching (Brown 1997). These disturbances vary in the scale and type of their impacts to coral reef communities. Cyclones for example, are capable of affecting medium to large areas of reef where they substantially modify the benthic habitat through physical scouring effects (Done 1992b; Harmelin-Vivien 1994). Crown-of-thorns (COTS) infestations disturb reefs at a similar magnitude (Chesser 1969; Lourey et al. 2000; Sweatman 2008), although in contrast to cyclones they remove only the living veneer of hard corals. More recently, coral bleaching has been causing damage to coral reefs at scales that, as recently as 20 years ago, were not really thought probable e.g. (Hoegh-Guldberg 1999; Wilkinson et al. 1999).

Because of the increasing scale (i.e. regional to global) at which bleaching is occurring and the possibility of more frequent episodes in the near future (Hoegh-Guldberg 1999), there has been a renewed focus on the relationship between coral reef fish and their hard coral hosts. From the fish’s perspective, coral bleaching has a similar impact on corals as COTS infestations, killing the living coral and leaving behind their calcium carbonate skeletons. These skeletons then erode at varying rates, dependent on the influence of such factors as depth, exposure and bio-eroding organisms (Chazottes et al. 1995; Tribollet et al. 2002). In the short term reef fish communities appear to be resilient to large changes in coral cover, as long as the remaining habitat is structurally complex and some residual coral cover remains (Arthur 2004; Downing et al. 2005; Lewis 1997; Sheppard et al. 2008; Syms & Jones 2000). For some reef systems however, the mortality to corals during the 1998 coral bleaching event was so extensive that the potential for recovery of hard corals was severely reduced e.g. the Seychelles (Graham et al. 2006). Without the return of significant levels of coral cover, which drives reef accretion, structural complexity cannot be maintained and the quality of habitat available to reef fish will continue to erode.

The longer term ramifications of reduced coral cover and habitat complexity on the structure of coral reef fish communities are not clear. A recent post-bleaching study in the Seychelles however, found that newly arrived cohorts of reef fish were the most affected by continually degrading habitat. While the large fish assemblages appeared unaffected there were significant reductions in the number of fish below 30cm in size (Graham et al. 2007). This result represents a ‘worst-case’ scenario but nevertheless provides significant insights into fish population dynamics in severely disturbed coral reef ecosystems. An important area for future research is discovering the thresholds at which such ‘worst-case’ scenarios may eventuate across other reef systems. Are the critical minimum limits of coral cover for reef fish communities to maintain their overall functional diversity comparable across reef systems? What is the range of responses possible from any given species, across different reef systems? These are some of questions that need to be answered before worthwhile predictions can be made about what the future holds for coral reef fish communities.

My work at Scott Reef provides detailed information on the response of reef fish assemblages to catastrophic bleaching. While Chapter 3 focused on community or assemblage level responses this chapter focuses on species-specific responses. This type of remote and isolated reef system has not been studied in detail before; hence the results make a significant contribution towards a clearer understanding of what makes a reef system resilient. In addition, the spatial extent of this study encompasses sites spread over 60-80 km's of reef all of which have been monitored annually over a period of ten years. Many studies have reported on the impacts of the 1998 bleaching event; however, few have a temporally continuous record providing both before and after sampling replication.

Following the dynamics of individual fish species over such a prolonged period provides a more complete picture of how these species respond to such drastic changes in their environment. The most common approach has been to obtain an absolute measure of the magnitude of changes between pre- and post-impact periods, e.g. Chabanet (2002), Garpe et al. (2006), Graham et al. (2006), Lasagna et al. (2008). While this approach is appropriate such 'snapshots' are not able to provide details of how species arrived at the end-point of such studies. The extra detail documented through temporal replication provides clearer insight into the processes behind the patterns.

In this chapter I provide an extensive analysis of the responses of individual fish species to the bleaching event of 1998. Four years of pre-impact data provides a powerful baseline to quantify the extent of changes post-1998 through to 2003. In addition I examine the strength of the relationship between each fish species and aspects of their local benthic habitat. By incorporating varying scales of disturbance and integrating through time, these results provide a rigorous assessment of the relationship between fish and the benthos.

Methods

For a detailed description of the study area, location of sites, and the survey methodologies used please refer to the Methods section in Chapter 3.

Data Analyses

A 2-step procedure was used to decide which fish species were suitable for analysis. Initially, all species with a continual presence during the pre-impact years were chosen. These species were then checked for normality and if transformation did not stabilise their variances they were discarded from any further investigation. Subsequent analyses indicated that of the 10 families investigated it was the Acanthuridae, Chaetodontidae, Scaridae and Pomacentridae that provided the most power to detect change. Hence the results presented here concentrate on these four families.

Univariate

Linear Mixed Effects Models (LMEM) (McCullagh & Nelder 1989) were used to examine spatial and temporal effects of disturbance on fish species abundances at Scott Reef. These models extend standard linear models by allowing for correlation and non-constant variability and provide the flexibility to model variances and covariances. Unbalanced and/or missing data and data collected at different times can also be accommodated.

Previous analyses of the Scott Reef fish community (see Chapter 3) indicated that a major spatial stratification exists between the lagoon and slope habitats. Consequently, the model fitted estimated fixed differences between ‘habitats’, among ‘years’, and the interaction between these terms. Variability among ’locations’ and ‘sites’ was estimated as random variance components. A first order autoregressive covariance structure provided the best fit to account for the serial dependence of variation through time. Where significant effects were identified, planned contrasts were used to partition the effects according to the *a priori* questions of interest. These related to differences in abundance averaged over the pre-impact years (i.e., 1994-1997) and each of the post-impact years (i.e., 1998, 1999, 2001 and 2003 respectively) and differences in these contrasts between habitats.

Coefficients of variation (CV's) were calculated for those species subject to LMEM analysis to examine whether there were systematic differences in variability between the Lagoon and Slope habitats. CV's were compared using paired t-tests. The rationale for this was to see whether the more complex habitat within the lagoons increased variation in the visual census counts of individual species because of impaired visual sitings of fish. Increased variation could ultimately reduce power to detect change and potentially confound real differences in bleaching responses between the two habitats.

Multivariate

Temporal relationships between each fish species and the benthic community over the 10 years of surveys were assessed using multiple regression. The benthic variables used in the analyses were Acropora branching (ACB) Acropora Tabulate (ACT), Acropora Bottlebrush (ACX), Acropora Digitate (ACD), Acropora Encrusting and SubMassive (ACES), non-Acropora Branching (CB), non-Acropora Encrusting (CE), non-Acropora Massive (CM), non-Acropora Foliose (CF), non-Acropora SubMassive (CS), Soft Coral (SC), Millepora Coral (CME), Turfing Algae (TA), Sponges (SP) and Sand (S).

To avoid problems with multicollinearity between many of the variables (Graham 2003) Factor Analysis was used to identify latent variables from the matrix of 15 benthic variables. The matrix contained 53 rows representing each Location x Year combination, e.g. Location L1 - ’94, ’95, ’96, ’97, ’98, ’99, ’01, ’03, Location L2 – ’94, ’95 etc. up to Location S3. Ultimately, three orthogonal factors with eigenvalues greater than one, and which explained 81 % of the total variability in the benthic data, were used as explanatory variables in the multiple regression analyses (see Table 4.6 for the loadings of the individual benthic variables on the 3 extracted factors). As the aim of the analyses was to assess relationships between temporal variability in the fish and benthos, differences in absolute abundance between locations were removed by subtracting the location means from the data (prior to the factor analysis) within each location. These deviations were used in subsequent analyses. Hierarchical multiple regression was then used to identify the components of temporal variation in the benthos that were associated with temporal abundance changes. The results were tabulated to show total variation explained by the 3 factors and how this variation was partitioned amongst the 3 factors (see Table 4.7).

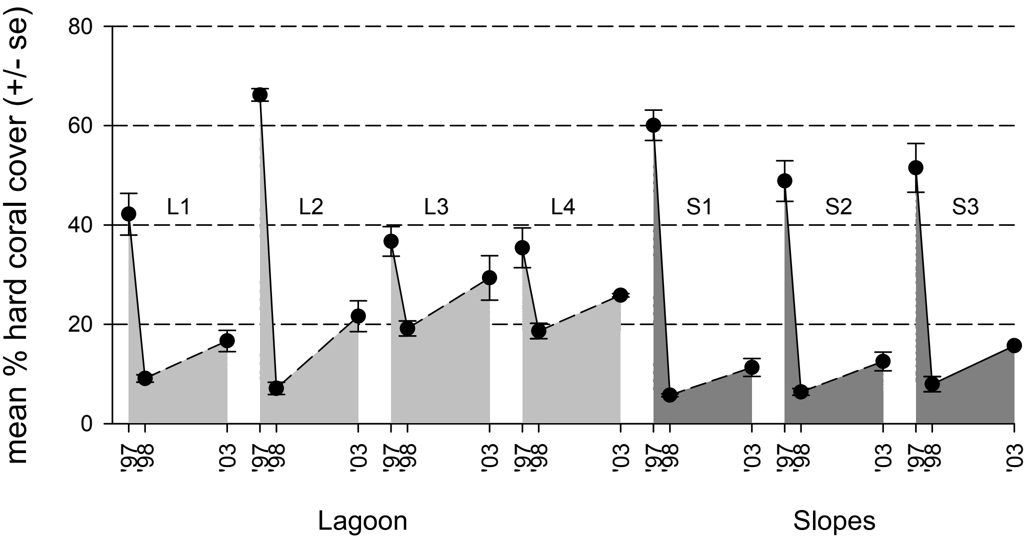


Fig. 4.1 Change in coral cover between 1997, 1998 and 2003, at all seven surveyed locations at Scott Reef

Results

Changes in the Benthic Assemblages

Reef-wide coral cover at Scott Reef before the bleaching was high, ranging between 40-65% with mean cover slightly higher on the slope sites (Fig. 4.1). Branching corals predominated in both the lagoon and slope habitats with minimal cover of turfing algaes (Fig. 4.2). However the bleaching in 1998 caused extensive mortality of hard corals in both habitats (Fig. 4.1) leading to complete dominance of the benthos by turfing algaes (Fig. 4.2). Mortality was disproportionately higher amongst branching coral species, especially on the outer slope sites which suffered decreases of close to 100 % (Fig. 4.2). By 2003 there were clear differences in the recovery rates of coral between habitats with recovery of the lagoon sites proceeding at a greater pace than on the slope sites (Fig. 4.1).

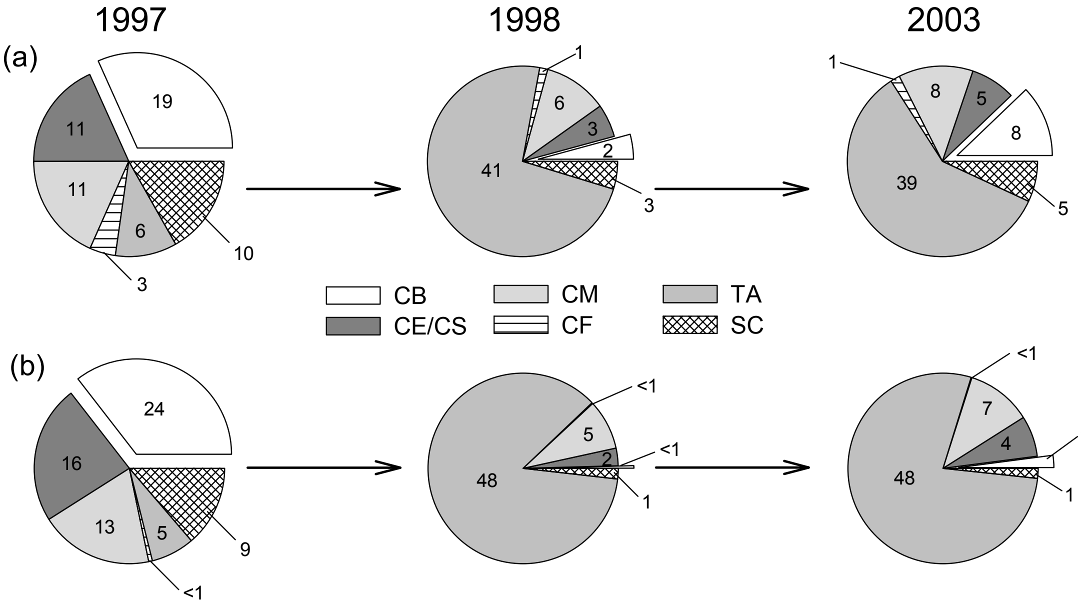


Fig. 4.2 Pie charts indicating the percentage cover of 6 composite benthic categories, for the Lagoon (a) and Slope (b) habitats, immediately before the bleaching event (1997), 6 months after (1998) and 5 years after (2003). NB. CB – Branching corals, CE/CS – Encrusting and sub-massive corals, CM – Massive corals, CF – Foliose corals, TA – Turfing algae, SC – Soft corals. Percentage cover values have been rounded to the nearest whole percent.

With significant loss of coral comes a concomitant drop in structural complexity, and this loss will be greater in areas where live coral is providing the majority of the structure. At the inner lagoon location of S2 branching corals provided a complex yet fragile structural matrix (Fig. 4.3). This matrix remained intact immediately after the bleaching but had collapsed completely by 2001. The subsequent loss of fine scale structural complexity is very clear (Fig. 4.3)

Fig. 4.3 Three screen shots taken from video footage of the inner lagoon site of L2 from the years 1997, 1998 and 2001. The gradual breakdown in structure can clearly be seen.

Species specific changes in the Fish Assemblages

The linear mixed model analyses revealed that of the 44 species analysed 29 (66 %) showed effects that could reasonably be attributed as a response to the bleaching event. The direction of change was positive for species within the Acanthuridae and Scaridae, and negative for the Chaetodontidae, while species within the family Pomacentridae displayed both positive and negative changes (Table 4.1). The remaining 15 species appeared to show no bleaching related effects (these species were spread across all of the four families).

Although earlier multivariate analyses (Chapter 3) indicated there were clear differences in the structure of fish assemblages from the Lagoon and Slope habitats these differences did not translate into differing responses of individual species between the two habitats. In no cases did a species show opposing responses between habitats. There were less statistically significant results across the lagoon habitat than there was for the slope habitats and this was initially hypothesized to be a possible function of increased variability as a result of doing visual census counts in very rugose habitat. However analysis of CV's indicated that this was not the case (of 29 species tested, 7 species with CV Lagoon > CV Slopes, 2 species CV Lagoon < CV Slopes, 20 species CV Lagoon = CV Slopes).

The responses of individual fish species to the bleaching could be categorised into 1. Those that showed an immediate and negative response (e.g. *Chaetodon baronessa*, *Dascyllus aruanus*) 2. Those that showed an immediate and positive response (e.g. *Acanthurus nigricans*, *Scarus schlegeli*) 3. Those that showed a delayed but negative response (e.g. *Amblyglyphidodon curacao*, *Pomacentrus moluccensis*). 4. Those that showed a delayed but positive response (e.g. *Zebrasoma veliferum*, *Plectroglyphidodon lacrymatus*) and 5. Those that showed no response (e.g. *Chaetodon kleinii*, *Scarus niger*, *Neoglyphidodon nigroris*). The most common

Table 4.1 Results of the Linear Mixed Model analysis for species within the families Acanthuridae, Chaetodontidae, Scaridae and Pomacentridae. Planned contrasts for each post-impact year were against the mean and variance of all pre-impact years combined. The complete model contains 4 lagoon locations and 3 slope locations. L – Lagoon, S – Slope, WR – Whole Reef. Significance Levels - p<0.05 (*), p<0.001 (**), p< 0.0001 (***). NS – non-significant

FAMILY						Planned Contrasts				Dir. of
Species	Locations in Model	Habitat	Year	Habitat*Year		1998	1999	2001	2003	Change
ACANTHURIDAE										
Acanthurus nigrofuscus	L1, L2, L3, L4, S1, S2, S3	NS	***	**	L	NS	NS	NS	***	▲
					S	***	**	***	***	▲
Ctenochaetus (grouped)	L1, L2, L3, L4, S1, S2, S3	*	***	***	L	NS	NS	NS	**	▲
					S	NS	NS	***	***	▲
Zebrasoma scopas	L1, L2, L3, L4, S1, S2, S3	NS	***	*	L	**	**	NS	NS	
					S	***	***	***	NS	
A. nigricans	L1, L3, L4, S1, S2, S3	NS	***	NS	WR	***	***	***	***	▲
Zebrasoma veliferum	L1, L3, L4, S2, S3	NS	**	NS	WR	NS	NS	*	***	▲
CHAETODONTIDAE										
Chaetodon adiergastos	L1, L2, L3, L4, S1, S2, S3	NS	NS	NS						
C. ephippium	L1, L2, L3, L4, S1, S2, S3	NS	NS	NS						
C. punctatofasciatus	L1, L2, L3, L4, S1, S2, S3	NS	***	NS	WR	**	***	***	***	▼
C. trifasciatus	L1, L2, L3, L4, S1, S2, S3	NS	***	NS	WR	***	***	***	**	▼
C. ornatissimus	L1, L2, L3, L4, S1, S2, S3	NS	*	**	L	NS	NS	*	NS	

					S	**	***	**	***	▼
C. ulietensis	L1, L2, L3, L4, S1, S2, S3	NS	NS	**	L	NS	NS	NS	NS	
					S	NS	**	NS	NS	
C. meyeri	L3, L4, S2, S3	NS	**	NS	WR	*	**	**	*	▼
C. baronessa	L1, L2, L3, L4		***		WR	***	**	***	**	▼
Forcipeger flavissimus	S1, S2, S3		NS							
C. kleinii	S2		NS							
C. trifascialis	L2		**		WR	**	**	**	**	▼
SCARIDAE										
Scarus dimidiatus	L1, L2, L3, L4, S1, S2, S3	NS	**	NS	WR	**	***	**	NS	
S. microrhinos	L1, L2, L3, L4, S1, S2, S3	NS	*	NS	WR	**	NS	*	NS	
S. niger	L1, L2, L3, L4, S1, S2, S3	NS	NS	NS						
S. schlegeli	L1, L2, L3, L4, S1, S2, S3	NS	***	NS	WR	**	***	***	***	▲
S. sordidius	L1, L2, L3, L4, S1, S2, S3	NS	***	NS	WR	***	***	***	***	▲
S. bleekeri	L1, L2, L4		NS							
S. flavipectoralis	L2		NS							
POMACENTRIDAE										
Chromis ternatensis	L1, L2, L3, L4, S1, S2, S3	NS	***	*	L	NS	*	**	**	▼
					S	NS	***	***	***	▼
Chrysiptera rex	L1, L2, L3, L4, S1, S2, S3	NS	***	*	L	NS	NS	***	**	▲
					S	**	NS	**	**	▲

Plectroglyphidodon lacrymatus	L1, L2, L3, L4, S1, S2, S3	NS	***	**	L	NS	***	*	***	▲
					S	*	***	***	**	▲
Pomacentrus vaiuli	L1, L2, L3, L4, S1, S2, S3	NS	***	**	L	***	***	*	**	▼
					S	**	**	NS	**	▼
P. lepidogenys	L1, L2, L3, L4, S1, S2, S3	NS	***	NS	WR	***	***	**	**	▼
Chromis atripes	L1, L3, L4, S1, S2, S3	*	***	NS	WR	NS	NS	**	NS	
Chromis lepidolepis	L1, L3, L4, S1, S2, S3	NS	***	***	L	NS	NS	**	NS	
					S	***	***	NS	**	▼
Chromis margaritifer	L1, L3, L4, S1, S2, S3	NS	**	NS	WR	NS	NS	*	NS	
Amblyglyphidodon aureus	L1, L4, S1, S2, S3	NS	***	NS	WR	NS	NS	***	***	▼
A. curacao	L1, L2, L3, L4		***		WR	*	***	***	***	▼
Pomacentrus moluccensis	L1, L2, L3, L4		***		WR	NS	***	***	***	▼
Plectroglyphidodon dickii	L3, L4, S2, S3	*	***	**	L	NS	*	**	NS	
					S	NS	***	***	***	▼
Amblyglyphidodon leucogaster	L2, L4, S1		***		WR	NS	**	***	***	▼
Plectroglyphidodon johnstonianus	S1, S2, S3		***		WR	NS	**	***	***	▼
Pomacentrus adelus	L2, L3		**		WR	NS	NS	**	**	▲
Chromis amboinensis	L1, S1		**		WR	NS	NS	*	**	▼
Chrysiptera hemicyanea	L2		***		WR	**	**	***	***	▼
Dascyllus aruanus	L2		**		WR	NS	***	**	***	▼
Neoglyphidodon nigroris	L2		NS							

Pomacentrus amboinensis	L2	**	WR	NS	NS	**	**	▲
Stegastes nigricans	L2	NS						

response was negative, whether immediately or delayed. These patterns are interpreted in the context of the habitat associations of individual species.

Table 4.2 The first 3 eigenvectors (components) extracted from the Factor analysis of 15 Benthic variables, and the amount of variance they explain. These components were subsequently used as independent variables in hierarchical regressions with individual fish species abundance. Only vectors with an eigenvalue of >1 were chosen.

	Extraction Sums of Squared Loadings			Rotation Sums of Squared Loadings		
Component	Total	% of Variance	Cum. %	Total	% of Variance	Cum. %
1	9.387	62.583	62.583	7.041	46.941	46.941
2	1.526	10.176	72.759	3.851	25.673	72.613
3	1.230	8.203	80.962	1.252	8.349	80.962

The three extracted components from the factor analysis explained ~81% of the variance in the benthic dataset with factors one and two of the rotated solution explaining the majority of the variance at ~47% and ~26% respectively (Table 4.2). The loadings of the individual benthic variables separated into three relatively clear groupings (Table 4.3) which were taken to define three separate components of the benthic habitat. Factor 1 represents the totality of morphology types that together represent a diverse, healthy hard coral community reef. It can be seen that turfing algaes (TA) load up strongly negative on this factor and this represents an obvious cause and effect such that where hard coral communities are thriving turfing algaes are not. Factor 2 represents the role of those coral morphologies that often form monospecific habitat types of their own. It is represented by Acropora tabulate and bottlebrush forms and foliose coral growth forms. The third factor represents

Table 4.3 Loadings of the individual benthic variables on the 3 extracted Factors. Only loadings > 0.6 were tabulated.

Benthic Variables	Factor 1	Factor 2	Factor 3
SC	0.944		
ACE & ACS	0.931		
CME	0.919		
CE	0.884		
CM	0.862		
TA	-0.830		
CB	0.808		
ACB et al.	0.750		
ACX		0.916	
ACT		0.775	
CF		0.750	
CS		0.680	
S			0.823
ACD			0.614

SC – Soft Coral, ACE – Acropora Encrusting, ACS – Acropora Sub-massive, CME – Millepora, CE – non-Acropora Encrusting, CM – non-Acropora Massive, TA – Turfing Algaes, CB – non-Acropora Branching, ACB – Acropora Branching, ACX – Acropora Bottlebrush, ACT – Acropora Tabulate, CF – non-Acropora Foliose, CS – non-Acropora sub-Massive, S – Sand, ACD – Acropora Digitate

discontinuous habitat where sandy areas are more prevalent. While this factor is also loading up on Acropora digitate corals this is not a reflection of a strong correlation between the two variables but rather a limitation of the factor analysis which was constrained to extract only those factors with eigenvalues greater than 1. Those fish species that significantly regressed against this factor were separately regressed against prevalence of sand and prevalence of digitate Acropora coral to see which of the two benthic variables was more influential.

