PATTERNS AND PROCESSES OF REEF RECOVERY AND HUMAN RESOURCE USE IN THE LAKSHADWEEP ISLANDS, INDIAN OCEAN

Thesis submitted by
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in August 2004

For the degree of Doctor of Philosophy
In the School of Tropical Environment Studies and Geography
James Cook University

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Abstract

PATTERNS AND PROCESSES OF REEF RECOVERY AND HUMAN RESOURCE USE IN THE LAKSHADWEEP ISLANDS, INDIAN OCEAN

Finding solutions that effectively conserve natural areas while simultaneously protecting the sustenance rights of resource stakeholders is a considerable challenge for ecosystem managers and scientists. In complex ecosystems like tropical coral reefs, the problem of management is further confounded by an inadequate understanding of how ecosystem function will respond to changes in environmental or management conditions. Given this uncertainty, managers are looking at ways to support and enhance the natural buffering capacity of ecosystems in the face of change, i.e. ecosystem resilience. Human use of natural areas can profoundly modify this resilience, particularly in the developing tropics, where a large proportion of the population depends directly on natural areas for daily sustenance. In these areas, developing and implementing effective management solutions requires a close understanding of both ecosystem processes and the factors affecting human interactions with the ecosystem.

This study examined the processes of ecosystem change after a major mass mortality of coral in the Lakshadweep Islands and the consequences that changes in resource use and policy have had on the recovery potential of these reefs.

The Lakshadweep Islands are a group of atolls in northern Indian Ocean. The El Niño Southern Oscillation (ENSO) of 1998 resulted in anomalous sea surface temperatures (SSTs) that caused extensive coral mortality in the reefs. I studied the patterns of recovery of coral and fish communities on outer reefs on three atolls, Agatti, Kadmat and Kavaratti from 2000 to 2003. Corals showed a mixed pattern of recovery: sites on the eastern aspects of islands showed little recovery of coral cover, while sites on the west showed a rapid increase in coral cover. This difference between aspects appears to be a function of the degree of exposure of these sites to seasonal monsoonal storms, and differences in the long-term stability of coral settlement substrate between aspects. Genera of coral that showed the most significant gains represented two very different life history strategies. *Porites* and *Goniastrea* were generally more resistant to bleaching stress. In contrast, *Acropora* was highly susceptible to bleaching, but recovered very quickly from disturbances by recruiting in large numbers, and sustaining high growth rates once established.

Fish communities in coral reefs are naturally very variable, but there were noticeable trends in fish assemblages after bleaching in the Lakshadweep. Species richness and diversity increased from 2000 to 2003 at all sites. Herbivorous fishes such as surgeonfish and parrotfish were very abundant in post-bleached reefs, representing up to 70% of all trophic guilds in the reef in 2000. The dominance of herbivores declined with time as coral took over from algal turf in many reefs. Multidimensional scaling (MDS) analysis of fish communities indicated that fish assemblages were moving towards increasing similarity with time, possibly approaching a post-disturbance equilibrium.

I interpret the recovery of Lakshadweep's reefs to disturbance within the conceptual framework of catastrophe theory. Catastrophe theory has been effectively used in several other ecosystems as a phenomenological model of ecosystem change, and the applicability of the two-factor cusp catastrophe is a useful conceptual model of reef responses to disturbance. This theory suggests that in the face of global warming, managers and scientists many need to invest their energies in understanding uncertainty on the one hand while managing for resilience on the other.

Biotic studies in the reefs of the Lakshadweep indicated that although the fine-scale patterns of recovery are variable, the reefs appear to be highly resilient after coral mortality. The current pattern of resource use practised in the Lakshadweep contributed in part to this high resilience. Despite being among the most densely populated locations in India, with over 2200 people/km^2, for most of the year the human population of the Lakshadweep do not depend on the reef for food. This situation largely results from a development initiative started by the Fisheries Department in the 1960s which actively converted reef fishers to pelagic tuna fishing with a series of subsidies and training programmes. This initiative was implemented solely to enhance economic development of the islands, but it has inadvertently released reefs from a potentially large resource extraction pressure. Thus local regulations have played an important if inadvertent role in controlling marine resource use in the Lakshadweep.

The Lakshadweep case study has important lessons for resource conservation in the developing tropics. The coral reefs of the Lakshadweep apparently possess considerable resilience in the face of catastrophic coral mortality. One of the major contributors to this resilience was the relatively low level of fishing pressure on these reefs, despite high human population densities. The policy change that was responsible for a shift away from reef fishing was designed primarily as a developmental activity, but it had significant, but completely unintended positive consequences for the resilience of the reef. The Marine Protected Area (MPA) is the principal tool currently used to manage the vanishing diversity of threatened ecosystems like coral reefs. While MPAs may still be the most effective solution in marine conservation, MPAs are often difficult and expensive to establish and maintain. It is even more difficult to get local communities to reconcile with a loss of access to resource areas. The Lakshadweep example suggests that there may be alternative paths to enhance ecosystem resilience that are perhaps as effective in achieving conservation goals. It is not often that ecosystem conservation and human development can pull in the same direction, but when they do, this synergy should be encouraged and supported.

Acknowledgements

My first experience of field research was on an island in the Gulf of Kutch – a tiny piece of land with mudflats and mangroves. I lived there for several months with a lighthouse keeper, a Forest Department watchman called *Dada*, and his wife, *Dadi*. *Dadi* was one of those rare innocents you find occasionally, whose world view was almost completely circumscribed by the 1.5 kms^2 of the island, her home for as long as she could remember. Talking with her one day as she cooked the evening meal, she asked me how long I had been studying. Seventeen years, I told her. She looked at me, aghast, and, after a small pause, said kindly, "You know, if you find it so difficult to pass the exams, there is no shame in giving up and trying something else".

Well, *Dadi*, I'm still at it. And, whether you realise it or not, you are part of the reason why I continue to do this. You, and numerous others, without whom my work would not only not have been possible, it would have very little meaning. You will forgive me if my attempt to thank all of you is ineffectual and incomplete.

I am an unruly researcher, and if anyone understands this well, it is my supervisory team. My supervisors, Terry Done, Helene Marsh and Vicki Harriott were indulgent with my most unrealistic ideas, and have nudged me in the right direction with quiet, insistent patience. You are an inspiration, and I am humbled by the unstinting dedication you showed for my work. Graeme Inglis supervised me in the initial years of this project, and he tried in vain to instil in me a rigor of approach, that I could only admire in him. Graeme, I still don't quite know what my question is exactly, but if you ask me enough times, perhaps I will discover it.

My field research was generously funded by the DIVERSITAS/TOTAL foundation, through a project headed by Terry Done. My studies in Australia were supported by an International Postgraduate Research Scholarship, and by the Tropical Environment Studies and Geography (TESAG) at James Cook University. Additionally, I was supported by the J. N. Tata Endowment for Higher Studies.

Doing field research in the Lakshadweep is a logistic nightmare, and it would not have been possible without the help of several wonderful organisations in Australia, mainland India, and the Lakshadweep Islands. The dive operation, Lacadives, made diving in the Lakshadweep a dream, providing boats, compressed air, tanks and helpful hands whenever I needed them. In mainland India, the Nature Conservation Foundation provided invaluable support in handling funds, and being my liaison between the islands and the rest of the world. James Cook University, and the Department of TESAG provided institutional support in Australia, along with the Australian Institute of Marine Science. Both Helene Marsh and Peter Valentine, as Heads of Department of TESAG were always encouraging and supportive, particular when dealings with the bureaucracy put my candidature at risk. I would also like to thank Susan Knight, Barbara Pannach, Susan Meehan, Beth Moore, Shirley Bruce, Clive Grant, Robert Scott, Jody Krueger, and all the wonderful administrative staff at TESAG for providing such unstinting support throughout these years.

The Lakshadweep Administration and all its contingent departments were remarkably open and welcoming of my research. I thank the Administrators, past and present, for the support and interest they showed my work. I owe a special debt of gratitude to Dr. Syed Ismail Koya, Deputy Director of the Department of Science and Technology, for sharing freely with me of his large experience and intimate knowledge of the island culture and ecology. My thinking about the Lakshadweep has been very largely influenced by you, and I look forward to more rewarding interactions in the future.

The Lakshadweep Islands have a special place in my heart, not merely for its trite picture postcard beauty (it gets old pretty quickly), but because the people of the Lakshadweep accepted me as one of their own. My field assistants and their families have been a vital part of my research – they are the people whose names seldom get on to scientific publications, but without whom so much of our research would be impossible. M.K. Ibrahim (Omni the Small), and Shah Jahan in particular accompanied me on most of my dives, and complained only when I pushed myself beyond what they thought were reasonable limits. Their friendship helped me through many of those long frustrating days in the field, when weather and inertia conspired to make working difficult. I also have to thank Captain Koya, Khalid, Latif, and all the lads in the Lakshadweep who helped in the field, and made living there a pleasure. I owe a special thanks to Prahlad and Mitali Kakkar, Sumer Verma, Anees Adenwala, Parinita Zia Nath, Shaukat Ali, Sarang Kulkarni, and all the good guys from Lacadives and Reefwatch.

For reading through endless drafts of chapters, and helping me think through ideas, I thank Oliver Floerl, Paul Marshall, Nadine Marshall, Joshua Cinner, Ameer Abdullah, James Moloney, Elisabeth Laman Trip, Dipani Sutaria, James Sheppard, Dan Salkeld, Teresa Alcoverro, Anindya Sinha, Simone Mariani, M.D. Madhusudan, T. R. Shankar Raman, Aparajita Datta, Charudutt Mishra, Divya Mudappa, Emre Turak, Vidya Athreya, Clive Wilkinson, Timothy McClanahan, Carden Wallace, Sean Connolly, Michelle Waycott, Arjan Rajasuriya, Mahesh Rangarajan, Vineeta Hoon, Dr. MVM Wafar, and a host of others.

NCF (Madhu, Charu, Sridhar, Divya, Aparajita, Rana, Suresha and all the rest) is my extended family, and no thanks I can give them would be adequate. The strength of their unconditional support has seen me through the hardest of times over these years. They have been my intellectual playmates, my carrots-and-sticks, my friends and my confidantes. I hope I can make it up to you all someday. Dipani, Smita, Simone, Teresa, Elisabeth and James, Josh, Paul, Nadine and Indiana, Anna, Amanda, Guido, Pia, Ameer, Dan and Kris, Sula, Ben, James, Phil, Gill and Oli, Brett and Karin, Ann, my parents my sisters, and all my friends have been quietly forgiving of all my erratic behaviour through these years, and have accepted my frustrating cynicism with the resigned grace that only those closest to you can. In my darkest moments, I remember a lovely trek I took through the Himalayas with one of you, and it helps me regain perspective.

Lastly, I would like to thank the Indian bureaucracy, for teaching me the art of gentle forbearance.

This thesis is dedicated to the memory of Zu, who would have loved the reef in all its irresponsible exuberance, and to the memory of Vicki, for her very responsible exuberance.

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Statement of Sources

Declaration

I declare that this thesis is my own work and has not been submitted in any other form for another degree or diploma at any university or other institutions 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.

Signature **Date**

Statement of Contribution of Others

I declare that this thesis is my own work, and has been supported by the following organisations and people. The field budget was funded through a DIVERSITAS/TOTAL Foundation Grant through the Australian Institute of Marine Science. Additional administrative support for the field project was provided by the Nature Conservation Foundation, India, Lacadives Dive School, and Reef Watch Marine Conservation.

Financial support for university fees and living expenses were funded through an International Postgraduate Research Scholarship (IPRS), and by departmental scholarships from the department of TESAG. Additional funds were also provided by the J.N. Tata Endowment for Higher Education, and the Ratan Tata Trust.

Editorial contributions to this thesis were provided by my supervisors, Terence Done, Helene Marsh and Vicki Harriott. Additional editorial contributors include Joshua Cinner, Paul Marshall, Nadine Marshall, T. R. Shankar Raman, Teresa Alcoverro, M.D. Madhusudan, Charudutt Mishra, Simone Mariani, and Dipani Sutaria.

Signature	**Date**

Declaration on Ethics

The research presented and reported in this thesis was conducted within the guidelines for research ethics outlined in the *National Statement on Ethics Conduct in Research Involving Humans* (1999), the *Joint NHMRC/AVCC Statement and Guidelines on Research Practice* (1997), the *James Cook University Policy on Experimentation Ethics, Standard Practices and Guidelines* (2001), and the *James Cook University Statement and Guidelines on Research Practice* (2001).

Signature **Date**

Chapter I

INTRODUCTION

Coping with Catastrophe: Coral reef recovery in the Lakshadweep Atolls, Indian Ocean

In this introductory chapter I explore links between human communities and natural ecosystems, and discuss the role of change as a structuring agent in human and social systems. I develop a simple model to describe the interaction between human communities as resource extractors and the ecological systems on which they depend. I then apply this model to the Lakshadweep, a group of coral atolls in the Indian Ocean. The Lakshadweep reefs were subjected to a catastrophic loss of coral in the wake of the 1998 El Niño event. This event provides a context for this study. I also briefly describe the rationale for, and structure of the thesis.

Chapter I: Introduction

Coping with Catastrophe: Coral reef recovery in the Lakshadweep Atolls, Indian Ocean

1.1 Change and its consequences

Dealing with change has never been easy. Despite its obvious ubiquity, change is often unpredictable and disruptive, and coming to grips with it has been a central human concern. Heraclitus, writing around 500 BCE, proposed that change was a fundamental character of nature, but that it possessed an underlying order (Barnes 1979). Understanding this underlying order has large implications, since if it does not allow us to completely command change, it may help us better prepare ourselves for it. Frazer proposes that the need to comprehend and control the forces of change in nature led human communities to turn progressively from magic to religion to science for answers (Frazer 1922). More recently, the need to understand change in the natural world has become an even more pressing subject of inquiry, as the rate of change increases, spurred on by human use and abuse of natural systems.

The history of human use of ecosystems has seen a progression from an environment dominated by natural change, to one that is highly influenced by human-induced change (Messerli et al. 2000). In time, human communities become progressively better at managing the uncertainties inherent in their access to natural resources, frequently modifying the system to reduce these uncertainties. Such modifications often trigger changes at different spatial and temporal scales from those being managed, and can lead, paradoxically perhaps, to increased vulnerability to environmental uncertainty (Holling 1973, Folke *et al.* 1996, Holling & Meffe 1996, Peterson *et al.* 1998). The growth of agriculture is the most familiar example of this trend. What started out as a means to protect people against the vagaries of food availability associated with a gathering lifestyle, led to a revolution in food production. Increased farming efficiency resulted in a homogenisation of cropping patterns. However, the success of agricultural monocultures meant that specialised crop predators could become equally successful, causing population explosions of ‘superpests’, with the ability to periodically devastate entire harvests (Messerli et al 2000). Holling (1986), reviewing trends in the history of man-managed systems (insect pests, forest fire, savannah grasslands, fisheries and human disease) proposes that human attempts to control ecological variables, lead, more often than not, to increased vulnerability to disturbance.

This outwardly spiralling arms race of management control and ecological ‘surprise’ (see Holling 1996) has had dramatic consequences for the natural world. The human footprint now extends to virtually every area of the globe, and few ecosystems exist today that are uninfluenced, directly or indirectly, by anthropogenic impact. Recent climate change has been linked conclusively to human lifestyle patterns and the modification of natural areas to fuel these lifestyles (Watson & Core Writing Team 2001). Climate change is an insidious threat from which no ecosystem is insulated. More importantly, it is not something that can be controlled at the level of an individual ecosystem using the traditional tools of management. The effects of climate change have been reported in a host of ecosystems including tropical forests, grasslands, coral reefs and seagrass meadows. Along with habitat loss and overexploitation, climate change is now being recognised as among the most significant threats to the continued survival of natural ecosystems (Hoegh-Guldberg 1999, Pounds *et al.* 1999, Holmgren *et al.* 2001, Lawton 2001, Wellington *et al.* 2001, Walther *et al.* 2002, Duarte 2002, Hughes *et al.* 2003).

In urban and developed regions of the world, human communities may be largely buffered (at least in the short term) from the immediate consequences of ecosystem change by elaborate networks of resource production and acquisition. However, in most of the developing tropics, many communities continue to be primary users of natural resources and derive their daily sustenance from these resources. These communities are more likely to be affected directly by changes to the functioning of the natural areas on which they depend. By severely testing the limits of ecosystems’ ability to absorb disturbance (Holling 1973), climate change also significantly threatens the livelihoods of local communities that depend on the products and services that these ecosystems provide.

1.2 Disturbance, resilience, and socio-ecological systems

In areas where human communities rely heavily on natural systems for sustenance or commerce, understanding how humans and the ecosystems they exploit deal with change is essential for effective management (Berkes & Folke 1998). It is becoming increasingly clear that there are important similarities in the way ecosystems and human communities respond to change (Adger 2000). Both social and ecological systems display different degrees of resilience when affected by external disturbances. Resilience is a measure of the amount disturbance or change a system is able to buffer before its social or ecological function is radically altered. This conception of resilience – the ability to absorb perturbations without significant change to the functioning of the ecosystem or the human community ('ecological resilience' Holling 1973), is markedly different from the more commonly accepted definition – the time a system takes to return to an earlier state after it has been disturbed (Pimm 1984, Tilman & Downing 1994), and is closer to the traditional definition of 'resistance'. The latter definition is what Holling terms 'engineering resilience', and is concerned mostly with maintaining the efficiency of function, whereas Holling's conception deals more with maintaining the existence of function (Gunderson *et al.* 2002).

1.3 A simplified model of human and ecosystem interactions

The ability of a human or ecological system to buffer change is dependent on the functional elements within the system, and the strength of the relationships between them. For a natural system this translates to species and/or functional diversity, competitive hierarchies, and food web architecture. In human systems, this translates to the strength of institutional frameworks within

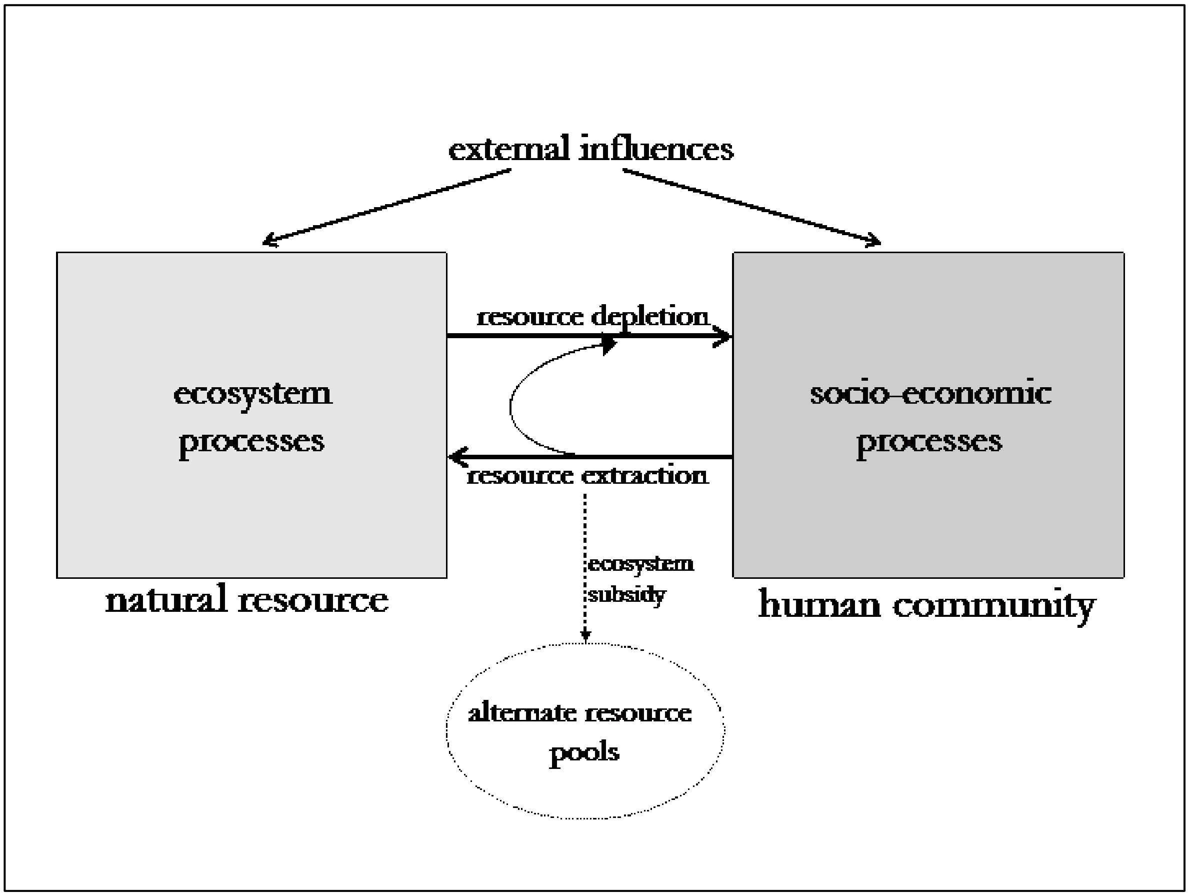


Figure 1.1 A simplified model of human interactions with natural resources

the system. In Figure 1.1, I present a highly simplified model of how human and natural ecosystems may influence each other. The two boxes represent a natural resource, and a human community that depends on it for ecological goods and services. Both boxes are essentially “black boxes” representing ecosystem and socioeconomic processes respectively. In this simplified conception, humans interact with the ecosystem primarily as resource extractors, either for subsistence (food, shelter, etc) or for commerce. The ecological system will affect the human system with changes in resource availability, either because of natural stochasticity caused by changes in population dynamics, external influences, or by overexploitation. The extent of human dependence is a function of the number of resource areas from which communities derive sustenance– isolated human communities may need to derive all their resource needs from a single ecological area, but often benefits are derived from a number of alternate resource pools. Both human and ecological systems are modified to different degrees by external influences that can result in major changes to the internal social or ecological processes. For ecosystems, this disturbance can be either natural (cyclones, lightening strikes, disease, etc), or anthropogenic (fire, climate change, etc). For human systems, disturbance manifests either through sudden, unexpected events (natural disaster, war, policy change, etc) or through insidious processes (attitude shifts, urbanisation, economic change, drying up of natural resources, etc). Because the functioning of the social and resource systems are so closely linked, changes in one system can often have serious implications for the functioning of the other system. Perhaps the most familiar example of this was the Irish potato famine of the 1840s, when potato harvests succumbed to black rot, fuelling a mass migration of the human population out of Ireland to North America (Hatton & Williamson 1998). After frosts devastated Brazilian coffee crops in the 1990s, there was an increase in global demand for Indian coffee, and estate-owners in southern India created a market for organic manure to bolster levels of coffee production. This initiative led to changes in the way communities in nearby villages used resources: there was a rapid conversion from agro-pastoralism to a dung-based economy, and a dramatic increase in livestock grazing in the adjacent forests, causing significant problems for native vegetation and forest ungulates (Madhusudan in press).

In this thesis, I apply the model outlined in Figure 1.1 to the Lakshadweep Islands, a group of atoll islands in the northern Indian Ocean, focussing attention on the response of the area’s coral reefs to change, and exploring the factors influencing the way human communities use the resource, and its consequences for the reef.

1.4 Thesis outline

My thesis examines the consequences of a catastrophic mortality event on the coral reefs of Lakshadweep in the Indian Ocean. The Lakshadweep Islands are a small group of atoll reefs at the northernmost tip of an archipelago that includes the Maldives and Chagos chains of islands. An unusually severe El Niño Southern Oscillation (ENSO) event in 1998 resulted in large-scale coral mortality to reefs in the region. This thesis is a case study of the patterns and processes of reef recovery in the wake of the 1998 coral mortality.

My primary motivation was to determine how benthic communities and reef fishes responded to the mass mortality of coral. I was additionally interested in understanding how patterns of resource use influenced the processes in the post-disturbed reefs. The Lakshadweep Islands are densely populated (more than 2000 people/km^2 in 2001), and the influence of human use on the surrounding ecosystems is likely to be large (Directorate of Census Operations 2001, Hoon 2003

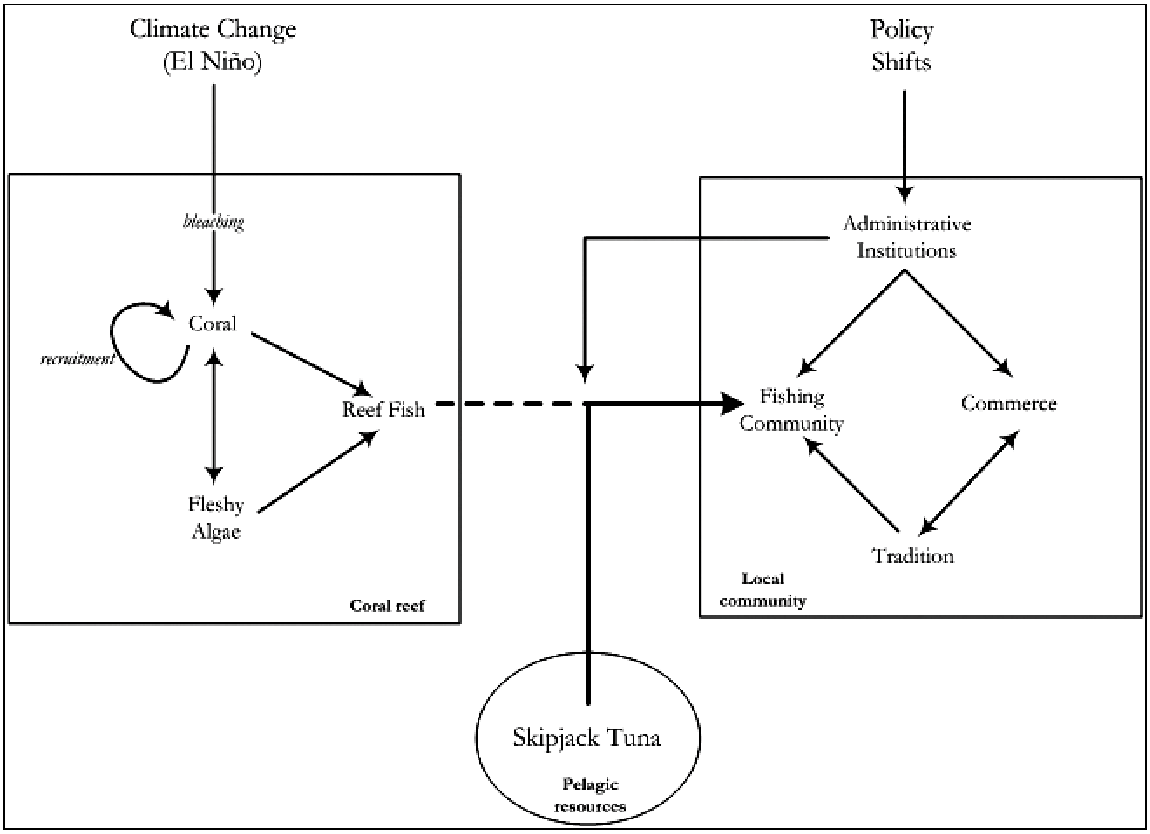


Figure 1.1. A simplified view of the socio-ecological system in the Lakshadweep islands

This thesis traces the history of policy and resource use on the Lakshadweep Islands, and how this has contributed (intentionally or unintentionally) to the resilience of the reef in the face of large infrequent disturbances.

Figure 1.2 applies the conceptual framework of figure 1.1 to the socio-ecological system of the Lakshadweep. It suggests interactions between the coral reef and the human communities that exploit it, and provides a framework for the rest of this thesis.

In **chapter two** I describe the Lakshadweep atolls and present the results of my broad-scale rapid assessment of benthic communities on six atolls in 2002, four years after the coral mass mortality.

Reefs subject to catastrophic coral mortality can sometimes switch over to a state dominated by fleshy macroalgae, from which recovery is often difficult (Done 1992). In **chapter three** I examine changes in benthic and coral communities to determine if such a phase shift occurred in the Lakshadweep atolls. I chose three atolls, Kadmat, Agatti and Kavaratti for detailed study and tracked changes to benthic substrate and coral size structure in these reefs, examining patterns of coral recovery and community assembly from 2000 to 2003.

Coral reef fish play important functional roles in reefs, and contribute to the overall resilience of the system. In particular, herbivorous fish help mediate competitive processes between scleractinian coral and fleshy macroalgae. Declines in fish communities have often been linked to protracted benthic recovery in reefs. Additionally, many trophic groups of fish depend heavily on coral either as a food resource, for shelter, or for ambush cover. The loss of coral after a mortality event could result in significant reductions in the populations of these fish. In **chapter four** I examine changes in the composition of different trophic groups of reef fish from 2000 to 2003, and explore the implications of fish community response to the overall recovery of the Lakshadweep reef system.

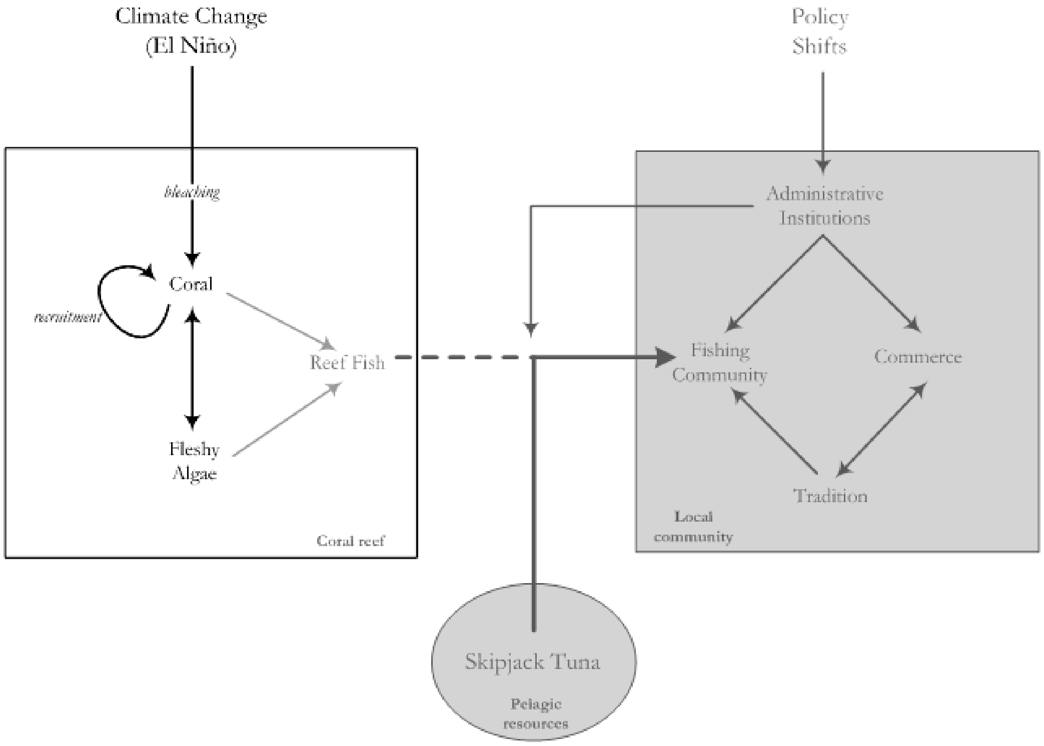
In **chapter five**, I attempt to understand patterns of reef recovery in the Lakshadweep within the conceptual framework of alternate ecosystem states. Catastrophe theory has been used successfully to describe state changes in a number of other ecosystems, and I explore its utility to coral reef systems. The cusp catastrophe is a simple topological model that integrates discontinuous ecosystem behaviours within an otherwise continuous system. The advantage of the cusp catastrophe model for the manager is that it is phenomenological and based on relatively few control variables. Observable management thresholds provide a tangible direction for management, allowing a constant assessment of management success against previously specified indices of ecosystem performance. The model suggests that, in an environment of increasing uncertainty, effective management requires an understanding the nature of ecological surprise while managing for ecosystem resilience.

In **chapter six** I present an historical analysis of fishing practices in the Lakshadweep, and the relationship between institutional structures that control it. Before the 1960s, the Lakshadweep fishery was a sustenance fishery, concentrated mostly in the lagoon and reef to meet daily requirements. Fish was an item of occasional barter but it was never a cash crop. The introduction of a government-sponsored programme to develop a fishery for pelagic tuna changed these traditional systems. I explore the success of this programme and its inadvertent consequences for the resilience of the reef.

In conclusion, **chapter seven** draws salient lessons from the Lakshadweep case study as it relates to the management of coral reef systems in the developing tropics. In the Lakshadweep, the reef was released from fishing pressure by an activity that was geared not towards reef management but towards fisheries development. The Lakshadweep example suggests that there is more than one path to achieving ecosystem resilience. While the marine protected area may still be our best bet to maximize ecosystem health in an unpredictable environment, it often threatens the basic food security of local communities and is expensive to establish and enforce. I argue that in these circumstances, it is easier to support a programme of proactive development than it is to promote conservation. In many areas of the developing tropics like the Lakshadweep, this approach might be the most effective way of ensuring ecosystem resilience in an era of rapid transformation.

Chapter II and Chapter III

BENTHIC CHANGE IN THE LAKSHADWEEP AFTER THE 1998 EL NIÑO



In Chapter 2 and Chapter 3 I examine the consequences of the 1998 El Niño on the benthic composition of Lakshadweep Reef. In Chapter 2, I introduce the Lakshadweep island, and provide a brief socio-historical overview of the islands. I then present the results of a 2002 rapid assessment of six atolls across the archipelago. The response of benthic communities was patchy, but there were clear differences in the cover of live coral and dead standing coral between aspects.

In Chapter 3, I look at temporal trends in benthic composition from 2000 to 2003. I look at changes in coral composition, and in the size distribution of coral populations through time. Recovery between aspects varied considerably at most atolls, driven by differences in substrate viability between the east and west. Corals with very different susceptibilities to bleaching appeared to be doing well in the post-bleached reefs, suggesting that species with different disturbance strategies could succeed after catastrophic mortality events.

Chapter II

A rapid assessment of Lakshadweep coral reefs four years after an El Niño-induced coral mass mortality

2.1 Introduction

2.1.1 Coral reef responses to climate change

The El Niño event of 1997-1998 raised sea surface temperatures (SSTs) significantly above seasonal averages, causing large-scale coral mortality at many reef locations across the tropics (Wilkinson 1998). Under stress, the chemical pathways that sustain the symbiotic relationship between algal zooxanthellae and their coral hosts are seriously compromised, and corals expel zooxanthellae, turning pale and then bleaching white (Douglas 2003). While bleaching may be a routine response to minor stresses, when unfavourable conditions are protracted, corals may bleach *en masse*, and eventually die (Brown 1997). Although temperature-related bleaching had been implicated in occasional mass mortality of coral prior to 1997 (Gleason 1993, Glynn 1993, Goreau & Hayes 1994), the effects of the 1997-1998 ENSO on reefs was unprecedented in intensity, duration and extent. Anomalous temperatures rose to previously unrecorded levels, causing mass bleaching of coral in reefs across the tropics at scales never recorded before. Many reefs recovered relatively quickly from this disturbance, but at several locations, corals were not able to recover and sustained considerable reductions to their populations (Baird & Marshall 1998, Wilkinson 1998, Edwards *et al.* 2001, Aronson *et al.* 2002, McClanahan *et al.* 2002a).

The severity of this event, and the response of reefs around the world to it, was interpreted as a clear signal of increasing climate change (Stone *et al.* 1999). Forecasts of climate data suggest that the 1997-1998 El Niño presages an environment where SST anomalies will increase in intensity and frequency, resulting in recurrent and wide-spread coral bleaching and mortality events, possibly every year (Hoegh-Guldberg 1999). It is unclear how long reefs will continue to be able to maintain ecological function under this sustained pressure. Corals are the dominant structural element in reefs, and their loss could result in major changes in benthic topography and flow-on consequences for other species, including fish. Additionally, the loss of coral could benefit opportunistic species like fleshy macroalgae, which often rapidly overtake benthic substrate, radically altering functional states, and potentially precluding the reestablishment of coral in these areas (Hay 1997, Miller 1998, McCook *et al.* 2001). Once precipitated, these changes in functional state, called phase shifts, can be remarkably difficult to reverse (Done 1992, McManus & Polsenberg 2004). Human communities in the developing tropics depend heavily on reefs for food security as well as a range of other ecosystem services (Moberg & Folke 1999), and the reduced function of reefs could potentially have a large impact on these economies (Bellwood *et al.* 2004).

