



PREPARING FOR climate change IN THE WESTERN INDIAN OCEAN

**IDENTIFYING CLIMATE
REFUGIA, BIODIVERSITY
RESPONSES
AND PREFERRED
MANAGEMENT**

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Identifying climate refugia, biodiversity responses and
preferred management

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“By failing to prepare, you are preparing to fail”

- Ben Franklin

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Abstract

The research presented in this report develops a synoptic view of the biodiversity and resilience of coral reefs to climate change in the western Indian Ocean. Studying reefs over a gradient of environmental variability, we tested for differences in the acclimatization and adaptation response of corals to climatic fluctuations and changes expected with global warming. The study had three major foci, one on the ecology of coral reefs, a second on the ecology of algal symbionts in corals, and finally an evaluation of the types of management restrictions that coral reef stakeholders in the region prefer and are likely to support. The combination of the ecological and management preference studies identified priority areas and conservation actions. Studies were undertaken throughout the western Indian Ocean and compared with all available published and unpublished data to develop the broadest view provided by the current science.

Ecological studies focused on assessing benthic cover (of corals and other functional groups), coral community structure, and bleaching response, and relating these to management type (fished reefs vs. fisheries closures), and physical environmental conditions (exposed vs. sheltered) and before, immediately after, and 7 to 10 years after the 1998 mass coral bleaching mortality). Coral cover was lowest in the period immediately after 1998 and decreased with latitude going northward. Fisheries closures had lower coral cover than fished reefs during this period. Analysis of late post 1998 data indicated that sheltered reefs (behind reefs and islands) had higher cover than exposed reefs. Acroporid and pocilloporid corals showed changes in cover that were opposite to those in Poritids and were more abundant on exposed reefs in the south, reflecting weaker patterns in bleaching in the south and, therefore, higher coral community susceptibility in the south. Coral taxonomic richness was higher in closures, particularly sheltered closures, and richness and diversity increased northward. Fleshy algae dominated on fished reefs in high-energy areas in the south. Patterns of coral and benthic composition in the region reflected the strong impact of the 1998-bleaching disturbance in the central northwestern Indian Ocean. The study suggests a strong positive relationship between total coral cover, and cover of bleaching susceptible taxa, such as *Acropora* and *Montipora*. Exposed reefs suffered the highest declines in cover in 1998, which is contrary to assumptions that exposure mitigates the impact of coral bleaching. The highest priority areas for securing corals against the future impacts of climate change and fishing are sheltered reefs, such as reefs behind islands, in enclosed bays, and back reefs.

Studies of the **algal symbionts** (*Symbiodinium* spp.) in these corals were undertaken to evaluate their ecology and potential value in promoting adaptation to climate change. Large-scale regional studies of algal symbiont distribution indicate that *Symbiodinium* in clade C is the most common and is a broad tropical generalist. Clade D is less common and found in more specific environments where temperatures are high and often variable, including dominance in some shallow fringing reefs of Kenya, and high abundance in northwest Madagascar. Changes in the relative frequency of clades C and D at different sites in Kenya depended on coral taxon, and interacted strongly with location (driven by variation in temperatures at different sites) and weakly with time.

Some coral taxa, such as *Pavona* and *Pocillopora*, frequently hosted clade D and are increasing on Kenya reefs. Branching *Porites* and *Acropora* have stronger associations with clade C and their populations are declining. There was some evidence that strong thermal anomalies can promote changes in symbionts from C to D in some coral taxa, but this change may not persist beyond five years after the disturbance unless background temperature anomalies, or continued warming, continue to promote clade D. Given that sheltered reefs are the most likely to persist under climate change due to associations with acclimatization and community changes in the symbionts, these reefs are high priority sites for increasing management restrictions.

The regional evaluation of **management preferences** indicated that there is generally broad-scale support for management restrictions, particularly gear and minimum size restrictions. There was support for restrictions on space, such as no-fishing closures, species and temporal closures, but there were also a number of communities (in all countries) that did not support these restrictions. Communities with a long history of marine protected areas tend to support closures, especially those

that are less reliant on marine resources, supporting the need for diversified and profitable alternative livelihoods. Consequently, we recommend the introduction and enforcement of broad-scale gear and size restrictions at the national and regional levels, and the immediate implementation of more site-specific closures and species restrictions in supportive communities. Greater interaction and communication between communities with positive views on restrictions and those with negative views is expected to increase support for the implementation and evaluation of these restrictions at the regional scale. There is an immediate need to increase successful co-management of sheltered coral reefs to ensure they persist as refuges from climate change.

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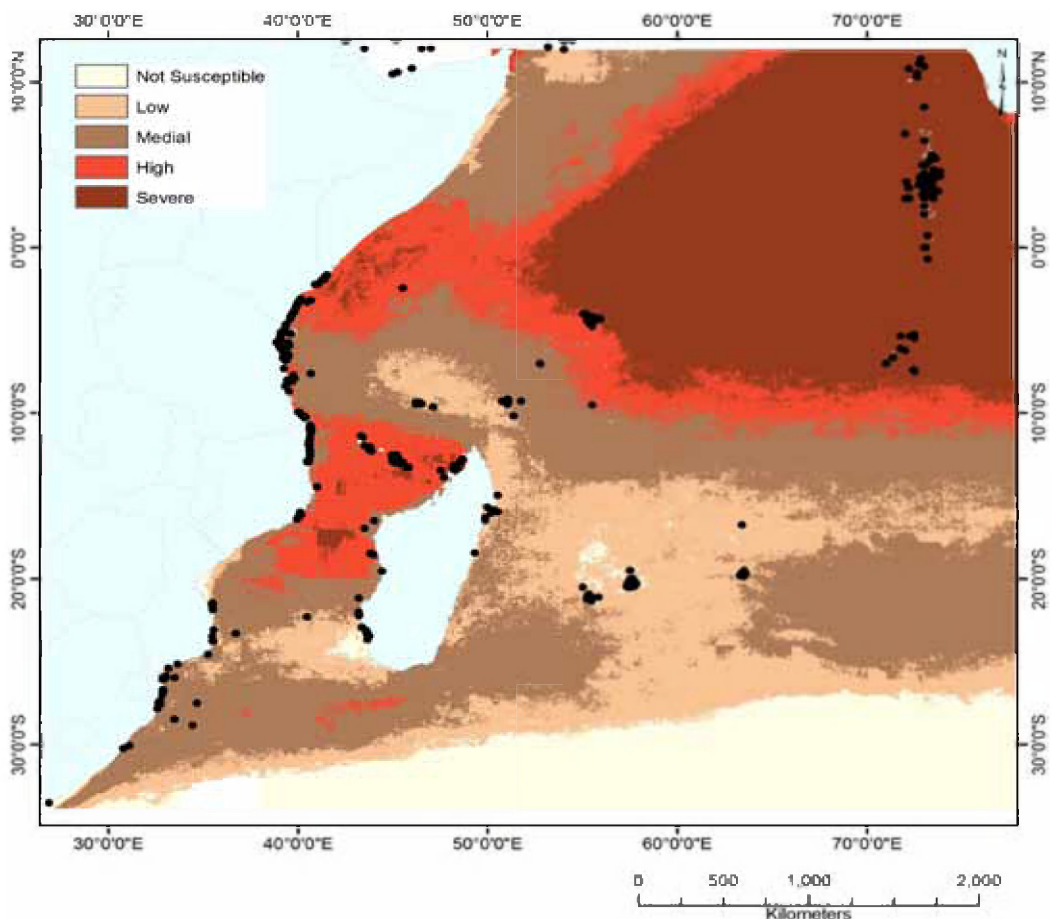
Introduction

A key concern of modern marine management and conservation is to determine the interactions between climate change and human resource use, and to identify the potential outcomes of those interactions. Particular objectives include identifying sites of high and unique biodiversity, connectedness, and resilience that will survive climate change, and developing appropriate management for these sites that will be adopted by resource users and managers and ensure the persistence of these potentially resilient biodiversity refugia. There is growing awareness of the need for these activities (West and Salm 2003; Wooldridge and Done 2005; McClanahan *et al.* 2011), but implementation requires an evaluation of large-scale patterns of environmental variation, connectivity, changes or resilience over time, projections into the future, and its consequences for adaptation and biodiversity preservation. Additionally,

to be confident about predictions for climate change, an improved understanding of the causation between environmental variation, adaptation, persistence, and biodiversity is needed. The patterns of causation are complex, sometimes counter-intuitive, an area for growth in understanding among biodiversity and climate change investigators (McClanahan *et al.* 2005a). Understanding climate change effects, adaptation and its consequences for biodiversity and the management preferences of resource users and managers were the impetus of this research and associated studies.

Ecological context

The Western Indian Ocean provides a unique environmental gradient to examine the relationships between environmental variation, climate change, connectivity, resilience, and



adaptation to climate and its consequences for biodiversity. The region's tropical to temperate range, complex currents that interact with the island of Madagascar and the African coastline create this complex gradient. Analyses of historical water temperature data from a section of this transect over the past 50 years indicate that there are strong gradients in mean temperature, variations in temperature, the rate of increase and cumulative anomalies during warm events, such as the 1998 ENSO episode (Fig. 1; Maina *et al.* 2008; McClanahan *et al.* 2011). The equatorial current has low variation but on the leeward side of Madagascar there are pockets of retention, warming, and high variation, which diminish as the island effect is reduced and current speeds increase towards the north. The rates of temperature rise are also affected by these patterns with temperate and retention areas warming fastest, particularly during strong warm ENSO years (Sheppard 2003; McClanahan *et al.* 2007a).

Natural gradients in the western Indian Ocean provide an opportunity to examine biodiversity and resilience in different environments and to determine how well these reefs have persisted over the early stages of climate warming and particularly since the 1998 ENSO (Goreau *et al.* 2000; McClanahan *et al.* 2011). There are likely to be taxa-specific responses to these changes and corals and some other benthic species are among the most vulnerable foundation taxa that are among the early responders to climate change (Hoegh-Guldberg and Bruno 2010). Study of the benthic taxa and how they interact with geography, habitat, and resource extraction is expected to improve understanding of the resilience of reef communities to climate change and the types of environments that will produce resilience and are high priority for management.

Symbiotic context

The potential adaptation or acclimatization of reef corals to rising temperatures is a critical but controversial question in contemporary coral reef science and conservation. Although there are a number of mechanisms by which corals, dinoflagellates (*Symbiodinium* spp.) and other symbiotic partners might respond to climate change (Gates and Edmunds 1999; Baird *et al.* 2009), most research has focused on whether or not corals are able to flexibly associate with diverse symbionts whose different physiologies provide greater resistance to environmental extremes (Buddemeier and Fautin 1993; Rowan *et*

al. 1997; Baker 2003; Baker *et al.* 2004; Berkelmans and van Oppen 2006; Jones *et al.* 2008; LaJeunesse *et al.* 2009; LaJeunesse *et al.* 2010). While changes within colonies have attracted the most attention, differential reproduction and survival of colonies with different symbiont associations is likely to be another important factor driving population level changes (Baker *et al.* 2004).

The future of coral reefs is uncertain as a result of rising seawater temperatures, decreasing aragonite saturation state, and increasing intense oceanographic oscillations that, when combined, have already begun to cause widespread loss of coral cover (Veron *et al.* 2009). These environmental changes are killing sensitive taxa and threatening losses in biological diversity and associated ecological processes (Bruno *et al.* 2007; Carpenter *et al.* 2008). The rates of climate change without regulation of greenhouse gases may be too rapid for compensatory genetic adaptations in reef corals or their algal symbionts (Hoegh-Guldberg *et al.* 2007; Baskett *et al.* 2009). The outcomes for sensitive coral taxa may depend on the types of bleaching and mortality, interacting with coral life histories and their ecological constraints (Day *et al.* 2008). A combination of acclimatization, community change, genetic adaptation and the ability of humans to collectively reduce greenhouse gas emissions and improve the management of coral reef resources will determine the outcomes (Baskett *et al.* 2010).

Social context

There is often considerable conflict between social and biological goals of fisheries and marine protected area management. This conflict frequently leads to poor success in the implementation of management (McClanahan 1999; Christie 2004; Hilborn 2007). Sustainable management relies heavily on the perceptions of resource users and managers and their ability to share and implement common values and goals (Nelson 1995; McClanahan *et al.* 2005b,c; Gelcich *et al.* 2005, 2006, 2007). Marine resource management can be grossly categorized into seven actions and their permutations, including restrictions on area, time, size, gender, species, gear and effort. Preferences for these restrictions can be based on real or perceived costs, culture, education, occupations, past history of interactions around resources, and be informed by scientific or qualitative investigations about the efficacy of different management strategies (Aswani 2005; McClanahan 2005a,b; Richardson

Table 1. Predictions or hypotheses of the effects of environmental gradients or extremes on ecological or community factors. (Here windward sides of islands would be high flow and low temperature variation and leeward sides would be low flow and high temperature variation).

Factor	High flow/Low temp Variation	Low flow/High temperature Variation
Coral host diversity	high	low
Coral symbiont diversity	low	high
Coral acclimation	low	high
Fish diversity	high	low
Productivity	high	low
Herbivory and predation	high	low
Algae diversity	low	high
Tolerance to rare disturbances	low	high
Diversity immediately after disturbance	low	high

et al. 2005). These preferences often lead to heterogeneity in perceptions and behavior, which can arise at a number of scales (from the individual, to the village, to managed and non-managed sites). Many of the conflicts over marine resources arise because of heterogeneity in perceptions about specific restrictions and identifying responsibility for control.

Management is likely to be successful when resource users and managers can agree on the types of management that they prefer, and work collaboratively towards their implementation (Jentoft *et al.* 1998; Jentoft 2003; Defeo and Castilla 2005). This may require a blending of ‘top-down’ and ‘bottom-up’ approaches to management (Berkes 2007), and a first step towards this blending is to evaluate the perceptions of these two groups and to identify areas of conflict and agreement (Cocklin *et al.* 1998). In principle, once this is achieved there is a greater chance that conflicts and agreement on shared perceptions can be recognized, constructively addressed, and potential solutions implemented (McClanahan *et al.* 2009a). Conflicts and the sustainable use of natural resources can be resolved in a number of ways, both in terms of the technologies and social organization around key institutions (Beddington *et al.* 2007; McClanahan and Castilla 2007).

Objectives

The project aimed at investigating environmental and biodiversity gradients created in the western Indian Ocean as a basis for understanding climate change effects, adaptation, and its consequences for biodiversity. Investigating this gradient

was not only expected to provide the basis for developing conservation and management priorities in the region, but also likely to uncover causative effects between environmental change and biodiversity. Two preliminary tests of this gradient had been completed, one focusing on the windward-leeward sides of the island of Mauritius (McClanahan *et al.* 2005d) and the second examining coral cover along a gradient from southern Kenya to Tanzania (McClanahan *et al.* 2007a). These studies suggested that as water flow is reduced by island effects along windward-leeward gradients water temperature variation rises and that this may result in fewer anomalous temperatures and adaptation to anomalous temperature events. The prediction for biodiversity was that the exposed windward sides of islands will have a high diversity of species but that they have low acclimation to environmental variability and leeward sides the opposite patterns (see hypothesis in Table 1). Windward sides being susceptible to rare environmental disturbances and sheltered leeward sides less so. The project therefore aimed at undertaking an evaluation of coral reef biodiversity across this regional gradient, focusing on corals, their endosymbionts, algae, and fish.

Because the proposed biodiversity evaluation would help to uncover the priority areas for management a simultaneous social survey in these sites was also undertaken to evaluate the management preferences of resource users and managers at each study area. It should be possible to both identify priority sites based on biophysical considerations and the management preferences most likely to be adopted by

communities at these sites. Consequently, this study examined the preferences and perceived benefits of management options in fishing communities with considerable heterogeneity in opinions and management systems - both between resource users and managers but also among fish landing communities. We evaluated and explored potential causes of this heterogeneity in perceptions and used this information to recommend future management plans. In this context, we were interested in examining how different types of hypothetical management options, including restrictions on time, size, gender, species, gear, and effort, would be viewed by resource users and managers and if these views could be predicted by their perceptions of who benefits from the management and their education, history of management, and their economies.

Specific goals included the following where biodiversity refers to the taxa described above:

- 1) Determine the differences in biodiversity on exposed windward and sheltered leeward sides of reefs and small and large islands.
- 2) Determine if there are gradients in biodiversity associated with these differences in environments along the African coastline along a latitudinal gradient and from coastline to oceanic sites.
- 3) Determine if there are differences in the functional categorization of this biodiversity along the above gradients.
- 4) Determine the distribution of high temperature tolerant types of *Symbiodinium* along this gradient, and determine associations between environmental variability and their distributions.
- 5) Determine the gross management preferences of the resource users and managers in each of the study sites.
- 6) Determine the role of local management on biodiversity by comparing fisheries closures and fished management treatments in each of the study areas.
- 7) Identify sites with high potential to survive climate change effects and suggest management interventions.

Literature review

Ecological studies

Preliminary use of gradients in the western Indian Ocean region have focused on the windward-leeward sides of the island of Mauritius (McClanahan *et al.* 2005d), a gradient along the East African coastline (McClanahan *et al.* 2007a), and the islands of Madagascar (McClanahan *et al.* 2009b). These studies suggest that currents and geography influence windward-leeward gradients and that water temperature variation rises and that this may result in fewer anomalous temperatures and adaptation to anomalous temperature (Ateweberhan and McClanahan 2010). The prediction for biodiversity is that windward sides of islands will have stable environments that promote high taxonomic diversity but that they will also have lower acclimation to environmental variability than leeward sides of islands and reefs. Windward sides are expected to be more susceptible to rare environmental disturbances than leeward sides of islands and reefs. Additionally, fishing is likely to further influence this interaction by reducing biodiversity and increasing taxa adapted to disturbance (Darling *et al.* 2010; Graham *et al.* 2011). Here, we combine and analyze a large database on the benthic communities in the Western Indian Ocean to develop a synoptic view of the biodiversity and resilience in response to climate change, habitat, human resource use, and environmental gradients. A number of the above hypotheses were tested on a regional scale where 170 coral reef sites were sampled using the same methods and observers.

Symbiont studies

The study of the symbiotic algae of reef-building corals has accelerated greatly in the past decade and is providing a basis for understanding acclimatization and adaptation of reef corals to climate change. It is now clear that the genus *Symbiodinium* is exceptionally diverse and consists of eight major clades, A-H, (Pawlowski *et al.* 2001; Pochon *et al.* 2001; Baker 2003). Members of five of these clades (A, B, C, D and F) have to date been documented in scleractinian (stony) corals. Many scleractinian corals are relatively flexible in the types of symbionts they can contain but one type is usually dominant in any given species and environment (Rowan and Powers 1991, Lajeunesse *et al.* 2003). Because reef corals are known to

associate with diverse algal symbionts and, in many cases are able to switch or shuffle these symbionts in response to environmental change (Rowan *et al.* 1997; Rowan 1998; Baker 2001; Baker 2003; Little *et al.* 2004), the facility with which these changes are reflected in the coral reef communities of the Western Indian Ocean was investigated. In particular, one type of symbiont (in *Symbiodinium* clade D), which appears to be unusually resistant to high temperature stress, was predicted to have become more abundant on these reefs following the 1997-98 El Nino (Baker *et al.* 2004). This project aimed at investigating and monitoring the abundance of this symbiont region-wide and contributes to an accumulating database on symbionts in this region.

Most studies of symbionts in the western Indian Ocean region have found a high dominance of clade C *Symbiodinium*, particularly in the cooler southwestern Indian Ocean region (MacDonald *et al.* 2008; Ruiz Sebastian *et al.* 2009, Lajeunesse *et al.* 2010), similar to the dominance of clade C found in the wider Indo-Pacific (Lajeunesse *et al.* 2003, 2004; Lajeunesse 2005). However, clade D *Symbiodinium* is frequently found in higher abundances in marginal regions, such as shallow Kenyan reefs, the Persian Gulf and the far eastern tropical Pacific (Baker *et al.* 2004). Clade D is also found at low levels in local areas of high temperature (Fabricius and van Oppen 2004), in various coral hosts at low levels (Corea *et al.* 2009a; Mieog *et al.* 2009), and can increase in dominance across temperature disturbances in some taxa (Jones *et al.* 2008; Lajeunesse *et al.* 2009; Mieog *et al.* 2010).

The fidelity of symbiont associations varies by coral taxon and the potential for change from one symbiont community to another, such as a change in dominance from clade C to clade D (Lajeunesse *et al.* 2004, 2010). Alternatively, conditions promoting shifts from one symbiont community to another may not yet have been reached on most reefs (Baker *et al.* 2004; Oliver and Palumbi 2009). Consequently, *Symbiodinium* in clade C may still represent optimal symbionts for the contemporary oceanographic conditions and temperatures on many Indo-Pacific reefs, particularly since they may be associated with faster coral skeletal growth rates than clade D (Jones and Berkelmans 2010). Some investigators consider members of clade D to be opportunistic taxa that colonize corals recovering from bleaching (Lajeunesse *et al.* 2009), but this association has not been found for infectious coral diseases (Correa *et al.* 2009).

Clade D may, however, offer corals some advantages or tolerance to unusually warm conditions, for example, and slower growth may increase survival in stressful warm temperature environments (Berkelmans and van Oppen 2006; Jones *et al.* 2008; Jones and Berkelmans 2010). Consequently, it is hypothesized that coral colonies can shuffle a diverse portfolio of symbionts or acquire novel symbionts from the environment that may perform better over disturbances and climate warming than those species that cannot (Buddemeier *et al.* 2004).

Management preferences and socioeconomic studies

Management informed primarily by natural science investigations seldom considers local and immediate social costs but considers the larger spatial and temporal scale of ecological benefits. These ecological benefits occur at the scale that educated technicians and managers, often employed at regional or national levels, perceive and value benefits (Hicks *et al.* 2009). Conversely, extractive users frequently perceive local and short-term costs and benefits from restrictions. These differing scales of perceived benefits can influence whether and how people engage in and comply with management measures (McClanahan *et al.* 2008; Thomassin *et al.* 2010). Resolution of these psychological, economic, and governance challenges of co-management of common-property resources holds promise for achieving higher compliance for sustainable resource use (Gutierrez *et al.* 2011).

What then are the factors that lead to divergent perceptions about management? Previous evaluations have shown that education, agriculture and salaried employment alternatives, and history of co-management, education and interactions with managers can be critical (Gelcich *et al.* 2009; McClanahan *et al.* 2005b; 2008). Restrictions that are perceived to benefit government or business elite as opposed to resource users (what is referred to as 'elite capture') are expected to lead to weak support (Christie 2004; Béné *et al.* 2009). Therefore, conflicts over marine resources can arise because of the heterogeneity in perceptions driven by perceived disparities in benefits (Béné *et al.* 2009). Identifying the specific restrictions that lead to higher degrees of perceived elite capture, and whether these are related to specific socioeconomic contexts assist the planning, research, management, awareness, and education needs.

Historical conflict between local social traditions and norms and legislated national-level management are common in Africa and the Indian Ocean (Béné *et al.* 2009; McClanahan *et al.* 1997; 2005e; Walley 2004). In some instances, participatory processes have reduced or resolved conflicts while in other instances they have stalled or failed to find solutions (McClanahan 2007; Walley 2004; Wells *et al.* 2010). For example, Kenyan national laws prohibit the use of pull seine nets and spearguns but an estimated 60% of fishers actively use these illegal gears (McClanahan *et al.* 2005c). Conversely, some fishing communities that adhere to traditional management see these nets and other gear and forms of management as “against tradition” but have had difficulties getting both local fisher and government support for their local rules (McClanahan *et al.* 1997). This has created a heterogeneous, fractioned, and often polarized management system that can often differ from place to place based on the interactions of various formal and informal organizations, power, and economic incentives at specific fisheries grounds (McClanahan 2007).

Methodology

The work presented here combines specific field studies supported by the WIOMSA grant combined with database that has been slowly developing over the course of the investigators studies, which in many cases exceeds over 100 study sites, depending on the particular metric used (Table 2). Below are some of the specific study sites evaluated as part of this grant but

many of the results presented here are part of a large database of sites where the specifics of the study sites will require examining specific papers. The results present the larger regional analyses that have been completed by the time of the writing of this report.

Study sites

Kenya

Field studies of fishing communities and resource managers were undertaken in 22 fish landing sites distributed along the entire Kenyan coastline, from the Lamu Archipelago in the north near the Somali border to Shimoni in the south near the Tanzanian border. The fish landing site communities were usually composed of groups of ~10-100 fishers who fished in nearshore mangrove, seagrass, and coral reef ecosystems using traditional handmade canoes, sailboats, various gear (lines, traps, spears and various nets) and landed their catch in a shared beach landing site. Some resource managers were interviewed in field situations but also in the local or regional offices of the park service (Kenya Wildlife Service) and the Fisheries Department. Many of the southern Kenyan sites have been part of long-term ecological monitoring work described in many papers (McClanahan 2008) whereas the northern Kenya sites in Kiunga were added during this study period.

Kiunga, Kenya

Five study sites were surveyed within the approximately 200 km² Kiunga Marine National

Table 2. Number of sampled sites in each country by period, management and exposure.
Period 1: 1994-1997; period 2: 1998-2003; period 3: 2004-2009.