Table 4.4 Results of Hierarchical Multiple Regressions of individual species abundance against the first 3 extracted factors from a PCA of 15 benthic variables. Results are interpreted in the context of loadings in Table 6. The amount of variance accounted for by each individual factor is expressed as an absolute percentage of the total explained variance, not a proportion. Negative percentages refer to the direction of the relationship between that factor and the dependent species. NS – No significant relationship at the p<0.05 level of significance.

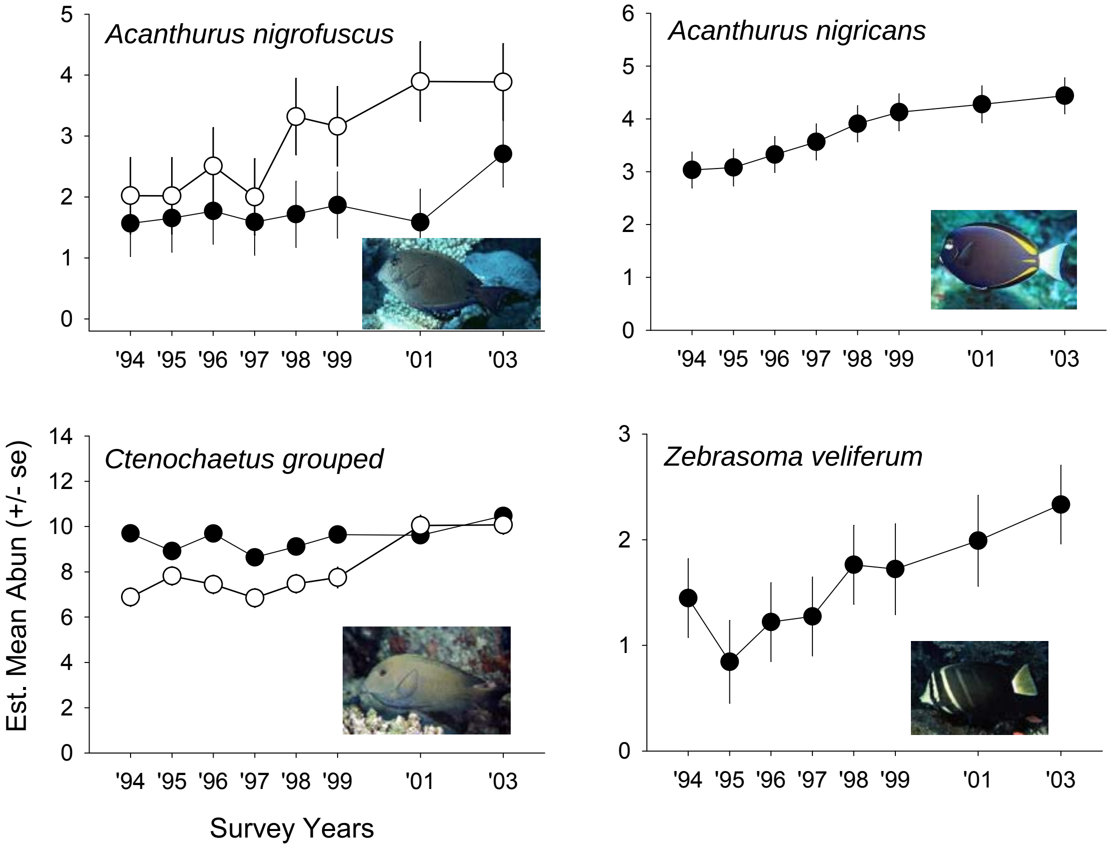
FAMILY *Species*	Spatial Scale	% Total Variance	p	Factors 1	 2	 3
ACANTHURIDAE						
Acanthurus nigricans	Lagoon	42.5	**	-26.5	NS	NS
	Slopes	60.5	***	-59.6	NS	NS
Acanthurus nigrofuscus	Lagoon	13.5	NS			
	Slopes	75.3	***	-72.1	NS	NS
Ctenochaetus (grouped)	Lagoon	19.2	NS			
	Slopes	50.3	**	-36.6	NS	NS
Zebrasoma veliferum	Lagoon	30.4	**	-25.5	NS	NS
	Slopes	44.5	**	-41.2	NS	NS
CHAETODONTIDAE						
Chaetodon punctatofasciatus	All Sites	54.1	***	46.0	5.4	NS
C. trifasciatus	All Sites	60.0	***	29.9	29.7	NS
C. ornatissimus	Lagoon	5.6	NS			
	Slopes	72.6	***	57.0	15.5	NS

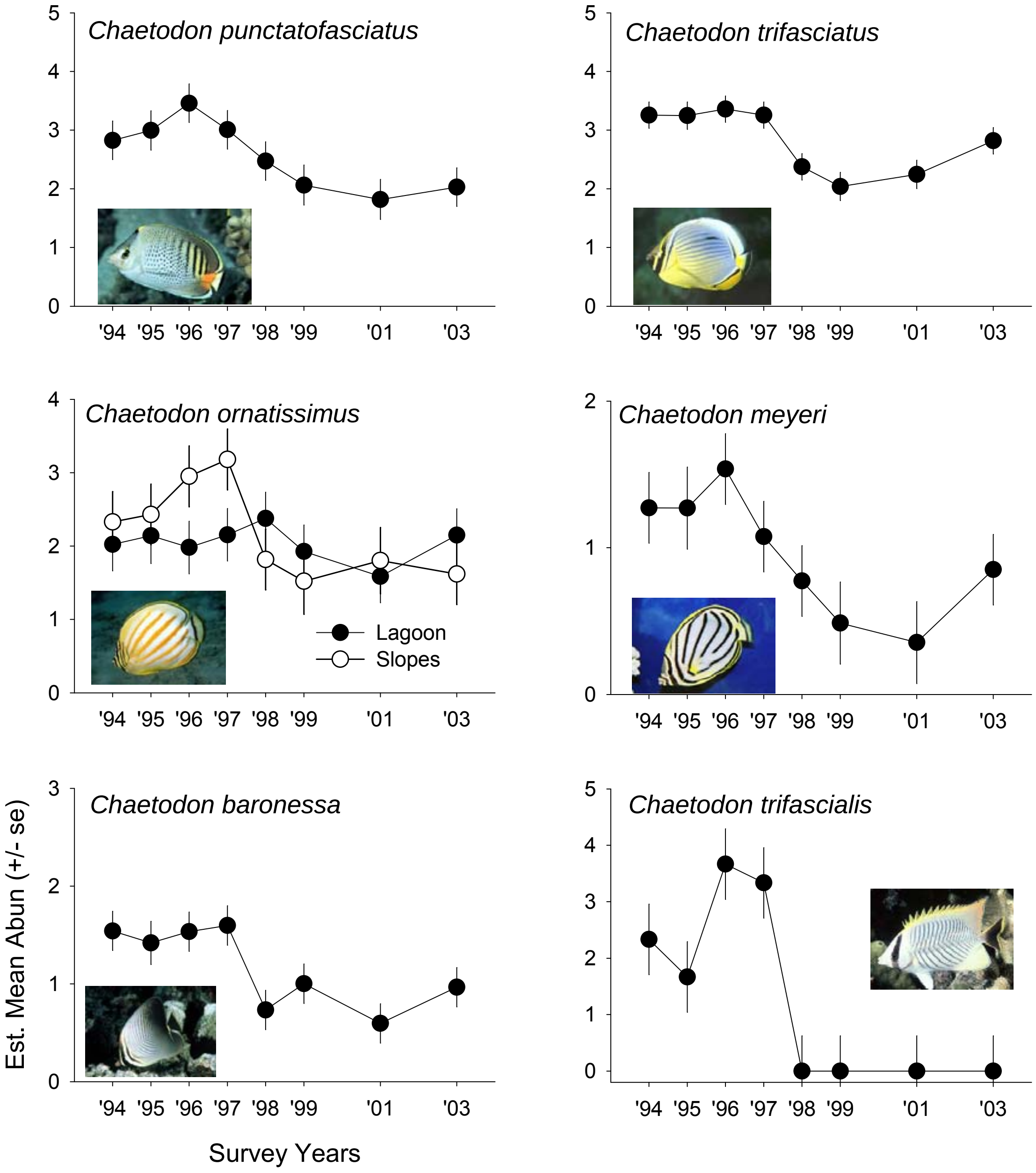
C. baronessa	Lagoon	59.0	**	29.1	28.0	NS
C. meyeri	L3, L4, S2, S3	54.0	***	47.6	NS	NS
C.. trifascialis	L2	93.3	***	NS	87.2	NS
SCARIDAE						
Scarus schlegeli	All Sites	56.1	***	-28.4	-16.1	11.7
S. sordidus	All Sites	53.8	***	-46.1	-7.7	NS
POMACENTRIDAE						
Pomacentrus lepidogenys	All Sites	33.9	***	33.2	NS	NS
Chrysiptera rex	Lagoon	18.4	*	NS	-16.2	NS
	Slopes	14.7	NS			
Chromis ternatensis	Lagoon	28.0	**	26.3	NS	NS
	Slopes	56.2	**	41.4	NS	14.6
Plectroglyphidodon lacrymatus	Lagoon	48.4	**	-19.2	NS	23.2
	Slopes	60.7	***	-59.9	NS	NS
Pomacentrus vaiuli	Lagoon	39.1	**	30.2	NS	NS
	Slopes	39.2	*	18.2	NS	-21.0
Chromis lepidolepis	L1, L3, L4	14.4	NS			
	Slopes	31	*	26	NS	NS
Amblyglyphidodon aureus	L1, L4, S1, S2, S3	53.3	***	13.4	2.6	-37.3
Plectroglyphidodon dickii	L3, L4, S2, S3	66.8	***	60.5	NS	NS
Amblyglyphidodon curacao	Lagoon	28.6	*	17.2	NS	NS
Pomacentrus moluccensis	Lagoon	46.7	**	24.3	17.9	NS
P. adelus	L1, L2, L3	35.3	*	NS	NS	22.1
P. amboinensis	L1, L2, L3	34.9	**	NS	NS	30.1

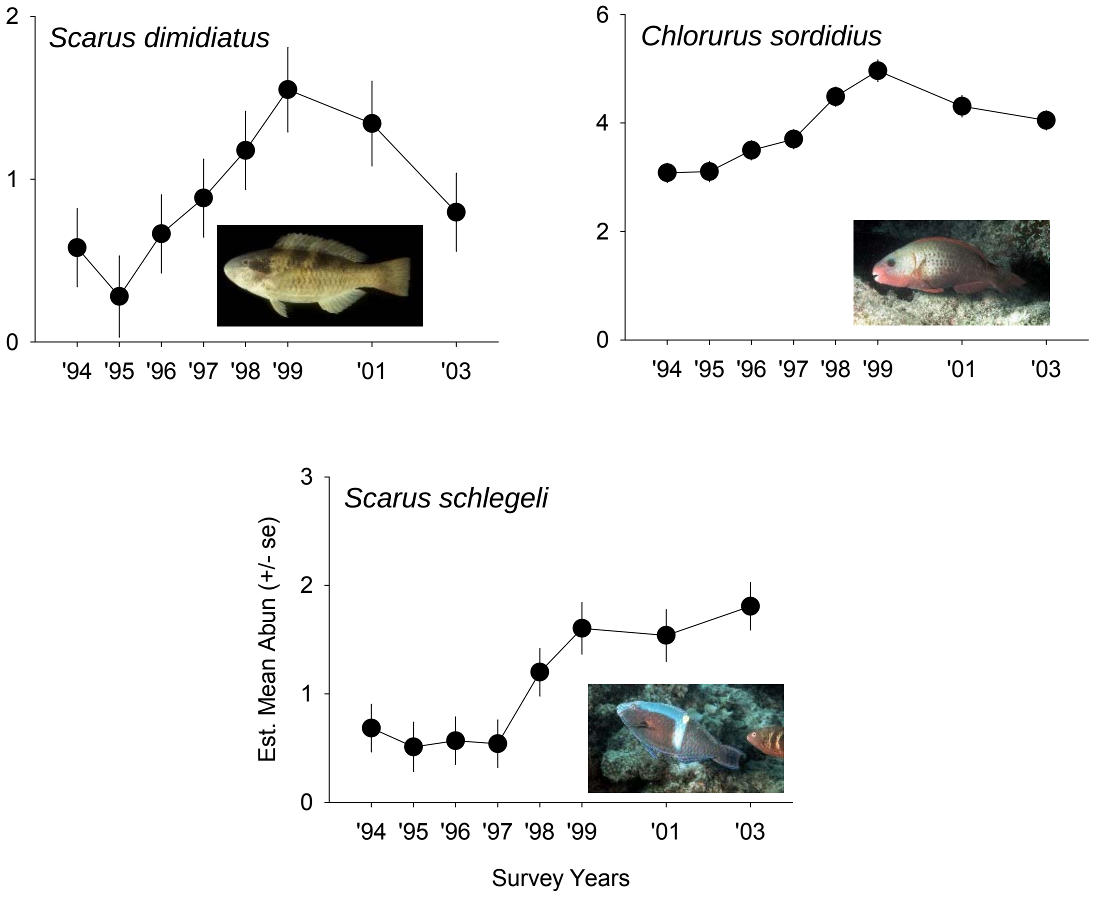
Plectroglyphidodon johnstonianus	Slopes	68.0	***	57.0	NS	-10.7
Amblyglyphidodon leucogaster	L2, L4, S1	41.1	**	37.4	NS	NS
Chromis amboinensis	L1, S1, S3	28.5	NS			
Dascyllus aruanus	L2	63.7	NS			

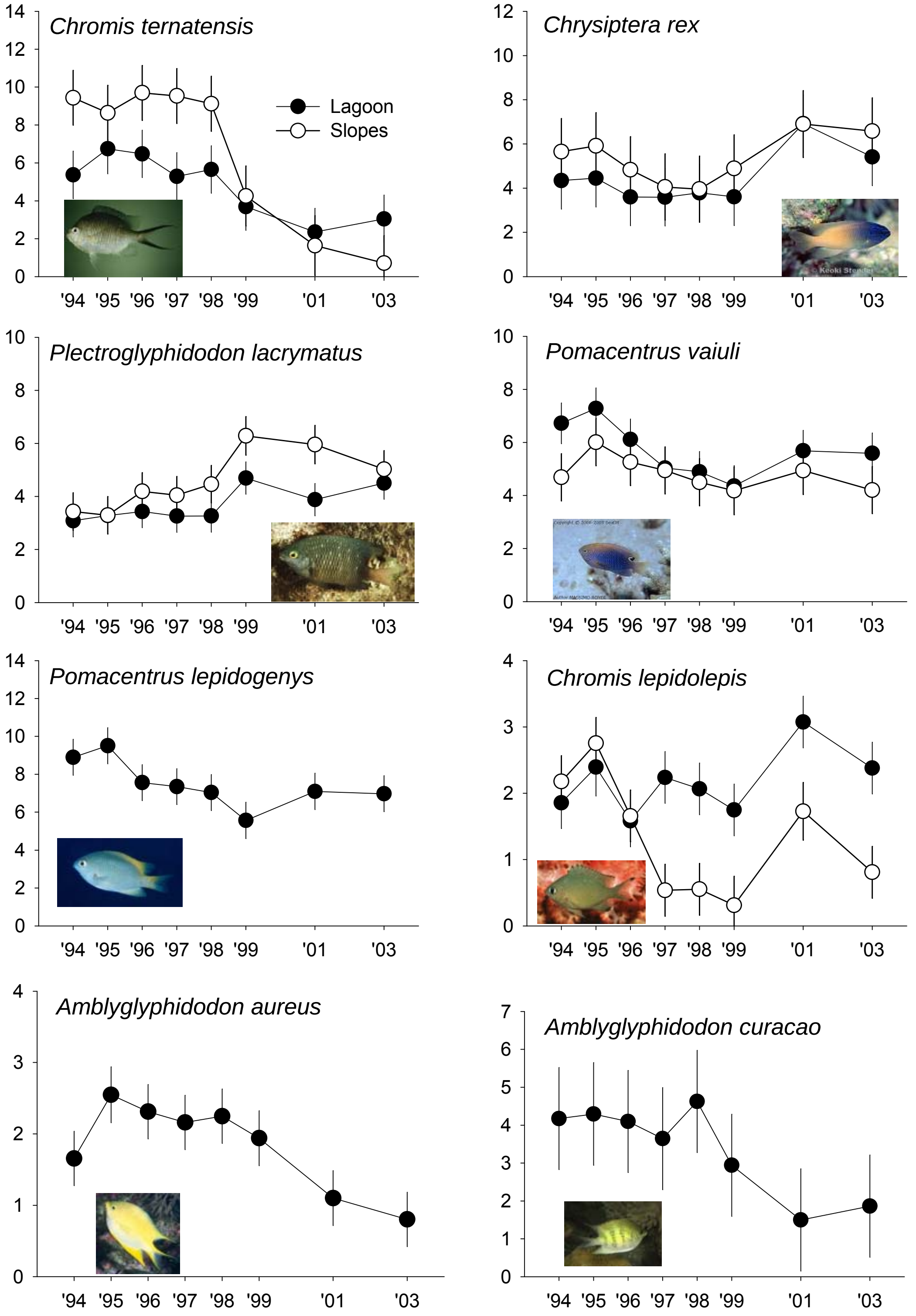
All of the four acanthurid species had significantly negative relationships with Factor 1 (Table 4.4). As all species showed relative stability in abundance during the years preceding the bleaching event, the change in their abundance was clearly heavily influenced by declines in the abundance of healthy coral reef areas after the bleaching and the subsequent increase in turfing algae. The strength of this response was strongest on the slope sites for all four of the species analysed (Fig. 4.4).

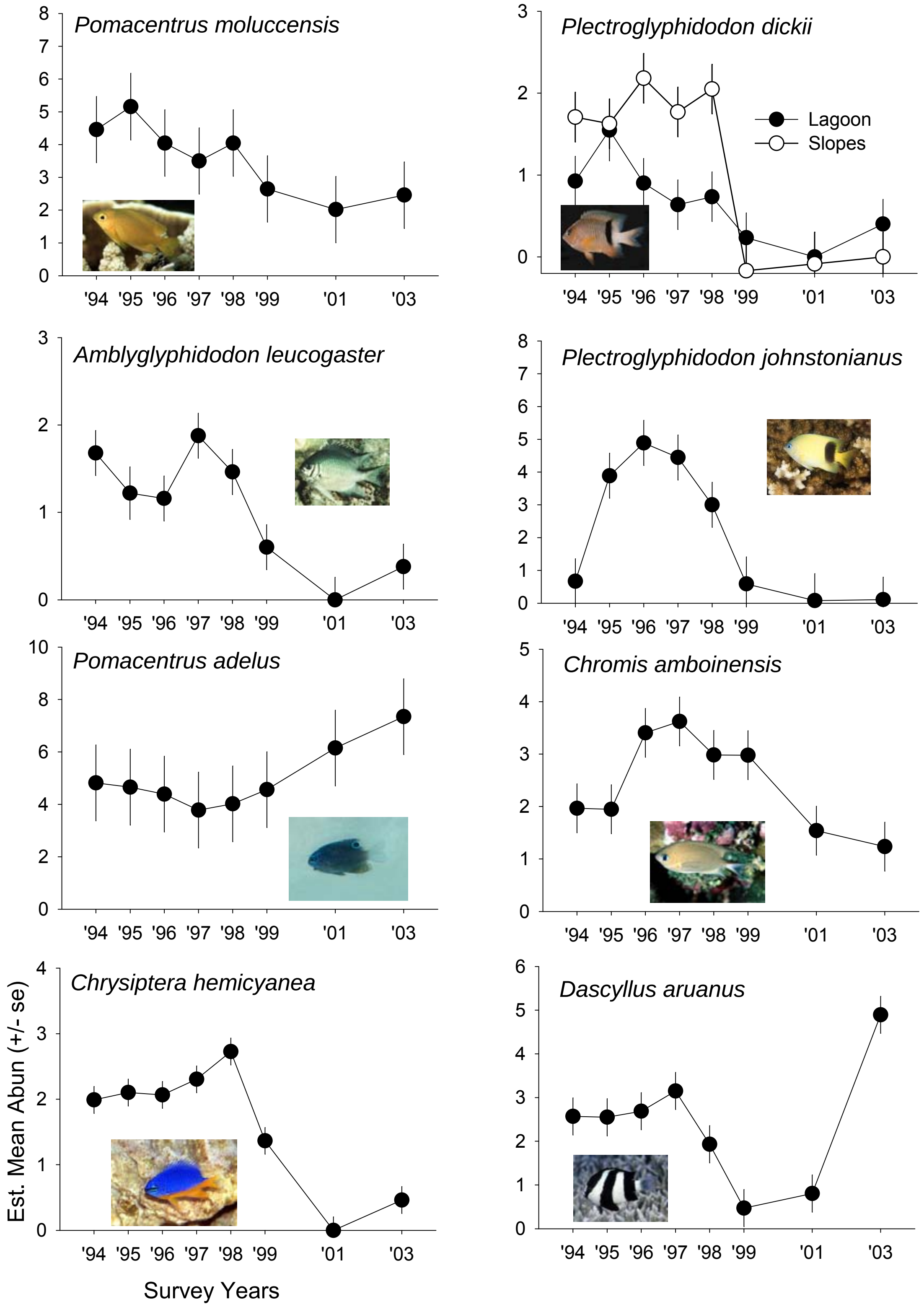
Of the 11 species of butterflyfish subject to analysis five did not show any effects that could reasonably be attributed to the bleaching event and these were all non-corallivorous species (see Table 4.1). The other six species were all obligately corallivorous and declined significantly, immediately following the bleaching (Fig. 4.4). Four of the impacted species had significant relationships with both Factor 1 and Factor 2 indicating a relationship to all aspects of the hard coral community. Of the remaining two species, *Chaetodon meyeri* was significantly associated with only Factor 1 while *C. trifascialis* was significantly associated with only Factor 2, representing the Acropora tabulate corals with which this species is wholly associated.


