# Coral Reefs and Climate Change in the Indian Ocean

## A case study of Watamu Marine National Park, Kenya and other Indian Ocean locations

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# Abstract

Coral reefs are arguably the most threatened marine habitat because of multiple anthropogenic stressors degrading the health and resilience of these systems. In the past 20 years there have been increasing observations of mass coral bleaching and mortality associated with increasing water temperatures in the tropics. Reefs provide ecosystem services worth billions of dollars to people living in tropical coastal areas and are the architects of one of the most beautiful structures found on earth. Conserving these habitats is paramount, and conservation planning must contend with climate change along with local and regional stressors. In this thesis Watamu Marine National Park in Kenya is used as a case study of the current challenges facing the conservation of reefs in a warming world. The Western Indian Ocean suffered dramatic bleaching during 1998, which caused the mortality of 70% of Watamu's corals. Using datasets from the 1980s to present the historical trajectory of Watamu's reef community is presented. The current ecosystem resilience is assessed to suggest how this reef will respond to future climate stress. It appears that Watamu's coral community has remained in an altered state post-1998, which, based on its past thermal stress and current coral community, should be resistant to future bleaching. Watamu's resilience and reef health is compared with other locations in the Indian Ocean, including reefs in Kenya and the Maldives that bleached in 1998 and examples from Mozambique and Sumatra of reefs with little evidence of historical thermal stress. Resilience is a multi-faceted process with different major components and numerous interacting factors, which act synergistically on the reef community. Conservation options and opportunities are discussed for the 6 locations examined, using current resilience models and theory as a framework for identifying priority actions. Local and regional-scale human impacts on shallow marine habitats during the last 50 years has been dramatic, and with global-scale climate change as an additional major threat, the next 50 years will be critical for the future of reefs. The locations visited during this study showed encouraging signs of resilience to past thermal stress, with evidence to suggest that corals are acclimatising and/or adapting to increasing water temperatures. The future of reefs in locations like Watamu is uncertain. Better understanding of reef ecology, appropriate conservation techniques and ultimately greater public concern for reefs is required to ensure that there is a future for these ecosystems in the Indian Ocean.

## Declaration

I declare that the work presented here is my own, under the supervision of Professor Alex Rogers with external supervision and guidance from Dr Robert Sluka from A Rocha Kenya and Dr. David Obura from CORDIO East Africa. In instances where others have contributed, the contributions have been specifically acknowledged. I have clearly indicated and referenced where I have quoted and discussed others' work throughout the document. In addition I can confirm this thesis has not been submitted for any other qualification at any institution. I hereby confirm this thesis is submitted in fulfillment of the requirements for the degree of Doctor of Philosophy.

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*I don't think we are going to become extinct. We're very clever and extremely resourceful - and we will find ways of preserving ourselves, of that I'm sure. But whether our lives will be as rich as they are now is another question. (David Attenborough)*

*I can mention many moments that were unforgettable and revelatory. But the most single revelatory three minutes was the first time I put on scuba gear and dived on a*

*coral reef. It's just the unbelievable fact that you can move in three dimensions.*
*(David Attenborough)*

Plate 1. Coral reefs provide a number of ecosystem services for people as well as creating one of the most beautiful natural structures on earth (B. Cowburn).

# Chapter 1. Literature Review

## 1.1 Coral reefs in crisis

Coral reefs are one of the most threatened marine ecosystems and deserve urgent conservation action, for three main reasons. Firstly, reefs possess very high biodiversity, with almost 800 species of coral (Veron 2000), a quarter of the world's marine fish species (Lieske and Myers 1994) and an unknown number of invertebrates and other taxa (Plaisance *et al.* 2011, Fisher et al. 2015). Secondly, this biodiversity is concentrated into only 0.089% of the surface area of the sea (Spalding *et al.* 2001), much of which is found within the highly-populated coastal zone, with an estimated 500 million people relying on reef resources for food, coastal protection, building materials and income (Wilkinson 2008). Lastly, many coral species are highly sensitive to stress, having narrow tolerance ranges for light levels, temperature, salinity and aragonite saturation (Kleypas *et al.* 1999).

The vulnerability of coral reefs is reflected by dramatic losses and declines in reef health around the world, to the point where some have claimed there are no longer any pristine coral reefs left (Knowlton and Jackson 2008). In the most recent "Status of Coral Reefs of the World" (Wilkinson 2008) it was estimated that 19% of all coral reefs had been functionally lost and only 46% could be considered healthy. Other reefs are in various states of decline because of multiple, and often, simultaneous stressors acting on them and even healthy reefs do not have a secure future as the magnitude of coral reef threats continue to grow (Bellwood *et al.* 2004, Graham *et al.* 2011).

The majority of coral reef declines can be attributed to three major categories of stress: climate change, over-fishing and pollution (Hughes *et al.*

2010, Graham *et al.* 2013). Stressors on coral reefs can be in the form of acute disturbances that influence corals over a narrow period of time, such as a mass-bleaching event, or long-term chronic disturbances, such as land-based run-off and sedimentation (Connell *et al.* 1997). Many reefs face several pressures simultaneously (Hughes *et al.* 2003, McClanahan *et al.* 2014) and the impacts on the coral-reef community include: declines in coral cover (Gardner *et al.* 2003), loss of biodiversity and ecosystem function (Graham *et al.* 2014), loss of structural complexity (McClanahan *et al.* 2009a), and, in extreme cases, phase-shift away from a coral-dominated ecosystem (Hughes 1994). From a global perspective, it has been suggested that climate change and more specifically mass coral bleaching and mortality, are now the most important stressors for reefs today (Hughes *et al.* 2003, Carpenter *et al.* 2008, Glynn 2012, Spalding and Brown 2015).

## 1.2 Conservation of coral reefs: successes and challenges

The alarming degradation of coral reefs has been met with a growing call from scientists, governments and local communities to conserve these habitats and the numerous ecosystem services and benefits they provide. Improvements in the understanding of reef ecology and impacts of specific stressors have allowed managers to identify conservation activities to improve reef health, such as fisheries quotas (Mumby *et al.* 2007a) and reducing land-based sources of pollution (Jouffray *et al.* 2015). However, the combined impact of multiple stressors acting on coral reefs and the complexity of the reef's ecological response to different pressures have highlighted Marine Protected Areas (MPAs) as a conservation tool to minimise numerous threats (Sheppard *et al.* 2012).

Well-managed MPAs can protect marine habitats from a range of human activities, such as resource extraction, construction and industry (Salm and Clark 2000). The percentage of territorial water protected by MPAs globally has increased dramatically from approximately 2% to 8% in the past decade (Juffe-Bignoli *et al.* 2014). This has been driven, in part, by nations attempting to fulfil their commitment to the Convention on Biological Diversity, Aichi Target 11, where countries are required to protect 10% of their marine habitats by 2020 (Juffe-Bignoli *et al.* 2014). The median MPA size is a relatively small 5km$^2$ (Wood *et al.* 2008), however, several very large (>300,000km$^2$) MPAs, such as the Chagos Marine Reserve and the Pacific Remote Islands National Monument exist, containing extensive areas of some of the least-impacted coral reef in the world (Knowlton and Jackson 2008, Sheppard *et al.* 2012).

Reviews of the effectiveness of MPAs in coral reef areas show that, on average, protection increases fish biomass, diversity and size (Halpern 2003) and prevents coral loss compared to unprotected areas, which are gradually losing coral cover over time (Selig *et al.* 2010). However, there are concerns that too few MPAs have adequate regulations or effective management to protect reefs sufficiently (Mora *et al.* 2006). In addition, the small size and placement of some MPAs may mean the reefs are still vulnerable to human threats and lack adequate connectivity to other habitats (Mora and Sale 2011). Mass coral bleaching and mortality is a global threat of particular concern as it has been observed to impact reefs far from human habitation (Obura and Mangubhai 2011) and irrespective of whether they are in MPAs or not (Selig *et al.* 2012).

## 1.3 Climate change, coral bleaching and its impacts on reefs

Climate change is predicted to have several negative influences on coral reefs (Hughes *et al.* 2003) including: acidification (Hoegh-Guldberg *et al.* 2007); increased storm impact (Gardner *et al.* 2005); increased prevalence of disease (Harvell *et al.* 1999); and mass coral bleaching (Glynn 1993). Mass coral bleaching has had the most widespread impact on coral reefs, especially since the mass-bleaching event of 1998, which affected coral reefs globally (Baker *et al.* 2008) and caused the death of approximately 16% of the world's shallow-water reef-forming corals (Wilkinson 2008). There has been significant confusion or misuse of terms when describing mass bleaching and its impacts (Obura 2005). Here, three different concepts relating to coral bleaching are defined: coral bleaching, bleaching-related mortality and mass bleaching events.