		Benthic composition				Coral taxonomic composition				Bleaching surveys			
		Sheltered		Exposed		Sheltered		Exposed		Sheltered		Exposed	
Country	Period	Closure	Fished	Closure	Fished	Closure	Fished	Closure	Fished	Closure	Fished	Closure	Fished
Kenya	1	5	4	0	0	3	3	1	0	0	0	0	0
	2	3	4	0	0	3	3	1	0	0	0	0	0
	3	5	11	0	3	9	7	5	0	6	6	1	0
Madagascar	3	1	6	1	3	8	3	3	1	2	4	6	5
Maldives	3	0	11	0	0	0	0	0	0	0	2	0	2
Mauritius	3	3	8	1	3	6	1	3	1	1	2	1	3
Mayotte	3	0	0	0	0	0	0	0	0	2	1	0	4
Mozambique	3	5	4	1	1	4	1	1	1	3	5	1	8
Seychelles	1	0	0	9	12	0	0	0	0	0	0	0	0
	2	0	0	4	0	0	0	0	0	0	0	0	0
	3	0	0	9	12	0	0	0	0	0	0	3	2
South Africa	0	0	0	0	0	0	0	0	0	0	0	2	0
Tanzania	1	4	7	0	1	6	5	1	0	0	0	0	0
	3	4	14	1	2	11	7	2	1	2	6	1	2

Reserve (KMNR) that lies in the Bajun Archipelago at the northern extreme of the Kenyan coast, bordering Somalia. Gazetted in 1979, KMNR is a priority site in the World Wide Fund for Nature (WWF) Eastern African Marine Ecoregion (WWF, 2001). It extends over some 50 km in length by 3–5 km in width (from about 1°42.25'S 41°31.78'E to 2°2.58'S 41°14.80'E) with the area being characterized by a linear series of barrier islands sheltering extensive mangrove stands in the protected lagoons, large areas of seagrass on rocky substrates on the shallow outer fringing reefs, and a series of patch and fringing coral reefs around the barrier islands and on the offshore rocky rock reef (Obura 2001). Biogeographically, reefs in the area have been reported to have lower species diversity than those farther south (Yaninek 1976, 1978, McClanahan 1990) and are transitional with coral reefs on the southern Somali coast and the upwelling system to the north (Carbone and Accordi 2001). Of the five study sites, three (Coral Garden, Mlango wa Muhindi and Boso) were of low flow with the latter site being a high fishing pressure site and the others experiencing low fishing pressure. Shimo la Tewa and Kui were both recorded as high flow habitats with the latter being a low fishing pressure zone.

Mafia Island, Tanzania

Mafia Island is a chain of small islets centered at 7.40° S and 39.41° E and located 20 km off the Tanzanian coastline east of the Rufiji River delta. Mafia District comprises an area of 972 km², of which 407 km² is dry land and 565 km² is seawater. Approximately 40,000 people live in the district (United Republic of Tanzania 2003, 2006) mostly within 20 villages. Mafia District is ~120 km southeast of the capital city Dar es Salaam, and trade is closely connected to the capital by boat traffic through a pier located at Kilindoni. The island is Pleistocene reef covered by a sandy loam, and rainfall is moderate, monsoonal and varies inter-annually. People largely depend on agriculture, notably coconuts, husbandry, artisanal crafts and fishing, but also tourism and trade with the capital (Caplan 2002). Local agriculture does not provide sufficient food, and food is therefore imported also from the mainland. Generally, fishing activities in Mafia Island are artisanal and mainly concentrated on inshore waters, and there is a surplus of fish that is exported to the mainland. The main reasons for shallow sea fishing are low travel costs and a lack of capital to purchase larger fishing vessels to engage in deep-sea fishing.

Six villages were surveyed for management preferences and socioeconomic information. Three of these (Bweni, Tumbuju and Mfuruni) are located on the main Mafia Island outside MIMP, and were not included in the 11 villages involved in the original community workshops and consultative meetings held by the Park from 1991 onwards. The three villages within MIMP that were included in the original village workshops and consultative meetings include Miburani on the western side of the main island, while Juani and Jibondo are located on small islands. Of the six villages studied, Jibondo is located on fossilized coral rock where crop farming and animal husbandry are unreliable and all non-marine food must therefore be imported from outside the village. Villagers in Jibondo conflicted with the Park management in 2001 when there was disagreement and arrests over establishing Kitutia Reef as a closed area, which was relied on by villagers for net and octopus fishing. Since that time, Jibondo has been one of the villages that do not follow Park regulations.

Vamizi Islands and Pemba Bay, Mozambique

Field surveys were conducted at three fished study sites in the coastal town of Pemba, and four sites at Vamizi Island, northern Mozambique. Of the study sites at Vamizi, two ecological study sites were within the closed area (i.e. Light House Point and Kisirwa Nkunga) and two sites in the fished reefs, namely Pangapanga and Pangapanga Point. Vamizi Island, located north of the Quirimbas Archipelago, is approximately 12 km long and 2 km wide with its main axis lying east to west (Davidson *et al.* 2006). The western-most tip of the island lies approximately 4 km from the mainland, across a shallow, deltaic system of mudflats and mangroves. The island appears to be an ancient uplifted patch reef of Pleistocene origin, surrounded by a submerged reef flat with broad 'terraced' reef slopes. The area has a complex bathymetry, rising shoals and variety of reef shapes, suggesting that the present structure may have been formed by a combination of local tectonic activity and global sea-level change (Davidson *et al.* 2006). Field studies were undertaken in October 2008.

Machangulo, Mozambique

Field surveys were carried out at two carbonate reefs at Inhaca and a mix of sites sandstone reefs ranging from the offshore Baixa reefs in the north to the Ponto Malongane sites in the south. The carbonate

reefs of Berreira Vermelha and Ponta Torres (adjacent to Inhaca) are, in fact, the most southern carbonate reefs in Africa at 26°S and only have similar low-latitude representatives in the Toliar reefs of southwest Madagascar. The Toliar reefs have been badly damaged in recent years due to a combination of climate and human disturbances. Coral cover, in these reefs, has been reduced to around 10% of the substratum, coral diversity is low, and large erect algae now dominate most reefs (McClanahan *et al.* 2009b). The experience in Toliar may suggest that the ecological condition of these isolated low-latitude carbonate reefs in Mozambique are of considerable conservation concern given their unique position and also the unique efforts to protect them by the University Eduardo Mondlane.

Nosy Tanikely Marine Reserve, Madagascar

Field surveys were carried out in the Nosy Be region of northwestern Madagascar. Two study sites were included within the Nosy Tanikely marine reserve (i.e. Tanikely 1, leeward and Tanikely 2, windward) and two sites in unmanaged reefs on the shorelines or nearshore islands of Nosy Be, namely Nosy Sakatia and Nosy Ambaritelo. Nosy Tanikely is a small island surrounded by a coral reef with a total area of ca. 1 km² and was declared a marine reserve in 1968 (Arrêté 4730 Journal Officiel 2232, 30 November 1968). Sakatia and Ambaritelo are both islands near small fishing villages and fishing was commonly observed at these sites. About 7-30% of the population are fishers and they do not consume most of their fish (Salimo and Gisele 2003). We studied shallow (<5 m deep at low tide) hard bottom areas that were formed from living and dead coral. Field studies were undertaken in March 2007.

Mayotte, France

We investigated coral reef communities at 19 sites around the island of Mayotte. Sites differed in fisheries management; seven sites were located within three national marine reserves and classified as closures (areas that are permanently closed to fishing). The remaining eleven sites were located in areas that are open to fishing and classified as open access. At each site, we also recorded the depth of the survey (m) as an indication of reef position and wave exposure. Sites occurred along a depth gradient from 1.5 to 20 m (mean \pm standard deviation: 8.7 \pm 5.2 m). The seven wave-exposed sites outside the barrier reef were deeper than the 12 less exposed sites inside the lagoon (outside sites, mean \pm SEM: 12.4 \pm 1.7 m; inside sites: 6.5 \pm 1.3 m).

Field methods

Field methods used included standard methods that have been used by WCS in the region since 1987 and described in detail in many publications (McClanahan *et al.* 1999). A brief description of these methods is provided below.

Ecological studies

Benthic and coral community studies

Benthic substratum functional groups and hard coral community structure were examined using standard line-intercept transects method (McClanahan and Shafir 1990) and relative abundance of the different coral genera and their health was estimated using search-sampling procedure (McClanahan *et al.* 2007b). The line-intercept method was based on 6 haphazardly placed draped 10 m line transects where all benthic substratum with cover greater than 3 cm were classified into 9 gross functional groups (hard coral, turf algae, calcareous algae, fleshy algae, coralline algae, sponge, soft coral, seagrass and sand) and their lengths measured to the nearest cm. Percentage cover was calculated based on the sum of each category divided by the total of substratum measured.

Search sampling was undertaken in all sites whereby observations were made in shallow (<3m) field sites while snorkeling for ~40 min period to observe their state of bleaching and the presence of diseases. Observer swam with eyes closed in haphazardly chosen directions and distances and periodically or haphazardly opened eyes and sampled the areas directly below. All hard coral colonies within ~2 m radius beneath the observer were identified to the genus and counted. Their bleaching state was determined on a scale from normal, pale, to various percentage of the surface bleached white. Any diseases were identified and noted. These observations were used to determine the health of the corals and also to estimate how susceptible the sites were to climate disturbances based on the relative abundance of the corals (McClanahan *et al.* 2007b).

Fish surveys

Fish numbers and wet weight estimates were quantified using 1 or 2 replicate 500m² belt transects per site (McClanahan 1994; McClanahan and Kaunda-Arara 1996). Wet weight and numbers estimates were then made by classifying each individual encountered in transects to the

family, estimating its length, and placing it into 10 cm size-class intervals, up to >80 cm and with no individuals less than 3 cm in length recorded. Data were collected and placed in 23 families and 1 group of 'others', if the individual was not a member of those pre-selected 23 families. Wet weight per family was estimated from length–weight correlations established from measurements of the common species in each family taken at local fish landing sites in Kenya (McClanahan and Kaunda-Arara 1996).

Symbiotic algae studies

Coral tissue samples were removed from source colonies using a hammer and a hollow steel punch to remove a core approximately 5mm deep and approx. ~0.5cm² in area. These biopsies are relatively non-destructive, and tissue typically re-grows over sampling scars within a month or so. Approximately 200 samples were collected from each country (1400 samples total over a 2-year period), focusing on the most abundant shallow-water (<7m) coral taxa across all sites to ensure meaningful comparisons. The exact sampling design depended on coral species composition in each country and site, but aimed at collecting ~35 samples from each of 6 locations in each country. At each site at least 5 colonies each of 5-7 cosmopolitan species were sampled. The depth of each coral sample was recorded, and samples transported to the surface in labeled zip-lock bags and preserved in 5mL vials containing 2-3mL saline DMSO or 95% ethanol. Racked samples in numbered vials were then sent for DNA analysis to the Baker lab at the University of Miami, USA. Scleractinian corals are listed under CITES Appendix II, and permits to export these samples were obtained from the appropriate government agencies.

In University of Miami laboratories, samples were processed by airbrush-blasting tissue from samples and extracting DNA from these tissues. *Symbiodinium* DNA was then purified and analyzed using established molecular methods in routine use in the Baker lab: Total DNA was extracted using conventional organic protocols (Rowan and Powers 1991) Baker *et al.* 1997), and Internal Transcribed Spacer-2 (ITS-2) ribosomal DNA of *Symbiodinium* was amplified using PCR and Denaturing Gradient Gel Electrophoresis (DGGE) used to analyze these amplified products (LaJeunesse 2001; LaJeunesse 2002) and distinguish mixed symbiont communities. Novel symbiont types were sequenced and

phylogenetically compared to a Genbank-archived database that currently comprises >100 distinct *Symbiodinium* taxa. These methods give results of high taxonomic resolution.

Within each study site the long-term water temperature patterns (mean, SD, skewness, and kurtosis) trends (annual rate of change, rate of change of ENSO years) and water flow measures were evaluated for patterns with community composition and diversity of corals and algal symbionts. Water temperature from various sources, namely Hadley, NOAA satellite, and JCOMM, and *in situ* recordings were used in the analyses.

Management preferences and socio-economic studies

Villagers and managers were interviewed in over 73 fishing villages in the region to elicit (1) their preferences for management, (2) their perceptions of who benefits from existing management measures, (3) reasons for the impacts and conflicts around management and (4) personal and household socioeconomic information. Villagers were asked to list and rank their household's occupations and, if they fished, to rank the importance of the gear they use. Managers were asked to identify their affiliation and job rank. Heads of household were interviewed, usually at their homes, but sometimes at landing sites during non-fishing days as they repaired fishing gear and vessels. To avoid bias every nth person or household was sampled where n was determined by size of the village, such that similar sample sizes were obtained for each village (~30 samples per village).

Interviewees were presented with questions and statements about six different management options, namely (1) area management, (2) spatial closures, (3) seasonal closures, (4) management of gear, (5) limits on size of fish captured and (6) limits on species caught, and asked to mark their level of agreement with these statements on a five point Likert scale from strong disagreement to strong agreement, with a 'don't know' option (six options in total) (McClanahan *et al.* 2005b,c). Questions were structured as such: 'do you believe that area management is a good way to sustain fisheries in this location?' where area management could be replaced by the various restrictions.

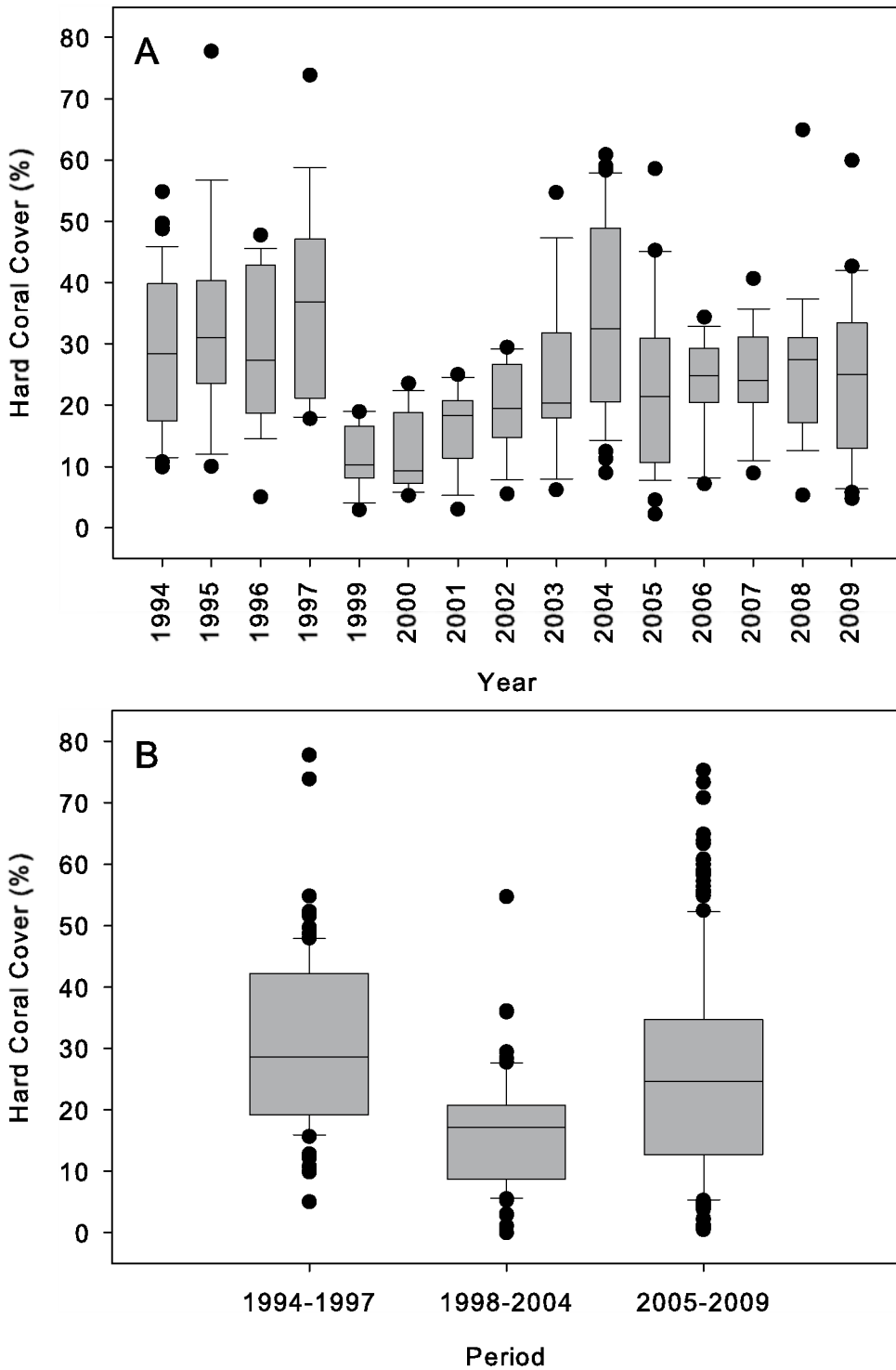


Figure 2. Temporal change in stony coral cover. A) Kenya; B) the whole region. Periods were: Period1: 1994-1997; period 2: 1998-2000; period 3: 2004-2009. Box: 25-75% percentiles; Horizontal bars: 2.5%, median (50%), 97.5% percentiles. Years before 1977 not presented due to small sample size and low regional representation. See Table 2 for sample sizes during each period.

Secondly, they were asked to scale their perceptions of benefits of six management options and who they perceived to benefit from each of these various management options, where three groups were identified, namely themselves, their community and the national government (10 point scale from 0 = no benefit to 10 = greatly benefits). They were also asked to state their reasons for the management preferences. These answers were grouped by their content and then tallied and presented if > 30% of the respondents in a village mentioned the same causative factor. Respondents were also asked about fishing gear that they believed should be restricted. Respondents were then asked to scale their perception of the need to restrict it by marking an 'x' along a 10-cm line with a low need to restrict it represented at one end and a high need to restrict it represented at the other end. The actual distance of the respondent's mark from the low end was treated as a Likert scale score.

Socioeconomic questions included fisher's typical biweekly expenditures, number of employed people and type of occupations among their household members, and the ownership of 33 material items. To further reduce the indicators and to develop a single material style of life index, we ran principal component analysis (PCA) based on the remaining material items. We performed several iterations of the PCA, removing items with low frequencies and weak loading scores. The resultant PCA scores were then used as a material style of life index in the analyses of respondent questions. The respondent was asked to provide

personal information, including age, gender, level of education, years in their current occupation and area of origin. The relative importance of each occupation was determined by having the respondent rank the occupations that their household undertook from least to most important.

Results

Ecological studies

The regional overview

Hard coral cover

Cover of stony corals was the highest in sheltered fisheries closures in period 3. It was lowest in period 2 in both exposed closures and fished reefs (Table 3). ANOVA results showed significant effect of period, its interaction with management, and the interaction between exposure and latitude (Table 4). In fisheries closures, coral cover was lower in period 2 than in periods 1 and 3 ($F = 6.29$; $p = 0.003$). There was no significant by period difference in the fished reefs ($F = 1.89$; $p = 0.16$). Comparison of exposed and sheltered reefs showed a significant difference only for period 3 when sheltered reefs had a higher cover than exposed reefs ($F = 25.26$; $p < 0.0001$). In both exposure types, period 2 had lower cover than periods 1 and 3 ($p < 0.005$). Comparison between fished and fisheries closures showed that closures had larger cover in exposed reefs in period 1 ($F = 6.97$; $p = 0.002$).

Table 3. Cover of major benthic functional groups at two exposure and management types for the three periods.

	Period Exposure Mgt N	Period 1				Period 2				Period 3			
		Sheltered Closure		Exposed Fished		Sheltered Closure		Exposed Fished		Sheltered Closure		Exposed Fished	
		9	11	9	13	3	4	4		18	54	13	24
Hard coral	Mean	37.53	33.85	36.31	23.28	10.96	10.37	6.00		39.01	34.09	14.01	18.23
	SEM	6.82	5.50	4.16	2.93	1.42	3.13	3.96		4.05	2.62	4.39	3.72
Turf algae	Mean	28.98	40.03	.	25.20	52.32	49.77	.		29.54	36.52	36.01	29.12
	SEM	4.69	3.35	.	.	1.21	2.15	.		1.84	2.29	6.19	3.96
Calcareous algae	Mean	2.91	0.30	.	0.00	4.65	0.66	.		1.39	0.89	0.04	1.21
	SEM	1.78	0.14	.	.	3.85	0.37	.		0.77	0.29	0.04	0.51
Fleshy algae	Mean	11.21	3.94	0.44	3.40	11.17	15.24	0.00		6.18	8.17	8.76	15.15
	SEM	4.71	1.74	0.23	1.85	1.38	5.73	0.00		2.34	1.70	3.88	4.07
Coralline algae	Mean	5.83	6.50	.	4.25	12.74	2.03	.		13.78	11.01	19.83	12.60
	SEM	1.24	2.14	.	.	3.52	0.59	.		3.01	1.03	7.32	2.48
Seagrass	Mean	2.71	4.41	.	0.00	2.07	12.48	.		0.58	1.40	0.03	0.16
	SEM	1.02	1.77	.	.	0.24	2.37	.		0.49	0.46	0.03	0.16
Soft coral	Mean	3.37	2.82	2.18	12.01	1.04	0.39	0.00		3.21	2.09	1.25	3.89
	SEM	0.98	0.65	1.79	2.73	0.59	0.14	0.00		1.23	0.49	0.63	1.41
Sand	Mean	7.26	7.80	9.53	6.69	4.88	8.38	11.58		5.51	5.29	9.60	3.59
	SEM	2.92	2.01	2.97	3.02	2.21	0.37	5.01		1.50	0.93	3.48	1.23
Sponge	Mean	0.19	0.34	.	0.27	0.18	0.68	.		0.79	0.53	0.29	0.48
	SEM	0.06	0.08	.	.	0.18	0.23	.		0.39	0.21	0.12	0.18

Table 4. Summary of Analysis of Variance on benthic functional groups by period, management, exposure, latitude and their main interactions. Missing values were due to lack of data on some functional groups for Seychelles.

Benthic category	Source	Time periods	Management	Exposure	Latitude	Per*Mgt	Time*Exp	Time*Lat	Mgt*Exp	Mgt*Lat	Exp*Lat
Hard coral	ANOVA F =	9.63	7.15	7.50	8.05	6.18	5.91	4.48	0.04	1.26	5.04
	P <	0.00	0.01	0.01	0.01	0.01	0.02	0.04	0.85	0.26	0.03
Turf algae	ANOVA F =	.	0.03	.	0.33	0.55	.	0.20	1.20	8.38	0.01
	P <	.	0.86	.	0.57	0.58	.	0.82	0.28	0.00	0.94
Coralline algae	ANOVA F =	.	0.07	.	11.83	0.00	.	8.87	1.57	4.38	0.97
	P <	.	0.79	.	0.001	0.97	.	0.001	0.21	0.04	0.33
Fleshy algae	ANOVA F =	1.17	1.62	0.36	0.05	0.16	2.02	0.24	1.10	9.13	1.94
	P <	0.28	0.21	0.55	0.82	0.69	0.16	0.63	0.30	0.001	0.17
Calcareous algae	ANOVA F =	.	1.01	.	0.80	0.32	.	1.74	0.74	1.92	1.20
	P <	.	0.32	.	0.37	0.57	.	0.19	0.39	0.17	0.28
Seagrass	ANOVA F =	.	3.91	.	20.10	4.51	.	19.46	0.02	0.00	0.07
	P <	.	0.05	.	0.0001	0.04	.	0.0001	0.90	0.99	0.79
Soft coral	ANOVA F =	0.65	6.54	3.12	0.01	3.93	5.12	0.05	10.88	0.28	0.01
	P <	0.42	0.01	0.08	0.93	0.05	0.03	0.82	0.001	0.60	0.93
Sand	ANOVA F =	0.81	0.65	0.21	1.84	0.49	1.06	1.73	2.07	0.52	3.02
	P <	0.37	0.42	0.65	0.18	0.49	0.31	0.19	0.15	0.47	0.08

Coral cover generally decreased northward with latitude and the decrease was stronger in exposed than sheltered reefs (significant interaction between exposure and latitude; Table 4). A separate analysis for period 3 when data was most complete indicated significant effect of exposure and latitude and the interaction between them ($p < 0.02$). Sheltered reefs had higher cover than exposed reefs. Cover decreased northward and the decrease was stronger on exposed reefs.

Algae

Fleshy algal cover was highest on exposed fished reefs in periods 2 and 3 (Table 3) and significantly affected by management and latitude (Table 4). The interaction between exposure and time was significant (Tables 3-4). Fleshy algal cover decreased northward on fished reefs ($F = 15.18$; $p = 0.0002$) but there was no effect of latitude for fisheries closures ($F = 1.34$; $p = 0.25$). A separate analysis for period 4 also indicated a significant

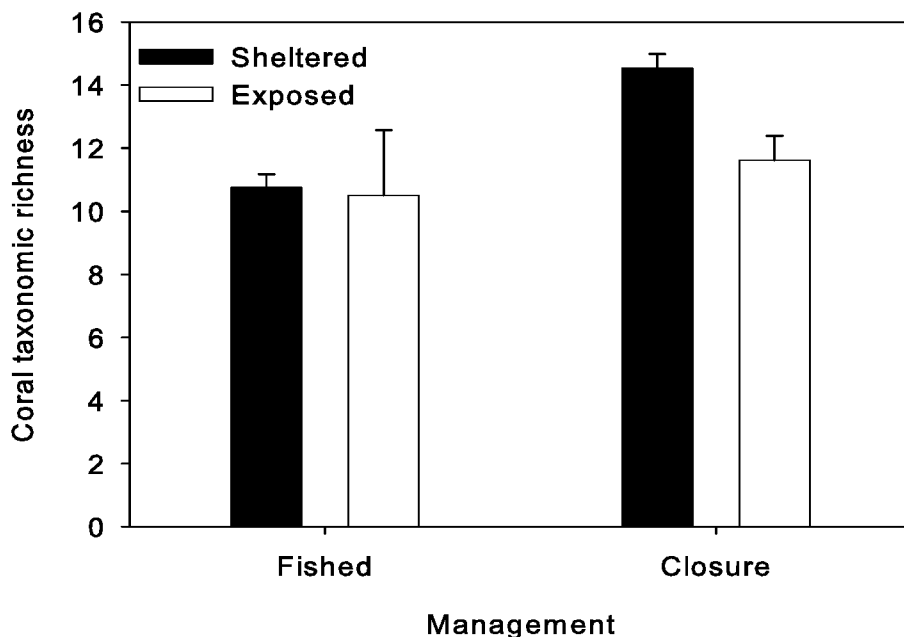


Figure 3. Relationship between coral taxonomic richness and management and exposure.