Acanthurus nigrofuscus
0
1
2
3
4
5
'94 '95 '96 '97 '98 '99 '01 '03
Acanthurus nigricans
0
1
2
3
4
5
6
'94 '95 '96 '97 '98 '99 '01 '03
Ctenochaetus grouped
0
2
4
6
8
10
12
14
'94 '95 '96 '97 '98 '99 '01 '03
Zebrasoma veliferum
0
1
2
3
'94 '95 '96 '97 '98 '99 '01 '03
Est. Mean Abun (+/- se)
Survey Years


Chaetodon punctatofasciatus
Chaetodon trifasciatus
Chaetodon ornatissimus
Chaetodon meyeri
Chaetodon baronessa
Chaetodon trifascialis
Lagoon
Slopes
Est. Mean Abun (+/- se)
Survey Years
0
1
2
3
4
5
'94
'95
'96
'97
'98
'99
'01
'03


Scarus dimidiatus
0
1
2
'94 '95 '96 '97 '98 '99 '01 '03
Chlorurus sordidius
0
2
4
6
'94 '95 '96 '97 '98 '99 '01 '03
Scarus schlegeli
Est. Mean Abun (+/- se)
0
1
2
3
'94 '95 '96 '97 '98 '99 '01 '03
Survey Years


Chromis ternatensis
Lagoon
Slopes
Chrysiptera rex
© Keoki Stender
Plectroglyphidodon lacrymatus
Pomacentrus vaiuli
Pomacentrus lepidogenys
Chromis lepidolepis
Amblyglyphidodon aureus
Amblyglyphidodon curacao
'94
'95
'96
'97
'98
'99
'01
'03
0
2
4
6
8
10
12
14


Pomacentrus moluccensis
Plectroglyphidodon dickii
Lagoon
Slopes
Amblyglyphidodon leucogaster
Plectroglyphidodon johnstonianus
Pomacentrus adelus
Chromis amboinensis
Chrysiptera hemicyanea
Dascyllus aruanus
'94 '95 '96 '97 '98 '99 '01 '03
Est. Mean Abun (+/- se)
Survey Years

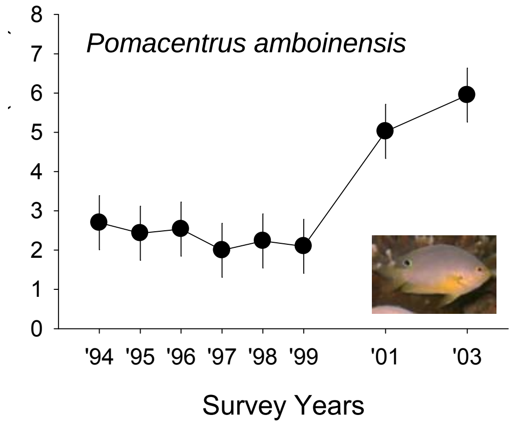


Fig. 4.4 Changes in abundance from pre- to post-bleaching for those species from the (a) Acanthuridae (b) Chaetodontidae (c) Scaridae and (d) Pomacentridae, identified as significant by the Linear Mixed Models. Abundance values are square root transformed estimated means (± 1 S.E.) as calculated by the linear mixed models.

Three of the seven species of parrotfish that were analysed showed effects that could be related to the bleaching event (Table 4.1, Fig. 4.4). However, of these three species *Scarus dimidiatus* abundance had declined to pre-disturbance levels by 2003 and hence it was not regressed against the three orthogonal factors representing aspects of the benthic community. The other two species were negatively associated with all aspects of the hard coral community while *S. schlegeli* was positively associated with Factor 3 (Table 4.4). A separate regression of this species against the two benthic variables loading on this factor indicated it was a positive relationship with sand that was driving this result.

There were more significant responses to the bleaching event in the damselfishes, compared to the other three families analysed, and their responses were also more varied (Table 4.1, Fig. 4.4). While most of the species analysed had significant and positive relationships with Factor 1, two of these species, *Amblyglyphidodon aureus* and *Pomacentrus moluccensis* also had significant relationships with Factor 2. Two species (*Chrysiptera rex* and *Plectroglyphidodon lacrymatus*) had negative relationships with Factors 1 or 2, with *P. lacrymatus* abundance in particular being strongly negatively correlated to areas of healthy coral cover. There were seven instances of significant correlation with factor 3 (Table 4.4) and for five of these species this was a relationship to sandy areas while for the other two it was reflective of a relationship with areas of digitate acropora corals (Table 4.4).

Discussion

The responses of reef fish species at Scott Reef to the global bleaching event of 1998 were in general agreement with what has previously been reported by other researchers throughout the Indo-Pacific e.g. (Booth & Beretta 2002; Graham et al. 2006; Graham 2008; Pratchett et al. 2006; Sano 2004; Spalding & Jarvis 2002; Wilson et al. 2006; Wilson et al. 2008c). I found the abundance of obligate corallivorous butterflyfish declined quickly after the extensive coral mortality; as was documented by Pratchett et al. (2006). Some herbivorous species from the Acanthuridae and Scaridae increased in abundance over the same period; as was documented by Wilson et al. (2006). These more immediate responses were then followed by lagged increases and declines from many of the damselfish species and one of the acanthurid species; similar to Booth and Beretta (2002). Some species however, responded differently to what has been recorded elsewhere and I interpreted this as local effects. These “local” effects represent the unique combination (amongst others) of tides, reef size, shape and type, prevailing currents, and geographic location that exist at Scott Reef. These factors influence reefs worldwide but their relative influence changes from location to location. My results here show a resilient reef system recovering from a large disturbance, albeit slowly. Continuous monitoring for five years after the bleaching revealed that as hard coral communities began to recover even species that appeared locally extinct returned.

There were a greater number of significant responses to bleaching on the slope locations. Analysis of CV's showed that this was a result of real differences between the two habitats rather than bias due to visual census. Although extensive, the coral bleaching at Scott Reef was patchy, especially within the lagoon, where two of the seven surveyed locations (L3 and L4) suffered considerably less coral mortality (Fig. 4.1). Despite higher hard coral cover on the slopes, rugosity was greater within the lagoon due to the greater complexity of the consolidated reef matrix. This combination of higher coral survival and greater residual rugosity has enabled many of the fish species within the lagoon to survive the bleaching to a much greater degree than their con-specifics on the slopes.

Because the first post-bleaching survey was conducted in November [1998] before the major recruitment period for reef fish at Scott Reef (Dec.- Mar.; A. Halford unpubl. data) the responses of fish at this time are considered independent of recruitment dynamics. Hence, the 1998 data point provides insights into the type of relationship that adult fish species have with their benthic environment without the confounding effects of recruitment. All the corallivorous butterflyfish had declined significantly from their pre-impact averages by the first post-impact survey in Nov. 1998, seven months after the bleaching. As the structural complexity of the dead coral skeletons remained intact at this time (see Fig. 4.3, 1998) these responses are likely due to the extensive decline in their preferred food; scleractinian corals e.g. (Pratchett & Berumen 2008). Hierarchical multiple regressions confirmed that in four of the six affected species their abundance was significantly linked to the entire hard coral community (i.e. Factors1 & 2; Table 4.4). One species, *Chaetodon trifascialis* was clearly linked to the fortunes of tabulate corals, its specific food preference (Pratchett & Berumen 2008) which loaded specifically on Factor 2 (87.2 % variance explained; Table 4.4). This species disappeared from the transects in 1998 and had still not returned by 2003.

The other species that responded immediately to the bleaching were the herbivorous acanthurids (*Acanthurus nigrofuscus* and *A. nigricans*), and scarids (*Chlorurus sordidus*, *Scarus dimidiatus* and *S. schlegeli*), all of which had increased in abundance seven months after the bleaching. These species had significantly negative relationships with Factor 1 indicating their numbers increased as coral cover decreased and was replaced by turfing algae (see Table 4.3). Because recruitment can be ruled out as a primary cause, the rapid initial increase in numbers is likely due to movement of individuals from undisturbed areas into areas of high turfing algal cover. Although the bleaching was extensive it was nevertheless patchy, more so in the lagoon (where there was less change in these species). Previous work at Scott Reef has shown many of these fish species extend to depths below the bleaching impact (Halford & Caley 2009). Highly mobile herbivores moving from undisturbed habitat refuges into heavily bleached areas would see their numbers increase rapidly in lieu of significant recruitment. Other studies have shown that herbivorous species can respond quickly to favourable feeding conditions brought on by biological (as distinct from physical) disturbances eg. (Garpe et al. 2006; Halford & Perret 2009) however by excluding recruitment here I provide a clearer picture of the mechanisms by which they initially respond.

Six other species also showed positive responses to the bleaching; two acanthurids (*Ctenochaetus* grouped and *Zebrasoma veliferum*) and four pomacentrids (*Chrysiptera rex*, *Plectroglyphidodon lacrymatus*, *Pomacentrus adelus* and *Pomacentrus amboinensis*), but unlike the others their responses were delayed by up to three years. While this delay makes it difficult to apportion bleaching effects it is reasonable to assume that as these species do not associate directly with live coral they found the post bleaching conditions favourable. The lagged response may represent the amount of time that is required for the favourable conditions to translate into reproductive success. In addition, inter-annual recruitment is inherently variable

(Doherty 1987) so even though conditions may have been favourable for settlement success between 1998 and 2001 a significant pulse of larvae still had to be available to take advantage of these conditions. The *Ctenochaetus* grouped and *Pl. lacrymatus* responses were the opposite of recent reviews which found these species had declined at numerous locations affected by bleaching (Pratchett et al. 2008; Wilson et al. 2006). It is not clear why so many other studies found declines in these species as they have no direct affiliation with live coral (either as recruits, juveniles or adult). A direct comparison of species that had differing responses across regions would be a worthwhile area for future studies. Are there fundamental life-history differences between locations that make the same species inherently more vulnerable, or is it just a reflection of the intensity of the disturbance effect at each location?

The most common response to the bleaching was a lagged decline between 18 months and 3 years after the event and only species within the Pomacentridae displayed this pattern. Moreover, of the four families examined in detail for this study the pomacentrids had the most number of species respond to the disturbance. This is not unexpected given they are small in size, and more closely associated with the benthos than larger fishes (see review by Munday and Jones (1998). The seven species that declined after 18 months (*Amblyglyphidodon curacao*, *A. leucogaster*, *Chromis ternatensis*, *Chrysiptera hemicyanea*, *Plectroglyphidodon dickii*, *P. johnstonianus* and *Pomacentrus moluccensis*) all associate with hard coral habitat both as adults and juveniles/recruits (Wilson et al. 2008a). The two species that took longest to respond to the bleaching (*Amblyglyphidodon aureus* and *Chromis amboinensis*) while not strongly associated with hard coral habitat as adults (Allen 1991; Myers 1991), do preferentially recruit to live coral. It is not possible in this study to separate the individual contribution of processes responsible for the observed declines in these species. Nevertheless a substantial body of evidence exists that highlights habitat as a key mediator of disturbance effects (see reviews by Wilson et al. (2006); Pratchett et al. (2008); Munday & Jones (1998)).

The patterns of decline seen in damselfish closely tracked observed declines in rugosity rather than live coral cover. This suggests they have a greater dependence on benthic habitat for shelter rather than food. Fig. 4.2 shows the structural integrity of dead corals breaks down incrementally and hence any effects associated with this tend to manifest more slowly. As adults, many reef fish species appear capable of withstanding the initial impacts of an intense bleaching event, as long as they are not depending on live coral as their primary food source. However as dead coral skeletons erode, they provide decreasing levels of protection which leads to higher levels of predation on adults, juveniles and recruits (Caley & St John 1996; Hixon & Beets 1993). Ultimately diversity is reduced and the structure of the resident fish assemblages changes considerably (Wilson et al. 2006). It has been shown recently for example, that even ecologically versatile species such as the damselfish *Pomacentrus amboinensis* are subject to higher mortality rates on bleached corals (McCormick 2009). Hence, it appears that structural complexity (independent of live coral) only slows down the rate of change in reef fish assemblages; it does not stop an inevitable process of decline.

To fully understand the processes by which fish species react to disturbance requires detailed demographic information, which is unfortunately lacking for most coral reef fish species. However, parallels can be drawn with those species for which such information does exist. Many small fish species are short lived, exhibiting early maturity, high reproductive output and high intrinsic rates of increase (Begon & Mortimer 1986 in Munday and Jones 2008). Under this life history pattern settlement failure is reflected very quickly in the adult population and changes in their abundance are quickly noted in post-disturbance surveys, which is the case in this study. However, there were many other larger species recorded during this study most of which can live for years to decades (Choat & Axe 1996; Doherty & Fowler 1994; Sale et al. 1994). These longer-lived species rely on a recruitment storage effect (Warner & Chesson 1985) to provide a buffer against prolonged periods of recruitment failure. Because of this storage effect the full impact of the 1998 bleaching may take decades to be fully realized.

Despite the damage inflicted on Scott Reef it has shown an ability to respond relatively quickly to positive stimuli, such as returning coral cover. The damselfish *Chrysiptera hemicyanea* and *Dascyllus aruanus* both recruit and reside in live coral and both these species' populations collapsed after the bleaching in 1998. However, by 2003 both species had begun to return with *D. aruanus* in particular recruiting in large numbers (Fig. 4.4). Small but significant increases in coral cover were enough to provide sufficient habitat for recruitment. Given the isolation of Scott Reef it seems likely that these recruits were derived from remnant breeding adults on the reef. Hence this reef system has been able to survive the bleaching and begin a process of recovery.

Although many reefs suffered extreme damage from the 1998 bleaching event there is evidence to suggest that many of the "true" coral reef systems are recovering. What these reefs have in common is extensive growth of corals below 40 meters depth, and reduced levels of the anthropogenic stresses that affect so many other reef systems of the world. I include the Chagos Archipelago (Sheppard et al. 2008), Aldabra atoll and more generally the southern Seychelles (Downing et al. 2005), the Maldives (Bianchi et al. 2006; Lasagna et al. 2008), Lakshadweeps (Arthur et al. 2006; Wallace et al. 2007) and the Great Barrier Reef (Diaz-Pulido et al. 2009; Maynard et al. 2008a). These reef communities are large enough to survive individual disturbance events with enough resources intact to begin the process of recovery. The underlying structural complexity of true coral reefs and the inherent patchiness of disturbance effects results in potential buffer zones from the effects of bleaching. Complex reef structures create complex water flow patterns (Chamberlain & Graus 1975) which may prevent pockets of reef being inundated with warm water during a bleaching episode. Small amounts of coral surviving in these pockets can provide a source for replenishment in the future. Moreover, many fish species may be able to survive prolonged periods of less-than-ideal conditions (e.g sub-lethal stress Pratchett et al. (2004)) within these heterogeneous reef areas until coral cover returns.

Chapter 5: Patterns of recovery in catastrophically disturbed reef fish assemblages

Halford, Andrew R. & Perret, Johan (2009) Patterns of recovery in catastrophically disturbed reef fish assemblages. *Marine Ecology Progress Series* 383: 261-272

Abstract

Direct and lethal natural disturbances to coral reef fish assemblages are rare, as their mobility usually allows for rapid migration away from such events. However, in 1989 and again in 2002, coral spawn ‘slicks’ off Coral Bay in Western Australia, caused many reef organisms to be asphyxiated, resulting in catastrophic mortality. A survey in 2002 revealed significant recovery of hard corals within the area disturbed in 1989 (6 % to 32%) but little recovery of the fish assemblages with their structure being highly skewed towards herbivorous species. The lack of recovery in the fish assemblages was unexpected for two reasons: (1) the existence of healthy fish populations in adjacent areas and (2) the well-known positive association between many species of reef fish and their benthic habitat. We identified a combination of minimal recruitment to the disturbed area of the bay and a significantly different coral community structure to be likely causes of the prolonged recovery process. Although just as lethal to the reef community, the 2002 disturbance was significantly smaller and patchy in its extent. In contrast to the 1989 event, the overall effects of this smaller disturbance were positive with species richness and abundance of fish increasing during the weeks after the event, primarily via migration from nearby areas of reef. Together, these results demonstrate the importance of scale when defining disturbance outcomes on coral reefs and highlight the significant role that ‘local’ factors can play in mediating outcomes from disturbance. This type of information is especially pertinent to reef managers trying to formulate effective plans for conservation of their local reef systems.

Introduction

The roles of a range of natural disturbances in influencing coral reef community dynamics have been extensively investigated e.g. storms (Done 1992, Dollar and Tribble 1993, Cheal et al. 2002, Halford et al. 2004), crown-of-thorns starfish infestations (Chesser 1969; Colgan 1987; Hart & Klumpp 1996; Lourey et al. 2000) and bleaching (Berkelmans and Oliver 1999; Aronson et al. 2000; Berkelmans et al. 2004; Graham et al. 2006). All of these disturbances impact coral communities directly but their effects on fish communities are mostly indirect. There have been some direct effects on fish assemblages through intense storms (Lassig 1983; Walsh 1983), cold temperatures (Bohnsack 1983) and phytoplankton blooms (Abram et al. 2003), but they remain for the most part, a rare occurrence on coral reefs.

A recent study however, documented the recovery of reef fish assemblages at Mururoa Atoll after underground nuclear testing (Planes et al. 2005). While the benthic habitat appeared undisturbed by the detonations, the fish assemblages were severely impacted, with multiple, instantaneous removal of fish over areas of approximately 12.5 km^2 (Planes et al. 2005). The fish community displayed remarkable resilience by recovering to a similar structure within 1-5 years of the tests (Planes et al. 2005). A similar outcome of rapid and deterministic recovery by fish assemblages from direct and catastrophic disturbance was also recorded by Syms and Jones (2000), although at a much smaller scale. After completely removing resident fish assemblages from otherwise undisturbed small patch reefs, they observed recovery of fish assemblages to their pre-removal structure within 3 months.

Both of these studies concluded that the deterministic nature of the recovery was mediated by the unchanged structure of the resident benthic communities and the ‘health’ of the greater area surrounding the disturbed zones. However, what happens if the benthic communities are also destroyed? In 1989 severe weather removed up to 95% of the benthic communities from the NE flanks of reefs at the southern end of the Great Barrier Reef, yet the benthos recovered to become similar to what existed previously with the fish assemblages then responding similarly (Halford et al. 2004). In contrast Berumen and Pratchett (2006) found that although the abundance of corals and butterflyfishes on their study sites on Tiahura Reef, Tahiti had recovered from numerous disturbances, the species composition of both the benthic and fish assemblages was very different to what was recorded previously.

A number of studies have identified the underlying rugosity of reef habitat rather than just coral *per se* as a major structuring force in fish communities (Lewis 1997; Ault and Johnson 1998; Jones and Syms 1998; Syms and Jones 2000). Lewis (1997), for example, found that coral cover had no effect on patch reef-specific patterns of relative abundance in the resident fish communities he was studying and concluded that the underlying heterogeneity of the hard substrata at each patch reef was affecting the composition of the fish communities independent of variations in coral cover. Hence recovery of a fish community is also likely when coral cover has been significantly reduced but structural complexity remains, such as after a bleaching or crown-of-thorns disturbance, or in this case after coral mortality through anoxia.

In March 1989 an unusual disturbance occurred within a small bay situated on the north-west coast of Australia (Fig. 5.1a). Corals within this bay spawned under anomalously benign conditions, effectively restricting the dispersal of the subsequent ‘slicks’ of coral spawn out of the immediate area (Simpson et al. 1993). Oxygen levels fell precipitously, resulting in a major proportion of the coral reef community within the

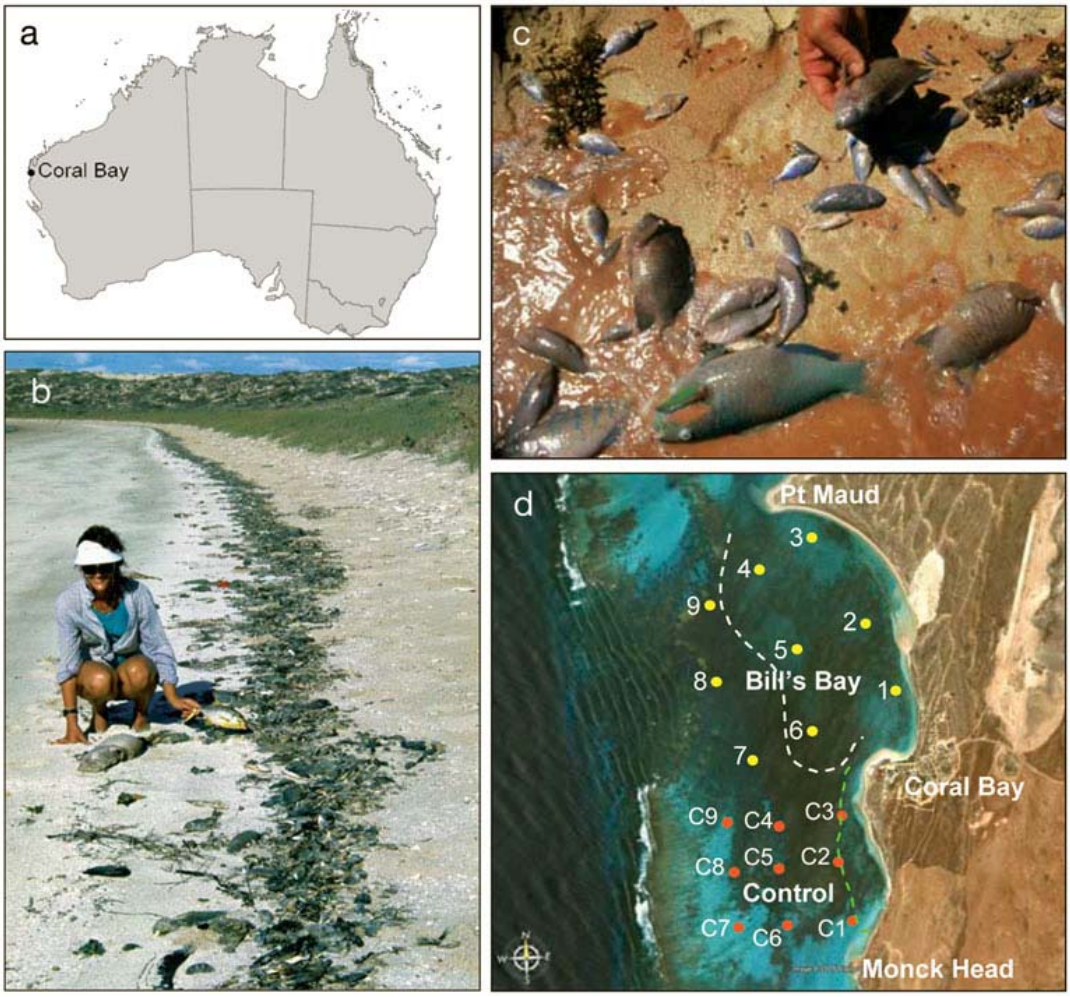


Fig. 5.1 (a) Location map of Coral Bay, Western Australia (b) Decomposing remains of fish and other organisms from the March 1989 coral spawning event in Bill's Bay. (c) Recently killed fish from the April 2002 coral spawning event in the inner Control Bay. The fish are parrotfishes and damselfishes. The reddish scum is coral spawn, with its colour indicative of how recent the mortality event was at the time the picture was taken. (d) The position of the survey sites within Bill's Bay and the Control Bay - the dashed lines indicate the outer extent of mortality caused by the two disturbances. The numbering of the survey sites in the Control Bay is the same as shown for Bill's Bay

inner half of the bay, being killed (Simpson et al. 1993). Over one million fish representing at least eighty species were washed up on the beach (Fig. 5.1b), with a similar number of dead fish remaining in the water (Simpson et al. 1993; Simpson pers.

