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CORAL REEF RESILIENCE: RECOVERY AND RESISTANCE ACROSS THE LAKSHADWEEP ARCHIPELAGO

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Coral reef resilience: Recovery and resistance across the Lakshadweep Archipelago

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Summary

The range of ecosystem services and rich biodiversity that coral reefs sustain are today being rapidly eroded under the influence of climate change and more regional human impacts. Coral reefs are perhaps among the most endangered tropical ecosystems and understand the inherent resilience of reefs in the face of catastrophic disturbances is critical for effective management of these systems. The reefs of the Lakshadweep Islands, Indian Ocean were considerably affected by catastrophic coral mass bleaching in the wake of El- Nino Southern Oscillation (ENSO) events in 1998 and more recently in 2010. In this study, coral reefs across 12 atolls of the Lakshadweep Archipelago were surveyed in 2010-11 to assess the impacts of the 2010 bleaching event on the reefs of the archipelago. We measured a range of more than 30 environmental and ecological parameters for each reef location, and calculated a Reef Resilience Score for every sampled reef based on a regionally sensitive modification of IUCN's Reef Resilience Assessment protocols. This score is designed to determine the putative ability of the reef to resist disturbance and recover from disturbance events when they occur. Using this score, we determined a gradient of reef resistance across the Lakshadweep islands, based on the response of different atolls to the 2010 bleaching. Our initial results indicate that although bleaching may have been widespread, post-bleaching survival differed widely between reefs. The resistance capacity of these reefs also varied across the archipelago, with some atolls like Kavaratti and Minicoy showing relatively high levels of potential buffer capacity while others like Agatti and Kadmat highly susceptible to disturbance impacts. In this report we describe the variation in multiple social-ecological factors that could potentially determine reef resilience, and suggest directions for future research on reefs in the Lakshadweep Islands.

Coral reef resilience: Dealing with a changing environment

Coral reefs are among the most diverse and productive ecosystems in the world, performing a range of vital ecosystem functions, and sustaining the livelihoods of local communities (Done et al. 1996; Moberg and Folke 1999). Reefs provide ecosystem services that are vital to human societies and industries through fisheries, coastal protection, and tourism. They are also one of the most threatened from global climate change and anthropogenic impacts. Ocean warming events (associated with anomalous El Niño currents), sea level rise and ocean acidification act in concert with coastal development, fishing and other local pressures to create multiple stressors that seriously threaten the existence and functioning of these systems (Carilli et al. 2009; Hughes et al. 2003b; Lesser 2007). Few natural systems are as susceptible to the forces of global change as low-lying coral atolls which have, over the last two decades, emerged as potent indicators of what we can expect of the world's ecosystems in an environment of increasing uncertainty and change. They are valuable laboratories to further our understanding of how socio-ecological systems respond to climate flux, and how these systems can be conserved at scales relevant to regional and local ecosystem management.

With the increasing frequency and intensity of climate-related coral mass mortality events, learning to predict and gauge the resilience and recovery potential of reefs is the holy grail of modern reef management. In the real world though, resilience, defined as the 'ability of an ecosystem to withstand change and/or return to its original or near-original state following a major disturbance event' (Batabyal 1998; Carpenter et al. 2001; Elmqvist et al. 2003; Gunderson 2000), can be difficult to identify and measure. It is becoming increasingly clear that, given the scale and pace of global climate change, the goal of local management has to shift from attempting to control the forces of change, to one of prophylaxis of natural ecosystem resilience in the face of an environment now increasingly characterized by inevitable surprise due to aberrant dynamic events. Determining the inherent ability of these ecosystems to sustain change is the first step towards management based on principles of resilience rather than control (Hughes et al. 2003a; West and Salm 2003). This will hopefully lead to a spatially explicit predictive framework of resilience that will enable a science-based prioritization of coastal management. In its broadest formulation, this will help determine which areas and ecosystem processes are most fundamental to be protected. This project takes the first step towards developing and validating a predictive resilience framework for the Lakshadweep Islands, an archipelago of low lying coral atolls in the northern Indian Ocean.

The processes linked to reef recovery after bleaching are multivariate and multidimensional, dependent on a range of physical, oceanographic, ecological and socio-economic factors. These factors may interact in a variety of ways, either independently or in combination, and lead to complex cross-scale patterns that might often be difficult to understand. Loss of habitat structure that is key to maintaining biodiversity is an important consequence of reef bleaching. On coral reefs, habitat structure is shaped by the spatial arrangement of sessile organisms (hard corals).

Structure, being biogenic in nature, is therefore highly vulnerable to environmental perturbations (Bozec and Doledec 2005, Madin and Connolly 2006). Interacting processes of fish recruitment, competition and predation (Hixon 1993, Almany 2004, Gratwicke 2005) are mediated by reef habitat structure, through provision of refuge and resources to fishes. Communities of coral-reef fishes are strongly influenced by changes in habitat structure and live coral decline caused by coral bleaching. Fluctuations in a range of physical variables, mediated by changes in global climate are predicted to affect directly the abundance, diversity, composition and demographic structure of the dominant habitat-forming corals, with repercussions for reef fishes as a result of change in habitat availability and quality (Pandolfi 2003, Feary et al. 2010).

Resilience and the Lakshadweep Archipelago

This project takes the first step towards developing and validating a predictive resilience framework for the Lakshadweep Islands, an archipelago of low-lying coral atolls in the northern Indian Ocean. Reefs of the Lakshadweep Islands, along with many island groups, were seriously affected, leading to death of considerable areas occupied by corals. The recovery of Lakshadweep coral reefs following the 1998-ENSO related bleaching event was found to be patchy and low. Furthermore, the recovery of these reefs was cut short by yet another mass bleaching ENSO event in early 2010. This project was aimed to conduct a comprehensive archipelago-wide survey to assess the impact of the 2010 bleaching event on these atolls. We assessed the status and intensity of damage to reefs, and the stages of ecological recovery of reefs across the islands. Reduction in structural complexity of reefs, intensity of bleaching, coral death and changes in reef fish community structure were also assessed.

Our goal was to evaluate the current benthic status of reefs, document impacts to fish communities, and measure a range of potential environmental and anthropogenic drivers that could help determine the overall resilience of these reef systems. Resilience scores were calculated for 42 reef sites on 12 atolls, with the guidelines provided by the Reef Resilience Assessment, International Union for Conservation of Nature (Obura and Grimsditch, 2008). Further, based on earlier long-term data (Arthur, 2005) we qualify the differential responses of reefs to bleaching-related disturbance, and evaluate the merits and shortcomings of the assessment. Finally, we discuss strategies for the conservation and management of coral reefs of the Lakshadweep Islands in times of increasing vulnerability to climate change impacts.