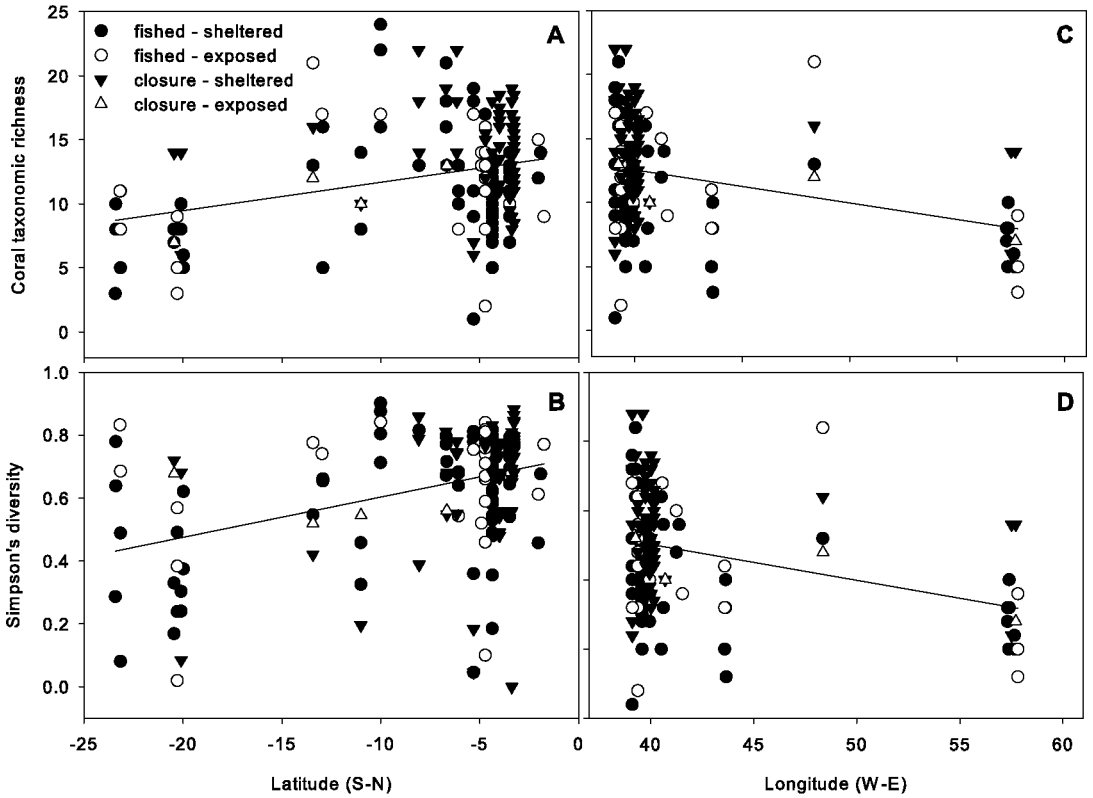


Figure 4. Relationship between coral species richness and diversity and latitude and longitude. A. Species richness-latitude: $R^2_{adj} = 0.22$; $F = 18.28$; $p < 0.0001$; $y = 0.22x + 13.88$; B. Diversity-latitude: $R^2_{adj} = 0.14$; $F = 32.36$; $p < 0.0001$; C. Species richness-longitude: $R^2_{adj} = 0.10$; $F = 20.39$; $p < 0.0001$; $y = -0.26x + 22.91$; $y = 0.01x + 0.73$; D. Diversity-longitude: $R^2_{adj} = 0.15$; $F = 33.93$; $p < 0.0001$; $y = -0.02y + 1.26$.

interactive effect of latitude and management ($F = 8.04$; $p = 0.006$) with fleshy algae decreasing northward on fished reefs ($F = 15.18$; $p = 0.0002$) while there was no effect of latitude on fisheries closures ($F = 1.34$; $p = 0.25$).

Coral diversity

Species richness did not vary with period and exposure ($p > 0.05$) but was higher in fisheries closures than fished reefs (Fig. 3; $F = 33.44$; $p < 0.0001$). Species richness increased northward with latitude and westward with longitude (Fig. 4). Multiple regression analysis indicated marginally significant interaction between management and exposure on species richness

patterns (Table 5). Separate, by management analysis, indicated that closures had higher species richness on sheltered areas but there was no difference in exposure levels on fished reefs (Fig. 3). Diversity, however, did not show any significant variation with management and exposure (Table 5). Diversity increased northward with latitude and decreased eastward with longitude (Fig. 4). Multiple regression analysis showed that period, its interaction with latitude and longitude, the interaction between management and latitude and longitude and the interaction between exposure and latitude had significant effects on diversity (Table 5).

Table 5. Summary of multiple regression models testing the effects of time period, management, exposure, latitude and longitude on coral species richness and diversity.

	Species Richness			Simpson's Diversity		
	R^2_{adj}	F Ratio	p	R^2_{adj}	F Ratio	p
	0.28	4.75	<0.0001	0.24	4.02	<0.0001
Source	F Ratio		p	F Ratio		p
Period	2.18		0.12	3.69		0.03
Management	3.09		0.08	1.13		0.29
Exposure	1.00		0.32	0.49		0.48
Latitude	0.09		0.76	1.50		0.22
Longitude	0.07		0.79	2.86		0.09
Period*Mgt	0.79		0.46	1.20		0.30
Period*Exposure	0.44		0.64	0.01		0.99
Period*Latitude	2.12		0.12	3.50		0.03
Period*Longitude	2.24		0.11	4.03		0.02
Mgt*Exposure	3.94		0.05	0.08		0.77
Mgt*Latitude	0.94		0.33	5.37		0.02
Mgt*Longitude	0.28		0.60	8.89		0.00
Exposure*Latitude	0.33		0.57	3.19		0.08
Exposure*Longitude	0.59		0.44	1.72		0.19

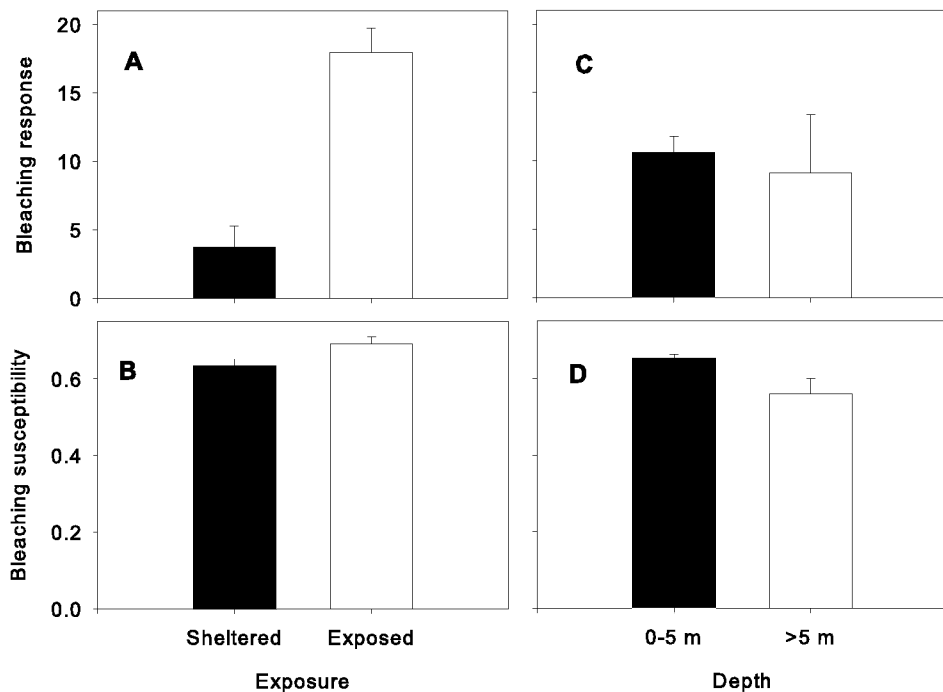


Figure 5. Variation in bleaching response and susceptibility by exposure and depth.

Table 6. Summary of multiple regression tests on the effects of management, exposure, latitude and longitude on bleaching response and bleaching susceptibility.

	Bleaching response			Bleaching susceptibility		
	R^2_{adj}	ANOVA F	p	R^2_{adj}	ANOVA F	p
	0.45	5.91	<0.0001	0.28	5.91	<0.0001
Source	F-ratio	p		F-ratio	p	
Depth	2.33	0.13		6.46	0.01	
Management	4.23	0.04		1.28	0.26	
Exposure	25.59	<0.0001		0.78	0.38	
Latitude	13.12	0.0005		19.60	<0.0001	
Longitude	4.18	0.04		0.01	0.92	
Management*Exposure	0.09	0.77		2.06	0.16	

Bleaching response and coral community susceptibility

Exposed areas of reefs had a higher bleaching response than sheltered areas ($F = 35.75$; $p < 0.0001$; Fig. 5); there was no effect of depth ($F = 0.15$; $p = 0.86$) and management ($F = 0.96$; $p = 0.33$). Bleaching response decreased northward but did not show any relationship with longitude (Fig. 6). Multiple

regression analysis gave significant effects for management, exposure, latitude and longitude - latitude having the strongest effect (Table 6). Coral community susceptibility was greater in deeper zones ($F = 5.87$; $p = 0.02$) and exposed areas ($F = 7.44$; $p = 0.008$) and decreased north- and eastward in the region (Fig. 6). Multiple regression analysis of the susceptibility metric showed only significant effects for latitude (Table 6).

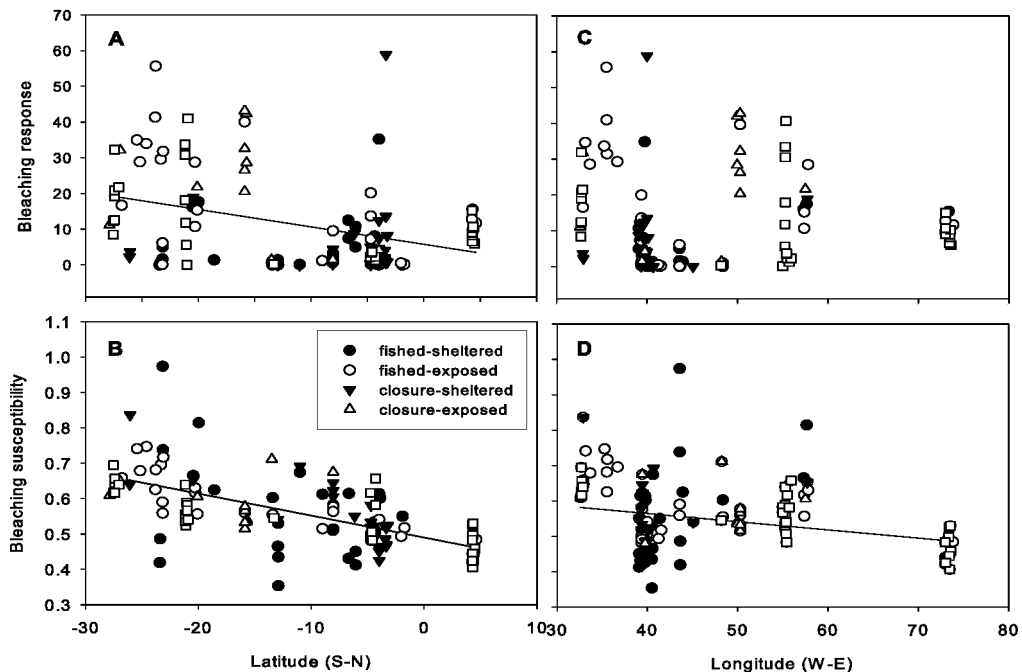


Figure 6. Relationship between bleaching response and bleaching susceptibility and latitude and longitude. A. Bleaching response-latitude: $R^2_{adj} = 0.21$; $F = 34.53$; $p < 0.0001$; $y = -0.59x + 3.79$; B. Bleaching susceptibility-latitude: $R^2_{adj} = 0.21$; $F = 33.45$; $p < 0.0001$; $y = -0.005x + 0.59$; C. Bleaching response-longitude: no significant relationship; D. Bleaching susceptibility-longitude: $R^2_{adj} = 0.03$; $F = 4.72$; $p = 0.03$; $y = -0.002y + 0.73$.

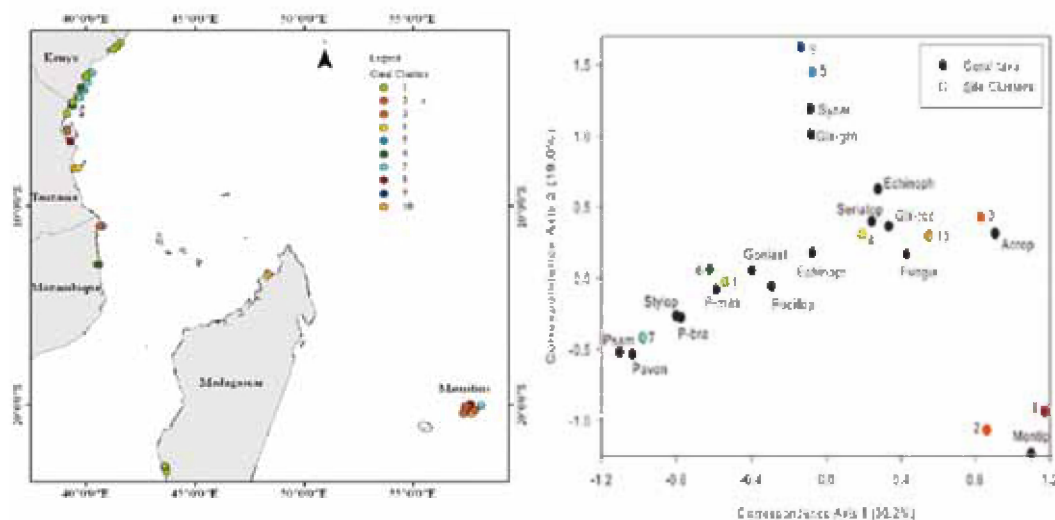


Figure 7. Multivariate analysis and the distribution of the coral communities in the western Indian Ocean.

Geographic distribution of the coral communities

Cluster analysis of the cover of the 12 most dominant coral taxa (with cover of >10% at any site during any period) by TWINSpan identified 10 cluster groups (Fig. 7). *Acropora*, *Montipora*, *Galaxea fascicularis*, *Synarea* and massive *Porites* were the most dominant coral taxa in a particular cluster. *Acropora* was most abundant in clusters 3 (Mauritius, northern Tanzania and the exposed side of Nosy Tanikely (NW Madagascar)).

Montipora was most abundant in cluster 8 along with *Acropora* (two sites in Mauritius and Mbudya before 1998) but also had high cover in cluster 2 (Mbudya and Watamu in period 1, Changale, Beantsy and Rose Garden in SW Madagascar in period 4). *Porites* branching was most abundant in cluster 7 on the fished reefs of southern Kenya and Mombasa before 1998 along with *Pavona*. *Porites* massive associated mostly with Mombasa after 1998 and Kiunga in northern Kenya, Ponta Maunhane and Baobab in Mozambique and Taa

Table 7. Summary statistics of temperature derived variables, PAR and mean UV by clade location, and tests of the relative contribution of each variable to the variability in clade distribution. Mean UV was not entered into the model because it did not meet the forward selection criterion of $P < 0.25$ during the stepwise regression.

Whole Model Test												
Model	DF		Chi-Square				R ² (U)				P	
Difference	18		428.5				0.11				<0.0001	
Clade	A		B		C		D		702			
Incidence	53		9		2211							
Variable	Entered	VIF	Mean	SD	Mean	SD	Mean	SD	Mean	SD	L-R ChiSquare	P
Mean SST	X	7.9	25.9	1.0	27.5	0.26	27.6	1.2	27.8	1.1	132.6	<0.0001
Skewness SST	X	5.0	0.1	0.2	0.0	0.12	0.1	0.2	0.1	0.2	69.6	<0.0001
SD SST	X	6.8	3.0	1.1	1.7	0.02	1.6	0.5	1.8	0.9	44.3	<0.0001
Mean PAR	X	3.1	46.0	1.8	47.0	0.0	47.1	2.5	47.6	2.5	29.7	<0.0001
Max SST	X	5.0	33.4	1.6	33.3	0.51	32.9	1.2	33.4	1.0	3.8	NS
Kurtosis SST	X	5.8	-0.8	0.4	-0.4	0.16	-0.3	0.5	-0.3	0.5	3.4	NS
Mean UV		5.9	230.4	19.7	272.0	1.32	262.9	20.0	263.6	16.4		

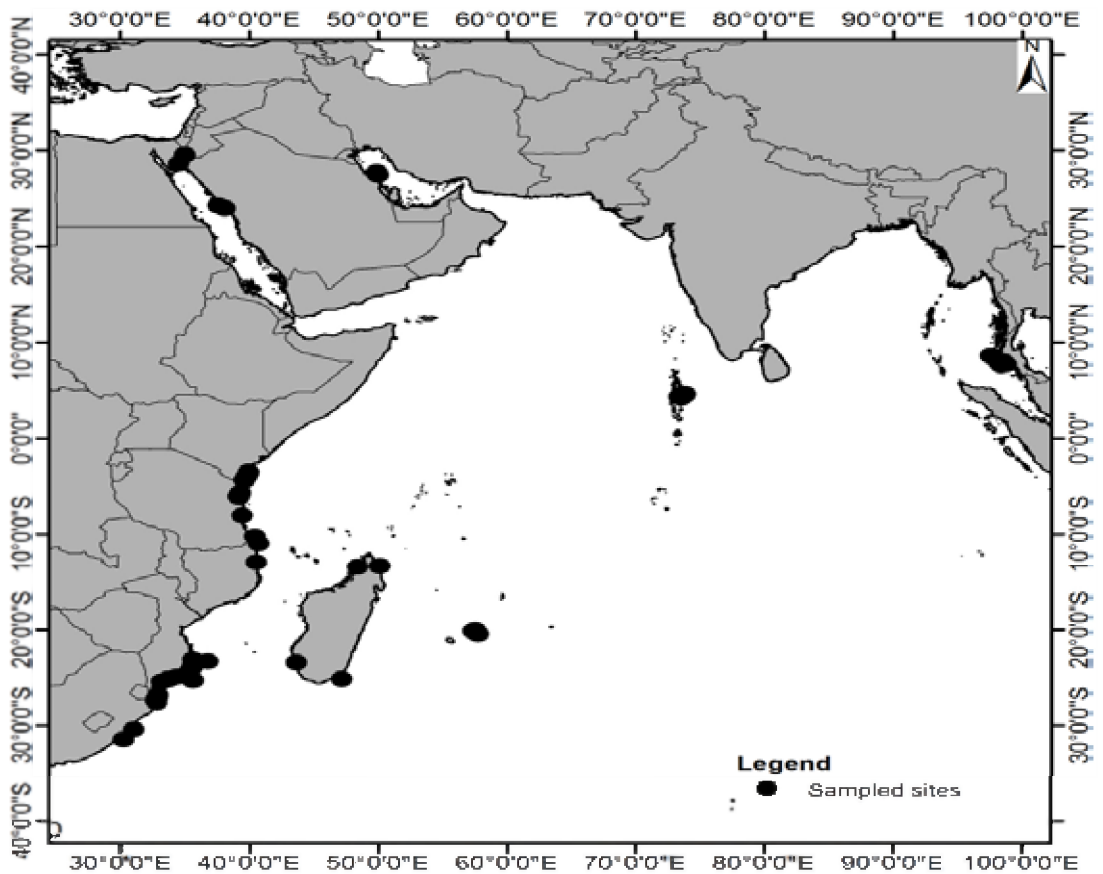


Figure 8. Distribution of *Symbiodinium* clades in the Indian Ocean using data collected in this project and data available in the published literature.

in Tanzania in cluster 6. *Porites* massive was also the most dominant taxon in cluster 1, composed of several reefs spread throughout the region. *Synarea* was associated with cluster 5, made of two fished reefs in Zanzibar (Changuu and Chapwani) and Nosy Ambaritelo, a high exposure site in NW Madagascar. *Galaxea fascicularis* dominated at Makome that formed its own cluster (cluster 9). It also had high cover in cluster 5 with *Synarea*. Cluster 4 was most common on reefs in northern Tanzania and not dominated by a particular taxon but with unusual amounts of *Seriatopora* and *Galaxea astreata*.

Symbiont studies

The regional overview

In total, there were 2975 incidences of *Symbiodinium* clades A-D in scleractinian corals from the combined studies in the Indian Ocean. Some samples were sometimes reported with two

clades, in which case the sample contributed an incidence score to each of the respective clades involved. Overall, there were 53 incidences of clade A (1.8%), 9 incidences of clade B (0.3%), 2211 incidences of clade C (74.3%) and 702 incidences of clade D (23.6%) (Fig. 8).

Symbiont niches

Stepwise multiple regression of all uncorrelated environmental variables found that SST mean, skewness and SD, as well as mean cumulative daily PAR, were significantly associated ($P < 0.0001$) with the incidence data for the four-clade *Symbiodinium* model (Table 7). The significance of the four-clade model was high ($P < 0.0001$) although its predictive power was relatively low ($R^2 = 0.11$). When the incidence data for each clade was analyzed separately, as presence/absence of each clade individually, multiple regression analysis found several significant factors that contributed to each model, but the factors differed among clades (Table 8). Mean PAR, mean UV

Table 8. Summary of results of multiple stepwise regression analyses showing significance level (P) and predictive power (R^2) of nominal logistic model for each of the response variables (*Symbiodinium* clade incidence). Also shown are the significant environmental variables contributing to the model for each clade, ordered by their frequency of contribution to the different response variables, and the R^2 value for multiple regression of the two principal factors in explaining *Symbiodinium* clade incidence. Blank entries indicate no significance.

Clade	A	B	C	D	All
R^2	0.27	0.56	0.06	0.17	0.11
Count	53	9	2211	702	2975
Whole model P	<0.001	<0.001	<0.001	<0.001	<0.001
Mean SST	0.06	<0.001	<0.001	<0.001	<0.001
Mean PAR	<0.001		<0.0008	<0.001	<0.001
SST SD			<0.001	<0.0003	<0.001
SST skewness		<0.001	<0.06		<0.001
Mean UV	<0.024	<0.002		<0.001	
SST kurtosis		<0.001		<0.001	
Max SST				<0.001	
PCA R^2	0.23		0.03	0.02	0.05

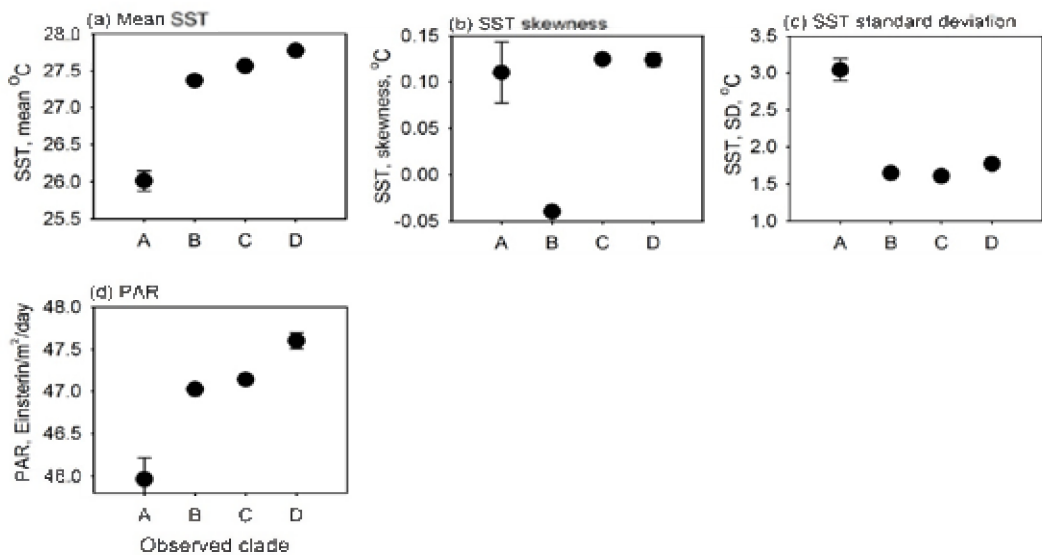


Figure 9. Scatter plots displaying mean ocean climate variables found to be significant in a multiple regression for all *Symbiodinium* clades. Error bars represent standard error of the mean.

and mean SST best explained the incidence of clade A ($R^2=0.27$). For clade B, these factors were mean SST, skewness, kurtosis and mean UV ($R^2=0.56$). Variability in clade C was not well explained by environmental variables ($R^2=0.06$), but significant factors were mean SST, SD, mean PAR and skewness. Clade D was best explained by mean PAR, maximum SST, kurtosis, UV, mean SST and SD ($R^2=0.17$). Scatter plots (Fig. 9) of the significant variables for each clade illustrate the environmental differences in the distributions of each clade in the Indian Ocean.

Temporal dynamics in Kenya

Symbiodinium clade C is the dominant clade in the study sites and over time, but clade D was the dominant in the poorly sampled years 2000 and 2010, but less abundant in the interim years (Fig. 10). Mixed communities of *Symbiodinium* C+D mix were found in low to moderate abundance in the early sampling years (2000-2004) but were uncommon afterwards. Clade C was most common in Mombasa, followed by Diani,

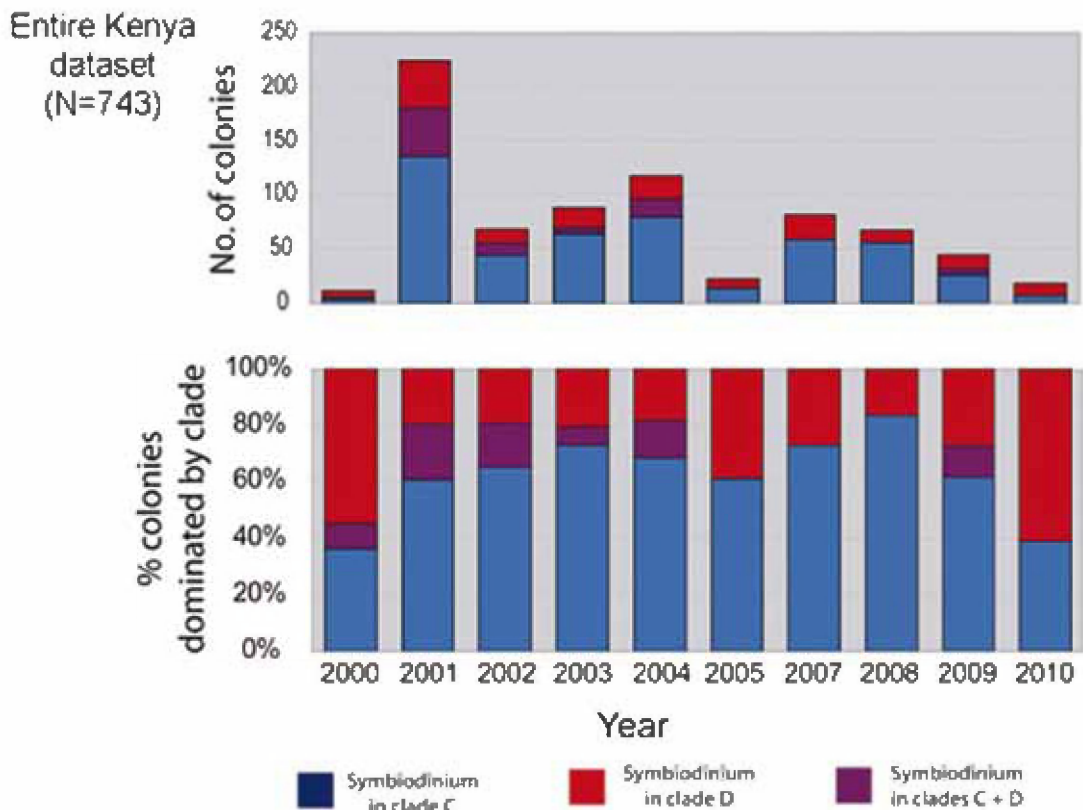


Figure 10. Distribution of *Symbiodinium* clades plotted for the 2000-2010 period pooling all sites and coral taxa.