Comm.). Hard corals were also devastated, with cover decreasing from 42.9% to 9.4% in the affected area (Simpson et al. 1993). The first post-disturbance survey of fish and coral was completed in 1995 and highlighted the extent of the disturbance and its continued effects six years later (Halford 1997). In April 2002 another similar disturbance event was recorded in an adjacent bay (herein called the Control). Although much smaller in spatial extent the immediate effects of this later disturbance were similar (Fig. 5.1c) with extensive coral and fish mortality within the affected area. This is the first study to report on the effects of simultaneous mortality to corals and fish and as such offers insights into fish-habitat relationships from a rarely seen perspective.

We report here on the progress of recovery from the 1989 disturbance in Bill's bay since 1997 and on the short-term effects of the 2002 disturbance in the Control bay. Previous work on fish-habitat relationships allows some predictions to be tested regarding the likely outcomes of the recovery process within Bill's bay. Although extensive mortality occurred in both the fish and benthic communities we predict that with the prevalence of healthy reef communities immediately adjacent to the disturbed areas, and with the skeletons of dead corals remaining largely intact within the very sheltered bay, recovery of the benthic and fish communities is likely. However, given the simultaneous demise of fish and live coral this recovery may be slower than expected. Whether the fish assemblages can recover their former structure will depend on the degree to which the benthic communities also recover their pre-disturbance structure. In the absence of any other major disturbances ten years is a median time-frame noted for recovery from natural disturbances (Connell 1997, Sano 2000, Halford et al. 2004, Downing et al. 2005).

Methods

Study Area

The area where this study was undertaken lies within the Ningaloo Reef Marine Park on the central coast of Western Australia (Fig. 5.1a). Ningaloo Reef is a contiguous, fringing reef, ~ 280 km long, with a shallow lagoon (mean depth at AHD is ~ 2 m) ranging in width from 0.5 to 6 km (Simpson et al. 1993). The study area consists of two adjacent bays that share a relatively contiguous coral reef community overlooked by the small township of Coral Bay. The northern most bay, Bill’s Bay, is approximately 2.5 km wide and 5 km long, being bounded by Point Maud in the north and the township at the southern end (Fig. 5.1d). This bay was severely impacted by entrained coral spawn slicks in March 1989 (Simpson et al. 1993). The second bay to the south is smaller than Bill’s Bay at 3 km wide and 2.5 km long, being bounded by the Coral Bay township to the north and Monck Head in the south.

Survey Design

A fish and habitat survey of Ningaloo Marine Park, two years before the initial disturbance by coral spawn slicks, indicated that Coral Bay was the most outstanding area within the Ningaloo Marine Park with respect to the cover of its hard coral communities (Ayling & Ayling 1987). This was still the case at the time of initiating this study and hence the reason why the bay directly adjacent to Bill’s Bay, was chosen as a comparable site for this study. We recognise that it was not ideal, but it nevertheless provided a comparison of temporal change in a section of undisturbed reef with levels of hard coral cover that were not to be found elsewhere at Ningaloo Reef.

The design for this study was outlined in detail in Halford (1997). Briefly, nine sites were established within Bill’s Bay and the adjacent bay to the south (herein called Control) (Fig. 5.1d) and 3 x 50 m transects located within each site, running parallel to the shore and separated from each other by 30-50 m. Benthic cover on each transect was recorded using a video camera following the standard operating procedure of Page et al. (2001) and the footage analysed in the laboratory using the point sampling technique of Carleton and Done (1995). Abundances of selected fish species were estimated by visual census following the standard operating procedure of Halford and Thompson (1994). On the first pass of a transect the relatively large and mobile fish species from the Acanthuridae (surgeonfishes), Chaetodontidae (butterflyfishes), Labridae (wrasses), Lethrinidae (emperors), Lutjanidae (snappers), Serranidae (groupers), Scaridae (parrotfishes), Siganidae (rabbitfishes), and Zanclidae were counted along a five meter wide corridor. On a return pass along the same transect, the smaller, site attached species from the family Pomacentridae (damselfishes) were counted along a one meter corridor.

Our initial survey was carried out in May 1995 and the results compared to Simpson et al. (1993) to monitor the rates of recovery in the ensuing years since 1989 (Halford 1997). Apart from the dead fish on the beach there was no quantitative data available on the fish assemblages within Bill's Bay prior to 1989; hence changes in the fish assemblage structure in Bill's Bay were assessed relative to the fish assemblages observed in the adjacent Control bay. A second survey of the fish and coral assemblages in both bays was completed in May 2002, allowing for a more rigorous assessment of changes in the fish assemblages since 1995. This survey was only a few weeks after the second, smaller disturbance event in the Control bay. These results are reported in detail here. Due to time constraints not all sites surveyed in 1995 could be re-surveyed in 2002. Effort was therefore concentrated in the inner bay sites where the impacts from both disturbances were most pronounced. Hence in 1995 all 18 sites were surveyed while in 2002 only sites 1-3, 4, 6, 7 and 9 were surveyed in both bays.

Data Analyses

Spatio-temporal changes in fish at the assemblage level were investigated using hierarchical clustering and non-metric multidimensional scaling (NMDS). Prior to analysis, fish abundance was summed across transects for all site x year combinations and then converted to a common density (nos. per 150m^2), a necessity because of the two transect widths used to count fish. Clustering and NMDS ordination was performed on a matrix of Bray-Curtis similarities calculated between all site x year combinations, from a data matrix of ln (x + 1) transformed counts of 44 fish species. This transformation reduces the dominance of the most abundant species, allowing rarer species to have a greater influence in the analysis. Exploratory analysis of the dataset using the BVSTEP procedure in PRIMER (Clarke & Warwick 2005) revealed eight species were providing the bulk of the structure in the data. These species were subsequently plotted as vectors on the NMDS ordination to indicate their contributions to the overall patterns. Species scores were calculated as weighted correlations between the original species vectors and the first two NMDS ordination axes (see Legendre and Gallagher (2001) pg 278 for calculation details).

A Linear Mixed Effects (LME) Model was used to test for disturbance effects on hard coral cover, fish species richness and abundance between 1995 and 2002. These models offer a useful alternative to standard linear models because the data are permitted to exhibit correlation and non-constant variability. By providing the flexibility to model not only the means of the data but also their variances and covariances, unbalanced and/or missing data, or data collected at different times, can all be accommodated (Lindstrom & Bates 1990). Only those species with a percentage occurrence of >10% across all 96, site x time combinations were considered for the LME analysis, with one exception *Stegastes lividus*, which was included because it was very common at a few sites. To stabilise variances and ensure normality of the residuals all abundances were either square root or natural log transformed prior to application of the LME model. Those species whose residuals remained highly non-normal even after transformation were discarded from any further investigation.

The LME model was fixed with respect to TREATMENT (Control Bay or Bill's Bay), LOCATION (Inner, Mid or Outer part of each Bay), and YEAR (1995 or 2002). YEAR was not considered a repeat effect due to the seven year gap between surveys. SITES and TRANSECTS were treated as random effects. Comparisons of Estimated Means were used to test for significant differences in individual factors and their interactions. Bonferroni corrections were applied to all comparisons to decrease the chances of Type I errors when multiple comparisons are made.

Hard coral cover from the surveys was input to a contouring and surface mapping program (Surfer -Golden Software Inc., CO, USA), to illustrate the spatio-temporal dynamics of coral recovery at Bill's Bay and the Control Bay. In combination with the Linear Mixed Model analysis this map provides an easily interpretable picture of the changes in hard coral abundance between 1995 and 2002.

Results

Hard Corals

Immediately prior to the major disturbance in March 1989, hard coral cover averaged ~ 42 % throughout Bills Bay (Simpson et al. 1993). As a result of the disturbance coral cover declined to ~ 5 % within the inner and middle parts of the bay, while remaining undisturbed in the outer part of the bay. Six years later in 1995, when this study was initiated, hard coral cover at the inner and middle sites within Bill's Bay, had shown little recovery, averaging 6.4 % (Halford 1997). However, between 1995 and 2002 hard coral cover approached pre-1989 levels having increased fivefold to ~ 32 %, within the impacted area of Bill's Bay (Fig. 5.2a). In the outer part of Bill's Bay coral cover had increased to ~ 62 %, an increase of 20 % compared to pre-impact levels.

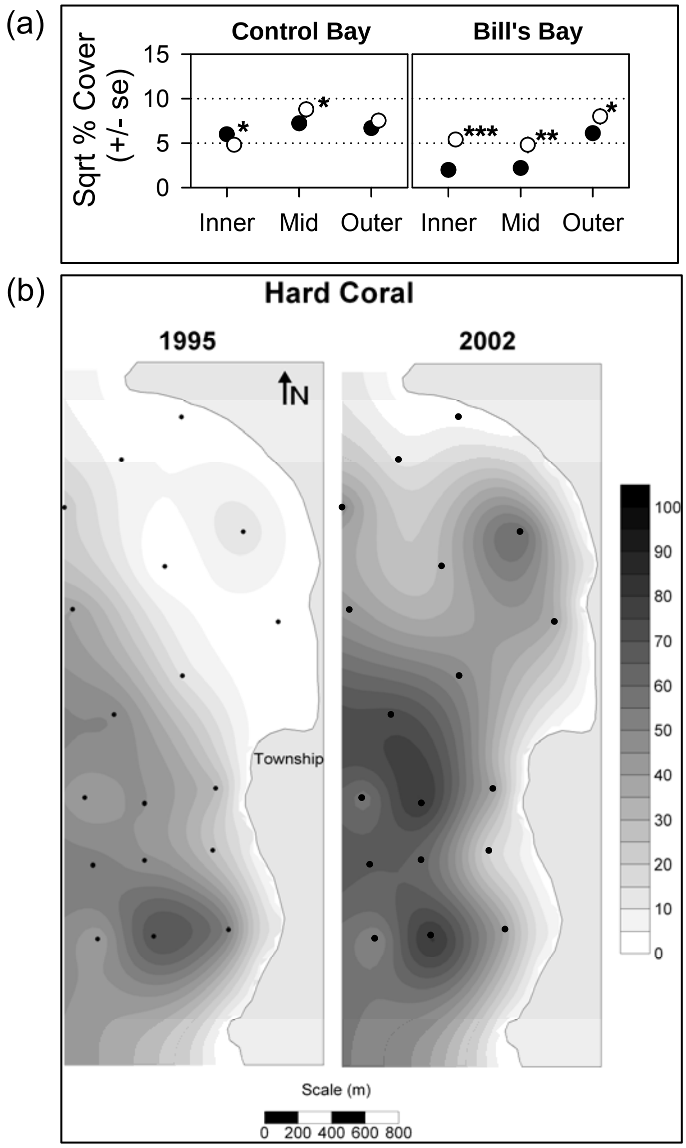


Fig. 5.2 (a) Hard coral cover by Treatment and Location, as estimated by the Linear Mixed Effects model. If transformation was necessary for the LME model analysis then transformed data was plotted. Significant differences between years for any given Treatment x Location are indicated thus * p<0.05, ** p<0.001, *** p<0.0001; ● 1995; ○ 2002 (b) Spatial contour plots of hard coral cover within the Control bay and BILL's bay, for 1995 and 2002. The shading scale represents the percentage cover of hard coral. The dots indicate the positions of the survey sites within each bay.

While total hard coral cover was returning to pre-impact levels, hard coral community structure had not. Faviids were dominant at many sites where previously Acropora was. However, recovery trajectories at most sites indicate that the benthic community is evolving towards its pre-impact condition, as Acropora species regain a foothold (van Schoubroeck & Long 2007). The hard coral community adjacent to Site 1 for example, has recovered its pre-disturbance acropora-dominated structure (van Schoubroeck & Long 2007) .

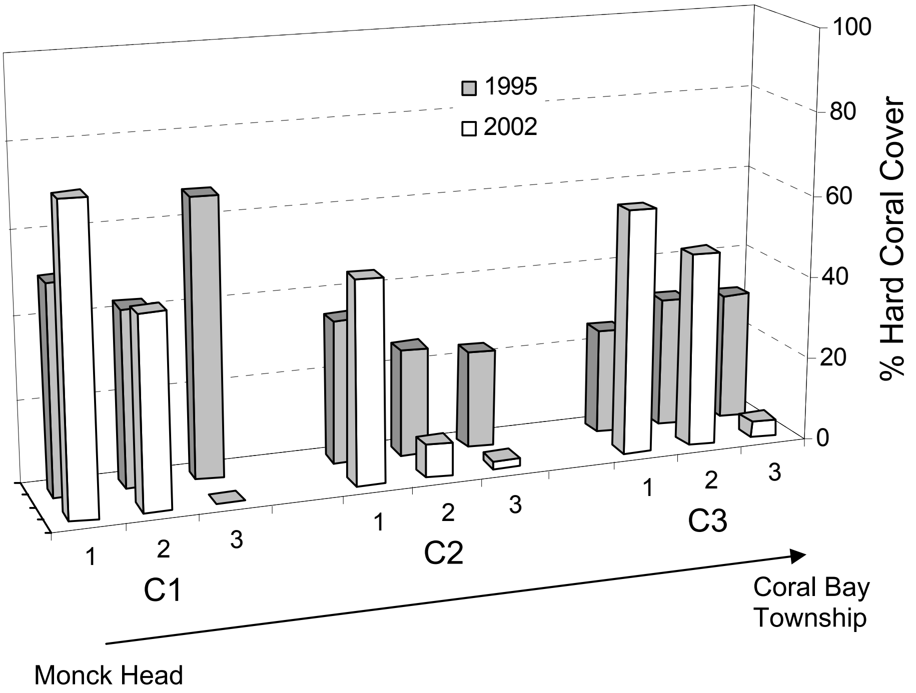


Fig. 5.3 Change in hard coral cover between 1995 and 2002, on the nine transects constituting the INNER Location within the Control bay (see methods for more details). The spatially patchy mortality effects of the 2002 coral spawn disturbance are evident.

In contrast to the Bill's Bay hard coral community, coral cover averaged ~ 45 % throughout the Control sites in 1995, increasing slightly at the middle and outer sites by

2002. As a result of the spawning disturbance in April 2002, there was however, a small decline in hard coral cover at the inner Control sites, from 36.8 % to 32 %, which was marginally insignificant at $p = 0.053$ (Fig. 5.2a). This decline was most pronounced at the middle inner Control site C2 (Fig. 5.2b). Although coral mortality following the second disturbance in 2002 was as high as 100% in some areas (e.g. Fig. 5.3 - Site C1, Transect 3,) the overall impact was patchy with only four of the nine transects significantly impacted (Fig. 5.3).

Fish Assemblages

There was little quantitative information available on the changes in the fish assemblages at Bills Bay after the disturbance in March 1989. Nevertheless, some conclusions could be drawn from the composition of the dead fish in the water and washed up on the beach (Fig. 5.1b). The damselfish, *Pomacentrus coelestis* and the parrotfish *Scarus schlegeli* constituted ~ 45% of the > 1 million dead fish on the beach (Halford 1997) and were also a significant part of the dead fish assemblage still in the water (Simpson pers. comm.). This is circumstantial evidence of the relative dominance of these species within the pre-impact fish assemblage residing within the mid- and inner parts of Bills Bay. Additionally, A Ningaloo-wide study of fish abundance conducted two years before the disturbance indicated *S. schlegeli* to be the most abundant scarid throughout Ningaloo (Ayling & Ayling 1987). In 1995 *S. schlegeli* was a dominant member of the fish assemblage and remained so in 2002. However, numbers of *P. coelestis* have never recovered, with only a few individuals seen in 1995 and 2002 (Table 5.1).

The major pattern in the fish assemblages, as identified by clustering and NMDS ordination, was the separation of sites impacted by coral spawn from all other

Table 5.1 Relative abundance (%), by Treatment and Year, for all species within the families Acanthuridae, Chaetodontidae, Scaridae and Pomacentridae

FAMILY	Control		Impact	
Species	1995	2002	1995	2002
ACANTHURIDAE				
Acanthurus dussumieri	0.0	1.9	1.5	0.9
A. grammoptilus	11.1	5.0	4.6	5.4
A. nigrofuscus	11.1	2.5	13.8	5.9
A. triostegus	66.7	82.5	72.3	84.2
Ctenochaetus striatus	0.0	3.8	3.1	0.0
Naso unicornus	0.0	3.1	1.5	0.5
Zebrasoma scopas	0.0	1.3	3.1	2.7
Z. veliferum	11.1	0.0	0.0	0.5
Total Abundance	**18**	**160**	**65**	**222**
CHAETODONTIDAE				
Chaetodon aureofasciatus	6.6	4.9	3.6	4.4
C. assarius	4.9	0.8	3.6	0.0
C. auriga	9.0	14.6	2.4	9.7
C. citrinellus	0.0	0.8	0.0	0.0
C. lineolatus	3.3	1.2	0.0	0.0
C. lunula	2.5	2.4	1.2	2.7
C. plebius	59.8	49.8	70.2	65.5
C. speculum	2.5	0.8	0.0	0.0
C. trifascialis	10.7	23.1	2.4	0.0
C. trifasciatus	0.8	1.2	16.7	15.9
C. unimaculatus	0.0	0.0	0.0	0.9
Chelmon marginalis	0.0	0.4	0.0	0.9
Total Abundance	**122**	**247**	**84**	**113**
POMACENTRIDAE				
Cheiloprion labiatus	0.8	0.6	0.6	0.0
Chromis atripectoralis	21.9	12.7	15.9	27.7
Dascyllus aruanus	29.8	29.1	11.6	12.9
D. reticulatus	0.2	0.3	0.3	0.0
D. trimaculatus	0.5	0.4	0.0	0.0
Dischistodus spp.	0.5	0.3	1.2	0.4
Neoglyphidodon melas	0.9	4.5	0.0	0.6
Plectroglyphidodon johnstonianus	0.0	0.1	0.0	0.0
P. lacrymatus	11.8	10.3	14.1	13.9
Pomacentrus coelestis	0.8	0.1	3.4	0.3
P. moluccensis	18.4	19.4	38.2	34.5
P. nagasakiensis	0.2	0.0	0.0	0.0
P. vaiuli	3.2	1.7	0.6	0.1
Stegastes lividus	4.9	15.1	1.5	5.9
S. nigricans	0.9	2.0	5.8	1.5
S. obreptus	5.4	3.3	6.7	2.2
Total Abundance	**652**	**691**	**327**	**676**
SCARIDAE				
Cetoscarus bicolor	0.2	0.0	0.0	0.0
Hipposcarus longiceps	1.5	1.3	1.1	1.5
Scarus chameleon	1.5	0.5	1.2	0.8
S. frenatus	1.7	1.7	0.7	0.3

S. ghobban	9.2	4.7	4.0	2.4
S. microrhinos	8.6	3.6	0.6	0.9
S. oviceps	0.0	0.4	0.0	0.0
S. prasiognathus	1.7	3.9	0.2	1.0
S. psittacus	0.0	0.4	0.0	0.0
S. rivulatus	3.9	4.4	2.8	2.3
S. schlegeli	41.9	51.1	65.1	58.5
S. sordidus	29.7	28.0	24.1	32.2
Total Abundance	**465**	**1116**	**964**	**1301**

sites (Figs. 5.4 & 5.5). Four main groups were identified, separating out from right to left on the first NMDS ordination axis, along a gradient of increasing disturbance intensity. The most “disturbed” group contained the three innermost sites in Bill’s Bay, which clustered together across years (Fig. 5.4) indicating minimal change in the inner Bill’s Bay fish assemblages through time, relative to the other groupings. Sites five and six from the middle part of Bill’s Bay also clustered together across years. Although Site 4 in Bill’s Bay was within the disturbed zone in 1989 it does not have relatively depauperate fish assemblages, grouping as it does with other un-impacted sites. In addition to those sites impacted by the much larger disturbance in 1989 there was also a clear change in the structure of the fish assemblages associated with the inner Control sites C2 and C3 which is where the 2002 disturbance impacted (Figs. 5.4 & 5.5). The NMDS biplot of the eight most influential species highlights the fact that impacted sites are different because their assemblages are depauperate in most species relative to the other sites. The two parrotfish *S. schlegeli and S. sordidus*, are the dominant components of the disturbed fish assemblages (Fig. 5.5, Table 5.1).