The Coral Reefs of the Lakshadweep Archipelago

The Lakshadweep atolls, Indian Ocean (Figure 1) are high diversity coral formations that appear to be particularly vulnerable to changes in sea surface temperatures. The pan-tropical 1998 El Niño resulted in a coral mass mortality of between 80-90% in most surveyed reefs (Arthur 2000), and our work over the last decade in this island group has focused on tracking the further decline and recovery of these systems from that event (Arthur 2005; Arthur 2008; Arthur et al. 2006; Arthur et al. 2005). The last 12 years have witnessed a mixed reef recovery in the Lakshadweep, including some surprisingly rapid rates of coral recolonisation and growth at some locations, and very shallow recovery at others. The summer of 2010 saw another major El Niño-related bleaching event in these waters, and our initial assessments indicated that its impact could be as wide as the 1998 event. The repeated coral die offs that these systems are subject to raises the question of how resistant and/or resilient individual reefs in the face of change, and serves as an ideal natural experiment to test the buffer capacity of these ecosystems. The western aspect of atolls is subject to 6 months of turbulent monsoon currents and storms, while the eastern aspect of atolls remains relatively stable throughout the year. These local hydrodynamic processes play an important role in determining post-bleaching recovery of reefs in the Lakshadweep archipelago (Arthur et al. 2006). Previous studies have indicated a dramatic loss of coral structure on the western reefs (as compared to eastern reefs) in response to bleaching events as a result of this monsoonal forcing (Arthur 2000, Arthur and Done 2005, Arthur et al. 2006).

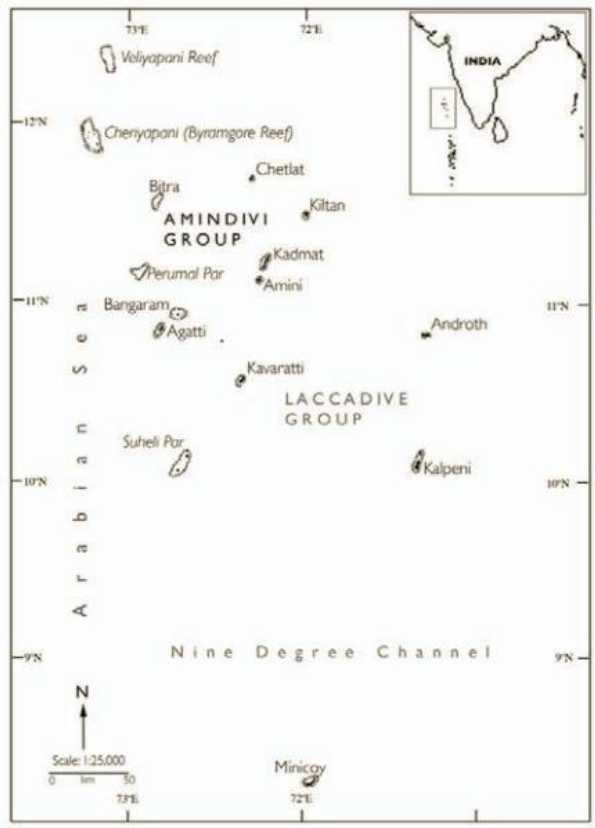


Figure 1.The Lakshadweep Archipelago

Field survey techniques and data analysis

Field Surveys

From November 2010 to April 2011, our team visited atolls across the Lakshadweep Archipelago and intensively sampled a total of 42 reef locations across 12 coral atolls (Figure 1). With the exception of Androth (a lagoonless island with fringing reefs) and Suheli (an uninhabited atoll), we surveyed every location in the archipelago including two submerged banks (Perumal Par and Cheriyapani). At each atoll we conducted in water SCUBA diving surveys, varying the number of reef sites we surveyed according to the size of the atoll. In addition, where considerable reef formations were present inside lagoons, we also surveyed the lagoon sites.

At each location we sampled reefs at two depth zones (where possible), between 10-20 m (deep) and between 5-10 m (shallow). Benthic condition was assessed using 1 m2 photographic quadrats established every 10 m along a 50 m free swim transect (5 quadrats per transect). In addition, we used scaled vertical photographs of the reefs cape to assess the structural complexity of each transect (5 measures per transect). We also collected a range of other reef- and island-based parameters that were used to assess the relative resilience of the reef location (Table 1). Data on reef fish species (abundance, size-class) was collected along this 50m x 5m strip transect using a visual assessment for individuals of all non-cryptic species larger than 5 cm. Biomass for each species was calculated using standard volumetric conversions from the website FishBase (Froese and Pauly 2011). Information on trophic guild and mode of feeding was also compiled for each species and a database was prepared.

Data Analysis

We used a modification of Obura and Grimsditch's (2008) Resilience Indicator protocol to rank the relative resilience of each location (Obura and Grimsditch 2008) on an ordinal scale. We used a set of 12 positive resilience parameters and 9 negative benthic parameters which were assessed at every reef location, in addition to 7 positive and 3 negative fish and bioeroder parameters. These included parameters that are assumed to either facilitate or reduce the resilience of reef locations. An average positive score and average negative score was calculated for the positive and negative indicators.

A net score, called the Resilience Score (RS), was calculated for each location as follows: Average Positive Score – Average Negative Score. Higher RS values indicated the best or least affected reef sites. We also compared pre-bleaching (2007, 2009) and post bleaching (2011) changes in benthic cover and fish biomass estimates, to assess relative change in reef condition. Trends in live coral cover were also assessed for three islands: Agatti, Kavarattii, and Kadmat from where long term data were available (1998-2007), to better qualify differential recovery potentials of these reefs.

Table 1. Resilience indicators measured in the Lakshadweep reefs for the post-bleaching resilience assessment (2010-11). Based on Obura and Grimsditch, 2008).