2.1.2 El Niño influences on coral reefs in the Indian Ocean

Many reefs in the Indian Ocean were severely affected by the anomalous SST event of 1997-1998. Coral mass bleaching and mortality was reported in various locations including the East African coast, the reefs of continental India, Sri Lanka, and from several oceanic islands (Wilkinson 1998, Öhman *et al.* 1999, Arthur 2000, Spencer *et al.* 2000, McClanahan *et al.* 2001). The reefs in northern Indian Ocean atoll chain were particularly badly affected: for instance, reefs in the Chagos and Maldives experienced large-scale bleaching of coral, with as much as 90% post-bleaching mortality in many reefs (McClanahan 2000a, Sheppard *et al.* 2002, Sheppard 2003). The Lakshadweep archipelago is situated at the northern end of this atoll chain, and its reefs have generally received far less attention than those of the Maldives or the Chagos. As part of a broader assessment of bleaching impacts on Indian coral reefs, I surveyed shallow-water sites in the Lakshadweep in mid-1998, at the peak of the SST anomaly (Arthur 2000). Bleaching was widespread, and much coral had already succumbed to temperature-related mortality. By December of 1998, surveys of deeper reefs indicated extensive bleaching mortality, with live coral reduced to less than 5% of benthic cover at many sites (Arthur 2000, Jason Rubens personal communication). These surveys were restricted to a few accessible islands, and it was unclear if reefs in other atolls in the chain were similarly affected.

The chain of archipelagos along the Lakshadweep-Chagos submarine ridge is relatively isolated from other major reef areas, and probably functions as a closed metapopulation with rare inputs from more distant reefs. Consequently, a short- to medium-term failure in coral recruitment may have resulted in a protracted period of benthic recovery in the aftermath of the 1998 coral bleaching event. Later chapters will trace temporal patterns of recovery of benthic (Chapter 3) and fish communities (Chapter 4) in three Lakshadweep atolls. In this chapter, I introduce the Lakshadweep islands, providing a brief description of the socio-ecological environment of the region. I then present the results of a rapid assessment of reefs in 2002, four years after the 1998 bleaching event. The purpose was to survey Lakshadweep's reefs extensively rather than intensively, with limited resources and time. I assessed benthic substrate at reefs sites on six atolls across the island chain to ascertain reef status at a broad spatial scale.

2.2 Study area: The Lakshadweep atolls

The Lakshadweep is an archipelago of small coral atolls situated at the northern end of the Lakshadweep-Chagos chain of reefs in the Indian Ocean. The Lakshadweep group comprises 27 coral islands occupying a total land area of approximately 32 km^2, between 8° N—12° N, and 71° E—74° E (Figure 2.1). The island chain has three separate administrative units. The

Figure 2.1 Atoll reefs of the Lakshadweep Archipelago in the northern Indian Ocean. The boxed region shows the area enlarged in Figure 2.2.

northernmost islands, Bitra, Chetlat, Kiltan, Kadmat and Amini form the Amindivi group. The Laccadive group comprises Androth, Kalpeni, Kavaratti, Agatti and Bangaram, together with several uninhabited islets and atolls. South of the Nine Degree Channel, the southernmost island of Minicoy forms an administrative unit of its own. My work on the islands was restricted to the islands of the Amindivi and Laccadive group (Figure 2.2).

Figure 2.2 Map of the Amindivi and Laccadive atolls. Triangles mark atolls chosen for rapid assessment

The region is strongly influenced by the southwest monsoonal system. The monsoon forms off the East African coast in early summer, and reaches the Lakshadweep in mid-May, bringing rain, rough wave conditions, and a strong easterly current to the atolls until the monsoon retreats in mid-September (Shankar 2000, Shankar *et al.* 2002). The atolls have a distinct windward (west) and a leeward (east) aspect in relation to the monsoon. Between May and September western reefs are subject to strong winds, high waves, and rough sea conditions. For the rest of the annual cycle the western reefs remain relatively calm. The eastern reefs on most atolls are largely protected from the rough wave and wind conditions of the monsoons.

The monsoonal system also profoundly affects island formation. Typically, atolls in the Lakshadweep atolls enclose between one and four islands, almost invariably located along the eastern rim of the atoll as thin arcuate strips of depositional coral and sand, away from the high-energy western aspect. The islands are low-lying and rarely rise above 5 msl. The lagoons are generally shallow (3-5 m on average) and are dominated by sand and seagrass beds with a few patchy corals (Rodrigues *et al.* 1997, Jagtap 1998).

The islands have been known to sailors and traders plying the Indian Ocean for several centuries; the earliest references to the atolls and its islands date back to 1 A.D. (Tripati 1999). There have been human populations on the Lakshadweep since at least 11 A.D. (Singh *et al.* 1993), although archaeological evidence suggests that they have been populated for 1,500 years if not longer (Saigal 1990). Local tradition has it that the islands of Amini, Androth, Kavaratti and Kalpeni were the first to be colonized and human populations gradually spread to every inhabitable island in the archipelago (Saigal 1990); a total of 11 of the 27 islands are populated at present. The major factors limiting the spread of populations to other islands are the area available for colonisation, and the presence of reliable potable ground water. Despite this, the most recent colonisation was on the northern island of Bitra, which has a land area of only 0.1 km^2 and a tiny reserve of fresh water prone to sea-water pollution when levels fall low every summer.

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Figure 2.3 Human population increase in the Lakshadweep Islands from 1901 to 2001. Data is from decadal censuses (Directorate of Census Operations 2001). The increase in growth rates after 1961 coincides with the introduction of a series of health and developmental programmes initiated by the Indian government after the Lakshadweep became a Union Territory of India in 1956.

Apart from for the island of Minicoy, the islanders share a close ethnicity with coastal communities in Kerala, in south-west India (Singh *et al.* 1993). The inhabitants speak *Jasseri*, a dialect of *Malayalam*, spoken in Kerala. The inhabitants of Minicoy, at the southern end of the chain, are ethnically closer to Maldivian communities, and speak *Mahl*, a variant of *Dwihehi* spoken in Maldives. Islam is the dominant religion, and most of the islanders belong the Sunni sect, though there is also a small following of mystic Sufism, and Sufi priests are highly revered in the community. Religion is an important part of life, and Muslim religious leaders play a pivotal role in the community. This is discussed further in Chapter 6.

With an average population density of nearly 2,000 individuals/km^2, the Lakshadweep is among the most densely populated non-urban regions in India. The first population census in 1901 recorded less than 14,000 individuals on the islands, and in the next 60 years, population numbers increased slowly to around 24,000 individuals in the 1961 census (Figure 2.3). By contrast, between 1961 and 2001, there was an approximate three-fold increase in population numbers, and at the last census, the human population comprised were more than 60,000 individuals. These data represent a decadal increase of 17%, which, though high, is lower than the overall rate of increase for India (Directorate of Census Operations 2001). The rapid rate of population increase after the 1960s coincided with a concerted programme of emancipation undertaken by the Indian government. The islands were declared a Union Territory of India in 1956, bringing them under direct administrative control of the central government; an action which marked a turning point in the socio-economic development of the islands (Saigal 1990, Singh *et al.* 1993). A series of developmental programmes was undertaken including the establishment of medical centres, schools, and marketing co-operatives. Additionally, there were marked improvements in shipping and transport, allowing far greater contact with the Indian mainland than was possible before. Much of this development is supported by a heavy subsidy culture, and its implications for marine resource use are discussed in Chapter 6.

In-water ecological studies of the Lakshadweep reefs are scarce. Gardiner (1903) described the corals of Maldives and Lakshadweep, but his observations of Lakshadweep were restricted to the southernmost island of Minicoy. Since then, taxonomic descriptions and surveys make up the bulk of the literature on Lakshadweep ecosystems, along with studies on the exploitation potential of reef and lagoon resources (Bakus 1994, Balasubramaniam & Khan 2001). No reliable estimates exist of reef benthic communities for Lakshadweep reefs prior to 1998. The bulk of available information on the state of the coral reefs in the Lakshadweep prior to the 1998 mass-bleaching event is from anecdotal accounts from local fishermen and islanders, recreational divers, and personal observations. From these accounts, and from my own casual observation, scleractinian coral dominated the benthic substrate at most sites in the Lakshadweep, with estimates of between 60% to 90% coral cover in reefs to a depth of 20 m. Benthic surveys in the Maldives and Chagos concur with these estimates, reflecting similar high-coral cover communities across the region (McClanahan 2000a, Sheppard *et al.* 2002).

2.3 The 2002 survey of the Lakshadweep atolls:

2.3.1 Methods

I surveyed six atolls in the Amindivi and Laccadive group of islands between March and May, 2002. These were Agatti, Bitra, Chetlat, Kadmat, Kavaratti and Kiltan (Figure 2.2). A brief profile of each atoll is provided in Table 2.1. I sampled three randomly located sites on the east and west aspects of each atoll. At each sampling location, I used a tape measure to mark a 5x5m quadrat area. Within the quadrat, I visually estimated cover of benthic components including live coral, dead standing coral, algal turf, coralline algae, fleshy macroalgae, calcareous algae, soft coral and other sessile organisms. I conducted a timed search within the quadrat to estimate the relative abundance of coral genera in each quadrat; all coral genera encountered in a 5 minute slow swim of the quadrat were recorded, along with the minute interval in which they was first seen. This technique assumes that, on average, the most abundant genera are more easily visible and are therefore encountered before rarer genera in a timed search. Five minutes was determined to be adequate to sample an area of 5x5 m, as the number of new genera recorded after the third minute declined to less than 1 on average (Figure 2.4). After sampling for genera, I swam in a random direction along the depth contour for 50m (measured with a tape measure) to establish a new sampling location. Six quadrats were sampled at each location in a depth range of 8 to 14 m, along the slope of the outer reef.

Table 2.1. Characteristics of atolls surveyed. Population figures are provisional data from the Directorate of Census Operations (2001).

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Average percent cover estimates were compared between islands to determine trends in benthic substrate. Sites on the east and the west were compared for differences between aspects. Coral genera recorded in each quadrat were assigned abundance values based on the minute interval in which they were first sighted in the timed count. This method resulted in a scale of relative abundance that ranged from 1 (genera recorded in the 5th minute: least abundant) to 5 (genera recorded in the first minute: most abundant). Relative abundance was averaged across all quadrats at sampled reefs on the east and west. I performed a hierarchical cluster analysis based on square-root transformed Bray-Curtis similarities of coral communities between sites to compare patterns of composition across the Lakshadweep (Magurran 1988). I used the software programme PRIMER 5 for cluster analysis (Clarke & Warwick 1994, Clarke & Gorley 2001). I used Excel for Windows for all other analysis.

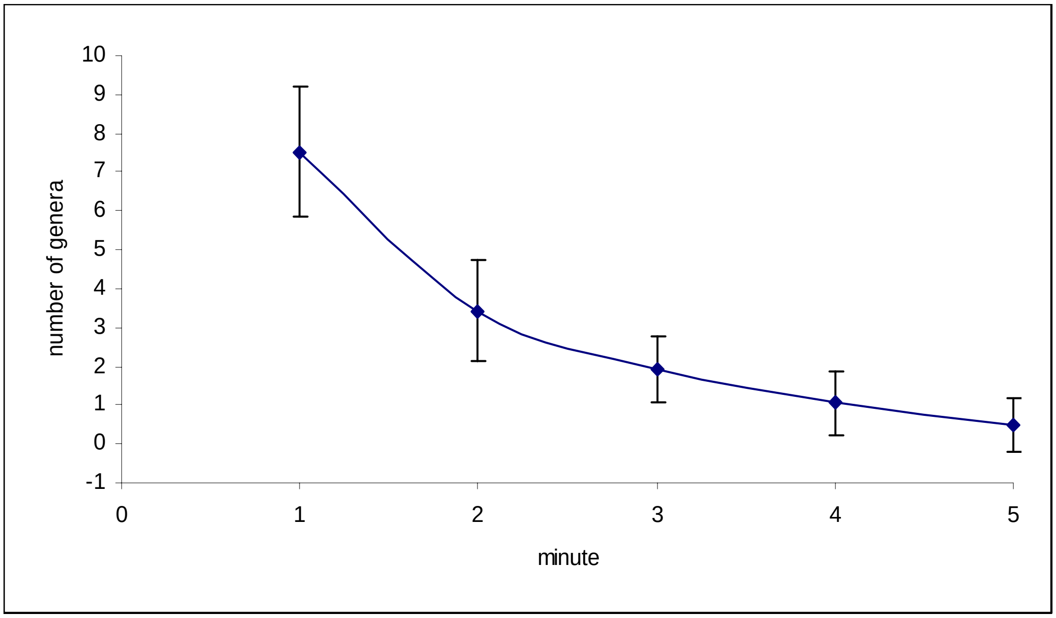

Figure 2.4 Average number of coral genera encountered on 5 minute time counts in 5x5 m benthic quadrats. There was a considerable decline in encounter rates with time, and in the 5th minute, less than 1 individual was recorded on average. This suggests that 5 minutes was an adequate search time to characterise the generic composition of these reefs.

2.3.2 Results

The cover of live coral varied considerably in reefs across the Lakshadweep. There were few noticeable geographical trends in cover between atolls (Figure 2.5). While northern atolls such as Chetlat and Bitra had relatively high live coral cover, this trend was not consistent: the northern atolls of Kiltan and Kadmat had the lowest recorded cover of live coral. However, there was a distinct difference in live coral cover between aspects. Reefs on the east had considerably lower coral cover than western reefs at most atolls (Figure 2.6). The exceptions to this pattern were Kavaratti and Chetlat, there were little observable differences in cover between aspects. By contrast, the cover of dead standing coral was considerably higher on eastern reefs in 2002, except at Kavaratti, where there were no noticeable differences (Figure 2.7).

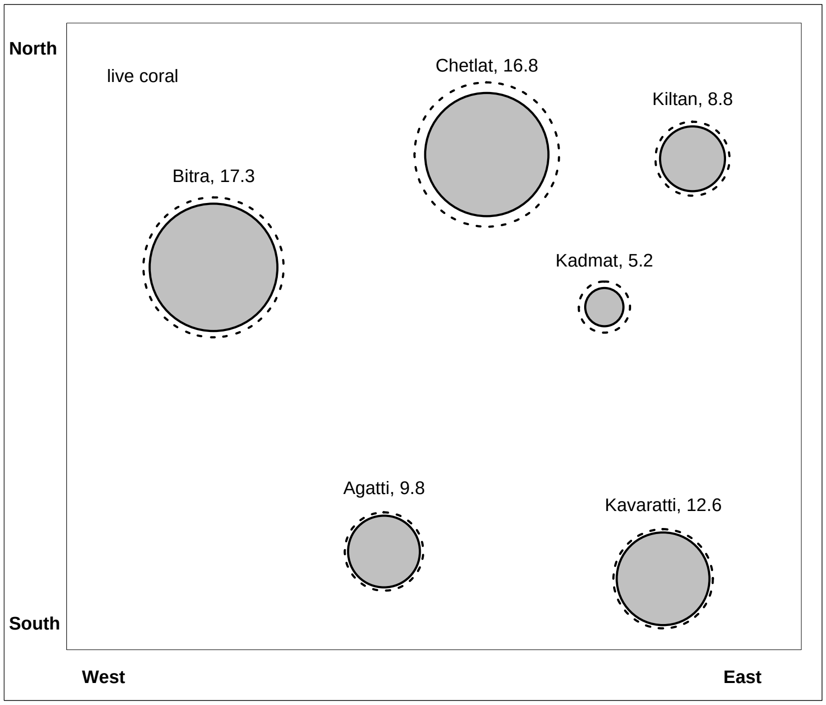

Figure 2.5 Live coral cover at Lakshadweep reefs in 2002. Bubble size represents relative percent cover of coral at each location. Dotted lines are positive standard errors

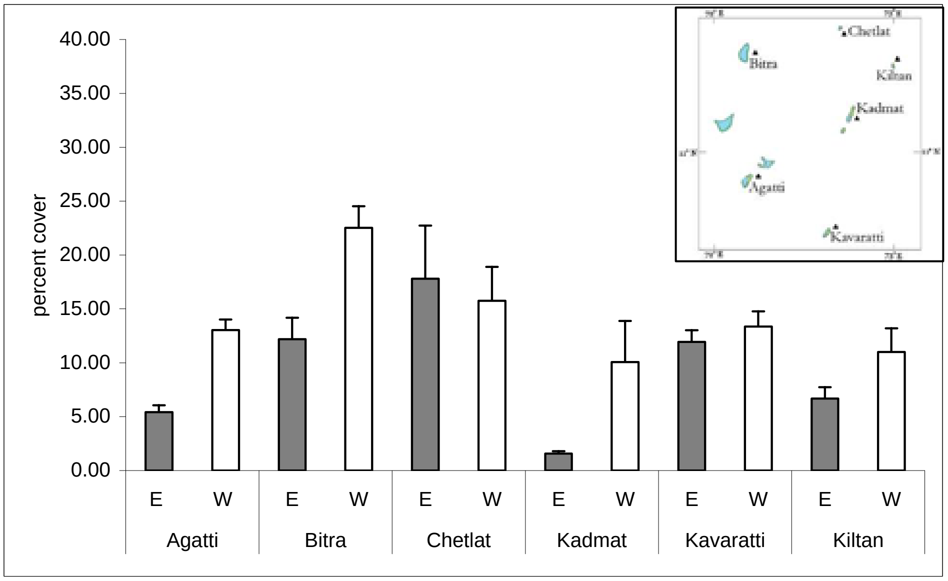

Figure 2.6 Percent cover of live coral in Lakshadweep reefs in 2002. Bars represent average live coral cover on the east (E) and west (W) aspects of sampled atolls. Error bars are standard errors.

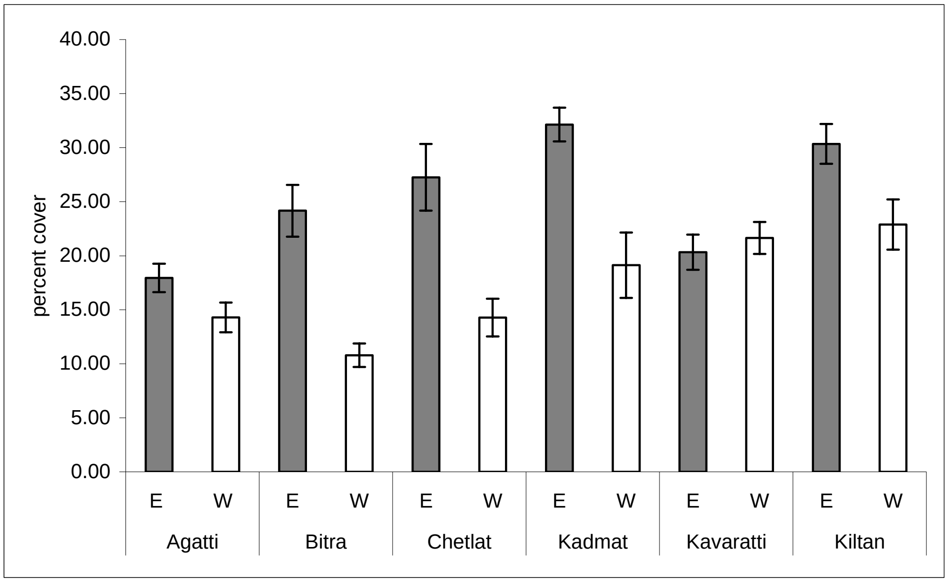

Figure 2.7 Percent cover of dead standing coral in Lakshadweep reefs in 2002. Bars represent average live coral cover on the east (E) and west (W) aspects of sampled atolls. Error bars are standard errors.

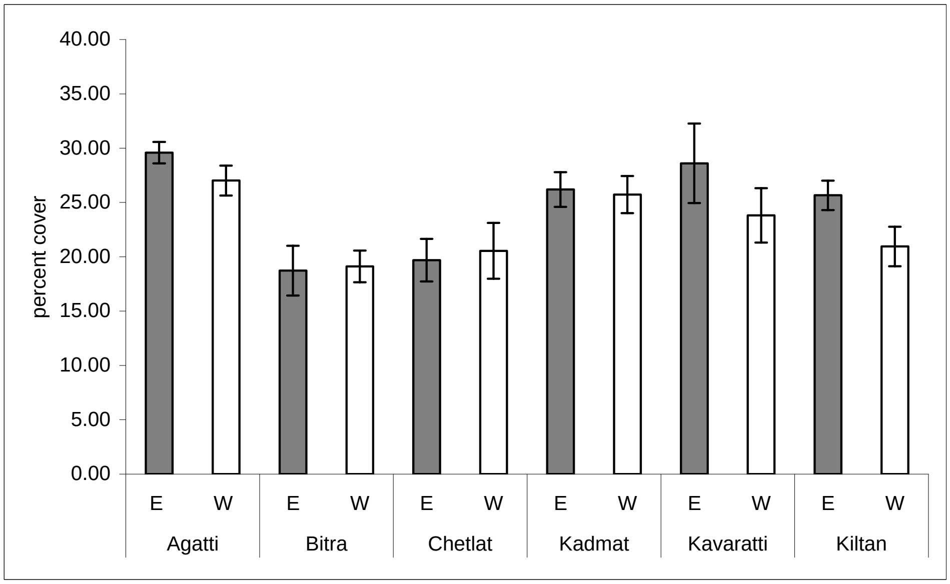

Figure 2.8 Percent cover of algal turfs in Lakshadweep reefs in 2002. Bars represent average live coral cover on the east (E) and west (W) aspects of sampled atolls. Error bars are standard errors.

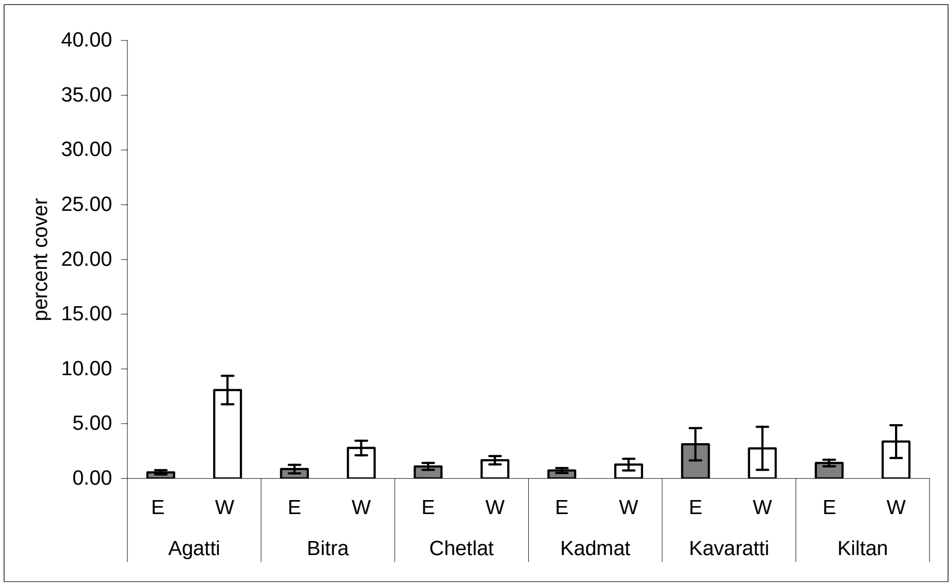

Figure 2.9 Percent cover of fleshy macroalgae in Lakshadweep reefs in 2002. Bars represent average live coral cover on the east (E) and west (W) aspects of sampled atolls. Error bars are standard errors.

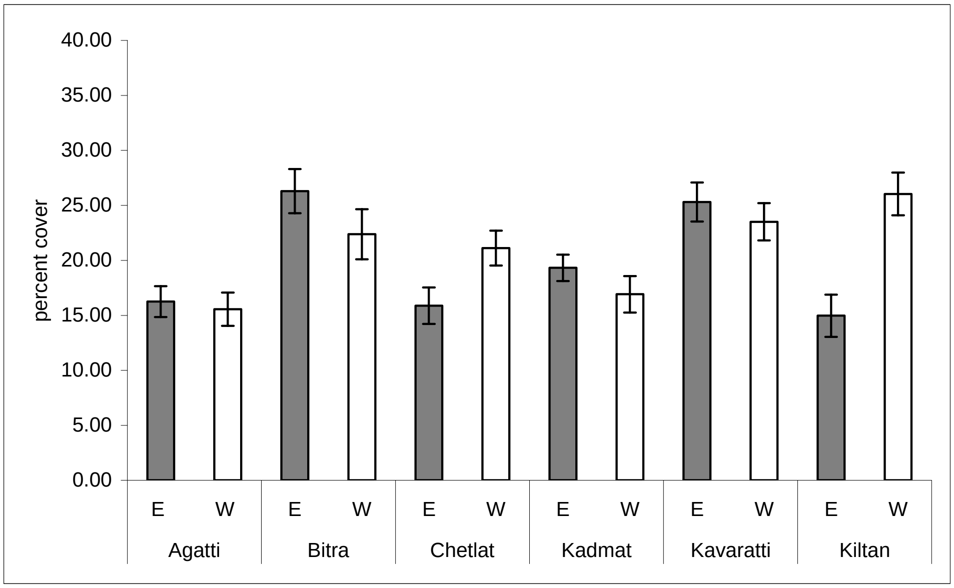

Figure 2.10 Percent cover of coralline algae in Lakshadweep reefs in 2002. Bars represent average live coral cover on the east (E) and west (W) aspects of sampled atolls. Error bars are standard errors.

Algal turf was a dominant benthic component in most reefs in the Lakshadweep, occupying 19% to 30% of the substrate (Figure 2.8). There were considerable differences in the cover of turf algae between atolls, but it did not differ much between aspects for most reefs. By comparison, fleshy algal cover was never dominant in outer reefs and generally occupied less than 3% of the substrate, except for the western reefs of Agatti, where fleshy macroalgal accounted for 8.1% of benthic cover (Figure 2.9). Coralline algae were also abundant at most sites, but there were few clear trends between atolls or aspects (Figure 2.10).

A total of 41 genera were recorded in timed counts from the Lakshadweep. The most common genera across all sites included *Porites*, *Favites*, *Acropora*, *Pavona*, and *Galaxea*. There were weak geographical trends in the composition of coral across the archipelago. The atolls of the Amindivi group in the north (Bitra, Chetlat, Kiltan and Kadmat), were more similar in generic composition than the more southern atolls of the Laccadive group, Agatti and Kavaratti (Figure 2.11). The composition of reefs on Kadmat West was the one exception to this trend, and was different from all other sites.

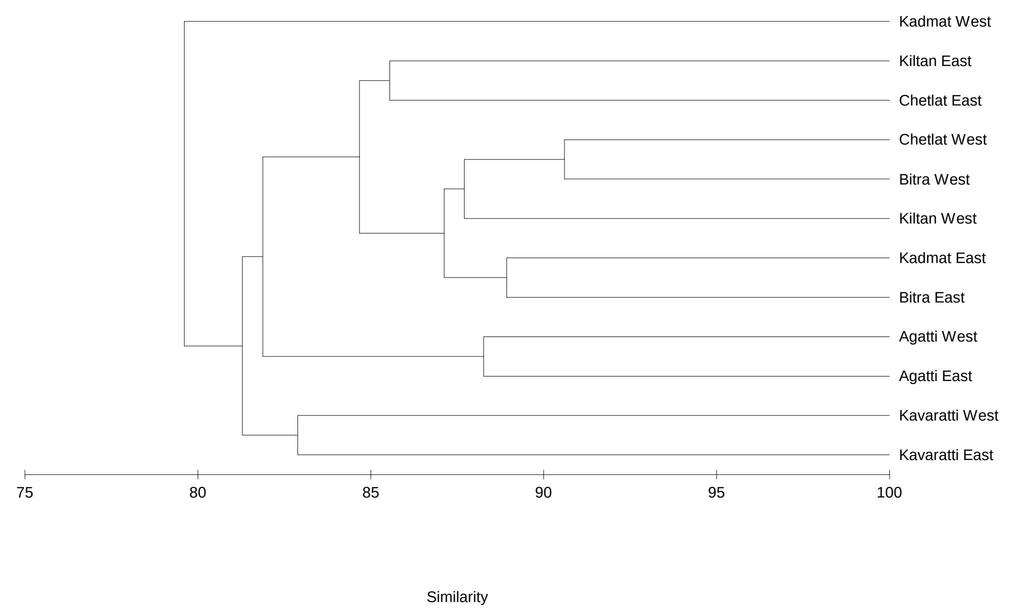

Figure 2.11 Similarity of coral composition in the Lakshadweep islands. The dendrogram is a group means clustering of Bray-Curtis similarity between sampled sites.

Aspect appeared to play an important part in determining coral composition, particularly at northern reefs, where there were closer affinities between aspects than between atolls. For instance, western reefs of Chetlat, Bitra and Kiltan cluster together, while the eastern reefs form two separate clusters (Kiltan and Chetlat, and Kadmat and Bitra). By contrast, at Kavaratti and Agatti, sites were more similar within atolls than between aspects (Figure 2.11).

2.4 Discussion

It is often difficult to predict how reefs will respond to catastrophic disturbances such as coral mass bleaching events (Berkelmans *et al.* 2004). The recovery of corals in reefs after such incidents is likely to be dependent on the interaction of several factors including the scale of the disturbance, the availability, settlement success, and growth of coral recruits, the mediation of competitive exclusion by other species, and the presence of anthropogenic stressors (Pearson 1981). Because of the complexity of these interactions, the recovery of reefs is highly variable: whereas in some instances, reefs may show few signs of recovery, and others take decades or more to begin returning to coral dominance, others may regain their full complement of coral cover in as little as five years (Loya 1976, Pearson 1981, Tomasik *et al.* 1996). In a long-term study of Heron Island reefs in the Great Barrier Reef, Connell and others (2004) found that recovery of coral species diversity and richness after catastrophic cyclones can vary from three to 25 years. This study was done at very small spatial scales (1m^2 quadrats), but variation in recovery after disturbance has been recorded at entire reef scales as well (Endean 1976). While Chapter 3 looks at temporal patterns in benthic recovery, the current survey was designed to establish the broader geographical response of Lakshadweep reefs to the 1998 coral mortality.

Without a comparative baseline, this rapid survey can only provide a snapshot of reef condition four years after the 1998 anomalous SST event. However, there is a strong indication that coral mortality was high throughout the atoll chain. Much of the live coral cover recorded was evidently from new growth, particularly in many western sites, where relatively small-sized colonies (~10 cm to 50 cm maximum diameter) of fast-growing genera like *Acropora* were growing rapidly. Despite this, coral cover was still less than 25% of the benthic cover at most reefs, and the substrate was conspicuously dominated by thin algal turfs that grew on the dead skeletons of coral. The fact that there were no discernable geographical trends in coral cover, points to the importance of local environmental conditions in determining the recovery of these reefs. Variability in the initial response of reefs to increased ocean temperatures may have resulted in patchy mortality across the archipelago. The subsequent regrowth of remnant populations and the settlement success of post-1998 coral recruits could also vary considerably between atolls, creating a response mosaic, with some atolls, like Bitra, recovering well, while others, like Kadmat and Kiltan, considerably slower in their recovery. This geographical patchiness is probably characteristic of disturbances like bleaching, where the response of coral may be influenced by a complex interaction of large scale and local-scale processes (Andréfouët *et al.* 2002, Wooldridge & Done 2004).

Despite individual variation between atolls, differences in coral cover between aspects were striking: for most atolls, coral cover was considerably higher on western reefs in comparison with eastern reefs (Figure 2.6). By contrast, the cover of dead standing coral was almost always higher on eastern reefs (Figure 2.7). This pattern reflects differences in hydrodynamic influences between aspects, particularly during the summer monsoon. Monsoon currents flow eastward across the Arabian Sea, bringing stormy conditions to the west-facing reefs of the Lakshadweep from May to September (Shankar 2000). These summer storms potentially perform a vital role in removing dead unstable coral from western reefs at a much faster rate than at eastern reefs. This difference could have differentially affected the long-term viability of settlement substrate on the east and west, and possibly drives the difference in live coral between aspects. The interaction of settlement substrate and coral recovery is discussed in more detail in Chapter 3.

Differences in environmental conditions between aspects likely also influenced generic composition of coral on the east and the west. For most of the northern atolls, community composition was more similar between aspects than within atolls (Figure 2.11), suggesting that differences in conditions between aspects may favour particular groups of genera over others. Northern reefs may share better connectivity than reefs further south: coral communities here have a high similarity, and clustered tightly together. In contrast, coral composition at Kavaratti and Agatti was distinct within atolls, suggesting that these more southern reefs may be less well connected to other reefs. A detailed knowledge of local currents and patterns of recruitment will be required before these trends can be fully understood.

Despite relatively low live coral cover at most reefs, fleshy macroalgae were not dominant at any of the sampled locations. This situation was encouraging for the future recovery of coral in these reefs, as it reduces the potential for competitive exclusion by fast growing, opportunistic macrophytes. Several factors could have contributed to low levels of fleshy algae. Open ocean atolls are generally nutrient poor, reducing the growth of algae in these well-flushed systems.

Perhaps more important though is the influence of herbivorous surgeonfishes (Acanthuridae) and parrotfishes (Scaridae). At all reefs surveyed, they were present in large numbers. The potential role of herbivorous fishes controlling algal biomass on Lakshadweep reefs is explored in Chapter 4.

Overall, although cover was relatively low at most atolls surveyed, coral was growing back well at many sites in the Lakshadweep. The genera that dominated the post-bleached reefs included a mix of hardy, bleaching-resistant taxa like *Porites* and *Favites*, and fast-growing taxa like *Acropora*, representing both remnant populations that survived the bleaching as well as cohorts that possibly recruited after 1998. The availability of new recruitment was important for this recovery to take place, and the patchiness of the initial response may have been extremely important to supply recruits to areas with high mortality. The long-term resilience of the Lakshadweep system may be dependent on these refuge sites, and it may be vital to identify, monitor, and protect them from other disturbances (Done 2001, Wooldridge & Done 2004). Global warming and its consequences are impossible to manage at a local scale, but pre-emptive management may help to bolster the natural capacity of coral reef systems to absorb environmental changes and recover from such catastrophic events.

Chapter III

Reef responses to a coral mass mortality: trends in benthic composition, and prospects for recovery

3.1 Introduction

The reefs of the tropical Indian Ocean were severely affected by unusually high sea surface temperatures (SSTs) as a result of the 1997-1998 El Niño Southern Oscillation (ENSO). Mass bleaching and mortality of coral was recorded in many locations from the region. Atoll reefs in the Lakshadweep-Chagos archipelagos in the Arabian Sea were badly impacted, and extensive bleaching of coral resulted in the loss of between 50-90% of coral cover in reefs across the island group (McClanahan 2000a, Sheppard *et al.* 2002, Sheppard 2003). My rapid assessment of shallow reefs at two atolls in the Lakshadweep indicated that after approximately 78 days of anomalous SSTs in 1998, more than 81% of corals had bleached, and more than 30% of bleached corals were already dead (Arthur 2000). By December of that year, live coral was reportedly as low as 5% of the benthic substrate at many reef sites (Arthur 2000).

This catastrophic mortality raised crucial questions about the recovery potential of these reefs, and the long-term resilience of the ecosystem to a changing climate regime. Given the high impact of mortality on adult coral populations, recovery was likely to be dependent more on recolonization by coral recruits than regrowth of remnant individuals. The Lakshadweep-Chagos archipelagos are relatively isolated from other reef systems, possibly functioning as a single metapopulation, dependent largely on local larval pools for recruitment. The intensity and extent of bleaching-related mortality in 1998 recorded across all three archipelagos (Chagos, Maldives and Lakshadweep) set the conditions for a breakdown in these recruitment processes, significantly retarding the pace of recovery, if not precluding it completely in the medium term (Arthur 2000, McClanahan 2000a). In this chapter, I examine three fundamental questions about the recovery processes in the Lakshadweep reefs:

3.1.1 Was there a shift in state away from coral dominance?

Scleractinian corals contend with each other and other sessile organisms like macroalgae for settlement space and light, using a number of competitive mechanisms including space pre-emption, overgrowth, shading, or direct competition (Lang & Chornesky 1990). The results of interactions between corals and macroalgae depend on the specific competitive abilities of different coral and algal species, and there is no clear competitive dominance of one group over the other (McCook *et al.* 2001, Jompa & McCook 2003). However, after a major die-off of corals, fast-growing macroalgae can often increase in biomass, and opportunistically occupy the released benthic space (Endean 1976). This can trigger a sudden switch in composition to an ecosystem state dominated by macroalgae, and it is often difficult for corals to re-establish in these reefs. This transition in benthic state or 'phase shift' is often difficult to reverse, and has cascading effects on other reef species, significantly lowering ecological functioning (Done 1992, Nyström *et al.* 2000, McManus & Polsenberg 2004). The phase shift from corals to macroalgae is almost invariably preceded by the loss of coral cover caused by a disturbance event, and may often be catalysed by environmental or anthropogenic conditions that favour algal growth, such as nutrient concentrations, or the reduction of herbivores by over-fishing or disease as was the case in Jamaican reefs (Hughes 1994). The scale of the coral mass mortality in the Lakshadweep, together with the possibility of a regional failure in recruitment, and the anthropogenic pressures of a high population density, made a phase shift a likely outcome in these reefs (see Bellwood *et al.* 2004). I monitored changes to benthic composition to determine if there was a change in dominance from coral to fleshy macroalgae.