In 2002 the fish assemblages on the inner and mid Bill’s Bay sites remained characterised by significantly lower species richness than all other sites in either Bill’s Bay or the Control Bay (Table 2; Fig. 5.6). When total species richness was partitioned by family it can be seen that this was primarily due to the paucity of damselfish species (Table 5.1; Fig. 5.6). The only fish species inhabiting this part of the bay in large

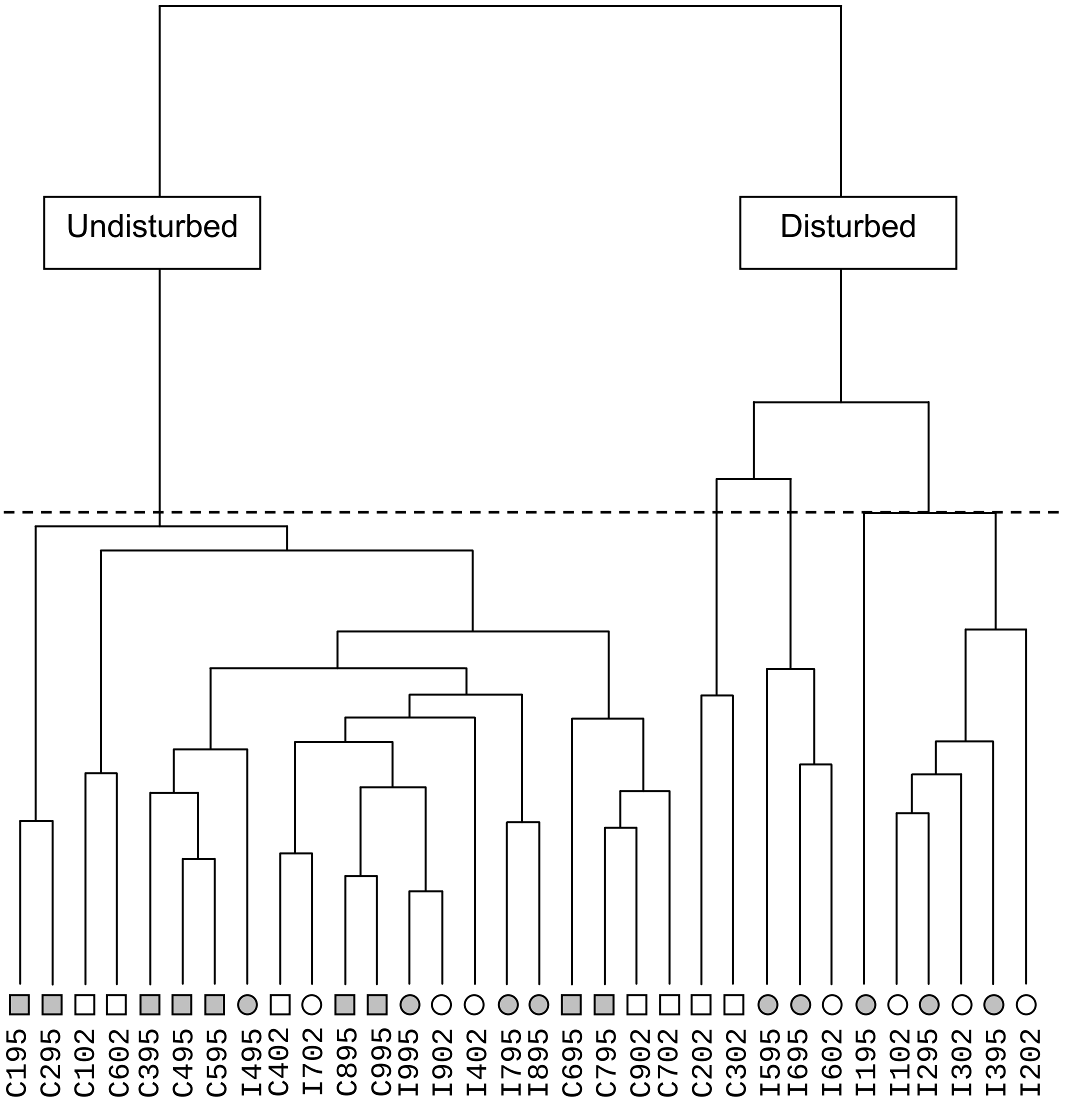


Fig. 5.4 Dendrogram illustrating the spatio-temporal relationships between the fish assemblages recorded at each site in 1995 and 2002. The abundance data matrix of 44 fish species was ln (x+1) transformed prior to calculation of Bray-Curtis similarities. Clustering was performed using UPGMA. The horizontal dashed line indicates four main groupings at 55% similarity. Coloured symbols allow for easier comparison with the ordination of Fig. 5.5

numbers relative to the other sites were the parrotfishes *Scarus schlegeli* and *S. sordidus*, and the surgeonfish *Acanthurus triostegus.*(Table 5.1; Fig. 5.7). While coral-associated species were poorly represented within the impacted area of Bill’s Bay this was not the case at the undisturbed outer sites where the most common coral-associated pomacentrids, i.e. *Chromis atripectoralis*, *Dascyllus aruanus and Pomacentrus moluccensis* all increased in abundance between 1995 and 2002 (Table 5.2; Fig. 5.7).

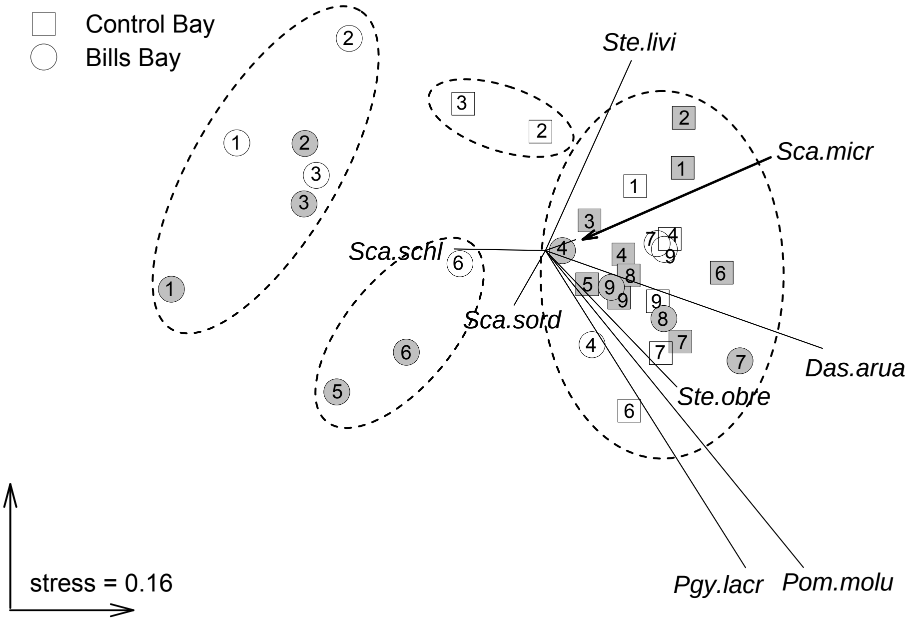


Fig. 5.5 Non-metric Multidimensional Scaling ordination of all Site x Year combinations. The similarity matrix underlying the analysis was the same one used for clustering. The four main groupings identified from the dendrogram are encircled. Biplots of the eight fish species most responsible for the observed patterns are superimposed – species were identified through the SIMPER routine in PRIMER (see methods for more detail). Das.arua – *Dascyllus aruanus*, Pgy.lacr – *Plectroglyphidodon lacrymatus*, Pom.molu – *Pomacentrus moluccensis*, Sca.micr – *Scarus microrhinos*, Sca.schl – *Scarus schlegeli*, Sca.sord – *Scarus sordidus*, Ste.livi – *Stegastes lividus*, Ste.obre – *Stegastes obreptus*. Symbol colours follow that of Fig. 5.4. Numbers 1-9 represent site locations as identified in Fig. 5.1b

In contrast to the persistent and negative changes on the impacted sites in Bill's Bay, species richness actually increased at the more recently impacted inner Control

Bay sites (Fig. 5.6). This was a pattern also manifested at the other undisturbed locations

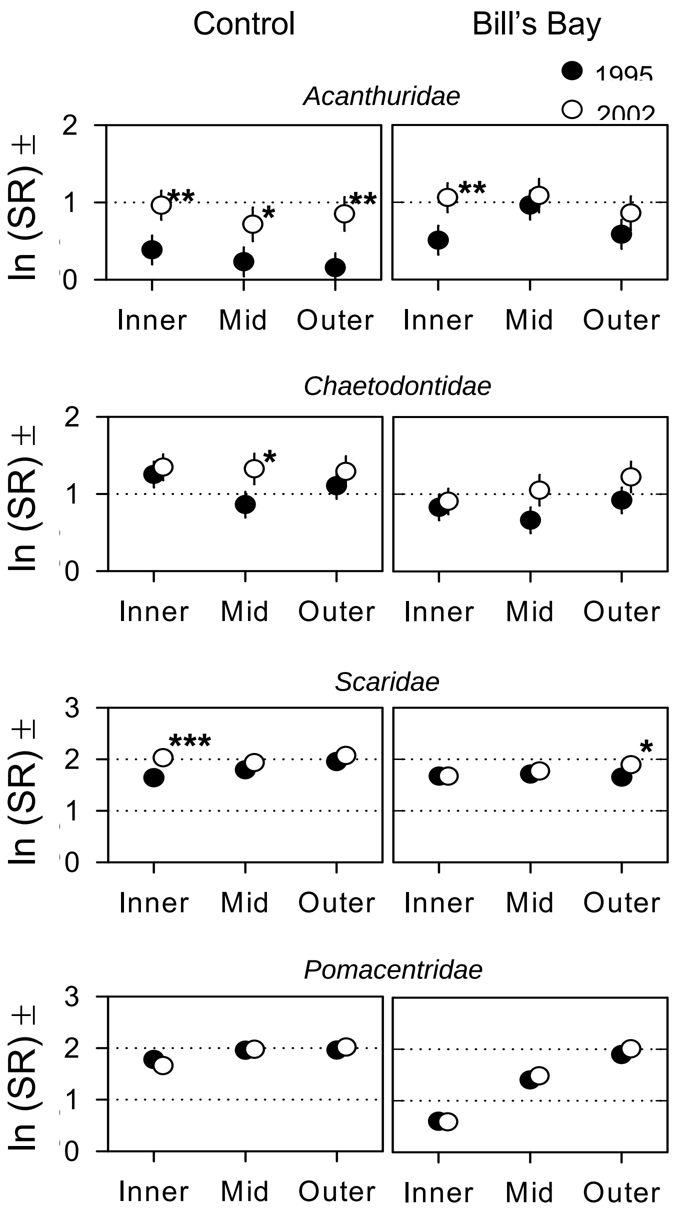


Fig. 5.6 Species richness of the families Acanthuridae, Chaetodontidae, Scaridae and Pomacentridae by Treatment and Location, as estimated by the Linear Mixed Effects Model. Legend is same as described in Fig. 5.2a

(Fig. 5.6; Table 5.1). Nevertheless, there were still significant decreases in the abundance of the coral associated damselfish *Dascyllus aruanu*s and *Pomacentrus moluccensis* within the inner Control Bay sites (Fig. 5.7; Table 5.2). While some of the coral associated fishes declined at the inner Control sites, some species that consume epilithic algae, such as *Scarus schlegeli*, *S. sordidus* and *Stegastes lividus* (damselfish) all increased in abundance as a result of the disturbance (Fig.5.7). For the scarid species, the scale of the increases in abundance at the inner Control Bay sites was not seen at any of the other sites. There was however a large increase in *S. lividus* numbers at the outer Bill's Bay sites which was even greater than the increase seen on the disturbed inner Control Bay sites (Table 5.1; Fig. 5.7)

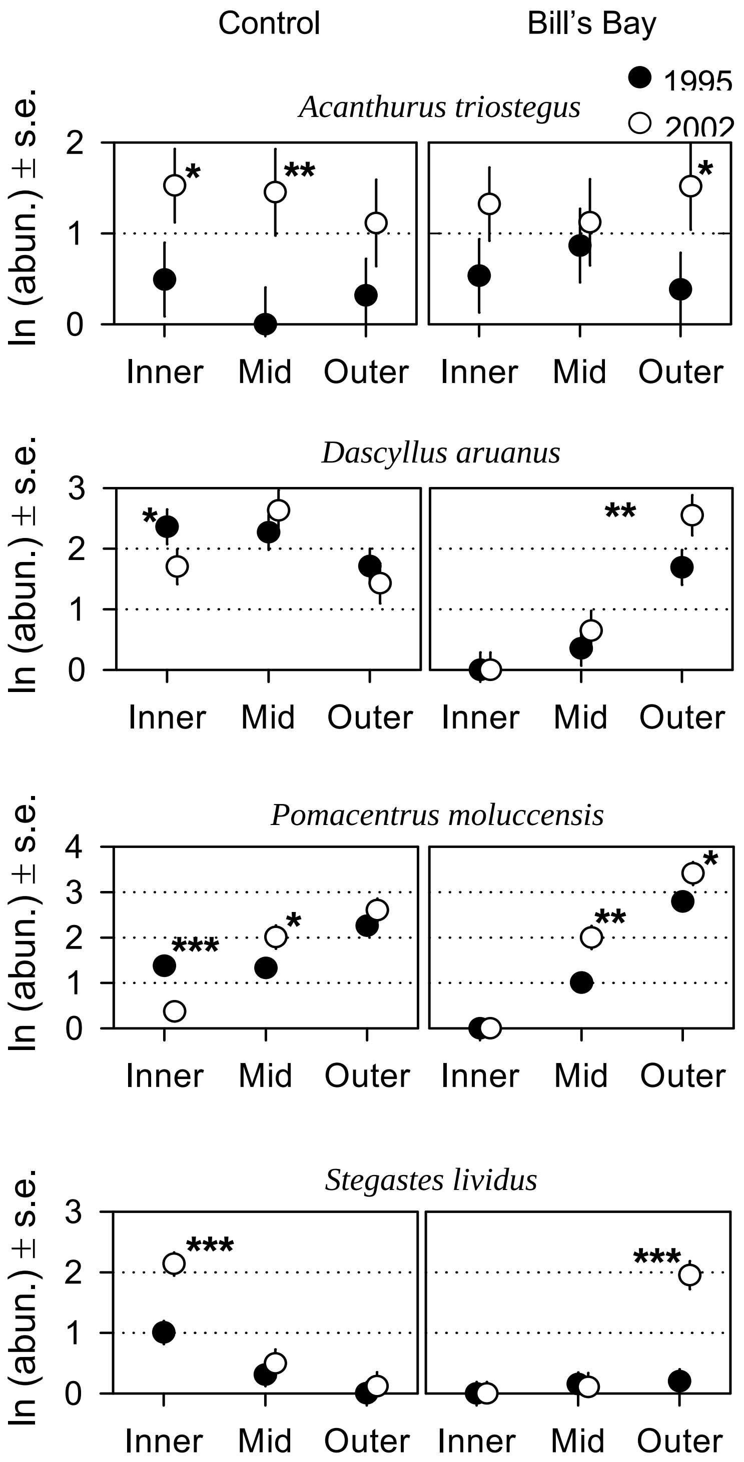
Discussion

Although there are ample studies documenting the effects of intense disturbances on coral reef communities e.g. (Aronson et al. 2000b; Chesser 1969; Harmelin-Vivien 1994), the nature of the 1989 and 2002 disturbances at Coral Bay nevertheless stand out. The direct removal of significant fish numbers, along with their [live coral] habitat, was an unusual and destructive event. Mobile organisms, such as fish, usually escape direct disturbance effects either by taking shelter elsewhere, as in the case of storms e.g. (Harmelin-Vivien 1994; Walsh 1983) or because they are not actually targeted; such as by bleaching e.g. (Berkelmans & Oliver 1999) or Crown-of-thorns starfish infestations e.g. (Chesser 1969). However, the atypical nature of the disturbance described here, provided an opportunity to investigate relationships between fish and their habitat, from a perspective not usually possible.

Coral recovery in Bill's Bay was negligible between 1989 and 1995; however, by 2002 percent cover had almost returned to pre-disturbance levels. The time-frame of this recovery is consistent with a number of other studies on disturbed coral assemblages (Colgan 1987) . Branching and tabulate coral species from the Acroporidae family dominated both Bill's Bay and the Control area prior to 1989. It was therefore not surprising that this coral family suffered most during the 1989 disturbance, with

Table 5.2 Results of the Linear Mixed Modelling for the dependent variables of Hard Coral, Species Richness and Abundance of the 4 main fish families, and Abundance of selected species. Significant results are indicated by ***** p<0.05, ****** p<0.001, ******* p<0.0001 Planned comparisons were made between years for each Treatment x Location combination with significant results annotated to the relevant graphics.

Dependent Variables	T'ment	Loc'n		Year			
	T	L	T*L	Y	T*Y	L*Y	T*L*Y
Hard Coral	**	*	*	***	***	ns	*
Species Richness							
Acanthuridae	*	ns	ns	***	ns	ns	ns
Chaetodontidae	*	ns	ns	**	ns	ns	ns
Scaridae	**	ns	ns	***	ns	ns	*
Pomacentridae	***	***	**	ns	ns	ns	ns
Abundance							
Acanthuridae	ns	ns	ns	***	ns	ns	ns
Chaetodontidae	ns	ns	ns	***	ns	*	ns
Scaridae	ns	ns	ns	**	**	*	*
Pomacentridae	**	***	**	**	**	ns	ns
Species							
Acanthurus triostegus (A)	ns	ns	ns	***	ns	ns	ns
Chaetodon auriga (C)	ns	ns	ns	***	ns	ns	ns
C. plebius (C)	ns	ns	ns	*	ns	**	ns
C. trifascilais (C)	*	ns	ns	*	**	ns	ns
Epibulus insidiator (L)	ns	***	ns	ns	ns	ns	ns
Hemigymnus melapterus (L)	*	ns	ns	ns	ns	ns	ns
Scarus ghobban (S)	ns	*	ns	ns	ns	ns	ns
S. microrhinos (S)	**	ns	ns	ns	ns	*	**
S. schlegeli (S)	*	*	ns	ns	**	*	ns
S. sordidius (S)	*	ns	ns	***	ns	ns	ns
Chromis atripectoralis (P)	ns	ns	ns	ns	*	ns	ns
Dascyllus aruanus (P)	***	*	**	ns	**	*	ns
Plectroglyphidodon lacrymatus (P)	ns	***	ns	ns	ns	ns	ns
Pomacentrus moluccensis (P)	ns	***	**	ns	**	***	ns
Stegastes lividus (P)	**	*	***	***	ns	*	***
S. obreptus (P)	**	***	ns	ns	ns	ns	ns


Control
Bill's Bay
● 1995
○ 2002
Acanthurus triostegus
ln (abun.) ± s.e.
0
1
2
*
**
*
Inner
Mid
Outer
Inner
Mid
Outer
Dascyllus aruanus
ln (abun.) ± s.e.
0
1
2
3
*
**
Inner
Mid
Outer
Inner
Mid
Outer
Pomacentrus moluccensis
ln (abun.) ± s.e.
0
1
2
3
4
***
*
**
*
Inner
Mid
Outer
Inner
Mid
Outer
Stegastes lividus
ln (abun.) ± s.e.
0
1
2
3
***
***
Inner
Mid
Outer
Inner
Mid
Outer

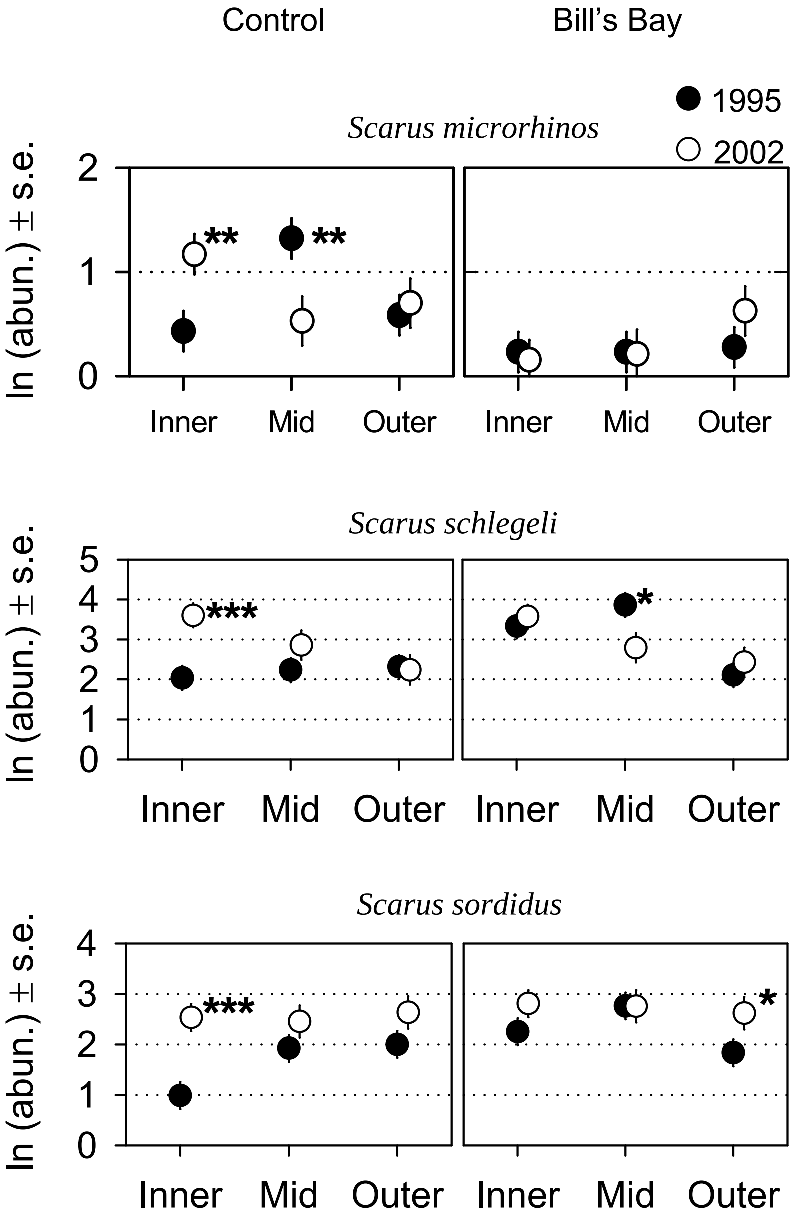


Fig. 5.7 (a) Abundance of fish species by Treatment and Location, as estimated by the Linear Mixed Effects model. Legend is the same as described in Fig. 2a. Only those species showing significant disturbance effects were plotted.

mortality of ~ 83% (Simpson et al. 1993). This was also the case during the 2002 disturbance when qualitative assessments of mortality indicated it was almost exclusively branching and tabulate acroporids that were affected (Halford, pers. obs.).

While the recovering coral communities were dominated by Faviids in 2002, the characteristics of high fecundity, rapid growth and competitive dominance (Stimson 1985; Baird and Hughes 2000) are enabling acroporid corals to regain their pre-eminence; albeit slowly. A recent report focussing on the recovery of coral communities within Bills Bay has demonstrated that at least one site within the inner part of Bill’s Bay has recovered its pre-impact community structure and that most sites within the affected area are all showing recovery trajectories heading in the same direction, i.e. towards a re-establishment of acropora dominance (van Schoubroeck and Long 2007).

While hard coral assemblages were recovering well within the previously impacted part of Bills Bay, this was not the case with the fish assemblages. Species diversity remained low with only a few herbivorous fish species prominent. This was despite ample live coral habitat for locally abundant coral-associated fish such as *Dascyllus aruanus* or *Pomacentrus moluccensis* to either recruit or migrate to, from the surrounding area. There are a number of possible reasons for this. Firstly, recovery of absolute abundance without a parallel recovery of pre-impact benthic community structure can result in different fish assemblage associations e.g. Berumen and Pratchett (2006) and the coral communities are now Faviid rather than Acropora dominated, as was previously the case. Secondly, there is a very shallow (<1m) raised ridge of live and dead coral that effectively bisects the bay parallel to the shore and encloses the middle and inner parts of the bay. Water temperatures can be up to 4^0C cooler on the shoreward side of this ridge indicating reduced water flow within the inner bay (Hearn et al. 1986). Reduced water flow has the potential to negatively affect recruitment of both fish and corals to the affected areas. Thirdly, given that the majority of live coral is adjacent to the reef crests where recruits cross over from the plankton to settle on the reef (Doherty & McIlwain 1996; McIlwain 2003), this is also the area where most coral-associated fish recruits will settle on the benthos. By the time the inner lagoon area is reached, any given patch of fish has already crossed significant amounts of habitat and hence substantial settlement has likely occurred such that very few coral-associated fish remain in the patch (see Lecchini (2005) and Lecchini and Galzin (2005) for a detailed investigation of habitat use strategies by recruiting reef fish).

While the coral associated fish have not returned to the affected areas in any number this is not the case for scarid species. Along with *P. coelestis*, scarid species were the most abundant group of dead fish recorded after the 1989 disturbance (Simpson et al. 1993), yet they have been able to recolonise the inner bay area in large numbers. Conditions within the disturbed area are favourable for these species with high cover of macroalgae; an observed food source for the two most abundant scarids, *S. schlegeli* and *S. sordidius* (A.Halford, pers. obs.) and an optimum habitat for their recruitment (Green 1996). Scarid species are also highly mobile and more likely to move significant distances over the reef in their daily foraging (Chapman & Kramer 2000).