Category	Subcategory	Variable	Direction	Details
Coral Condition	Current	Bleached coral	-	Photographic recording of cover in 1 sq.m. quadrats (% occurrence)
	Current	Recent mortality (any cause)	-	Based on amount of algal growth on dead coral (%)
	Current	Coral Disease	-	Photographic recording of cover in 1 sq.m. quadrats (% cover)
	Historic	Coral mortality old	-	Based on amount of algal growth on dead coral (%)
	Historic	Recovery old Acropora	+	Observations on standing live Acropora corals (Rank)
	Historic	Recovery old Pocillo-pora	+	Observations on standing live Pocillopora corals (Rank)
	Population Biology	New Recruitment	+	Photographic recording of cover in 1 sq.m. quadrats (% occurrence)
	Population Biology	Live fragmentation	+	Observations on large fragmented corals (massive, encrusting forms; Rank)
	Population Biology	Dominant Size class and Size class diversity	+	Observations on standing live corals (Rank)
	Population Biology	Largest Coral Massive (avg of 3)	+	Observations on standing live corals (Rank)
	Population Biology	Largest Coral Tabular (avg of 3)	+	Observations on standing live corals (Rank)
	Population Biology	Largest Coral Branching (avg of 3)	+	Observations on standing live corals (Rank)
Coral Associates	Positive	Obligate Corallivores	+	Abundance recorded in 50m x 5m belt-transects along different depth contours of reef site (Density per 500 sq.m.)
	Positive	Branching Obligates/ Residents	+	Abundance recorded in 50m x 5m belt-transects along different depth contours of reef site (Density per 500 sq.m.)
	Negative	Competitors (Algae, sponges, etc)	+	Observations on randomly selected corals (Rank)
	Negative	External Bioeroders (urchins, clams, etc)	-	Count of bioerosion signs at 5-10 Porites coral heads (Number)
	Negative	Internal Bioeroders (sponges, etc)	-	Observations on randomly selected corals (Rank)
	Negative	Negative Corallivores (COTS, Drupella, etc)	-	Abundance recorded in 50m x 5m belt-transects along different depth contours of reef site (Density per 500 sq.m.)

Category	Subcategory	Variable	Direction	Details
Herbivores	Herbivores	Herbivore abundance	+	Abundance recorded in 50m x 5m belt-transects along different depth contours of reef site (Density per 500 sq.m.)
	Herbivores	Excavating grazers	+	Abundance recorded in 50m x 5m belt-transects along different depth contours of reef site (Density per 500sq.m.)
	Herbivores	Scrapers	+	Abundance recorded in 50m x 5m belt-transects along different depth contours of reef site (Density per 500sq.m.)
	Herbivores	Grazers/browsers	+	Abundance recorded in 50m x 5m belt-transects along different depth contours of reef site (Density per 500sq.m.)
Predators	Piscivores	Predator Abundance	+	Abundance recorded in 50m x 5m belt-transects along different depth contours of reef site (Density per 500sq.m.)
Connectivity	Dispersal	Self seeding	+	Based on Connectivity and Adjacency with other reefs (Rank)
	Dispersal	Local seeding (10 km)	+	Based on Connectivity and Adjacency with other reefs (Rank)
	Dispersal	Distant seeding (100 km)	+	Based on Connectivity and Adjacency with other reefs (Rank)
	Transport	Oriented/Directed Current flow	+	GIS, Oceanographic Charts
	Transport	Dispersal Barriers	-	None recorded
	Transport	Reef Fragmentation	-	Observations of reef from boat and on dives (Rank)
	Transport	Photic Submersed Ridges etc	-	GIS, Oceanographic Charts (y/n)
Human influences	Substrate	Point sources of pollution	-	Direct observation (Rank)
	Substrate	Anchor and other physical damage	-	Direct observation (Rank)
	Fishing	Fishing pressure on reef	-	Based on knowledge of local informants/observations on fishing boats (Rank)
	Fishing	Destructive fishing	-	Direct observation (Rank)
	Pollution	Human population density per sq km of island	-	Human Population Census figures (2011; Density per sq.km)
	Fishing	Fisher density per sq km of reef/lagoon	-	Encounter-rates derived from fisher census figures (2006) and daily observations on Fishing boats (boats/km reef)
Management	Traditional	Traditional Resource Management	+	Based on local knowledge/literature (y/n)
	Community/NGO	Community Reserves, recent local management	+	Based on local knowledge/literature (y/n)
	Governmental	Presence of Resource Extraction Limits etc	+	Based on local knowledge/literature (y/n)

Results of the Survey

Our initial results paint a mixed picture of the benthic status of the Lakshadweep reefs. This rapid loss of coral structure could have major flow-on consequences for a host of ecological processes dependent on the complexity the reef framework provides, and our ongoing studies will focus on examining the impact of this structural loss on key ecosystem processes like predation, coral recruitment, and post-recruitment survival. Our initial attempts to quantify post-bleaching mortality based on standing recent dead coral (Figure 3) is likely to be an overestimation because of the quick turnover of dead structures on these reefs due to the monsoon. This is particularly true for reefs dominated by *Acropora* spp.

Benthic cover

Western shallow reefs showed the highest impacts of bleaching, with the highest coral mortality and decline in live coral cover (Fig.2, Fig.4). Western deep reef sites, largely dominated by massive, bleaching resistant coral species, showed relatively low bleaching impacts (Fig. 4). Eastern reefs too showed a similar trend, but owing to inherently low pre-bleaching coral cover, showed less declines in coral cover than western reef sites (Fig. 6b). Lagoon sites had the highest live coral cover, owing, most probably, to adaptation to hotter temperatures in shallow, ponded environments (Fig. 4). Atolls such as Agatti, Kadmat, Amini and Cheriyapani showed overall high declines in live coral, and post-bleaching mortality was higher in these reefs (Fig. 2). On the other hand, reefs such as Kavaratti and Minicoy seemed to be resistant to the 2010 bleaching, with lesser coral death and structural damage (Fig. 7).

Structural complexity and physical factors

Deeper reef sites, both on the eastern and western aspects, had high physical shading, and abundance of large, canopy-like corals (Fig. 5a). Being reefs sheltered from monsoonal storms, eastern reefs exhibited overall higher structure than western reefs (Fig. 5a). Atolls with structurally complex reefs were Perumal Par, Minicoy, and eastern aspects of Kalpeni and Kavaratti. Other islands such as Amini, Kadmat, Agatti, Bangaram, Kavaratti (western reefs) showed alternating spur-and-groove formations that continued for large areas at shallow depths. Most of the eastern reefs (with exceptions in Amini and Bitra) were located deeper and had steep drop-offs. These factors contributed to overall reef structure, highest in Minicoy and Perumal Par and lowest in Kadmat (Fig.12).

Coral mortality and recovery

Recent coral mortality was highly variable across the archipelago, with reefs in Kavaratti, Minicoy, Perumal Par and Bitra showing moderate to high resistance to the 2010 bleaching, whereas islands such as Agatti, Kadmat, Amini and Kalpeni (western sites) had low resistance and suffered high coral mortality (Fig.11). Post-bleaching mortality (magnitude) was evident in most surveyed reefs (Fig.3, 5b), and many shallow areas were dominated by recently dead *Acropora* tables and a mixture of dead massive genera, colonised by turfing algae. Although shallow reefs were the worst impacted, bleaching related mortality was recorded in many deep locations as well, up to 20 m. However, live coral cover varied considerably between locations, and, at some outer reefs we surveyed, coral cover was, on average, more than 40% of the benthic substrate (Fig. 2), dominated by massive genera like *Porites*, *Goniastrea* and *Montipora*, among others, known to be less susceptible to bleaching.