3.1.2 How did coral populations respond to the mass mortality?

No detailed in-water studies of coral community structure in the Lakshadweep exist prior to 1998. It is therefore not possible to compare pre- and post-disturbed reef conditions to determine how coral populations responded to the bleaching event. However, an analysis of coral size structure can serve as a valuable proxy for the dynamics of post-disturbance change. For instance, an examination of skews in size distributions can shed light on trends in recruitment, survival and growth of populations after a major disturbance event (Bak & Meesters 1998). From 2001 to 2003, I tracked changes in coral size distributions in the Lakshadweep, to examine these population patterns.

3.1.3 Was there a shift in coral composition to more bleaching-resistant genera?

Corals appear to be surprisingly plastic in their life-history strategies, and the classic trade-off between competitive ability and disturbance resistance is far less established for coral species. Competitive interactions between species are often complex and diffuse rather than hierarchical (Chornesky 1989, Lang & Chornesky 1990). Community composition and species turnover in recovering reefs is therefore contingent on a suite of factors that make it difficult to predict the response of coral assemblages to disturbance. With respect to temperature stress however, corals show relatively consistent patterns of susceptibility to bleaching (McClanahan *et al.* 2004), though the degree of tolerance may vary with location, and the history of environmental influences in the region (Loya *et al.* 2001, Obura 2001, Fitt *et al.* 2001, Brown *et al.* 2002b). The susceptibility of coral species to bleaching is emerging as a potentially important trait in predicting community patterns in post-bleached reefs as communities 'adapt' to changing environmental conditions (Done 1999, Done 2001). In reefs dominated by frequent temperature stress, coral species with higher temperature stress should be favoured (Loya *et al.* 2001). I analysed relative change in the cover of coral genera to determine if bleaching susceptibility could adequately explain the relative success or loss of genera in recovering reefs.

3.2 Methods

3.2.1 Field Methods

Three atolls were chosen for this study: Agatti, Kavaratti and Kadmat (Figure 3.1). Reefs at all three atolls were affected by the coral mass mortality of 1998 but to differing degrees. Kadmat and Agatti suffered extensive post-bleaching mass mortality. Post-bleaching coral mortality was considerably less in Kavaratti. One of the primary aims of this study was to provide a baseline for the region, documenting spatial and temporal patterns of benthic change after the mass mortality of 1998. Two sampling sites were established on each atoll, one on the windward west and one on the leeward east (Figure 3.1). Sites were sampled with SCUBA from 2000 to 2003, except at Kavaratti, where sampling began in 2001. At each site, benthic communities were sampled in 1 m^2 quadrats placed at 10 m intervals along a randomly located tape measure of 50 m, laid along the depth contour of the reef. The Lakshadweep reefs often do not have a distinct crest, and all sampling was done along the slope between 5 m and 12 m depth. Within each quadrat, the areal cover of major benthic components was estimated. A PVC quadrat, subdivided into a grid of 25 squares, was used to estimate cover: each grid square represented 4 % of total cover. The areal cover of benthic communities was estimated in the following broad groups: live coral, algal turf, fleshy macroalgae, crustose coralline algae, filamentous and calcareous algae, and other sessile invertebrates, including soft coral. Other substrate components estimated included dead coral rubble, and sand. In the absence of pre-1998 data on live coral cover, it was conceivable that the cover of dead standing coral could be used as a surrogate for pre-1998 conditions. However, this was abandoned because, two years after the mass mortality, it was very difficult to differentiate bleaching mortality from other mortality, either before or after the 1998 event. Additionally, rates of coral erosion were not homogenous between aspects, seriously biasing any estimate of pre-1998 conditions. Corals were identified to the highest taxonomic resolution possible in the field, and analysed at the level of the genus.

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Figure 3.1 The Lakshadweep islands and surveyed atolls. Study sites were established on the east and west of the outer reefs of Agatti, Kadmat and Kavaratti, represented by stars. Atolls not drawn to scale.

The population size structure of coral communities can reveal trends in recruitment, survival and growth, as well as changes in the relative dominance of species over time. I estimated the distribution of coral size classes in 1 m^2 quadrats from 2001 to 2003. Size structure data was not collected from Kadmat West in 2001. Within each quadrat, the maximum diameter of coral individuals was estimated in seven size classes: <1 cm, 1-3 cm, 3-5 cm, 5-10 cm, 10-20 cm, 20-50 cm and >50 cm. All corals visible within the quadrat were counted. Colonies with more than 50% cover outside the quadrat were excluded. Size classes were used instead of direct measurements to allow more extensive sampling. During an initial period of familiarisation, I measured coral colonies using vernier callipers or a tape measure (depending on the size) before assigning them to size classes to reduce misclassification errors. In all later sampling, doubtful size classifications were verified with a calliper or tape measure. A potential bias in this technique is that individuals in smaller size classes will be under-sampled because they are inherently less detectable, and settle in more cryptic locations than larger size classes. To reduce this bias, the area of the quadrat was thoroughly scanned for smaller size-class corals.

3.3.2 Analytical Methods

The cover of substrate components was averaged across quadrats for each reef and compared between years. Changes in benthic cover over time between aspects was analysed for each atoll independently using a nested ANOVA with the following design: Year + Aspect(Year).

Population size structure of coral communities was estimated as the average number of corals present in each size class averaged across all quadrats at a site. Size structure data was calculated for each coral genus. All genera were pooled together to compare overall size structure between reefs and years.

While the average number of corals in size classes is a valuable indicator of coral establishment and recovery in the reef, the contribution of size classes to areal cover is likely to be very different, with relatively few large size class individuals contributing considerably more to overall cover than several small size class individuals. To estimate the contribution of each size class to total cover, the area of each size class was estimated by first approximating coral colonies to a circle and calculating area based on the average diameter for the size class. Area was then summed across all corals in the quadrat and then scaled to the independently-assessed coral cover estimate for each quadrat. This method reduced the potential overestimate of the contribution of individual coral to overall cover that could result because:

1. Coral were often found in crevices or oriented vertically. They could thus still occupy a large area that would not be reflected in areal cover, which is a two-dimensional projection of a complex three-dimensional space.
2. Larger size classes as defined by this study had a greater size range than the smaller size classes. Therefore, the midpoint diameter used to estimate the area of larger size classes could often overestimate (or underestimate) the actual size of coral individuals. This becomes additionally important since larger size classes contribute much more to overall cover than smaller size classes.

While there is still a level of bias in this method, it provides a more comparable estimate of the distribution of coral size classes based on their cover. The relative contribution of coral sizes to overall cover was compared between reefs and across years.

Changes in percent cover of different genera through time were calculated as the change in generic cover between subsequent years and averaged across all years. A positive change indicates the genus is increasing its relative, while a negative change indicates it is declining in relation to other genera. Relative change in composition was calculated for each reef independently, and for all sites together.

Multidimensional scaling (MDS) was used to elucidate spatial and temporal trends in coral community composition. MDS iteratively ordinates similarity values between samples to produce a relative distribution of points with minimum stress in two or three dimensions (Kruskal & Wish 1978). The similarity index used for the analysis was the Bray-Curtis similarity index, calculated between samples based on percent composition of generic cover. The Bray-Curtis similarity index is given by: $S_{jk} = 100\left(1 - \frac{\sum_{i=1}^{p} \left| y_{ij} - y_{ik} \right|}{\sum_{i=1}^{p} (y_{ij} + y_{ik})}\right)$, where $\mathbf{S_{jk}}$ is the similarity between sites **j** and **k**, $\mathbf{y_{ij}}$ is the cover of the $\mathbf{i^{th}}$ species in the $\mathbf{j^{th}}$ sample, and $\mathbf{y_{ik}}$ is the cover of the $\mathbf{i^{th}}$ species in the $\mathbf{k^{th}}$ sample, summed across all **p** species (Magurran 1988). Relative composition was used rather than average cover/m^2 to standardise for large differences in overall abundance between sites and years, which could otherwise swamp the analysis. The data were then square-root transformed, to reduce the influence of highly abundant genera. Kruskal Stress, a measure of the overall stress of the ordination was calculated for the ordination. The differences between community similarity values between reefs and years was analysed with analysis of similarity (ANOSIM). ANOSIM is analogous to analysis of variance, and examines differences between the similarity values of groups, testing for significance using a Monte Carlo permutation test (Clarke & Warwick 1994). The statistical programme PRIMER was used for MDS and ANOSIM analyses (Clarke & Gorley 2001). The spreadsheet programme Excel for Windows, and the statistical programme Statistica were used for all other analysis.

3.3 Results

3.3.1 Trends in coral and algae: was there a phase shift?

Nearly two years after the mass mortality, coral cover in 2000 was still relatively low in the reefs of Agatti and Kadmat, occupying less than 6% of benthic substrate on average at all sites surveyed (Figure 3.2). Although systematic sampling at Kavaratti only began in 2001, dives off these reefs in

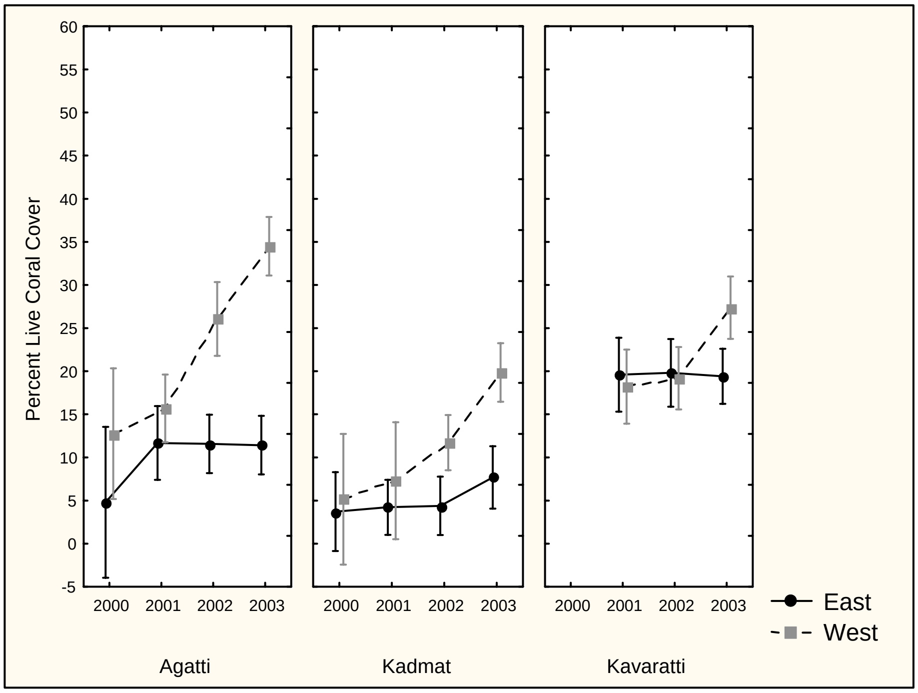


Figure 3.2. Change in live coral cover between aspects at Agatti, Kadmat and Kavaratti from 2000 to 2003. Reefs at Kavaratti were not sampled until 2001. Error bars are 95% confidence intervals.

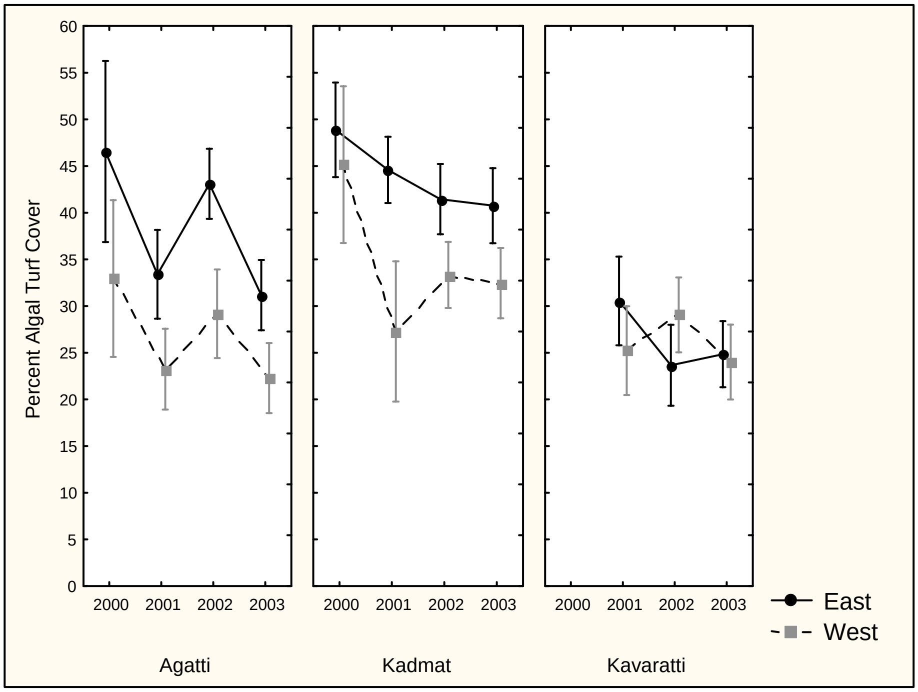


Figure 3.3. Change in cover of algal turfs between aspects at Agatti, Kadmat and Kavaratti from 2000 to 2003. Reefs at Kavaratti were not sampled until 2001. Error bars are 95% confidence intervals.

Table 3.1. Benthic change in the Lakshadweep. ANOVA table for the nested ANOVA comparing trends in benthic components with time (2000 to 2003) and aspects (East and West)

Benthic Component	Atoll	Factor	SS	d.f.	MS	F value	P value
Live Coral	Agatti	Year	4155.39	3	1,385.13	**8.14**	<0.01
		Aspect(Yr)	14315.56	4	3,578.89	**21.03**	<0.01
		Error	35062.41	206	170.21		
	Kadmat	Year	2591.21	3	863.74	**17.90**	<0.01
		Aspect(Yr)	3994.73	4	998.68	**20.70**	<0.01
		Error	11435.62	237	48.25		
	Kavaratti	Year	812.76	2	406.38	2.66	0.07
		Aspect(Yr)	1276.23	3	425.41	2.79	0.04
		Error	28823.72	189	152.51		
Turf Algae	Agatti	Year	4509.47	3	1,503.16	**16.69**	<0.01
		Aspect(Yr)	6604.65	4	1,651.16	**18.34**	<0.01
		Error	18549.52	206	90.05		
	Kadmat	Year	2223.09	3	741.03	**3.45**	0.02
		Aspect(Yr)	5209.84	4	1,302.46	**6.07**	<0.01
		Error	50889.83	237	214.73		
	Kavaratti	Year	381.36	2	190.68	1.57	0.21
		Aspect(Yr)	838.15	3	279.38	2.29	0.08
		Error	23024.95	189	121.83		
Fleshy Macroalgae	Agatti	Year	135.03	3	45.01	**8.54**	<0.01
		Aspect(Yr)	279.97	4	69.99	**13.28**	<0.01
		Error	1085.84	206	5.27		
	Kadmat	Year	1797.52	3	599.17	**14.49**	<0.01
		Aspect(Yr)	490.40	4	122.60	2.96	0.02
		Error	9802.65	237	41.36		
	Kavaratti	Year	90.04	2	45.02	**9.06**	<0.01
		Aspect(Yr)	143.23	3	47.74	**9.60**	<0.01
		Error	939.50	189	4.97		
Crustose Coralline Algae	Agatti	Year	1292.84	3	430.95	**4.46**	<0.01
		Aspect(Yr)	2192.84	4	548.21	**5.68**	<0.01
		Error	19899.51	206	96.60		
	Kadmat	Year	6472.80	3	2,157.60	**16.83**	<0.01
		Aspect(Yr)	2716.38	4	679.10	**5.30**	<0.01
		Error	30383.41	237	128.20		
	Kavaratti	Year	1591.85	2	795.93	**4.32**	0.01
		Aspect(Yr)	4838.18	3	1,612.73	**8.75**	<0.01
		Error	34834.08	189	184.31		
Filamentous Algae	Agatti	Year	236.07	3	78.69	**13.76**	<0.01
		Aspect(Yr)	315.55	4	78.89	**13.79**	<0.01
		Error	1178.16	206	5.72		
	Kadmat	Year	219.83	3	73.28	**9.94**	<0.01
		Aspect(Yr)	311.23	4	77.81	**10.56**	<0.01
		Error	1746.88	237	7.37		
	Kavaratti	Year	136.09	2	68.04	3.56	0.03
		Aspect(Yr)	374.61	3	124.87	**6.52**	<0.01
		Error	3616.96	189	19.14		

Benthic Component	Atoll	Factor	SS	d.f.	MS	F value	P value
Other benthic invertebrates	Agatti	Year	6.93	3	2.31	0.59	0.62
		Aspect(Yr)	123.55	4	30.89	**7.90**	<0.01
		Error	805.50	206	3.91		
	Kadmat	Year	11.27	3	3.76	1.73	0.16
		Aspect(Yr)	11.53	4	2.88	1.33	0.26
		Error	514.21	237	2.17		
	Kavaratti	Year	65.33	2	32.67	2.30	0.10
		Aspect(Yr)	29.81	3	9.94	0.70	0.55
		Error	2688.77	189	14.23		
Rubble	Agatti	Year	651.45	3	217.15	**4.57**	<0.01
		Aspect(Yr)	2397.93	4	599.48	**12.61**	<0.01
		Error	9795.17	206	47.55		
	Kadmat	Year	3784.43	3	1,261.48	**24.22**	<0.01
		Aspect(Yr)	402.74	4	100.68	1.93	0.11
		Error	12342.36	237	52.08		
	Kavaratti	Year	700.02	2	350.01	4.27	0.02
		Aspect(Yr)	355.40	3	118.47	1.45	0.23
		Error	15485.89	189	81.94		
Sand	Agatti	Year	11353.32	3	3,784.44	**36.28**	<0.01
		Aspect(Yr)	1304.17	4	326.04	3.13	0.02
		Error	21489.24	206	104.32		
	Kadmat	Year	4784.28	3	1,594.76	**7.57**	<0.01
		Aspect(Yr)	1553.13	4	388.28	1.84	0.12
		Error	49940.45	237	210.72		
	Kavaratti	Year	707.67	2	353.83	**7.95**	<0.01
		Aspect(Yr)	3976.93	3	1,325.64	**29.79**	<0.01
		Error	8410.81	189	44.50		

1999 and 2000 indicated that while there was considerable coral mortality, it was not as extensive as Agatti and Kadmat. In 2001, live coral was approximately 19% at Kavaratti (Figure 3.2). The pace of recovery was not uniform across the Lakshadweep, and while coral cover increased considerably at some reefs, others showed few signs of recovery. Recovery rates at all three atolls were significantly different between aspects (Table 3.1). Relatively exposed west-facing reefs rapidly increased in coral cover, while the more protected reefs of the east were much slower to recover. This pattern was evident in all reefs, although at Kavaratti, the difference in cover between years and aspects was not pronounced in 2001 and 2002 (Table 3.1).

With the loss of living coral, algal turf quickly claimed the newly released space and grew abundantly in the Lakshadweep. Observations in mid-1998 indicated that algal turf had quickly colonised the newly dead skeletons of coral, and within the first two years of detailed sampling, between 25—48% of the reef substrate was occupied by thin layers of algal turfs. Trends in turf abundance showed considerable variability, but there was a pattern of overall decrease in

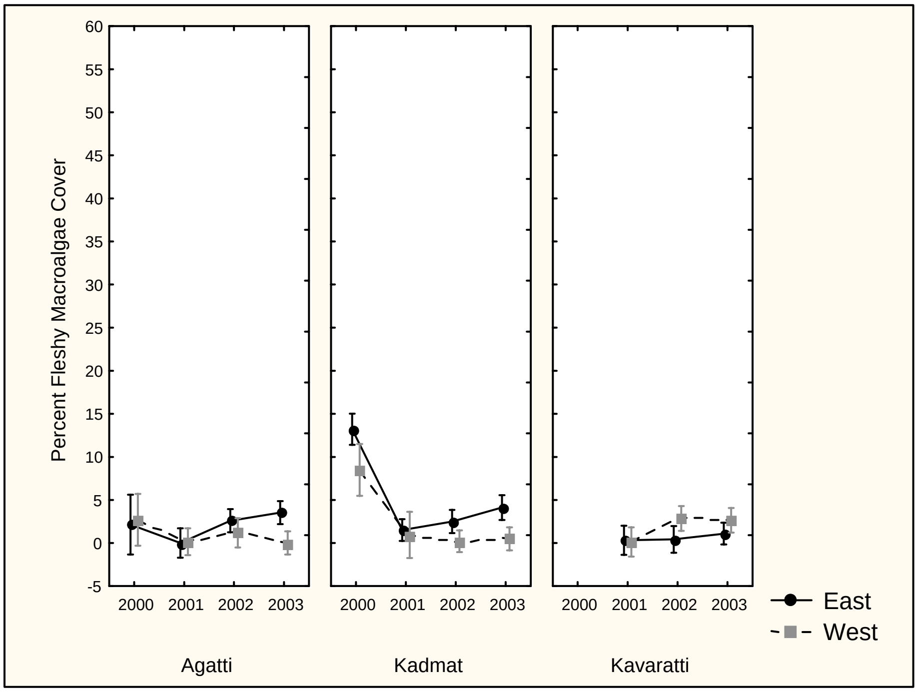


Figure 3.4. Change in cover of fleshy macroalgae between aspects at Agatti, Kadmat and Kavaratti from 2000 to 2003. Reefs at Kavaratti were not sampled until 2001. Error bars are 95% confidence intervals

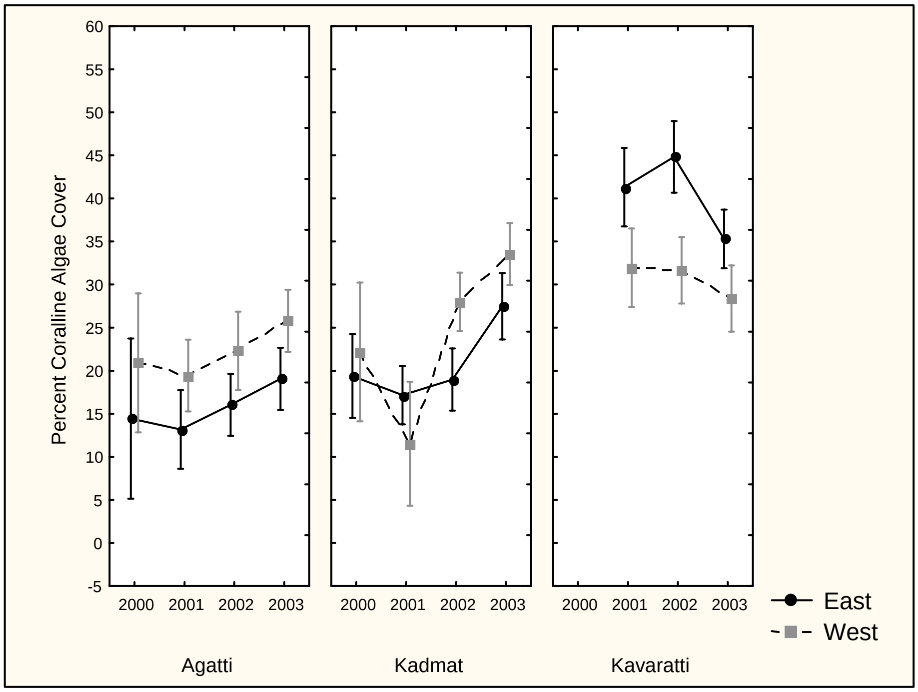


Figure 3.5. Change in cover of coralline algae between aspects at Agatti, Kadmat and Kavaratti from 2000 to 2003. Reefs at Kavaratti were not sampled until 2001. Error bars are 95% confidence intervals.

abundance as coral recovered (Figure 3.3, Table 3.1). The eastern aspects of atolls generally had higher cover of turf algae, and though cover decreased at most reefs with time, algal turf continued to be a dominant biotic component in Lakshadweep reefs in 2003. The reefs of Kavaratti by contrast showed little difference between aspects, and the cover of algal turf did not change much through time (Figure 3.3, Table 3.1).

At most reefs, the fleshy macroalgae (represented by *Dictyota*, *Padina*, *Hypnea* among others) changed significantly through time at all sites, and was different between aspects (Table 3.1). However, cover was never more than 5% at most reefs (Figure 3.4). The exception was Kadmat in 2000, where the fleshy algae *Turbinaria* was very common in surveyed reefs: macroalgal cover on Kadmat East was 13.2 ± 1.37 S.E., and on Kadmat West was 8.5 ± 2.27 S.E. In subsequent years, the cover of *Turbinaria* declined considerably. Although *Turbinaria* and other fleshy macroalgae were abundant in (unsampled) sheltered lagoonal patch reefs, their abundance was never large on the outer reefs, except for the bloom recorded at Kadmat in 2000. The biomass of turfs and fleshy macroalgae was apparently limited to low levels by herbivorous fishes, particularly Acanthurids and Scarids (see Chapter 4). Unlike fleshy algae, crustose coralline algae were common at most reefs in the Lakshadweep, and increased in cover at most sites (Figure 3.5, Table 3.1). The cover of coralline algae was highest in Kavaratti reefs, and its abundance showed little change, and perhaps even declined marginally at this atoll. Cover was significantly higher on western reefs of Agatti and Kadmat (Table 3.1), though this pattern was reversed for Kavaratti.

3.3.2 How did coral communities respond?

Multidimensional Scaling: trends in space and time

The two-dimensional MDS of coral genera showed a clear separation of communities (Figure 3.6). Kruskal Stress for the MDS was low (Stress=0.11), indicating that the 2-D ordination was a good representation of the multidimensional scatter. There was considerable change in the coral community at most reef sites as recovery progressed, but apart from an overlap between west-facing sites of Kadmat and Kavaratti, there was a clear separation between sampled reefs (ANOSIM with reef site as a factor, Global R=0.77, significance=0.1%). West-facing reefs clustered closer together while eastern reefs were less similar in composition. Coral composition changed progressively in time at reef sites, and this was particularly evident for Kadmat East, Agatti East and Agatti West. East-facing reefs changed directionally from 2001 to 2003 approaching closer together in the scatter, suggesting a possible convergence of community composition. By contrast, Agatti West moved away from the central cluster of points, driven by the rapid re-establishment of *Acropora* at this site, while composition at other west-facing reefs showed small non-directional changes at the centre of the scatter.

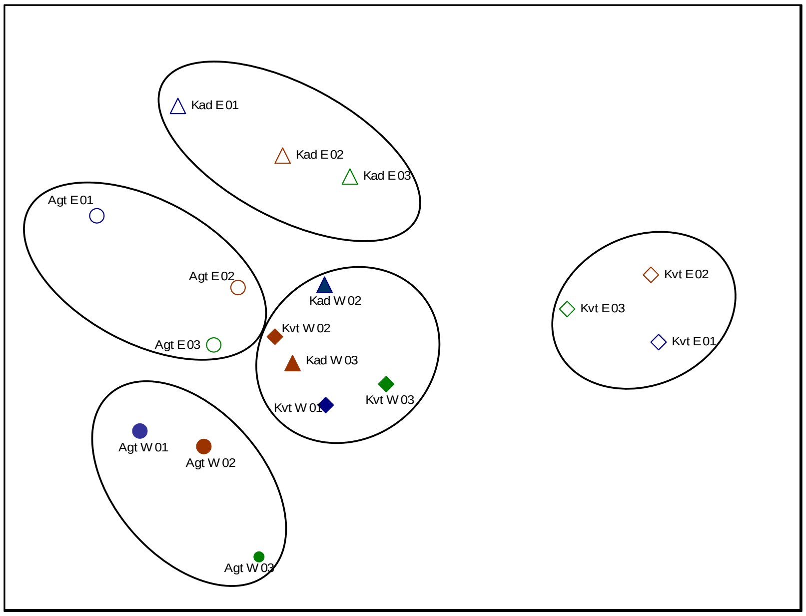


Figure 3.6. Multidimensional scaling (MDS) analysis of coral composition in the reefs of the Lakshadweep from 2001 to 2003. The data represent Bray Curtis similarities of percent composition of coral genera measured in Western (W) and Eastern (E) reef sites on Kavaratti (Kvt), Agatti (Agt) and Kadmat (Kad) in 2001 (01), 2002 (02), and 2003 (03). Kruskal Stress for the 2-D MDS was low (0.11), and ANOSIM analysis indicates significant separation between reef sites (Global R=0.77, significance=0.1%).

Relative change of coral genera: winners and losers

The composition of coral varied considerably both between reefs, and as recovery progressed. From 2001 to 2003, the east-facing reefs, while recording little change in benthic cover of coral, saw the largest changes in the relative cover of genera between years (Figure 3.7 a, c, e). Although overall coral cover increased significantly on west-facing reefs they did not show the large changes in relative cover of genera recorded on the east-facing reefs (Figure 3.7 b, d, f).

In Kavaratti East, the relative composition of genera changed dramatically (Figure 3.7e). This site was dominated by large stands of *Lobophyllia corymbosa* before 1998. Many coral individuals of this species showed signs of considerable partial mortality after 1998, but in 2001 it was still a dominant species in the reefs. By 2003 however, the cover of *L. corymbosa* had declined rapidly as erosional processes took over, and the coral broke apart into rubble. It is possible that partial mortality of the coral caused by bleaching led to a weakening of the structural stability of *L. corymbosa*, resulting in gradual loss of coral cover (Figure 3.7e). In contrast, the large change in genera evident in Agatti

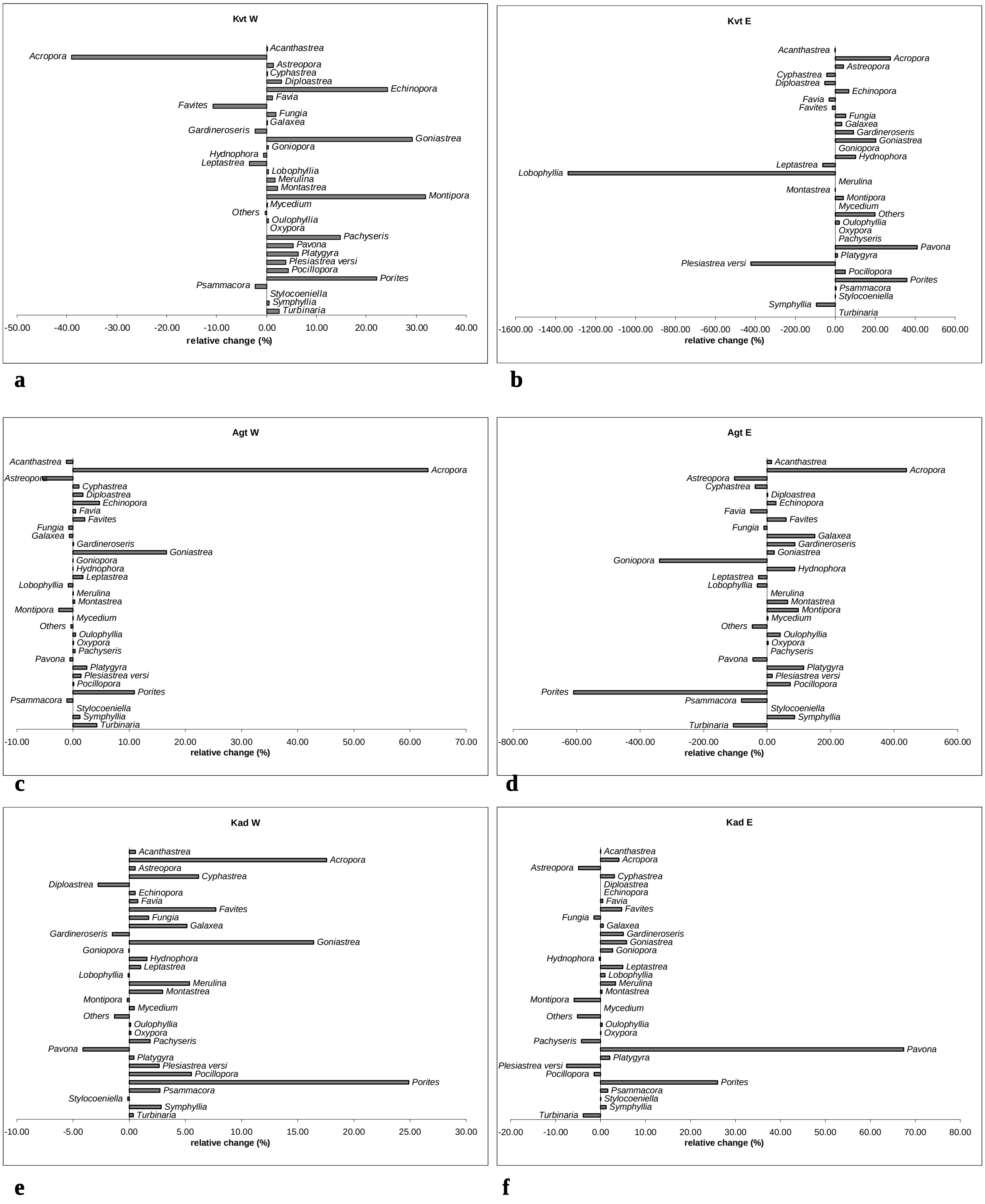


Figure 3.7. Relative change of coral genera across six reefs in the Lakshadweep from 2001 to 2003. The change in percent coral cover/m² was calculated for each reef site between years, and averaged across years. Bars represent proportional change across all genera.

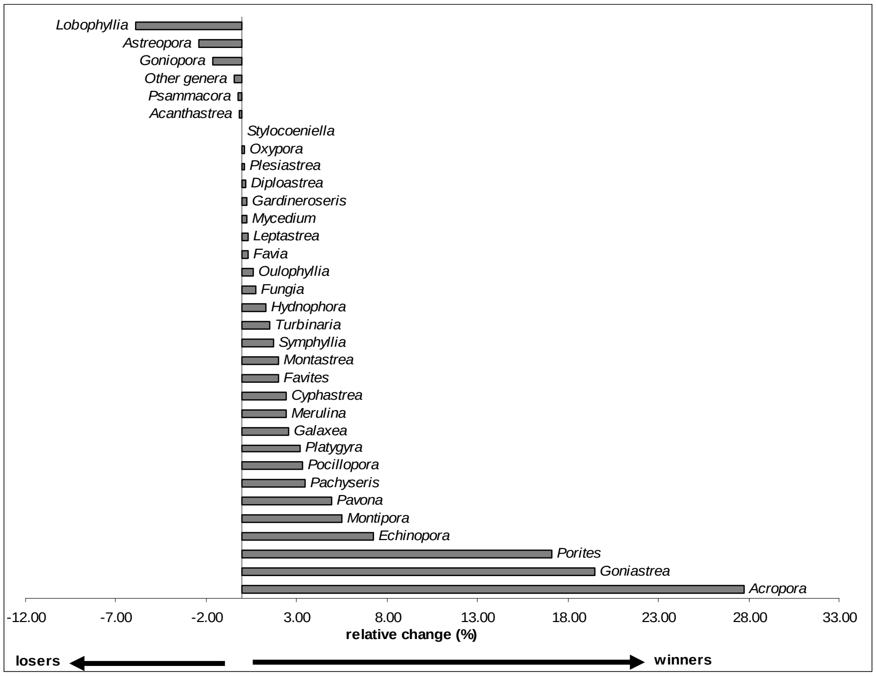


Figure 3.8. Relative change of coral genera across six reefs in the Lakshadweep from 2001 to 2003, averaged across all reefs. The change in percent coral cover/m^2 was calculated for each reef site between years, and averaged across years. Bars represent proportional change across all genera.

East was due to the combined effects of the loss of genera like *Porites* and *Goniopora* with an increase in areal cover of *Acropora* (Figure 3.7a). In Kadmat East, relative change was driven by gains in cover by *Pavona*; this reef was characterised by a large individuals of *Pavona clavus*, a species that often grows to occupy vast areas of reef substrate. Partial mortality was evident in *P. clavus* in the aftermath of the mass bleaching, but in contrast with *L. corymbosa* in Kavaratti East, *P. clavus* recovered quickly over the years, showing considerable increases in cover (Figure 3.7c).

Averaging relative change of genera across all reef sites from 2001 to 2003 is helpful in elucidating overall trends in change across the Lakshadweep (Figure 3.8). As the reefs of the Lakshadweep recovered, more genera showed relative gains rather than losses in cover. Among the biggest "winners" (Loya et al. 2001) in the Lakshadweep reefs were *Acropora*, *Porites* and *Goniastrea*. *Acropora* is a generally fast-growing genus, and its cover increased in the Lakshadweep at all sites save the Kavaratti West. Similarly, the cover of *Porites* increased in all sites except Agatti East, while *Goniastrea* increased in abundance at all sampled sites.