The term 'coral bleaching' is used to describe when corals reduce the amount of cholorphyll in their tissues, either by the expulsion of chlorophyll from their endosymbiotic algae (zooxanthellae) or the expulsion of zooxanthellae cells altogether, leaving the coral pale or white (Brown 1997, Obura 2009). The coral animal remains alive, but is unable to accrue nutrients from the photosynthetic activity of its' symbionts, instead relying on heterotrophy through filter-feeding (Glynn 1993). If bleaching occurs for an extended period the coral starves and dies, a process known as 'bleaching-associated mortality', or in this context, just mortality. It is important to note that bleaching does not always lead to mortality, and corals are able to regain their zooxanthellae should the environmental conditions ameliorate (Gates 1990). An individual colony may completely die, or suffer partial mortality, which is seen especially among larger corals (Harriot 1985; Bak and Meesters 1993). 'Mass bleaching events' are where numerous corals in the same area bleach simultaneously in response to extreme conditions. Mass bleaching events can be considered as either minor/non-lethal events where coral mortality is low or major/lethal events where mortality can be as high as 95% of all corals on a reef (Obura 2005).

Several environmental stressors including, pollution and flushing of cold water can cause coral bleaching (Baker *et al.* 2008), but it is most commonly observed in situations of increased water temperature and high solar radiation (Drollett *et al.* 1994, Fitt et al. 2001). Most corals operate near their thermal upper limits and a small increase in temperature of 1-2 degrees can lead to bleaching (Glynn and D'Croz 1990). The temperature rise required to trigger a bleaching event is not absolute, but rather is relative to the ambient conditions and the average maximum summer temperatures (SSTmax) (Eakin *et al.* 2009). Hughes *et al.* (2003) noted that the Persian/Arabian Gulf and Lord Howe Island are located at opposite extremes of the Indo-Pacific spectrum of reef environments, with average summer temperatures of 36$^{o}$C in the Gulf and 24$^{o}$C at Lord Howe, but still share 24 species of coral in common. Both sites have experienced bleaching.

The length of time that coral is exposed to thermal stress is important, as this increases chances of starvation and mortality (Glynn 1993). The most commonly used indicator of “thermal pressure” is Degree Heating Weeks (DHW) or Months (DHM) (Liu *et al.* 2003). A rise in temperature of 1 degree over SSTmax for 1 week equals 1 DHW and hence a rise of 2 degrees over SSTmax for 1 week or a rise of 1 degree over 2 weeks equals 2 DHW. Coral reef scientists and the National Oceanographic and Atmospheric Administrations (NOAA) have used this metric extensively for predicting the severity of mass coral bleaching (Eakin *et al.* 2009). However, it has also been noted that in areas with higher temperature variation (or chronic thermal stress) that corals have higher thresholds above SSTmax to bleaching and mortality (McClanahan *et al.* 2007a).

The overall impact of mass bleaching on the coral community is varied and less predictable than the initial bleaching response (Anthony *et al.* 2007). There are compounding factors beyond temperature, such as pollution, sediment, water flushing, and light intensity, which determine the fate of bleached corals (Baird and Marshall 2002, Anthony *et al.* 2007). For example, Reunion and Mauritius during 1998 were largely spared from widespread mortality, despite high water temperatures, because of shading from cloud cover at that time (Obura 2005). Nakamura and Woesik (2001) observed that water flow is important for reducing thermal stress within the coral colony.

During lethal mass bleaching events, some corals have been shown to be more sensitive to thermal stress than others (e.g. *Acropora* and *Pocillopora*)

(Loya *et al.* 2001), which lead to selective mortality of these colonies (Berklemans *et al.* 2009). The remaining coral community tends to be more tolerant to bleaching, dominated by merulinids (previously the favids) and *Porites* (McClanahan 2014) and hence the reef experiences community-level adaptation for higher thermal stress (Donner *et al.* 2009). In non-lethal conditions, corals have been shown to re-shuffle their symbiotic algae and select zooxanthellae clades with higher thermal tolerance (Thornhill *et al.* 2006) and hence bleaching can cause colony- level acclimatisation to increasing thermal stress (Buddemeier and Fautin 1993).

Even with the positive processes of adaptation and acclimatisation occurring within coral communities, the future of reefs does not look hopeful (Hoegh-Guldberg 1999). Coral reefs will have to contend with between 0.5°C and 2.8°C of warming over the next century depending on future emissions scenarios (Donner *et al.* 2009). It is not clear that reefs can acclimatise fast enough to cope with this level of change (Hoegh-Guldberg 2014) and it is thought that if bleaching occurs too frequently, coral communities will not be able to recover between bleaching events (Sheppard *et al.* 2003). Under these worrying future scenarios the resilience of reef systems to remain as productive coral-dominated ecosystems is not certain (Graham *et al.* 2014).

## 1.4 Ecological resilience and its application in coral reef systems

Ecological resilience is defined as the ability of an ecosystem to maintain a stable state (Holling *et al.* 1973), which when applied to coral reefs means maintaining a coral-dominated benthic community. In the 1980s, Hughes (1994) noted that some reefs in the Caribbean experienced a phase-shift to a macroalgal-dominated state, which was interpreted as a loss of resilience resulting from chronic human stressors, and a subsequent phase-shift caused by an acute disturbance, in this case a hurricane. With rising human pressure on reefs (Hughes *et al.* 2003), and predicted increases in disturbance through mass coral bleaching (Hoegh-Guldberg 1999), understanding the resilience of coral reefs has received increasing scientific attention (Graham *et al.* 2011).

When applied to coral reefs that have experienced mass bleaching and mortality, the resilience concept has several key components. Reefs that experience thermal stress, but not mortality are described as being 'resistant' (West and Salm 2003). This can either be because of factors that prevent the coral from bleaching in the first place, or factors that allow bleached corals to recover (Obura 2005). Resistance is distinct from avoidance (West and Salm 2003) or thermal protection (Obura 2005), where upwelling or cool water or other localised temperature reductions, avoid thermal stress altogether. Factors that promote resistance to bleaching include intrinsic factors such as coral physiology (Brown *et al.* 2002) and the thermal tolerance of zooxanthellae symbionts (Baker *et al.* 2004). Extrinsic factors refer to any environmental factors that prevent mortality, including local currents, shading and water quality (Penin *et al.* 2013).

Reefs that experience mortality associated with thermal stress can recover to a coral-dominated state. After the 1998 mass-bleaching event in the Western Indian Ocean (WIO), it was noted that reefs, which suffered similar mortality of approximately 80%, had radically different recovery rates (Obura 2005). Some reefs bounced back rapidly (e.g. Maldives; Edwards *et al.* 2001, and Chagos; Sheppard *et al.* 2012), others recovered slowly (Seychelles; Ledlie *et al.*

2007) and yet others showed no recovery at all (Kenya; Lambo and Ormond 2006). Some authors refer to a reef's ability to recover as its 'resilience', referring to resistance as a separate process (West and Salm 2003, Nystrom *et al.* 2008). However, because both resistance and recovery are important for a reef to maintain a coral-dominated state when impacted by thermal stress (West and Salm 2003), in this thesis the term 'resilience' encompasses both of these concepts.

The factors that influence the resilience of a particular location are diverse. They can be organised into broad categories, depending on the focus of a particular study, disturbance, or spatial scale (Obura 2005). Obura (2005) and West and Salm (2003) have produced a comprehensive list of these categories, which can be placed into the following sub-categories:

- Physical factors: e.g. local currents and water retention influences the temperature regime, and the general daily heterogeneity in the reef environment (Nakamura and Woesik 2001, Wall et al. 2015).
- Population factors: e.g. the variation of genes, species, and genera within the coral community of the reef will affect the degree to which corals will be resistant to bleaching (Baker *et al.* 2004, Coles and Riegl 2013).
- Community factors: e.g. herbivores play a key role in regulating algal populations and creating space on reefs for new coral recruits to settle and grow. The diversity, abundance and biomass of the herbivorous fish community will influence when and how phase-shifts occur (Green and Bellwood 2009).
- Anthropogenic factors: e.g. sediments and nutrients in the water column from dredging, coastal development and soil erosion can influence health,

reproduction, primary productivity and settlement rate of corals before, during, and after, a bleaching event (Fabricius *et al.* 2013).

The individual factors related to resilience combine to produce the overall resilience of the system through the complex ecological interactions that exist on reefs (Mumby *et al.* 2007b). In some cases, these influences and trajectories may be operating in opposite directions, e.g. eutrophication may strengthen resilience to the reef as it promotes heterotrophy, by which bleached corals can obtain their nutritional needs, and causes shading (Fabricius *et al*. 2013). However, eutrophication may also weaken resilience through smothering, heightened stress to corals and by conferring a competitive advantage to macro-algae (Fabricius *et al.* 2013). Corals with high thermal tolerance, such as massive Merulinidae and *Porites* are important for the resistance of the reef, but their slow growth may reduce the recovery potential of the reef (McClanahan *et al.* 2012). The interplay of feedbacks and interactions within the ecosystem form the bases of how stable states form and phase-shifts occur (Mumby *et al.* 2007b, Graham *et al.* 2013).