Table 9. Results of the logistic model testing for the effects of taxa, site, and time on the frequency of the symbiont clade groups C, D, and C+D.

Whole Model Test				
Model	-LogLikelihood	DF	ChiSquare	P<
Difference	360.26	104	720.53	0.0001
Full		273.02		
Reduced	633.29			
R ² = 0.57				
N = 741				
Individual factors and interactions				
Source	DF	ChiSquare	P<	Conclusion
Genus	26	44.09	0.015	Significant effect
Site	8	0.00	1.0	Not significant
Year	2	0.00	1.0	Not significant
Genus*Site	50	83.59	0.002	Strong interaction
Genus*Year	12	19.32	0.081	Marginal
Site*Year	6	13.78	0.032	Weak interaction

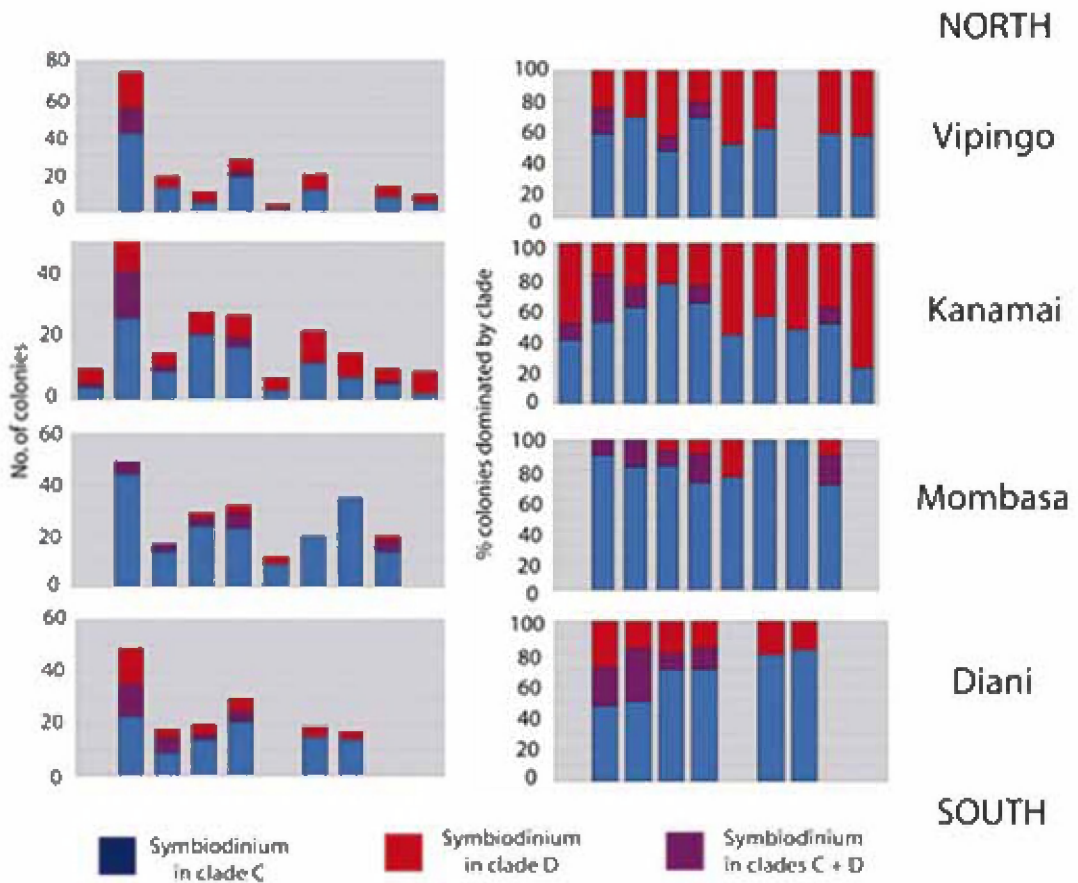


Figure 11. Distribution of *Symbiodinium* clades for the 2000-2010 period at five study sites pooling all coral taxa.

Vipingo and Kanamai (Fig. 11). Clade D was consistently found in more than half of the coral colonies in Kanamai. Clade C (specifically C15) was the dominant symbiont in *Porites*, with only one 2001 sample containing clade D.

When testing for differences between taxa (genus), site, and time separately, there were statistically significant differences among all the variables. However, when testing these factors simultaneously for all samples, genus was the most significant single factor ($P=0.015$). Genus interacted very strongly with site ($P=0.002$), site and year interacted weakly, and the overall model was relatively powerful ($R^2=0.57$) (Table 9). When reducing the analysis to the four dominant genera (*Acropora*, *Pavona*, *Pocillopora*, *Porites*), genus was again the most significant factor and interacted strongly with site ($P<0.0001$), site and year was marginal ($P=0.055$), and the power of all factors combined was also high ($R^2=0.54$) (Table 10).

Stepwise logistic regression of temperature variables with the frequencies of the clades revealed a number of significant but weak factors (Table 11). Temperature variables obtained directly from field gauges delivered significantly better predictive value than temperatures obtained from satellites, which were not significant. Mean temperature was not a significant predictor but most measures of temperature variation were significant. Maximum annual temperature in the year before sampling was the most significant factor in predicting symbiont distributions at the level of clade ($P<0.0001$), followed by minimum annual temperature in the year before sampling ($P=0.006$) and standard deviation of temperature in the year of sampling ($P=0.02$).

A nominal logistic fit of *Symbiodinium* clade for all sites and taxa pooled found that the maximum

Table 10. Testing effects of taxa, site, and time on the abundance of four dominant clades Results of the logistic model testing for the effects of taxa, site, and time on the frequency of the symbiont clade groups C, D, and C+D for only the dominant four genera (*Acropora*, *Pavona*, *Pocillopora* and *Porites*)

Whole Model Test				
Model	-LogLikelihood	DF	ChiSquare	P<
Difference	313.80	61	627.60	0.0001
Full	268.58			
Reduced	582.39			
R ² = 0.54				
N = 685				
Individual factors and interactions				
Effect Likelihood Ratio Tests				
Source	DF	ChiSquare	P<	Conclusion
Genus	8	44.49	0.0001	Significant
Year	2	0.00	1.0000	Not significant
Site	8	0.00	1.0000	Not significant
Genus*Site	28	72.05	0.0001	Strong
Genus*Year	8	11.33	0.184	Not significant
Site*Year	7	13.78	0.055	Marginal

annual temperature was highly significant ($P<0.0001$) but a weak predictor of the clade distributions ($R^2=0.04$) (Fig. 12). A 5°C increase in maximum annual temperature (from 30°C to 35°C) resulted in a three- to four-fold increase in the number of colonies dominated by *Symbiodinium* in clade D, with no change in the number of colonies containing mixtures of clades C and D. The influence of temperature and taxa was

explored by taxon-specific analyses (Fig. 13). All genera showed similar patterns but only the symbiont communities of *Pocillopora* and *Porites* were significantly associated with maximum annual temperatures ($P<0.0001$ and $P=0.037$, respectively). In these two genera, maximum annual temperature was a much better predictor of *Symbiodinium* distribution than for the pooled dataset ($R^2=0.30$ and $R^2=0.17$, respectively,

Table 11. Statistical results of the stepwise logistic regression model for the temperature variables and the frequency of the clades C, D, and C+D. Only the results from the field temperature gauges were significant and shown.

LogLikelihood = 601.1				
R ² = 0.049				
Parameter	Estimate	nDF	Wald/Score	P<
Intercept[CD]	3.86	1	0.00	1.00
Intercept[D]	4.47	1	0.00	1.00
Maximum	-0.61	1	6.66	0.01
Minimum	1.05	1	7.63	0.006
Average	-0.43	1	1.20	NS
Standard Deviation	2.54	1	5.11	0.023
Skewness	-1.65	1	3.77	0.052
Kurtosis	0.73	1	2.96	0.085
Step History				
Step	Parameter	ChiSquare	P<	R ²
1	Maximum	42.34	0.0001	0.03
2	Minimum	7.51	0.006	0.04
3	Average	2.39	0.121	0.04
4	Standard Deviation	5.34	0.021	0.05
5	Skewness	0.96	0.327	0.05
6	Kurtosis	2.85	0.091	0.05

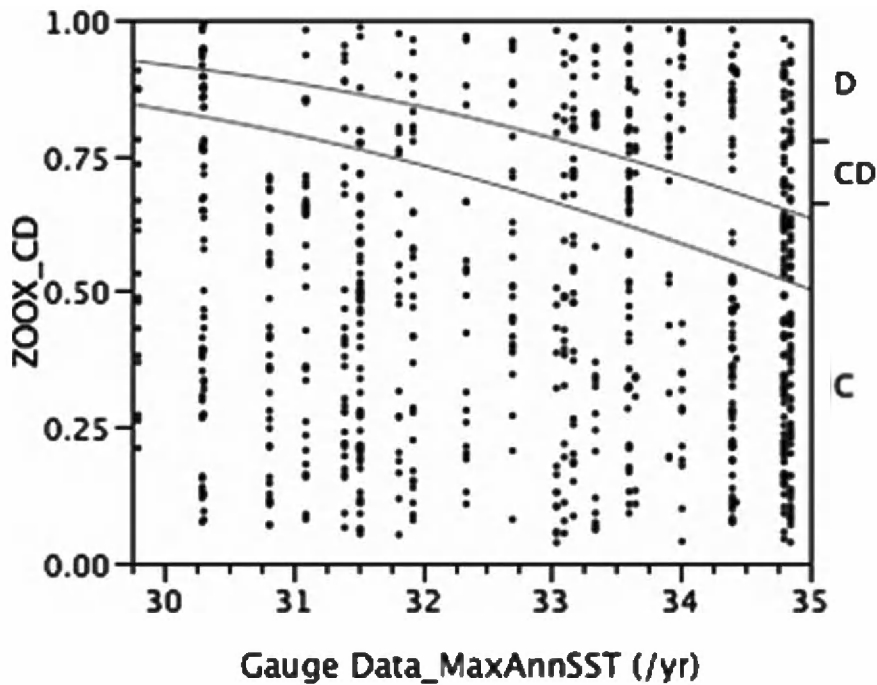


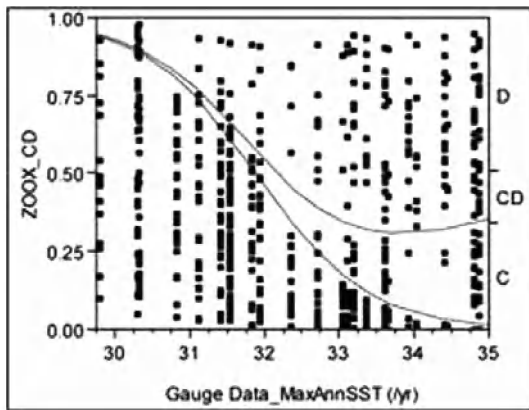
Figure 12. Nominal logistic fit of *Symbiodinium* clade in shallow scleractinian corals in Kenya, against maximum annual temperature from in situ gauges in the year of sampling.

Table 12. Summary of mean annual water temperature metrics taken from temperature gauges within Kenyan reefs and tests of significance (two-tailed *t* test) for comparisons between protected/unfished and unprotected/fished reefs. Based on 30 replicate and 29 replicate annual averages in the protected and unprotected reefs collected between 2001 and 2009.

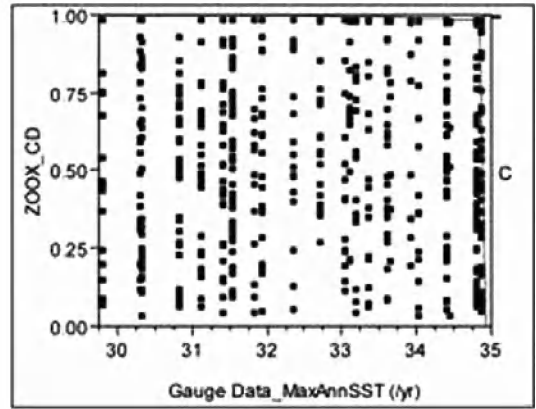
Management	Site	Average Temperature	Average Maximum Temperature	Average Minimum Temperature	Average SD Temperature	Average Skew Temperature	Average Kurtosis Temperature
Unprotected	Diani	27.39	33.05	24.45	1.64	0.40	-0.61
	Kanamai	27.56	33.91	23.83	1.81	0.61	0.06
	RasIwatine	27.66	31.84	24.77	1.38	0.26	-0.62
	Vipingo	27.60	33.34	24.28	1.61	0.49	-0.05
	Mean (SD)	27.55 (0.12)	33.03 (0.87)	24.33 (0.39)	1.61 (0.18)	0.44 (0.15)	-0.31 (0.36)
Protected	Kisite	26.90	30.50	24.16	1.22	0.25	-0.61
	Malindi	27.19	30.58	25.10	1.13	0.31	-0.32
	Mombasa	27.34	31.07	24.64	1.23	0.29	-0.55
	Watamu	27.20	31.06	24.76	1.42	0.39	-0.74
	Mean (SD)	27.16 (0.18)	30.80 (0.30)	24.67 (0.39)	1.25 (0.12)	0.31 (0.06)	-0.55 (0.18)
T test statistic		3.62 (0.01)	4.83 (0.00)	1.20 (0.27)	3.35 (0.02)	1.64 (0.15)	1.25 (0.26)
(p value)							

compared to $R^2=0.04$). Clade D within *Pocillopora* was the most strongly associated with maximum temperatures, with very few colonies containing detectable *Symbiodinium* in clade D when

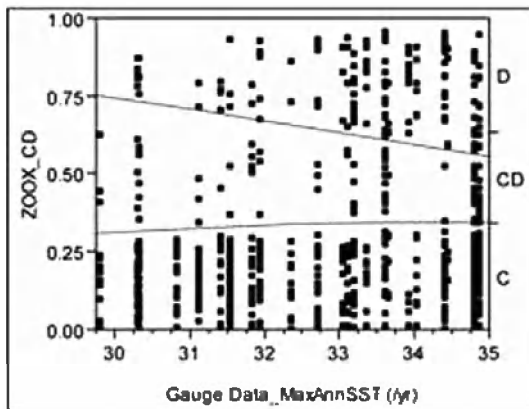
maximum temperature was 30°C but nearly all colonies containing detectable clade D and majority containing only clade D when maximum temperature reached 34°C.



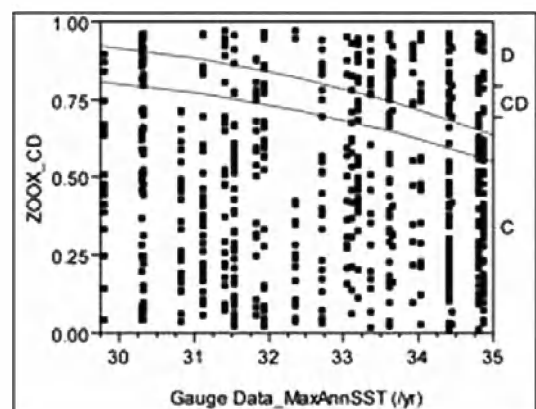
Pocillopora $P < 0.0001$ $R^2 = 0.3024$



Porites $P = 0.0374$ $R^2 = 0.1739$



Pavona $P = 0.1340$ $R^2 = 0.0112$



Acropora $P = 0.3441$ $R^2 = 0.0289$

Figure 13. Nominal logistic fit of *Symbiodinium* clade against maximum annual temperature in the year of sampling, based on the four most commonly sampled coral genera (*Acropora*, *Pavona*, *Pocillopora*, and *Porites*).

Influences on coral populations in Kenya

Kenyan sites differed for most temperature metrics with generally greater variation in temperature in the fished sites (Table 12). Some of the differences were, however, small such as mean temperatures of 27.16 and 27.55° C in protected and unprotected reefs, respectively. Temperature variation in unprotected was about 25% larger than protected reefs and this was largely reflected in the higher standard deviations, maximum temperatures, skewness and kurtosis in the unprotected reefs.

Mean population density estimates indicated that branching *Porites* was the most common and widespread coral taxon. *Acropora* was common at unfished sites and uncommon on fished reefs, while

Pavona had the opposite distribution. *Pocillopora* was more evenly distributed across sites but about twice as abundant in unfished than fished reefs. The combined effects of coral taxon and management regime were statistically significant for differences in absolute cover, relative cover, and colony number (ANOVA; $P < 0.01$). The effect of coral taxon was significant for colony size, but not management regime (ANOVA; $P < 0.01$).

A total of 737 coral tissue samples were taken over the 10-year sampling period, of which 203 were collected in protected fisheries closures and 534 from unprotected fished reefs. At the level of resolution provided by DGGE, only members of *Symbiodinium* clades C and D were detected in Kenyan reef corals among the four focal genera (Fig. 11). Diversity within clades (based on DGGE analysis of ITS-2 region) revealed the presence of types C1, C2, C3, C15, C42, D1, D1a, and Ddh

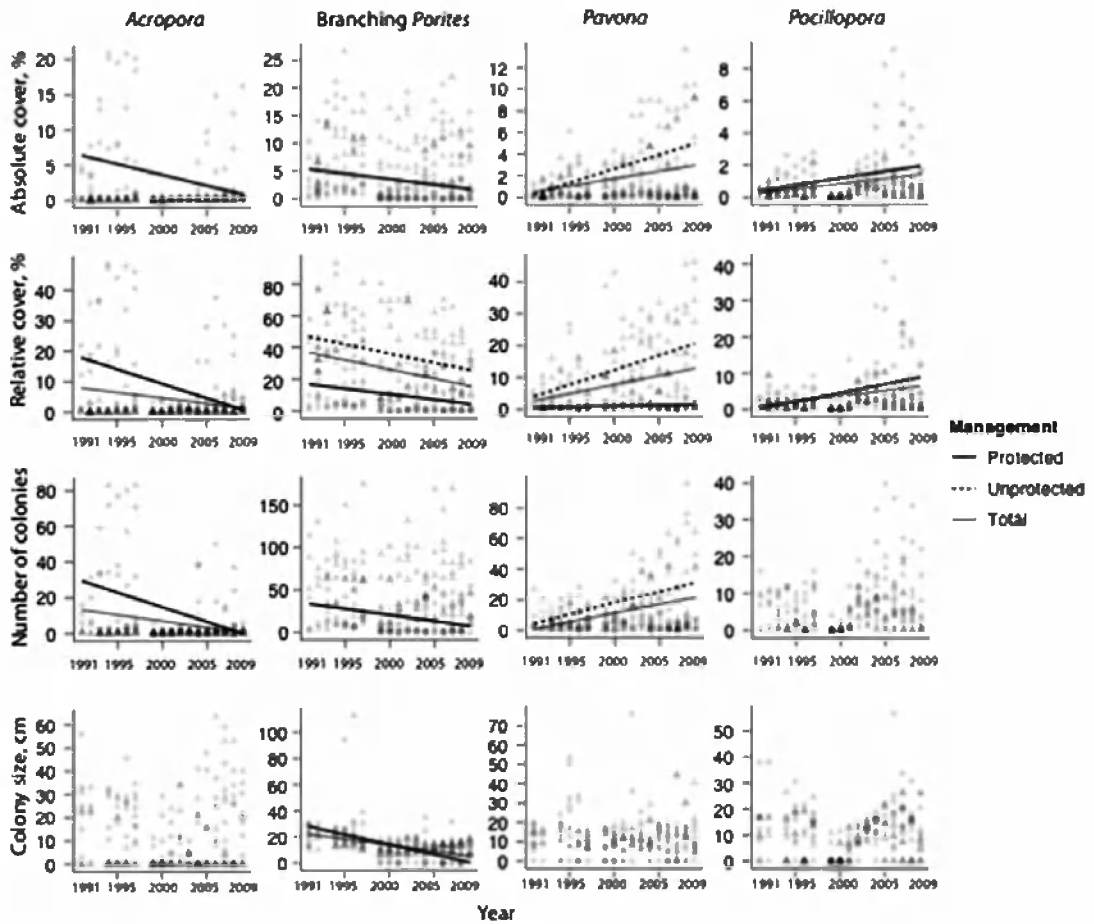


Figure 14. Time series charts for the four coral genera and four population metrics. Black, dashed and gray lines represent only those linear regressions that were statistically significant.

in the 4 focal taxa. There were differences in the relative proportions of clade D by management regime and coral taxon. Fished areas had a higher proportion of clade D dominance ($G = 11.1$, $df = 3$, $p = 0.011$) and clade D incidence ($G = 27.2$, $df = 3$, $p < 0.00001$) compared to unfished reefs. Branching *Porites* was the least symbiotically variable, and contained only *Symbiodinium* C15.

Acropora had 23% of samples containing only clade D, and *Pocillopora* and *Pavona* were the most symbiotically variable between management regimes. *Pavona* contained the least clade C and the most clade D, with incidence of clade D reaching 64% of samples.

The absolute cover of *Acropora* and branching *Porites* declined significantly, while *Pocillopora* increased significantly on unfished and all reefs over the 20-year period (Fig. 14). Absolute cover

of *Pavona* increased significantly on fished reefs, but was uncommon and remained unchanged on unfished reefs. In all sites combined, *Pavona* and *Pocillopora* absolute cover increased. The relative cover of branching *Porites* declined significantly under all management regimes, as did *Acropora* in unfished sites and overall, although it was uncommon on fished sites. The relative cover of *Pavona* significantly increased under all management regimes and *Pocillopora* increased in unfished sites and overall. The number of colonies declined significantly for *Acropora* and branching *Porites* on unfished reefs as well as overall for *Acropora*. The mean number of *Pavona* colonies increased significantly on fished reefs and overall. The only taxon that exhibited a decline in colony size was branching *Porites*, which experienced significant declines on unfished reefs and overall.

Table 13. Cluster analysis results based on respondents' mean level of agreement on various management options - based on Ward hierarchical clustering-method where the communities are placed within the eight dominant clusters.