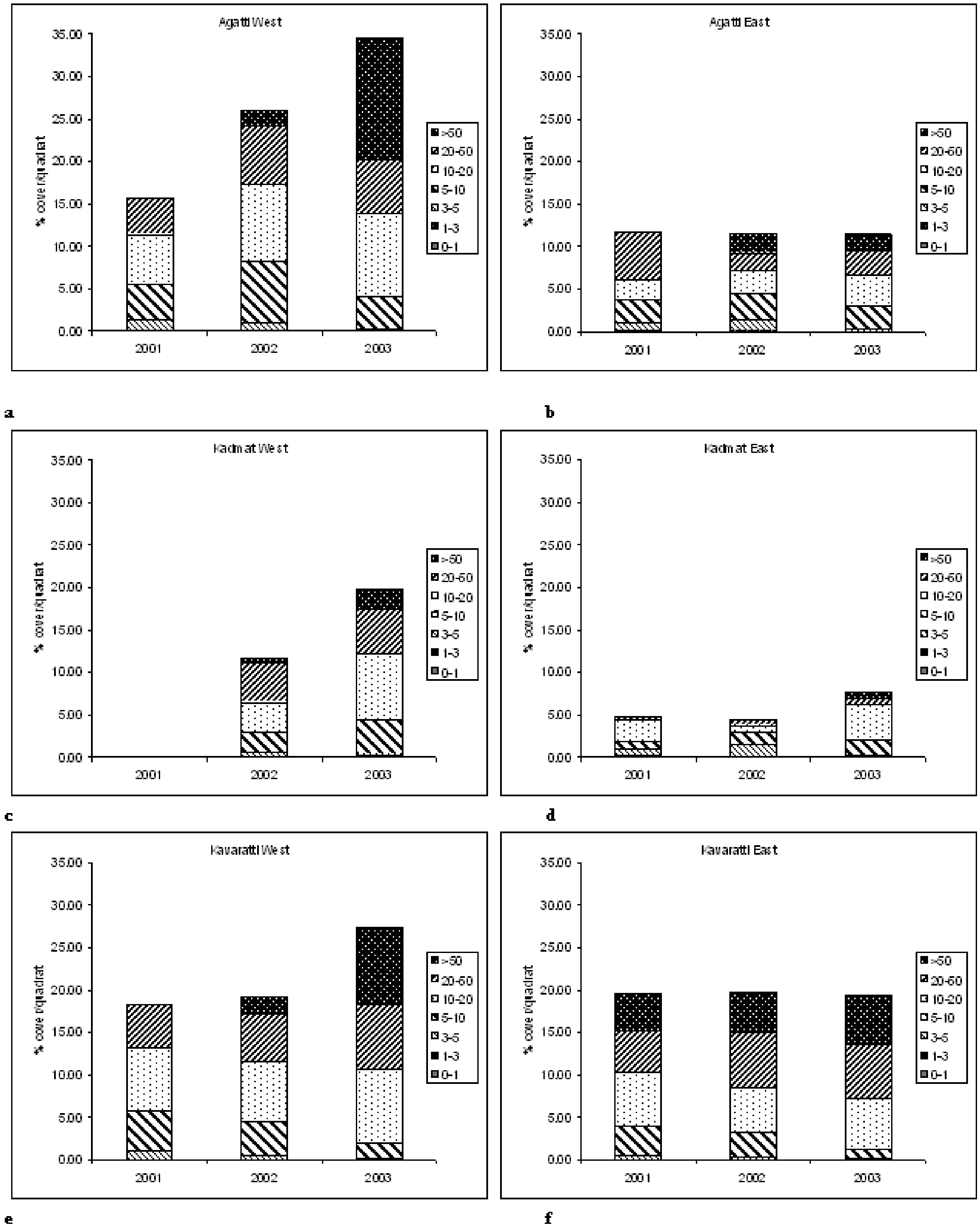


Figure 3.9. Size structure distribution of coral based on percent cover occupied. **a.** Agatti West, **b.** Agatti East, **c.** Kadmat West, **d.** Kadmat East, **e.** Kavaratti West, **f.** Kavaratti East. Sizes were estimated in the size classes based on the maximum diameter of individuals (in cms). Kadmat West was not sampled in 2001.

Coral Size Distributions

Nearly two years after the coral mass bleaching in 2000, the extensive mortality of large individuals was evident as dead standing coral. However, by mid 2001, the reefs were dominated by corals in smaller size-classes, many of which had settled on dead stony coral skeletons (Figure 3.9). Across all reefs, approximately 82% on average of individuals surveyed were below 10 cm in maximum diameter. By 2003, this predominance had reduced by nearly a fifth, to around 63% of coral below 10 cm across all sites, as individuals grew into larger size-classes.

Though numerically scarce, individuals in larger size-classes contributed significantly more to overall cover than smaller size-class individuals (Figure 3.9). For instance, in 2001, less than 18% on average of individuals were in size-classes larger than 10 cm, yet they constituted approximately 69% on average of the total coral cover across all sites. By 2003, this had increased to 37% on average of individuals greater than 10 cm contributing more than 83% of the total coral cover (Figure 3.9). Corals larger than 50 cm diameter were rare in most reefs in 2001, and, apart from Kavaratti East, were not recorded in any quadrats. At Kavaratti East, the overall distribution of size-class cover did not change much from 2001 to 2003 (Figure 3.9 f), though it did change considerably at other reefs. Coral cover in western reefs (Figure 3.9 a, c, e) increased as coral individuals recruited to size-classes greater than 20 cm. By contrast, at east-facing reefs, the increase in the cover of larger size-class individuals did not translate into significant changes in overall coral cover. The reduction in smaller size-classes on east-facing reefs can be partially explained by coral growing to larger size-classes. However, the fact that overall cover did not increase in these reefs suggests that high mortality of smaller individuals compensated for the increase in cover of larger size-classes. The east reefs (Figure 3.9 b, d, f), protected from monsoonal currents, maintained a large proportion of dead standing coral, which proved a good settlement substrate for coral recruits. By 2003 however, dead standing coral had rapidly eroded and broken away on eastern reefs, resulting in significant mortality of coral that had settled on them. This was particularly true of dead tabular *Acropora* which fragmented and overturned easily, killing juvenile corals growing on their upper surfaces. In contrast, at the time of first sampling on western reefs, dead standing tabular and branching corals were not as common, and, in all probability, had been broken and swept clean by the high-energy waves of the south-west monsoon.

3.4 Discussion

3.4.1 Benthic change in the Lakshadweep

Five years after the 1998 mass-mortality, coral cover in the Lakshadweep was increasing once again. Two distinct trends in benthic change were evident: rapid gains in coral cover on all west-facing reefs from 2000 to 2003, and little net change in coral cover on east-facing reefs, apart from the early gain in Agatti (Figure 3.2). This striking difference in recovery between aspects was also evident in observations made at other atolls across the island chain (Chapter 2). This pattern suggests that there is a consistent difference between aspects in the availability of settlement substrate, survival of recruits, and hydrodynamics. These issues are discussed in more detail later.

The mass coral mortality of 1998 created the opportunity for macroalgae to quickly increase in biomass, potentially precluding the recovery of coral, and precipitating a phase shift. With a human population density of nearly 2000/km^2, and without adequate sewage treatment facilities on the islands, the potential for land-based nutrients leaching into the surrounding waters, promoting macroalgal growth, is high. Fleshy macroalgae grow in high density in lagoonal patch reefs in Agatti, Kadmat and Kavaratti (personal observation, Dhargalkar & Shaikh 2000) but did not attain high abundances in outer reefs in this study (Figure 3.4). There was no evidence in four years of sampling of the community switching to macroalgal dominance. Several possible hypotheses could explain the failure of macroalgae to increase in dominance, including **nutrient limitation**, **space pre-emption** and **herbivore pressure**.

In contrast to the enclosed lagoon, nutrients are probably diluted and flushed away fairly rapidly from outer reefs in the Lakshadweep, making them relatively nutrient poor (Wafar 1986), and potentially limiting the growth of macroalgae. On western reefs, rapid increases in coral cover could in principle have pre-empted the establishment of fleshy macroalgae. However, observations on eastern reefs suggest that this mechanism was unlikely to be important: here, coral cover remained relatively low through time, yet the substrate was still not overrun by macroalgae.

Herbivory was probably much more important than either nutrient-limitation or space pre-emption on these reefs. As discussed in detail in chapter 4, one of the clearest trends after coral mortality was the very high abundance of herbivorous fishes in the first few years of sampling. Large mixed schools of surgeonfish and parrotfish were ubiquitous, and large grazing aggregations were commonly observed as schools roved between patches, grazing down available algae.

Another indication of high herbivory on these reefs was the gradual increase of algal crusts in most reefs, a common response of benthic communities to intense herbivory (Steneck 1986, Steneck & Dethier 1994 Figure 3.5). Reefs have been shown to persist for long periods of time dominated by algal turfs and crusts, maintained in this state by high densities of herbivores (possibly scraping off settled coral), low nutrient levels, or factors such as water-flow and disturbance (Sammarco *et al.* 1974, Cheroske *et al.* 2000, McClanahan *et al.* 2002b). This descriptive study cannot conclusively separate the factors limiting the abundance of fleshy algae, and further experimental evidence would be required to explore the precise mechanisms of macroalgal control in Lakshadweep reefs. If current levels of herbivory and nutrients are maintained however, the eastern reefs of Lakshadweep could well persist as turf-dominated communities with little coral, until corals successfully recruit and grow back to dominance (See chapter 6 for a conceptual model).

3.4.2 Coral size structure

One of the biggest difficulties in understanding recovery in the Lakshadweep reefs is the absence of baseline benthic data with which to compare it. Thus, while it may be possible to record changes in coral cover post-disturbance, without information on the pre-disturbance community, it is impossible to know, with any degree of certainty, if reefs are returning to an earlier assemblage, or being populated by a different suite of species after the disturbance (Pearson 1981). There is dubious merit in measuring the recovery of ecosystems with respect to a hypothetical ‘pristine’ past. However, different assemblages may have varying functional values for the reef, and consequently could mean very different outcomes for reef diversity and resilience. Answering the ‘recovery to what?’ question may therefore be crucial for diversity conservation, as well as for the management of reefs in the face of repeated disturbances.

Coral size structure holds potentially valuable information about community responses and recovery after disturbance events. For instance, Bak and Meesters (1999) propose that reefs subject to disturbance will have right skews in coral size distributions, larger size-classes dominating the population. Right-skewed size distributions can arise when smaller individuals suffer greater whole-colony mortality in the face of disturbance than large individuals, and/or short- to mid-term failure in coral recruitment. Absence of young coral from the reef further skews populations towards larger size-classes. By contrast the population size structure of corals in the Lakshadweep showed clear skews to the left. In 2001, nearly three years after the coral mass mortality, Lakshadweep reefs were dominated by corals in smaller size classes, and individuals larger than 50 cm were rare in most reefs surveyed. These observations are thus apparently at variance from those of Bak and Meesters, and reflect the possibly limited recruitment success in Caribbean reefs on which they based their observations (see below).

Size specific whole-colony mortality patterns appear to have been reversed in the Lakshadweep reefs in the wake of the mass bleaching. In rapid assessments six months after the bleaching, many large individuals suffered whole-colony mortality while smaller size-class individuals appeared to have fared considerably better. This is reflected in the detailed size-class data recorded in 2001 where small individuals dominated the distribution (Figure 3.9). In the specific instance of bleaching-related disturbance, smaller individuals may actually have an advantage over larger corals. Studies have shown that shading by macroalgae for instance could serve to protect corals from bleaching (Diaz-Pulido & McCook 2002), perhaps through a protection from PAR or UV irradiance in particular (Brown *et al.* 2002b). Small size-classes could thus have been shielded from bleaching by growing in crevices, or in the shade of larger individuals. It is also possible that young corals are inherently more tolerant of heat stress than older individuals. For instance, a recent study (Little *et al.* 2004) suggests that the zooxanthellae clade in juvenile *Acropora millepora* and *A. tenuis* was more resistant to heat stress. Also, juvenile corals are possibly more heterotrophic than adults, and therefore less reliant on coral-algal symbiosis for food production.

The death of reproducing adults in the population could well result in a failure of coral to recruit until remnant corals grow to reproductive age. Post-1998 recruitment of coral was low in the Lakshadweep: a preliminary study of coral recruitment in Agatti, Kadmat and Kavaratti in 2002 recorded densities of approximately 0.26 recruits/tile after four months of deployment (n=108, unpublished data). Despite this, juveniles of several coral families were present in high densities in reefs, with up to 90% of individuals in size classes below 10 cm in 2001 (Figure 3.9). These most likely represent a cohort that recruited to the reef before or immediately after the bleaching event. Juveniles were able to successfully colonise the substrate in large numbers, skewing the size-distribution to the left. Thus, while post-disturbance recruitment may not be reliable in the Lakshadweep, smaller size-classes were not limited in the reef. In fact, disturbance appeared to favour the growth of smaller size-class corals by releasing them from competition for space and light with larger individuals.

Done (1999), contrary to Bak and Meesters (1999) predicted that repeated disturbance will skew coral populations to smaller size-classes and earlier successional stages. For instance, following a catastrophic loss of coral after a volcanic eruption on Banda Islands in Indonesia, coral size distributions showed a pronounced left skew, as the reef was rapidly re-colonised by new recruits (Tomasik et al. 1996). Though Bak and Meesters (1999) consider these distributions to be "deviant", they may be characteristic of many disturbed Indo-Pacific reefs where connectivity is high and settlement space is often limiting in reefs. Right skews may still result in the immediate aftermath of a major disturbance event, but they could be rapidly reversed in areas that are not recruit-limited. Recruits to these sites may experience higher settlement and survival rates after a disturbance. Chronic, low-impact disturbances may result in higher whole-colony mortality of smaller individuals than larger colonies, while catastrophic disturbances like storms may affect large and small colonies equally (Done & Potts 1992, Bak & Meesters 1999). The evidence presented here suggests that in the particular instance of mass bleaching, larger size-class individuals may actually be disadvantaged relative to smaller colonies.

Reefs on the east and west of Lakshadweep atolls provide an interesting contrast in recovery processes. On the west, larger size classes were largely responsible for the rapid increase in coral cover. In contrast, the increasing dominance of larger size classes on the east was offset by a concomitant reduction in smaller size classes, resulting in few net gains to benthic cover (Figure 3.9). This difference in recovery rates between aspects was not peculiar to Agatti, Kadmat and Kavaratti, but was noted in other atolls across the archipelago (Chapter 2).

The difference in recovery patterns between aspects is most likely driven by differences in environmental conditions and post-settlement survival of coral recruits between east and west. The Lakshadweep atolls are influenced by the summer monsoon for four months, between mid-May and mid-September. The monsoon, arriving from the East African coast, brings strong currents and waves to the exposed west, while the east remain relatively protected through the year. The timing of the 1998 mass mortality in relation to the monsoon played a vital role in driving recovery patterns. Anomalous SSTs were experienced from late March 1998 in the Lakshadweep, and by the time the monsoons set in, considerable coral mortality had already occurred (Arthur 2000). The strong energy conditions on the west resulted in a rapid loss of unstable dead coral. However, on the east, there was much dead standing branching and tabular lifeforms that were dominant in pre-bleached reefs, and that continued to persist beyond 1998 (personal observation). However, these substrates provide little viability for the long-term survival of coral recruits (Endean 1976, Bellwood *et al.* 2004). Juvenile coral (< 5 cms diameter) were observed in high densities in these sites in 2000, growing on the dead tops of tabular coral and dead branches. These recruits did not survive long. In time, dead standing coral either fragmented because of wave damage and natural bioerosional processes, or toppled over as the weight of the growing recruits made them structurally unstable. By 2003, most dead branching coral had fragmented to rubble, and very few dead tabular coral remained standing. The available substrate on western reefs in contrast proved more viable, as most of the unstable branching and tabular forms had been washed away in the 1998 monsoon. Early coral survival appears to have been considerably higher, leading to rapid increases in cover, as more recruits grew to higher size classes. Long-term stability of settlement substrate is vital for coral recovery (Endean 1976). In this instance, the rate and timing of removal of dead standing coral played a large role in determining the rate at which coral cover recovered.

3.4.3 Coral community composition and recovery

Differences in generic composition between reefs were clearly evident in MDS analysis, and reefs separated well in the ordination. These differences between sites were maintained for most reefs despite considerable change in composition with time. The MDS suggests a strong directionality in the change in coral composition at east-facing sites on all atolls. From 2001 to 2003, these sites moved closer together in the ordination space, increasing in overall similarity as recovery progressed. This suggests that recovery at these sites is being driven by a similar suite of genera. It remains to be seen if this successional convergence is maintained as the reefs continue to recover. Interestingly, though coral cover was quicker to recover in western reefs, changes in composition with time were strongly directional only in Agatti West, where *Acropora* quickly grew to generic dominance.

As may be expected in the first few years of recovery, there were more relative gains than losses in coral cover from 2001 to 2003 (Figure 3.8). Three genera, *Acropora*, *Goniastrea* and *Porites* dominated the recovery in the Lakshadweep. These are an interesting group because their species have very different responses to disturbance. Neither *Goniastrea* nor *Porites* comprise particularly fast-growing species. However, species of both genera appear to have a high tolerance of heat stress (Brown *et al.* 2000, Brown *et al.* 2002a, McClanahan *et al.* 2004). *Goniastrea* is often found in shallow and even intertidal reefs, and can presumably tolerate several hours of daily aerial exposure. Most species of massive *Porites* also deal with heat stress well, and, while they bleach rapidly, are also fairly quick to recover (Loya *et al.* 2001).

Acropora in contrast is often among the worst affected genera in bleaching episodes, suffering high mortality during these events (Loya 1976, Baird & Marshall 1998, McClanahan *et al.* 2004). *Acropora* was an important community element in the Lakshadweep prior to bleaching, with many reefs dominated by branching and tabular species, as well more robust forms like *A. palifera*. These species were severely affected by the bleaching in 1998, their populations drastically reduced in reefs throughout the chain (Arthur 2000, McClanahan 2000a, Sheppard *et al.* 2002). Despite these losses, *Acropora* proved an important driver of post-1998 recovery in most reefs in the Lakshadweep, growing rapidly from a cohort of juveniles to quickly reclaim benthic cover.

There has been much speculation about the response of coral communities to changing climate regimes. It has been suggested that coral communities subjected to an increasing frequency of anomalous SSTs may be skewed towards species that have higher tolerance of heat stress (Loya *et al.* 2001). In the Lakshadweep, these temperature-tolerant genera were favoured, but bleaching-susceptible genera dominated new recruitment to the damaged sites. With further bleaching events, the success of a species is likely to be determined not merely by its susceptibility to disturbance, but by a combination of its recruitment and life history strategies, growth rates, and the return time of disturbances. Prolific recruitment coupled with fast growth rates in *Acropora* species could favour the continued dominance of this important genus in reefs. The caveat to this is the return time of ocean warming events: if the frequency of catastrophic anomalous temperatures increases causing extensive mortality before genera like *Acropora* grow back, it is likely that their abundance will ratchet further downwards. Under these conditions, it is likely that stress-tolerant genera like *Porites* and *Goniastrea* will become increasingly important elements of the benthic assemblage.

3.4.4 Disturbance, recovery, and the Lakshadweep atolls

The stochastic nature of large infrequent disturbances on natural ecosystems introduces an inherent unpredictability in ecological communities. A range of rate-limiting factors control the recovery of ecosystems from major disturbances, and it is often difficult to predict with any degree of certainty, the path and duration an ecosystem will take to recovery. In general, processes relating to recruitment, the subsequent survival of recruits, and resource competition, will together determine the potential for recovery after a catastrophic event (Pearson 1981). In complex ecosystems like coral reefs, these processes are often governed by a stochasticity of their own, often varying with temporal and spatial scale.

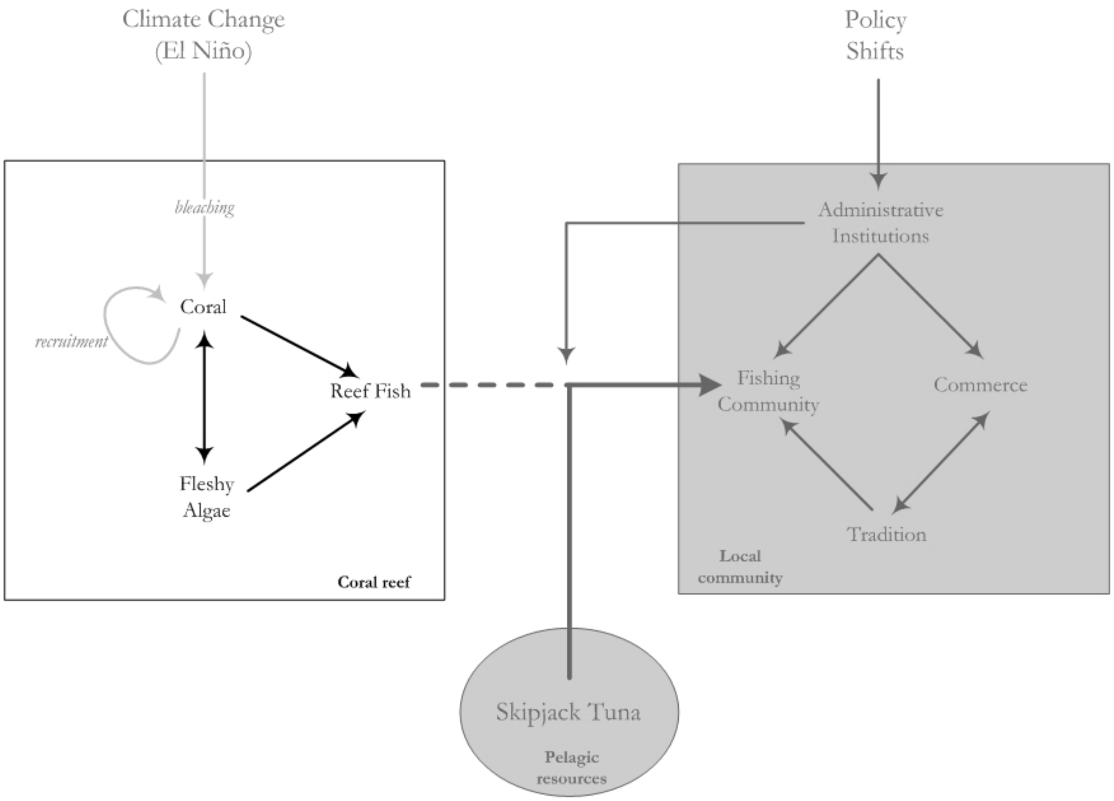
For the Lakshadweep, this study cannot separate the influence of environmental factors from community composition factors in determining recovery rates. Since this is essentially a post-disturbance study with practically no benchmarks to compare it to before the bleaching event, it is difficult to know what factors led to the dominance of *Acropora* in eastern reefs before the mortality.

Also, very little information exists on recruitment patterns in this archipelago – spawning periods, current patterns, source and sink dynamics etc – and this knowledge would be essential in a more complete understanding of recovery on the reefs.

From a management standpoint, the Lakshadweep reefs provide important lessons. Managing for ecological surprise is never easy. Increasingly, managers and conservation biologists are advocating the use of spatial closures (National Parks, no-take zones, etc) as a means of reef conservation. These set-aside zones are meant to maximise resilience, and serve as an insurance against disturbances. The Lakshadweep reefs show that it might be additionally important to have detailed knowledge of the community composition of these areas, and understand the susceptibilities of these communities to different disturbances and environmental influences. This information would be useful in determining where spatial closures would be most effective in maximising resilience, and where they would serve little purpose.

Chapter IV

RESPONSES OF CORAL REEF FISH TO BENTHIC CHANGE



In this chapter, I examine the consequences of coral mortality on reef fish communities. I track changes in the trophic composition of reef fish in three Lakshadweep atolls. Overall, fish communities remained relatively stable from 2000 to 2003. Herbivorous fishes were dominant in the reefs, comprising up to 70% of fish biomass in the first year of sampling, and remained abundant throughout. Their numbers was important in maintaining low algal biomass in the reef, and possibly set the stage for a relatively rapid rate of benthic recovery. Of the group to be most affected by the coral mortality were the corallivorous species, though, by 2003, the abundance of corallivores was increasing, in response to increases in coral cover.

Chapter IV

Recovery of fish communities after a coral mass mortality event

4.1 Introduction

As the pace of change of the global environment continues unabated, the ability of ecosystems to maintain the structure and function of their dominant communities is being called increasingly into question (Pounds *et al.* 1999, Hughes 2000, Walther *et al.* 2002). Few habitats are affected as intensely by this rapid change as coral reefs. The pantropical bleaching and mortality of coral that resulted after the severe 1997-1998 El Niño event was a dramatic indicator of the detrimental impacts of climate change on reef ecosystems (Wilkinson 1998, Hoegh-Guldberg 1999). There was considerable variability in the extent of decline and recovery of coral and other benthic elements after this disturbance (Wilkinson *et al.* 1999, Arthur 2000, Sheppard *et al.* 2002, Diaz-Pulido & McCook 2002, Baird & Marshall 2002, Wilkinson 2002, this thesis Chapter 3). The effects of coral mortality on reef fish are less well documented. Fish species have different degrees of dependence on corals, both directly, as a food resource, and indirectly, as a refuge from predators or for ambush cover. The death of coral and subsequent loss of topographic structure could therefore have important flow-on consequences for reef fishes (Caley & St.John 1996, Jones & Syms 1998, Angel & Ojeda 2001, Fox *et al.* 2003). Changes in the composition of fish communities have been linked to major declines in reef condition (Roberts 1995, McClanahan 1997, Jennings & Kaiser 1998). Fish play vital functional roles in maintaining ecosystem resilience on reefs, both as keystone predators and as efficient grazers, and their response to disturbance is an important driver of reef recovery.

As discussed in Chapter 3, the reefs of the Lakshadweep suffered catastrophic mortality of coral during the 1997-1998 El Niño. Coral recovery appeared to be progressing well at some sites, while at others, recovery was slow. However, the biomass of fleshy macroalgae was consistently low, facilitating reef recovery. Fish communities, and in particular, herbivorous fishes may have had a large role to play in reducing the cover of algae. While herbivorous fish could be benefited from the loss of corals from these reefs, several other functional groups could presumably have been badly affected. This chapter examines change in the functional composition of fish communities from 2000 to 2003, to determine the response of fish assemblages to mass bleaching and subsequent mortality.

Fish responses to bleaching and coral mortality

Several species of fish are reliant on coral as a primary food resource, and are likely to be most directly affected by bleaching mortality. The 1998 bleaching episode resulted in population declines of several corallivores, including the file fish, *Oxymonocanthus longirostris* (Kokita & Nakazono 2001, Spalding & Jarvis 2002), and other obligate coral-feeders (Spalding & Jarvis 2002, Sano 2004). Many other species use coral as cryptic habitat, and may be disadvantaged as they are exposed by bleaching to predators or potential prey. Post-bleaching declines were noted in the abundances of strongly coral-dependent damselfish, *Plectroglyphidodon johnstonianus* (Spalding & Jarvis 2002), *P. dickii*, and *Dascyllus carneus* (Lindahl *et al.* 2001). In contrast, predatory fish that feed on these species may benefit from the loss of cryptic habitat, though this may be evident only in the short term as they rapidly deplete their resources: Spalding and Jarvis (2002) show an increase in the abundance of several invertebrate feeders after bleaching, though Chabanet (2002) found the opposite trend.

Qualitatively, there is little to suggest that the indirect consequences of bleaching mortality to fish communities will be very different from other natural and anthropogenic disturbances that result in loss of reef structure, though they may differ in their spatial extent and intensity. Coral disease, red tides, and outbreaks of the coral-feeding sea star *Acanthaster planci* in particular, likely cause similar changes in reef fish communities, characterised by an initial loss of live coral, followed, in time, with accelerated reduction of topographic complexity. For instance, in a study of the responses of a coral-feeding pufferfish to El Niño and red tide-induced coral mortality, Guzmán and Robertson (1989) found that *Arothron meleagris* individuals adapt to changes in the availability of coral by switching diets to less favoured foods, including coralline algae, suffering costs to their growth rates as a result.

The genus *Acropora*, a structural dominant in many reefs worldwide, and an important habitat for a large number of fish, is particularly susceptible to both bleaching and *A. planci* outbreaks. The response of reef fish to *A. planci* outbreaks and to cyclones and hurricanes depend to a large extent on the scale and intensity of the disturbance, and the life-history characteristics of the fish species (Walsh 1983, Williams 1986, Sano *et al.* 1987, Hart *et al.* 1996, Lewis 1997, and others).

Bleaching mortality often leads to large-scale modifications in habitat composition as turf and fleshy algae opportunistically occupy the space released by coral, and bioerosion causes the rapid collapse and compaction of reef rugosity. These habitat changes could lead to a host of flow-on effects for reef fish communities. While some of these indirect effects may manifest themselves relatively quickly after a bleaching event, many may be insidious and not immediately apparent. Thus, herbivore and planktivore abundances often quickly increase after bleaching (Lindahl *et al.* 2001, Chabanet 2002, Spalding & Jarvis 2002), but the longer-term consequences to fish communities have not been studied. Nor is there much information on how bleaching mortality influences fish feeding, growth-rates, fecundity and behaviour.

In this chapter I examined patterns of fish community composition in reefs recovering from a catastrophic El Niño-related bleaching event in 1998. Fish communities were sampled in reefs off three Lakshadweep atolls for four years from 2000 to 2003. I examined trends in guild composition of fish assemblages and discuss implications for the resilience and recovery of the reef ecosystem.

4.2 Methods

4.2.1 Field Methods

Three Lakshadweep atolls were chosen for study: Kadmat, Agatti, and Kavaratti (Chapter 3). These reefs were differently affected by coral mortality: Kadmat suffered the highest coral mortality, while Kavaratti was the least affected. The atolls have a north-south orientation and therefore have a distinct eastern and western face, exposed to differing environmental conditions through the year. A sampling site was randomly located on both aspects of each atoll. These reefs were sampled between April and May of 2000 (Kadmat and Agatti only), 2001, 2002 and 2003.

Fish were sampled along 50m × 5m belt transects, randomly located on the reef slope between 5m and 12m. Horizontal visibility, estimated visually as the metre at which an upright rod (length: 100cm, width: ~2.5cm) was still clearly visible, was always greater than 10m, and was typically between 20m and 30m. Every attempt was made to conduct fish sampling at the same time in relation to the tide (within an hour before or after High Water: tidal range~2m). The transect line was left unattended for at least 10 minutes after it was laid and its length was then swum slowly. Fish species and number were noted, and grouped into the following size classes: 5-10cm, 10-20cm, 20-50cm and >50cm; fish smaller than 5cm were ignored. Fish species were identified using standard field guides, principally Lieske and Myers (2001). Numbers of fish in large schools were estimated to the nearest 5 or 10 individuals, depending on the size of the school. The midpoint of each fish size class was used to estimate fish biomass based on growth parameters extracted from published literature (Froese & Pauly 1997) as well from as a length-weight relationship database compiled by Michel Kulbiki and others (unpublished data). Where growth parameters were unavailable, average values of available species within the genus or close relatives were used (see appendix for a species list with parameter values). Fish density was calculated as the number of fish recorded in a $250m^2$ area (the area of coverage of the transect). A total of 158 species of fish, belonging to 28 common reef fish families were counted. The species sampled represent a wide variety of feeding groups and habitat uses. Cryptic species are generally underrepresented in visual transects of this nature, and no attempt was made to target them specifically. Two diverse reef families, the Gobiidae and Blennidae were excluded because most species are small and cryptic.

4.2.2 Analytical Methods

Defining fish guilds

Data on fish diets were extracted from a database compiled by Michel Kulbiki (Kulbiki, unpublished data), with supplementary data from published literature (Froese & Pauly 1997) for species not present in Kulbiki's database. Food groups in the database included microalgae (turf), macroalgae, coral, microinvertebrates (<2cm length), macroinvertebrates (>2cm length), plankton (zooplankton and phytoplankton), detritus and fish. Fish were assigned to seven functional food guilds, based on the proportional composition of food groups in the diet. These included:

1. Herbivore: Diet predominantly (>50%) micro or macroalgae
2. Corallivore: Diet predominantly coral (>50%)
3. Macro Invertebrate Feeder: Diet largely comprising large invertebrates (>50%)
4. Micro Invertebrate Feeder: Diet largely comprising small invertebrates (>50%)
5. Piscivore: Predominantly fish-eating species (>50%)
6. Planktivore: Fish with phyto- or zoo-plankton as a dominant part of their diet (>50%)
7. Omnivore: Fish feeding unselectively from several food groups

A list of fish species and their functional guilds is provided in Appendix I.

Tracking changes in fish communities

Significant shifts in community composition often take place after major disturbances as species adjust to changes in local habitat, availability of resources, and shifting competitive environments. I used MDS analysis to explore spatial and temporal patterns in community structure as the reef recovered. Biomass estimates of fish species along transects were square-root transformed to reduce the influence of skews in the data set. Bray-Curtis similarity was calculated between samples and ordinated using group mean clustering with the software package PRIMER (Clarke & Warwick 1994). I tested for the significance of community changes between reef sites and years using ANOSIM.

I looked for site-wise changes in a range of community characteristics. I used ANOVA techniques to compare species richness (N), diversity (H'), as well as total abundance and biomass summed across all fish species between sites and years. The index of diversity used was the Shannon-Weiner diversity index, measured as $-\sum_{i=1}^{n} pi \times \log_e pi$, where *pi* is the proportional abundance of species *i* in a sample with *n* species (Magurran 1988). Changes in abundance and biomass of individual trophic guilds were compared between sites and years. In addition, I looked for trends in the proportional distribution of trophic guilds based on biomass and abundance.

The reefs at Kavaratti could not be sampled in 2000 due to logistic constraints. I therefore tested the dataset first with all available sites and years included, then with the incomplete year (2000) excluded from the analysis, and finally with the incomplete site (Kavaratti) excluded from the analysis. Taken together, the analyses provide more reliable conclusions about the direction of community change than if an incomplete design is interpreted in isolation. I used a nested ANOVA design, with sampling times (2000 to 2003), atolls (Agatti, Kadmat and Kavaratti), and aspects (East and West) as fixed factors, and the community measure (species diversity, family biomass, guild biomass, etc) as the dependent variables. Atolls were nested in time, and aspects were nested in atolls with the following design: Year+Atoll(Year)+Aspect(Year x Island). Few samples met the condition of homogeneity of variances (using the Cochran's C-test), and in most cases, transformations (log+1 transformations for continuous data, arc-sin transformations for proportional data) did not improve homogeneity conditions. The ANOVA is considered fairly robust even when this assumption is violated (Sokal & Rohlf 1981) and I conducted the tests on untransformed data.

4.3 Results

4.3.1 Fish Responses

Community composition

As benthic recovery progressed in the wake of coral mass mortality, the composition of fish assemblages changed considerably at most Lakshadweep reefs. There was a distinct temporal

Table 4.1: Anosim results of changes in fish species composition in the Lakshadweep between years. Global R=0.309, significant at 0.2%, based on a randomisation test with 999 permutations. Presented are the ANOSIM results of pairwise comparisons of similarities between years. The number of permutations used to calculate significance level is also presented. R values in bold are significant at 5% or less.

Years	R Statistic	Significance Level %	Possible Permutations	Actual Permutations	Number >=R
2000, 2001	-0.048	58.1	210	210	122
2000, 2002	**0.544**	1.	210	210	2
2000, 2003	**0.81**	0.5	210	210	1
2001, 2002	**0.23**	2.8	462	462	13
2001, 2003	**0.35**	0.2	462	462	1
2002, 2003	0.109	15.2	462	462	70

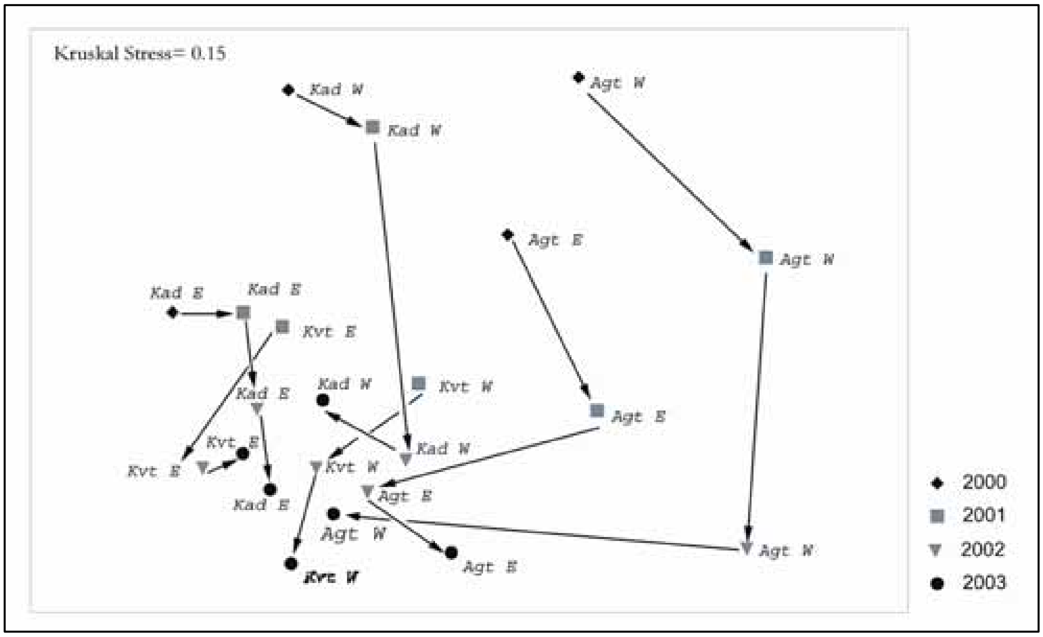


Figure 4.1 MDS ordination of fish composition in the Lakshadweep atolls. Fish species biomass was used for calculating similarity values. Kruskal Stress for the 2D solution was 0.15. The arrows show the direction of change with time.
Abbreviations: Agt=Agatti, Kad=Kadmat, Kvt=Kavaratti, E=East, W=West

trend evident in the MDS ordination of fish species biomass (Figure 4.1). Fish assemblages at Kadmat and Agatti showed a pattern of increasing convergence, moving closer to Kavaratti reefs in the MDS scatter. By 2002 all sites except for Agatti West had clustered close together in the ordination, and by 2003, all six reefs had very similar fish assemblages. A one-way ANOSIM with Sampling Year as a factor confirms this trend: global R was 0.31, significant at the 0.2% level (Table 4.1). The magnitude of community change between years was more evident in Kadmat and Agatti than at Kavaratti. The composition of fish assemblages at all reefs became increasingly similar with time from 41.8% (±1.86 SE) in 2000 to 53.7% (±1.52 SE) in 2003.