The trajectory of the reef state and the reef's resilience are difficult to detect from data collected in a snapshot of time (Spalding and Brown 2015). In addition, the state of a reef and its resilience can be decoupled, so that it is possible to have a reef with high coral cover, but low resilience and *vice versa* (Hughes *et al.* 2010). Nystrom *et al.* (2008) distinguish a phase-shift as a shift in state of the reef, and a regime-shift as a shift in the resilience value of the reef (Fig. 1.1). In Fig. 1.1a the change in state of the reef is dramatic, but resilience is not weakened below a critical point and hence recovery is quick. An example of such a classically resilient reef is described by Diaz-Pullido and McCook (2009) on a reef in the Great Barrier Reef, which bleached, died and became colonised entirely by macro-algae 1 year after bleaching, but 2 years after bleaching had returned to a coral-dominated state. Fig 1.1b represents the opposite of this, where the impact causes a phase-shift, which then degrades the resilience of the reef until a regime shift occurs and hence there is little to no recovery on the reef. Fig 1.1c demonstrates the complexity added with multiple stressors where the critical resilience threshold is crossed, as a result of a different chronic impacts (e.g. pollution) on the reef, leading to a long steady decline in reef condition until an acute impact, such as thermal stress or a storm, finally triggers a complete phase-shift (Hughes *et al.* 2010). Reflecting on the catastrophic collapses seen around the world in 1998 and with other acute stressors, it has been suggested that many reefs were, and many currently may be in this critically vulnerable situation, where resilience is weakened beyond a point to provide any recovery should the reefs be impacted (Jackson *et al.* 2001; Wilkinson 2008).

The examples above also demonstrate the importance in understanding thresholds or tipping points within a resilience framework. It should be noted that the threshold value for a certain resilience factor when moving from coral-dominated to macroalgal (or less desirable) state is not necessarily the same as the threshold when moving back to the coral-dominated state (Nystrom *et al.* 2008). This effect is called 'hysteresis' and occurs because of different feedback mechanisms that operate in a particular state to maintain the different directions (Fig. 1.2). A good example of this comes from Bellwood *et al.* (2006), where phase shifts were simulated using herbivore exclusion cages. In the absence of grazing parrotfish (Scaridae) and surgeonfish (Acanthuridae), macro-algae quickly took over, demonstrating the drop in herbivory was great enough to cross a threshold and cause a phase-shift. However, once the cages were removed the parrotfish and surgeonfish had no interest in the fully-grown algae. The mechanism for returning to a coral-dominated state was mediated by a single species of batfish (*Platax pinnatus*), which removed the algae allowing coral to recolonize the area.

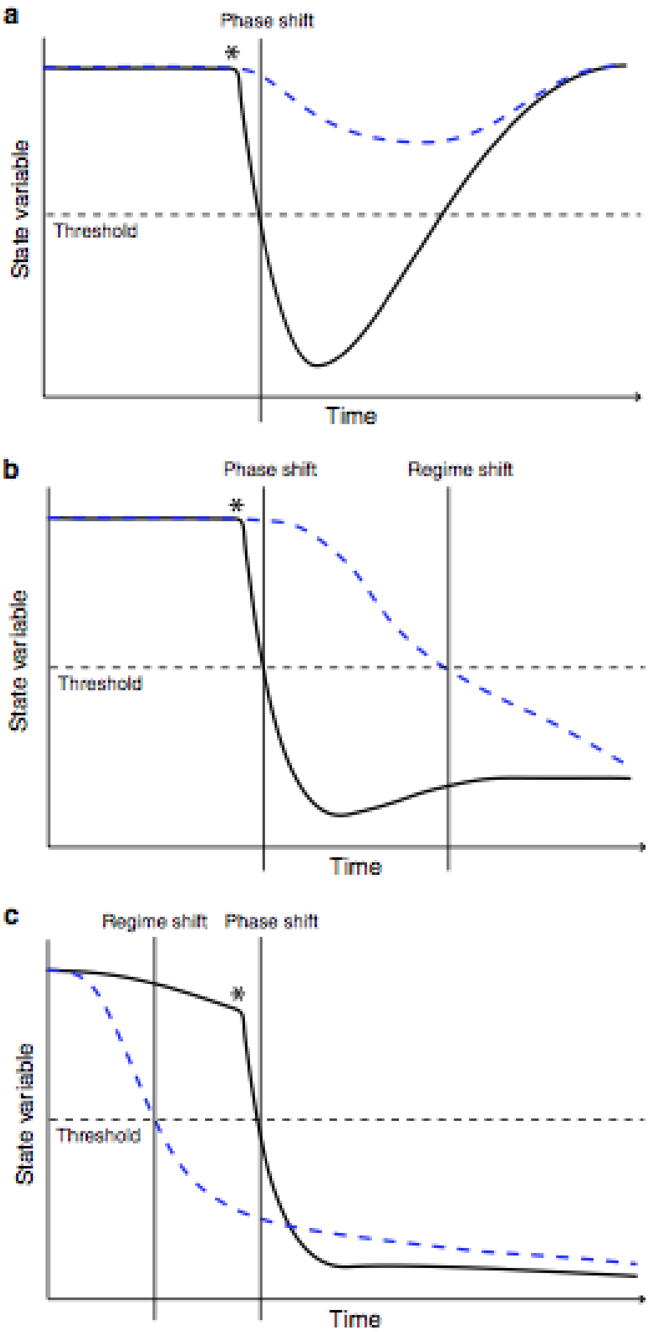


**Figure 1.1 The interaction between resilience (blue-dashed) and coral cover (black) in three different scenarios of acute disturbances (*). A) Disturbance causes a large drop in coral cover (phase-shift), but resilience is maintained (no regime shift). B) Drop in coral cover (phase-shift) reduces resilience to a critical theshold and regime shift occurs. C) Resilience is lost (regime shift) before the acute disturbance, but coral loss (phase-shift) is only experienced when a disturbance occurs. Reproduced from Nystrom *et al.* (2008).**

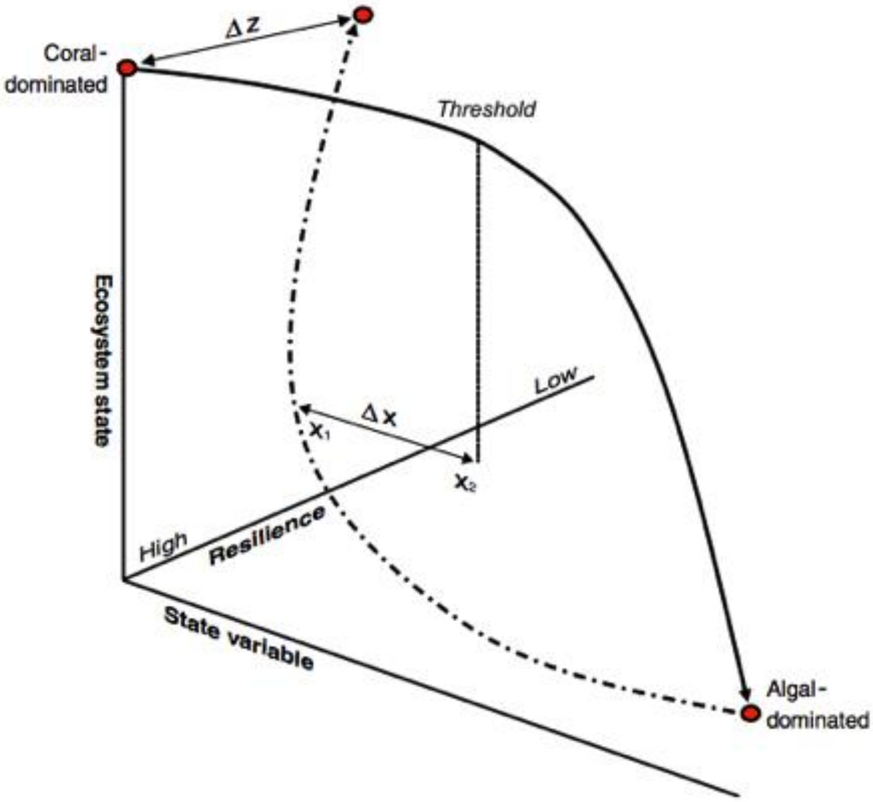


**Figure 1.2 The relationship between resilience, critical thresholds and the phenomenon of hysteresis. The solid line represents the decline in ecosystem state once a state variable hits a critical threshold. The dashed line represents the recovery to a favourable coral dominated ecosystem state. ΔX represents the difference in theshold value of the state variable between system decline and recovery (Hysteresis effect). ΔZ represents the difference in resilience between pre-disturbance and post-recovery reefs (Reproduced from Nystrom *et al.* (2008).**