In contrast, reefs once dominated by branching and tabular species appeared to have had the most significant damage, and many were reduced to rubble banks, with a major loss of reef structure. This was, in all probability, due to the combined impacts of bleaching related mortality (that peaked between April and May 2010), and the subsequent monsoon storms (that begin in mid May and continue until September). While most branching coral were particularly susceptible to the mass bleaching, *Pocillopora verrucosa* showed an opposite trend and seems to have resisted the bleaching. This one species, from comprising less than 5% of the coral composition after 1998, is beginning to take over as the dominant species of branching coral in many shallow Lakshadweep reefs. There is thus a noted shift in dominance from species of *Acropora* to *P. verrucosa* among the branching coral community on the reefs. However, *P. verrucosa* has a branching structure very different from the *Acropora* species that once dominated these reefs.

Lagoon reefs: acclimatization and adaptation

At most lagoon sites (apart from Agatti), coral cover was significantly higher than the outer reef sites, and these locations were among the only surveyed locations where bleaching susceptible genera like *Acropora* were thriving. Interestingly, these locations experienced high levels of bleaching in April and May of 2010, but corals appear to have recovered since then. These shallow locations are highly entrained or ponded, and are typically subject to higher temperatures through the year, often climbing to 31ºC during the peak of a normal summer.

Coral populations in these lagoon locations are potentially better able to cope with anomalous temperature events because of a longer period of acclimatisation.

Coral associates

Interestingly, *P. verrucosa* that became dominant on the reefs post the 2010-bleaching, had an entire retinue of facultative and obligate associates, and their numbers are also apparently increasing considerably as this species is gaining ground in the post-bleached reef communities. Within lagoon reef sites, *Acropora* species dominated and *Acropora*-linked species continued to persist, although in outer reefs, they were never observed (with the exception of Minicoy) because of heavy declines in *Acropora*. Crown-of-thorns starfishes were most abundant in the Agatti, Amini and Kadmat reefs, whereas they were not recorded in Minicoy, Kalpeni, Bitra and some northern islands. Boring sponges dominated in Amini, Kadmat and Agatti reefs. Positive associates of corals are mainly fish species, esp. corallivorous butterfly fishes of the family Chaetodontidae that enhance growth rates of corals by regulated feeding on coral polyps. The persistence and diversity of these species depend directly on live coral condition. Kavaratti had the highest net positive scores for coral associates among all islands, followed by Minicoy, whereas Agatti and Kalpeni had low scores. Net positive coral reef associates scores were highest in lagoon areas (Fig. 5c).

Reef fish trophic guilds

The highest reef fish biomass scores were recorded at Amini, Kavaratti and Kalpeni (Fig. 8). Herbivores and zooplanktivores respectively showed moderate and huge increases in biomass post-bleaching, but all other trophic guilds showed declines. The most critically affected trophic guild was of the corallivorous fishes, due to declines in live coral cover. Amini, Kadmat and Agatti, atolls with the highest levels of coral mortality, recorded high herbivore biomasses. Overall, reef fish biomass was exceptionally high in most reefs, largely due to the low-impact reef fishing across the Lakshadweep Archipelago. The high biomass values led to eastern and western sites showing no significant differences in reef fish abundance scores (Fig. 6b).

Connectivity

Coral larval dispersal and seeding (self-, local- and distant-) was assumed similar across the Amindivi group of islands, with the exception of Minicoy. The Minicoy reefs, owing to distance, were assumed to receive less distant seeding than other closer islands (although the Maldives' reefs could be a likely source). Natural reef fragmentation by intervening sandy zones was seen only in the northern islands of Bitra and Cheriyapani;

whereas photic submerged zones were present south of Amini (covering an area of 155 km2) and along the sea between Agatti and Bangaram islands.

Anthropogenic and management factors

No significant impacts of anthropogenic disturbance were noted on corals or benthic composition. Levels of pollution, physical damage from anchors and fishing were higher inside lagoon reefs than outer reefs, but were negligible to produce any significant effect. Fishing pressure on the reefs, though low in general, was higher in eastern reefs (closer to islands and thus more accessible) than the western reefs. Overall, no significant differences in human impacts were seen on the eastern or western reefs (Fig. 5d). Bangaram, Cheriyapani and Perumal Par being uninhabited reefs / islands, had relatively low human impacts than most others, except for the occasional fishing activity of Agatti and Bitra fishers (Fig. 9). Agatti, Amini and Kavaratti were the most human-impacted reefs as per our survey.

Table 2. Lakshadweep reefs ranked from best to worst as per resilience scores.

Rank	Atoll	Resilience Score	Resistance	Remarks
1	Kavarae	1.43 (SD 0.61)	High	Highly resistant reefs, could act as source populations for coral and fishes
2	Minicoy	1.31 (SD 0.43)	High	Resisted the 2010 bleaching, especially in deeper reefs > 15m
3	Bangaram	0.99 (SD 0.68)	Moderate	Coral indicators poor, but lagoon sites and fish indicators high; this is also an uninhabited area
4	Kalpeni	0.96 (SD 0.68)	Moderate	Highly variable response on the western and eastern aspects
5	Perumal Par	0.93 (SD 0.34)	Moderate	Uninhabited submerged bank
6	Kiltan	0.91 (SD 0.52)	Moderate	
7	Chetlat	0.89 (SD 0.45)	Moderate	
8	Bitra	0.84 (SD 0.49)	Moderate	
9	Amini	0.78 (SD 0.54)	Low	Shallow profile of reefs might have led to high coral decline
10	Cheriyapani	0.68 (SD 0.25)	Low	Uninhabited submerged bank
11	Kadmat	0.62 (SD 0.57)	Low	Highly affected. Possibly tito repeated bleaching events
12	Agae	0.40 (SD 0.34)	Low	Severely hit by the 1998 and 2010 bleaching

Overall resilience scores

Kavaratti, Minicoy and Perumal Par, along with highly variable reefs such as Bangaram and Kalpeni, showed the highest resistance indices. Kiltan, Chetlat, and Bitra islands showed moderate resistance; whereas Amini, Kadmat and Agatti were rated the worst-affected by bleaching (Fig. 13, Table 2).