Abundance, biomass and diversity

There was considerable variation in total fish density (abundance $250m^{-2}$) among sites, but there was a general trend of increase from 2000 to 2003 (Figure 4.2a, Table 4.2a). Fish numbers were consistently highest in Kavaratti, and stayed relatively low in Agatti until 2003. Reefs on the east supported slightly higher total numbers of fish, though this pattern was not consistent between years. With the exception of Agatti, total density approximately doubled from 2000 to 2003. In Agatti, density peaked in 2001, driven by ubiquitous mid-water aggregations of the planktivorous triggerfish *Odonus niger*, which reached average densities of around 97 individuals $250m^{-2}$ on Agatti West. Such high densities were not encountered after 2001 in Agatti or at any of the other atolls. The removal of this species from the analysis did not noticeably alter the trends in fish density at Kavaratti and Kadmat, but showed that abundance at Agatti was relatively unchanged until 2003, when Agatti West saw a sharp increase in fish numbers (Figure 4.2b).

Trends in total biomass of species were much less clear. On the whole, there was an increase in total biomass across all surveyed sites from 2000 to 2001, but little noticeable change was apparent post-2001 (Figure 4.3a, Table 4.2a). Eastern reefs generally supported higher biomass than western reefs. At Kadmat, this difference was maintained throughout the study, whereas at Kavaratti and Agatti, it remained higher only until 2002. Fish biomass on western reefs increased regularly through time everywhere except at Kavaratti, where it varied considerably between years. The removal of *O. niger* from the analysis did not significantly alter these trends (Figure 4.3b, Table 4.2b).

Species richness and diversity per $250m^2$ increased gradually with time as the reef recovered. Richness at Kavaratti was always higher than other atolls, while Agatti always maintained lower richness, relative to other atolls (Figure 4.4, Table 4.2a and b). This difference between atolls was not reflected in Shannon Weiner diversity (Figure 4.5, Table 4.2a and b). Neither richness nor diversity differed significantly between aspects (Table 4.2a and b).

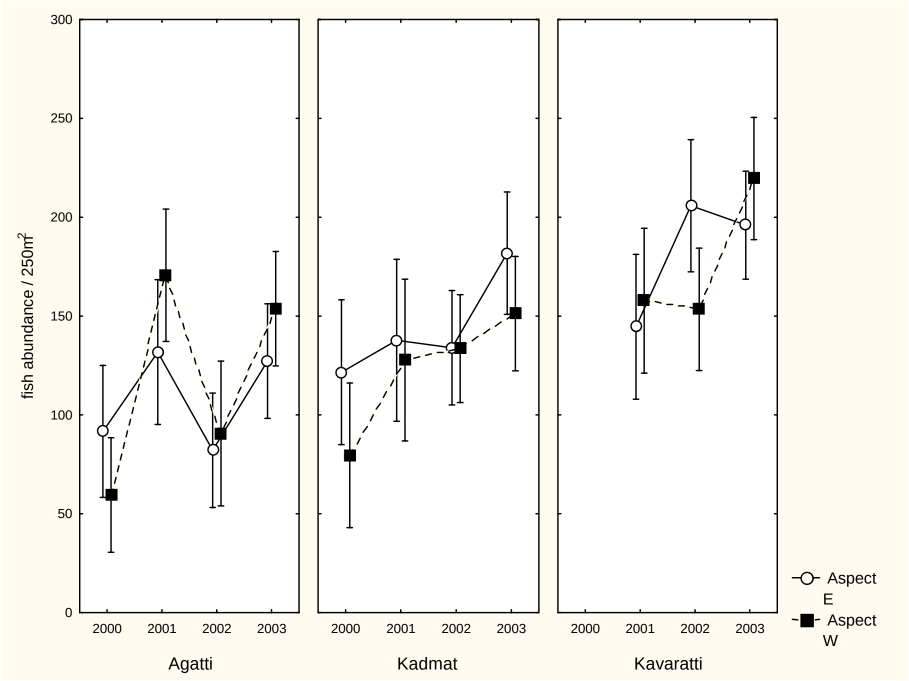


Figure 4.2a: Total fish abundance / 250m^2 in Lakshadweep reefs from 2000 to 2003. Reefs in Kavaratti could not be sampled in 2000. Error bars are 0.95 confidence intervals

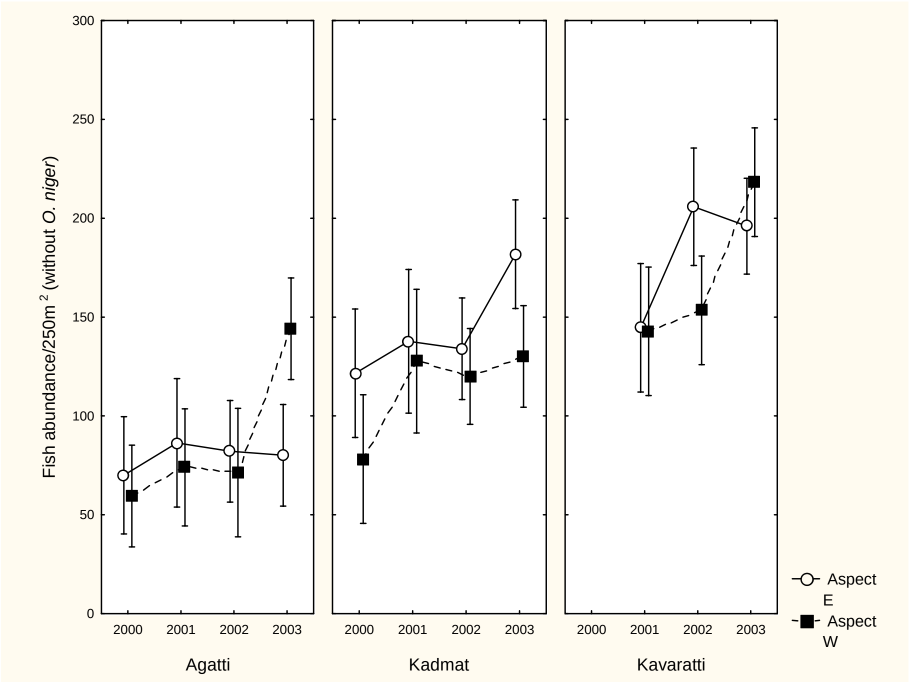


Figure 4.2b: Total fish abundance / 250m^2 in Lakshadweep reefs from 2000 to 2003 without *O. niger*. Reefs in Kavaratti could not be sampled in 2000. Error bars are 0.95 confidence intervals

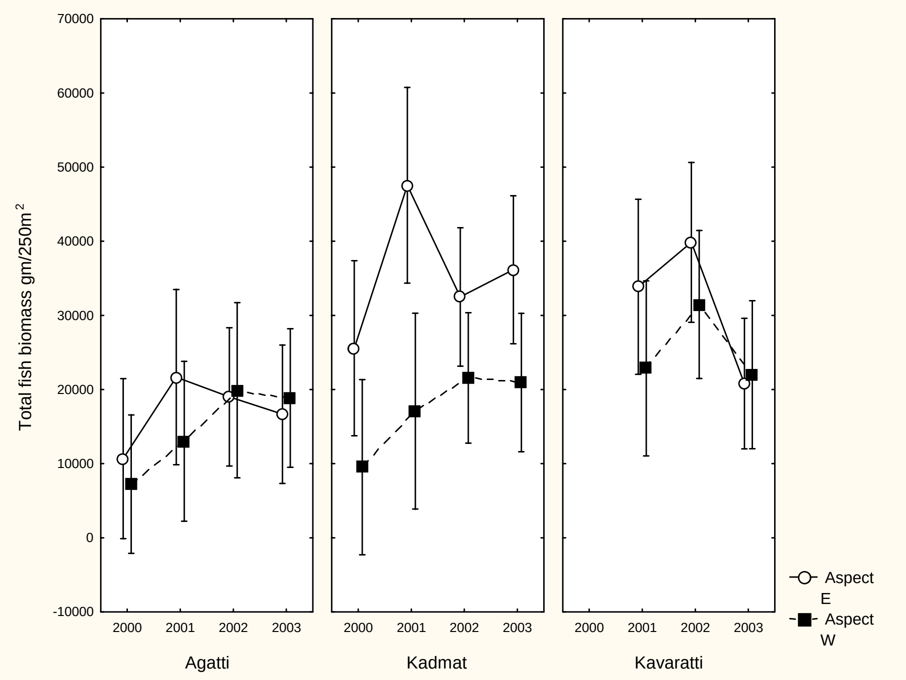


Figure 4.3a. Total fish biomass/250m² in Lakshadweep reefs from 2000 to 2003. Reefs in Kavaratti could not be sampled in 2000. Error bars are 0.95 confidence intervals

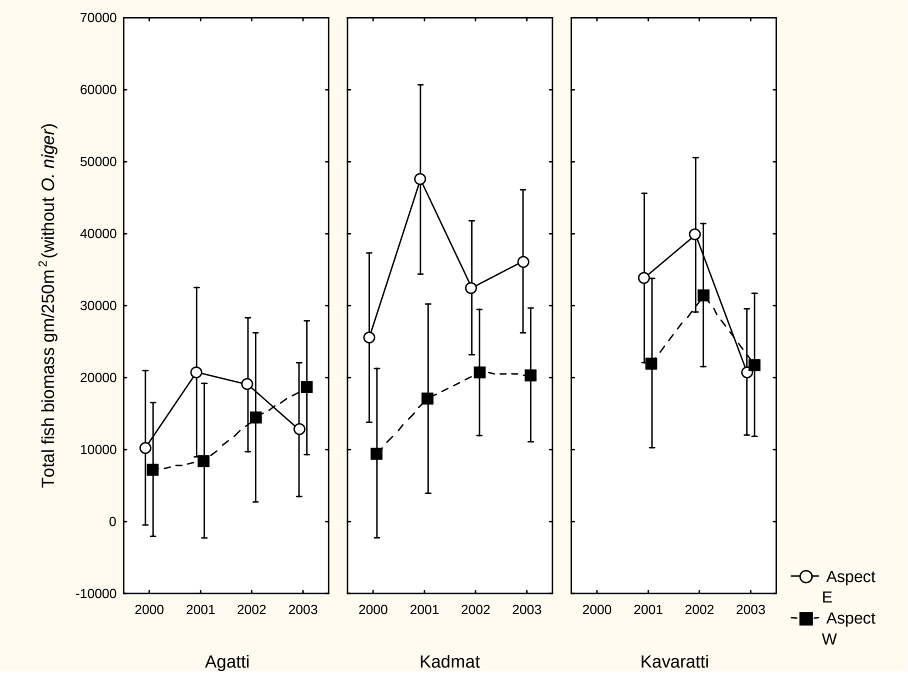


Figure 4.3b. Total fish biomass gm/250m² in Lakshadweep reefs from 2000 to 2003 without *O. niger*. Reefs in Kavaratti could not be sampled in 2000. Error bars are 0.95 confidence intervals.

Table 4.2a. Changes in fish species richness, Shannon Weiner diversity, total fish abundance and biomass, in the Lakshadweep reefs: Mean and standard errors

Measure		**West**			**East**		
Diversity (H')	**Year**	**Agatti**	**Kadmat**	**Kavaratti**	**Agatti**	**Kadmat**	**Kavaratti**
	2000	2.2 ± 0.11	2.5 ± 0.14		2.2 ± 0.13	2.3 ± 0.14	
	2001	1.9 ± 0.13	2.5 ± 0.15	2.7 ± 0.14	2.4 ± 0.14	2.6 ± 0.15	2.5 ± 0.14
	2002	2.5 ± 0.14	2.4 ± 0.1	2.7 ± 0.12	2.7 ± 0.11	2.5 ± 0.11	2.7 ± 0.13
	2003	2.7 ± 0.11	2.6 ± 0.11	2.9 ± 0.12	2.4 ± 0.11	2.6 ± 0.12	2.9 ± 0.1
Richness (S)		**West**			**East**		
species/250m^2	**Year**	**Agatti**	**Kadmat**	**Kavaratti**	**Agatti**	**Kadmat**	**Kavaratti**
	2000	14.88 ± 1.57	19.2 ± 1.98		19.17 ± 1.81	22.8 ± 1.98	
	2001	21.17 ± 1.81	22.5 ± 2.22	27.2 ± 1.98	21.4 ± 1.98	26.5 ± 2.22	25 ± 1.98
	2002	17.8 ± 1.98	22.78 ± 1.48	26.43 ± 1.68	22.13 ± 1.57	24.5 ± 1.57	29.17 ± 1.81
	2003	25.88 ± 1.57	24.38 ± 1.57	29.29 ± 1.68	20.88 ± 1.57	26.57 ± 1.68	29 ± 1.48
Abundance		**West**			**East**		
(all species)	**Year**	**Agatti**	**Kadmat**	**Kavaratti**	**Agatti**	**Kadmat**	**Kavaratti**
(Individuals/250m^2)	2000	59.5 ± 14.62	79.6 ± 18.49		91.7 ± 16.88	121.6 ± 18.49	
	2001	170.7 ± 16.88	127.8 ± 20.67	157.8 ± 18.49	131.8 ± 18.49	137.8 ± 20.67	144.6 ± 18.49
	2002	90.6 ± 18.49	133.6 ± 13.78	153.4 ± 15.63	82.1 ± 14.62	134 ± 14.62	205.8 ± 16.88
	2003	153.8 ± 14.62	151.3 ± 14.62	219.6 ± 15.63	127.3 ± 14.62	181.9 ± 15.63	196 ± 13.78
Abundance		**West**			**East**		
(without *O. niger*)	**Year**	**Agatti**	**Kadmat**	**Kavaratti**	**Agatti**	**Kadmat**	**Kavaratti**
(Individuals/250m^2)	2000	59.5 ± 12.98	78.2 ± 16.42		70 ± 14.99	121.6 ± 16.42	
	2001	74 ± 14.99	127.8 ± 18.36	142.8 ± 16.42	86.4 ± 16.42	137.8 ± 18.36	144.6 ± 16.42
	2002	71.4 ± 16.42	120 ± 12.24	153.4 ± 13.88	82.1 ± 12.98	134 ± 12.98	205.8 ± 14.99
	2003	144.1 ± 12.98	130.1 ± 12.98	218.3 ± 13.88	80.1 ± 12.98	181.9 ± 13.88	196 ± 12.24
Total Biomass		**West**			**East**		
(all species)	**Year**	**Agatti**	**Kadmat**	**Kavaratti**	**Agatti**	**Kadmat**	**Kavaratti**
(gms/250m^2)	2000	7245.5 ± 4716.46	9529.4 ± 5965.9		10688 ± 5446.1	25563.2 ± 5965.9	
	2001	13029.9 ± 5446.1	17085.2 ± 6670.08	22850 ± 5965.9	21668.2 ± 5965.9	47548.7 ± 6670.08	33856 ± 5965.9
	2002	19901.8 ± 5965.9	21572.6 ± 4446.72	31473.3 ± 5042.11	19011.4 ± 4716.46	32488.9 ± 4716.46	39853 ± 5446.1
	2003	18864.5 ± 4716.46	20942 ± 4716.46	22003.4 ± 5042.11	16672.3 ± 4716.46	36161.6 ± 5042.11	20793 ± 4446.72
Total Biomass		**West**			**East**		
(without *O. niger*)	**Year**	**Agatti**	**Kadmat**	**Kavaratti**	**Agatti**	**Kadmat**	**Kavaratti**
(gms/250m^2)	2000	7245.5 ± 4696.3	9501.2 ± 5940.4		10251.3 ± 5422.82	25563.2 ± 5940.4	
	2001	8457.4 ± 5422.82	17085.2 ± 6641.57	22022.9 ± 5940.4	20753.1 ± 5940.4	47548.7 ± 6641.57	33856 ± 5940.4
	2002	14476.3 ± 5940.4	20716.2 ± 4427.71	31473.3 ± 5020.55	19011.4 ± 4696.3	32488.9 ± 4696.3	39853 ± 5422.82
	2003	18604.9 ± 4696.3	20385.1 ± 4696.3	21790 ± 5020.55	12770.3 ± 4696.3	36161.6 ± 5020.55	20793 ± 4427.71

Table 4.2b: Summary ANOVA table for fish species richness, Shannon Weiner diversity, total fish abundance and biomass, with and without the outlying species, *Odonus niger*. To account for the absence of data from Kavaratti in 2000, the ANOVA was conducted first with all data included, then with 2000 excluded and then with Kavaratti excluded. F values in bold are significant at the 0.05 level. See appendix for complete ANOVA tables.

		F Values		
Variable	**Factor**	**All data**	**Year 2000 excluded**	**Kavaratti excluded**
Species Richness (S)	Year	**1060.59**	**1286.21**	**726.04**
	Atoll(Yr)	**5.53**	**5.81**	**3.11**
	Aspect(Yr*At)	1.48	1.21	1.91
Species Diversity (H')	Year	**2415.62**	**2972.36**	**1333.77**
	Atoll(Yr)	**4.35**	**5.04**	**2.73**
	Aspect(Yr*At)	1.33	1.60	1.41
Abundance (All species included)	Year	**416.59**	**480.16**	**223.88**
	Atoll(Yr)	**8.37**	**8.68**	**3.65**
	Aspect(Yr*At)	1.74	1.49	1.30
Abundance (without *O. niger*)	Year	**445.962**	**524.9812**	**239.1401**
	Atoll(Yr)	**17.972**	**18.9687**	**10.3617**
	Aspect(Yr*At)	**2.9745**	**3.0376**	**3.2675**
Biomass (All species included)	Year	**109.66**	**126.21**	**70.17**
	Atoll(Yr)	**3.36**	**3.21**	**4.09**
	Aspect(Yr*At)	**2.39**	**2.27**	**3.06**
Biomass (without *O. niger*)	Year	**102.638**	**117.8783**	**63.48113**
	Atoll(Yr)	**4.5339**	**4.4378**	**5.69455**
	Aspect(Yr*At)	**2.7003**	**2.6206**	**3.4821**

Changes in guild abundance and biomass

The most striking feature of the post-bleach fish communities in the Lakshadweep reefs was the predominance of herbivores – mostly algal turf feeders. Several species of surgeonfish (Acanthuridae) and parrotfish (Scaridae) roved the reef in dense schools, scraping the turf that grew in abundance on the dead coral skeletons. Herbivore numbers were high, reaching densities of greater than $120/250m^2$ in Kadmat and Kavaratti, far outnumbering other guilds in the reef (Figure 4.6, Table 4.3a). In 2000, they constituted between 60-70% of total biomass, and between 48-72% of total abundance. Over four years of benthic recovery, they maintained their numbers, but declined in relative terms as other functional groups increased in importance (Figure 4.8). By 2003, herbivores continued to be among the most dominant fish guilds, but represented only 23-52% of biomass, and between 23-65% of abundance. Herbivore density in Agatti was lower than Kavaratti and Kadmat, a pattern that persisted through time.

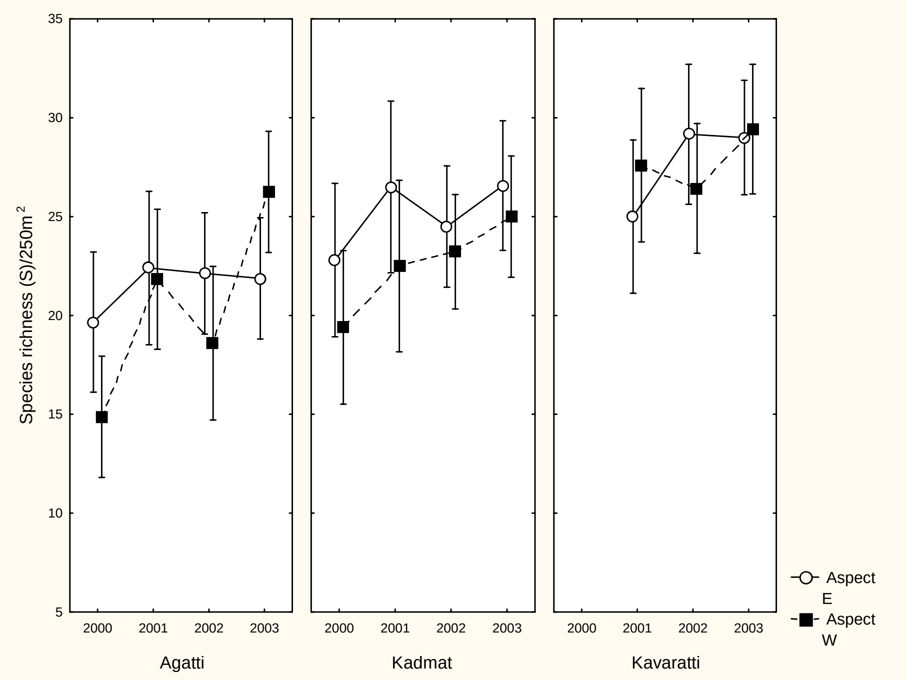


Figure 4.4. Species richness/250m^2 (S) in Lakshadweep reefs from 2000 to 2003. Reefs in Kavaratti could not be sampled in 2000. Error bars are 0.95 confidence intervals.

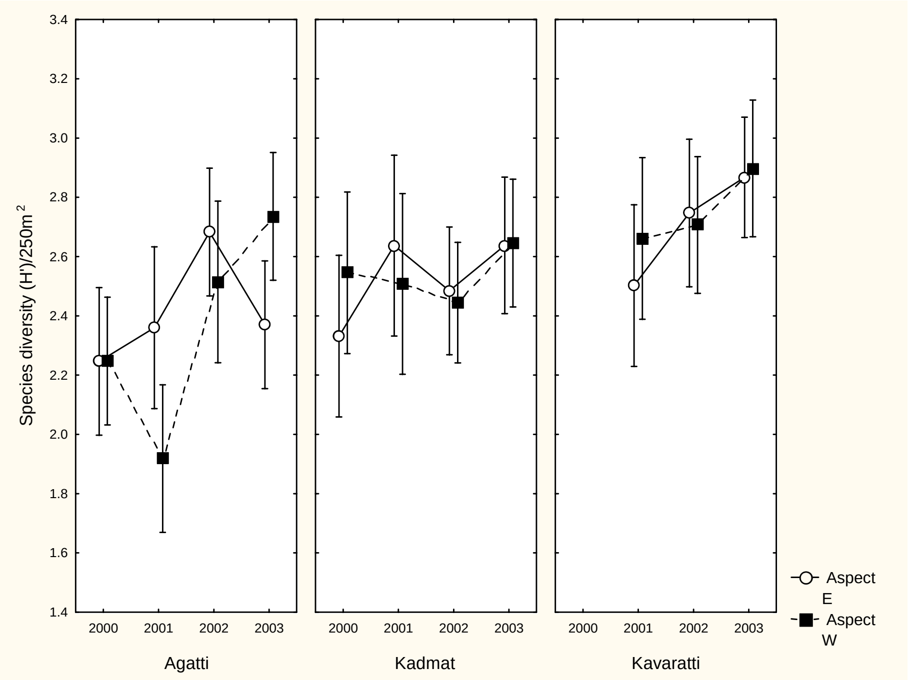


Figure 4.5. Fish species diversity/250m^2 (H') in Lakshadweep reefs from 2000 to 2003. Reefs in Kavaratti could not be sampled in 2000. Error bars are 0.95 confidence intervals.

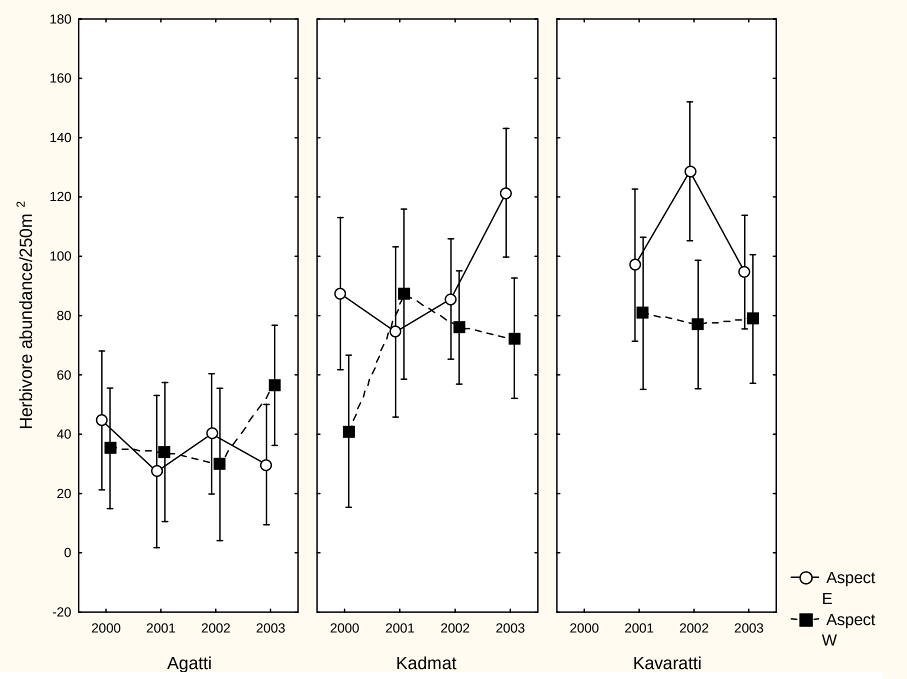


Figure 4.6. Herbivore abundance / 250m^2 in the Lakshadweep atolls from 2000 to 2003. Reefs in Kavaratti could not be sampled in 2000. Error bars are 0.95 confidence intervals.

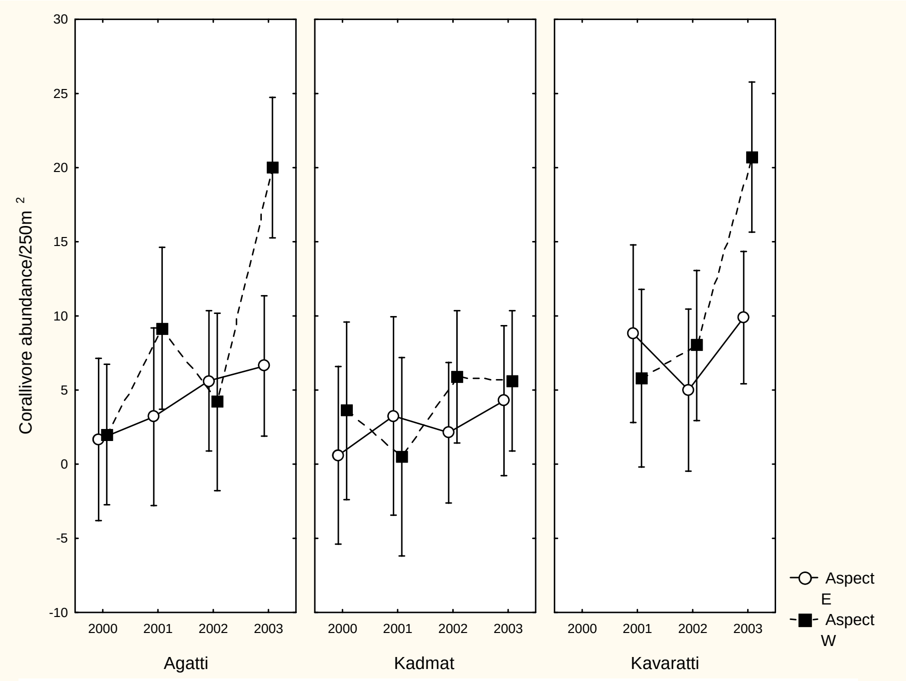


Figure 4.7. Corallivore abundance / 250m^2 in the Lakshadweep atolls from 2000 to 2003. Reefs in Kavaratti could not be sampled in 2000. Error bars are 0.95 confidence intervals.

Table 4.3a. Changes in guild abundance/250m^2 in the Lakshadweep reefs from 2000 to 2003: Means and standard errors

Guild		West			East		
Herbivores	**Year**	**Agatti**	**Kadmat**	**Kavaratti**	**Agatti**	**Kadmat**	**Kavaratti**
	2000	35.3 ± 10.25	41 ± 12.96		44.7 ± 11.83	87.4 ± 12.96	
	2001	34 ± 11.83	87.3 ± 14.49	80.8 ± 12.96	27.4 ± 12.96	74.5 ± 14.49	97 ± 12.96
	2002	29.8 ± 12.96	76 ± 9.66	77 ± 10.95	40.1 ± 10.25	85.6 ± 10.25	128.7 ± 11.83
	2003	56.5 ± 10.25	72.4 ± 10.25	78.9 ± 10.95	29.8 ± 10.25	121.4 ± 10.95	94.7 ± 9.66
Corallivore		**West**			**East**		
	Year	**Agatti**	**Kadmat**	**Kavaratti**	**Agatti**	**Kadmat**	**Kavaratti**
	2000	2 ± 2.39	3.6 ± 3.02		1.7 ± 2.76	0.6 ± 3.02	
	2001	9.2 ± 2.76	0.5 ± 3.38	5.8 ± 3.02	3.2 ± 3.02	3.3 ± 3.38	8.8 ± 3.02
	2002	4.2 ± 3.02	5.9 ± 2.25	8 ± 2.56	5.6 ± 2.39	2.1 ± 2.39	5 ± 2.76
	2003	20 ± 2.39	5.6 ± 2.39	20.7 ± 2.56	6.6 ± 2.39	4.3 ± 2.56	9.9 ± 2.25
Macroinvertebrate Feeder		**West**			**East**		
	Year	**Agatti**	**Kadmat**	**Kavaratti**	**Agatti**	**Kadmat**	**Kavaratti**
	2000	13.4 ± 3.63	20.8 ± 4.59		15.3 ± 4.19	14.6 ± 4.59	
	2001	17 ± 4.19	21.5 ± 5.13	22.8 ± 4.59	23.8 ± 4.59	21.3 ± 5.13	21.8 ± 4.59
	2002	25 ± 4.59	18 ± 3.42	24.7 ± 3.88	20 ± 3.63	19.1 ± 3.63	22 ± 4.19
	2003	26.5 ± 3.63	18.8 ± 3.63	32.7 ± 3.88	25.9 ± 3.63	26.1 ± 3.88	29.7 ± 3.42
Microinvertebrate Feeder		**West**			**East**		
	Year	**Agatti**	**Kadmat**	**Kavaratti**	**Agatti**	**Kadmat**	**Kavaratti**
	2000	4 ± 1.61	3.3 ± 1.27		2.3 ± 1.47	1.8 ± 1.61	
	2001	7.3 ± 1.47	3.7 ± 1.2	5.9 ± 1.27	3.9 ± 1.27	9.4 ± 1.61	2.5 ± 1.27
	2002	2.8 ± 1.8	4.7 ± 1.47	4.4 ± 1.2	1 ± 1.61	3.5 ± 1.27	5.4 ± 1.27
	2003	15 ± 1.8	5.6 ± 1.36	5.6 ± 1.36	5 ± 1.61	2.8 ± 1.61	4.4 ± 1.36
Omnivore		**West**			**East**		
	Year	**Agatti**	**Kadmat**	**Kavaratti**	**Agatti**	**Kadmat**	**Kavaratti**
	2000	3.6 ± 1.38	3.8 ± 1.74		2.5 ± 1.59	3.6 ± 1.74	
	2001	2.5 ± 1.59	1.8 ± 1.95	4.4 ± 1.74	4 ± 1.74	7 ± 1.95	5.6 ± 1.74
	2002	3 ± 1.74	2.2 ± 1.3	7 ± 1.47	2.4 ± 1.38	4.6 ± 1.38	4.2 ± 1.59
	2003	6.8 ± 1.38	3.3 ± 1.38	5.7 ± 1.47	5.1 ± 1.38	4.1 ± 1.47	6.2 ± 1.3
Piscivore		**West**			**East**		
	Year	**Agatti**	**Kadmat**	**Kavaratti**	**Agatti**	**Kadmat**	**Kavaratti**
	2000	1.3 ± 1.87	4 ± 2.37		2.3 ± 2.17	3.4 ± 2.37	
	2001	3.8 ± 2.17	1.8 ± 2.65	4.4 ± 2.37	4.4 ± 2.37	6 ± 2.65	4.2 ± 2.37
	2002	4.8 ± 2.37	6.7 ± 1.77	8.7 ± 2	5.4 ± 1.87	4.5 ± 1.87	11.7 ± 2.17
	2003	4.9 ± 1.87	6.3 ± 1.87	15.3 ± 2	5.8 ± 1.87	5.7 ± 2	13 ± 1.77
Planktivore		**West**			**East**		
	Year	**Agatti**	**Kadmat**	**Kavaratti**	**Agatti**	**Kadmat**	**Kavaratti**
	2000	0.1 ± 10.8	1.4 ± 13.66		22.8 ± 12.47	11 ± 13.66	
	2001	96.8 ± 12.47	0 ± 15.27	30.2 ± 13.66	65 ± 13.66	23 ± 15.27	5.4 ± 13.66
	2002	21 ± 13.66	21.1 ± 10.18	22.4 ± 11.55	5.1 ± 10.8	14.8 ± 10.8	29.7 ± 12.47
	2003	33.8 ± 10.8	39.1 ± 10.8	60.7 ± 11.55	51.6 ± 10.8	15.7 ± 11.55	38.1 ± 10.18

In contrast with algal feeders, corallivores were conspicuously underrepresented in the reefs in 2000. At that time, they contributed less than 1% to the total fish biomass – around 3% of total abundance (Figure 4.7, Table 4.3a). They increased relative dominance in time, though they were still at fairly low densities and biomass in 2002. However, in 2003, concomitant with considerable gains in coral cover (see Chapter 3), the western sites of Agatti and Kavaratti saw a surge in corallivore numbers. In 2003, corallivores in these reefs were dominated by high densities of coral-associated butterflyfish such as *Chaetodon trifasciatus*, *C. collare*, *C. citronellus*, and *C. meyeri*, the majority of them being in the smallest size class (below 10cm). By 2003, pairs of the obligate coral specialist filefish, *Oxymonocanthus longirostris*, were recorded at all western reefs, where coral was growing fastest (see Chapter 3). This species was not recorded in transects nor observed on extensive free swims in either 2000 or 2001, and was first sighted as isolated pairs from Kadmat and Kavaratti in 2002.

Table 4.3b: Summary ANOVA table for fish trophic guilds based on abundance values. To account for the absence of data from Kavaratti in 2000, the ANOVA was conducted first with all data included, then with 2000 excluded and then with Kavaratti excluded. F values in bold are significant at the 0.05 level. See appendix for complete ANOVA tables.

		F Values		
Variable	**Factor**	**All data**	**Year 2000 excluded**	**Kavaratti excluded**
Herbivore	Year	**201.15**	**236.68**	**112.98**
	Atoll(Yr)	**13.58**	**14.76**	**16.10**
	Aspect(Yr*At)	**3.13**	**3.00**	**2.88**
Corallivore	Year	**42.47**	**47.37**	**26.35**
	Atoll(Yr)	**3.46**	**3.41**	**4.71**
	Aspect(Yr*At)	**2.86**	**2.91**	**3.44**
Macro-invertebrate Feeder	Year	**168.54**	**179.59**	**147.94**
	Atoll(Yr)	1.19	1.12	0.96
	Aspect(Yr*At)	0.51	0.44	0.87
Micro-invertebrate Feeder	Year	**60.93**	**70.68**	**47.81**
	Atoll(Yr)	1.15	1.25	1.33
	Aspect(Yr*At)	**4.02**	**4.21**	**4.71**
Piscivore	Year	**53.37**	**59.10**	**40.44**
	Atoll(Yr)	**5.03**	**4.91**	0.47
	Aspect(Yr*At)	0.37	0.37	0.60
Planktivore	Year	**34.08**	**39.20**	**22.92**
	Atoll(Yr)	**5.30**	**5.38**	**6.49**
	Aspect(Yr*At)	1.36	1.25	1.34
Omnivore	Year	**43.84**	**47.83**	**30.95**
	Atoll(Yr)	1.22	1.27	1.04
	Aspect(Yr*At)	0.81	0.87	1.07

Macroinvertebrate feeders are a diverse guild of species in the Lakshadweep, comprising 11 families, including several triggerfish, wrasses, snappers and goatfish. Their abundance showed signs of increasing through time at Agatti and Kavaratti, while at Kadmat, no overall change was apparent (Figure 4.8, Table 4.3a, b). Microinvertebrate feeders are a much smaller guild which includes several small labrid species and species from a few other families (see Appendix I). In contrast to macroinvertebrate feeders, their abundance stayed low at all reefs (Figure 4.8, Table 4.3a, b). The abundance pattern of planktivores was dominated by the spike in *O. niger* densities described earlier, and shows few clear trends beyond this (Figure 4.8). Piscivores showed a consistent increase in abundance in Kavaratti, but remained unchanged at other sites (Figure 4.8).