Of all the fish species affected by the disturbance in 1989, it was the neon damselfish *Pomacentrus coelestis* that appears to have suffered most. There has been a complete failure of this species to recolonise the inner bay, where it was once a dominant species. This is despite the abundance of appropriate habitat for them to recruit to - *P. coelestis* settlers prefer disturbed habitat with low coral cover (Doherty et al. 1996) - and evidence of significant recruitment of this species to other parts of Ningaloo reef in previous years (McIlwain 2001; Meekan et al. 2003). There also exists significant numbers of *P. coelestis* within the reef passes adjacent to Coral Bay (pers. obs.). While environmental conditions within the inner bay may retard recruitment the absolute failure of this species to return to the inner bay is highly correlated with the decimation of the previous adult population and hence it is likely that the inner bay population of *P. coelestis* was largely self-seeding. Recovery of this species to the inner bay is uncertain.

Given the time it is taking for the fish assemblages to recover in the inner part of Bills Bay this type of disturbance must be relatively infrequent at the scale of the 1989 event - as evidenced by the 12 year hiatus before the next disturbance of this type occurred, albeit very much smaller in scale. In contrast to Bill's Bay the effects of the 2002 disturbance within the inner part of the Control bay appeared to be mostly positive, with species richness and abundance increasing significantly within the disturbed area. The positive nature of the response was likely a reflection of the smaller scale and patchy nature of the coral mortality which created opportunities without decreasing reef health overall. In addition, the reef surrounding the disturbed area was very healthy with relatively high abundance and diversity of fish, some of which may have been attracted to the recently dead corals which were covered in a dense epilithic turfing algae. This is known to be a preferred food source for some species (Wilson et al. 2006).

The increases in species richness and abundance within the inner Control area were in fact confined to the Acanthuridae and Scaridae families, both of which contain mostly herbivorous species (Randall et al. 1990). There were no significant family-level changes in either the Chaetodontidae or Pomacentridae although there were significant changes in some individual species. Given the timing of our survey, within one month of the 2002 disturbance, and the lack of any other obvious disturbance effects we believe the increase in abundance and diversity of herbivorous fish within the inner Control area must have been due to migration from adjacent areas. This conclusion is supported by a concomitant drop in the abundance of the parrotfish *Scarus schlegeli* and *S. sordidus* from the inner and middle part of Bill's Bay. Scarid species such as these have been found to respond numerically to turfing algae of the type found on newly killed corals (Wilson et al. 2006).

The other dominant species of the post-disturbance fish community in the inner Control bay was *Stegastes lividus*, a territorial, herbivorous damselfish (Allen 1991). Because this species defends a territory it is unlikely to migrate as an adult, hence the increased abundance of this species within the inner Control area was most likely due to a successful recruitment event sometime between 1995 and 2002, independent of the disturbance. This species also increased significantly in outer Bill's Bay where no disturbance has been recorded, reinforcing the likelihood of a recruitment event. Although the staghorn corals which *S. lividus* resides in were dead, their skeletons were still intact and continuing to provide effective shelter for the fish. We expect *S. lividus* numbers will decline as the dead skeletons erode and eventually collapse.

Conclusions

Given the abundance of healthy fish and coral communities surrounding the disturbed area of Bill's Bay we expected recovery of the fish assemblages to be well advanced within 5-10 years of the disturbance; a time frame encapsulating the results of other studies investigating disturbance effects on reef fish e.g. Halford et al (2004), Planes et al (2005) and Sano (2000). We also predicted habitat to be a major mediator of fish assemblage structure during the recovery process, irrespective of whether live coral or structure was the primary catalyst. Surprisingly this has not been the case as the fish assemblages in the inner part of Bill's Bay have remained depauperate of all but a few herbivorous species. While it is difficult to pinpoint what is sustaining the slow recovery of the fish assemblages it is clear that a considerable time period is required for a coral reef community to recover from a disturbance of such magnitude. Regardless of what factors are influencing the recovery a significant recruitment event is most likely necessary before the inner bay fish assemblages can regain some semblance of their pre-impact state. However, the lack of recovery by *Pomacentrus coelestis* indicates such recruitment events are not very common in the inner Bay. In contrast to the enduring and negative effects of the 1989 spawning disturbance, the 2002 disturbance provided a positive stimulus, even though the nature of the disturbance was the same. The nature of the smaller disturbance is akin to gaps opening in the canopy of a rainforest and providing opportunity for others to exploit e.g. Connell (1978). The opposing outcomes from the same type of disturbance confirms the multi-scalar nature of coral reef systems (Sale 1998) and highlights the continued need to acknowledge scale when discussing disturbance effects on coral reefs. Moreover, in the continual search for generality in patterns and processes operating on coral reefs our study provides evidence of the influence that ‘local’ factors can have in influencing outcomes.

Chapter 6: General Discussion

Although the storm/s that struck the reefs of the Capricorn Bunker sector of the Great Barrier Reef (GBR) caused extensive damage (Halford et al. 2004), they also provided a baseline against which to test emerging models of large-scale community structure (e.g. Hanski ,(1998), Wu & Loucks(1995)). Were metapopulation dynamics a valid model of landscape-scale stability on the GBR then the proximity of the individual reefs and the presence of substantial healthy communities remaining on each reef should have provided ideal conditions for renewal of denuded areas. The results of fourteen years of monitoring provided a clear answer with the reef flanks recovering to their pre-disturbance condition and the asymptotic nature of the recovery providing evidence of the influence of larger scale processes e.g. Caley & Schluter (1997), Hughes *et al.* (1999), Cheal *et al.* (2007).

The nature of this disturbance also provided the opportunity to investigate relationships between reef fish and benthic habitat. Previous studies had shown that underlying rugosity moderates the effects of disturbance to corals e.g Lewis (1997), Syms & Jones (2000). As there was very little underlying rugosity on the reef flanks with hard corals providing most of the structure, we would expect that the effects of coral removal on the reef fish assemblages would have been more substantial than if some habitat complexity remained. This was indeed the case with virtually no fish present on these reefs in the years immediately following the disturbance (Doherty et al 1997). The coral and fish communities nevertheless recovered to be similar to their pre-impact structure. This pattern of recovery occurred on each of five individual reefs spread out over 80 kilometers and is therefore compelling evidence not just of the resilience of reef communities at larger scales but also for the influence of habitat in structuring fish communities.

While similar results have been reported on a small scale, e.g. Lewis (1997), Syms & Jones (2000) and more recently Holbrook *et al.* (2008), such recovery has rarely been demonstrated at large scales, as this study has done. One large-scale study of disturbance does however provide similar results. Nuclear tests at Mururoa Atoll provided a comparable large-scale test of the role of habitat in structuring reef fish assemblages and the resilience of its associated reef fish populations (Planes et al. 2005). The benthic habitat remained untouched from the tests but reef fish assemblages were killed by the blast percussion. Yet, reef fish communities reestablished within five years and were no different in structure to what was there previously. Both of these studies (Halford et al. (2004) and Planes et al. (2005)) demonstrate the stabilising influence of larger-scale processes and how deterministic community structure can be at these scales (Caley 1995). Unlike at Mururoa Atoll, the benthic habitat had to first recover in the Capricorn Bunkers before fish communities could reassemble, this makes the ten year time period to recovery for a disturbance of this scale, impressive. Indeed, a decadal time frame for substantial recovery is becoming a common feature of many disturbances on coral reefs e.g. (Connell 1997; Sano 2000; 2008) and likely reflects the minimum time required for processes of growth and reproduction to re-establish benthic structure.

The spatial arrangement of thousands of individual reefs embedded in a highly inter-connected matrix makes the GBR an ideal system for testing the efficacy of metapopulation theory in a coral reef environment. It is less clear, however, whether the metapopulation concept is as appropriate for isolated reefs or fringing reef systems? Long-term monitoring of locations on the west coast of Australia provided the opportunity to investigate this question and see whether patterns of recovery from disturbance would proceed in a similar way as on the GBR. At Scott Reef, coral bleaching was extensive but considerable areas of reef were not badly damaged. Five years after bleaching when my study ended, the coral and fish assemblages were clearly recovering and appeared to be heading towards their pre-impact structure as defined in multivariate space (see Fig. 3.4 & 3.7 in Chapter 3). Full recovery within a decade – a similar time frame to recovery as on the southern GBR - would therefore appear possible. Given the isolation of this reef system, do the recovery dynamics support a model of metapopulation dynamics? They appear to for a number of reasons.

Firstly, the minimum size for an effective metapopulation has not been determined (Sale et al. 2006), so there is no *a-priori* reason why a large and isolated reef system like Scott Reef could not function under such a model. Secondly, there is evidence that local production contributes significantly to local recruitment in some corals at Scott Reef (Smith et al. 2008; Underwood et al. 2007) so it is reasonable to assume that this may also be the case for many fish species (i.e. it is a semi-closed system). In addition, recruitment patterns of reef fish can be synchronous within Scott Reef but not with reefs to the south (Halford, unpublished data), supporting the assumption of a relatively closed system operating at Scott Reef. However, if Scott Reef circumscribes the boundaries of a metapopulation what are the sub-populations? One of the requirements for a metapopulation is a degree of asynchrony between local populations such that their demographics differ but they still receive significant input from other sub-populations (Kritzer & Sale 2004). Recent studies indicate that demographic variability can be very pronounced over small distances (100’s of metres to kilometers), resulting in large differences in the relative contributions of these sub-populations to an overall metapopulation (Figueira et al. 2007). These demographically distinct areas on the reef can be considered ‘patches’ surrounded by unfavourable habitat, with the scale of these patches varying according to the scale of movement of a particular species or group (Williams et al. 2003). These demographically different patches likely reflect habitat patchiness and I have shown that there is clear spatial structuring of fish populations at Scott Reef and that this spatial structure remained unchanged following coral bleaching.

The resilience of Scott Reef to coral bleaching is evidence of a dynamic ecosystem that is able to recover even after major damage. How it could do this given its relative isolation on ecological time-scales can be explained through metapopulation dynamics. However, fish assemblages at this location could not have recovered without appropriate habitat. I found that rugosity, independent of live coral was a major mediator of reef fish dynamics. Although the slope locations at Scott Reef were high in coral cover they were low in residual rugosity and the recovery of the fish assemblages was much slower than those in the lagoon where rugosity was and remained much greater. The Scott Reef study is one of the first to illustrate such responses through time at a large scale. Moreover, the results concur with work done at smaller scales (Holbrook et al. 2008; Jones & Syms 1998; Lewis 1997; Syms & Jones 2000) providing empirical evidence that the nature of the fish - habitat relationship is to some extent scale independent.

While the size of Scott Reef was likely influential in its ability to withstand a major coral bleaching event, two other factors contributed to its resilience. Firstly, prolonged tidal cooling of surface waters at locations L3 and L4 (Bird 2005) by upwelled deep water, allowed large sections of reef to survive with relatively minimal damage. Finding out whether such processes operate in other reef systems should be afforded high priority for future research. Reef areas associated with such local-scale hydrodynamic features will be future ‘sources’ for recovery of reefs under projected climate change scenarios e.g. Baker et al. (2009). While the position of these areas of reef gave them access to cooler water, it also made them more susceptible to storms with this being reflected in lower average coral cover prior to the bleaching. Another probable reason why Scott Reef survived as it did was the presence of deep water coral reef communities (down to 60 metres) within the lagoon (Heyward et al. 2000). The existence of deep water refuges has also been implicated in the recovery of the

Maldives and Chagos Archipelagoes (Graham et al. 2008; Sheppard et al. 2008). The vertical dimension of older, well-developed reef systems throughout the Asia-Pacific region provides a vast area for refuge and increases the possibility of recovery from large-scale disturbances. In contrast, these buffers to disturbance were lacking in the northern reefs of the Seychelles and these reefs remain in poor condition post-1998 (Graham et al. 2006).

The third system that I monitored for my thesis was part of a fringing reef that provided a contrast to the other two systems studied here. Ningaloo Reef is very healthy, although fishing impacts are quite high in some areas (Westera et al. 2003). However, when I started monitoring at Coral Bay on Ningaloo Reef in 1995 it had been 6 years since coral spawn ‘slicks’ had caused catastrophic mortality of most organisms within the inner half of the bay. Coral cover had only increased from 5 to 6.5 % and the fish assemblages reflected a habitat dominated by dead coral skeletons and stands of the macroalgae, *Sargassum sp*. A repeat survey in 2002 indicated that coral cover was approaching levels that existed prior to 1989, a time-frame of approximately 13 years. However, the benthic community structure was still very different from what existed previously, supporting the idea that there was recovery without resilience (Berumen & Pratchett 2006) and the fish assemblages remained depauperate and little changed from 1995. Ningaloo is a fringing reef system that is broken up by a series of passes through the reef. Water flows over the reef crests, along the lagoon, and out through the passes, providing a good environment for larval supply and connectivity at medium scales (up to 5 kilometres) (McIlwain 1997; McIlwain 2003). In addition, the areas of reef in the outer part of the affected bay and in areas to the north and south all contained healthy corals and associated reef fish assemblages. The distance between healthy reef communities and impacted reef communities within the bay was less than 100 meters. It was expected therefore that recovery should have been more advanced by 2002. At the scale of this study it is clear that a metapopulation dynamic was not operating and there was low resilience to large-scale disturbance within Coral Bay. A primary reason for this slow recovery was a raised portion of reef which bisected the middle of the bay, inhibiting water flow and therefore larval dispersal. What this study illustrates is that local factors can often have a significant influence on the dynamics of an area, to the extent that predicting outcomes is very difficult. In the search for mechanisms that structure coral reefs it can sometimes be easy to overlook such effects.

The influence of local dynamics is also highlighted by comparison of species-specific effects of disturbance between locations. A number of reviews published over the past few years have summarised reef fish responses to climate change - related effects (Graham et al. 2008; Munday et al. 2008; Munday et al. 2007; Pratchett et al. 2008; Wilson et al. 2006) providing a means to compare my results with many other studies that have looked at disturbance effects on reef fish. While the majority of species that I analysed for changes in chapter 5 behaved as described in the reviews (Pratchett et al. 2008; Fig. 2 pg 258 and Wilson et al. 2006; Fig. 2 pg 6), there were some notable exceptions; all herbivores. For example, the territorial, herbivorous damselfish *Plectroglyphidodon lacrymatus* responded very positively to coral bleaching at Scott Reef with substantial recruitment (Halford, pers. Obs.) and increased abundance of adults. This result is in direct contrast to the synopsis in the reviews where this species has undergone substantial decreases after loss of coral cover. This species has no direct affiliation with live coral (either as a recruit, juvenile or adult) so it is unclear why it should have declined in so many studies. A direct comparison of those species that had differing responses across regions would be a worthwhile area for future studies. Are there fundamental life-history differences between locations that make the same species inherently more vulnerable, or is it just a reflection of the intensity of the disturbance effect at each location? Given that the density of a species can vary across its distribution range, is there a density threshold at which individual species are more susceptible to disturbance? Whatever the reasons, there is no single set of predictions applicable to the response of coral reef communities to disturbance with species-, reef-, region- and ocean-specific patterns prevalent.

This work reinforces the value of monitoring programs, which were the means by which the data used here were collected. Such programs can provide the observational data on which large-scale studies depend. It remains the case that a more complete understanding of larger-scale processes such as metapopulation dynamics requires a combination of empirical and theoretical studies that bridge the gap between smaller scale field experiments and larger scale phenomena that are presently explored mostly by theory (Hixon et al. 2002). This thesis is one of the first examples to use such an approach on coral reefs.

Looking ahead, if future climate predictions are true e.g. (Veron et al. 2009) then coral reefs along with many other ecosystems will likely face tough times. However, there remains considerable uncertainty as to exactly how the disturbance regimes of the future will affect coral reefs. Some of the most dire predictions; for example, that corals are living close to their upper thermal limits and are unlikely to adapt or acclimatize to projected rates of change, are not yet supported by sufficient data (Maynard et al. 2008b). While experimentation will start to shed light on the effects of particular climate scenarios e.g. Dixson *et al.* (2010), from a field ecologist’s perspective it makes sense to concentrate on understanding what are the characteristics that have enabled particular reef communities to remain resilient. In this context, monitoring programs that are long-term and adaptive will continue to be essential tools for obtaining the data that are missing at intermediate to large-scales.

References

Allen, G.R. 1991. *Damselfishes of the World* Germany, Mergus Publishers.

Aronson, R.B., Precht, W.F., Macintyre, I.G., & Murdoch, T.J.T. 2000a. Coral bleach-out in Belize. *Nature*, 405, (6782) 36

Aronson, R.B., Precht, W.F., Macintyre, I.G., & Murdoch, T.J.T. 2000b. Coral bleach-out in Belize.(bleaching of corals from high sea temperatures). *Nature*, 405, (6782) 36 (1)

Arthur, R. 2004. *Patterns and processes of reef recovery and human resource use in the Lakshadweep Islands, Indian Ocean.*

Arthur, R., Done, T.J., Marsh, H., & Harriot, V. 2006. Local processes strongly influence post-bleaching benthic recovery in the Lakshadweep Islands. *Coral Reefs*, 25, 427-440

Ault, T.R. & Johnson, C.R. 1998. Spatially and temporally predictable fish communities on coral reefs. *Ecological Monographs*, 68, (1) 25-50

Ayling, A. M. & Ayling, A. L. 1987, *Ningaloo Marine Park: Preliminary fish density assessment and habitat survey.*, Sea Research, Daintree, Qld. Australia.

Baird, A.H. & Hughes, T.P. 2000. Competitive dominance by tabular corals: an experimental analysis of recruitment and survival of understorey assemblages. *Journal of Experimental Marine Biology and Ecology*, 251, 117-132

Baker, A.C., Glynn, P.W., & Riegl, B. 2009. Climate change and coral reef bleaching: An ecological assessment of long-term impacts, recovery trends and future outlook. *Estuarine, Coastal and Shelf Science*, 80, (4) 435-471

Bell, J.D. & Galzin, R. 1984. Influence of live coral cover on coral-reef fish communities. *Marine Ecology Progress Series*, 15, 265-274

Bellwood, D.R. 1988. Ontogenetic changes in the diet of early post-settlement Scarus species (Pisces: Scaridae). *Journal of Fish Biology*, 33, (2) 213-219

Bellwood, D.R., Hoey, A.S., Ackerman, J.L., & Depczynski, M. 2006. Coral bleaching, reef fish community phase shifts and the resilience of coral reefs. *Global Change Biology*, 12, 1587-1594

Berkelmans, R. & Oliver, J.K. 1999. Large-scale bleaching of corals on the Great Barrier Reef. *Coral Reefs*, 18, 55-60

Berumen, M.L. & Pratchett, M.S. 2006. Recovery without resilience: persistent disturbance and long-term shifts in the structure of coral and coral communities at Tiahura reef, Moorea. *Coral Reefs*, 25, (4) 647-653

Bianchi, C. N., Morri, C., Pichon, M., Benzoni, F., Colantoni, P., Baldelli, G., & Sandrini, M. Dynamics and pattern of coral recolonization following the 1998 bleaching event in the reefs of the Maldives, Y. Suzuki et al., eds., Japanese Coral Reef Society, pp. 30-37.

Bird, J.C. 2005. *Modelling sub-reef thermodynamics to predict coral bleaching: a case study at Scott Reef, WA.* (MEngSc). James Cook University.

Blackburn, T.M. & Gaston, K.J. 2004. Macroecology. *Basic and Applied Ecology*, 5, 385-387

Bohnsack, J.A. 1983. Resiliency of reef fish communities in the Florida Keys following a January 1977 hypothermal fish kill. *Environmental Biology of Fishes*, 9, (1) 41-53

Booth, D.J. & Beretta, G.A. 2002. Changes in a fish assemblage after a coral bleaching event. *Marine Ecology Progress Series*, 245, 205-212

Bormann, F.H. & Likens, G.E. 1979. Catastrophic disturbance and the steady state in northern hardwood forests. *American Scientist*, 67, 660-669

Bouchon-Navaro, Y., Bouchon, C., & Harmelin-Vivien, M. 1985. Impact of coral degradation on a Chaetodontid fish assemblage (Moorea, French Polynesia). *Proceedings of the 5th International Coral Reef Symposium*, 5, 427-432

Bray, J.R. & Curtis, J.T. 1957. An ordination of the upland forest communities of southern Wisconsin. *Ecological Monographs*, 27, (4) 325-347

Brown, B.E. 1997. Coral Bleaching: Causes and consequences. *Coral Reefs*, 16, 129-138

Brown, J.H. & Maurer, B.A. 1989. Macroecology: The division of food and space among species on continents. *Science*, 243, (4895) 1145-1150

Buddemeier, R. W. & Fautin, D. G. Large-scale dynamics: the state of the science, the state of the reef, and the research issues. Coral Reefs 21[1]. 2002.

Bythell, J.C., Hillis-Starr, Z.M., & Rogers, C.S. 2000. Local variability but landscape stability in coral reef communities following repeated hurricane impacts. *Marine Ecology Progress Series*, 204, 93-100

Caley, M.J. 1995. Reef-fish community structure and dynamics: an interaction between local and larger-scale processes? *Marine Ecology Progress Series*, 129, 19-29

Caley, M.J., Carr, M.H., Hixon, M.A., Hughes, T.P., Jones, G.P., & Menge, B.A. 1996. Recruitment and the local dynamics of open marine populations. *Annual Review of Ecology and Systematics*, 27, 477-500

Caley, M.J. & Schluter, D. 1997. The relationship between local and regional diversity. *Ecology*, 78, (1) 70-80

Caley, M.J. & St John, J. 1996. Refuge availability structures assemblages of tropical reef fishes. *Journal of Animal Ecology*, 65, 414-428

Carleton, J. & Done, T.J. 1995. Quantitative video sampling of coral reef benthos: large-scale application. *Coral Reefs*, 14, (1) 35-46

Chabanet, P. 2002. Coral reef fish communities of Mayotte (western Indian Ocean) two years after the impact of the 1998 bleaching event. *Marine and Freshwater Research*, 53, 107-113

Chabanet, P., Ralambondrainy, H., Amanieu, M., Faure, G., & Galzin, R. 1997. Relationships between coral reef substrata and fish. *Coral Reefs*, 16, (2) 93-102

Chamberlain, J.A. & Graus, R.R. 1975. Water flow and hydromechanical adaptations of branched reef corals. *Bulletin of Marine Science*, 25, (1) 112-125

Chapman, M.R. & Kramer, D.L. 2000. Movements of Fishes Within and Among Fringing Coral Reefs in Barbados. *Environmental Biology of Fishes*, 57, (1) 11-24

Chazottes, V., Le Campion-Alsumard, T., & Peyrot-Clausade, M. 1995. Bioerosion rates on coral reefs: interactions between macroborers, microborers and grazers (Moorea, French Polynesia). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 113, (2) 189-198

Cheal, A.J., Coleman, G., Miller, I.R., Delean, S., Osborne, K., & Sweatman, H. 2002. Responses of Coral and Fish Assemblages to a Severe but Short-Lived Tropical Cyclone on the Great Barrier Reef, Australia. *Coral Reefs*, 21, 131-142

Cheal, A.J., Delean, S., Sweatman, H., & Thompson, A.A. 2007. Spatial synchrony in coral reef fish populations and the influence of climate. *Ecology*, 88, (1) 158-169

Chesser, R.H. 1969. Destruction of Pacific corals by the sea star Acanthaster planci. *Science*, 165, 280-283

Chesson, P. L., Case, T. J., & Diamond, J. 1986, "Overview: non-equilibrium community theories: chance, variability, history and coexistence," *In Community Ecology*, New York: Harper & Row, pp. 229-239.