Long-term changes in reef resistance and recovery

Long-term data from three reefs (Agatti, Kadmat, Kavaratti) were compiled over a period of 13 years (based mainly on Arthur, 2005; Arthur et al., 2006, and recent reef surveys by the authors of this report). The three islands showed different trajectories of live coral recovery across the bleaching events of 1998 and 2010 (Fig. 14a). Agatti showed the highest rates of change (both decline and subsequent increase) among the three islands. Kavaratti reefs responded to bleaching impacts in a more stable manner, and coral cover did not decline majorly post-bleaching. Kadmat, on the other hand, showed significant declines not matched up by recovery rates in the subsequent years. Eastern and Western reef aspects also showed important differences in their responses to bleaching (Fig. 14a). Overall, the three atolls with their eastern and western reefs (6 sites in total) were ranked along a gradient of recovery post-bleaching and resistance to bleaching. Kavaratti had highly resistant reefs, the western reefs of Agatti showed highly dynamic states between high decline and high recovery, whereas Agatti (eastern reefs) and Kadmat reefs showed low resistance and low recovery (Fig. 14b).

Understanding Reef Resilience in the Lakshadweep Archipelago

Reef-level differences in the response of reefs

Aspect and depth play important roles in influencing resilience across this atoll chain. While for eastern reefs, there is not too much of a difference between resilience scores for shallow and deep reefs, resilience on eastern reefs tended to be low. In contrast, western reefs differed widely between deep and shallow locations, with deep reefs scoring highest in the resilience index, while the shallow western reefs scoring significantly lower than all other reef locations (Figure 4). The differences in resilience behaviour between reef aspects is most likely because of the clear hydrodynamic contrasts between eastern and western faces of these atolls. The south-west monsoon influences the western front of these atolls profoundly, while eastern reefs generally tend to be less exposed to four months of continuous monsoon battering.

In a post-bleaching scenario, this makes the shallow western reefs particularly susceptible to a rapid loss of dead structure, while on the east, this structure is not eroded as quickly (Arthur et al. 2006). However, shallow western reefs also saw the most rapid rates of recovery after the bleaching of 1998. Their recovery was dominated by fast-growing branching and tabular *Acropora*, which is also highly susceptible to bleaching mortality. These shallow western reefs score very low on the resilience index, but represent potentially dynamic sites. Thus while the resilience index, as currently constructed, may be effective in identifying sites with large buffer capacity (the ability to withstand disturbance events without changing), it may be less sensitive to a location's ability to recover from major disturbances.

In addition to large differences between aspects, lagoon sites, despite being shallow, scored higher on the resilience index than all but the deeper western sites on the outer reef. The lagoon reefs of Kadmat and Agatti were notable exceptions that scored very low on the resilience index. The Agatti lagoon is peculiar in that it is not as enclosed (ponded) as other lagoon sites because of a very large break in the reef framework on its western front. This may result in a lower acclimation potential for this lagoon site, lowering its overall resilience. We provide atoll-wise characteristics for all surveyed locations: the relative resilience of an atoll appears not to be based on island connectivity, although large, isolated atolls with low to moderate fishing pressure appear to fare better in the resilience index. Although uninhabited atolls like

Perumal Par and Bangaram had high resilience scores; merely having low population densities did not protect reefs from fishing pressure or from being vulnerable to climate related events. It has to be clarified that the fishing pressure characterisations are relative indications, and, in general, reef fishing in the Lakshadweep is low and limited to largely non-commercial subsistence fishing. However, even at this relatively low level of fishery, it is possible for ecosystem-wide consequences to accrue to these reefs, and, in post-mortality reefs, could compromise the overall resilience of the system.

Lagoon reefs: Getting used to change

There has been much debate about the potential adaptive capacity of corals and entire reefs to cope with repeated bleaching events (Brown et al. 2002; Coles and Brown 2003; Kinzie et al. 2001; Thompson and van Woesik 2009). One line of evidence for the potential for corals to 'learn' from their environment comes from lagoon reef sites in the Lakshadweep.

Lagoon reefs are typically small patch formations, but, in the context of repeated mass mortality events on outer reefs, these may serve as potentially vital source areas for recolonisation. Whether potential reseeding from lagoon reefs is sufficient to compensate the large losses experienced by the outer reefs remains to be seen. Another intriguing possibility is that these populations could transfer their acquired temperature plasticity to the newly seeded reefs, leading to new colonisation that is better able to resist future sea surface temperature increases. Given their importance, these shallow lagoon reefs need particular protection, since these locations among the most susceptible in the Lakshadweep to the combined effects of bait fishing, anchor and keel damage, nutrient pollution, etc.

Resistance, recovery and resilience in the Lakshadweep reefs

The snapshot resilience assessment of Obura and Grimsditch (2008) provided useful information on relative resilience across reefs, and gave a good idea of immediate post-bleaching impacts. It thus stands as an efficient index to document reef resistance to bleaching. However, there is a need to consider longer-term trajectories of recovery of reefs also. Long-term studies on the post-1998 bleaching impacts (Arthur et al. 2004; Arthur et al., 2005) have shown that reefs in the Lakshadweep Archipelago can have differing buffer capacity (ability to withstand resistance), and recovery potentials. The Agatti reefs, for instance, showed considerable damage after the 1998 bleaching, but also the highest recovery rates, and rapidly improved in indicators such as live coral cover. On the other hand, Kavaratti showed relatively lower impact of the 1998 as well as the 2010-bleaching events. The reefs of Kavaratti are classified as resistant reefs, which tend to be more stable in response to even catastrophic disturbances. Reefs such as Agatti are likely to be inherently dynamic, going through drastic changes (e.g. coral population decline as seen in the 2010-11 survey) in response to periodic disturbances. Reefs of Kadmat, between 1998 and 2011, showed overall low recovery and low resistance, and are likely to be highly susceptible to bleaching impacts. These differential responses of resistance and recovery could be attributed potentially to oceanographic and physical factors.

The nature of differential responses provides useful hints to conservation and management strategies that may be used for sustaining coral reefs in an age of increasing uncertainty about catastrophic disturbances caused by climate change. Conservation of coral reefs can benefit from an understanding of relative resistance and recovery potentials of reefs for more pragmatic allocation of funding and management inputs. For instance, protecting more resistant reefs would be the most crucial, but affording higher protection to dynamic recovering reefs would also be high priority. Resistant reefs may provide source populations to degraded reefs and act as vital replenishing agents for corals and fishes.