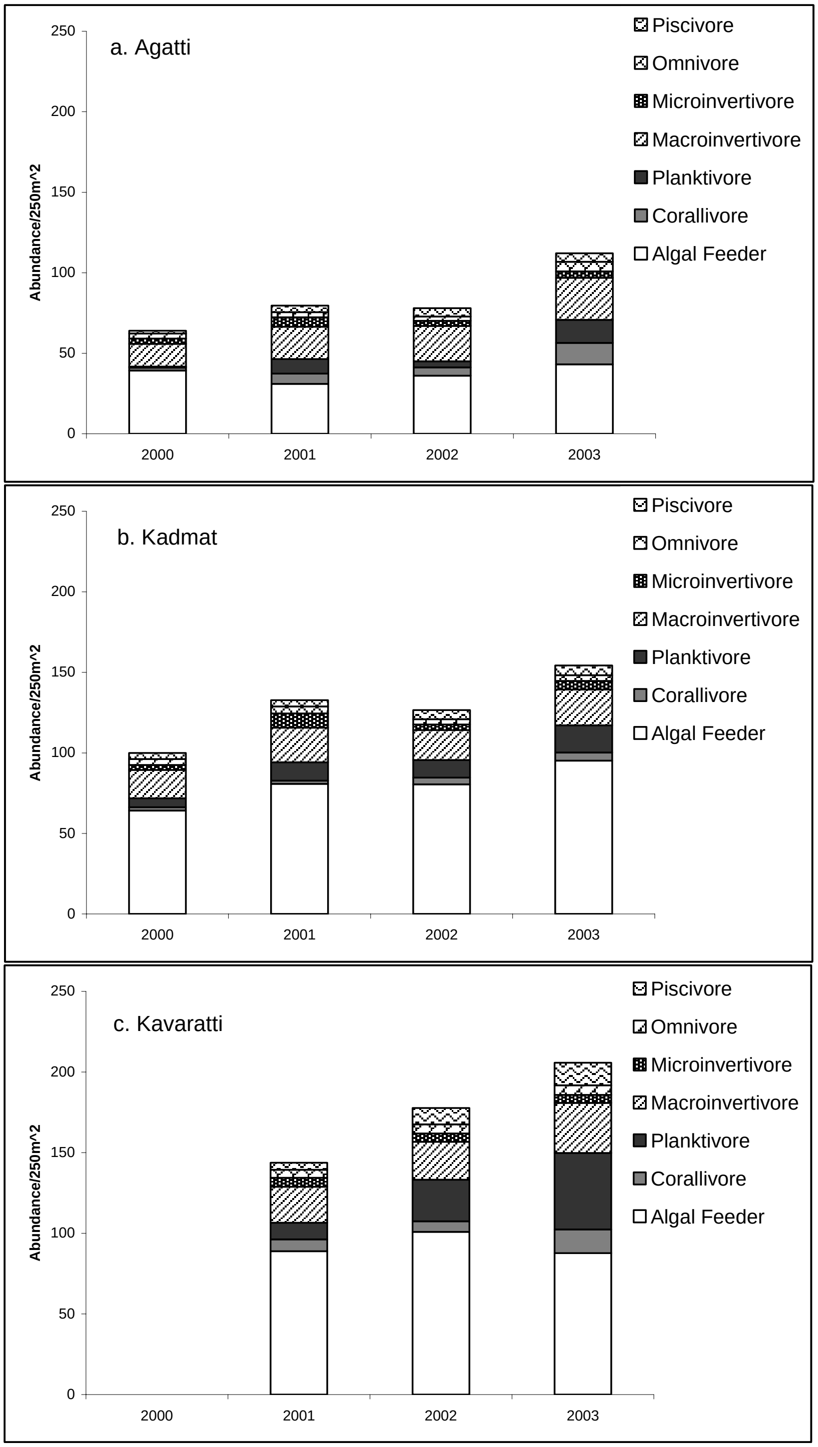


Figure 4.8: Change in guild distribution in the Lakshadweep reefs from 2000 to 2003. Stacked bars represent average values of guild abundance/250m^2. Reefs at Kavaratti could not be sampled in 2000. a: Agatti, b: Kadmat, c: Kavaratti

4.4 Discussion

The response of fish communities to changes in benthic composition is likely the result of a complex interaction between fluctuations in food availability, benthic topography, larval recruitment processes and inter-specific interactions (Sale 1977, Hixon & Beets 1993, Doherty & Fowler 1994, Ault & Johnson 1998, Holbrook *et al.* 2002). The naturally dynamic processes of the reef can be thrown into even greater flux when catastrophic events result in the mortality of a dominant structural element like coral, and it is not unreasonable to expect major shifts in the composition of species either directly or indirectly dependent on it. We may be certain that the 1998 coral bleaching at Lakshadweep was one such event, despite the lack of before and after data. This study focuses on the longer-term consequences of this event to fish abundance, trophic structure and composition. Of particular note are:

1. Fish composition changed considerably from 2000 to 2003, as evidenced from the MDS scatter of similarity between sites
2. Kavaratti experienced the least overall change in composition
3. Total fish abundance, richness and diversity increased, though biomass showed a more variable pattern
4. Guild composition was dominated by herbivores in the first years of sampling, becoming more even with time
5. Corallivores were at very low abundances in 2000, but increased in time, particularly in 2003, when abundance (but not biomass) peaked at some sites
6. In general, fish abundance was lower at Agatti than at Kadmat or Kavaratti

The Lakshadweep fish assemblage thus experienced major directional shifts in composition from 2000 to 2003 (Figure 4.1). Perhaps unsurprisingly, the sites most affected by coral mortality (Kadmat and Agatti) showed the greatest overall change in fish composition. By contrast, at Kavaratti, fish assemblages remained remarkably stable, and communities at other reefs became increasingly similar to the Kavaratti fish community with time. Circumstantially this suggests that assemblages were returning to a pre-disturbance community, although, in the absence of data before 1998, it is impossible to assert this with any certainty. Studies elsewhere have shown that fish communities can be surprisingly resilient to coral mass-mortality events (Williams 1986, Hart *et al.* 1996, Spalding & Jarvis 2002, Sano 2004). For instance, Walsh (1983), tracking the recovery of fish communities after a storm-induced coral mortality, showed that assemblages regained their initial composition within as little as 16 months after the disturbance, despite significant losses to habitat structure. Walsh suggests that plasticity in habitat choice by vagile fish species could well have worked to mitigate the potentially large impact of the storm on community structure. The presence of deeper refugia to which fish could temporarily retreat was crucial to the rapid recovery. Such habitat refuges could well have played an important role in the recovery of Lakshadweep fish in Agatti and Kadmat. Early benthic surveys at these atolls indicated that such availability of refuges may have been limited: coral mortality was extensive throughout the atoll, and not limited to shallow reefs (personal observation, and see Chapter 2). However, both these locations are close to other atolls (Amini, Bangaram, Perumal Par and others – see map in Chapter 2) that could likely have retained fish populations in pockets that escaped bleaching: these could have been an important source of immigrants as the reefs recovered. The reefs of Kavaratti did not sustain as high levels of coral mortality as seen at Kadmat and Agatti, and this possibly helps explain the relative stability of its fish assemblages.

Other studies of bleaching that focus on immediate consequences fail to provide a clear picture of the likely response of fish communities. A month after a mass-bleaching event in southern Japan, Shibuno et al (1999) reported no change in abundance and density, but marked a decline in fish diversity at bleached reefs. By contrast, a year after a similar bleaching-induced coral mortality in Tanzania, Lindahl et al (2001) found no apparent change in diversity, but a striking increase in the abundance of fish. In the Seychelles, Spalding and Jarvis (2002) found little change to fish numbers, while in Japan, Sano (2004) reported declines both in richness and abundance a year after a similar disturbance in 2002. Unlike storm damage, where fish often die as a direct result of disturbance (see references in Walsh 1983), the effects on fish of mass bleaching are likely more insidious. There could be a considerable lag before the consequences of coral death are manifest in fish communities, possibly explaining the variability in response reported by these studies. In relation to the Lakshadweep, it is safe to conjecture that the increases in diversity and abundance from 2000 to 2003 do represent recovery from an initial post-bleaching decline rather than a continuation of an existing trend that predated 1998. Trends in the abundance of trophic groups (for instance, the increase in corallivores in parallel with the increase in corals from 2000 to 2003) support this argument.

Much of the variability of fish community response to coral mass mortality is consistent with differential responses of trophic groups to changes in their resource availability. In the Lakshadweep, the trophic composition of fish was highly skewed towards herbivores in the first few years of sampling. Acanthurids and scarids in particular dominated trophic structure. In 2000, they constituted nearly 75% of total fish abundance in some reefs, exploiting large areas of filamentous and turf algae that had colonized dead coral in the wake of the 1998 mass coral mortality. Opportunistic increases in the abundance and biomass of algal feeders has been consistently reported after such events: for instance, Lindahl et al (2001) recorded surges in the numbers of parrotfish and surgeonfish, being the main contributors to a 39% increase in total fish abundance post-bleaching. Other studies demonstrate similarly disproportionate increases in herbivore numbers after bleaching episodes, often seen within a few months of the bleaching event (Shibuno *et al.* 1999, Chabanet 2002, Shibuno *et al.* 2002). In the Lakshadweep, the relative abundance of herbivores declined with time, but this was driven not by a decrease in herbivore numbers but by increases in the abundance of other groups, as the reef attained a more even guild distribution.

A rapid decline of corallivores is common after mass bleaching (e.g. Kokita & Nakazono 2001, Lindahl *et al.* 2001, Chabanet 2002, Spalding & Jarvis 2002, Sano 2004). While some species of corallivore may become more catholic in their food choice in times of adversity thus resisting extinction (Guzman & Robertson 1989), others suffer significant losses because of their strict fidelity to coral (Kokita & Nakazono 2001, Spalding & Jarvis 2002). The coral filefish *Oxymonocanthus longirostris* appears to have been universally affected by declines in live coral cover, going virtually extinct in the Maldives (M. Saleem, quoted in Dulvy *et al.* 2003). In the Lakshadweep, *O. longirostris* was not recorded in 2000 despite being relatively common before 1998 (personal observation). They were occasionally sighted every year since then, though their numbers remained low. Species like *O. longirostris*, with strong affinities to coral show a very rapid response to coral mortality, and, if refuge sites are unavailable, may even face local extinction. In the Lakshadweep, the significant recovery of corallivores with time (see Figure 4.7) is encouraging, particularly given the extent of coral mortality in some reefs. Young corallivore butterflyfish (10 cm TL) were recorded in large numbers in Kavaratti and Agatti in 2003. While coral mortality was patchy in Kavaratti, allowing coral feeders to thrive in potential refuge sites, the extent of coral mortality at Agatti was far more uniform across all depths and locations, and refuge sites, if present, were in all probability very scarce. This supports the notion that these reefs may be supplied by external recruitment from source reefs elsewhere in the Lakshadweep archipelago. Understanding recruitment patterns and connectivity between atolls in the archipelago will be crucial to the future management of these reefs, in particular, the identification and protection of source reefs.

There is increasing theoretical, experimental and observational evidence of the link between species diversity and the maintenance of ecosystem processes (Walker 1992, Chapin *et al.* 1998). Ecosystem resilience (the ability of ecosystems to absorb disturbance without changing state, (sensu Holling 1973), is linked conceptually to both the diversity of functional groups in a system, and the number of individual species in each group, i.e. functional redundancy (Naeem 1998, Fonseca & Ganade 2001). Ecosystems with high redundancy and functional evenness can often sustain species loss without a state change so long as functional roles are not compromised.

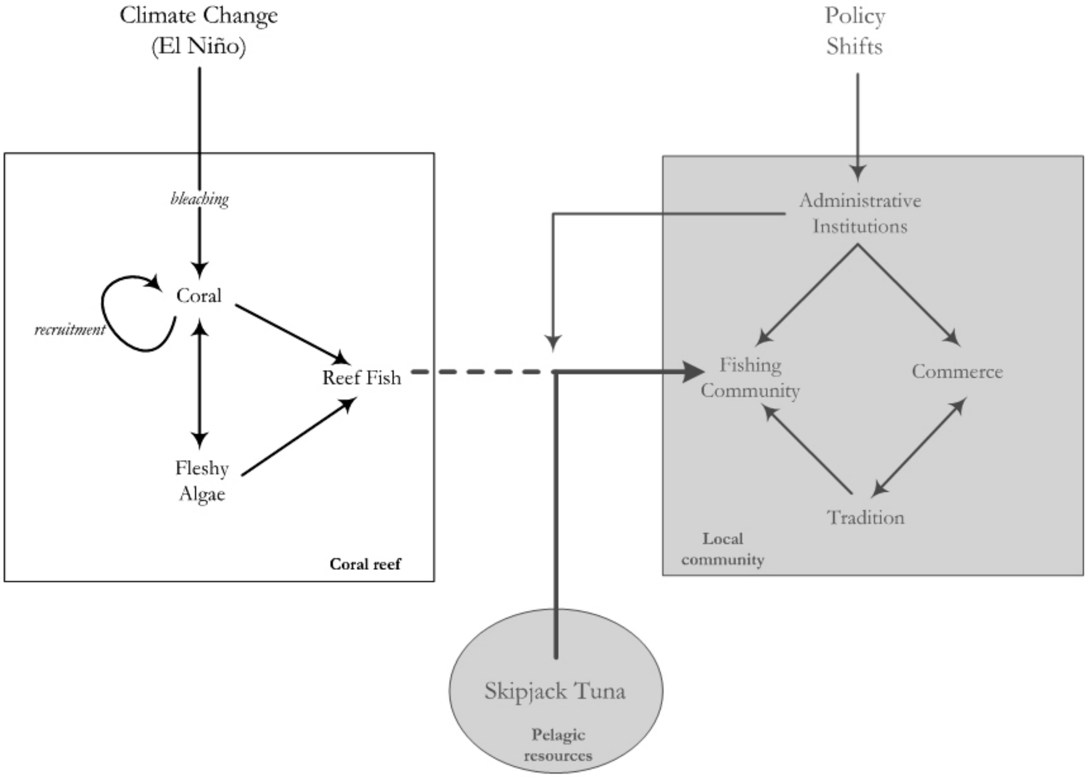
For coral reef systems, fish guilds play vital roles in maintaining ecological functioning, and their response to coral mortality may be a key factor driving reefs towards recovery or decline in the wake of major disturbances (Sammarco *et al.* 1974, Endean 1976, Hughes *et al.* 1987, Done 1992, Hixon & Brostoff 1996, Steele 1998, Lirman 2001). Changes in the functional composition of fish assemblages on reefs have been implicated in dramatic transitions in benthic composition. These ‘phase shifts’ are sometimes reversible. Overfishing reduced populations of a predatory triggerfish, *Balistapus undulatus* in Kenyan reefs, causing sea urchin numbers to burgeon, resulting in considerable reduction of coral cover (presumably because of urchin spine abrasion); with the establishment of no-fishing reserves, triggerfish populations increased in the parks, urchin numbers declined, and coral cover increased (McClanahan *et al.* 1994, McClanahan 1994, McClanahan *et al.* 2001, McClanahan & Arthur 2001). In other instances however, the community shift is more difficult to reverse, as in the reefs of Jamaica, where a combination of overfishing, a hurricane-induced coral mortality, and a disease of herbivorous sea-urchins resulted in the opportunistic predominance of fleshy macroalgae, which has effectively out-competed coral for several decades (Hughes 1994, Hughes & Tanner 2000, Gardner *et al.* 2003). In both these instances, as well as in several others across the developing tropics, heavy fishing pressure has played in major role in modifying the trophic structure of fish communities, resulting in depressed ecosystem function (Roberts 1995).

Fishing on Lakshadweep reefs in contrast is surprisingly low given the large human densities that depend on fish as a major protein source. The history of fishing on the islands is important in this context and is discussed in Chapter 5. Effort is diverted away from reef fishing by heavy subsidies of a pelagic tuna fishery. Except for the monsoon months, the reefs are not the main source of fish (Hoon 2003). However, even such a small, occasional fishery could have a sizeable impact on reef fish populations, particularly as Lakshadweep’s human populations have tripled in the last two decades. For instance, I recorded consistently lower fish abundances from Agatti than at other atolls: Agatti had the highest number of pelagic fishers in the Lakshadweep (Hoon 2003), and in interviews with local people, considerably more men in Agatti engaged in occasional reef fishing than in Kadmat and Kavaratti. It warrants further investigation to establish if the small-scale reef fishery on these reefs is sufficient to depress fish numbers in atolls like Agatti.

It is becoming increasingly apparent that maximizing the natural resilience of reef systems in the face of environmental uncertainty is perhaps the best strategy for their long-term conservation. Maintaining a functional fish community appears to be vital in ensuring that reefs have the best opportunity to recover from coral mass mortality events. This preliminary study showed that fish communities in the Lakshadweep are in a state of transition, with some strong indications of convergence. The increasing abundance and diversification of reef fishes suggest an encouraging level of resilience in these reefs. Relatively low human extraction pressures may have contributed considerably to the reefs recovery. Maximizing such natural resilience through adoption of ecosystem-based approaches to management is perhaps the soundest strategy for their long-term conservation.

Chapter V

BENTHIC CHANGE IN THE LAKSHADWEEP: MODELS AND MANAGEMENT



In this chapter, I attempt to understand the recovery of Lakshadweep's reefs within the framework of catastrophe theory. I explore the applicability of the two-factor cusp catastrophe as a potential phenomenological model of reef response to large infrequent disturbances. The model is driven by two principle axes. The first axis represents the intensity of state-changing pulse disturbances on the system. The second axis incorporates a range of intrinsic reef conditions that promote or hinder resilience. Here, I explore the management applicability of this model to coral reef systems.

Chapter V

The cusp catastrophe as a management tool for coral reef ecosystems

5.1 Introduction

In earlier chapters, I examined the recovery of Lakshadweep reefs after a coral mass mortality event. Although the disturbance resulted in wide-spread death of coral in reefs across the archipelago, recovery was swift at many sites (Chapter 3). At many sites, benthic substrate was dominated by a thin cover of algal turf, maintained in that state by high densities of herbivorous fishes (Chapter 4). In an environment of changing climate, disturbance events such as the 1998 coral mortality are likely to become more frequent and intense (Hoegh-Guldberg 1999), and being able to predict how reefs respond to these disturbances is going to be become crucial to their management. While in some instances, like the Lakshadweep, coral recovery can take place relatively quickly, in many other instances recovery can be protracted, and it is difficult to predict which path the reef will take after a pulse disturbance. In this chapter I examine the role of disturbance on coral reefs, and suggest a model based on catastrophe theory as a potential conceptual model for managing reefs subject to pulse disturbances.

5.1.1 Disturbance and coral reefs

Coral reefs are subject to a host of disturbances, both natural and human-induced. Reefs communities persist in the face of routine disturbances like wave battering and low tide aerial exposure as well as large infrequent disturbances like storms, crown-of-thorns outbreaks and mass bleaching events (Done 1983, Done 1999). Coral reefs also incur significant impacts from human activities, either through extractive processes like fishing (Roberts 1995, McManus *et al.* 1997), non-extractive uses of reefs like anchoring and recreational activities, or through off-reef processes like land-use practices that result in sediment run-off (McClanahan & Obura 1997). The impact of these disturbances has been extensively studied, and they have been found to profoundly influence both the structuring of reef communities as well as the functioning of the ecosystem (Pearson 1981, Done *et al.* 1988, Dollar & Tribble 1993, Connell *et al.* 1997, Guldberg-Hoegh 1999, Done 1999, Ninio *et al.* 2000, Nyström *et al.* 2000).

In the wake of global warming and coral bleaching, coral reefs face a future of increasing uncertainty (Guldberg-Hoegh 1999, Hughes *et al.* 2003). The key question for managers, conservationists and users of the resource is how to effectively protect a reef system with local measures, against a force that is at once global, and inherently unpredictable in nature. Much recent attention has focussed on the management of natural ecosystems to maximize resilience against such ecologically surprising, and essentially uncontrollable events (Done 2001, West & Salm 2003, Bellwood *et al.* 2004). For instance, while it may not be possible to predict with much degree of certainty where and when an ocean warming episode will take place, it may be possible to determine the susceptibility of reef locations and communities to bleaching (Obura 2001, West & Salm 2003). Such information can help prioritize where management should concentrate efforts, either by a strategic selection of protected areas, or by limiting other impacts that may exacerbate reef decline. Thus far however, we do not have a sufficiently general and satisfactory model of coral reef resilience to disturbance that encompasses the full range of variability that this complex ecosystem shows.

Complex ecosystems like coral reefs seldom behave in predictable ways, and are inherently dynamic. The path a coral reef will take after a disturbance is contingent on several factors working synergistically or antagonistically, favouring either recovery or further decline of coral populations. After a large disturbance event like a crown-of-thorns outbreak or a bleaching mortality, coral communities on healthy reefs may respond by gradually returning to pre-disturbance conditions, following a predictable successional path back to normality that will, in time, reach a dynamic equilibrium at, or close to, the pre-disturbance community (Loya 1976, Pearson 1981, Done 1999, Ninio *et al.* 2000).

Often though, reefs do not behave this predictably. A disturbance event sometimes causes a discontinuous switch of community state in the reef that does not revert to the original community even after the disturbance has abated. Recovery of the pre-disturbance community is often difficult, and the consequences of this change to ecosystem functioning is large (Hughes 1994, Hughes & Tanner 2000).

Although changes of community state in coral reefs have received considerable attention (Done 1992, Hughes 1994, Steele 1998, McCook 1999, McManus & Polsenberg 2004), there has been little attempt to integrate simple successional paths with more complex ecosystem behaviours in a single model of coral reef response to disturbance. In managed grasslands and freshwater lakes in contrast, such models have become increasingly important in furthering our understanding and management of these systems (Rietkerk *et al.* 1997, Rietkerk & Van den Koppel 1997). The framework of topological catastrophes has been used effectively in predicting ecosystem behaviour in the wake of disturbance, and there is a strong case for extending this framework to other natural systems that show complex behaviours (Zeeman 1976, Saunders 1980). Catastrophe theory was developed by René Thom as a topological model specifically for representing systems that can display both discontinuous and continuous behaviours (Thom 1975). Depending on the number of control variables, several topological 'catastrophes' or discontinuities can arise in a system, that otherwise follows a predictably continuous path (Saunders 1980). For ecological systems, the cusp catastrophe, with two major control variables, has particular applicability and has been used most successfully in understanding grasshopper dynamics in grasslands (Lockwood & Lockwood 1991), the effects of grazing on rangeland plant communities (Lockwood & Lockwood 1993, Rietkerk *et al.* 1996, Rietkerk & Van den Koppel 1997), in modelling the effects of wildfire and soil moisture on forest plant communities (Hesseln *et al.* 1998, Frelich & Reich 1999) and the effects of eutrophication on freshwater lakes (Scheffer 1998). Here I review the utility of the cusp catastrophe in relation to to coral reef systems subject to disturbance. I first describe the catastrophe model as it could be applied to coral reef communities, and assess if the model is a valid description of reef systems. Finally, I briefly outline how the cusp catastrophe model can be an effective tool in the planning and application of management for coral reef ecosystems.

5.1.2 Coral reef response to disturbance as a cusp catastrophe

The cusp catastrophe is given by the equation (Saunders 1980):

$$V(x)=x^4+px^2+qx \qquad (1)$$

where p and q are control variables, and x is the response or state variable. The equilibrium solutions of (1) provide the response surface of the state variable x which has a three-dimensional geometry as shown in Figure 5.1, with an infolded cusp (or catastrophe), becoming gradually less infolded along the p-axis. The control variable q (Figure 5.1) is a gradient of disturbance intensity, and directly affects the state variable by reducing the dominant community element, in this case hard coral. Low levels of disturbance may merely stress coral individuals without causing mortality. As disturbance severity increases however, coral individuals are killed sequentially, depending on the susceptibility of species to the disturbance. The control variable q represents conditions largely external to the ecosystem that can still have a large effect on it. The response surface x (Figure 5.1), is a "landscape" of community states that the reef can attain. Most of these states will be transitory, and there exist two relatively stable community states (coral dominant and fleshy macroalgae dominant) corresponding to the upper and lower regions of the figure, and an intermediate state where bare space and algal turf dominates.

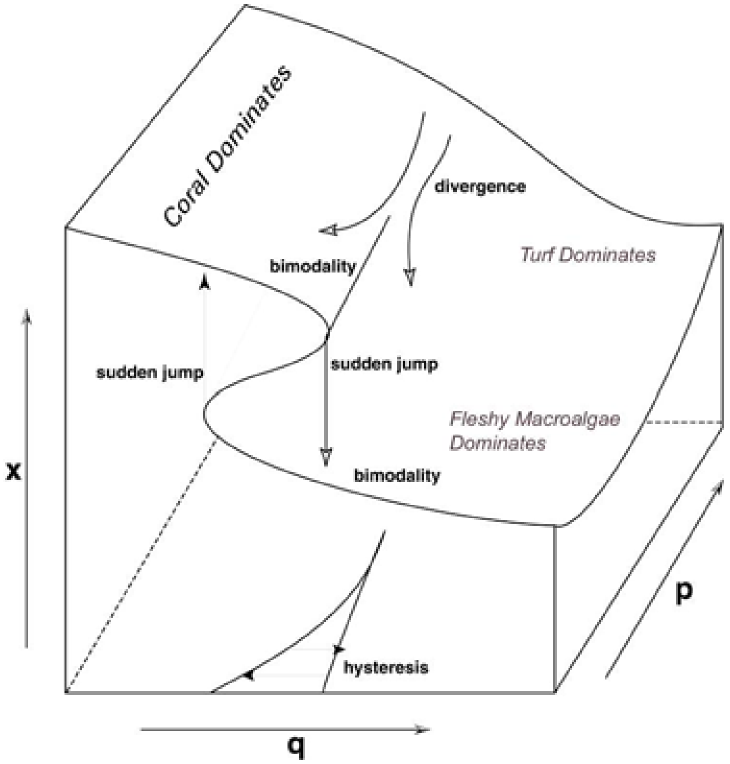


Figure 5.1 A cusp catastrophe model for coral reefs. The control variables q and p drive community responses. See text for details.

The control variable p constitutes the gradient of ecological and environmental conditions present at a reef site. At one extreme of this gradient (the far end of p in Figure 5.1), the reef changes from coral to algal dominance and back through a series of unstable, intermediate (successional) states. An increase in disturbance will see a predictable increase in turf algae as observed in the Lakshadweep; when the disturbance abates the system will move gradually back to coral dominance. At the other extreme of p however, the reef behaves in a discontinuous manner. Under these conditions, after a certain threshold of disturbance (the cusp in Figure 5.1), the reef will abruptly switch to fleshy algal dominance. When the disturbance is removed, the system does not revert back to coral dominance, and may maintain algal dominance until conditions change.

The control variable p represents factors that are inherent to a particular location, independent of the external factors that influence it. In the context of community disturbance and recovery, the inherent factors most important in characterising a reef include:

1. the availability, settlement and survival of coral recruits
2. the prevalence and control of coral competitors, most significantly, the abundance and biomass of fleshy macroalgae, the influx of nutrients that may favour their growth, and the ability of herbivores to contain them
3. anthropogenic factors (like fishing) that influence 1. and 2.

The variable p is likely a combination of these factors, and is important in determining which point of stability the reef community moves towards on the response surface of the cusp catastrophe. Presumably there exist critical levels of these factors that could push ecosystems from continuous to discontinuous change. Where a reef site lies on this gradient will determine if it will follow a successional path, or undergo a phase shift after a major disturbance event (Table 5.1). These factors are not necessarily independent of each other and interact in various ways. For instance, if herbivores are not able to adequately contain fleshy algae in the wake of a disturbance, it could well limit the settlement and survival of coral recruits. The ability of herbivores to maintain algal populations may in turn be compromised by heavy fishing pressure.

Table 5.1 Intrinsic factors contributing to catastrophe axis p favouring either succession or phase shifts in reefs subject to coral mortality

Factor	**Succession**	**Phase Shift**
Recruitment Processes		
Connectivity	**High**	**Low**
Recruit production	**High**	**Low or absent**
Settlement and growth	**High**	**Low**
Recruit Mortality	**Low**	**High**
Competitive Processes		
Macroalgal abundance and growth		
Nutrient influx	**Low**	**High**
Herbivory	**Low**	**High**
Anthropogenic impacts	**High**	**Low**
Fishing pressure		
Structure reducing activities like anchoring, etc	**Low**	**High**
	Low	**High**

In modern day reefs, the effects of removal of fish have become an important part of ‘p’. While it may be argued that routine human uses of reefs like fishing are not inherent to the system, and are external to it. However, within the context of the model, fishing (p) is qualitatively different from disturbances (q) that directly modify ecosystem state. Its influence on benthic communities is that of a chronic rather than a pulsed driver. Also, unlike external disturbances such as ocean warming events and storms, fishing is more predictable, measurable, and, at least in theory, manageable.

5.3 Catastrophic symptoms: reviewing the evidence for coral reefs:

Catastrophe theory's great strength is that it integrates concepts of states, transitions and succession into a single theory whose mathematics is well understood. For the theory to be applicable however, it is necessary for ecological systems to show the following characteristic properties or 'symptoms' associated with cusp catastrophes (Zeeman 1976): modality, sudden switches between modes, hysteresis, inaccessibility and divergence. Here, we briefly discuss the evidence for these five properties in coral reef ecosystems.

Modality indicates that the system can exist in more than one distinct state at equilibrium. Bimodality in coral reef ecosystems has been widely discussed and reviewed, both from theoretical models as well as real world examples, often set in the context of the multiple stable state (Knowlton 1992, Gunderson 2000). While the concept of multiple stable states has been around for a while in the coral reef literature, it is unclear if the case studies in the literature meet the strict criteria specified by Connell and Sousa (1983). They suggest for instance that in order to demonstrate stable alternate states, the community should remain unchanged for at least one turnover of all individuals in the population (Connell & Sousa 1983). With clonal organisms of indeterminate age like corals, it is difficult to unambiguously define a clear turnover time. Coral colonies can be naturally very long lived (Done & Potts 1992), and few examples exist from the field to show that reef communities remain stable over periods extending a few decades. Where the ecosystem is subject to state-changing disturbances at intervals considerably shorter than the potential generational time of corals, it may be impossible to demonstrate the existence of stable alternate state in real-world conditions. Done (1992), borrowing a term from the physical sciences, suggests the concept of the phase shift as an alternative to the stable state. This views the ecosystem as considerably more dynamic and fluid than the multiple stable state, and specifies the existence of at least two modes, or phases, that the ecosystem can exist in. The modes most frequently identified in coral reefs are a community dominated by hard coral which can be replaced by a community dominated by fleshy macroalgae. Although phase shifts have been described for reefs across the tropics from the Caribbean (Hughes 1994) to the GBR (McCook 1999), the precise mechanisms driving change are not completely clear. The competitive mechanisms between coral and algae are seldom straightforward, and different species and lifeforms of coral and algae have different competitive effects on each other (Jompa & McCook 2003). In most cases where a phase shift from coral dominance to algal dominance occurs, it is preceded by a disturbance event that kills off a large proportion of the coral, leaving the substrate open to takeover by algae. Herbivory is an important control in coral reefs, and herbivore reduction by fishing appears to be as a major cause in generating phase shifts (Hughes 1994, Hughes & Connell 1999, McManus *et al.* 2000). The role of nutrients that promote the growth of fleshy algae has also been implicated in encouraging a push towards algal dominance (Miller & Hay 1996, McCook 1999, Mccook 2001, Smith *et al.* 2001). It is also unclear how temporally stable phase shifts in reefs are, though case studies from the Caribbean indicate little change after two decades of a phase shift in the 1980s (Hughes 1994, Hughes & Tanner 2000, Lugo *et al.* 2000, but see Knowlton 2001).

The presence of **sudden switches** between community modes is also fairly well documented in the reef literature. The reefs of Jamaica are a classic case in point where the combination of overfishing, a devastating hurricane and a disease of sea urchin herbivores resulted in the rapid switch between community states from coral to macroalgae (Hughes 1994). Done (1992) and McManus *et al.* (2000) discuss rapid switches of state in response to a range of disturbance factors. Defining the time span of a sudden switch may be problematic particularly because coral and algae have strikingly different life spans.

Hysteresis indicates that, under unvarying conditions of p, the path the coral reef takes to reach an alternate state is different from the path back to the original state. This is represented by the infolded region of the catastrophe surface (Figure 5.1). Practically this means the pre-disturbance community may not be achieved even when the conditions that precipitated the change abate. In Jamaican coral reefs for instance, the phase shift to macroalgae has resulted in the exclusion of coral recruitment and recolonization, resulting in the long-term dominance of the macroalgal community (Hughes & Tanner 2000). This may show some of the characteristics of hysteresis (the community did not recover long after the disturbance conditions – Hurricane Allen – had passed), but it is difficult to prove hysteresis conclusively until we understand the conditions under which the reef reverts back to coral dominance, if at all it does. If the exclusion of fishing (which contributes to p on the cusp catastrophe) results in coral recovery in Jamaican reefs, it would be symptomatic of divergence rather than hysteresis. The dominant organisms that constitute the phases in coral reef systems (coral and algae) have very different growth rates and lifespans. Thus, while the switch from coral to algae can take place very quickly, corals, which grow much slower, may take much longer to regain dominance. The time span of a ‘sudden’ switch from coral to algae may be very different from a switch back to coral dominance. Reefs are subject to a host of stochastic processes that may reduce coral cover at rates faster than the regrowth of coral, and this could prevent rapid switches from taking place. Where these switches do take place, it is likely to be driven by relatively fast growing coral species.

Another symptom of the cusp catastrophe is **inaccessibility**, and it indicates that the system precludes certain community states from existing stably. This represents the infolded region of the catastrophe cusp in figure 5.1. There is insufficient evidence in the reef literature to support this, though inaccessibility may be an important character of reefs that show phase shifts.

Divergence is a property of cusp catastrophes that causes large changes in the response surface with small changes in condition (see Figure 5.2). For coral reefs, there is little evidence that profound changes of community state can result from minor changes in environmental conditions, but this is probably because most studies of reef decline and recovery have not been geared to answering this question. Examples exist of ecosystem decline with the loss of a single species, and this may be evidence of divergent behaviour of reefs. In Jamaica, the population collapse of the sea urchin *Diadema antillarium* to disease signalled a switch of reefs to a seemingly stable macroalgal phase. However, in this instance, the loss of sea urchins was the final trigger in a chain of events that had earlier included the depletion of herbivorous fish, and a hurricane that caused large coral mortality (Hughes 1994). The Jamaican reefs are not therefore a clear-cut case of divergence. The coral reefs of Kenya supply a more convincing example of possible divergent behaviour in reefs. Here, the loss of the Redline Triggerfish (*Balistapus undulatus*) to fishing resulted in population explosions of sea urchins and a decline of corals (because of abrasion by sea urchin spines) and fish communities (Carreiro-Silva & McClanahan 2001). Fishing intensity is apparently the major cause that drives divergent behaviour in Kenyan reefs: when fishing was stopped, triggerfish abundance increased, controlling urchin populations and resulting in a reversion of the reef community to coral dominance (McClanahan 1994, McClanahan 2000b, McClanahan & Arthur 2001).

In summary, there is some evidence that coral reef communities may show the symptoms of a cusp catastrophe. Bimodality and sudden switches are both common in reefs and have been extensively discussed. There is evidence from a few studies to show that reef systems may behave in divergent ways and it may be possible to test the divergence of reefs with a well-designed experimental approach. Hysteresis in contrast may be more difficult to demonstrate in field conditions because of differences in life history of the community dominants, and the frequency of stochastic disturbances. It is also difficult, from studies done thus far to conclude that certain configurations of community compositions are ‘inaccessible’.

5.4 P’s and Q’s: the cusp catastrophe as a tool for management

The cusp catastrophe generates specific hypotheses on the effect that small changes in environmental conditions will have on community structure within a single response model of coral reef disturbance. While it does not tease apart causal ecological mechanisms of decline or recovery, it can be very effective in assessing the likelihood of reef sites to recover or decline after a major disturbance. Its control variables have distinct ecological characters applicable to the management of reefs. Additionally, it identifies thresholds on both control axes that have relevance to coral reef management.