Cluster number	Country	Sites	People interviewed
Cluster 8 – Positive towards all restrictions	Kenya	Managers, Fisheries officer	14
	Kenya	Managers, Park service	15
	Kenya	Vipingo	32
	Kenya	Wasini	6
	Madagascar	Ambodipaka	18
	Madagascar	Antsirakivolo	5
	Madagascar	Maintimbato	10
	Madagascar	Managers	12
	Madagascar	Rantohely	25
	Madagascar	Tanantsara	22
	Mozambique	Chwiba	19
	Mozambique	Vamizi	48
	Mozambique	Managers	14
	Mozambique	Ruela	36
	Tanzania, Mafia	Managers	14
	Tanzania, Mtwara	Managers	14
Cluster 1 - Weaker support for size and species restrictions	Kenya	Mkwiro	11
	Kenya	Shimoni	16
	Kenya	Mkokoni	13
	Madagascar	Ambarono	30
	Madagascar	Ambariotelo	30
	Madagascar	Ambodilaitra	7
	Madagascar	Ampasimena Sakatia	29
	Madagascar	Imorona	20
	Madagascar	Navana	8
Cluster 7 – Weak support for closures and species restrictions	Madagascar	Nosy Komba	30
	Madagascar	Ambohitsabo	30
	Madagascar	Anakao	30
	Mozambique	Museu	4
	Mozambique	Nacaramo	15
	Mozambique	Passa-mar	25
Cluster 3 –Negative views on marine protected areas and species restrictions	Kenya	Kanamai	13
	Kenya	Marina	14
	Kenya	Kizingitini	12
	Madagascar	Ankiembe	31
	Madagascar	Ankilibe	60
	Madagascar	Saint Augustin	30
	Madagascar	Saradrano	30
	Madagascar	Soalara	30
	Madagascar	Amboaboake	10
	Madagascar	Ambotsibotsiky	10
Cluster 2 – Weak support for gear, minimum sizes, and species restrictions	Kenya	Bamburi	24
	Kenya	Chale	19
	Madagascar	Madiorano	10
	Tanzania	Mafia, Bweni	31
	Tanzania	Mafia, Mfuruni	30
Cluster 5 – Weak support for marine protected areas and negative views closed seasons, areas, and species restrictions	Kenya	Mvuleni	15
	Kenya	Mwape	19
	Kenya	Mwanyaza	13
	Kenya	Pate	27
	Kenya	Gazi	14
	Kenya	Kiunga	26
	Kenya	Msanakani	18
	Kenya	Nyali	13
	Kenya	Shanga Ishakani	27
	Tanzania	Mtwara-, Miburani	35
	Tanzania	Mtwara-, Tumbuju	30
Cluster 6 – Weak support for species restrictions, negative views on close seasons, areas, and marine protected areas	Kenya	Shanga Rubu	22
	Kenya	Tradewinds	12
	Madagascar	Kalakajoro	5
	Mozambique	Areal	16
	Tanzania	Mtwara-Mngoji	22
	Tanzania	Mafia, Jibondo	30
	Tanzania	Mafia, Juani	28
	Tanzania	Mtwara-Msangu mkuu	20
Cluster 4 – positive on gear restrictions and negative on all other restrictions	Kenya	Reef	13
	Madagascar	Nosy-Lava	10
	Tanzania	Mtwara-Msimbati	24
	Tanzania	Mtwara-Nalingu	23

Branching *Porites*, which contained no detectable clade D, showed consistent declines in all population metrics on unfished reefs, losses of relative cover in fished reefs and overall, and overall declines in colony size (Fig. 14). Unfished reefs had the lowest dominance of clade D and

this was associated with losses in two taxa, the exception being an increase in *Pocillopora* and no change in the uncommon *Pavona*. Fished reefs showed positive responses for *Pavona* population metrics. Overall, the two taxa with the lowest dominance of clade D, *Acropora* and branching

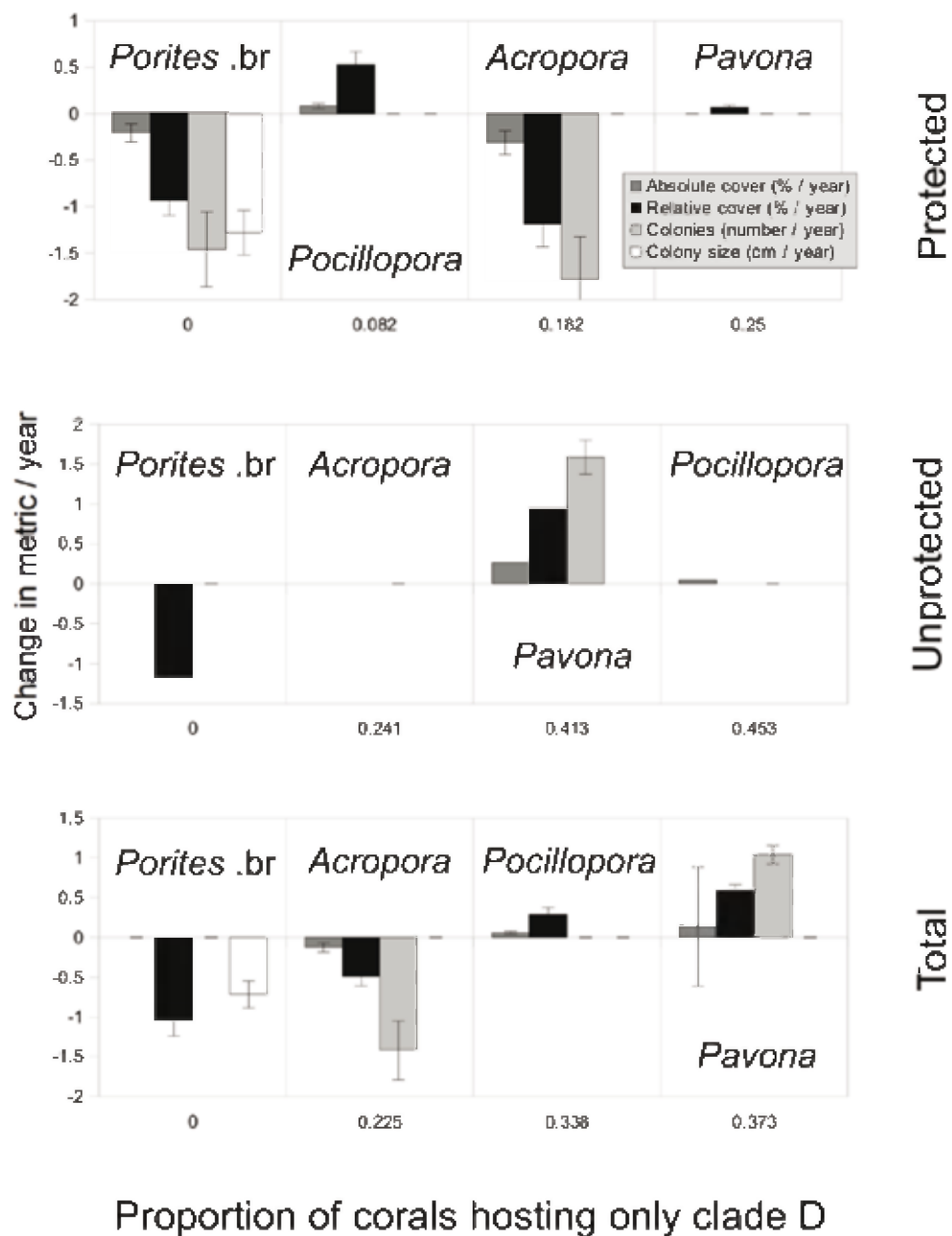


Figure 15. Proportion of corals hosting *Symbiodinium* D only as their dominant symbiont relative to the mean slope of the four population metrics in (a) protected/unfished (b) unprotected/fished and (c) all sites pooled. Statistically insignificant slopes are given a value of zero.

Porites had the largest declines in population metrics. *Pocillopora* and *Pavona*, the two taxa with the highest dominance of clade D, had the most increases in population metrics (Fig. 15).

Management preferences

The regional overview

The regional analysis presents the broad overview and is based on a total of 1437 respondents from 73 landing sites in 5 countries. This included 88 managers, including fisheries officers and marine attendants. Hierarchical clustering method identified 8 clusters with a mix of different landing sites from various countries (Table 13). Countries differed slightly with certain countries dominating in various

clusters but with examples of spread that suggest that management preferences do not often follow national borders (Table 14). The national government managers in all countries scaled all restrictions positively. The country of Tanzania had the biggest dichotomy between managers and resource users, the managers ranking all restrictions positively but resource users having less positive views of restrictions.

Plotting the six management options by the scaling of the specific preferences showed how each cluster differed in their preferences (Fig. 16). Cluster 8 scaled all restrictions positively while cluster 1 had weaker preference for species restrictions and cluster 7 also scaled closed areas low. Clusters 2 and 3 were more intermediate in their scaling and cluster 2 scaled gear restrictions and minimum sizes of fish low where as cluster

Table 14. Summary of the study sites and their distribution among the eight management preference clusters in the four studied sites. The clusters are scaled from positive on the left to most negative towards restrictions on the right. The numbers of managers groups are in parentheses.

Country	Positive towards restrictions			Neutral towards restrictions		Negative towards restrictions		
Cluster number	8	1	7	3	2	5	6	4
Kenya	4(2)	3	0	3	2	9	2	1
Mozambique	11(7)	1	3	0	1	0	1	0
Madagascar	11(5)	6	3	7	1	0	1	1
Tanzania - Mafia	3(3)	0	0	0	3	2	4	2

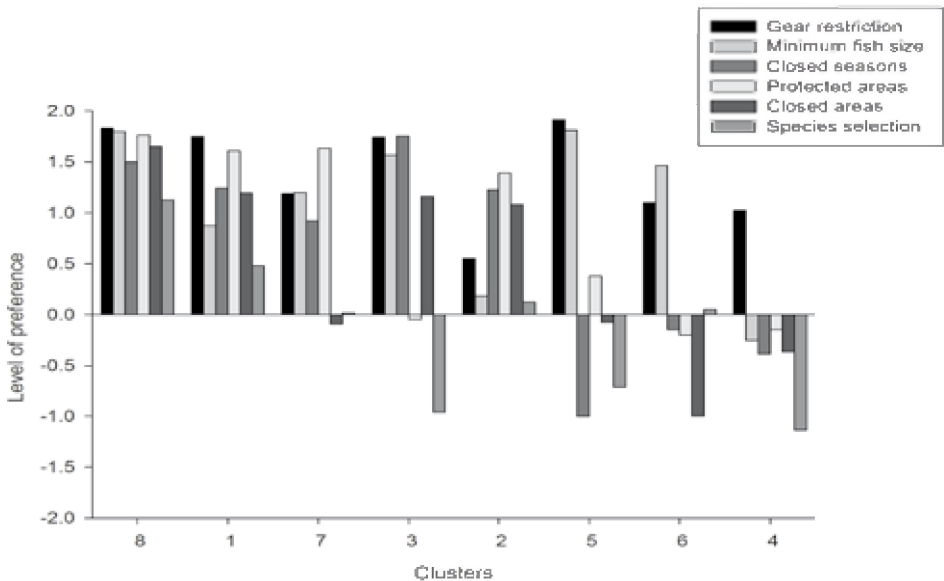


Figure 16. Scaling of the six management preferences in the 8 clusters based on the sites in Table 13.

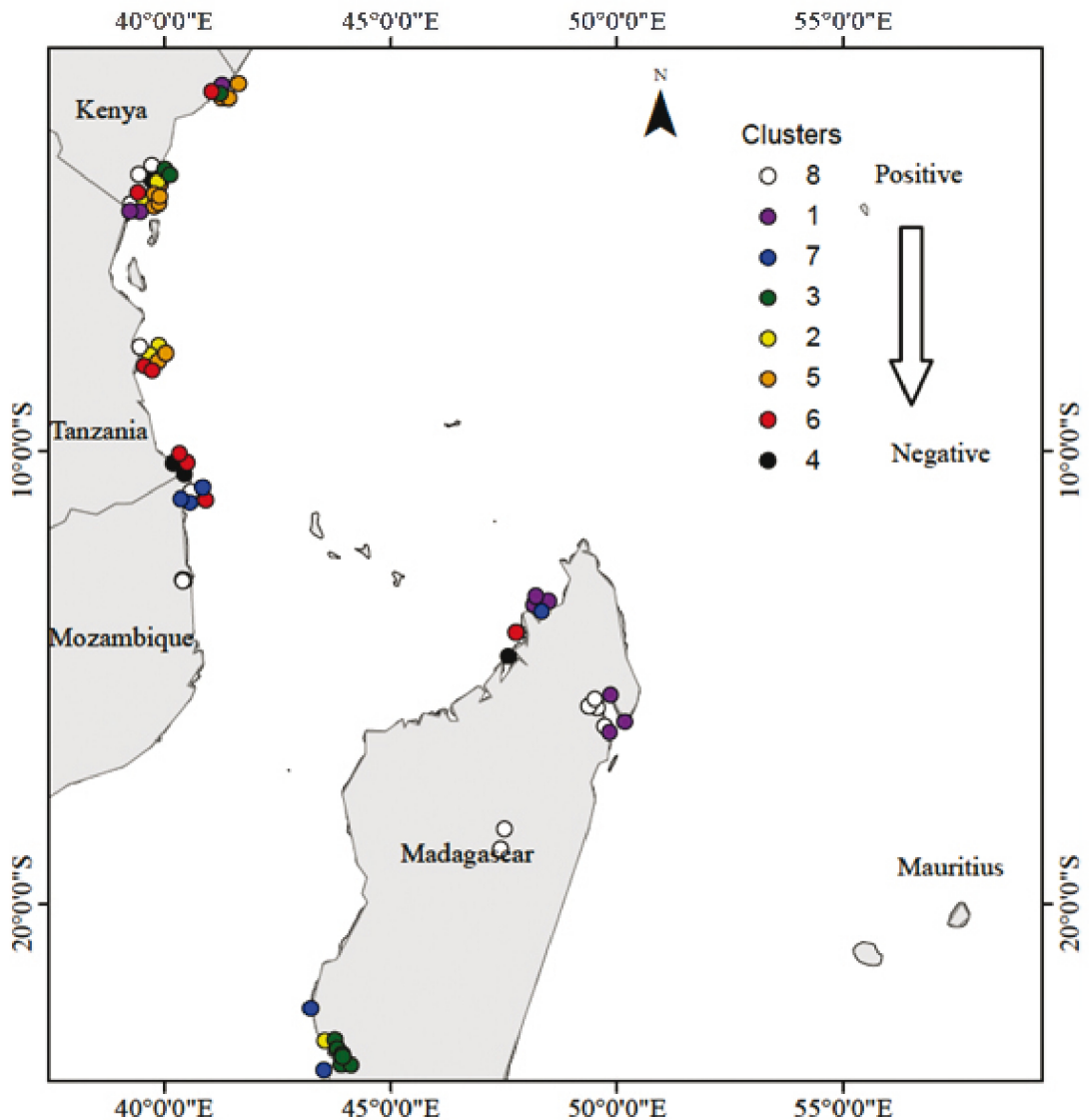


Figure 17. Geographic location of the 8 management preference clusters based on the six management preferences as described in Table 13.

3 scaled these higher but had a negative view of species selection. Clusters 4, 5, and 6 had a number of negative scaling and differed as to whether they disliked closed seasons (cluster 5), species selection (cluster 4 and 5) or closed areas (cluster 4, 5 and 6). Cluster 4 had the most negative scaling, only scaling gear restrictions positively.

The distribution of these cluster varied by country (Table 14, Fig. 17). Kenya had a broad spread among the clusters but with the most

number of sites in the most positive scaling clusters. A number of Mozambique and Madagascar sites were in cluster 2, suggesting positive perceptions towards closed seasons, protected areas, and closed areas but less so for gear restrictions, minimum size of fish, and species restrictions. Tanzania had a number of sites in cluster 5, which suggests positive perceptions towards gear restrictions and minimum size of fish but not other management systems. Regardless, there is considerable spread in the sites scaling of preferences.

Site-specific studies

Kenya

Fishers in Kenya had a mean age of 40 years, just over five years of education, 2.2 jobs per household and, on average, lived 31-km from the nearest marine protected area. Fishers differed from government employees in being older and having more household jobs. The government employees had 12-13 years of education and a lower perceived disparity of benefits than fishers (Table 15). Cluster analysis of the responses to the management restrictions indicates that there were three broad groupings with the cluster group, management, and their interaction being statistically significant (Fig. 18). The group that scaled restrictions most positively included government employees and fishers at four landing sites (Vipingo, Mkokoni, Shimoni, Mkwiro) (Figs. 18, 19). Seven landing sites scaled the restrictions in a more neutral and eleven in a more negative way depending on the restriction.

Respondents in the positive preference cluster undertook all jobs except gleaning and ~80% were involved in fishing but less than half rated it as their primary occupation (Fig. 19). The most important job among the positive cluster was salaried job where more than 50% of those involved rated it as their primary occupation. Other important jobs in this cluster were informal sector and subsistence jobs where ~25% rated them as their primary job. Jobs in the neutral cluster included fishing, informal sector and subsistence farming of 90, 32, and 28% involvement respectively with none involved in mariculture or cash crop farming. Somewhat less than 20% were involved in tourism and salaried job but over 50% of those involved rated it as their

primary occupation. There were many jobs listed in the negative cluster but most were involved in fishing and cash crop farming, 81% and 40% involvement respectively, and other jobs had less than 20% involvement.

The different management preference clusters had statistically significant differences in the key descriptions of the respondents with the exception of the biweekly expenditures (Table 15). The group with the most negative view of restrictions had a lower level of education, a higher perception of disparity in benefits from restrictions, a lower material style of life, and was farthest from marine protected areas. This group and the neutral group both had similar high rankings for fishing as of importance to their household and the total number of jobs per household.

There were statistically significant differences between the three management preference clusters regarding their level of agreement with all restrictions except species and gear (ANOVA, $P < 0.01$, Fig. 19). All groups had equally high levels of agreement with gear restrictions and this was scaled as the most agreeable of all potential restrictions. In contrast, all groups had low levels of agreement with species restrictions. There were statistically significant but weaker differences in minimum length restrictions, which were scaled high for all clusters. The largest differences among the three clusters were their level of agreement with protected areas, and closed areas, and closed seasons. These restrictions were what largely distinguished the clusters. The positive cluster scaled all restrictions positively, but had higher levels of agreement with minimum length and gear restrictions than for closed seasons. The neutral

Table 15. Summary of key descriptions (mean \pm SEM) of the respondents in the three clusters of management preferences and one-way ANOVA test of significance. Material style of life metric is a multivariate PCA scaling based on ownership of various household items where positive values indicate greater material assets and vice versa. Results of a post-hoc Tukey test comparing individual means where values preceded the same letter (A, B, C) are not significantly different from each other.

	Age of respondent, years	Level of education years	Biweekly expenditure, US\$	Perceived mean disparity	Fishing ranking	Total jobs per household	Distant from park	Material style of life
Cluster								
Negative	B 40.0 \pm 0.5	A 4.6 \pm 0.12	A 63.6 \pm 0.8	A 2.8 \pm 0.11	B 1.1 \pm 0.02	B 2.1 \pm 0.02	A 37 \pm 0.5	A -2.0 \pm 0.2
Neutral	A 42.0 \pm 0.7	B 5.1 \pm 0.2	A 63.7 \pm 1.2	B 1.9 \pm 0.16	B 1.1 \pm 0.0	B 2.0 \pm 0.03	B 26 \pm 7.4	AB -0.12 \pm 0.0
Positive	B 38.0 \pm 0.9	C 7.2 \pm 0.2	A 64.8 \pm 1.4	B 1.9 \pm 0.20	A 1.3 \pm 0.0	A 2.4 \pm 0.04	C 15 \pm 9.6	B 0.26 \pm 0.04
ANOVA								
R ²	0.0005	0.05	0.00003	0.01	0.03	0.03	0.21	0.04
F ratio	6.6	52.1	0.27	14.4	29.9	30.5	276.3	41.5
P <	0.0014	0.0001	NS	0.0001	0.0001	0.0001	0.0001	0.0001

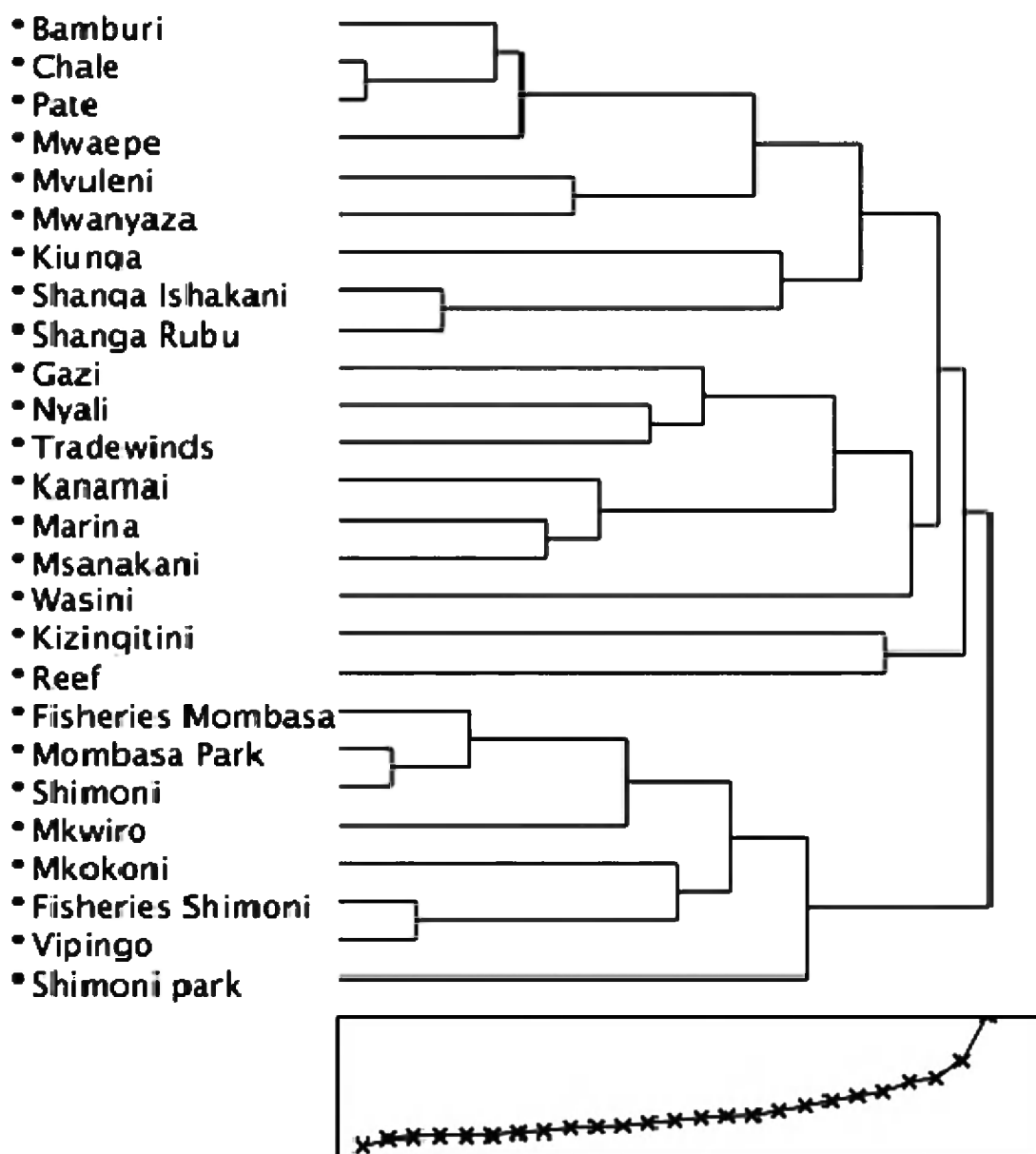


Figure 18. Cluster analysis of similarities in the respondents' level of agreement with the various management options. Includes the 22 fish landing sites and the government fisheries and park management officers or marine attendants. Kizingitini and Reef responses were more negative and pooled into the negative cluster in subsequent analyses.

group scaled closed seasons positively but was neutral on protected areas and negative on closures. The negative group was neutral on protected areas but scaled closed seasons, closed areas, and species selection negatively.

When asked about reasons for their level of agreement, the common explanations for gear restriction were that this ensured less destruction to fish and their habitat and also it reduced

mortality of juvenile fish. Reasons for supporting minimum length restrictions included ensuring future fish stocks, the ease of selling, and better prices. Reasons for not supporting species selection was that it was not possible to control, that catch was a natural phenomenon determined by God, there was no benefit to fishers for these restrictions, and that size was more important than species. Among those respondents that did support species restrictions, explanations

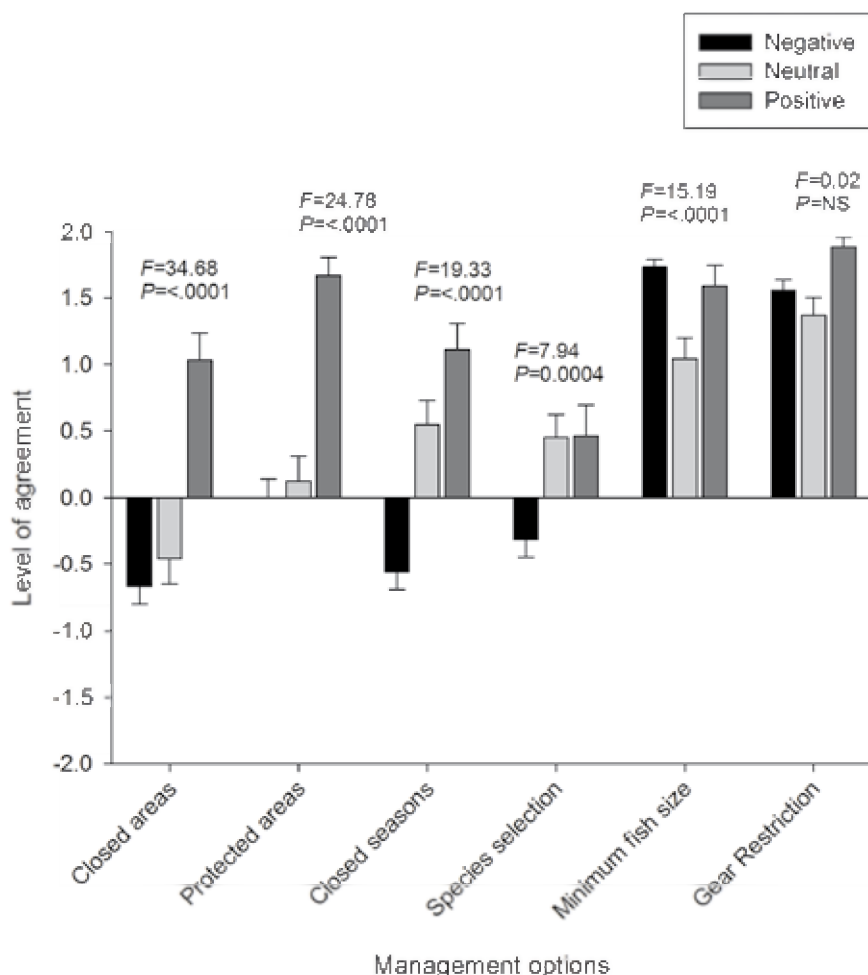


Figure 19. Scaling of the management preference restrictions pooling responses into the three major management preference clusters.

Table 16. Summary of sizes given for minimum caught fish, closed and protected areas (mean + SEM) for the three different cluster groups and result of ANOVA nested analysis for landing sites nested within clusters.

Figure 21 shows the values presented as cumulative frequency distributions. The number of the 402 total respondents that would not answer the question, could not give quantitative estimates, or gave zero as their answer is indicated below the "non or zero responses" sub-heading.