## 1.5 Applying coral bleaching science and reef resilience theory to coral reef conservation

Contemporary conservation attitudes value healthy natural ecosystems and the ecosystem goods and services they provide (Mace 2014). However, without historical records and a baseline of past reef state it is difficult for conservation managers to know how their ecosystem has changed over time (Knowlton and Jackson 2008). Chapters 2, 3 and 4 of this thesis develop a baseline of relevant contemporary data to understand the ecological status, trajectory and bleaching impact on reefs in Watamu Marine National Park (WMNP), Kenya. Data are presented on habitats and biodiversity found within the park, the current status and health of the coral community and the impacts of a non-lethal bleaching event. The findings are compared with available data and published scientific records that have been collected in WMNP over the four decades since the park was gazetted in 1968. These three chapters aim to understand the overall resilience of reefs in a small area and in a highly contextualised setting. The final chapter expands the geographical range to the scale of the entire Indian Ocean, and attempts to understand a snapshot view of resilience across six locations in four countries, including WMNP. Unlike Watamu, many locations that conservation scientists wish to understand do not have extensive historical data available (Knowlton and Jackson 2008) and hence management decisions must be made by interpreting contemporary data on resilience indicators (Obura and Grimsditch 2009). This fifth chapter aims to demonstrate how these snapshot data can be used to predict a reef's vulnerability or resilience to future climate stresses, which are expected to increase over the next century (Donner 2009).

WMNP is located on the rim of the Western Indian Ocean (WIO) eco-region (Obura 2012), which is part of the wider Indo-Pacific marine tropical province (Hughes *et al.* 2002). The park contains 10km$^2$ of shallow lagoonal and back-reef habitats found in the continental fringing reef, which runs 200km along Kenya's coastline from Kiunga to Malindi (Stoddart 1971) (Figs. 1.3 and 1.4). The park was gazetted in 1968 and made into a UNESCO biosphere reserve in 1979, along with Malindi Marine National Park and the wider Watamu-Malindi Marine National Reserve. It is one of the oldest MPAs in the world (Juffe-Bignoli *et al.* 2014) and as such has an extensive record of past reef states and impacts that the reef has sustained (e.g. Jones 1969, Obura 1995, McClanahan 2014). Muthiga (2009) assessed the effectiveness of WMNP as an MPA and found that the park had been successful at promoting higher fish biomass and in conserving keystone species, which maintain key ecological processes. However, the reefs in Watamu, like much of the rest of Kenya and WIO, suffered extensive mortality during the 1998 El Niño Southern Oscillation (ENSO) (McClanahan *et al.* 2001).

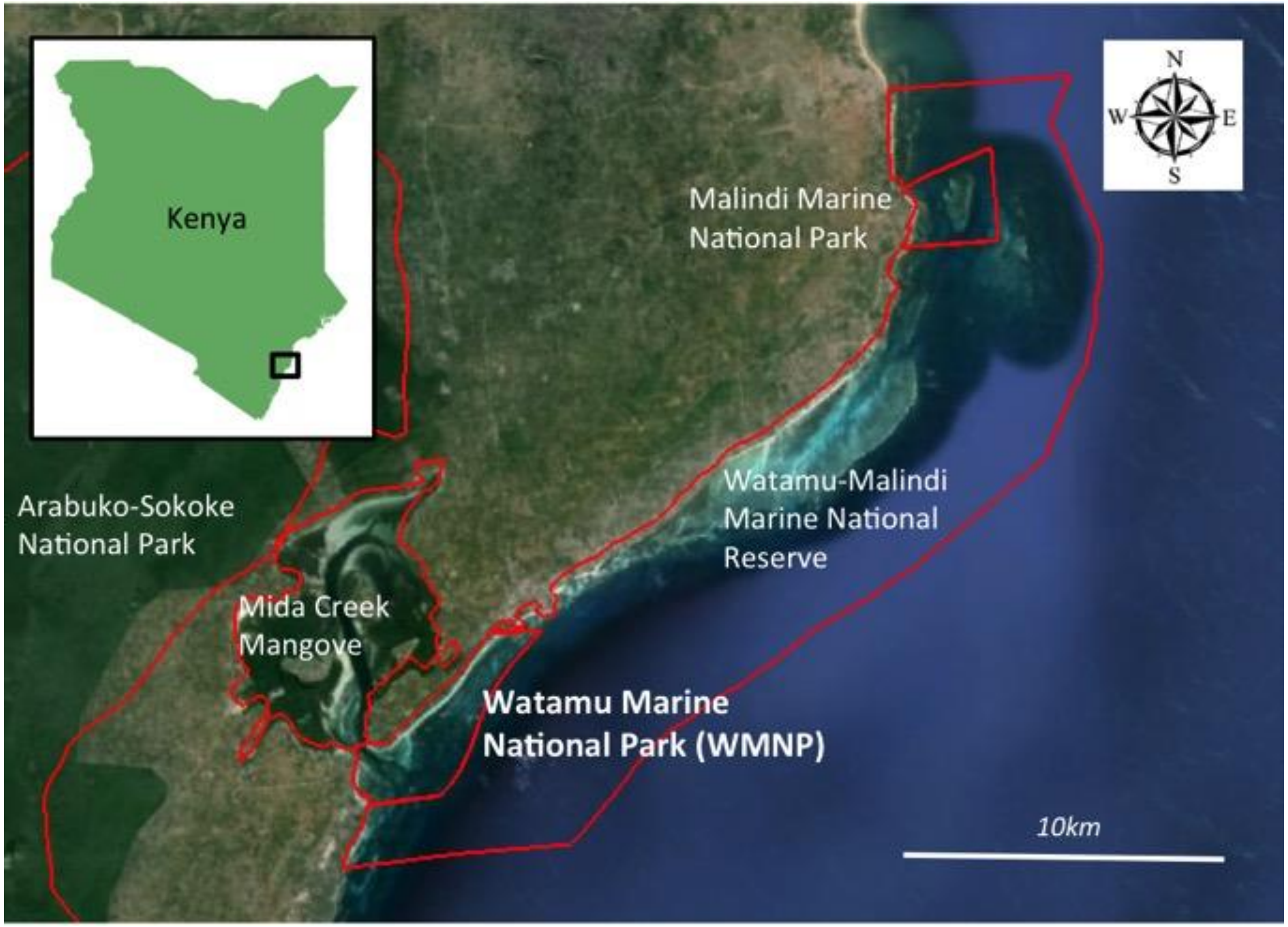


Figure 1.3 Satellite image of Watamu Marine National Park (WMNP) and three other protected areas nearby, including Arabuko-Sokoke National Park, Malindi Marine National Park and Watamu-Malindi Marine National Reserve (including Mida Creek).

In the second chapter of this thesis, a broad perspective of WMNP is presented, including the distribution and biodiversity of coral reefs in the park, as well as the non-coral habitats it protects. In addition, a bibliography of relevant ecological and conservation reports and published papers is compiled to contextualise the current patterns of biodiversity, reef health and resilience explored in this thesis. It is hoped that the products of this chapter, including the habitat map, species lists of different taxa and bibliography can provide a comprehensive baseline for informing management and conservation planning in the park and provide useful information for future researchers to build on. The findings from this chapter are used to discuss the conservation value of the park and the conservation challenges facing WMNP. With concern over the effectiveness of MPAs and their validity as a conservation strategy (Sale 2008), this study represents a detailed and long-term case study of marine conservation effectiveness in a less economically developed tropical nation.

The third chapter investigates changes in the health of reefs in WMNP using data spanning from 1983 to 2014. Changes in coral cover, recruitment, growth and mortality rate are investigated over this time frame, with a focus on major changes that occurred during the 1998 mass-bleaching event. In response to human pressures and climate stress, coral cover has declined in many coral reef regions (Wilkinson 2008), but the Indian Ocean has maintained healthier coral cover than other areas (Ateweberhan *et al.* 2011). Changes in coral cover and genus composition of the coral community have ecological repercussions in the wider reef community (Graham *et al.* 2007, Beldade *et al.* 2015) and influence the resilience of the reef (Hughes 1994). The current coral community in Watamu and the changes it has experienced over time are used to infer the resilience of the reef and its future trajectory. The demographic processes of coral recruitment, growth and mortality are measured twenty years apart in 1994 and 2014 to understand why the coral community has changed over time and highlight potential human pressures driving these trends. The aim of this chapter is to present past trends, current state and predicted trajectory of the coral community in WMNP and suggest conservation options to promote the resilience of the coral community into the future.