Choat, J.H. & Axe, L.M. 1996. Growth and longevity in acanthurid fishes: An analysis of otolith increments. *Marine Ecology Progress Series*, 134, 15-26

Choat, J.H., Clements, K.D., & Robbins, W.D. 2002. The trophic status of herbivorous fishes on coral reefs. I: Dietary analyses. *Marine Biology*, 140, 613-623

Clarke, K. R. & Warwick, R. M. Change in marine communities: an approach to statistical analysis and interpretation. 2005. Plymouth Marine Laboratory, PRIMER-E Ltd.

Colgan, M.W. 1987. Coral reef recovery on Guam (Micronesia) after catastrophic predation by *Acanthaster planci*. *Ecology*, 68, (6) 1592-1605

Connell, J.H. 1978. Diversity in tropical rainforests and coral reefs. *Science*, 199, 1302-1310

Connell, J.H. 1997. Disturbance and recovery of coral assemblages. *Coral Reefs*, 16, 101-113

Connell, J.H., Hughes, T.P., & Wallace, C.C. 1997. A 30-year study of coral abundance, recruitment and disturbance at several scales in space and time. *Ecological Monographs*, 67, (4) 461-488

Connell, J.H. & Sousa, W.P. 1983. On the evidence needed to judge ecological stability or persistence. *The American Naturalist*, 121, (6) 789-824

Cornell, H.V. & Karlson, R.H. 1996. Species Richness of Reef-Building Corals Determined by Local and Regional Processes. *Journal of Animal Ecology*, 65, 233-241

Davies, P.J. & Marshall, J.F. 1979. Aspects of holocene reef growth, substrate age and accretion rate. *Search*, 10, (7-8) 776-779

Davies, P.J. & Marshall, J.F. 1980. A model of epicontinental reef growth. *Nature*, 287, 37-38

Diaz-Pulido, G., McCook, L.J., Dove, S., Berkelmans, R., Roff, G., Kline, D.I., Weeks, S., Evans, R.D., Williamson, D.H., & Hoegh-Guldberg, O. 2009. Doom and Boom on a Resilient Reef: Climate Change, Algal Overgrowth and Coral Recovery. *PLOS One*, 4, (4) e5239

Dixson, D.L., Munday, P.L., & Jones, G.P. 2010. Ocean acidification disrupts the innate ability of fish to detect predator olfactory cues. *Ecology Letters*, 13, (1) 68-75

Doherty, P.J. 1987. The replenishment of populations of coral reef fishes, recruitment surveys, and the problems of variability manifest on multiple scales. *Bulletin of Marine Science*, 41, (2) 411-422

Doherty, P. J. 1991, "Spatial and temporal patterns in recruitment," *In The ecology of fishes on coral reefs*, P. F. Sale, ed., San Diego, California: Academic Press, pp. 261-293.

Doherty, P.J. & Fowler, A. 1994. An empirical test of recruitment limitation in a coral reef fish. *Science*, 263, 935-939

Doherty, P.J., Kingsford, M., Booth, D., & Carleton, J. 1996. Habitat selection before settlement by Pomacentrus coelestis. *Marine and Freshwater Research*, 47, 391-399

Doherty, P.J. & McIlwain, J.L. 1996. Monitoring larval fluxes through the surf zones of australian coral reefs. *Mar Freshwat Res*, 47, 383-390

Doherty, P.J., Meekan, M., Miller, I.R., Osborne, K., & Thompson, A.A. 1997. Catastrophic loss of coral cover from reefs in the southern Great Barrier Reef and the impact on fish recruitment. *Proceedings of the 8th International Coral Reef Symposium*, 1, 1005-1010

Done, T.J. 1992a. Constancy and change in some Great Barrier Reef coral communities: 1980-1990. *American Zoologist*, 32, 655-662

Done, T.J. 1992b. Effects of tropical cyclone waves on ecological and geomorphological structures on the Great Barrier Reef. *Continental Shelf Research*, 12, 859-872

Done, T. 1993. On tropical cyclones, corals and coral reefs. *Coral Reefs*, 12, (3-4) 126

Downing, N., Buckley, R., Stobart, B., LeClair, L., & Teleki, K. 2005. Reef fish diversity at Aldabra Atoll, Seychelles, during the five years following the 1998 coral bleaching event. *Philosophical Transactions of the Royal Society of London Series A*, 363, 257-261

Faith, D.P., Minchin, P.R., & Belbin, L. 1987. Compositional dissimilarity as a robust measure of ecological distance. *Vegetatio*, 69, 57-68

Feary, D.A., Almany, G.R., McCormick, M.I., & Jones, G.P. 2007. Habitat choice, recruitment, and the response of coral reef fishes to coral degradation. *Oecologia*, 153, 727-737

Figueira, W.F., Lyman, S.J., Crowder, L.B., & Rilov, G. 2007. Small-scale demographic variability of the biocolor damselfish, Stegastes partitus , in the Florida Keys USA. *Environmental Biology of Fishes*, 81, (3) 297-311

Fowler, A.J. 1990. Spatial and temporal patterns of distribution and abundance of chaetodontid fishes at One Tree Reef, Southern GBR. *Marine Ecology Progress Series*, 64, 39-53

Fowler, A.J., Doherty, P.J., & Williams, D.M. 1992. Multi-scale analysis of recruitment of a coral reef fish on the Great Barrier Reef. *Marine Ecology Progress Series*, 82, 131-141

Friedlander, A.M. & Parrish, J.D. 1998. Habitat characteristics affecting fish assemblages on a Hawaiian coral reef. *Journal of Experimental Marine Biology and Ecology*, 224, 1-30

Garpe, K.C., Yahya, S.A.S., Lindahl, U., & Ohman, M.C. 2006. Long-term effects of the 1998 coral bleaching event on reef fish assemblages. *Marine Ecology Progress Series*, 315, 237-247

Graham, M.H. 2003. Confronting multicollinearity in ecological multiple regression. *Ecology*, 84, (11) 2809-2815

Graham, N.A.J., Wilson, S.K., Jennings, S., Polunin, N.V.C., Bijoux, J.P., & Robinson, J. 2006. Dynamic fragility of oceanic coral reef ecosystems. *Proceedings of the National Academy of Sciences*, 103, (22) 8425-8429

Graham, N.A.J., Wilson, S.K., Jennings, S., Polunin, N.V.C., Robinson, J., Bijoux, J.P., & Daw, T.M. 2007. Lag Effects in the Impacts of Mass Coral Bleaching on Coral Reef Fish, Fisheries, and Ecosystems. *Conservation Biology*, 21, (5) 1291-1300

Graham, N.A.J. 2008. *Effects of Coral Bleaching on Coral Reef Fish Assemblages.* Doctor of Philosophy.

Graham, N.A.J., McClanahan, T.R., MacNeil, M.A., Wilson, S.K., Polunin, N.V.C., Jennings, S., Chabanet, P., Clark, S., Spalding, M.D., Letourneur, Y., Bigot, L., Galzin, R., Ohman, M.C., Garpe, K.C., Edwards, A.J., & Sheppard, C.R.C. 2008. Climate Warming, Marine Protected Areas and the Ocean-Scale Integrity of Coral Reef Ecosystems. *PLOS One*, 3, (8) e3039

Green, A.L. 1996. Spatial, temporal and ontogenetic patterns of habitat use by coral reef fishes (Family: Labridae). *Marine Ecology Progress Series*, 133, 1-11

Green, A.L. 1998. Spatio-temporal patterns of recruitment of labroid fishes (Pisces: Labridae and Scaridae) to damsefish territories. *Environmental Biology of Fishes*, 51, 235-244

Halford, A.R. 1997. Recovery of a fish community six years after a catastrophic mortality event. *Proceedings of the 8th International Coral Reef Symposium*, 1, 1011-1016

Halford, A.R., Cheal, A.J., Ryan, D., & Williams, D.M. 2004. Resilience to large-scale disturbance in coral and fish assemblages on the Great Barrier Reef. *Ecology*, 85, (7) 1892-1905

Halford, A. R. & Thompson, A. A. 1994, *Visual census surveys of reef fish*, Australian Institute of Marine Science, Townsville, Australia, 3.

Halford, A.R. & Caley, M.J. 2009. Towards an understanding of resilience in isolated coral reefs. *Global Change Biology*, 15, (12) 3031-3045

Halford, A.R. & Perret, J. 2009. Patterns of recovery in catastrophically disturbed reef fish assemblages. *Marine Ecology Progress Series*, 383, 261-272

Hanski, I. 1998. Metapopulation dynamics. *Nature*, 396, 41-49

Harmelin-Vivien, M. 1994. The effects of storms and cyclones on Coral Reefs: A review. *Journal of Coastal Research*, 12, (1) 211-231

Hart, A.M. & Klumpp, D.W. 1996. Response of herbivorous fishes to Crown-of-thorns starfish Acanthaster planci outbreaks. I. Substratum analysis and feeding ecology of Acanthurus nigrofuscus and Scarus frenatus. *Marine Ecology Progress Series*, 132, 11-19

Hart, A.M., Klumpp, D.W., & Russ, G.R. 1996. Response of herbivorous fishes to Crown-of-thorns starfish Acanthaster planci outbreaks. II. Density and biomass of selected species of herbivorous fish and fish-habitat correlations. *Marine Ecology Progress Series*, 132, 21-30

Hart, A.M. & Russ, G.R. 1996. Response of herbivorous fishes to Crown-of-thorns starfish Acanthaster planci outbreaks. III. Age, growth, mortality and maturity indices of Acanthurus nigrofuscus. *Marine Ecology Progress Series*, 136, 25-35

Harvell, D., Aronson, R., Baron, N., Connell, J., Dobson, A., Ellner, S., Gerber, L., Kim, K., Kuris, A., McCallum, H., Lafferty, K., McKay, B., Porter, J., Pascual, M., Smith, G., Sutherland, K., & Ward, J. 2004. The rising tide of ocean diseases: unsolved problems and research priorities. *Frontiers in Ecology and the Environment*, 2, (7) 375-382

Hearn, C. J., Hatcher, B. G., Masini, R. J., & Simpson, C. J. 1986, *Oceanographic processes on the Ningaloo coral reef.*, Centre for Water Research, University of Western Australia.

Heinselman, M. L. Fire intensity and frequency as factors in the distribution and structure of northern ecosystems, H. A. Mooney, T. M. Bonnicksen, & N. L.

Christensen, eds., Washington, D.C., USA: U.S. Dept. of Agriculture, Forest Service, pp. 7-57.

Heyward, A. J., Halford, A. R., Smith, L., & Rees, M. 1998, *Temporal and spatial patterns of coral and fish assemblages at Scott Reef, 1994-1997*, AIMS, Dampier, Australia.

Heyward, A. J., Rees, M., Cappo, M., Smith, L., Speare, P., & Halford, A. R. 2000, *Characterisation of Scott Reef lagoon biota - fish and macrobenthos*, Australian Institute of Marine Science, Dampier, WA.

Hixon, M. A. 1991, "Predation as a process structuring coral reef fish communities," *In The ecology of fishes on coral reefs*, P. F. Sale, ed., San Diego, California: Academic Press, pp. 475-408.

Hixon, M.A. & Beets, J.P. 1993. Predation, prey refuges, and the structure of coral-reef fish assemblages. *Ecological Monographs*, 63, (1) 77-101

Hixon, M.A., Pacala, S.W., & Sandin, S.A. 2002. Population regulation: Historical context and contemporary challenges of open vs closed systems. *Ecology*, 83, (6) 1490-1508

Hobbs, R.J. 1994. Landscape ecology and conservation: moving from description to application. *Pacific Conservation Biology*, 1, 170-176

Hoegh-Guldberg, O. 1999. Climate change, coral bleaching and the future of the world's coral reefs. *Marine and Freshwater Research*, 50, 839-866

Holbrook, S.J., Schmitt, R.J., & Brooks, A.J. 2008. Resistance and resilience of a coral reef fish community to changes in coral cover. *Marine Ecology Progress Series*, 371, 263-271

Holling, C.S. 1973. Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics*, 4, 1-23

Hughes, T.P. 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science*, 265, 1547-1551

Hughes, T.P., Baird, A.H., Bellwood, D.R., Card, M., Connolly, S.R., Folke, C., Grosberg, R., Hoegh-Guldberg, O., Jackson, J.B.C., Kleypas, J.A., Lough, J.M., Marshall, P., Nystrom, M., Palumbi, S.R., Pandolfi, J.M., Rosen, B., & Roughgarden, J. 2003. Climate change, human impacts and the resilience of coral reefs. *Science*, 301, 929-933

Hughes, T.P., Baird, A.H., Dinsdale, E.A., Moltschaniwskyj, N.A., Pratchett, M.S., Tanner, J.E., & Willis, B.L. 1999. Patterns of recruitment and abundance of corals along the Great Barrier Reef. *Nature*, 397,

IPCC 2007, *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*, Cambridge University Press, Cambridge, United Kingdom and New York, USA.

Jones, G. P. 1991, "Postrecruitment processes in the ecology of coral reef fish populations: A multifactorial perspective," *In The ecology of fishes on coral reefs*, P. F. Sale, ed., San Diego, California: Academic Press, pp. 294-330.

Jones, G.P., Srinivasan, M., & Almany, G.R. 2007. Population connectivity and conservation of marine biodiversity. *Oceanography*, 20, (3) 100-111

Jones, G.P. & Syms, C. 1998. Disturbance, habitat structure and the ecology of fishes on coral reefs. *Australian Journal of Ecology*, 23, 287-297

Karlson, R.H. & Hurd, L.E. 1993. Disturbance, coral reef communities, and changing ecological paradigms. *Coral Reefs*, 12, 117-125

Kritzer, J.P. & Sale, P.F. 2004. Metapopulation ecology in the sea: from Levin's model to marine ecology and fisheries science. *Fish and Fisheries*, 5, 131-140

Landsberg, J.H. 2002. The effects of harmful algal blooms on aquatic organisms. *Reviews in Fisheries Science*, 10, (2) 113-390

Lasagna, R., Albertelli, G., Giovannetti, E., Grondona, M., Milani, A., Morri, C., & Bianchi, C.N. 2008. Status of Maldivian reefs eight years after the 1998 coral mass mortality. *Chemistry and Ecology*, 24, (S1) 67-72

Lassig, B.R. 1983. The effects of a cyclonic storm on coral reef fish assemblages. *Environmental Biology of Fishes*, 9, (1) 55-63

Lecchini, D. & Galzin, R. 2005. Spatial repartition and ontogenetic shifts in habitat use by coral reef fishes (Moorea, French Polynesia). *Marine Biology*, 147, (1) 47-58

Legendre, P. & Gallagher, E.D. 2001. Ecologically meaningful transformations for ordination of species data. *Oecologia*, 129, 271-280

Levin, S.A. 1992. The problem of pattern and scale in ecology. *Ecology*, 73, 1943-1967

Lewis, A.R. 1997. Effects of experimental coral disturbance on the structure of fish communities on large patch reefs. *Marine Ecology Progress Series*, 161, 37-50

Lewis, A.R. 1998. Effects of experimental coral disturbance on the population dynamics of fishes on large patch reefs. *Journal of Experimental Marine Biology and Ecology*, 230, 91-110

Lindahl, U., Ohman, M.C., & Schelten, C.K. 2001. The 1997/1998 mass mortality of corals: Effects on fish communities on a Tanzanian coral reef. *Marine Pollution Bulletin*, 42, (2) 127-131

Lindenmayer, D.B. & Likens, G.E. 2009. Adaptive monitoring: a new paradigm for long-term research and monitoring. *Trends in Ecology and Evolution*, 24, (9) 482-486

Lindstrom, M.J. & Bates, D.M. 1990. Nonlinear mixed effects models for repeated measures data. *Biometrics*, 46, 673-687

Littell, R.C., Henry, P.R., & Ammerman, C.B. 1998. Statistical analysis of repeated measures data using SAS procedures. *Journal of Animal Science*, 76, 1216-1231

Lourey, M.J., Ryan, D.A.J., & Miller, I.R. 2000. Rates of decline and recovery of coral cover on reefs impacted by, recovering from and unaffected by crown-of-thorns starfish Acanthaster planci: A regional perspective of the Great Barrier Reef. *Marine Ecology Progress Series*, 196, 179-186

Lovett, G.M., Burns, D.A., Driscoll, C.T., Jenkins, J.C., Mitchell, M.J., Rustad, L., Shanley, J.B., Likens, G.E., & Haeuber, R. 2007. Who needs environmental monitoring? *Frontiers in Ecology and the Environment*, 5, (5) 253-260 Luckhurst, B.E. & Luckhurst, K. 1978. Analysis of the influence of substrate variables on coral reef fish communities. *Marine Biology*, 49, (4) 317-323

Massel, S.R. & Done, T.J. 1993. Effects of cyclone waves on massive coral assemblages on the Great Barrier Reef: meteorology, hydrodynamics and demography. *Coral Reefs*, 12, (3/4) 153-166

Maynard, J., Anthony, K., Marshall, P., & Masiri, I. 2008a. Major bleaching events can lead to increased thermal tolerance in corals. *Marine Biology*, 155, (2) 173-182

Maynard, J.A., Baird, A.H., & Pratchett, M.S. 2008b. Revisiting the Cassandra syndrome; the changing climate of coral reef research. *Coral Reefs*, 27, (4) 745-749

McCormick, M.I. 1994. Comparison of field methods for measuring surface topography and their associations with a tropical reef fish assemblage. *Marine Ecology Progress Series*, 112, 87-96

McCormick, M.I. 2009. Behaviourally Mediated Phenotypic Selection in a Disturbed Coral Reef Environment. *PLOS One*, 4, (9) e7096

McCullagh, P. & Nelder, J.A. 1989. *Generalized Linear Models* London, England, Chapman and Hall.

McIlwain, J.L. 1997. Hydrodynamic flows and the flux of larval fishes across the crest of Ningaloo Reef, Western Australia. *Proceedings of the 8th International Coral Reef Symposium*, 2, 1133-1138

McIlwain, J.L. 2001. *Replenishment patterns of coral reef fish to Ningaloo Reef, Western Australia.* PhD University of Western Australia.

McIlwain, J.L. 2003. Fine-scale temporal and spatial patterns of larval suply to a fringing reef in Western Australia. *Marine Ecology Progress Series*, 252, 207-222

Meekan, M.G., Carleton, J.H., McKinnon, A.D., Flynn, K., & Furnas, M.J. 2003. What determines the growth of tropical reef fish larvae in the plankton: food or temperature? *Marine Ecology Progress Series*, 256, 193-204

Meekan, M.G., Wellington, G.M., & Axe, L.M. 1999. El Nino southern oscillation events produce checks in the otoliths of coral reef fishes in the Galapagos Archipelago. *Bulletin of Marine Science*, 64, (2) 383-390

Miller, I. R., Thompson, A. A., Baker, V. J., Bass, D. K., & Christie, C. A. 1991, *Widespread coral mortality on reefs in the capricornia region of the great barrier reef marine park*.

Minchin, P.R. 1987. An evaluation of the relative robustness of techniques for ecological ordination. *Vegetatio*, 69, 89-107

Munday, P.L. 2004. Habitat loss, resource specialization, and extinction on coral reefs. *Global Change Biology*, 10, 1642-1647

Munday, P.L., Jones, G.P., Pratchett, M.S., & Williams, A.J. 2008. Climate change and the future for coral reef fishes. *Fish and Fisheries*, 9, 1-25

Munday, P.L. & Jones, G.P. 1998. The ecological implications of small body size among coral-reef fishes. *Oceanography and Marine Biology: An Annual Review*, 36, 373-411

Munday, P. L., Jones, G. P., Sheaves, M., Williams, A. J., & Goby Gillian 2007, "Vulnerability of fishes of the Great Barrier Reef to climate change," *In Climate change and the Great Barrier Reef*, J. Johnson & P. Marshall, eds., Townsville, Australia: Great Barrier Reef Marine Park Authority, pp. 357-391.

Myers, R.F. 1991. *Micronesian reef fishes* Guam, USA, Coral Graphics.

Ninio, R. & Meekan, M.G. 2002. Spatial patterns in benthic communities and the dynamics of a mosaic ecosystem on the Great Barrier Reef, Australia. *Coral Reefs*, 21, (1) 95-104

Ninio, R., Meekan, M.G., Done, T.J., & Sweatman, H. 2000. Temporal patterns in coral assemblages on the Great Barrier Reef from local to large spatial scales. *Marine Ecology Progress Series*, 194, 65-74

Nott, J. & Hayne, M. 2001. High frequency of `super-cyclones' along the Great Barrier Reef over the past 5,000 years. *Nature*, 413, (6855) 508-512

Odum, E.P. 1969. The strategy of ecosystem development. *Science*, 164, 262-270

Page, C., Coleman, G., Ninio, R., & Osborne, K. 2001, *Surveys of benthic reef communities using underwater video*, Australian Institute of Marine Science, Townsville, Australia, 7.

Paine, R.T. & Levin, S.A. 1981. Intertidal landscapes: disturbance and the dynamics of pattern. *Ecological Monographs*, 51, 145-178

Pickett, S.T.A. & White, P.S. 1985. *The ecology of natural disturbance and patch dynamics* Orlando, Florida, Academic Press.

Pineda, J., Hare, J.A., & Sponaugle, S. 2007. Larval transport and dispersal in the coastal ocean and consequences for population connectivity. *Oceanography*, 20, (3) 22-39

Planes, S., Galzin, R., Bablet, J.P., & Sale, P.F. 2005. Stability of coral reef fish assemblages impacted by nuclear tests. *Ecology*, 86, (10) 2578-2585

Pratchett, M.S. & Berumen, M.L. 2008. Interspecific variation in distributions and diets of coral reef butterflyfishes (Teleostei: Chaetodontidae). *Journal of Fish Biology*, 73, (7) 1730-1747

Pratchett, M.S., Munday, P.L., Wilson, S.K., Graham, N.A.J., Cinner, J.E., Bellwood, D.R., Jones, G.P., Polunin, N.V.C., & McClanahan, T.R. 2008. Effects of climate-induced coral bleaching on coral-reef fishes - ecological and economic consequences. *Oceanography and Marine Biology: An Annual Review*, 46, 251-296

Pratchett, M.S., Wilson, S.K., & Baird, A.H. 2006. Declines in the abundance of Chaetodon butterfly fishes following extensive coral depletion. *Journal of Fish Biology*, 69, 1269-1280

Pratchett, M.S., Wilson, S.K., Berumen, M.L., & McCormick, M.I. 2004. Sublethal effects of coral bleaching on an obligate coral feeding butterflyfish. *Coral Reefs*, 23, (3) 352-356

Randall, J.E., Allen, G.R., Steene, R.C., & Steene, R. 1990. *Fishes of the Great Barrier Reef and Coral Sea* Bathurst, Australia, Crawford House Press.