	Minimum fish size, cm	Closed areas, km ²	Protected areas, km ²
Cluster			
Negative	16.9 ± 0.5	3.0 ± 1.8	4.6 ± 4.3
Neutral	15.3 ± 0.7	4.4 ± 2.5	11.2 ± 5.0
Positive	18.4 ± 1.2	13.8 ± 3.3	34.7 ± 9.1
Non or zero responses			
Negative cluster	Nil	34.0%	22.4%
Neutral cluster	Nil	14.4%	8.2%
Positive cluster	Nil	8.7%	3%
Nested analyses			
Clusters	F=4.7, P <0.009	F=6.1, P <0.003	F=6.8, P <0.001
Landing sites	F=3.0, P <0.0001	F=2.0, P <0.009	F=2.1, P <0.006

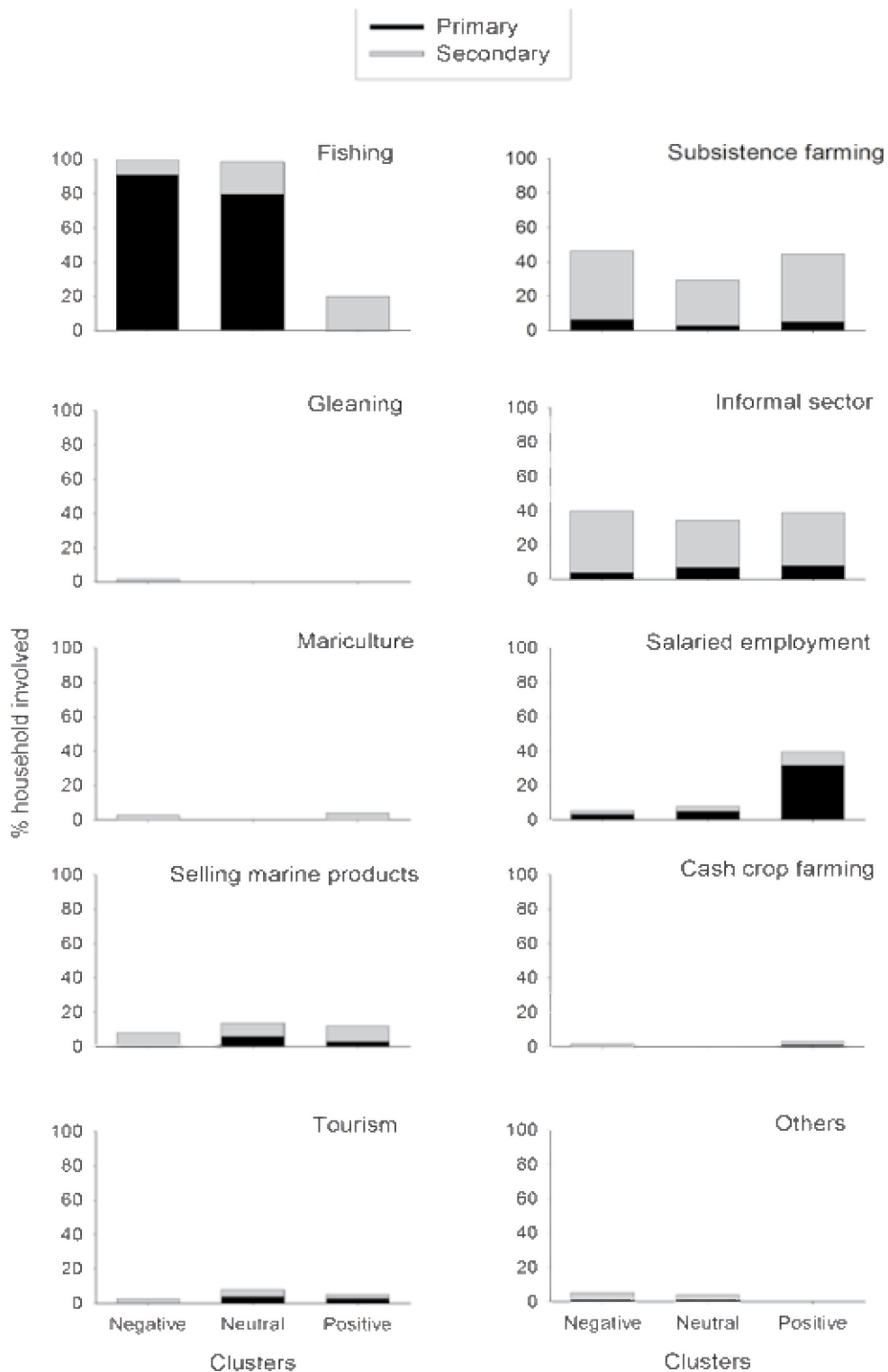


Figure 20. Frequency of the ranks of dependency on fishing and other livelihoods in the three management preference clusters.

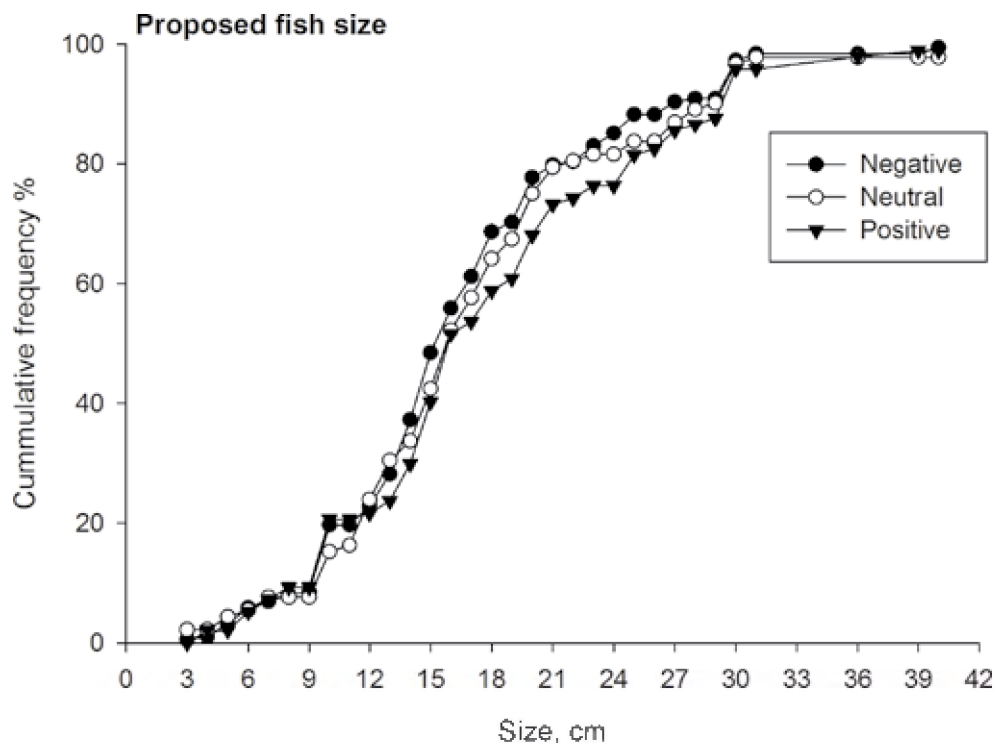


Figure 21. Cumulative frequency distributions of the minimum size of captured fish pooling respondents by the three major management preference clusters.

included the importance of stopping extinction and preserving predatory species and their ability to attract tourists, which led to jobs. Respondents that scaled parks and closures high saw them as breeding sites and useful in improving catch through spillover effects while those that scaled them negatively said they restricted their movements and reduced the area of their fishing grounds.

Responses to questions about the appropriate sizes for the minimum length of landed fish, closures, and protected areas indicate that all comparisons among the three clusters were statistically significant and differences among clusters were stronger than the sites (Table 16). Differences in the suggested minimum lengths of landed fish were, however, not large among the three groups ranging from 15.3 to 18.4 cm for the mean lengths. The range of individual responses was larger, however, ranging from 3-cm at the smallest to

42-cm at the largest, but 90% of the responses suggested minimum sizes below 30 cm (Fig. 21).

When asked about the acceptable sizes of closures and protected areas, a significant portion of respondents were either not able to estimate sizes, would not give suggested sizes, or gave zero as their answer for closures and protected areas, particularly in the neutral and negative clusters. For those that did answer with quantitative values, there was small spread in responses for closed areas but a large spread for the size of protected areas among the three clusters (Fig. 22). Respondents in the negative and neutral groups that gave answers for closed areas, the mean values were between 3.0 and 4.4 km² where as respondents in the positive group gave a mean value of 13.8 km². The size of protected areas ranged from 4.6, 11.2, and 34.7 km² with fairly large variation around these values and with the positive cluster as having the most variation. Testing for differences in scaling of benefits for

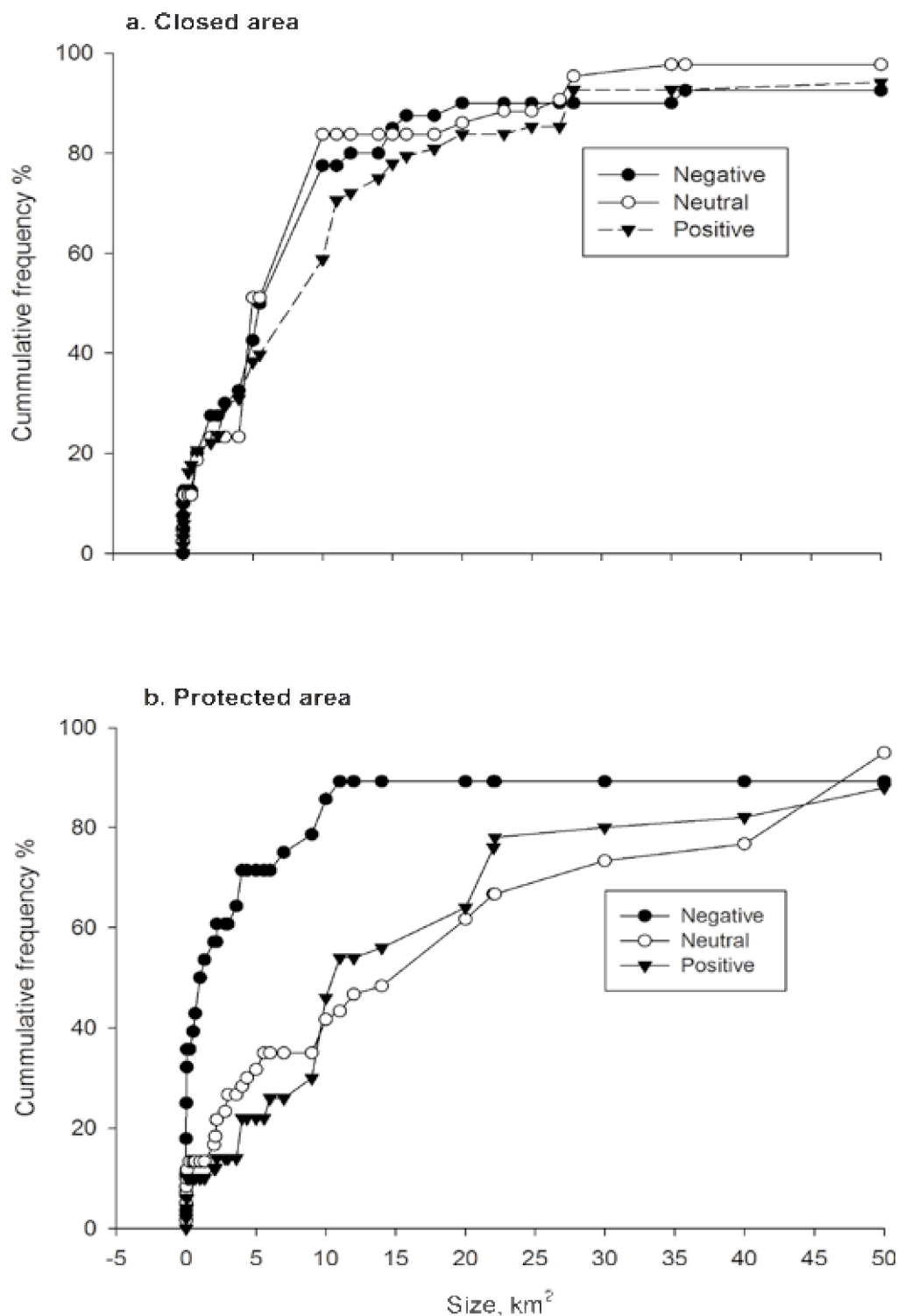


Figure 22. Cumulative frequency distributions of sizes of fisheries closures and sizes of marine protected areas based on the pooled responses of the three major management preference clusters.

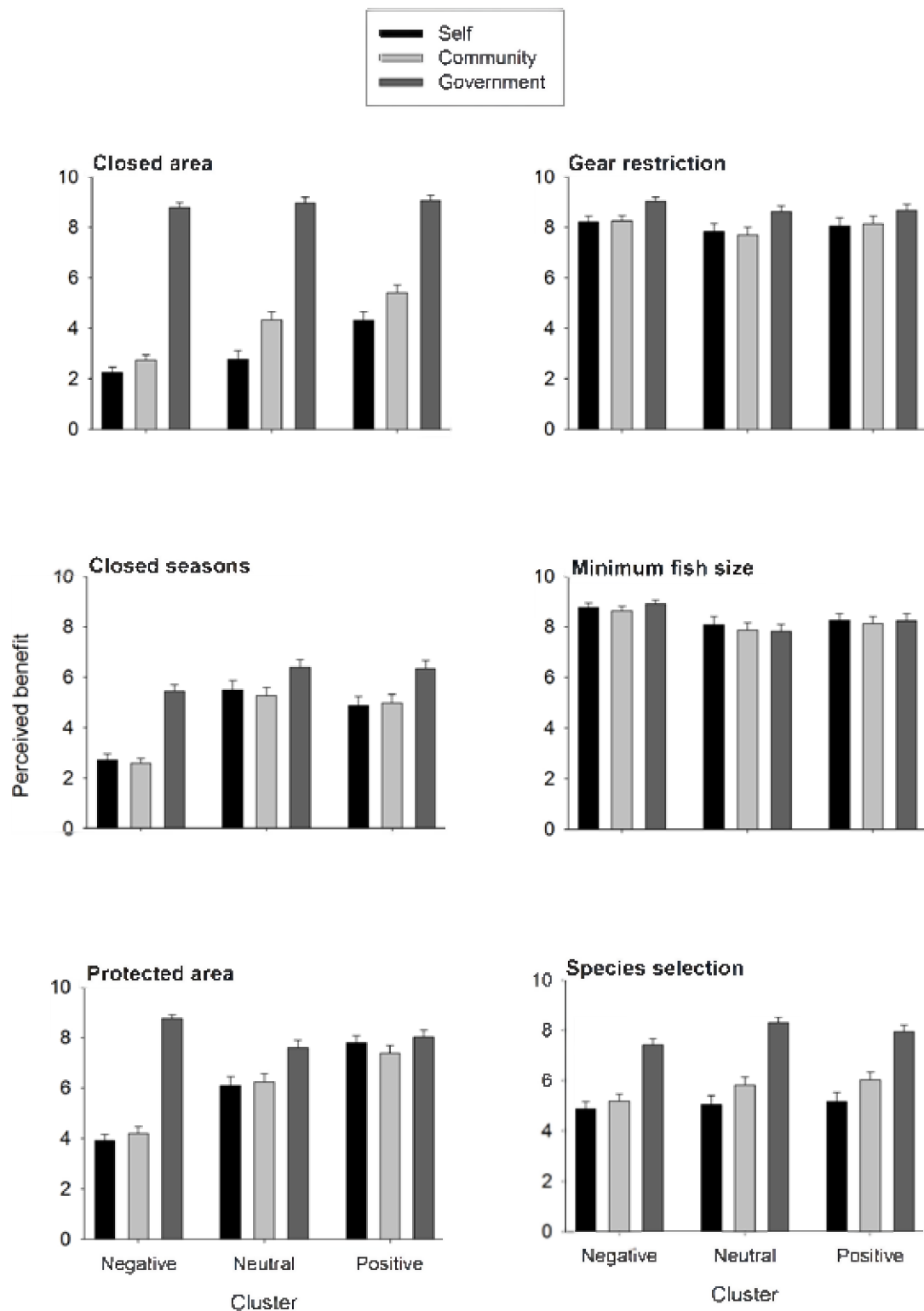


Figure 23. Scaled perceived benefits for the 3 beneficiaries (self, community, and government) of the management restriction options as rated by the respondents in the three clusters. Tests of significance compare differences between the three management preference clusters for the three beneficiaries.

the six management restrictions by the three beneficiaries - self, community, and government, indicated differences by the types of restrictions for the three management preference clusters (Fig. 23). One exception was gear restrictions, which were perceived to benefit all beneficiaries equally by all preference clusters. Minimum length restrictions were also seen to benefit most groups with the negative cluster scaling the benefits higher than the neutral and positive cluster respondents for all beneficiaries. The negative group also scaled protected areas as a greater benefit to the government than the other clusters. Most respondents scaled government as the main beneficiary to restrictions, followed by community, and self but the extent of this varied for the three preference clusters and restrictions. Generally, the most negative benefits to the self and community were associated with the negative and neutral clusters. Consequently, the negative and neutral cluster respondents generally scaled the restrictions that they did not like as of lower benefit to themselves and their community but they did recognize the benefits to the government.

Pair-wise regression comparisons of the differences in perceived benefits to the three scales of beneficiaries suggest that the largest disparities are seen between the government and individual scales, but this is highly correlated with the government-community disparities. In other words, the respondents did perceive similar levels of benefits that accrued to both themselves and their communities, but did perceive differences in benefits that accrued to the government. Consequently, in the evaluation of disparities below we used the government-self as the metric of 'perceived disparity'.

Logistic step-wise multiple regression analyses of the socio-economic variables and perceived disparity on the level of agreement with the six management restrictions indicate generally high variability and weak multivariate models but a number of statistically significant associations (Table 17). The most frequent statistically significant factor was perceived disparity, which was a significant predictor in all six restrictions - the greater the perceived disparity the weaker the level of agreement with the restriction. Distance to the park was significant for four of the restrictions with higher levels of agreement with restrictions the closer the respondents were to the park, for the restriction of closed areas, closed season, minimum fish

lengths, and species selection restrictions. The total number of jobs of the respondents was significant for three of the restrictions. Higher levels of agreement with closed areas, minimum size, and gear restrictions were associated with fewer reported numbers of jobs. Ranking of fishing as the number one occupation was more common in the negative and neutral clusters (Fig. 23). Higher levels of agreement with closed area restrictions increased with the respondent's level of education and preferences for species restrictions declined with the age of the respondent.

Mafia Island, Tanzania

Average age for the occupations and villages in Mafia was 39 ± 12.1 (\pm SD) years, with the youngest individual respondent being 19 years and the oldest 76 years. Fishers using each gear type were well represented with hook and line, gillnets, sharknet and traps being the commonly used gears. Education and biweekly expenditure were significantly higher among government officials than villagers (education $F = 62.2$, $p < 0.01$; expenditures $F = 37.5$, $p < 0.01$). Government officials had 12.0 ± 1.6 years of education and biweekly expenditure of Tanzanian Shillings (Tsh) $71,500 \pm 38,500$, respectively, compared to 6.0 ± 2.7 years of education and biweekly expenditures of Tsh $37,668 \pm 16,422$ among villagers (US\$ 1 = 1000 Tsh). Non-Park villagers had both higher levels of education and expenditures compared to Park villagers (education $F = 34.6$, $p < 0.01$; expenditures $F = 23.4$, $p < 0.01$). Government officers had fewer workers ($F = 20.2$, $p < 0.0001$) and jobs ($F = 16.9$, $p < 0.0001$) per household but a higher ratio of the two than villagers.

There were also differences in these measures between Park and non-Park villagers and within non-Park villagers. Non-Park villagers had a lower number of jobs per household than Park villagers, except at Mfuruni, which had the highest jobs per worker ratio among all villagers and occupations, having high employment in the informal sector and salaried jobs (Fig. 24). Fishing was the most important occupation, undertaken by 21–30% of working people in all the villages. Generally those who undertook fishing and salaried jobs ranked it as their primary occupation. Subsistence farming occurred in all the villages except Jibondo, and no cash crops or salaried employment were recorded at Jibondo and Juani, which had the highest employment in mariculture.

Table 17. Factors influencing fisher's level of agreement with various management options based on logistic step-wise multiple regression analysis. Variables included are those that remained after the step-wise screening procedure.

Management option	Variables	N	R ²	Chi-square	P value
Closed areas	Perceive mean disparity	373	0.07	16.29	0.0001
	Distant from park			11.42	0.0006
	Level of education			4.77	0.03
	Total jobs			3.86	0.05
Closed seasons	Perceived mean disparity	366	0.03	13.8	0.0002
	Total jobs			2.02	0.16
	Distant from park			1.42	0.23
Protected areas	Perceived mean disparity	370	0.09	43.25	0.0001
Species selection	Perceived mean disparity	353	0.04	11.37	0.0007
	Age of respondent			8.84	0.002
	Distant from park			3.85	0.05
	Biweekly expenditure			2.93	NS
	Total jobs			1.59	0.21
Minimum fish size	Total jobs	372	0.02	6.42	0.01
	Distant from park			6.16	0.01
	Perceived mean disparity			2.00	NS
	Level of education			1.91	NS
Gear restriction	Perceived mean disparity	366	0.08	26.18	0.0001
	Total jobs			6.79	0.009
	Fish ranked importance			3.09	0.08

All occupations rated the management benefits of gear and minimum size restriction highly, with no statistical differences between occupations (ANOVA, $P < 0.01$; Fig. 25). Government officials listed a larger, but not statistically different ($F = 2.2$, $p = 0.14$), minimum size restriction on target species (14.5 ± 2.2 cm) than villagers (11.2 ± 4.8 cm). Common reasons given for gear restrictions were that they were destructive and killed juvenile fishes. Reasons given for minimum lengths included the need to protect future stocks, the lack of a market, being wasteful and protecting target species.

There were a number of significant relationships between the agreement with restrictions, perceptions of who benefits, and socioeconomic variables. Despite weak relationships among villagers for the whole model, there were a number of statistically significant variables (Table 18). Agreement with protected areas was negatively related to years in occupation, but positively related to age. Perceived benefits from protected areas was also negatively related to years in occupation, but positively related to biweekly expenditures.

Support for closed areas was negatively related to years in occupation and biweekly expenditures, while perceived benefits were negatively related to years in occupation and age. Agreement with and perceived benefits from minimum sizes of fish were negatively related to material style of life and years in occupation, but agreement was positively related to age and biweekly expenditures. Agreement with gear restrictions was negatively related to years in occupation, and benefits were positively related to level of education.

There were stronger whole model relationships between government officials and socioeconomic characteristics for a few of the responses, but low sample sizes were unlikely to produce statistical significance for weak relationships (Table 19).

Nonetheless, all government officials agreed with restrictions on gear and minimum sizes with no statistically significant relationships with their socioeconomic characteristics. There was a positive association between government official's level of education and perception of who

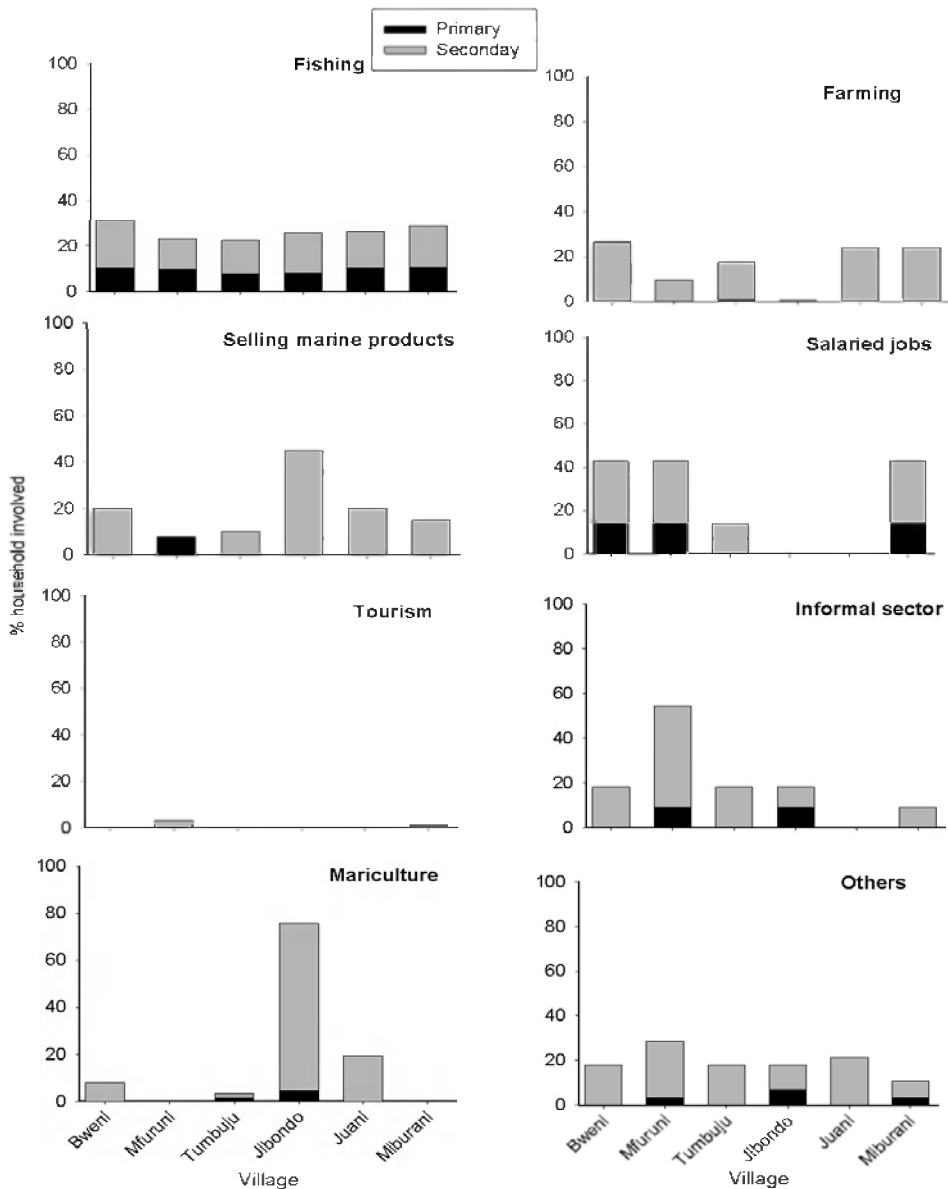


Figure 24. Percentage of individuals employed by sector in six villages, where the villages Bweni, Jibondo and Juani are in or close to the Park, and Miburuni, Mfuruni and Tumbuju are outside the Park.

benefits from minimum size restrictions. There were marginally positive ($p < 0.07$) associations between government official's biweekly expenditures and perceptions of who benefits from minimum size and gear restrictions.

The agreement with restrictions and perceived benefits of marine protected areas, permanent and seasonal closures, and species restrictions were different between occupations (Fig. 25). Government officials were in agreement with

and saw large benefits from protected areas, closed areas and closed seasons and generally saw these as benefiting self, community and national government. Agreement and perceived benefits were shared by all officials, as there were no significant associations between the collected socioeconomic variables and the levels of agreement with the exception that the perceived benefits of closed areas were negatively associated with the number of years in the occupation.