WMNP has been shown to be effective at protecting against direct human pressures on various habitats (Muthiga 2009), but like many MPAs around the world, was unable to protect against the severe impacts of mass bleaching and mortality (Selig *et al.* 2012). Building on the findings of the general reef health presented in Chapter 3, the fourth chapter in this thesis explores the impacts of thermal stress, coral bleaching and mortality in WMNP. Many of the studies investigating the impacts of coral bleaching and mortality on reef communities have been conducted in locations that have experienced high mortality (Suggett and Smith 2010), and only consider the impacts of a single event (e.g. Loya *et al.* 2001). However, non-lethal bleaching events and past acute thermal stress allow corals to adapt and acclimatise to thermal stress (Obura 2009, Berkelmans 2009) and hence there is a need to understand how these positive impacts of bleaching are balanced with the more commonly reported deleterious effects. WMNP experienced major bleaching in 1998 and several cases of minor bleaching, including an event in 2013 where the bleaching response and mortality of corals was recorded. This chapter investigates the overall impact of repeated thermal stress on the reefs in WMNP in order to better understand how reefs will respond to increasing thermal stress (Donner *et al.* 2009).

Since the 1998 mass-bleaching, there have been increasing research efforts to understand and incorporate reef resilience into conservation (Graham *et al.* 2011). In order to provide accurate information on reef resilience to managers, indicators were selected based on ecological and environmental factors that are known to affect reef resilience (Obura and Grimsditch 2009). The final chapter in this thesis presents the results of resilience surveys in 6 locations across the Indian Ocean. These results are interpreted in the light of explanatory variables, such as human pressure and past thermal stress, to explore what factors influence a reef's resilience to future climatic stress. By using the best current models of resilience (McClanahan *et al.* 2012, Maynard *et al.* 2015), this chapter aims to demonstrate how resilience indicators can be used to inform managers about the resilience of their reefs, as well as commenting on areas where our current model is inadequate. Resilience indicators were originally intended to be used in conservation planning (Obura and Grimsditch 2009), but to date there are few examples where indicators have been applied (Maynard *et al.* 2012). It is hoped the findings of this chapter will help bridge the gap between our current scientific understanding of resilience and its use in conservation.

## 1.6 Habitat characteristics and main study locations in WMNP

In Chapter 2 data are presented on species abundance and richness from a wide variety of locations in the park in both coral-dominated reef structures and non-reef habitats, such as intertidal rocky platforms and subtidal seagrass beds. The landward boundary of the Marine National Park is considered as 100m behind the mean high water (MHW) line in the dunes, cliffs and coastal scrub habitat of the littoral fringe (Fig. 1.3). The seaward boundary of the park is on the reef slope parallel to the reef crest. Between shoreline and the reef crest the majority of the park is <2m below mean low water (MLW), with a maximum depth of ~10m in channels (Fig. 1.4). The tidal range in Watamu is approximately 4m (McClanahan 1988) and it is the daily flushing of tidal waters that produce the main currents in the park. Oceanic water is pushed into the lagoon of WMNP along two main channels running parallel to the shore, which join the open ocean near Whale Island. A small channel also exists at the northern part of the lagoon near Turtle Bay (Fig. 1.4). In areas of the lagoon more distant from the reef crest and these channels, the water rentention time is higher, which appears to result in higher localised temperatures and suspended particulate matter (B. Cowburn pers. obs.) At the southern end of the park there is a deep channel that bisects the lagoon from the mouth of Mida Creek to the reef crest north of Whale Island, through which water flows inland into the creek on a rising tide and out to sea on a falling tide. The creek used to be the mouth of the River Sabaki, which now flows out to sea 20km to the North (D. Obura pers. comm.) and hence today, the main channel and surrounding mangrove forest (Fig. 2.2) in Mida Creek have no major source freshwater input.

The majority of coral growth and lagoon reef strucutures are found along the landward slope of these channels or in the centre of channels (Fig. 1.4). Massive *Porites* colonies, some >2m wide, dominate the coral community, with a range of coral forms and genera growing on the patch reef structures formed by the *Porites* heads. In all the chapters of this thesis data are presented from the same 6 main research sites (Fig. 1.4), some of which were also studied (using the same site names) in various historical research as well (Chapter 2). Coral Gardens is the best-known site scientifically in Watamu and is where most snorkel tourism takes place (B Cowburn pers. obs.). Coral Gardens and nearby Bennett's Reef consist of several *Porites* dominated reef patchs between 20-50m on their longest axis starting at the channel floor ~ 4m deep to MLW. Lambis Reef and Bara Bara are located further south along this channel from Coral Gardens, where the depth increases to 6-8m below MLW, these reefs are similar in ecological character to Coral Gardens and Bennett's reef, but are slightly more exposed to oceanic conditions and outflow from Mida Creek. Uyombo Reef is located on a small channel running south of Whale Island and Turtle Reef on a similar channel in the northern part of WMNP (Fig. 1.4). Coral growth at these sites begins at a depth of 10m and rises to MLW. These two reefs are still broadly lagoonal in character, dominated by large *Porites* structures, but because they are nearest to the reef crest they have the most exposure to waves and flow of oceanic waters. As such, these two reefs also have some of the features of a fore-reef slope in ecology, including deeper water corals such as *Plerogyra sinuosa* and *Blastomussa merleti.* In Uyombo there is also a higher abundance and cover of branching Pocilloporids and Acroporids, compared to other sites.

The earliest records from Watamu, come from a study conducted by the University of Radboud in 1983 (Chapter 3), which examined reef sites in Watamu that are marked on Figure 1.4. Except for Coral Gardens, none of these sites were confirmed to be from the same study locations used in this thesis, but are found in ecologically similar areas <500m away from contemporary sites and hence are used to compare reef condition.

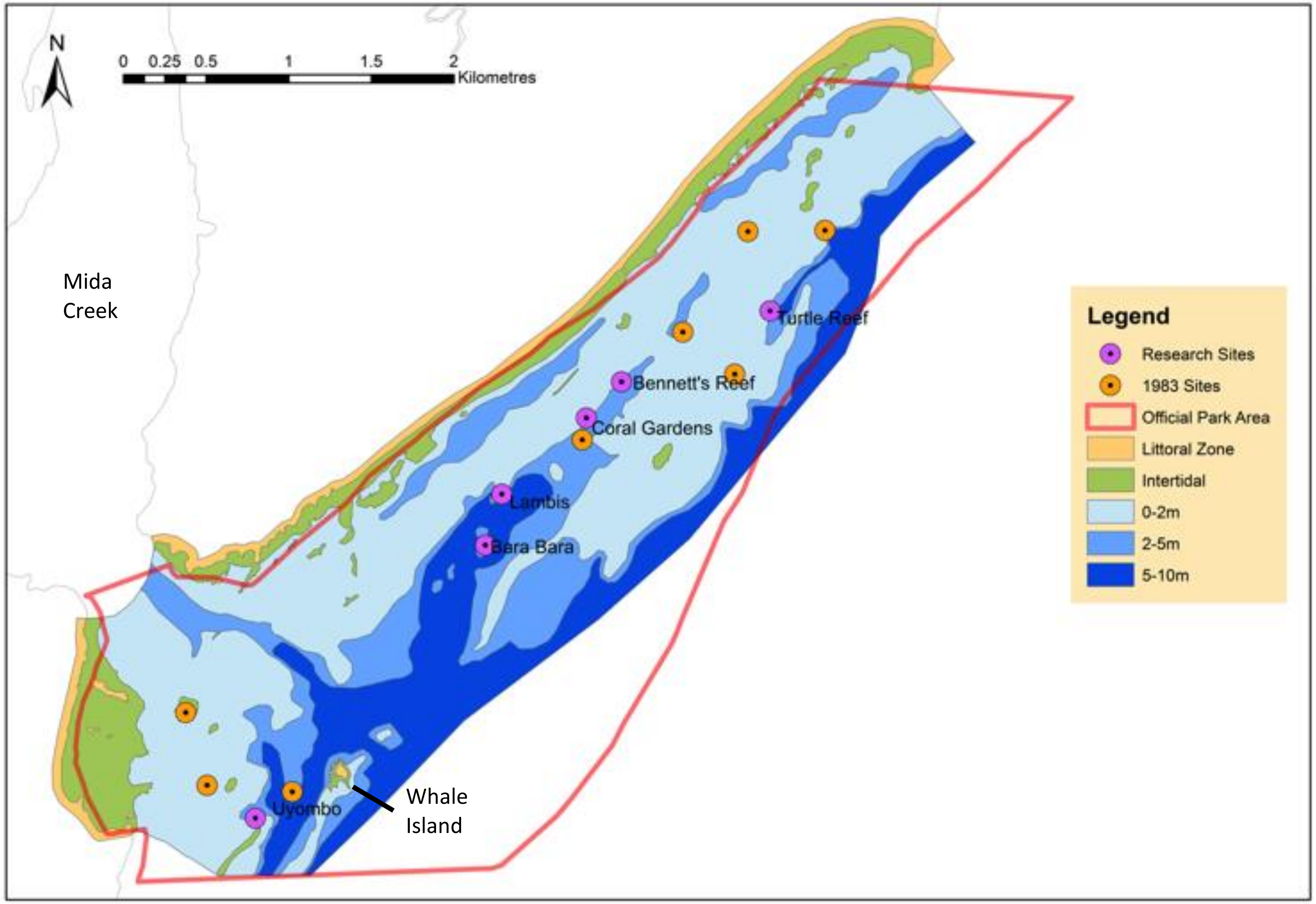


**Figure 1.4 A map of Watamu Marine National Park (WMNP), showing the boundary and approximate depth of the protected area. Named research sites (pink) are used throughout the thesis and in previous work (e.g. Obura 1995). Sites in 1983 (orange) were assessed during the earliest quantitative work on coral communities in WMNP (Chapter 3)(Blom *et al.* 1985).**