If reefs are susceptible to climate impacts irrespective of having a suite of apparently favourable indicators, such as Kadmat, it might make sense to rank these reefs lower on the priority lists, as management actions may only be as good as the ability of the reefs to respond. Because of this, it is critical to understand how reefs change in the long term, and fundamentally necessary to understand what factors and processes drive the dynamics of reef resistance. The nature of the underlying processes might strongly affect management success, and a detailed understanding of these factors will be helpful in assessing the suitability of management interventions in different reefs. In the case that the major factors governing reef resistance are mainly linked to oceanography, seasonal current patterns, or local hydrodynamics, i.e. factors essentially beyond the scope of effective conservation; the wise approach shall be to merely protect resistant reefs from external influences, and thus maintaining their important function as it is governed by the oceanographic factors. On the other hand, if pollution and fishing, i.e. factors within human control; are identified as factors critical to reef resilience, active intervention to curb these threats to the coral reef in question. It is highly likely that these two factors could interact, and then the manager has to decide how the human factors could be prevented first, to achieve the maximum possible recovery given large-scale factors beyond control. In this sense, long-term planning for conservation of coral reefs can greatly benefit from a detailed understanding of where different reefs may fall on the axes of resistance and recovery.

In this report we establish a gradient of resistance, recovery and susceptibility to bleaching along which the Lakshadweep reefs may be placed. Across this gradient we plan to conduct a series of ecological studies over the next few years to tease apart the specific drivers of climate resilience to help us better understand the mechanisms that need the most attention while attempting to manage these climate-challenged ecosystems.

RESULTS FIGURES

Figure 2. Percent live coral cover in the Lakshadweep reefs (early 2011)

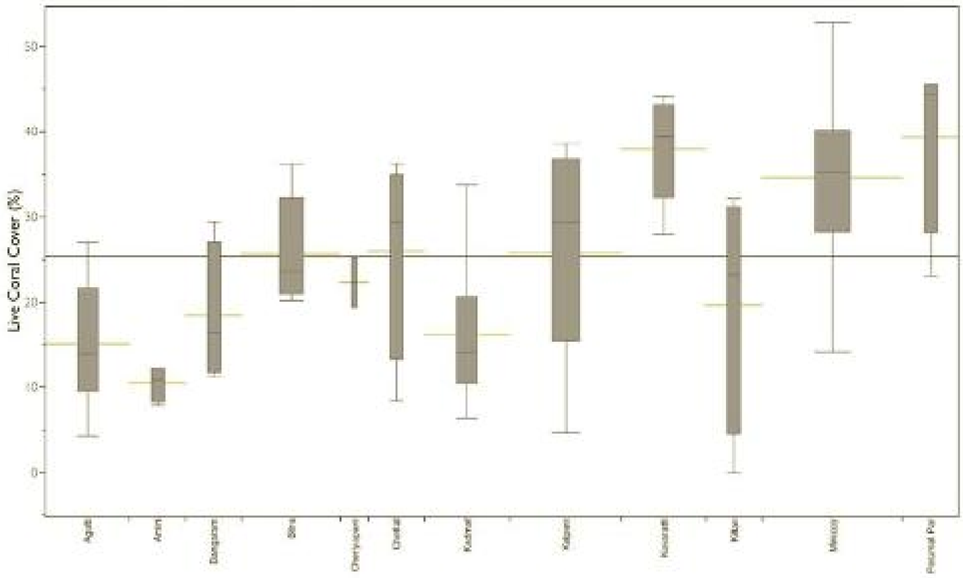


Figure 3. Initial assessments of post-bleaching mortality based on evaluations of recent dead standing coral compared with present live coral cover in the Lakshadweep atoll

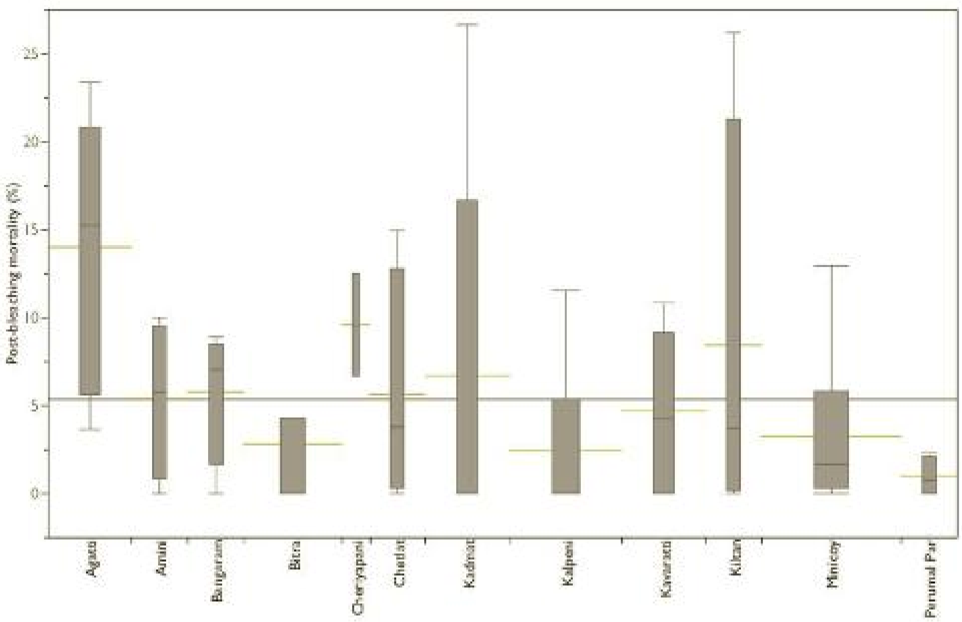


Figure 4. Average resilience scores based only on coral mortality at lagoon sites, deep and shallow locations in western and eastern aspects of the Lakshadweep Islands. Error bars are standard errors

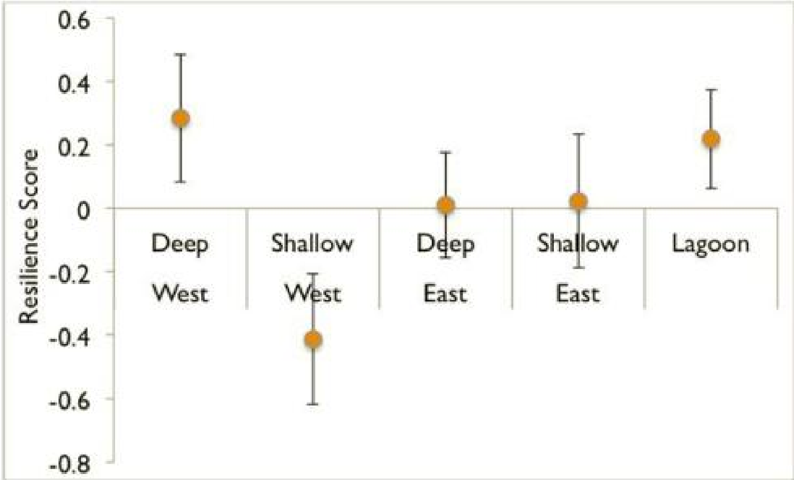


Figure 5. Boxplots showing net resilience scores for physical factors, coral recovery, coral associates and human impacts across lagoon sites, and shallow and deep reefs along western and eastern aspects. Note the low and similar human impacts across all these sites. ED=East Deep, ES=East Shallow, L=Lagoon, WD=West Deep, WS=West Shallow