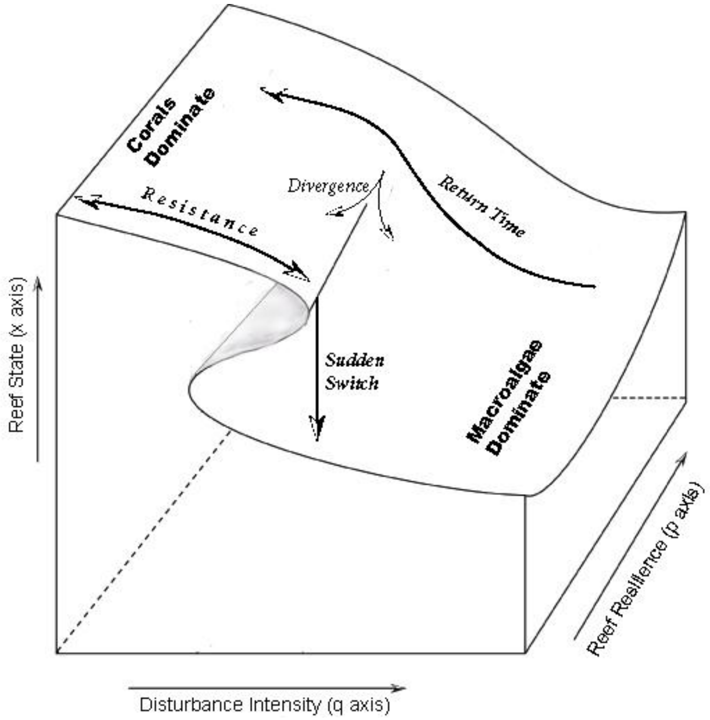


Figure 5.2 A catastrophe model of coral reefs, showing management thresholds (divergence and sudden switches).

5.4.1 The q-axis: Unmanageable impacts

As the axis of disturbance intensity, variable q is largely outside the bounds of what managers can control (Figure 5.2). It therefore encompasses the exogenous dynamic uncertainty of ecosystem response. The location of the cusp on the response surface represents the intensity of disturbance that a reef will sustain before it switches community state (Figure 5.2). Its position is highly contingent on the species and lifeform composition, and the susceptibility of dominant coral species to the disturbance. The kind of disturbance is also important: susceptibility to a storm may be very different from susceptibility to a heat wave.

5.4.2 The p-axis: Management for resilience

The variable p can be viewed as an axis of resilience. For a given place, the necessary attributes of resilience for the coral state are good conditions for coral growth, settlement and repair after major losses, summarized in Table 5.1. At high values of p, these conditions are in place in good measure, and reef has the potential to recovery relatively quickly after a disturbance event. At values of p below the infolded cusp of the response surface, recovery will be considerably protracted.

The p axis is the principle management axis of the model, in that it represents environmental and biological conditions that managers can aspire to control: recruitment processes, water quality, competitive and herbivory processes. These will be different for each reef area. For instance, isolated reefs like the Lakshadweep may be less well-connected to fecund coral metapopulations – the strength and reliability of new recruits may be the most important factor driving local resilience. In contrast, nearshore reefs, well supplied with recruits may be rendered ‘non-resilient’ by negative impacts of terrigenous nutrient inputs that encourage the growth of macroalgae. Determining the contribution of each of the factors listed in Table 5.1 to local resilience is the major requirement to develop the catastrophe model as a working management tool.

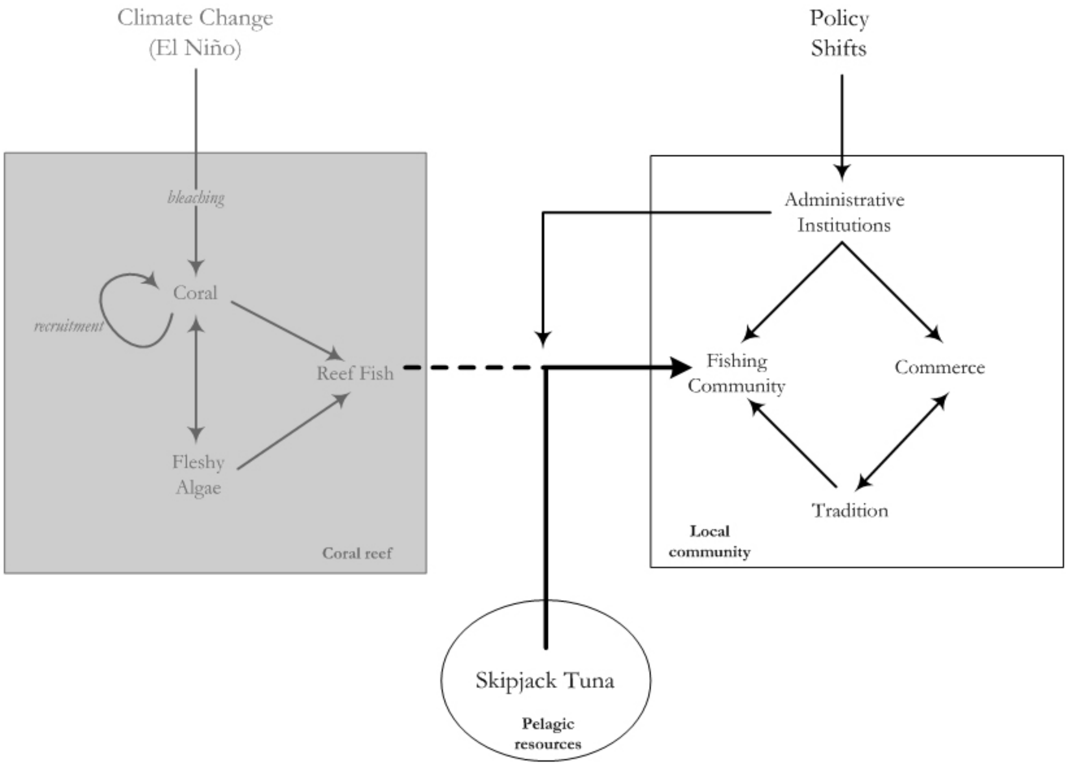
5.5 Conclusion

Managing along the p-axis has two significant benefits. It provides an objective way of assessing reef sites for their resilience potential, based on indicators of connectivity, community composition and human use. This approach would allow a manager to rate the susceptibility of an area to phase shifts, and could help in deciding where protected areas might be most effective. Particularly in the developing tropics, where the process of setting up protected area networks is in its infancy, the model could be a useful means of deciding priority areas for management. Additionally, the p-axis forms a firm basis of monitoring ecosystem performance in terms of the factors that contribute most to resilience.

The management of complex ecosystems is scarcely simple, particularly when we have a poor understanding of the underlying processes that shape the system. While considerable research could be done to validate the model for reef systems, it already provides a conceptual model and and heuristic tool for coral reef managers. There is already a paradigm shift taking place that is attempting to incorporate the dynamism inherent in coral reefs in the management strategies we adopt to conserve them. In an era of increasing environmental uncertainty, catastrophe theory provides a coherent and intuitive model of reef response to disturbance, and could prove a powerful tool in the development of this new paradigm.

Chapter VI

INSTITUTIONAL CONTROLS AND MARINE RESOURCE USE IN THE LAKSHADWEEP



In this chapter, I look at patterns of resource use in the Lakshadweep, and examine the influence of local institutions on the way marine resources are extracted. I discuss the implications of an historical change in marine resource use from a primarily reef-based fishing to a commercial exploitation of pelagic tuna. The success of this programme has significantly reduced fishing pressure on the reef. I argue that this may be an example of epiphenomenal conservation, where the benefits accrued to the ecosystem were the incidental bi-product of a development scheme.

Chapter VI

Managing reefs by *non sequitur*: institutional control, marine resource use, and unintended consequences

6.1 Introduction

The paradigm of natural area management is graduating from a purely preservationist ideology to a more inclusive one, where social and ecological systems are seen to be inextricably linked (Berkes & Folke 1998, Berkes 2004). Humans have exploited natural areas for millennia, and are a significant agent of ecosystem change, modifying them intentionally as well as unintentionally. Changes in human systems can impact ecosystems just as strongly as changes in natural resources can influence human communities. Any attempt to understand ecosystem behaviours is incomplete without an additional understanding of the cultural, economic and political institutions that control the way humans use ecosystems. Central to this is the appreciation that the study of ecosystems is as much a discipline of history as it is a discipline of the natural and social sciences (Berkes *et al.* 2000, Davidson-Hunt & Berkes 2000). Historical disturbances to social or ecological status quo are largely unpredictable, characteristically discontinuous, and can wield an often disproportionate influence on the functioning of ecological systems. Ecosystem response takes place on a canvas of history, nudged along diverse ecological pathways by contingency and circumstance. Given this uncertainty, management within this paradigm should focus less on maintaining a system at a putative steady state, and attempt instead to maximize the buffer capacity (ecological resilience, Holling 1973) of the system against inevitable surprises.

While the chapters 2 through 4 of this thesis dealt primarily with ecosystem processes in the Lakshadweep reefs after a coral mass mortality, this chapter looks briefly at the history of marine resource use, and the institutions that control it in the Lakshadweep. I argue that historical changes in fishing practices associated with changes in institutional policy have had important and completely unintended consequences for the resilience of the coral reef ecosystem. I discuss these consequences in relation to the recovery of Lakshadweep's reefs in particular, and its broader implications for reef conservation management.

6.1.1 Resource use, traditional management and epiphenomenal conservation

Much of the debate on the use and abuse of natural resources by human communities has centred around Hardin's influential 'tragedy of the commons' proposition (Hardin 1968). Collectively owned, open access natural resources are doomed to overexploitation since each individual is likely to behave as a "rational calculator" of their own needs. The resource will eventually succumb to extraction regimes that maximize individual efficiency rather than common good, pushing systems past sustainable levels of harvest. However, examples exist of traditional communities sustainably harvesting natural resources for centuries, leading to the suggestion that humans in many traditional societies may be using their resources judiciously, operating as a 'prudent predator' (Slobodkin 1968), and carefully self-regulating extraction through a series of resource management strictures, often couched in religious or cultural belief systems. For instance, several communities in India employ traditional practices that restrain resource extraction including the protection of spawning periods, species taboos, and the maintenance of sacred groves, patches of forest which have special religious significance, from which extraction is forbidden (Gadgil 1985, Gadgil *et al.* 1998).

There has been considerable doubt cast over the continued effectiveness of traditional systems in sustaining natural resources as ecosystems fragment and are rapidly depleted, and the population numbers of people directly dependent on them burgeon (Madhusudan & Raman 2003a). Merely demonstrating that traditions of voluntary restriction are practiced is not proof enough that these practices represent traditional conservation. Few communities are completely immune from the influences of modernisation, and though traditional practices may still thrive, they may be subtly modified by improvements in gear or increase in access which could significantly alter the sustainability of the practice. When traditional communities interact with commercial markets, traditional practices can often be employed to supply external demand rather than the sustenance needs of the community, radically altering the human-resource relationship (Madhusudan 2004, Mishra 2000). The "ecologically noble savage" may not exist in even the most isolated societies: Alvard (1993, 1995) has shown that Piro hunters in the Amazonian Peru hunt game in a manner completely predicted by optimal foraging theory rather than as prudent predators. The fact that their hunting techniques are 'sustainable', Alvard claims, is an example of "epiphenomenal conservation" – an unintended consequence of an essentially non-altruistic practice, resulting either from low population density, or because logistic constraints limit how much communities can extract (Hunn 1982).

Epiphenomenal conservation has been discussed largely within the context of traditional management systems. However non-indigenous forms of natural resource management could also have conservation benefits that are completely unintended, and the history of fishing in the

Lakshadweep appears to present one such example. Here, a development activity, engineered to provide employment, kick-start an economy, and tap into underexploited natural resources, has had potentially far-reaching consequences for the archipelago's coral reefs.

6.1.2 Coral mass mortality and Lakshadweep reefs

Earlier in the thesis I outlined patterns of change to Lakshadweep's reefs after the 1998 El Niño-induced coral mass mortality. Fleshy macroalgae can sometimes opportunistically overrun a reef after such events, precipitating a radical change in ecological function, termed a 'phase shift' (Done 1992, McCook 1999). However, despite sustaining large-scale losses of coral, the Lakshadweep reefs did not undergo such a phase shift (Chapter 2). This set the conditions for rapid recovery of coral at some sites (Chapter 3). Coral growth was not uniform in different reefs, and was driven largely by differences in the long-term viability of settlement substrate and post-settlement mortality of coral. In reefs where corals settled on stable substrate, recovery was rapid, in areas of unstable substrate, new recruitment was offset by losses because of structural erosion, and recovery was delayed.

As explained in Chapter 4, the composition of reef fish was important in facilitating this recovery. Overall, reef fish assemblages showed signs of considerable stability. While highly coral-dependent groups had very low abundances in 2000, their populations showed encouraging signs of increase by 2003. This included species like the coral filefish (*Oxymonocanthus longirostris*), that were previously thought to have gone locally extinct in the wake of the bleaching.

Fishing often has a large impact on reef communities, and overfishing is among the most significant proximate causes of reef decline in reefs across the tropics (Roberts 1995, Jennings & Lock 1996, McClanahan 1997). Fishing in many parts of the developing world follows a familiar pattern of exploitation, targeting species lower down the trophic chain as higher trophic groups are depleted, resulting eventually in an over-exploitation of herbivores (Pauly *et al.* 1998). Algal herbivores play an important mediating role in the competitive interactions between coral and fleshy macroalgae (McCook *et al.* 2001, Lirman 2001), and their reduction in reefs has often been implicated as a precipitant of detrimental phase shifts in reefs (Hughes 1994, McManus *et al.* 2000, McManus & Polsenberg 2004).

For the Lakshadweep in contrast, herbivorous fish (principally surgeonfish and parrotfish) were abundant and burgeoning at all surveyed reefs from 2000 to 2003 (Chapter 4). Unlike many other reefs in the developing tropics, the Lakshadweep atolls sustain relatively low levels of reef fishing despite high human populations living in close proximity to the reef. In this chapter I explore the institutions that influence and control fishing practices and marine resource use in the Lakshadweep. I briefly outline historical changes in fishing practices in the Lakshadweep, and the implications of these changes for the resilience and conservation of the coral reef.

6.2 Methods

I used participant observation, semi-structured interviews and document analysis to understand the institutions and institutional structures that influence and control resource use in the Lakshadweep (Bunce *et al.* 1999, Bunce *et al.* 2000). Participant observation is an experiential technique central to much ethnographic research, and involves observing communities 'on the inside', participating actively in community activities while still maintaining relative distance (Bernard 1995). This technique directly contrasts with 'passive' observation, acknowledging that observers inevitably modify community behaviours. For instance, M. N. Srinivas, studying the consequences of modernisation on the Indian caste system, lived in the village of Rampura as participant and observer, fully recognizing that community members in the village related to him according to his caste (Srinivas 1980). However, this gave him access to patterns of community behaviour and belief that may have been hidden from passive observation.

I visited the Lakshadweep every year from 1997 to 2003, spending between 1 to 6 months on the islands. I lived largely on Kadmat, Kavaratti and Agatti, with shorter periods spent on other islands. During that time I integrated within the Lakshadweep community: wherever possible I lived in the village, I participated actively in the daily life of the community, and attended ceremonial functions (weddings, circumcisions, religious celebrations, etc). I accompanied fishers on fishing trips, and interviewed them as they processed fish on the beaches, and in their homes. My identity within the community was an important part of establishing trust with the islanders. I was identified as a 'scientist' and a 'student', and was not affiliated with local or central government institutions. This was important in establishing that I had no vested interests in obtaining information from community members, particularly in relation to their attitudes to the local administration. In my discussions with local islanders on the role of religion in daily life, I was identified as 'Christian', and therefore a '*kitabi*' (one who shares the same holy book). Narratives and opinions obtained through participant observation were validated by triangulating with key informant interviews and document analysis (Bernard 1995, Bunce *et al.* 2000).

I interviewed key informants from the fishing community and government departments in Kadmat, Kavaratti and Agatti:

1. Fishers: I conducted semi-structured interviews with 32 fishers in Agatti, Kadmat and Kavaratti. Fishers were all male, and ranged between 14 and ~70 years old. For the purposes of this study, I asked questions about current and historical fishing practices and preferences, fishing habits through the year, and the species of fish they caught. I asked questions about how they were introduced to the fishery, and the factors that influenced current fishing practices. Additionally, I questioned informants about taboo marine species, and why these species were taboo.

2. Government department officials: I interviewed officials at various levels of government in order to understand the administration's role in influencing marine resource use on the islands. I spoke to individuals in the Department of Science and Technology, Department of Environment and Forests, Department of Fisheries, Lakshadweep Development Corporation, and the Island Administrator. One of my principal key informants was the Deputy Director of Science and Technology, one of the few island inhabitants who occupied a high position in the governing bureaucracy. He was able to provide a unique bridge between the island community and the Lakshadweep administration. I asked questions relating to economic and environmental policies, and the administration's perceptions of marine resource use in the Lakshadweep.

In addition to participant observation and interviews, I also used previously published literature on the Lakshadweep and published data from Department of Fisheries, Planning Commission, and the Directorate of Census Information for the Lakshadweep.

6.3 Results

6.3.1 Institutions of control in the Lakshadweep

Among the institutions that influence community behaviours, the two that principally affect resource use in the Lakshadweep are religion (couched within the larger institution of local culture), and local government. Both are strong forces, and have a series of explicit rules and implicit norms that seek to control resource use on the islands. I first briefly describe how each of these institutions affects daily life, and how the community perceives them. I use case studies of dolphin hunting and shark fishing to discuss how these institutions interact to influence marine resource use. I then outline the history of reef and pelagic fishing in the Lakshadweep, and discuss its implications for reef recovery.

Cultural identity and religion

The Lakshadweep islands were declared a Union Territory of India in 1956, ushering in a number of important rural development activities, and bringing the islands in much closer contact with economies on the Indian mainland (See Chapter 2). Despite this, the Lakshadweep islands have been fairly resistant to cultural invasion (Singh *et al.* 1993). The islanders maintain a strong sense of local island identity; many islanders I interviewed resented the comparison with the inhabitants of coastal Kerala, despite acknowledging the close ties they share: *Jasseri*, the language spoken on most Lakshadweep Islands is a dialect of Malyallam spoken in Kerala, and the social structure of the Lakshadweep still maintains several important affinities with Kerala, most notably, a matrilineal system of inheritance (Mannadiar 1977, Dube 1996). After marriage, men are traditionally required to share their time equally between their wife's and their mother's house, and may typically spend half the day at each residence (Singh *et al.* 1993). This makes inter-island marriage difficult to sustain, and although traditions are slowly breaking down, the population still tends to marry within the island of their birth. This further strengthens a sense of identity with the native island: the people of Agatti for instance see themselves as distinct from the people of Kadmat or other islands, and even have accents and idioms that distinguish them from other islanders.

Cultural pride and separateness is strongly promoted by the islands' religious leaders. The vast majority of the local population follow the *Shafi'i* school of Sunni Islam, and religion plays an important part in daily life (Mannadiar 1977, Singh *et al.* 1993). Religious education begins early, a system of *madrassas* (religious schools) is well established, and children are exposed to religious studies even before they attend regular school. Religious elders are well respected on the islands, and their dictates are rarely opposed. Their influence is not restricted to moral mores and they have a large influence in decision-making on the islands. For instance, till 2002, religious leaders actively opposed the introduction of cable television (the predominant way that much of India receives television) to the islands, citing cultural pollution and moral depravity that could result from exposure to western-oriented media.

Religion also influences patterns of natural resource exploitation (Jha 1998, and see later). For instance, the islanders adhere firmly to the weekly day of prayer (*juma*) that falls on Friday; none of the fishers interviewed would take their boats out to sea between Thursday night and late Friday afternoon, until after the mid-day prayers (*namaz*). Islam has strict codes about the consumption and preparation of pure (*halal*) and impure (*haram*) foods. The islanders consider most marine species to be *halal* and there are no religious limits placed on their extraction. However, molluscs, crustaceans, and any shell-bearing marine species are considered *haram*, and are not eaten. The notable exceptions are squid and octopus which are significant harvests from the reef (Hoon 2003, personal observation); presumably their internal shells make them acceptable targets for consumption.

Local governance and the subsidy culture

The institution that plays an even more direct role in the economy of the islands is the Indian government and its contingent departments and bureaucracies. After independence from Britain, the Lakshadweep was quickly recognised as a strategically important Indian Ocean outpost, economically important, because it significantly extended India's Exclusive Economic Zone (EEZ), and politically sensitive, being a strongly Islamic culture on the ocean border with rival Pakistan (Rajiv Talwar, Administrator, personal communication).

Beginning in the early 1960s the government instituted a policy of heavy subsidies for the island. Today, almost every aspect of daily life is subsidized in some way by the government. This includes food, agriculture and fishing, fuel, transport, electricity generation and supply, telecommunications, and other essential goods and services (Department of Planning and Statistics 2003). Most development and commercial activities are also controlled by the government through government-run co-operatives. Being a Union Territory, the Lakshadweep has lower tax structures than the full federal states of India, and agriculture and fishing are largely tax exempt. Indigenous islanders who are born in the Lakshadweep are afforded 'Scheduled Tribe' status, a listing that entitles them to a significant range of benefits including non-merit based, reserved positions in schools and universities, as well as in government jobs.

However, although some middle-level management positions in the government are chaired by islanders, the top tier of the Lakshadweep administration is appointed by the central government, chosen from cadres of career bureaucrats; the top job of the island Administrator has never been held by an indigenous Lakshadweepan. The demand for lower-level positions in government departments however is high. The government is the largest full-time employer on the islands. I came to quickly recognise that for the islanders, 'employment' is synonymous with 'government employment'. An interesting indication of this is that one of the many active youth groups in the capital Kavaratti calls itself "The Unemployed Youth Association" (UYA), dedicated to helping out in environmental and social causes. In interactions with the UYA, I discovered that most of the young men in the group were, in fact, gainfully employed as fishers or shopkeepers. However, they did not consider these professions to be ‘employment’ because it did not provide the same benefits (a monthly salary, stability, status) that a government job would afford them.

6.3.2 Institutional control and marine resource use

The interaction between the administration and religion in the Lakshadweep is complex, and can have far-reaching implications for resource use. Two brief case studies help illustrate this interaction and its consequences for marine resource use on the islands. The first describes the cessation of dolphin hunting in the Lakshadweep in the 1970s, and is based on a narrative history I encountered repeatedly from Kadmat. Key informants in Kadmat (M.K. Ibrahim, Mohammed Hanifa) claimed that this applied other islands as well, but I was unable to verify this independently. The second example describes a more recent attempt to restrict shark fishing on the islands, in 2001. This event took place while I was on the islands, and I had occasion to interview fishers, community members and administration authorities as it unfolded.

Dolphin hunting

Populations of spinner dolphins (*Stenella longirostris*) are common in the waters surrounding many Lakshadweep atolls, and till the 1970s, these populations were traditionally hunted on an annual basis on the island of Kadmat. The tradition involved the whole village, and dolphin meat was highly prized. Fishing boats would locate a dolphin pod, and collectively ‘herd’ the pod through the narrow entrance to the lagoon. Once inside the shallow lagoon, the dolphins were trapped, and clubbed to death. The meat was then collected and eaten, and the leftover meat was dried for later consumption. A single hunt could result in a harvest of between 100 to 500 dolphins. After the early 1970s the practice died out, and dolphins are not hunted in large numbers anymore. I spoke to administration officials in the Department of Environment to understand what led to the decline of this practice. According to department officials, the tradition was stopped after the enforcement of the Indian Wildlife (Protection) Act of 1972, which prohibited hunting of cetaceans, placing them in a restricted schedule (Schedule II, Government of India 1972). The specific details of enforcement however are unclear.

None of the islanders I interviewed mentioned the legislation or its enforcement as a reason for the cessation of the practice. They link the discontinuation of the annual hunt with a specific incident that took place in the early 1970s, although no one I interviewed to could confirm the exact year. Tradition required that a prize dolphin caught in the hunt was presented to a village religious leader called the *Thangal*. The *Thangals* of Lakshadweep claim direct descent from Prophet

Mohammed, and, as Sufi priests, are reputed to have mystical and healing powers (M.K. Ibrahim personal communication). In the year in question, the *Thangal* was presented the dolphin without its head. This was apparently viewed as a direct insult of the religious leader, and he 'cursed' the tradition, proclaiming that it should not happen again. According to the islanders, the dolphin hunt has never taken place after that event. Dolphins are still harpooned opportunistically, but never in large numbers.

Shark fishing

Sharks form a small but important fishery in the Lakshadweep (Directorate of Fisheries 1990). In July 2001, a Gazette notification of the Indian government promoted a host of marine species, including all shark species, to Schedule I of the Wildlife (Protection) Act of 1972, a schedule reserved for highly endangered species. This effectively made illegal the hunting of all shark species along the coasts of India. The notification began with the efforts of zealous conservation organizations and animal rights groups to curb the hunting of whale sharks on the north-west coast of India, and expanded to include several other groups. There appears to have been no consultative process undertaken with coastal communities and shark fishers, nor any formal analysis of the level of dependence on the fishery, nor what impacts the ban would have on local economies (Vivekanandan 2001). The Lakshadweep Department of Environment faced serious and violent opposition to its attempts enforce this ban, culminating in an environmental warden in Kadmat being severely beaten up by local villagers, his bicycle was strung up on a coconut tree, and he was placed under police protection for several weeks to avoid any further violence. Similar protests took place in other parts of coastal India, and the Indian government had to finally succumb to this sustained pressure in December 2001 by removing several species from the schedule, including all but 9 species of shark. At no point was the enforcement of the shark ban effective in the Lakshadweep, and there was practically no compliance with the law for the five months that it was in effect. What it served to do however was to effectively alienate the fishing community from the administration, reinforcing previously held perceptions of the heavy-handedness of management actions in the Lakshadweep.

6.3.3 Tuna fishing in the Lakshadweep

The government-sponsored development activities that took place in the 1960s (see Chapter 2) included a transformation of how local communities used the reef. Until the 1960s, fishing effort concentrated on reef fish caught in the lagoon or the reef, and on near-shore pelagic species caught in deeper waters close to the reef. Fish was, and continues to be, the major protein source in the island diet. However, prior to 1960, fish were rarely sold, and an organised system of barter existed where any fish not consumed by the family was bartered for rice in the village (Hoon 2003). Several traditional wooden craft were employed for this fishery, and a variety of fishing methods predominated, from trolling and angling, anchor and cast nets, and fish poisons (Mannadiar 1977). Few reliable figures of fishing effort exist prior to 1960 when the Lakshadweep Fisheries Department began systematic data collection, though fish landings were estimated to be less than 500 mt in the late 1950s, feeding a population of approximately 21,000. The vast majority of this catch consisted of reef fish such as coral cods, triggerfish, perches, snappers, parrotfish and surgeonfish, though pelagic species were caught as well (Directorate of Fisheries 1990).

The establishment of a local Department of Fisheries on the islands in 1959 saw the beginning of organised fisheries development, with the administration keen to convert the sustenance, largely artisanal fishing practice into a commercially viable industry. The stated aim of the department was *"achieving a sustained growth in the economy by exploiting the natural resources hitherto untouched, and to open up a way for permanent employment for the people."* (George Varghese, Director of Fisheries, in Directorate of Fisheries 1990). In exploring viable alternatives, the Fisheries Department looked to fishery practices in the Maldives, where a successful pelagic fishery for skipjack tuna (*Katsuwonus pelamis*) was already well established. The southernmost island in the Lakshadweep chain, Minicoy, also had considerable success with tuna fishing (Jones 1958), and it was considered logical to extend this practice to other islands in order to exploit this as-yet underexploited resource (Silas *et al.* 1986). Training programmes and a suite of subsidies on mechanised vessels, equipment and fuel were introduced in a concerted attempt to convert fishers in the Lakshadweep to this fishery. Experienced fishers from Minicoy employed to train the community in the pole-and-line fishing technique: after the sighting of a tuna shoal, live bait fish are released into the water to create a feeding frenzy; the tuna are then caught with barbless hooks attached to long bamboo poles with thick nylon lines. The technique requires close co-ordination between members of the fishing team, which typically consist of between 9 to 10 fishers, each assigned a specific task during the operation. A successful fishing trip will normally return with up to 1000 fish (Varghese & Shanmugham 1983).

Apart from the southern island of Minicoy, none of the other islands have facilities for tinning tuna, and there are few cold storage facilities on the islands. This places restrictions on processing of freshly caught fish. Fish are sold fresh directly from the boats, on the piers, or in the village centre, and the vast majority of the catch is processed on the beaches to be sold as dried fish. Dried tuna (*mas*) is delivered to government cooperatives that transport and market the produce in the coastal cities of mainland India.

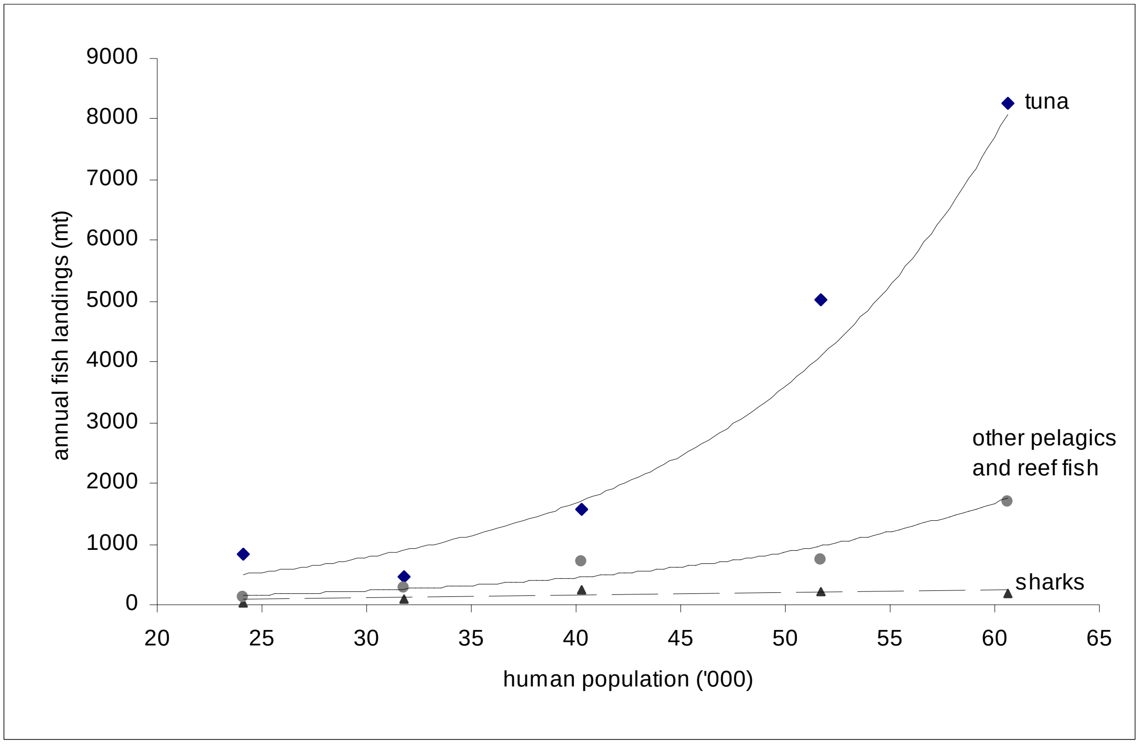


Figure 6.1 Human population increase and annual fish landings (metric tonnes) in the Lakshadweep from 1961 to 2001. Fish landing values were averaged by decade to compare with decadal censuses. There were increases in the catch of all categories of fish with time, reflecting the needs of a population with a 17% decadal growth since 1961. The increase in tuna catch is a direct result of the success of a commercial exploitation programme set up by the government (see text for details). Shark fishing is a small but important fishery in the Lakshadweep, and its numbers do not appear to have increased with human populations. Sources: Population figures (Census of India 2001). Fish catch data (Directorate of Fisheries 1990)

From an occasional fish caught in angling lines prior to 1960, the tuna industry has transformed the Lakshadweep culturally and economically. The fishing season runs from September to late May (Hoon 2003), and for this time, tuna largely replaces the diversity of reef fish as the staple protein consumed on the island; the ferial cuisine of the islands is monotonously dominated by tuna. There is no doubt that economically, tuna fishing is a valuable source of income. In 1998 the tuna catch was valued at approximately INR 240,000,000 (~US$ 5,205,000) for the dried meat

(Directorate of Fisheries 1990). This is a gross value, and does not represent the true profitability of the industry, as will be discussed later.

The tuna industry has not completely replaced extraction of fish from the reef (see Figure 6.1). During the monsoon (from late May to September) the open ocean waters are too rough to fish, and the islanders revert to fishing reef fish, either in the shallow lagoons and seagrass beds, or in the reef (Hoon 2003). Reef fish are also occasionally caught through the year, particularly by older fishermen who cannot (and often, will not) join a tuna crew. Most fishers I interviewed over the age of 50, poured scorn over the new-fangled technique of catching tuna. These fishers continued to fish using traditional crafts methods.

Although extraction of other fish has increased consistently since the 1960s, the skipjack tuna industry has grown in importance (Figure 6.1). In the first decade of the introduction of the industry to the Lakshadweep, tuna averaged 56% of the total fish landings. By contrast, in the 1980s and 1990s, tuna contributed 80% of the total catch on average. The 1998 El Niño event in the Indian Ocean did not appear to have any immediate deleterious impacts on this fishery. Though tuna catches fluctuate annually, fish catches continued to increase; 1998 was a bumper year for the tuna fishery with more than 12,000 metric tonnes extracted in that year.

6.4 Discussion

6.4.1 Reef resilience and fishing pressure

Coral reefs do not appear to be able to sustain high levels of fishery, and overfishing has important population and ecosystem consequences for reefs (Roberts 1995, Jennings & Lock 1996). Overfishing in Jamaican reefs has been implicated as one of the principal factors responsible for a long-term failure of coral recovery after a catastrophic mortality (Hughes 1994). Similarly, a fishing density of 10 fishers/km of reef was enough to result in reductions of keystone predators in East African reefs, resulting in an increase in sea urchin numbers, a consequent reduction in live coral cover, and an overall decline in reef condition (McClanahan & Kaunda-Arara 1996, McClanahan 1997).

In contrast, the reefs of the Lakshadweep appeared to possess considerable natural resilience, and, for the most part, were recovering well from the 1998 bleaching disturbance. Coral and fish populations recovered rapidly at many of the study sites (See chapters 3 and 4). Several factors possibly contributed to this recovery, including a good recruitment event, quick growth of coral at some sites, and consistently low biomass of fleshy macroalgae. While macroalgal growth may be limited by low nutrient levels in these open-ocean atoll reefs, high herbivorous fish numbers also likely played a vital role in maintaining a low algal biomass in these reefs, thus promoting the recovery of coral in these areas.

Reef resilience therefore appears to have been maintained, at least in part, by relatively low level of reef fishing despite a burgeoning human population, dependent on fish as their major protein source. Ironically perhaps, this low level of fishing is the direct result of the success of a programme to exploit hitherto unexploited fish resources. The pelagic tuna fishery introduced to the islands by the government was established principally as an economic development and employment generating activity, yet it has had fortuitous, epiphenomenal consequences for the resilience of the reef: as much as 80% of Lakshadweep's fish requirements are being currently provided by pelagic tuna, significantly subsidizing potential fishing pressure on the reef.

6.5.2 Natural resource management, ecosystem conservation, and human communities

The Lakshadweep case study shows that while natural disturbance plays a vital role in structuring ecosystems, changes in the way human communities use resources can have equally dramatic consequences for natural systems. Some modifications in human resource use are insidious, arising as a result of gradual population increase, cultural change, or progressive changes in technology. However, changes in law, institutional policy, leadership or ideology can often transform the way a community interacts with natural areas in radical and instantly observable ways. Among the most common examples of this in modern natural resource management is the establishment of protected areas which limit human access to natural areas, and restrict, or completely ban, resource extraction from these zones. There are no marine protected areas (MPAs) in the Lakshadweep, and only one uninhabited islet (Pitti) protected as a tern breeding sanctuary. However, the introduction of the Fisheries Department-sponsored tuna fishing programme to the Lakshadweep has reduced reef fishing in the Lakshadweep since the 1960s at least as effectively as a formal MPA would have done. Institutional policies can thus often affect resource use in completely unintended ways, both positive as well as negative.

Local community institutions can exert subtle influences in the way natural areas are exploited. Communities may often employ socially and religiously imposed resource extraction limits, for instance by establishing sacred groves, restricting extraction at certain times of the year, or placing taboos on the killing of specific species (Gadgil 1985). Similar religious beliefs shape the way the

Lakshadweep fishers use the marine resource, prohibiting the extraction of most shellfish for instance.