Roberts, C.M. & Ormond, R.F.G. 1987. Habitat complexity and coral reef fish diversity and abundance on Red Sea fringing reefs. *Marine Ecology Progress Series*, 41, 1-8

Sale, P.F. 1998. Appropriate spatial scales for studies of reef-fish ecology. *Australian Journal of Ecology*, 23, (3) 202-208

Sale, P.F., Guy, J.A., & Steel, W.J. 1994. Ecological structure of assemblages of coral reef fishes on isolated patch reefs. *Oecologia*, 98, 83-99

Sale, P.F. & Steel, W.J. 1989. Temporal variability in patterns of association among fish species on coral patch reefs. *Marine Ecology Progress Series*, 51, 35-47

Sale, P. F., Hanski, I., & Kritzer, J. P. 2006, "The merging of metapopulation theory and marine ecology: establishing the historical context," *In Marine Metapopulations*, J. P. Kritzer & P. F. Sale, eds., Burlington, MA, USA: Elsevier Academic Press, pp. 3-28.

Sano, M. 2000. Stability of reef fish assemblages: responses to coral recovery after catastrophic predation by Acanthaster planci. *Marine Ecology Progress Series*, 198, 121-130

Sano, M. 2004. Short-term effects of a mass coral bleaching event on a reef fish assemblage at Iriomote Island, Japan. *Fisheries Science*, 70, 41-46

Sano, M., Shimizu, M., & Nose, Y. 1984. Changes in structure of coral reef fish communities by destruction of hermatypic corals: Observational and experimental views. *Pacific Science*, 38, (1) 51-79

Sano, M., Shimizu, M., & Nose, Y. 1987. Long term effects of destruction of hermatypic corals by Acanthaster planci infestation on reef fish communities at Iriomote Island, Japan. *Marine Ecology Progress Series*, 37, 191-199

Sheppard, C.R.C., Harris, A., & Sheppard, A.L.S. 2008. Archipelago-wide coral recovery patterns since 1998 in the Chagos Archipelago, central Indian Ocean. *Marine Ecology Progress Series*, 362, 109-117

Simpson, C.J., Cary, J.L., & Masini, R.J. 1993. Destruction of corals and other reef animals by coral spawn slicks on Ningaloo Reef, Western Australia. *Coral Reefs*, 12, 185-191

Smith, L.D., Gilmour, J.P., & Heyward, A.J. 2008. Resilience of coral communities on an isolated system of reefs following catastrophic mass-bleaching. *Coral Reefs*, 27, (1) 197-205

Sousa, W.P. 1984. The role of disturbance in natural communities. *Annual Review of Ecology and Systematics*, 15, 353-391

Spalding, M.D. & Jarvis, G.E. 2002. The impact of the 1998 coral mortality on reef fish communities in the Seychelles. *Marine Pollution Bulletin*, 44, 309-321

Spalding, M.D., Ravilious, C., & Green, E.P. 2001. *World atlas of coral reefs* Berkeley, USA, University of California Press.

Stimson, J. 1985. The effect of shading by the table coral Acropora hyacinthus on understorey corals. *Ecology*, 66, 40-53

Sweatman, H. 2008. No-take reserves protect coral reefs from predatory starfish. *Current Biology*, 18, (14) R598-R599

Syms, C. 1998. Disturbance and the structure of coral reef fish communities on the reef slope. *Journal of Experimental Marine Biology and Ecology*, 230, 151-167

Syms, C. & Jones, G.P. 2000. Disturbance, habitat structure and the dynamics of a coral-reef fish community. *Ecology* 2714-2729

Thompson, A.A. & Mapstone, B.D. 2002. Intra- vs Inter-annual variation in counts of reef fishes and interpretations of long term monitoring studies. *Marine Ecology Progress Series*, 232, 47-57

Tribollet, A., Decherf, G., Hutchings, P.A., & Peyrot-Clausade, M. 2002. Large-scale spatial variability in bioerosion of experimental coral substrates on the Great Barrier Reef (Australia): importance of microborers. *Coral Reefs*, 21, 424-432

Underwood, J.N., Smith, L.D., van Oppen, M.J.H., & Gilmour, J.P. 2007. Multiple scales of genetic connectivity in a brooding coral on isolated reefs following catastrophic bleaching. *Molecular Ecology*, 16, 771-784

van Schoubroeck, P. & Long, S. 2007, *Disturbance history of coral reef communities in Bill's Bay, Ningaloo Marine Park, 1989-2007*, Marine Science Program, Department of Environment and Conservation, Perth, Western Australia.

Van Woesik, R., Ayling, A.M., & Mapstone, B. 1991. Impact of Tropical Cyclone "Ivor" on the Great Barrier Reef, Australia. *Journal of Coastal Research*, 7, (2) 551-558

Vecchi, G.A. & Soden, B.J. 2007. Global warming and the weakening of the tropical circulation. *Journal of Climate*, 20, (17) 4316-4340

Veron, J.E.N., Hoegh-Guldberg, O., Lenton, T.M., Lough, J.M., Obura, D.O., Pearce-Kelly, P., Sheppard, C.R.C., Spalding, M., Stafford-Smith, M.G., & Rogers, A.D. 2009. The coral reef crisis: The critical importance of <350 ppm CO2. *Marine Pollution Bulletin*, 58, (10) 1428-1436

Wallace, C.C., Venkatesh, M., & Muir, P.R. 2007. Post-bleaching renewal of the dominant reef-building coral Acropora abrotanoides in the Lakshadweep islands of India. *Coral Reefs*, 26, 45

Walsh, W.J. 1983. Stability of a coral reef fish community following a catastrophic storm. *Coral Reefs*, 2, 49-63

Warner, R.R. & Chesson, P. 1985. Coexistence mediated by recruitment fluctuations: A field guide to the storage effect. *The American Naturalist*, 125, (6) 769-787

Warwick, R.M. & Clarke, K.R. 1993. Comparing the severity of disturbance: a meta-analysis of marine macrobenthic community data. *Marine Ecology Progress Series*, 92, 221-231

Wellington, G.M. & Victor, B.C. 1985. El Nino mass coral mortality: a test of resource limitation in a coral reef damselfish population. *Oecologia*, 68, 15-19

West, J.M. & Salm, R.V. 2003. Resistance and resilience to coral bleaching: implications for coral reef conservation and management. *Conservation Biology*, 17, (4) 956-967

Westera, M., Lavery, P., & Hyndes, G. 2003. Differences in recreationally targeted fishes between protected and fished areas of a coral reef marine park. *Journal of Experimental Marine Biology and Ecology*, 294, 145-168

Wilkinson, C. 2004, *Status of coral reefs of the world: 2004*, Australian Institute of Marine Science, Townsville, Qld Australia, 1.

Wilkinson, C., Linden, O., Cesar, H., Hodgson, G., Rubens, J., & Strong, A.E. 1999. Ecological and socioeconomic impacts of 1998 coral mortality in the Indian Ocean: An ENSO impact and a warning of future change. *Ambio*, 28, (2) 188-196

Williams, A.H. 1984. The effects of Hurricane Allen on back reef populations of Discovery Bay, Jamaica. *Journal of Experimental Marine Biology and Ecology*, 75, 233-243

Williams, A.J., Davies, C.R., Mapstone, B.D., & Russ, G.R. 2003. Scales of spatial variation in demography of a large coral reef fish - an exception to the typical model? *Fisheries Bulletin*, 101, 673-683

Williams, D.M. 1986. Temporal variation in the structure of reef slope fish communities (central Great Barrier Reef): short-term effects of Acanthaster planci infestation. *Marine Ecology Progress Series*, 28, 157-164

Wilson, S.K., Burgess, S.C., Cheal, A.J., Emslie, M.J., Fisher, R., Miller, I., Polunin, N.V.C., & Sweatman, H.P.A. 2008a. Habitat utilization by coral reef fish: implications for specialists vs. generalists in a changing environment. *Journal of Animal Ecology*

Wilson, S.K., Dolman, A.M., Cheal, A.J., Emslie, M.J., Pratchett, M.S., & Sweatman, H.P.A. 2008b. Maintenance of fish diversity on disturbed coral reefs. *Coral Reefs*

Wilson, S.K., Fisher, R., Pratchett, M.S., Graham, N.A.J., Dulvy, N.K., Turner, R.A., Cakacaka, A., Polunin, N.V.C., & Rushton, S.P. 2008c. Exploitation and habitat degradation as agents of change within coral reef fish communities. *Global Change Biology*, 14, (12) 2796-2809 Wilson, S.K., Graham, N.A.J., Pratchett, M.S., Jones, G.P., & Polunin, N.V.C. 2006. Multiple disturbances and the global degradation of coral reefs: are reef fishes at risk or resilient? *Global Change Biology*, 12, 1-15

Woodley, J.D., Chornesky, E.A., Clifford, P.A., Jackson, J.B.C., Kaufman, L.S., Knowlton, N., Lang, J.C., Pearson, M.P., Porter, J.W., Rooney, M.C., Rylaarsdam, K.W., Tunnicliffe, V.J., Wahle, C.M., Wulff, J.L., Curtis, A.S.G., Dallmeyer, M.D., Jupp, B.P., Koehl, M.A.R., Neigel, J., & Sides, E.M. 1981. Hurricane Allen's impact on Jamaican coral reefs. *Science*, 214, (4522) 749-755

Wu, J. & Loucks, O.L. 1995. From balance of nature to hierarchical patch dynamics: a paradigm shift in ecology. *The Quarterly Review of Biology*, 70, (4) 439-466

Appendices

Appendix 2.1

Details of the mixed linear models that were fitted independently to the benthic and fish data. Estimates of benthic cover, fish species richness and abundance were obtained using restricted maximum likelihood as implemented in the SAS MIXED procedure (Littell et al. 1996). The models included (a) the fixed effects of method and the polynomial for the change of benthic cover, species richness and fish abundance over time, for the periods before and after the disturbance, and (b) the random effects for the polynomial over time for each reef

Benthos

Under the assumption that the benthic cover estimates collected using the Manta Tow, Line Intercept and the LTMP video transects are spatially and temporally consistent, the following mixed linear model was used to describe the change in hard coral cover for the Capricorn Bunker reefs for the period, 1984 to 1998:

$$y_{ijk} = \mu_i + \beta_{o,pre} + \beta_{1,pre} X_k + \beta_{o,post} + \beta_{1,post} Z_k + \beta_{2,post} Z_k^2 + \\ + \alpha_{\mathrm{o,pre:j}} + \delta_{1,pre:j} X_{jk} + \alpha_{\mathrm{o,post:j}} + \delta_{1,post:j} Z_{jk} + \delta_{2,post:j} Z_{jk}^2 + \varepsilon_{ijk}$$

where y_{ijk} represents the transformed response for method *i*, reef *j* and year *k*; μ_i represents the mean response for method *i*, $\beta_{o,pre}$ represents the mean transformed response in 1988 prior to the disturbance, $\beta_{1,pre}$ represents the rate of change of the transformed response prior to the disturbance; X_{jk} a coded variable equal to the actual year - 1988 for all observations taken before 1988, and zero for all observations taken after 1988; similarly, $\beta_{o,post}$ represents the mean transformed response after the disturbance in 1988, $\beta_{1,post}$ represents the linear change in coral cover after the disturbance, $\beta_{2,post}$ represents the quadratic component of the change in coral cover after the disturbance, Z_{jk} equals 0 for all observations taken before 1988 and the actual year - 1988 for all observations taken after 1988, $\alpha_{o,pre:j}$ and $\delta_{1,pre:j}$ represent the random deviations of the intercepts and slopes from $\beta_{o,pre}$ and $\beta_{1,pre}$ for reef *j* respectively, $\alpha_{o,post:j}$, $\delta_{1,post:j}$ and $\delta_{2,post:j}$ represent the random deviations of the intercepts, slopes and quadratic terms from $\beta_{o,post}$, $\beta_{1,post}$ and $\beta_{2,post}$ for reef *j* respectively, and ε_{ijk} represents the errors for method *i*, reef *j*, and time *k*. It was assumed that the α's, δ's and ε_{ijk} were independent, normally distributed random effects with mean zero and variance $\sigma^2_{Component*}$. Since all years were "connected" (Table 1) the temporal change in coral cover could be estimated because there was a measure of the differences between methods (Hocking 1985).

Effects of Interest

Comparisons of the coral cover pre- to post- impact were estimated using linear combinations of the model effects (Table A2.1).

Table A2.1 Definition of comparisons of interest and the combination of the model effects used to estimate these comparisons.

Comparison	Estimator
Change in coral cover from just prior to impact (1987) to just after the impact (1991)	$\beta_{o,pre} - \beta_{o,post}$
Change in coral cover from just prior to impact (1987) to present (1998)	$\beta_{o,pre} - \left(\beta_{o,post} + \beta_{1,post}10 + \beta_{2,post}10^2\right)$
Change in coral cover from immediately after the impact (1991) to present (1998)	$\beta_{1,post}10 + \beta_{2,post}10^2$
Change in growth rate (per year basis) from just prior to the impact (1987) to present (1998)	$\beta_{1,pre} - \left(\beta_{1,post} + \beta_{2,post}20\right)$

Fish

Under the assumption that the abundance and species richness estimates of the fish are consistent spatially and temporally, the following mixed linear model was used to describe the changes for the Capricorn Bunker and Swains reefs for the period, 1983 to 1998, using the calibration trip in the Central GBR:

$$y_{ijkl} = \mu_i + \beta_{ol,pre} + \beta_{ol,post} + \beta_{1l,post} Z_{kl} + \beta_{2l,post} Z_{kl}^2 + \alpha_{ol,pre:j} + \alpha_{ol,post:j} + \delta_{1l,post:j} Z_{jkl} + \delta_{2l,post:j} Z_{jkl}^2 + \varepsilon_{ijkl}$$

where y_{ijkl} represents the transformed response for method *i*, reef *j*, year *k* and sector *l*; μ_i represents the mean response for method *i*, $\beta_{ol,pre}$ represents the mean transformed response in 1988 prior to the disturbance for sector *l*, $\beta_{ol,post}$ represents the mean transformed response after the disturbance in 1988 for sector *l*, $\beta_{1l,post}$ represents the linear change in fish abundance for the period 1988 to 1998 for sector *l*, $\beta_{2l,post}$ represents the quadratic component of the change in fish abundance for the period 1988 to 1998 for sector *l*, Z_{jkl} equals 0 for all observations taken before 1988 and the actual year - 1988 for all observations taken after 1988, $\alpha_{ol,pre:j}$ represent the random deviations of the intercepts from $\beta_{ol,pre}$ for reef *j*, $\alpha_{ol,post:j}$, $\delta_{1l,post:j}$ and $\delta_{2,post:j}$ represent the random deviations of the intercepts, slopes and quadratic terms from $\beta_{o,post}$, $\beta_{1,post}$ and $\beta_{2,post}$ for reef *j* respectively, and ε_{ijkl} represents the errors for method *i*, reef *j*, time *k* and sector *l*. It was assumed that the α's, δ's and ε_{ijkl} were independent, normally distributed random effects with mean zero and variance $\sigma^2_{Component*}$.

Since all years were "connected" (Table 1) the temporal change in fish abundances could be estimated, because there was a measure of the differences between methods (Hocking 1985)

Effects of Interest

Comparisons of the fish abundance and species richness pre- to post- impact, and between the different sectors, were estimated using linear combinations of the model effects (Table A2.2).

Table A2.2 Definition of comparisons of interest and the combination of the model effects used to estimate these comparisons.

Comparison	Estimator
Change in fish abundance/species richness from 1983 (last year fish data was available pre impact) to just after the impact (1992) in the Capricorn bunker sector	$\beta_{oC,pre} - \left(\beta_{oC,post} + \beta_{1C,post}4 + \beta_{2C,post}4^2\right)$
Change in fish abundance/species richness from 1983 to just after the impact (1992) in the Swains sector	$\beta_{oS,pre} - \left(\beta_{oS,post} + \beta_{1S,post}4 + \beta_{2S,post}4^2\right)$
Difference in the change of abundance/species richness pre to post impact for the Capricorn bunker sector and the swains sector	$\beta_{oC,pre} - \left(\beta_{oC,post} + \beta_{1C,post}4 + \beta_{2C,post}4^2\right)$ - $\beta_{oS,pre} - \left(\beta_{oS,post} + \beta_{1S,post}4 + \beta_{2S,post}4^2\right)$
Change in fish abundance/species richness from just after impact (1992) to present (1998) for the Capricorn bunkers sector	$\beta_{1C,post}6 + \beta_{2C,post}84$
Change in fish abundance/species richness from just after impact (1992) to present (1998) for the Swains sector	$\beta_{1S,post}6 + \beta_{2S,post}84$
Difference in the change post impact between the Capricorn bunker and Swains sectors.	$\beta_{1C,post}6 + \beta_{2C,post}84$ - $\beta_{1S,post}6 + \beta_{2S,post}84$

Appendix 3.1

Fig. 3.8 Species abbreviations and their complete names

Chaetodontidae	
CHA.ADIE	*Chaetodon adiergastos*
CHA.AURI	*Chaetodon aureofasciatus*
CHA.BARO	*Chaetodon baronessa*
CHA.BENN	*Chaetodon bennetti*
CHA.CITR	*Chaetodon citrinellus*
CHA.EPHI	*Chaetodon ephippium*
CHA.KLEI	*Chaetodon kleinii*
CHA.LINE	*Chaetodon lineolatus*
CHA.LUNU	*Chaetodon lunula*
CHA.MELO	*Chaetodon melannotus*
CHA.MEYE	*Chaetodon meyerii*
CHA.OCTO	*Chaetodon octofasciatus*
CHA.ORNA	*Chaetodon ornatissimus*
CHA.PUNC	*Chaetodon punctatofasciatus*
CHA.RAFF	*Chaetodon rafflesi*
CHA.RETI	*Chaetodon reticulatus*
CHA.SEME	*Chaetodon semeion*
CHA.SPEC	*Chaetodon speculum*
CHA.TLIS	*Chaetodon trifascialis*
CHA.TTUS	*Chaetodon trifasciatus*
CHA.ULIE	*Chaetodon ulietensis*
CHA.UNIM	*Chaetodon unimaculatus*
CHA.VAGA	*Chaetodon vagabundus*
FOR.FLAV	*Forcipiger flavissimus*
FOR.LONG	*Forcipiger longirostrus*

Acanthuridae	
ACA.AUBL	*Acanthurus auranticavus/ blochii*
ACA.BARI	*Acanthurus bariene*
ACA.DUSS	*Acanthurus dussumieri*
ACA.FOWL	*Acanthurus fowleri*
ACA.GRAM	*Acanthurus grammoptilus*
ACA.LEUC	*Acanthurus leucocheilus*
ACA.LINE	*Acanthurus lineatus*
ACA.NANS	*Acanthurus nigricans*
ACA.NCUS	*Acanthurus nigrofuscus*
ACA.NUDA	*Acanthurus nigricauda*
ACA.OLIV	*Acanthurus olivaceus*
ACA.PYRO	*Acanthurus pyropherus*
ACA.THOM	*Acanthurus thompsoni*
ACA.XANT	*Acanthurus xanthopterus*
CTE.GROP	*Ctenochaetus (grouped)*
NAS.ANBR	*Naso annulatus/brevirostris*
NAS.LITU	*Naso lituratus*
NAS.THOR	*Naso thorpei*
NAS.UNIC	*Naso unicornus*
NAS.VLAM	*Naso vlamingi*

ZEB.SCOP	*Zebrasoma scopas*
ZEB.VELI	*Zebrasoma veliferum*

Scaridae

CHL.SORD	*Chlorurus sordidius*
BOL.MURI	*Bolbometapon muricatum*
CET.BICO	*Cetoscarus bicolor*
CHL.MICR	*Chlorurus microrhinos*
HIP.LONG	*Hipposcarus longiceps*
SCA.BLEE	*Scarus bleekeri*
SCA.CHAM	*Scarus chameleon*
SCA.DIMI	*Scarus dimidiatus*
SCA.FLAV	*Scarus flavipectoralis*
SCA.FORS	*Scarus forsteni*
SCA.FREN	*Scarus frenatus*
SCA.GLOB	*Scarus globiceps*
SCA.LONG	*Scarus longiceps*
SCA.NIGR	*Scarus niger*
SCA.OVIC	*Scarus oviceps*
SCA.PRAS	*Scarus prasiognathus*
SCA.PSIT	*Scarus psittacus*
SCA.RUBR	*Scarus rubroviolaceus*
SCA.SCHL	*Scarus schlegeli*
SCA.SPIN	*Scarus spinus*

Pomacentridae

AMB.AURE	*Amblyglyphidodon aureus*
AMB.CURA	*Amblyglyphidodon curacao*
AMB.LEUC	*Amblyglyphidodon leucogaster*
CHR.AMBO	*Chromis amboinensis*
CHR.APES	*Chromis atripes*
CHR.ATVI	*Chromis atripectoralis/viridis*
CHR.LEPI	*Chromis lepidolepis*
CHR.LIVA	*Chromis lineata/ vanderbiltii*
CHR.MARG	*Chromis margaritifer*
CHR.TERN	*Chromis ternatensis*
CHR.WEBE	*Chromis weberi*
CHR.XANT	*Chromis xanthura*
CHY.HEMI	*Chrysiptera hemicyanea*
CHY.REX	*Chrysiptera rex*
CHY.TALB	*Chrysiptera talboti*
DAS.ARUA	*Dascyllus aruanus*
DAS.RETI	*Dascyllus reticulatus*
DAS.TRIM	*Dascyllus trimaculatus*
DIS.PERS	*Dischistodus perspicillatus*
NEG.MELA	*Neoglyphidodon melas*
NEG.NIGR	*Neoglyphidodon nigroris*
PGY.DICK	*Plectroglyphidodon dickii*
PGY.JOHN	*Plectroglyphidodon johnstonianus*
PGY.LACR	*Plectroglyphidodon lacrymatus*
POM.ADEL	*Pomacentrus adelus*
POM.AMBO	*Pomacentrus amboinensis*
POM.BANK	*Pomacentrus bankanensis*

POM.COEL	*Pomacentrus coelestis*
POM.LEPI	*Pomacentrus lepidogenys*
POM.MOLU	*Pomacentrus moluccensus*
POM.NIGR	*Pomacentrus nigromanus*
POM.PHIL	*Pomacentris phillipinus*
POM.VAIU	*Pomacentrus vaiuli*
PRE.BIAC	*Premnas biaculeatus*
STE.NIGR	*Stegastes nigricans*