## 1.7 Climate and oceanography of Watamu and the Indian Ocean

Watamu, like much of the WIO region, is heavily influenced by the Inter-Tropical Convergence Zone (ITCZ), which moves across the region twice annually creating a monsoonal climate (McClanahan 1988, Schott *et al.* 2009). During December the ITCZ sits at 10°S in northern Mozambique, with Kenya being influenced by the Northeast trade winds and drier conditions (Griffiths 1977). During the first half of the year the ITCZ moves north bringing wet weather and a shift in wind direction to the southeast, a season known as the 'long-rains' in Kenya, which begins in April (McClanahan 1988). During the second half of the year the ITCZ moves south, bringing a second rainy season to Kenya in October, known as the 'short-rains' and a reversal in wind direction back to the northeast. In Chapter 5, data are presented from Watamu and Kisite (Kenya), Vamizi (Mozambique), Kuramathi (Maldives) as well as Tikus and Enggano in Sumatra. Kisite has a similar climate to Watamu, whereas Vamizi is generally cooler and only has one rainy season during January to March when the ITCZ is at its southerly limit on the East African coastline (Schott *et al.* 2009). Kuramathi in the Maldives and Tikus and Enganno in Sumatra are also affected by a reversal of wind associated with the change in the Indian Ocean monsoon, with a northeast wind from November to March and a westerly wind from April to October (Kench *et al.* 2009, Schott *et al.* 2009).

The main currents in the WIO are displayed in Fig. 1.5. The Southern Equatorial current travels from the east at approximately 10°S (Düing *et al.* 1978). In northern Madagascar this current forms a complex series of gyres and eddies, which continue south down the Mozambique Channel. Part of the equatorial current heads north as the East African Coastal Current, which continues during the southeastern monsoon along the Somali coast to the Horn of Africa. During the northeastern monsoon, the Somali Counter Current pushes southwards to a maximum of 4°S, where it meets the East African Coastal Current and is pushed east (Johnson *et al.* 1982). As these two currents meet and leave the African coastline a seasonal upwelling occurs off the northern coast of Kenya.

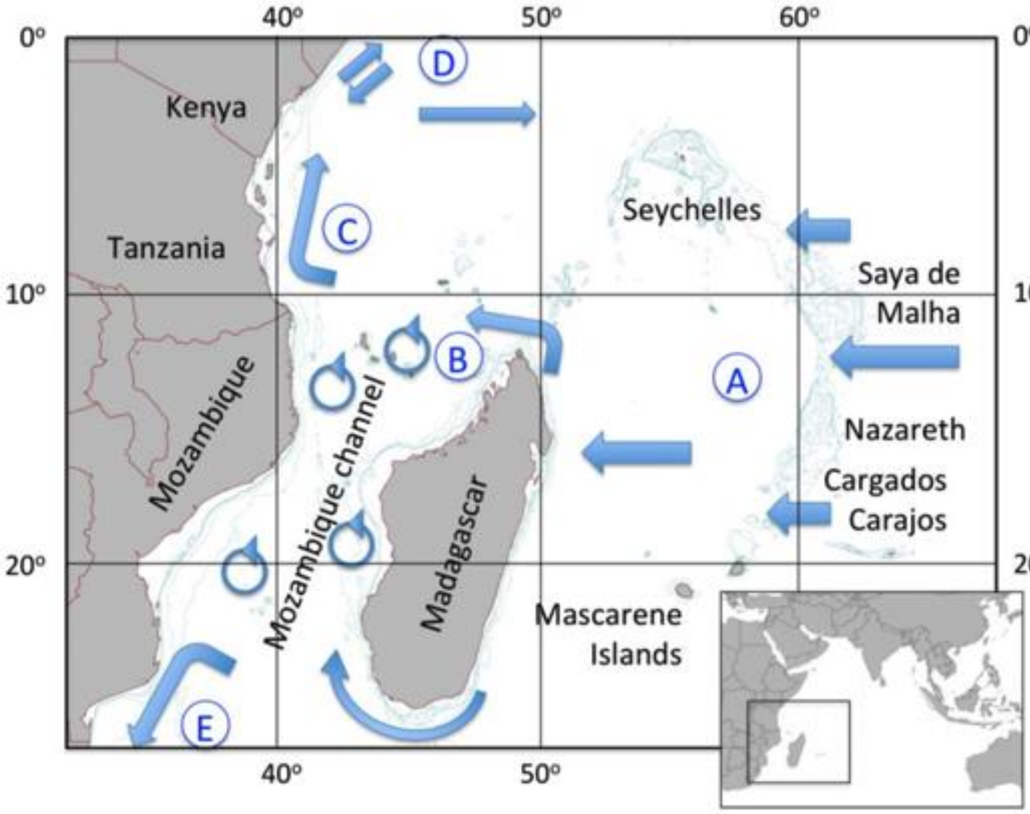


**Figure 1.5. The WIO and the main oceanic currents; A) Southern Equatorial Current, B) Comoros Gyre and Mozambique Channel eddies, C) East African Coastal Current, D) Somali Counter Current and E) Agulhas Current. Reproduced from Obura 2012.**

The climatic conditions described above are observed in normal years. However, the Indian Ocean is subject to sporadic climatic events where conditions change dramatically (Meyers *et al*. 2007). The El-Nino Southern Oscillation (ENSO) is generated in the eastern Pacific where anomalous calm conditions cause the cold upwelling off equatorial South America to fail, leading to higher than average sea temperatures. The impacts of ENSO events are felt worldwide, including the tropical Indian Ocean. In the WIO ENSO years are associated with higher than average sea temperatures and heavy rainfall (Cole *et al.* 2000). Interestingly, these conditions are also generated during the Indian Ocean Dipole (IOD) (Saji *et al.* 1999). During a positive IOD phase, anomalously strong easterly winds cause cold upwelling off Sumatra in the eastern Indian Ocean, causing an increase of rain and high sea temperatures in the WIO (Meyers *et al*. 2007). ENSO and IOD operate independently (Saji *et al.* 1999), but can take place during the same year (Meyers *et al*. 2007). The catastrophic coral bleaching event in 1998 was caused by extremely high sea temperatures as a result of the combined effects of ENSO and IOD in 1997. In negative phases of IOD and ENSO East Africa experiences drought conditions. A negative IOD phase causes warmer than average SSTs in the eastern Indian Ocean with anomalously high rainfall (Horii *et al.* 2013).

Plate 2. View across WMNP from the shore to the reef crest near A Rocha Kenya (Photo: B. Cowburn).

# Chapter 2. Protecting marine habitats and biodiversity for nearly 50 years in East Africa: a case study of Watamu Marine National Park, Kenya

## Abstract

Watamu Marine National Park (WMNP) is one of the oldest no-take Marine Protected Areas (MPAs) in the world. Since its establishment in 1968, it has been host to a number of scientific studies as well as suffering from a range of modern threats to coastal marine habitats. This chapter aims to understand the current status of WMNP, in terms of habitat, biodiversity and available scientific literature. There were 101 published references relating to WMNP found, which mostly focus on coral reef ecology, with less attention to other habitats and topics, such as biodiversity or socio-economics. During fieldwork nine habitat categories were mapped; revealing that the most dominant habitat type is seagrass and the least is coral reef.  Species lists were collected and analysed for fish, echinoderms, molluscs, crustaceans, corals and seagrass. There were 18 species identified which were IUCN red-listed as categories of conservation concern and 8 species found which may be un-described. The findings of this chapter emphasise the importance of non-coral habitats in the WMNP, such as seagrass beds and the need for more research into these areas. There is also a need for understanding the connectivity of WMNP to other areas and more research into some of the potential threats facing the park. The baseline of information provided in this chapter should provide a comprehensive overview to any scientist or conservationist wanting to carry out further work in WMNP.