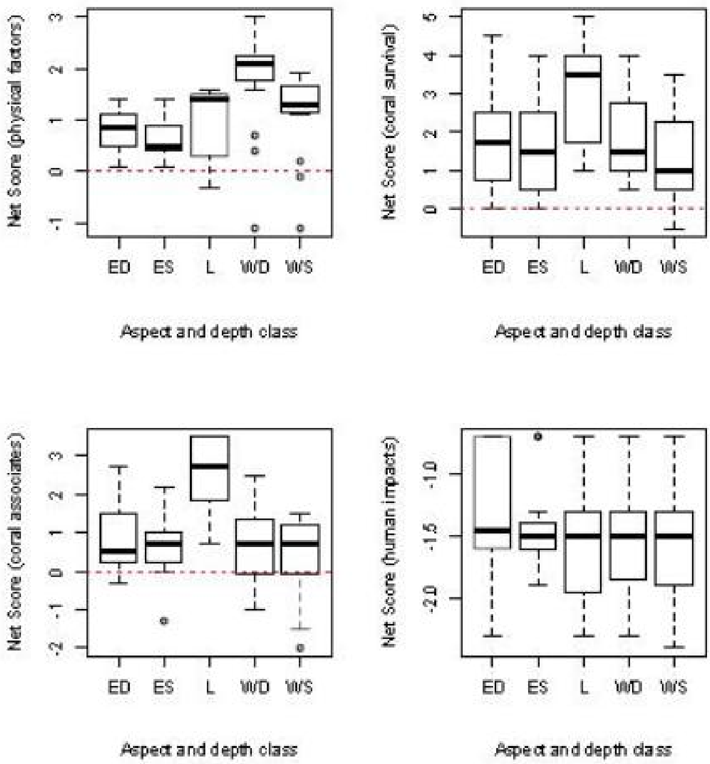


Figure 6. Lagoon reef sites had higher benthic cover scores. Fish biomass values are overall high across the Lakshadweep reefs, due to low-intensity fishing. ED=East Deep, ES=East Shallow, L=Lagoon, WD=West Deep, WS=West Shallow

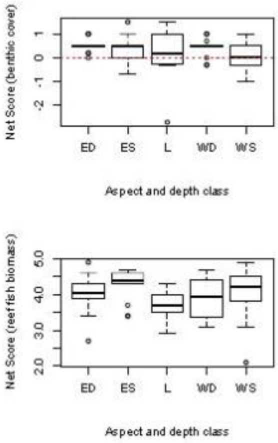


Figure 7. Benthic cover scores across atolls. Kavaratti, Minicoy, Chetlat and Perumal Par have high scores, whereas Kadmat, Kalpeni, Agatti and Amini have the worst-affected sites. ED=East Deep, ES=East Shallow, L=Lagoon, WD=West Deep, WS=West Shallow

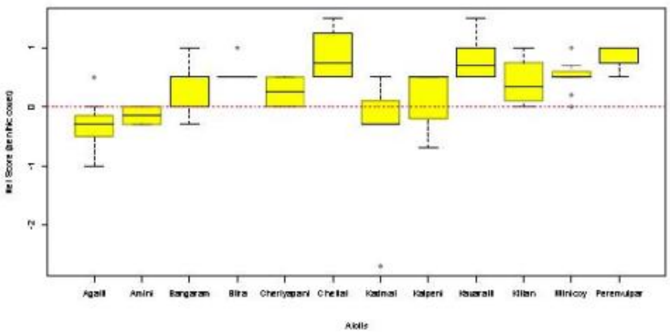


Figure 8. Reef fish biomasses are high across atolls, with Kavaratti and Amini having the highest fish scores.

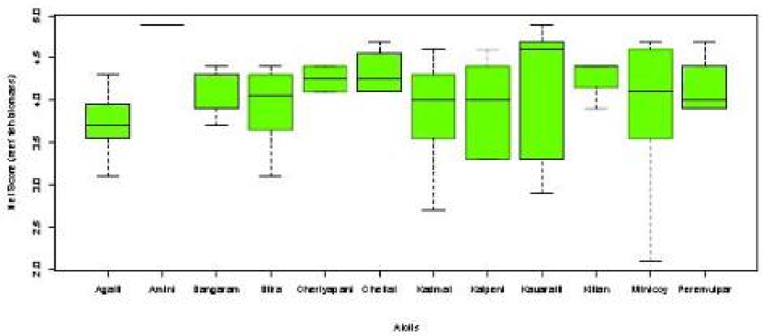


Figure. 9. Human impacts are overall similar across islands, with Amini and Kavaratti the most impacted, and Perumal Par, Cheriyapani and Bangaram (uninhabited islands) having low impacts.

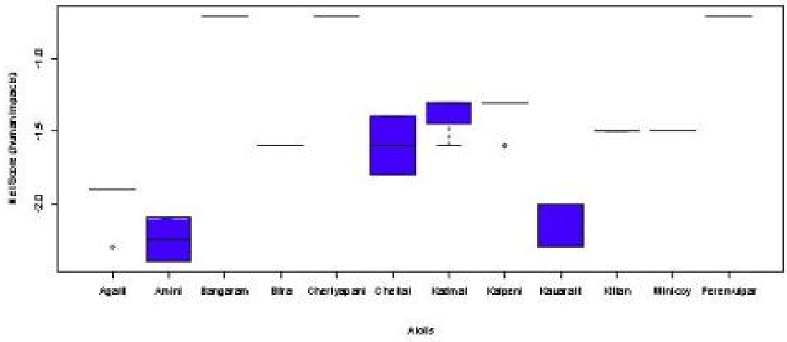


Figure. 10. Net score of coral associate abundance (weighted towards positive) shows Agatti to be highly affected by negative coral associates such as Crown-of-Thorns starfish, while most other islands have similar scores.