Considerable debate surrounds whether these measures (governmental or social) are the best way to maximize ecosystem resilience in the developing world, where human and social systems interact so closely (Madhusudan & Raman 2003a, 2003b). What is clear is that the success or failure of these measures lies to a large extent on the level of control each institution wields over the local populace, and the degree of compliance with these measures. In the Lakshadweep, the principal institutions that influence marine resource use are the local government (the administration) and religion (belief systems and Muslim religious leaders). Though the mechanisms of control they employ are different, they both exert a strong influence on the community. Most Lakshadweepans regard the administration as an external force, both benefactor and dictator. Islanders I interviewed expressed an inability to influence important decisions of local governance with the perception that they had no voice in the upper management of the administrative bureaucracy. On the other hand, the all-pervasive subsidy economy created by the administration is a powerful mechanism of control, and the islanders are beholden to the government for supporting the economy, providing jobs and promoting local enterprise. While religion does not play a direct role in the economic institutions of the islands, cultural and religious beliefs are a strong influence on island daily life. Cultural indoctrination begins early in life and the islanders exhibit a fervent religious conservatism. Religious control is effected by Islamic clerics, and their pronouncements are strictly respected.

The case studies of dolphin and shark hunting give some indication of the relative control religious and governmental institutions wield over the community. In the case of dolphin hunting, it is difficult to separate which narrative – the administrations' or the islanders' – is a 'truer' history of discontinuation of dolphin hunting. While the islanders' version of religious insults and holy curses leading to the cessation of the practice has a touch of a fanciful folk fable, it may be argued that the administrations' version of effective enforcement of a legal pronouncement is equally fabulous, and merely derived from a different mythological tradition. Whatever the 'real' course of events, it has resulted in a significant modification of resource use practices, with spinner dolphins not being hunted in large numbers anymore.

The more recent failed attempt to ban shark fishing on the islands provides an interesting contrast. The protests in the Lakshadweep were certainly not solely responsible for the Indian central government retreating from shark bans, because the law was protested by coastal communities across the country. What it did however was to illuminate the limits of control that a top-down policy can wield in the Lakshadweep. Communities will comply with management policies when they respect the authority of the institutions advocating them, and when they understand the benefits of the policy.

Though compliance may be best achieved with the active participation of the community, this is not always necessary. For instance, Brockington (2002) shows that wildlife conservation in Mkomazi, a terrestrial wildlife park in Tanzania, can be enforced effectively even in the face of strong community resentment. This was possible because government and conservation institutions held a much stronger sway, politically and economically, than rural community institutions (Brockington 2002). While this 'fortress conservation' may be possible for as long as these power inequalities remain, it requires a level of enforcement and funding that is often difficult to sustain, besides dispossessing the primary users of the natural area.

The tuna fishing programme in the Lakshadweep presents a possibly less inequitable solution that may be more sustainable in the long run. In design, the programme was a top-down management policy, yet it was embraced by the Lakshadweep fishers, and is rightly hailed as one of the big development successes for the Lakshadweep economy, having effectively transformed a small sustenance fishing community into thriving commercial traders. Much of the reason for its success is that it was sold to the Lakshadweep community as a means of developmental emancipation, not as a policy to restrict access to a resource. The Lakshadweep Fisheries Department in the 1960s and 1970s were more concerned with maximizing exploitation potential of marine resources than they were with conserving ecological diversity and function, and the fact that its policies resulted in significantly reducing extraction pressure on the reef was incidental to the cause. Yet, as a form of serendipitous reef management, there are few examples of alternative livelihood programmes that can claim to be as effective.

6.4.3 Subsidies and sustainability

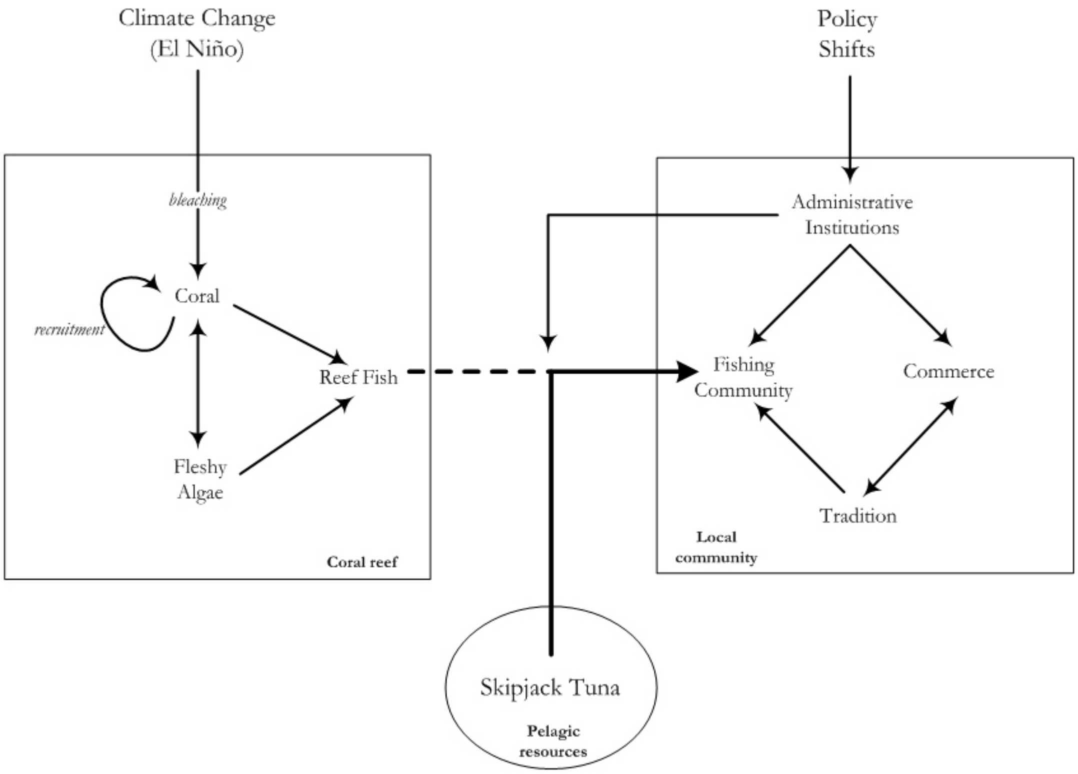
While the relatively low-level reef fishery in the Lakshadweep reef certainly promotes reef resilience, it is maintained by a heavily subsidized tuna industry. The presence of these subsidies makes it difficult to gauge the true economic sustainability of this practice. Apart from subsidizing boat and fuel costs, the government also controls the transport and marketing of dried tuna. However, in an era of economic rationalism in India, the rampant subsidies of the 1970s and 1980s are being called increasingly into question. It is difficult to know what effect the reduction or removal of subsidies will have on the tuna industry in the Lakshadweep. It is possible that Lakshadweep fishers may look elsewhere to maintain their incomes. A possible option would be to move away from the pole-and-line fishing technique. While being relatively low-cost, this technique is fairly labour-intensive, and is not as efficient as trawl netting. Trawling will increase extraction efficiency considerably, but this increased extraction pressure will affect the long-term sustainability of tuna stocks is unknown. Another option, with more direct relevance for reef resilience, would be a resumption of year-round reef fishing, both for daily consumption, as well as to supply the live-fish trade. Given the growing population of the Lakshadweep, this could very quickly lead to over-harvesting, and decreased reef resilience.

From the point of view of reef conservation therefore, there is a strong case for preserving the tuna industry in its present form, while weaning it away from the subsidies it currently relies on. The tuna caught today is still largely sold as dried meat because of a lack of tinning factories on most islands. Unlike bluefin and yellowfin tuna, the skipjack tuna is not high quality fresh fish, but it is an ideal candidate for tinning. Careful positioning and marketing of tinned tuna could boost the profitability of this fishery considerably. The pole-and-line method utilised by the Lakshadweep fishers is a dolphin and turtle-friendly technique with practically no bi-catch, and can be positioned to fetch higher prices in markets (like Australia, North America and western Europe) that are sensitive to issues of ethical fishing.

As will be discussed in later chapters, the Lakshadweep case study suggests that there may be several ways to maximizing the resilience ecosystems like coral reefs need to deal with disturbances. While marine protected areas and other reservationist management actions are perhaps still the most reliable and effective way to ensure the long term survival of ecosystems, these alternatives may be equally successful in achieving ecosystem benefits. Rarely is it possible to devise win-win solutions that integrate community development and conservation objectives, and there are strong arguments against the currently fashionable attempts to marry the two in community-based conservation programmes (Redford & Sanderson 2000). Many attempts to include local communities in conservation are only marginally successful (Kellert *et al.* 2000), but where they do manage to work towards the same eventual goal, either by intention or by *non-sequitur*, they should be supported and strongly encouraged.

Chapter VII

SYNTHESIS



Chapter VII: Synthesis

Paths to resilience: Marrying socio-economic development with ecosystem conservation in the Lakshadweep islands

7.1 Introduction

Learning to adapt to change is, perhaps, the principal challenge of ecosystem management. The problems of habitat fragmentation, pollution and overexploitation apart, ecosystem managers have to additionally deal with an increasingly stochastic and unpredictable global environment. Climate change has increased the frequency and heightened the intensity of environmental fluctuations, with often catastrophic consequences for ecosystems (Hughes 2000, Lawton 2001, Walther *et al.* 2002, Parmesan & Yohe 2003, Thomas *et al.* 2004). Little, if anything, can be done to control the occurrence of these global events at the regional scales at which most ecosystem management takes place, and attention is now rapidly shifting to the need to preserve and enhance the natural ability of ecosystems to absorb disturbances when they happen – ecosystem resilience (Holling 1973, Holling 1986, Batabyal 1998, Allison *et al.* 2003).

The vast majority of the world's natural areas today are human-dominated (Messerli *et al.* 2000), and ensuring the resilience of these ecosystems requires an understanding of how humans interact with them (Berkes & Folke 1998). Humans use natural areas for a range of ecological goods and services, and often have well-developed social institutions that govern resource extraction (Gadgil 1985, Colding & Folke 2000). Just as ecological communities are influenced by external disturbances, human communities can also change the way they use the resource, fuelled by internal pressures or external forces. These historical processes can have profound implications, both positive as well as negative, for the natural areas being exploited.

In this study, I examined the consequences of a mass bleaching and mortality of corals on the reefs of the Lakshadweep, and attempted to understand how local resource use influenced reef responses. The case study demonstrates how historical changes in resource use by human communities may have contributed to the maintenance of reef resilience in the face of a large-scale pulse disturbance. In this final chapter I briefly summarise the findings and major conclusions of the thesis. I argue that the reefs of the Lakshadweep demonstrated considerable resilience in the wake of the coral bleaching and mortality event of 1998. I look at the role of local institutions in regulating fishing on the reefs, and suggest that this has had important consequences for reef resilience. I suggest that the Lakshadweep is an example of 'epiphenomenal conservation', where benefits accrued to the ecosystem were an incidental bi-product of a programme designed principally to boost the local economy. Although unintended, I argue that the Lakshadweep example is at least as effective as more conventional forms of management in promoting reef resilience. I explore the implications of this for the further management of Lakshadweep reefs in particular and the conservation of tropical reefs in general.

7.2 Reef recovery in the Lakshadweep: a brief summary of major results

The El Niño event of 1997-1998 raised ocean temperatures to unprecedented levels above seasonal averages, and led to widespread bleaching of corals in many tropical reefs (Wilkinson 1998, Wilkinson 2002). Most reefs in the Indian Ocean were affected by this event, and a few months after the bleaching, benthic cover of coral was reduced to as little as 2% to 5% in surveyed reefs in the Lakshadweep (Arthur 2000). Although no benthic studies exist prior to this work, anecdotal accounts and my own personal observations indicate that the Lakshadweep reefs were typically high in coral cover, comprising 50% to 80% of benthic substrate (personal observation, Shaukat Ali, personal communication). In Chapter 2, I presented the results of a rapid survey I conducted in 2002, attempting to assess the consequences of coral mass mortality to benthic composition, four years after the bleaching event. Benthic response was characteristically patchy across the atoll chain, and few strong geographical trends were apparent in substrate composition across the six atolls surveyed. The strongest pattern observable was between aspects: live coral cover was considerably higher on west-facing reefs than on eastern reefs on most atolls. In contrast, the amount of dead standing coral was higher on the east than on the west. Additionally, generic composition of coral differed between aspects.

In Chapter 3, I described temporal changes in benthic composition from 2000 to 2003 at three Lakshadweep atolls. The temporal study suggested mechanisms to explain the differences in benthic recovery between aspects recorded in the broad spatial survey (Chapter 2). The striking differences in coral cover between east and west appeared to be driven by differences in the long-term viability of settlement substrate between aspects. The recovery of coral on eastern reefs appeared to be directly offset by a loss of benthic structure, and the subsequent mortality of coral individuals, resulting in a reduced rate of recovery in comparison with western reefs. Importantly, smaller coral individuals appeared to be relatively advantaged in post-bleached reefs, either through competitive release by larger corals or by being naturally more tolerant of temperature stress. Although there were significant changes in coral genera composition through time, there was no clear indication that bleaching-resistant genera were doing better in these reefs. Corals with very different life history responses to bleaching appeared to be successful; the recovering coral community was dominated by a mix of resistant genera as well as highly bleaching-susceptible genera like *Acropora*. Given enough time between catastrophic pulse disturbances, species with fast-growing life histories could well retain their dominance in reefs, despite high susceptibility to disturbances.

Initial concerns that fleshy macroalgae would overtake the benthic substrate, precipitating a shift in ecological state (or phase shift) were largely unmet. Crucial to this was the abundance and biomass of algal herbivores. Chapter 4 examined temporal changes in the composition of herbivorous fish and other fish guilds in Lakshadweep reefs. Herbivore numbers remained high through the study and accounted for more than 70% of total abundance in 2000, dominated by several species of Acanthurids and Scarids. Although herbivore dominance reduced somewhat through time, they were still the most abundant functional group in the reef. The largest detrimental impacts of the coral mortality were apparent on corallivores. However, by 2003, the abundance of coral feeders was increasing, in response to the quick re-establishment and growth of corals in several reefs. Some obligate corallivore species like *Oxymonocanthus longirostris* were not sighted in any surveyed reefs in 2000, but were observed in small numbers in 2003. Overall, fish communities were remarkably stable, despite the large changes in benthic composition. The assemblages at different reef sites became increasingly similar in composition with time, and were largely indistinguishable from each other by 2003. Without a pre-1998 baseline, it is not possible to speculate if the community resembled the pre-disturbance community, however, fish composition appeared to become increasingly similar to communities at reefs least affected by bleaching mortality, suggesting a return to a less disturbed community state. Refuge sites at other reefs or at deeper water sites were probably important in maintaining the stability of fish communities in the face of massive benthic change, as has been demonstrated elsewhere (Walsh 1983).

In Chapter 5, I explore the utility of a simple conceptual model in understanding the factors influencing and affecting the recovery and resilience of reef systems like the Lakshadweep from major pulse disturbances such as coral bleaching. The Lakshadweep reefs demonstrated considerable resilience despite massive losses in coral cover. However, in many other instances across the tropics, similar pulse disturbances have led to a significant loss of ecological function that have, in some instances, been difficult to reverse for decades or longer, termed a ‘phase shift’ (Done 1992). Characteristically, after a major die-off of corals, fleshy macroalgae opportunistically overtake the released substrate and preclude the re-establishment of new coral growth, stalling reef accretion, and reducing structural complexity for several reef species, including fish (Done 1992, McManus & Polsenberg 2004). Although the possibility of phase shifts has received much attention in recent literature, reefs can also rapidly regain coral cover after a mass mortality, through the regrowth of adult remnants and the establishment and growth of new coral recruits (Endean 1976, Pearson 1981, Tomasik *et al.* 1996). The cusp catastrophe model presented in Chapter 5 attempts to understand these dichotomous responses of reefs to similar disturbance events in terms of simple control variables. The model is a topological ‘response surface’ which represents a continuum of community states the reef can attain, some more ‘stable’ than others. Chapter 5 identifies two main control axes that determine community state. The q-axis is an axis of external influences to the reef system that include state-changing disturbance events. The p-axis is an axis of intrinsic reef conditions that determine resilience, including herbivory and nutrient levels, larval supply and connectivity, and local fishing pressure. Reefs with high p values may be more stable in the face of disturbances, and, post-disturbance, will move rapidly from bare space to coral dominance. On the other hand, reefs with low values of p may be quickly taken over by fleshy macroalgae because of a combination of low herbivory, high nutrient inputs and high fishing pressure. In this model, the Lakshadweep reefs possessed considerable resilience because high herbivore abundances and low nutrient conditions helped preclude the dominance of fleshy macroalgae on the reef, allowing a gradual return to coral dominance.

The high herbivorous fish numbers in the Lakshadweep presents a conundrum given that these islands have among the highest human population densities anywhere in rural India, with fish a major component of the islanders’ diet. In Chapter 6, I examine the history of resource use and trace changes in fishing practices on the islands. Before the 1960s, most of the fish eaten came from the reef, and the islanders had a long tradition of reef fishing. A fisheries department programme begun in the 1960s was instrumental in dramatically changing resource use patterns. The principal aim of the programme was to explore the exploitation potential of pelagic fisheries and as an employment generation scheme for the local islanders (Directorate of Fisheries 1990). The programme was overwhelmingly successful, and the vast proportion of fish now caught during the non-monsoon months comprises oceanic skipjack tuna, having largely replaced reef fish as the primary protein source of the islanders. This significant reduction in reef fishing was instrumental in maintaining the ecological buffer capacity of the reef, and facilitated a rapid recovery process.

This was a completely unanticipated ('epiphenomenal') consequence of the fisheries department programme, but it has resulted in considerable benefit for the reef, despite its inadvertency. The perceived power and legitimacy of local institutions was crucial to effecting this change. In Chapter 6, I explored the institutional relationships in the Lakshadweep, in particular, looking at the interaction between local administration and religion, and its capacity to influence and change resource use patterns. Both institutions wield considerable control on the islands, but while the islanders respect and obey the control of religious leaders, their relationship with the administration is a little more ambivalent. The bureaucratic machinery is seen as an outside force, and their control is often resented. However, the government is also by far the largest full-time employer and Lakshadweepans recognise that the government brings with it considerable services and subsidies which would otherwise be unavailable to them. This dual view of the administration as controller and benefactor also influences the perceived legitimacy of the administration to govern resource use. While the programme to develop tuna fisheries was very successfully implemented, a more recent attempt to ban the fishing of sharks was viewed as a direct assault by the local administration on the economic livelihood of the islanders, and was met with fierce resistance. I argue that an understanding of these institutional relationships is essential for effective management on the islands.

7.3 Change, contingency and caveats: Lessons for the Lakshadweep

Lakshadweep's reefs have been strongly influenced by historical events that have modified both ecological functioning and patterns of human extraction. The mass bleaching event of 1998 significantly reduced coral cover and structural complexity, and threatened the ecological functioning of the reef. High herbivore densities were instrumental in ensuring that coral re-established well in many areas, and that fleshy macroalgae did not take over the bare substrate. This in turn was linked to relatively low levels of reef fishing, because of a government initiative to encourage commercial pelagic fishery for skipjack tuna. Since its inception in the 1960s, this scheme was successful in weaning local fishers away from reef fishing, and in significantly reducing potential extractive pressures on the reef.

Historical events are unplanned, badly designed experiments, and it is perhaps impossible to speculate how the system would respond if they had not occurred. With the high human population densities in the Lakshadweep, it is unlikely that fish communities could sustain levels of extraction if current demand for commerce and sustenance were to be met solely from the reef. Nevertheless, if tuna fishing had not been introduced to the Lakshadweep by the government, it would perhaps only be a matter of time before the islanders adopted the practice themselves. They would not have to look far to see the obvious success of this fishery in Minicoy, the southernmost island of the Lakshadweep group, and in neighbouring Maldives (Jones 1958, Directorate of Fisheries 1990). The release of reef fish from exploitation documented here (Chapter 6) was perhaps only inevitable. Equally though, a combination of private enterprise and the global demands for live reef fish as food could have as likely sparked unmitigated exploitation of the abundant fish of the Lakshadweep reefs.

The Lakshadweep tuna fishery has had the unintended but fortunate consequence of supporting the resilience of Lakshadweep's reefs. However, the fishery is still supported by a number of government subsidies. In an era of increasing economic rationalisation, and the movement away from protectionist economic practices, the Indian government is under increasing pressure to rethink its subsidy policy. Already, several important agricultural subsidies have been revoked. It is a matter of debate if the Lakshadweep economy will have the resilience to absorb a cessation of subsidies and compete effectively in a global marketplace. It is also unclear what effect increases in extraction would have on tuna populations. Estimates of tuna stocks suggest that the fishery may not yet have reached its full exploitation potential (Varghese & Shanmugham 1983, Silas *et al.* 1986), but changes in fishing technology may radically alter the long-term viability of these stocks.

From the point of view of enhancing reef resilience, there are strong reasons to preserve the *status quo* of fishing practices in the Lakshadweep. At present, the amount of tuna caught is limited by the number of boats the Fisheries Department issues, the lack of processing facilities, and the technique of fishing itself. The pole-and-line fishery is not a high-volume technique, and a successful fishing will return with up to 1000 fish (Varghese & Shanmugham 1983). Innovative marketing strategies could easily capitalize on the dolphin- and turtle-friendly nature of this fishery, marketing tinned tuna at a premium in urban and western markets. If successful, a scheme like this could be useful in valuing the pole-and-line technique, and reduce the incentive to move away from this technique towards more intensive, high-volume fishing techniques such as purse seining or trawling.

This study describes some important patterns in the relationship between ecological functioning and local resource use. However, there are several vital gaps that need addressing. At a fundamental level, our knowledge of the distribution of these reefs and their present status is, at best, patchy. Importantly, there is virtually no information available on the source-sink dynamics of this reef system, and there is little reliable knowledge on coral recruitment patterns anywhere from the region. The results of this study pertain particularly to the three atolls of Agatti, Kadmat and Kavaratti, where most of my detailed sampling was done. A more complete understanding of recruitment and connectivity patterns will require research efforts across a broader spatial area of the Lakshadweep as well as the Maldives and Chagos. This study has pointed to the importance of refuge source sites in supporting reef recovery, both for coral as well as for fish species (Chapters 3 and 4). Understanding where these potential sites are will be essential for effective management.

Open ocean reefs are generally considered to be nutrient poor, limiting the possibility of macroalgal growth. The relative role of nutrients and herbivores in the Lakshadweep has not been addressed in this thesis and requires further study. My observations in lagoons in Kadmat, Kavaratti and Agatti indicate that macroalgae may not be limited by nutrients in these enclosed areas. In a pilot herbivore exclusion experiment I conducted in 2002 in the outer reefs in Kadmat, fleshy macroalgae grew after two weeks of the establishment of exclusion plots, suggesting that, even here, nutrients may not be limiting (unpublished data). However, more work will be required to resolve this issue conclusively.

It has often been said that natural resource management is really an issue of people management. The Lakshadweep case study is a striking example of this. While this study provides a useful descriptive analysis of institutional and economic drivers that govern resource use on the islands, it leaves many questions unanswered. The success of the tuna industry is, in my estimation, vital in protecting the buffer capacity of the reef, yet little is known of the true profitability of the industry today. A detailed economic analysis will be required to look at the influence of subsidies on the profitability of the trade, and to suggest workable alternatives. Additionally, without a rigorous stock assessment, it is difficult to know conclusively if tuna stocks are being exploited sustainably, and if the fishery can be further strengthened.

Finally, this study provides a valuable ecological baseline from an area of the tropics where little in-water work has taken place. Climate change is rapidly becoming the background reality for managers and reef ecologists, and continuing to monitor change in these systems will be crucial to designing strategies for conserving reef function.

7.4 Paths to resilience: Lessons from the Lakshadweep

7.4.1. No Take Areas and experiments with co-management

With environmental stochasticity increasing in an era of global change, managers have begun to view the No Take Area (NTA) as an invaluable management tool in protecting the buffer capacity of ecosystems. There is gathering theoretical, experimental and empirical evidence to show that NTAs, when successful, can go a long way in preserving ecosystem function, and nurturing resilience (Gunderson 2000, Bruner *et al.* 2001). For marine areas, the marine protected area (MPA) has increasingly become an important management tool, used both for protecting ecosystem resilience, as well as for perceived fisheries benefits (Agardy 1994, Roberts *et al.* 2001, Russ 2002, Allison *et al.* 2003, Gell & Roberts 2003). It has been suggested that the MPA may also play a vital role in protecting ecosystems like coral reefs against the vagaries of climate change and bleaching (Done 2001, West & Salm 2003, Bellwood *et al.* 2004).

Despite their obvious appeal, both marine and terrestrial NTAs face considerable challenges to their establishment and implementation, particularly when they compromise the food security and economic viability of dependent human communities (Madhusudan & Raman 2003). In order to transcend the divide between ecosystem conservation and economic necessity, many recent efforts have attempted to marry the two, providing local residents with incentives to reduce resource extraction, and involving communities in ecosystem conservation (Johannes 2002). These experiments with co-management have received plenty of interest, but there are remarkably few examples of unequivocal successes (Kellert *et al.* 2000, Berkes 2004) . Objective studies of these programmes suggest several reasons why they meet with lukewarm success or outright failure, including poor planning and implementation, underfunding, unrealistic time frames, poorly defined conservation and community goals, and an inadequate understanding of community institutional frameworks (Becker & Ostrom 1995, Kellert *et al.* 2000, Barrett *et al.* 2001, Goldman 2003). In other instances, conservation benefits are accrued at the cost of perceived or real community disenfranchisement, with only lip-service paid to co-management (Alexander & McGregor 2000, Brockington 2002, Christie in press). In fact, Redford and Sanderson (2000) suggest that the dual goals of economic sustainability and ecosystem viability are, perhaps, mutually exclusive, and should not be attempted to be achieved together.

7.4.2 Searching for Win-Win solutions: the Lakshadweep example

The history of resource use changes in the Lakshadweep is an encouraging example that, under some circumstances, win-win solutions may be possible, where economic development matches the goals of ecosystem conservation, albeit (in this case) by accident. In many parts of the developing world, high human dependence on reefs make NTAs difficult to establish and implement. When the basic food security of populations is in question, communities will be unlikely to give up access to resource areas in favour of more or less intangible concepts like biodiversity conservation. At the same time, overexploitation can seriously threaten the long-term food security of communities, apart from reducing ecological functioning and ecosystem resilience. Maintaining ecosystem values is even more urgent and necessary when attempting to manage systems in the face of an increasingly unpredictable climate regime, and the NTA appears to be our best bet in order to do this.

The case study of the Lakshadweep suggests however, that there may be more than one path to achieve resilience. Despite the fact that none of the reefs of the Lakshadweep have extractive limitations on them, the tuna industry has deflected fishing efforts away from the reef. It is possible to argue that at least one of the reasons for the success of the tuna fishery programme, is that it was designed and promoted as an economic development scheme to develop commercial potential and generate employment (Directorate of Fisheries 1990). Biological conservation has never been a stated mandate of the tuna fishing industry in the Lakshadweep. Yet its consequences for Lakshadweep's reefs have been at least as effective as any MPA could have achieved, and with considerably less opposition.

Alternate livelihood programmes have, of course, been a major tool in the community co-management arsenal, attempting to wean local communities away from unsustainable extractive practices. These programmes have had different degrees of success, dependent on a host of continent factors that will differ from location to location (Pollnac *et al.* 2001, Christie *et al.* 2003). One of the biggest difficulties in the implementation of these programmes is the degree of identity communities hold with the professions they are being weaned away from. With few occupations is this stronger than with fishing, and it is often difficult to convince fishers to abandon their professions, even in favour of more profitable alternatives (Ikiara & Odink 1999). In the Lakshadweep, at least part of the reason why the transition away from reef fisheries was embraced was that it allowed communities to retain their identity as fishers, despite effecting radical changes in target species, technology and technique. Being sensitive to issues of identity may bolster the success of future alternative livelihood programmes. In an increasingly stochastic human-dominated environment, the NTA will undoubtedly continue to be the most powerful and effective tool in ensuring the maintenance of ecosystem values and ecological resilience. While the ecological bottom line should always be paramount, more effort and imagination needs to be directed at discovering alternatives to the reservationist ideal.

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Appendix I

Fish species list for the Lakshadweep atolls with trophic guilds

FAMILY	FISH SPECIES	TROPHIC GUILD
ACANTHURIDAE	*Acanthurus auranticavus*	Herbivore
	Acanthurus leucosternon	Herbivore
	Acanthurus lineatus	Herbivore
	Acanthurus nigrofuscus	Herbivore
	Acanthurus thompsoni	Planktivore
	Acanthurus triostegus	Herbivore
	Acanthurus xanthopterus	Herbivore
	Ctenochaetus striatus	Herbivore
	Naso brachycentron	Planktivore
	Naso brevirostris	Omnivore
	Naso hexacanthus	Planktivore
	Naso literatus	Herbivore
	Naso tuberosus	Herbivore
	Naso unicornis	Herbivore
	Naso vlamingii	Planktivore
	Paracanthurus hepatus	Herbivore
	Zebrosoma desjardinii	Herbivore
	Zebrosoma scopas	Herbivore
BALISTIDAE	*Balistapus undulatus*	Macroinvertebrate feeder
	Balistoides conspicullum	Macroinvertebrate feeder
	Balistoides viridescens	Macroinvertebrate feeder
	Melichthys niger	Herbivore
	Odonus niger	Planktivore
	Pseudobalistes flavimarginatus	Macroinvertebrate feeder
	Rhinecanthus aculeatus	Omnivore
	Rhinecanthus rectangulus	Omnivore
	Sufflamen bursa	Macroinvertebrate feeder
	Sufflamen chrysopterus	Macroinvertebrate feeder
	Sufflamen fraenatus	Macroinvertebrate feeder
CAESIONIDAE	*Caesio caerulaurea*	Planktivore
	Caesio lunaris	Planktivore
	Caesio xanthonota	Planktivore
	Pterocaesio tile	Planktivore
CARANGIDAE	*Caranx ignobilis*	Piscivore
	Caranx melampygus	Piscivore

FAMILY	FISH SPECIES	TROPHIC GUILD
	Elegatis bipinnulata	Piscivore
	Seriola lalandi	Piscivore
CHAETODONTIDAE	*Chaetodon auriga*	Omnivore
	Chaetodon bennetti	Corallivore
	Chaetodon citrinellus	Corallivore
	Chaetodon collare	Corallivore
	Chaetodon decussatus	Omnivore
	Chaetodon falcula	Corallivore
	Chaetodon kleinii	Planktivore
	Chaetodon lunula	Corallivore
	Chaetodon madagascariensis	Corallivore
	Chaetodon melannotus	Corallivore
	Chaetodon meyeri	Corallivore
	Chaetodon plebius	Corallivore
	Chaetodon triangulum	Corallivore
	Chaetodon trifascialis	Corallivore
	Chaetodon trifasciatus	Corallivore
	Chaetodon unimaculatus	Corallivore
	Chaetodon xanthocephalus	Microinvertebrate feeder
	Forcipiger flavissimus	Microinvertebrate feeder
	Hemitaurichthys zoster	Planktivore
	Heniochus acuminatus	Omnivore
	Heniochus chyrsostomus	Corallivore
	Heniochus pleurotaenia	Corallivore
CIRRHITIDAE	*Oxycirrhitus typus*	Planktivore
	Paracirrhites arcatus	Macroinvertebrate feeder
	Paracirrhites forsteri	Piscivore
EPHIPPIDAE	*Platax orbicularis*	Omnivore
FISTULARIIDAE	*Fistularia commersonii*	Piscivore
HAEMULIDAE	*Plectrorhinchus orientalis*	Piscivore
HEMIGALEIDAE	*Triaenodon obesus*	Piscivore
HOLOCENTRIDAE	*Myripristis berndti*	Macroinvertebrate feeder
	Sargocentron rubrum	Macroinvertebrate feeder
	Sargocentron spiniferum	Macroinvertebrate feeder
	Sargocentron violaceum	Macroinvertebrate feeder
KYPHOSIDAE	*Kyphosus cinerascens*	Herbivore
LABRIDAE	*Anampses lineatus*	Microinvertebrate feeder
	Anampses meleagrides	Microinvertebrate feeder
	Bodianus axillaris	Macroinvertebrate feeder
	Bodianus diana	Macroinvertebrate feeder

FAMILY	FISH SPECIES	TROPHIC GUILD
	Cheilinus chlorourus	Macroinvertebrate feeder
	Cheilinus fasciatus	Macroinvertebrate feeder
	Cheilinus trilobatus	Macroinvertebrate feeder
	Cheilinus undulatus	Macroinvertebrate feeder
	Cheilio inermis	Piscivore
	Cirrhilabrus exquisitus	Planktivore
	Diproctacanthus xanthurus	Corallivore
	Epibulus insidiator	Macroinvertebrate feeder
	Gomphosus caeruleus	Macroinvertebrate feeder
	Halichoeres hortulanus	Macroinvertebrate feeder
	Halichoeres nebulosus	Macroinvertebrate feeder
	Halichoeres scapularis	Microinvertebrate feeder
	Halichoeres vrolikii	Macroinvertebrate feeder
	Hemigymnus fasciatus	Microinvertebrate feeder
	Hemigymnus melapterus	Macroinvertebrate feeder
	Hologymnosus doliatus	Piscivore
	Labroides dimidiatus	Microinvertebrate feeder
	Novaculichthys taeniourus	Macroinvertebrate feeder
	Pseudocheilinus hexataenia	Microinvertebrate feeder
	Pseudodax moluccanus	Macroinvertebrate feeder
	Stethojulis interrupta	Microinvertebrate feeder
	Stethojulis strigiventer	Microinvertebrate feeder
	Stethojulis trilineata	Microinvertebrate feeder
	Thalassoma hardwickei	Microinvertebrate feeder
	Thalassoma janseni	Microinvertebrate feeder
	Thalassoma lunare	Microinvertebrate feeder
LETHRINIDAE	*Lethrinus harak*	Macroinvertebrate feeder
	Monotaxis grandoculis	Macroinvertebrate feeder
LUTJANIDAE	*Aphareus furca*	Piscivore
	Lutjanus biguttatus	Piscivore
	Lutjanus bohar	Macroinvertebrate feeder
	Lutjanus fulviflamma	Macroinvertebrate feeder
	Lutjanus gibbus	Macroinvertebrate feeder
	Lutjanus kasmira	Piscivore
	Lutjanus spp	Macroinvertebrate feeder
	Macolor niger	Macroinvertebrate feeder
MALACANTHIDAE	*Malacanthus latovittatus*	Macroinvertebrate feeder
MONACANTHIDAE	*Amanses scopas*	Microinvertebrate feeder
	Cantherhines dumerili	Corallivore
	Oxymonacanthus longirostris	Corallivore

FAMILY	FISH SPECIES	TROPHIC GUILD
MULLIDAE	*Mulloidichthys flavolineatus*	Microinvertebrate feeder
	Parupeneus barberinus	Macroinvertebrate feeder
	Parupeneus bifasciatus	Macroinvertebrate feeder
	Parupeneus cyclostomus	Piscivore
	Parupeneus macronema	Macroinvertebrate feeder
MURAENIDAE	*Gymnothorax flavimarginatus*	Piscivore
NEMIPTERIDAE	*Scolopsis bilineatus*	Macroinvertebrate feeder
PEMPHERIDAE	*Pempheris cf. oualensis*	Planktivore
POMACANTHIDAE	*Apolemichthys trimaculatus*	Microinvertebrate feeder
	Centropyge multispinis	Omnivore
	Pomacanthus imperator	Macroinvertebrate feeder
	Pomacanthus semicirculatus	Omnivore
	Pygoplites diacanthus	Macroinvertebrate feeder
SCARIDAE	*Cetoscarus bicolor*	Herbivore
	Chlorurus atrilunula	Herbivore
	Chlorurus sordidus	Herbivore
	Chlorurus strongylocephalus	Herbivore
	Scarus cf. falcipinnis	Herbivore
	Scarus frenatus	Herbivore
	Scarus ghobban	Herbivore
	Scarus globiceps	Herbivore
	Scarus niger	Herbivore
	Scarus prasiognathos	Herbivore
	Scarus psittacus	Herbivore
	Scarus rubroviolaceus	Herbivore
	Scarus scaber	Herbivore
	Scarus spp	Herbivore
SERRANIDAE	*Aethaloperca rogaa*	Piscivore
	Cephalopholis argus	Piscivore
	Cephalopholis miniata	Piscivore
	Cephalopholis urodeta nigripinnis	Piscivore
	Epinephelus fasciatus	Piscivore
	Epinephelus malabaricus	Piscivore
	Epinephelus polyphekadion	Macroinvertebrate feeder
	Epinephelus spilotoceps	Piscivore
	Gracila albomarginata	Piscivore
	Plectropomus laevis	Piscivore
	Variola louti	Piscivore
SIGANIDAE	*Siganus argenteus*	Herbivore
	Siganus corallinus	Herbivore

FAMILY	FISH SPECIES	TROPHIC GUILD
	Siganus stellatus	Herbivore
SPHYRAENIDAE	*Sphyraena quenie*	Piscivore
TETRAODONTIDAE	*Arothron nigropunctatus*	Corallivore
ZANCLIDAE	*Zanclus cornutus*	Omnivore

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2005