## 2.1 Introduction

### 2.1.1 Conserving reefs with marine protected areas (MPAs)

Marine protected areas (MPAs) are the dominant form of marine conservation around the world, seeing a threefold increase in the area covered by these zones in the past decade (Juffe-Bignoli *et al.* 2014). The purpose of MPAs varies from location to location, although broadly they are established for the protection of biodiversity and habitats, managing fisheries, promoting sustainable use of marine resources, and promoting tourism (Salm and Clark 2000). More recently MPAs contribute towards national commitments to the Convention on Biological Diversity, through Aichi Target 11, to conserve 10% of marine areas through the use of protected areas and other spatial management measures (Juffe-Bignoli *et al.* 2014).

Various attempts have been made to assess how effective MPAs are as a conservation strategy (Wood *et al.* 2008, Lester *et al.* 2009, Fox *et al.* 2014). These assessments have shown some broadly positive successes, such as maintenance of higher biomass (Lester *et al.* 2009) and preventing coral loss (Bruno *et al.* 2010), but with areas of concern around the small size of MPAs (Mora *et al.* 2006), the effectiveness of MPA management (Sale 2008) and the equitable sharing of benefits within local communities (Juffe-Bignoli *et al.* 2014). A common theme is the difficulty in actually assessing the effectiveness of MPAs, because of a paucity of information available on the ecology for the areas being protected and effectiveness of the protection (Wood *et al.* 2008, Juffe-Bignoli *et al.* 2014).

Watamu Marine National Park (WMNP) is a single MPA located on the coast of mainland East Africa in Kenya. Like many MPAs it is relatively small (Mora and Sale 2011), covering just 10km$^2$ and it has been unable to resist the impacts of external stressors (McClanahan *et al.* 2001). However, it is one of the oldest marine parks in the world, being established in 1968 (Wells *et al.* 2007) with a history of scientific investigation and conservation activity. Its location in a tropical emergent economy means it possesses both high biodiversity (Richmond 2002) and high levels of pressure from a growing population and economy (Muthiga 2009). As such WMNP offers a case-study for assessing the conservation of biodiversity and habitats in an important yet threatened area.

### 2.1.2 Marine conservation in the western Indian Ocean and Kenya

The western Indian Ocean (WIO) is a biogeographically distinct region of the wider tropical Indo-Pacific realm (Richmond 2002, Obura 2012), including the Red Sea, oceanic islands, such as the Seychelles and the Maldives, and the tropical East African coastline. It has moderately high biodiversity with over 60 genera of corals (Obura 2012) and 2000 species of fish (Richmond 2002). However, compared to other shallow tropical marine areas it has received much less scientific attention (Sheppard 2000).

The WIO has a long history of marine conservation, with many countries establishing their first MPAs in the 1960s (Wells *et al.* 2007). In Kenya there are four no-take marine 'parks' where fishing and all forms of extraction are forbidden and six 'reserves' where fishing and other activities are regulated for sustainability (Fig. 2.1), of which WMNP is the oldest. Continuous fringing coral reef is present along the southern coastline of the country, but because of local geology and currents, is more patchily distributed in the north (McClanahan 2000). The continental shelf in this section of coastline is relatively narrow, but within shallow marine environments are a range of habitats including coral reefs, seagrass beds and extensive mangrove areas (Stoddart 1971). In addition Kenya also has a relatively large tidal range of ~4m (McClanahan 1988) producing a range of intertidal habitats including mudflats, beaches and rocky shorelines (Nordlund 2012)

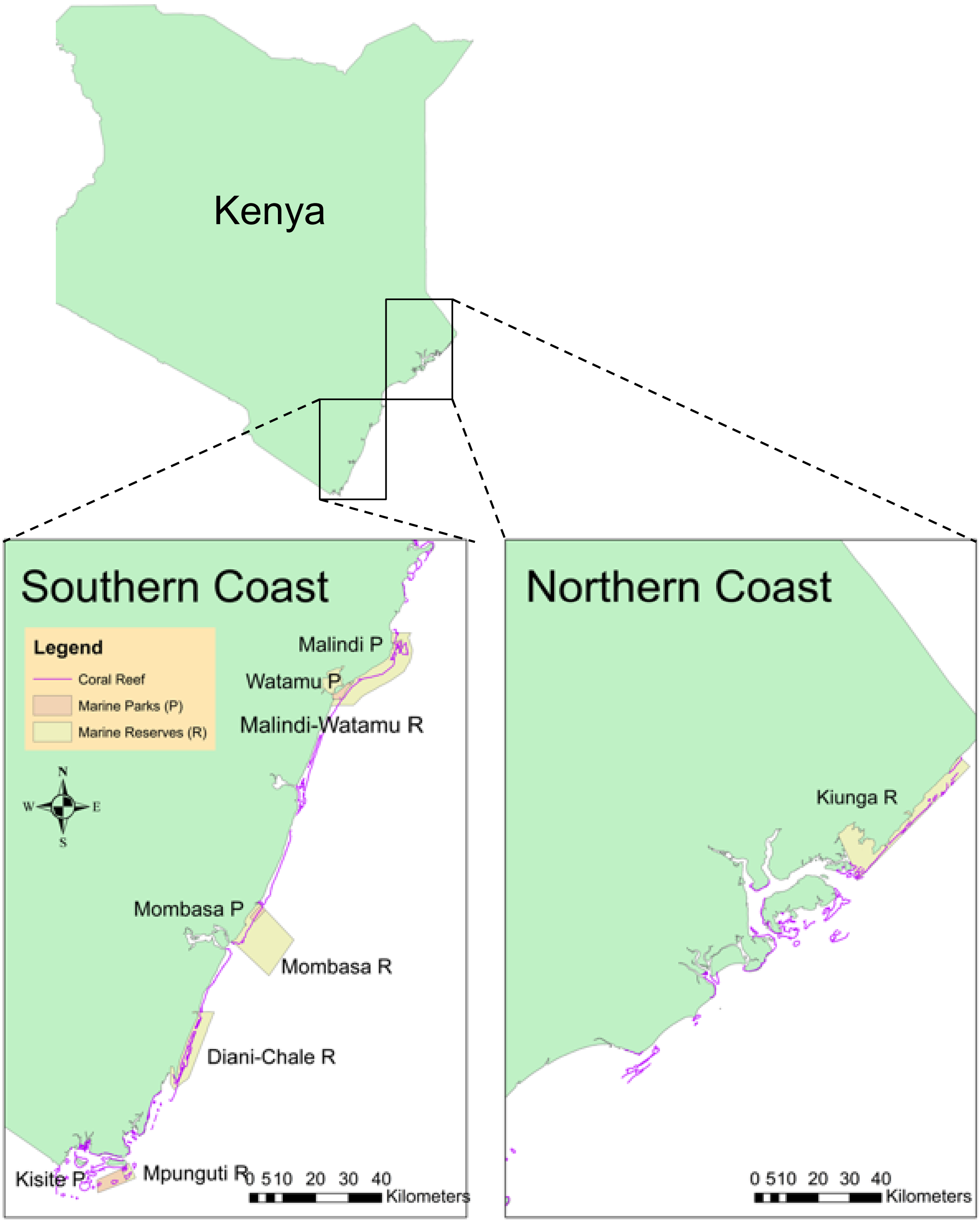


**Figure 2.1 A map of Kenya's coastline and coral reefs, showing the locations of MPAs.**

The majority of WMNP is located in the lagoon and back-reef of a sheltered section of coastline, south of Watamu village (Fig. 2.2). At its southern end a deeper channel formed by Mida Creek flows out to sea, which is a large tidal inlet containing mangrove forests, but with no river input or overland flow (Fig. 1.5). To the north it is bounded by the steep cliffs of the Kibirijini Headland and by the reef crest along its seaward edge. Both Mida Creek and the fore-reef slope beyond the park are part of the Watamu-Malindi Marine National Reserve, which extends 20km to the north and also encompasses Malindi Marine National Park (Fig. 1.5).

The park is officially managed by Kenya Wildlife Service (KWS) who are responsible for the management and conservation of both marine and terrestrial parks in Kenya. In addition there is a cross over in responsibility with the Ministry of Fisheries (Muthiga 2009). As well as governmental protection four non-governmental organisations (NGOs) focus on marine issues in the area;

- Watamu Turtle Watch: This group has focussed on the conservation and rehabilitation of Watamu's two main turtle species *(Chelonia mydas* and *Eretmochelys imbricata)*, through protecting nesting sites, preventing illegal hunting of turtles and carrying out marine education in the local area.
- Watamu Marine Association: With a wide suite of programmes covering various issues surrounding WMNP, Watamu Marine Association have focussed their activities on community involvement and sharing of benefits from the MPA, as well as monitoring the dolphins and whales found in the reserve offshore from the park.
- Watamu Beach Management Unit: Beach management units (BMUs) are a national strategy for fishing communities to deal with issues arising within their own communities and between themselves and other

agencies such as KWS or the Ministry of Fisheries. They monitor fish yields and collect other data relating to local fisheries.