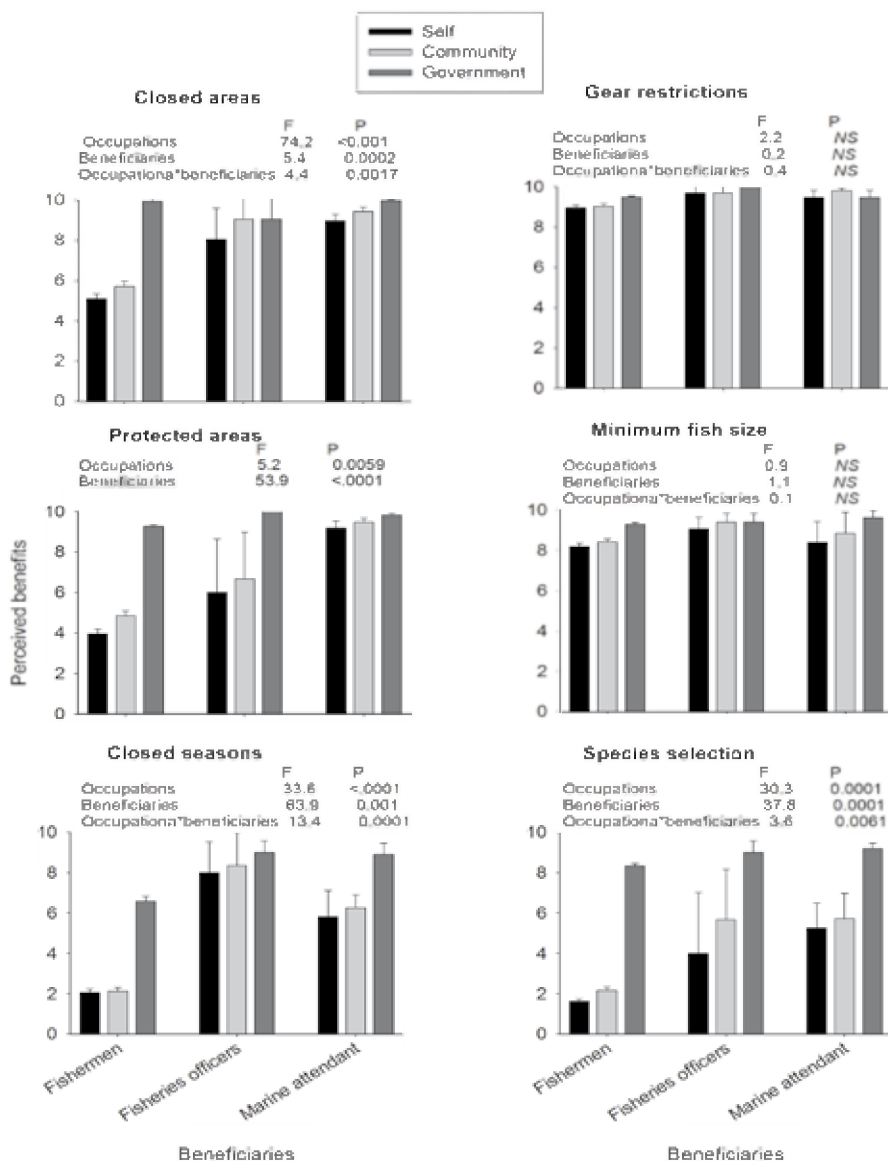


Figure 25. Lickert scale (relative 0 to 10) responses for people pooled by occupations (fishers, fisheries officers and marine attendants) of their perceptions of the benefits of management options (namely protected areas, closed areas, closed seasons, gear restrictions, minimum fish restrictions and species selection) and those who are perceived to benefit.

Villagers did not see protected and closed areas as benefiting themselves and their communities, but they did see it benefiting the national government. There were negative associations between the agreement with restrictions and perceived benefits with protected and closed areas and the years in their occupation and biweekly expenditures (Table 18). There was, however, a positive relationship between perception of who benefits from protected areas and biweekly expenditures. Respondents

who supported protected areas said that they reduced illegal gear and that they had no negative effect on them. Respondents who did not support protected areas said they reduced the fishing grounds and that control of resources was attributable to natural phenomena or God (as opposed to management). Villagers who supported closed areas said that they had no negative effect on them, acknowledged benefits if they were small and improved conservation of resources. Villagers who disagreed with closures

Table 18. Factors influencing fishers' levels of agreement and perceived benefits responses for various management options based on step-wise multiple regression analysis. Variables included are those that remained after the step-wise screening procedure. * $p < 0.05$.

Management option	R ²	t-ratio	F-ratio	p<
Agreement				
Protected areas	0.03			
Years in occupation		-2.12	4.51	0.03*
Age of respondent		1.56	2.44	0.12
Closed area	0.07			
Years in occupation		-2.33	5.42	0.02*
Biweekly expenditure	-2.21	4.41	0.04*	
Minimum fish size	0.16			
Material style of life		-2.17	4.78	0.03*
Years in occupation		-4.38	19.45	< 0.001*
Age of respondent		2.39	5.69	0.02*
Biweekly expenditure	2.3	5.28	0.02*	
Species selection	0.03			
Years in occupation		1.23	1.50	0.22
Biweekly expenditure	1.8	3.22	0.07	
Gear restriction	0.05			
Years in occupation		-3	9.00	0.01*
Age of respondent		1.46	2.14	0.15
Benefits				
Protected areas	0.07			
Years in occupation		-2.47	6.09	0.02*
Biweekly expenditure		2.34	5.47	0.02*
Closed area	0.12			
Years in occupations		-4.49	20.14	< 0.001*
Age of respondents		-1.74	3.02	0.08
Closed season	0.02			
Biweekly expenditure		-1.57	2.46	0.12
Minimum fish size	0.1			
Material style of life		-2.59	6.69	0.01*
Years in occupations		-2.9	8.43	0.01*
Biweekly expenditure		1.23	1.52	0.22
Species selection	0.06			
Material style of life		-1.73	2.99	0.09
Level of education		1.27	1.61	0.21
Biweekly expenditure		2.57	6.61	0.01*
Gear restriction	0.04			
Level of education		2.52	6.34	0.01*

mentioned increased conflicts, a lack of benefits or alternatives, reduced fishing grounds or ineffectiveness because natural phenomena or God controlled changes in resources.

Villagers saw lower benefits of closed seasons than government officials, but saw moderate to high benefits for the national government (Table 18). Government officials and villagers agreement with closed seasons was not associated with the socioeconomic variable, but villagers' scaled perceptions of benefits was negatively associated

with years in the occupation and positively associated with biweekly expenditures (Table 19). Respondents who agreed with closed seasons stated that it improved the resource, while those that did not listed reduced yields and incomes, a lack of alternatives and the control of resources by natural phenomena or God.

All occupations saw species restrictions as benefiting the national government, but not self or communities, with villagers more strongly viewing this disparity in the beneficiaries

Table 19. Factors influencing managers' agreement response and perceived benefits of various management options for government officials' responses based on step-wise multiple regression analysis. Responses and variables included are only those that remained after the step-wise screening procedure where only those whole models that were statistically significant are presented. * $p < 0.05$.

Management options	R ²	t-ratio	F-ratio	p<
Agreement				
Protected areas	0.16			
Component wealth		-1.46	2.13	0.173
Closed season	0.14			
Years in occupation		1.34	1.79	0.208
Species selection	0.48			
Level of education		2.27	5.13	0.047*
Biweekly expenditure		-2.56	6.56	0.028*
Benefit				
Closed area	0.67			
Component wealth		1.74	3.03	0.120
Years in occupation		-2.87	8.25	0.021*
Level of education		-1.34	1.79	0.218*
Biweekly expenditure		2.20	4.84	0.059
Closed season	0.17			
Level of education		1.51	2.28	0.159
Minimum fish size	0.65			
Level of education		3.06	9.35	0.012*
Biweekly expenditure		2.04	4.17	0.068
Species selection	0.48			
Age of respondent		-3.00	9.01	0.013*
Biweekly expenditure		1.30	1.70	0.222
Gear restriction	0.33			
Level of education		-1.24	1.53	0.245
Biweekly expenditure		2.10	4.42	0.062

(Fig. 25, Table 18). This view was pervasive among villagers, as there were no significant relationships between socioeconomic variables and agreement with this restriction apart from a positive association with their biweekly expenditures. Respondents who agreed with species restrictions listed protecting future stocks or climate effects on the stocks as reasons for restrictions. Government officials' agreement with species restrictions was positively associated with the level of education and negatively with biweekly expenditures, while the perception of benefits was negatively associated with the age of the respondent (Table 19). Respondents who disagreed with restrictions believed it was not possible to enforce them, that they would have a bad effect on the economy or that these species were not under control by human management.

Comparison of respondents in villages nested within Park and non-Park categories found that Park villages perceived lower benefits from

protected and closed areas, gear restrictions, minimum fish lengths and species selection, but greater benefits from closed seasons than non-Park villages (Fig. 26).

Village respondents nested within these categories were different for protected areas, closed areas and closed season as the Park villages of Jibondo and Juani differed from Miburani; villagers in Miburani perceived benefits in a manner similar to the non-Park villages. There was general agreement among occupations on the gears to be discouraged by managers and villagers ($F = 1.47$, $p = \text{NS}$) with beach seines and spearguns rated the highest for restrictions, poisons and explosives rated moderately, and traps and hook and line rated the lowest.

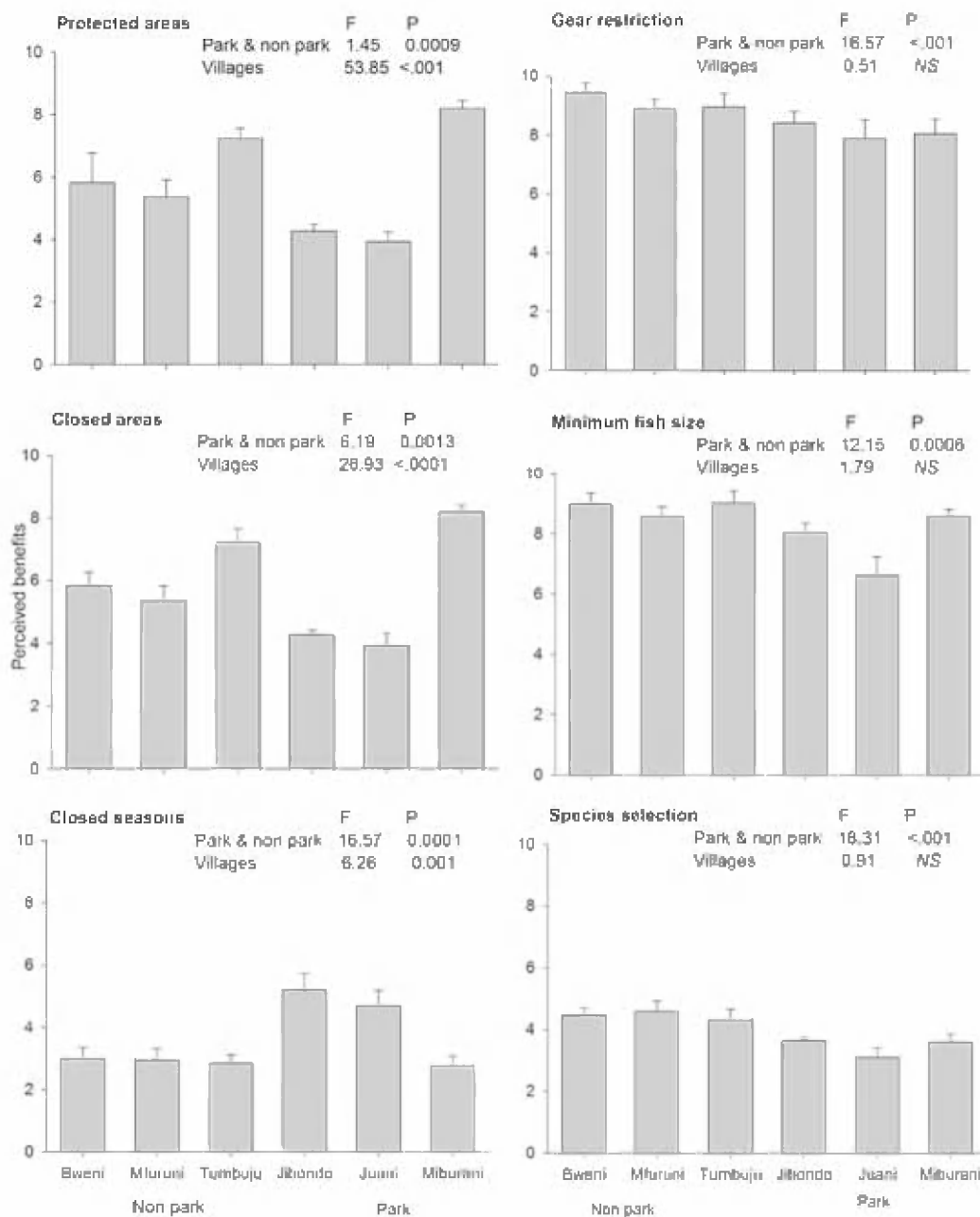


Figure 26. Lickert scale perceptions (relative 0 to 10 scale) of benefits of management options (namely protected areas, closed areas, closed seasons, gear restrictions, minimum fish size restrictions and species selection) within six studied villages. Bweni, Jibondo and Juani villages are in or close to the park, and Mibureni, Mfuruni and Tumbuju are outside the Park. Results of nested ANOVA testing for differences between Park and non-Park sites with villages nested within these categories are presented (ns=not statistically significant).

Discussion

Ecological studies

The overview

Benthic community structure

The ecological condition of coral reefs in the western Indian Ocean (WIO) greatly represents the historical climate and bleaching disturbances, the extent to which reefs have been disturbed by past thermal anomalies. For example, the low coral cover recorded in the period 2 of the analysis and the decrease in cover northward reflects the impact of the 1998 ENSO. Period 2 represents the time immediately after 1998 when areas in the central-northern WIO suffered larger mortalities than reefs in the southern WIO (Ateweberhan and McClanahan 2010). The increased sampling in the third period included more locations from the south and should have influenced the higher cover of hard coral during this period. Probably linked to their higher cover and dominance by bleaching susceptible taxa, closures had lower cover than fished reefs in period 2 (McClanahan 2008a; Darling *et al.* 2009). This difference, however, disappeared in period 3 probably due to the higher region wide post-bleaching recovery in fisheries closures (Ateweberhan *et al.* 2011).

Analyses during the final sampling period, when the data was more complete, indicated that sheltered reefs had higher cover than exposed reefs. Considering their higher cover in period 1 and the lack of difference in period 2, exposed reefs probably suffered higher decline in cover in 1998. They may also have had a lower recovery after 1998. Although high water flow environment in exposed reefs may be more suitable for coral growth during normal conditions (Obura 2005; Van Woesik *et al.* 2005), it may create narrow environmental conditions for acclimation resulting in higher bleaching impacts (McClanahan *et al.* 2007a,b). Exposed reefs provide conditions conducive for maximum photosynthesis, capture of particles and uptake of nutrients, thereby allowing dominance of fast growing corals (Jokiel 1978; Aronson *et al.* 2002; Sebens *et al.* 2003). These fast growing and dominant taxa are among the most susceptible to bleaching. Following a mass mortality various algae that grow better in high-energy environments can dominate these areas. The

pre-emption of space by these algae may, then, result in reduced coral recruitment and overall decreased coral recovery.

Results indicate that there was a decline in coral cover due to overfishing, destructive fishing, bleaching and their interaction with other stressors that can result in a quick take over by various algae after a mortality event (McClanahan *et al.* 2001; McClanahan 2008). Nevertheless, fleshy algae dominated fished reefs on high-energy areas in the south and their distribution may be more influenced by the physico-chemical environment than by management.

Coral community structure

The overall change in coral cover described above reflects the dynamics of coral bleaching where susceptible and tolerant coral taxa are associated with the sampling period, exposure, and management depending on the history of thermal anomalies interacting with these factors. For example, Acroporids had lower cover in fisheries closures during the second period, suggesting a strong response to the 1998 ENSO in these reefs. As mentioned above, fisheries closure often promote dominance of fast growing coral taxa. These taxa are also the most susceptible to bleaching (McClanahan *et al.* 2004; Obura 2005) underlining the differential mortality related to management.

Pocilloporids, despite their high bleaching susceptibility, showed fast recovery in the old parks of Kenya. Recovery of other coral species in these old parks has been slow and probably due to poor recruitment and predation (McClanahan *et al.* 2005a). Pocilloporids can have stronger coral skeletons in comparison to Acroporids and this combined with their disturbance-induced reproduction and lower reliance on coralline algae substrate may be responsible for their recovery after the mass mortality.

A strong negative relationship between recovery of coral cover and crustose coralline cover has been observed in Kenya (Ateweberhan and McClanahan in review). Some corallines induce coral larval settlement while others do not (Harrington *et al.* 2004) but most recruitment studies suggest Pocilloporid are not highly reliant on corallines (O'Leary and Potts 2011). There does appear to be higher recruitment of corals onto coralline algae in Kenya (O'Leary *et al.* 2011)

but there may also be higher post-settlement mortality associated with higher predator abundance. Corallines suffered some loss across the 1998 event (O'Leary and McClanahan 2010), probably due to increases in fast growing algae, and this may have promoted recruitment of coral taxa, such as Pocilloporids that are not greatly reliant on corallines.

The fact that Faviids remained proportionally high in fisheries closures in all periods indicates that they were more influenced by management than the thermal anomalies. In contrast, Poritiids remained constant in all periods with little by management difference indicating that they were less influenced by either factor. We suggest that the opposing pattern in Acroporid, Pocilloporid and Poritiid cover with latitude reflects this differential response in susceptibility and the impact of the 1998 ENSO. For example, McClanahan and colleagues (2007) showed a strong decreasing linear relationship between post 1998 distribution of *Acropora* and *Montipora*. The pattern was opposite for the less susceptible massive *Porites*. Corals grouped under the category 'other' were probably most influenced by fisheries management, as they showed fewer differences across time, similar to the Faviids.

Bleaching responses and susceptibility

Most of the bleaching was observed during this study in the southern WIO and after 1998 when there was high mortality of bleaching sensitive taxa, particularly in the northern Indian Ocean (McClanahan *et al.* 2007b). Areas in the south were probably spared mass mortality of sensitive taxa in 1998 because their SST and hydrodynamic properties promoted greater resistance to bleaching (McClanahan *et al.* 2007a; Maina *et al.* 2008; Ateweberhan and McClanahan 2010), rather than their benthic and coral community structure, which is now dominated by taxa that declined greatly in the northern Indian Ocean. We believe this higher bleaching reflects the higher abundance of these bleaching sensitive taxa in the southern part of the region, rather than the south having warmer temperatures.

Bleaching responses were also higher in closures and exposed areas. The positive response of bleaching to exposure is likely to result from either a narrow environment for coral taxa for acclimatization, thus their inability to resist extreme conditions, or by promoting dominance of fast growing bleaching susceptible coral taxa

in closures and exposed reefs. Consequently, the south was observed to bleach more because they still have the species that do bleach and closures and exposed areas promote corals that are susceptible to bleaching (Darling *et al.* 2010).

Bleaching response decreased northward and latitude had positive interaction with exposure and management in its effect. The northward decrease in bleaching response could be due to a sampling bias because most of the post 1998 bleaching events occurred in the south. The bleaching susceptibility is, however, a reflection of the coral community structure. The relationship with latitude is most likely a function of the differential effect of the 1998 ENSO, which resulted in higher relative dominance by bleaching resistant forms in the north. The southern WIO still supports healthy populations of *Acropora* and other bleaching susceptible taxa.

Symbiont studies

Biogeographic spatial patterns

On a regional scale, the most common symbionts of scleractinian corals in the central and western Indian Ocean are Symbiodinium in clade C, but there are pockets of clades A, B, and D throughout the region. Clade G has also been found in corals in intertidal environments at Cape Panwa in the Andaman Sea (Thailand). However, only three colonies of *Coeloseris mayeri* and one colony of *Montastraea valenciennesi* were reported, and all of these colonies contained mixtures of both clades G and D (LaJeunesse *et al.* 2010). We excluded clade G from our analyses because the unusual environmental conditions experienced by these intertidal corals are unlikely to be reflected in the satellite environmental data that we obtained. Therefore, although it is clear that an apparent intertidal niche exists for these symbionts, we cannot define it on the basis of these satellite data.

At some sites, notably the Arabian Gulf, clade D replaces clade C as the dominant symbiont of scleractinian corals. There were also additional sites where clade D is common, such as Kenya, Madagascar, and Thailand. The only locations where clade D appears to be absent (at the level of resolution of these studies) are the farthest latitudinal extremes, including South Africa (~30°S) and Israel (30°N).

Clade A was found in the Red Sea and Arabian Gulf in the northern hemisphere and Madagascar and Mauritius in the southern hemisphere. These sites also represent higher latitude areas of the study, although they do not include the most southerly sites in South Africa. Clade B was found at just one site (Mtwara in Tanzania, where 9 colonies of *Pocillopora* were found only hosting clade B), and we included them in the analysis because, unlike clade G, these corals were not intertidal, and therefore reliable environmental data could be obtained from satellites. Clade B is also much more common than clade G in scleractinian corals worldwide (being particularly common in the Caribbean) and hence its niche parameters in the WIO are of more potential relevance to corals elsewhere.

Reef-scale spatial patterns in Kenya

There were clear taxon-specific differences in symbiont communities, with genus being the most significant factor in explaining variability in the symbiont clade data. Although site and year were significant on their own, when tested simultaneously with genus, they were not significant. This was true both for all coral taxa sampled, as well as for the four dominant coral genera. However, the relatively strong interactions between genus and site, and the relatively weak interactions between genus and year, indicate that the effect of specificity on symbiont distributions is, itself, influenced by location and time.

The proximate causes underlying the interaction with site and year are revealed by analysis of the temperature data collected from *in situ* gauges. Bivariate relationships and stepwise regression analysis showed that maximum, minimum, mean and standard deviation all contribute significantly to the model, although their overall contribution was relatively weak ($R^2=0.05$). For example, the threshold maximum annual temperature at which clade D becomes dominant varied from $\sim 32^\circ\text{C}$ in *Pocillopora* to $>35^\circ\text{C}$ in *Porites* (if it indeed it ever becomes dominant in this genus, $N=1$). This supports the hypothesis that coral specificity contracts niche space for *Symbiodinium* clade D among different hosts, although it may never be entirely absent, as indicated by the single colony of *Porites* dominated by clade D.

The rank of different coral hosts in their propensity to host clade D at high temperatures is as follows: *Pocillopora* = *Galaxea* > *Pavona* > *Acropora* > *Porites*. Coral genera at the high end of this ranking (e.g.

Pocillopora) are the most “thermally labile” taxa; defined here as those most likely to experience changes in their symbiont communities in response to temperature changes over space and time. Thermal lability in symbiont communities is one axis for identifying taxa with the highest capacity for adaptation/acclimatization, although it is only one factor among a complex suite of traits that might contribute to identifying “winners” and “losers” in a climate change context (Baird *et al.* 2009).

The significant interaction between genus and site, combined with the results of the regression analysis against temperature variables, indicates that site-specific temperature regime plays an important role in determining differences in symbiont communities. Although all sites had similar mean temperatures (ranging from 27.34°C to 27.60°C), tidal variability at each the four sites results in localized heating and cooling over short time scales as a result of restricted water exchange between the lagoons and the fore reef. This results in considerable differences in temperature variability between sites.

Kanamai had the highest frequency of colonies containing clade D *Symbiodinium* and had the highest mean annual maximum water temperatures over the study period (33.91°C), lowest mean annual minimum temperatures (23.83°C), and highest standard deviation (1.81°C). Kanamai also had the highest positive skewness; a long right-hand tail in the temperature distribution, indicating rare but extremely high temperatures and was the most leptokurtic site (positive kurtosis in the temperature distribution), indicating a narrow peak around the mean and fatter tails to the distribution.

In contrast, Mombasa had the lowest incidence of clade D and had the lowest annual maximum temperature (31.07°C), highest minimum temperature (24.64°C) and lowest standard deviation (1.23°C). It had the lowest positive skewness (i.e. fewer occurrences of extreme high temperatures) and is one of the most platykurtic sites (negative kurtosis), indicating wider peaks in the temperature distribution and thinner tails in the distribution.

Together, these data suggest that no single temperature metric determines the relative frequency of clade D in reef corals among different sites. Instead, the overall temperature regime drives the abundance of clade D, with high maximum temperatures, high variability, high positive

skewness and leptokurtosis all helping to drive the relative frequency of clade D. In this study, low minimum temperatures were also associated with high frequency of clade D, but this is probably an artifact of high variability; low minimum temperatures without high maximum temperatures are probably unlikely to drive the clade D found in Kenya (but see Chen *et al.* 2005 for an unusual clade D commonly found in subtropical Taiwan).

Temporal patterns in Kenya

There was no sustained directional change in the relative abundance of clades C and D in Kenya over the period 2000-2010. However, during the first half of the study (2000-2004) colonies containing mixed communities of C+D were relatively frequent, whereas in the second half of the study (2005-2010) mixed colonies were rare, occurring only in 2009. The resolution of DGGE limits the detection of symbionts unless they represent at least 5-10% of the total community (LaJeunesse *et al.* 2008), and it is likely that more colonies contained mixed communities than were detected in this study (Baker and Romanski 2007; Silverstein *et al.* in review). Nevertheless, the fact that clade D symbionts were detected in mixed communities from 2000-2004, but became rare afterwards, indicates that they may have fallen below threshold limits in the latter half of the study. This suggests that the changes in the relative frequency of clade D in this study were the result of shuffling of pre-existing symbiont communities (Baker 2003; Stat *et al.* 2006).

One hypothesis why mixed communities were relatively common from 2000-2004 is that these corals were still recovering from the effects of 1998 bleaching. If some of the colonies that survived 1998 experienced increases in clade D (Baker *et al.* 2004), the disappearance of mixed communities by 2005 may indicate that these increases were sustained for as much as 6 years following the event. There is also some evidence for a brief increase in clade D in 2005 that was lost again from 2006-2008 before another spike in clade D occurred in 2009-2010. Bleaching was observed in these study sites in 2005 but did not sustain high mortality (T. McClanahan, personal observation). These patterns are more apparent in *Pocillopora* and *Pavona* from Kanamai and Diani but are absent from Mombasa, suggesting that temperature regimes at Kanamai and Diani may have favored clade D during those years. In contrast, in Mombasa, a warming trend from 2002 to 2005 coincides with an increase in clade D over the same timeframe (C. Starger, unpublished analyses).