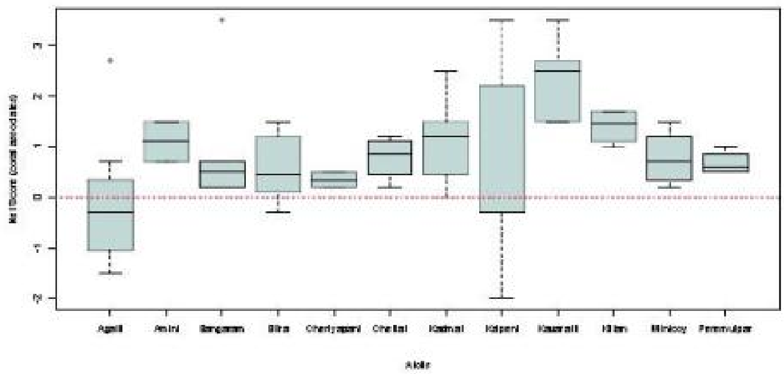


Figure. 11. Overall coral recovery and survival are the highest in Minicoy, Kalpeni and Kavaratti.

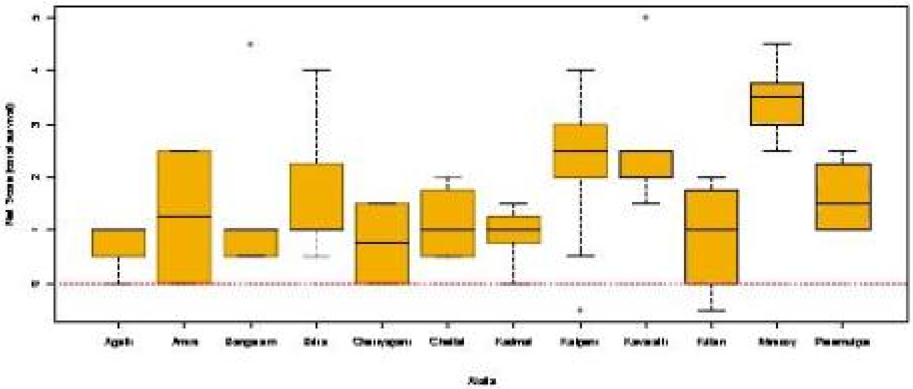


Figure. 12. Kadmat reefs were found to rank the lowest in terms of physical factors such as shading, slope and canopy coral cover.

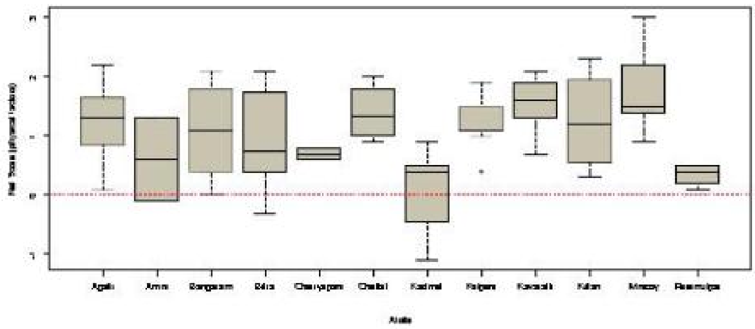


Figure. 13. Total resilience scores for all atolls in the Lakshadweep Archipelago.

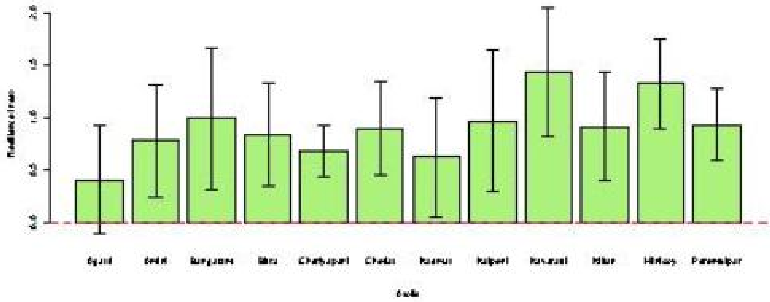
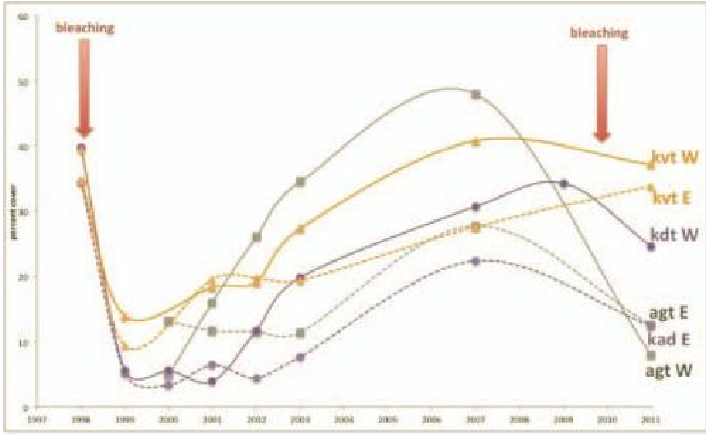
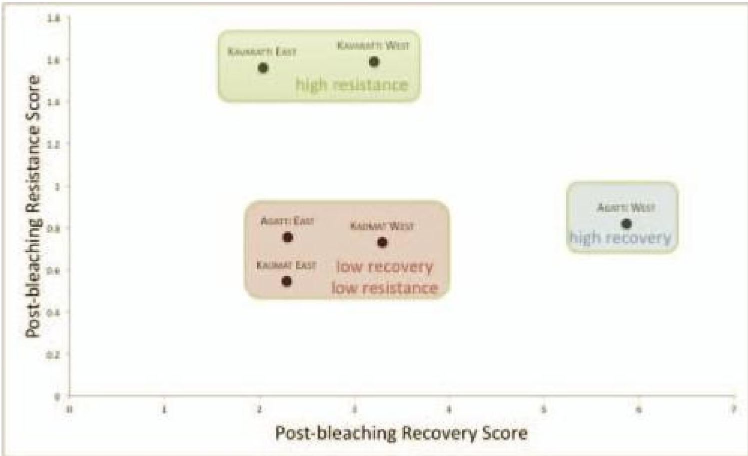


Figure. 14. (Above) Trajectories of live coral decline and recovery in Agatti, Kadmat and Kavaratti over a period of 13 years and 2 bleaching events. (Below) Based on observed trends in live coral cover, individual atolls classified into a) high resistance areas (e.g. Kavaratti); b) Low recovery and Low resistance (Susceptibility) (e.g. Kadmat, Agatti-East), and c) Low resistance but high recovery (e.g. Agatti- West).





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