Symbiont communities on shallow Kenyan reefs are relatively dynamic, and unidirectional shifts to favor particular symbionts are rarely maintained over multiple years, given that the prevailing temperature regime is determined by short-term tidal variability that varies between sites. Indeed, site-specific tidal variation in temperature overrides any climate signal in our 2000-2010 data, although the possibility of longer-term interactions with episodic ocean-atmosphere oscillations, such as the El Niño-Southern Oscillation and the Indian Ocean Dipole, remains.

Our data suggest that any disturbance that affects the temperature metrics investigated here is likely to affect the abundance and distribution of *Symbiodinium* in clade D. Consequently, the composition of symbiont communities and their dynamics cannot be explained solely as the result of acute disturbance (Baker *et al.* 2004) or by long-term environmental conditions (LaJeunesse *et al.* 2010). Instead, on Kenyan reefs, both acute and chronic stressors caused by oceanographic and tidal oscillations, interact with taxa to produce highly dynamic symbiotic communities. High maximum temperatures and high variability allow clade D to be maintained at relatively high levels in Kenya, although its relative abundance varies significantly from year to year because tidal variability causes frequent stress periods that are likely to disrupt these communities over lunar time scales. Since the immediate effects of tidal variability are far greater than that of climate warming, the emerging picture is one in which gradual changes in symbiont communities as a result of warming are masked by larger changes over shorter timescales.

These results contrast with and complement monitoring studies in other areas. In Panama, extreme temperature fluctuations do not occur, despite high tidal ranges, because reef geomorphology still allows water exchange. Consequently, intra-annual disruptions are infrequent and gradual changes in symbiont communities following acute disturbance, such as the 1997-98 El Niño, are more detectable (Baker *et al.* in prep.). In Barbados, annual maximum temperatures are moderate and temperature variation is low; therefore transient spikes in clade D following bleaching cannot be maintained (LaJeunesse *et al.* 2009). In the Florida Keys and Bahamas temperatures are also moderate, but variability is higher than in Barbados, although less extreme than the tidal fluctuations found in Kenya, and consequently

clade D is maintained in the short-term but cannot persist in the absence of further bleaching or other acute disturbances (Thornhill *et al.* 2006).

This perspective suggests that *Symbiodinium* in clade D are not inherently opportunistic (LaJeunesse *et al.* 2009; Stat and Gates 2010) but rather, on most reefs, the environmental niche that supports these symbionts is rarely maintained. Periodic disruptions due to mass bleaching will increase the relative abundance of clade D and warming baselines may tend to increase the longevity of these shifts, but we should not expect all bleaching events to lead to dramatic or sustained changes in symbiont communities, since equilibrium conditions will quickly weed out these symbionts once conditions return to normal. These results provide a mechanistic basis for the observation that corals from warm yet variable conditions are the best able to survive climate change (McClanahan *et al.* 2005d) and support assessments of thermal regime as a means of economically identifying conservation priority sites in anticipation of continued climate change.

Effects on coral populations

These results of the long-term monitoring of Kenyan corals indicate generally declining population trends in *Acropora* and branching *Porites*, some increasing trends in *Pocillopora* and *Pavona*, and interactions with the temperature and fisheries management environments. The declining taxa were generally more abundant (*Acropora* on unfished reefs and branching *Porites* on fished reefs) and had lower dominance of *Symbiodinium* in clade D than the increasing taxa. The increasing taxa were less abundant and had greater or more variation in the dominance of clade D. *Pavona* had the highest dominance of clade D but was only common and increased on fished reefs. *Pocillopora* increased overall and on unfished reefs but the larger increase was on the unfished reefs, which had lower dominance of clade D. These results suggest a complex interaction between the structure of the *Symbiodinium* community, the relative abundance of different coral taxa and fish communities, and the temperature environment. Given that these reefs have been well studied, it is possible to evaluate some of these additional factors and their influence on our results.

Dominance of clade D had been associated with stressful conditions, warmer temperatures and recent bleaching (Toller *et al.* 2001; Berkelmans and van Oppen 2006; Oliver and Palumbi 2011) but mostly at local, rather than regional scales (Oliver and Palumbi 2009). There were very small differences in mean seawater temperatures among studied Kenyan reefs that were unlikely to have affected symbiont dominance but there were notable differences in temperature variation. Notably, higher temperature variation, flatter distributions and maximum temperatures are likely to have been among the factors that promoted clade D in the fished reefs. In particular, two of the fished reefs, Vipingo and Kanamai, have elevated reefs and shallow lagoons that have the highest temperature variance (McClanahan and Maina 2003). These reefs also have lower numbers of coral taxa than the more stable temperature environments in the protected areas but also have greater resilience to temperature anomalies (McClanahan 2008). Consequently, it may largely be the temperature environments more than fishing that influences clade D dominance in these reefs.

This conclusion assumes that it is warm or variable temperatures that drive the dominance of clade D versus clade C but it may also be the taxonomic composition of corals on reefs, which can be influenced by biological as well as environmental interactions. Studies of predation on corals, for example, have shown that branching *Pavona* and *Porites* transplanted from fished to unfished reefs were rapidly consumed by predators (McClanahan *et al.* 2005a). Consequently, the dominance of *Pavona* and clade D could be associated with differential survival of coral taxa under different management systems. However, branching *Porites* was quite common on fished reefs and contained no detectable clade D. It also experienced the fastest and highest mortality of all coral taxa across the 1998 thermal anomaly, whereas *Pavona* was considerably more resistant (McClanahan *et al.* 2001). Previous long-term studies have shown differential responses to thermal disturbances between the two management systems (McClanahan 2008). Biological interactions are expected to influence the mortality and recovery of the coral taxa, particularly higher predation on some taxa of corals in unfished reefs (McClanahan *et al.* 2005a).

The complexity of the patterns we observed likely result from changes in coral community composition in different environments as well as differences in the flexibility of the coral-symbiont

relationship among different coral taxa. Some of the site- and management-level variability may be attributable to finer scale taxonomic patterns in different coral genera/subgenera that cannot be evaluated at the coarser taxonomic resolution of this study. For example, *Pocillopora* currently contains two dominant recognized species in Kenya, but the number of taxa may increase as more molecular studies are undertaken (Souter 2010; Pinzon and LaJeunesse 2011). The more robust form, *P. verrucosa*, is the more common taxa on unfished reefs compared to *P. damicornis*. This may explain the lower dominance of clade D on unfished reefs, if *P. verrucosa* more commonly associates with clade C than clade D compared to *P. damicornis*. The more fragile *P. damicornis* may be more susceptible to predation than *P. verrucosa* and this may, like *Pavona* and branching *Porites*, reduce their numbers where coral predators are abundant (Neudecker 1979). *P. damicornis* may either have more clade D or a more flexible symbiotic relationship than *P. verrucosa*. Each of these factors, either alone or in combination, was likely to have contributed to the observed patterns.

Given this variability, we suggest that the observed patterns are the result of complex interactions between different species of coral host (which vary in their symbiotic flexibility), the thermal environment of different reefs, and biological interactions within these reef communities. The physico-chemical environment is influenced by factors at the local scale (such as water depth and reef height, which affect temperature variability), and the biological environment is mediated by the intensity of fishing. This ecological complexity promotes a variety of possible outcomes following large-scale human disturbance associated with climate change. The presence of clade D alone is not a panacea for corals facing climate change, given the considerable physical, biological and ecological variability that can influence survival outcomes.

Local fisheries management practices, environmental history, and the coral association with symbiont clades all play a role in determining the future of these reefs and require a reevaluation of priorities for conservation in the face of climate change. This study suggests that a coral's ability to host clade D *Symbiodinium* can influence the relative success of coral taxa in response to increasing climate disturbances expected with climate change. Yet, environments typically selected as priorities for conservation (Myers *et al.* 2000) are not the same as those that create conditions for resilience to climate

change. Given that protected areas are frequently located in areas of high environmental stability and diversity and these may be most affected by temperature anomalies (McClanahan 2008), there may also be a need to insure that resilient locations and taxa are also being well managed, such that they contribute to the regional stability of coral reefs. Consequently, including stressed reefs in the portfolio of conservation and management systems is expected to improve the chances for reef persistence by including taxa with the ability to adapt to the warm and variable environments expected in the future.

Management preferences and socioeconomics

The regional overview

There is considerable diversity of opinions over the types of management that are supported by fishers and managers in the region. These are not always closely related to national laws and suggest the need for site-specific management implementation. Kenya, the country with the oldest and most developed marine protected area management system (Wells *et al.* 2007; McClanahan *et al.* 2009c) had the most communities with positive views towards all management. Nevertheless, there were also communities with antagonistic views to a number of management restrictions, often those communities far from protected areas. This suggests that there is a need for increased interactions and possible peer-to-peer dialogues and education programs in order to share concerns and experiences with various management options. These may be useful both within and between nations to diversify the shared experiences. The causes of these heterogeneity in opinions will be explored in future analyses of the data but the cases of Kenya and Mafia have been well analyzed and can be useful in understanding the contexts that produce these opinions.

Lessons from Kenya

Socioeconomic context

The results from Kenya suggest that restrictions, such as gear and minimum length restrictions, had large-scale appeal but area, species, and closure management had more limited support. These preferences are weakly associated with socio-economics of the respondents as well as the

spatial distribution and history of management. In general, restrictions were scaled positively but three distinct groupings of management preferences were found among the landing sites and government offices. The majority of fishers and particularly those most dependent on fishing incomes were most opposed to closed area and species restrictions, partially generated from or justified by a perceived sense of disparity in the benefits of these forms of management.

The sense of economic disparity is probably not entirely based on direct experience, as the landing sites closest to the government managed areas had among the most positive views towards area and closure management. In addition, high dependence on fishing and low incomes and educations are expected to heighten this sense of unease with closure management and lost fishing area and potential income (McClanahan *et al.* 2008; Cinner *et al.* 2009). Consequently, there are opportunities for greater compliance of some restrictions on a broad national scale. Additionally, it may be possible to change perceptions in those areas without direct area and closures management experiences if more information about the costs and benefits of closure and area management is shared among these fishers. Programs like site exchanges between fishing communities may help to exchange both information about and experience with protected areas. Nevertheless, information and education alone are not expected to change preferences or behaviors without greater financial wealth, stability, and decreased dependence on fishing (McClanahan *et al.* 2008).

Positive views of closure and area management were shown to increase with the age of closures and education in Kenya for closures ranging in age from a few to 35 years (McClanahan *et al.* 2005b). In the youngest closure of that study (Kenyatta Beach), which originally had the most negative views, there had since been reduced level of conflict since the closures (McClanahan *et al.* 2005e). Evaluations of fishing income in Kenya showed that fishing grounds next to closures with gear restrictions had rising incomes associated with larger and more valuable fish (McClanahan 2010). Consequently, changes in perception and reduced conflicts with time since closure may be stimulated by the increased incomes that may follow after some period of closure. In some cases, increased income may be associated with reduced effort associated with restrictions on gear and increases in catch for the remaining fishers (McClanahan 2010).

There is also an expected lag effect where catch may drop shortly after the closure but may increase as the biomass and migration out of the closures increases (Halpern *et al.* 2009; Vandeperre *et al.* 2010). Additionally, the creation of closures may stimulate the tourism economy and fisher families and communities may receive some benefit from these developments (Hicks *et al.* 2009; Cinner *et al.* 2010). Some of the initial negative perceptions towards closures may be balanced if information about these long-term case studies are shared, which is largely that there are initial costs but potential long-term benefits to closures

The socio-economic context in which fishers operate is critical to perceptions and compliance. Poorer fishers who's ability to change their behavior and adapt to immediate disturbances may depend on their household economies. For example, Cinner *et al.* (2009) found that fisher's reporting their likelihood of exiting a fishery increased with their household wealth and job opportunities. Some fishers may continue to fish and resist closure and other management efforts if they do not see or have other opportunities, which can lead to behaviors that have the potential to reinforce ecological degradation (Cinner *et al.* 2011).

The causes and consequences of livelihood diversity in rural communities are complex (Barrett *et al.* 2001; Ellis 1998, 2000). Consequently, attempts to indiscriminately add more jobs to already diverse livelihood portfolios in some fisher communities may have marginal or no benefits (Allison and Ellis 2001; Pomeroy *et al.* 2006). More specifically, alternative foods, stability, and wealth may influence perceptions towards losses in fishing grounds and lags in fish catch that can result from closures.

Size restrictions

Restrictions on the size of fish caught and closures have been examined from the normative theoretical and empirical approaches of fisheries and conservation scientists (Halpern and Warner 2003; Ault *et al.* 2008; White *et al.* 2008). These approaches are useful for understanding biophysical expectations based on these metrics and assumptions but do not necessarily assure adoption and compliance, which may depend as much on local perceptions and knowledge. In the case of minimum fish lengths, the theoretical-empirical scientific approach produced mean values that differ from the local Kenyan

suggestions. For example, the dominant three species in the fish catch, which compose 80% of the catch, were *Siganus sutor* (rabbitfish), *Leptoscarus vaigensis* (seagrass parrotfish) and *Lethrinus mahsena* (pink-ear emperor) and have lengths at an estimated optimum yield of 32.7, 22.7, and 29.6, where as the estimated age at first maturity are 29.1, 21.2 and 26.7 cm, respectively (www.fishbase.org). These scientific values generally lay above the mean values for minimum lengths given by fishers, between 15.3 to 18.4 cm. Fisher suggestions are closer to the ages at first maturity, which are more likely to be something that fishers can view and appreciate as important. Beyond these differences in means and metrics, the main practical difference between the scientific calculations and fisher's expert opinions is the higher variability among fisher's responses. High variability and weak consensus can lead to conflicts and low compliance. Consequently, we suggest that combining these two approaches and informing fishers of the fisheries science approach and recommendations will improve the chances for consensus and compliance.

The acceptable or minimum size of closures is more difficult to evaluate, as the responses were more variable and based on the respondent's ability to estimate sizes and willingness to answer this question. The mean number of years of education among fishers was 5.2 years, so this may have been a limitation to their responses but this may also have arisen if the fisher did not see benefits from closure and area management, in which case they would not estimate the size. Among those who did answer the question, the preferred size of the closure varied from 3.0 to 13.8 km² and protected areas from 4.6 to 34.7 km², increasing from the negative to positive preference clusters. Conservation scientists have suggested that minimum viable size of a closure is 3.1 km² (Halpern and Warner 2003) and a preferable size of 12.5 to 28.5 km² (Shanks *et al.* 2003). Based on more than 4000 marine protected areas, the median size of marine protected areas globally is 4.6 km² and the mean is 544 km², which is greatly skewed by a few very large marine protected areas (Wood *et al.* 2008). No-take closure areas are only ~13% of these protected areas and therefore sizes are likely to be smaller. Nevertheless, without assuming the causes of the non-responses in our survey and the few very large protected areas in the global compilation, the estimates of sizes for closure, protected areas for our respondents were similar to those provided by conservation scientists and what is found globally.

Consequently, it should be possible to create and maintain closures that are above some suggested minimum viable size using the recommendations of fishing communities. There are, however, many closures that are created and maintained by communities that are considerably smaller than the minimum viable size and they do show responses in fish abundance to closure, if given sufficient time to recover (Russ and Alcala 2004). They may not be sufficient on their own to meet conservation needs but, if part of a larger network and some larger nationally protected areas, more conservation and management goals can be met (Weeks *et al.* 2010).

These findings can be seen as an opportunity to guide more context-appropriate management where technical biophysical and local knowledge approaches can be combined (Aswani and Hamilton 2004). The above results indicate that heterogeneity in perceptions and actual benefits of management restrictions can be considerable and this potentially creates challenges for successfully implementing management, particularly where decisions and potential benefits are determined at the national but considerable short-term costs can potentially accrue at the local level. The costs and benefits of specific restrictions may also be variable in space, time, and individual economies, which can cause considerable disparity among stakeholder's views. Poor consideration of these socioeconomic and perception considerations and the open-access nature of fisheries are arguably the reasons for poor compliance with fisheries management (Ostrom 2007). Nevertheless, the findings are hopeful for planning management at multiple scales where local management is a mix of national laws and local bylaws and many of the suggestions of the respondents are similar to those provided by theoretical-empirical findings of conservation scientists.

Lessons from Mafia

In Mafia, there was general agreement about the benefits of gear restrictions and minimum size of catch. The national government was perceived to receive the largest benefits, and these declined from there to the community and individual. Nevertheless, we found considerable differences among the perceptions of who benefits from restrictions, which may be among the primary causes for conflicts between local social norms governing marine resource use and the legislated and national-level management

systems. For example, government officials saw the communities as a whole benefiting from restrictions more than the resource users themselves. This reveals a fundamental problem of observer subjectivity in prescribing the most appropriate actions for resolving conflicts. Conflicts are molded by factors such as the person's history and knowledge of resources and management effects, reliance on the resource, the time and social scale of their perceptions of benefits. These are further influenced by socioeconomic and educational status, connections to wider sources of information and alternative resources and markets, politics over the control of resources and complex interactions between these factors.

Socioeconomic context

Preferred management and perceptions of benefits differed based on occupations, the location of the villages in relationship to the Park and other geographic and socioeconomic factors. Positive views on restrictions were frequently associated with education and, in some cases, biweekly expenditures. Perception of benefits and management options was frequently associated with the interviewees' time employed in their occupation but the relationships were often negative, particularly for closure benefits. These general findings are consistent with several recent studies exploring factors related to heterogeneity in fishers' perceptions of management and the environment (McClanahan *et al.* 2005b,c; Gelcich *et al.* 2005, 2008). Studies of management restrictions in southern Kenya found fishers to be more supportive of gear than other forms of management (McClanahan *et al.* 2005c). Perceptions can change with experience however, as McClanahan *et al.* (2005a) found stronger support for closures with the increasing age of the closure and Gelcich *et al.* (2008) found greater concern for water quality issues with that length of time that Chilean fishers were engaged in co-management.

There were weak associations between agreements on restrictions and perceived benefits and most of the socioeconomic variables for the villagers. In some cases they became increasingly negative with increased length of time in their occupations and material wealth of their household. Biweekly expenditures of villagers were, however, both positively and negatively associated with various restrictions. The strongest factors in the villagers' responses was the position of the villages in terms of Park boundaries,

management, history of interaction with the Park service and other economic options. Jacobson and Maynowski (1997) reported similar findings, where the most knowledgeable resource users had more negative views towards conservation and ecosystem management than recreational users and the general public. Consequently, positive attitudes towards conservation may be enhanced by a general education, but adversely affected when there has been a history of conflicts between resource users and managers and restrictions directly affect access to known resources required for income or survival.

Differences among Mafia villages and comparison with Kenyan findings (McClanahan *et al.* 2005b,c) may provide insight into how perceptions at Mafia were formed. In Kenya, those fishers having higher levels of education and fishing adjacent to older managed areas had more positive perceptions of restrictions and management. Additionally, Kenyan fishers had more positive perceptions towards gear restrictions than permanent closures, and the wealth of the resource user and the history of community programs at the landing sites was not associated with positive perceptions towards restrictions. In Mafia, we found similar responses, but unlike the Kenyan study we compared Park and non-Park villages and found that respondents in two Park villages with a history of interacting with Park and conservation employees (namely Jibondo and Juani) had the most negative perceptions towards restrictions and benefits. The Park villagers of Miburani had a similar history, but more positive perceptions towards restrictions than the other Park villagers. Miburani village is closest to the pier, and associated trade at Kilindoni and their fishing grounds (Mange) restrict the use of gears and collection of species. This contrasts with the full closures adjacent to Jibondo and Juani and suggests the presence of full closures, limits to trade, and the lack of salaried employment are largely responsible for the negative perceptions of management in Jibondo and Juani. Interactions with conservation authorities have failed to improve the villagers' perceptions.

Livelihood diversity is often seen as an important economic buffer for people living near parks but, ironically, MIMP villages had higher household job diversity than non-Park villages. Consequently, livelihood diversity was not associated with positive perceptions towards restrictions and higher compliance. Better access

to markets or salaried employment associated with proximity to Kilindoni may be more important than the number of livelihoods. A large number of livelihoods may be a risk-spreading strategy that can arise from poverty and not a sign of increased economic security (Campbell 1990; Carter 1997). Accordingly, heavy reliance on marine resources, fewer options for involvement in that cash and tourism economy, historical conflicts with management and resources contained within closures could combine to produce the lower levels of support for national government area management and some of the associated restrictions.

Both long-serving government officials and villagers shared negative perceptions towards closures and some other restrictions. This is likely to reflect a long history of conflict and some cynicism about their value or likelihood of reconciliation (Walley 2004). In contrast, older villagers did not always hold these negative perceptions, and so it is unlikely to arise from a simple increase in cynicism over restrictions with age, but rather with occupational experience that might be associated with a conflict or knowledge about the economic value of closures. Although resources in these closures have responded positively to the closure (Kamukuru *et al.* 2004), a long-term study of closures in Kenya has found that it can take many years for the full biomass to recover and that spillover effects can be limited to areas very close to closures (McClanahan and Mangi 2000; McClanahan 2010). Many of the parks in the region may not be economically competitive with resource extraction options in the absence of high levels of tourism (McClanahan 1999). Various conflicts that arose in the early years have still not been resolved 12 years after the Park's implementation (Walley 2004). It is possible that the transition to the benefits of closures has not and may not be made until these issues are resolved.

Mafia Island has a long and complex history that has been characterized by centuries of domination by Arabs, Persians, mixed-African-Arabs, merchants, slavers and plantation owners, followed by German and British colonialists. The indigenous people of Mafia are the Wambwera, who are culturally similar to the people living between Kisiju and the mouth of Rufiji river delta (Mahongo 1994). Most of them are Muslims, which is their source of morality and social organization. Despite historically having a rigid social hierarchy based on slavery and colonialism, much of the social hierarchy inherited from the past has been dissipated by the legacy of the socialist policies from the 1960s (Mahongo 1994; Walley 2004). As a consequence of these policies and because all children inherit by Islamic law, the wealth of the indigenous people has reduced. Decline in the global price of coconuts in recent years has reduced many household incomes.

The government took an initiative to gazette Chole Bay and Kitutia reef as marine reserves in 1975, but without implementing effective enforcement. MIMP was the first marine park to be successfully established in Tanzania in 1995, and covers an area of about 822 km², more than 75% of it below the high water mark. The managed area is located on the southern section of the main island and is part of a 33-km long broken reef that ends in one of the two fisheries closures at Kitutia reef (Wells *et al.* 2007b). Landward of the fringing reef, the seabed is shallow (<50 m deep) and contains a number of large patch reefs that are within the managed area. MIMP's general management plan includes a zoning scheme of core, specified use and general use zones (URT 2000). Core zones are fisheries closures in areas with high or unique biodiversity and include Kitutia Reef and Kinasi Pass. Specified use zones have intermediate levels of protection that allow resource-users to fish with restrictions on gear and species, whereas general use zones have levels of protection that are similar to national laws (no illegal and destructive gear).

Conclusions and Recommendations

This study investigated the ecology of coral reefs in the context of climate disturbances and their expected continued influences on reef ecology. Additionally, the management preferences of stakeholders were studied in order to determine the management systems that might be most easily achieved in this region and in specific communities. These studies uncovered a number of key points that will be helpful in planning adaptation that will improve the chances for the persistence of reefs and the communities that depend on them.

The ecological studies indicate that climate disturbances are not uniform at regional, habitat, or management scales. Specifically, the sheltered reefs appear to have persisted better than exposed reefs after the 1998 thermal anomaly. These sheltered reefs include back reef environments, reefs on the leeward sides of islands, and in bays. The calm conditions may promote periodic warming and stressful conditions that lead to acclimatization and community change that make the rare anomalies less devastating than exposed reefs adapted to more stable conditions. These reefs are also frequently under high fishing, pollution, and tourism pressure, and illustrate the need to increase the level of management and restrictions on these factors in order to improve the chances of coral reef persistence in the region.

Studies of the algal symbionts of corals (*Symbiodinium* spp.) suggest that most of the region is dominated by tropical generalists in clade C that may be more host- than environment-specific. This may challenge the ability of reef corals to compensate through adaptive changes in symbiont communities. However, there is some evidence that warm-environment specialists in clade D can increase in frequency and persist for a few years after major thermal disturbances but this response may be limited to sites that regularly experience high temperatures due to background thermal variability. Some taxa at these sites, such as *Pavona* and *Pocillopora*, do have high dominance

of clade D, but they also may not survive well at all sites due to strong biological interactions on some reefs. This complicates the prioritization of conservation actions but also emphasizes that managing shallow reefs as well as reefs in warm environments, which are not typically considered management priorities, is a new conservation priority. Some sheltered sites are quite stressful and are not as diverse as exposed reefs (McClanahan and Maina 2003) but nevertheless still support the important clade D symbiont, which appears to promote the success of some coral taxa. There are some reefs, notably along the Tanzanian and northern Mozambique that have both the elements of moderate temperature variability and high diversity (McClanahan *et al.* 2007a). We found that some of these sheltered closures had high levels of coral diversity, which is a good prognosis for these management recommendations.

Evaluations of stakeholder communities indicate that government employees charged with the management of natural resources in different countries have positive and similar views towards restrictions. However, the resource users opinions are more variable and can vary considerably within and between countries. The dichotomy between managers and users is particularly large in Tanzania but also exists in Kenya and elsewhere. Many resource users in Madagascar were positive about restrictions, but there is also widespread noncompliance with many restrictions in this country, suggesting a possible limit to the sincerity of responses and usefulness of these answers towards successfully implementing management. Mozambique fishers had more intermediate responses, and there are few evaluations of compliance. Nevertheless, we believe that identifying and understanding differences in stakeholder views and attitudes toward management is a valuable first step towards resolving conflicts. This information can be useful for developing constructive dialogues among stakeholders that can reduce polarization, increase the chances for conflict resolution, and lead towards higher levels of adoption and compliance. Conflict resolution and increased compliance are badly needed in the region if coral reef resources are to maintain their capacity to adapt to a changing climate.

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Appendix – Bibliography of papers produced by the project and associations

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