- A Rocha Kenya: Traditionally A Rocha Kenya focussed mainly on terrestrial conservation issues, but from 2010 began its marine programme, the focus of which was to understand the broad-scale ecology and conservation threats faced by WMNP from a scientific perspective.

**Figure 2.2 Satellite image of WMNP used in habitat mapping, showing the locations of Kenya Wildlife Services, conservation groups and main villages surrounding the MPA.**

### 2.1.3 Constructing a baseline for WMNP

A baseline can be defined as a snapshot in time for the state and condition of an area. The lack of historical baselines in coral-reef biology has hampered our understanding of some of the impacts that reefs have seen (Knowlton and Jackson 2008). For example, without any data documenting the historical fish stocks in WMNP, it is impossible to determine whether the poaching and other potential impacts are significantly affecting the reef's fish community and hence decide what management action to take. There are many aspects of the park's biodiversity and ecology that remain unclear. The aim of this chapter is to construct a contemporary baseline for the park, which allows discussion of the conservation effectiveness of Watamu as an MPA so far and highlights the need for future scientific study and management of the park. Specifically I aim to;

- Collate the existing literature available for the park to identify available information and highlight gaps in our understanding of WMNP.
- Produce a habitat map for the park to demonstrate the range and extent of the habitats being protected.
- Assess the biodiversity of major taxa in the different habitats of the park as a first step towards understanding the biota of WMNP as an integrated system.

## 2.2 Methods

### 2.2.1 Literature review

A detailed bibliography of all published papers, grey literature and reports was compiled by Muthiga and Kawaka (2010) for all the marine protected areas in Kenya. An initial bibliography for WMNP was compiled from this (excluding references relating to Mida Creek), and then augmented with more recent records through the Author's knowledge of local marine science and searching Web of Knowledge using the key words 'Marine' and 'Watamu'.

The information on historical work conducted in WMNP was summarised by the type of publication, the topic and the geographical scope of the work. The topic was ascertained by reading the abstract of each piece of work and assigning it several keywords in an annotated bibliography. Each reference was also assigned one of three topic categories; 'social' for anything relating to social sciences and human interaction with the park, 'biodiversity' for references documenting species information or taxonomy and 'ecology' for work looking at biotic interactions or response to environmental and human pressures. The geographical scope of each reference was defined as 'Watamu' if WMNP was the only study site, 'Kenya' if WMNP was one of several sites in the country or 'International' for any study including data from outside of Kenya.

### 2.2.2 Habitat mapping

Habitat classifications were chosen *a priori* based on similar habitats defined in Jones (1969). These were based on dominant benthic component and divided among the littoral zone as follows;

*Subtidal*

- Coral reef
- Subtidal rock
- Subtidal sand
- Subtidal seagrass
- Mixed

*Intertidal*

- Tidepool
- Beach
- Intertidal seagrass

*Supralittoral fringe*

- Islands, dunes and cliffs

The general structure of the park and location of key features were known, based on the Author's personal knowledge of the area through extensive fieldwork experience. A formal assessment of subtidal habitats was conducted over a 4-day period in February 2013. The park was divided into zones (2-3km$^2$) and systematically traversed from the low tide mark to the reef crest, with an observer in the water and a second person on a boat recording GPS positions. Notes were made on the dominant benthic substratum and particular attention was paid to the presence of patch reefs. Intertidal habitats were recorded by walking around habitat patches with a hand-held GPS tracking the path taken at the lowest tide of each tidal cycle.

The GIS software used to process these data into polygons and habitat layers was ArcMap 10.0 (ESRI 2011). Intertidal polygons were converted from the tracks. Subtidal ground-truthed waypoints were plotted onto ArcMap's base map of satellite imagery (Fig. 2.2). Habitat polygons were made by a technique called 'heads up digitising' whereby the mapper uses visible colour patches, the ground-truthed points and knowledge of the area to manually draw around habitat patches.

### 2.2.3 Sampling methods and estimating WMNP's biodiversity

Species lists were prepared for fish, echinoderms, molluscs, crustaceans and seagrass, and corals were identified to genus level. These lists are based on both quantitative sampling and chance incidental observations during the three years the Author was based at A Rocha Kenya's marine programme, located on the shore of the MPA (Fig. 2.2). Eleven affiliates of the marine programme contributed to data collection (Table 2.1). The eight intertidal and subtidal habitats defined for habitat mapping were condensed into three zones to structure data collection: coral reef, intertidal (beach, tidepool and intertidal seagrass), and lagoonal (rocky reef, sand, seagrass and mixed). The supralittoral zone, composed of dunes, rocky cliffs and islands in the park was not surveyed for biodiversity.

**Table 2.1 Data collection for fish, echinoderm, mollusc, crustacean, seagrass and coral diversity by zone. Incidental and quantitative data collection (blue) and incidental records only (yellow) are indicated. Data collectors in addition to the author include Robert Sluka (RS), Dawn Goebbles (DG), Victoria Sindorf (VS), Cassie Raker (CR), Peter Musembi (PM), Hannah Hereward (HH), Aline Porteus (AP), Mattias Horion (MH), Jack Kamire (JK), Benjamin van Baelenberghe (BB) and Dorothea Kohlmeier (DK). All collectors are affiliated with A Rocha Kenya's marine programme.**

| ***Taxon*** | ***Zone*** | | |
|---|---|---|---|
| | **Coral Reef** | **Intertidal** | **Lagoonal** |
| **Fish** | RS, DG | VS | CR |
| **Coral** | The Author | VS, BB | *Not sampled* |
| **Echinoderms** | PM, AP | CR, PM | The Author |
| **Molluscs** | PM, HH, AP | MH, JK, PM | The Author |
| **Crustacea** | HH | HH | *Not sampled* |
| **Seagrass** | *Not sampled* | DK | DK |

Quantitative sampling counted the abundance of different species in a standardised area, which was replicated across the park. Quantitative data were collected for fish, echinoderms and molluscs in coral reef and intertidal areas. In lagoonal areas only fish were assessed quantitatively (Table 2.1). Data collection for the coral reef zone was conducted at the six main research sites in the lagoon (Fig. 1.5) at depths between 1-8m below mean low water (MLW). Biodiversity data from intertidal areas were collected on rocky platforms (~1m above MLW) at regular intervals along the beach (Sindorf *et al.* 2015). Lagoonal fish data were collected along 4 transects which traverse the park at regular intervals (~2km apart) from the beach to the reef crest. Data from these transects did not include fish observed in any coral habitat encountered.

Reef habitats were sampled using belt transects. Fish transects were 40x5m (200m$^2$) and for echinoderms and molluscs, 20x2m (40m$^2$). Because of difficulties in creating a truly random sampling design under water, transects were placed 'haphazardly' across patch reefs. Lagoonal fish were recorded in a similar manner using 100x5m (500m$^2$) with belt transects arranged end-to-end traversing the entire lagoon. In intertidal areas $1m^2$ quadrats were placed at random on tidepool areas (Sindorf *et al.* 2015).

Incidental records for various taxa were collected based on chance observations across the period of the Author's residence in Watamu from September 2011 until April 2014 and augmented with observations made by other collectors (Table 2.1). When a new species was found it was added to the relevant species list and where possible, with a location and date. Some records were added based on photographs. Incidental records were collected for fish, molluscs, echinoderms alongside quantitative records and in addition included seagrasses, crustacea and coral genera. Intertidal incidental records also include beach and intertidal seagrass habitats, which were not surveyed during quantitative intertidal sampling.

### 2.2.4 Analysis of species information

Both quantitative and incidental species data were analysed to reveal basic patterns of biodiversity and conservation importance of the species found in WMNP. In addition to species richness and abundance from the raw data, species richness estimates, species diversity and dominance, community similarity between habitats, and biogeographical affinity were analysed and presented (see below for specific details). Threatened species and species of high conservation importance are highlighted based on their IUCN Red List status and other relevant information (www.iucnredlist.org).

The total richness for a taxon in a particular habitat was estimated by plotting individual-based rarefaction curves to visually estimate sampling completeness and by calculating richness estimates. Four common richness estimates were used: Chao, Jackknife 1, Jackknife 2 and Bootstrap (Kindt and Coe 2005) to give a range of estimated values.

Diversity was calculated using an index known as Probability of Interspecific Encounter (PIE) (Equation 2.1), where '*n*' is the total abundance of all individuals observed and '*p*' is the proportional abundance each species represents of the total abundance. The advantage of this method is that it is unaffected by sampling method or sample size, meaning that the diversity number generated is comparable across habitats and taxa (Gotelli and Ellison 2013). Dominance was visually compared from rank abundance curves.

**Equation 2.1 Probability of Interspecific Encounter (PIE)**

$$PIE = \frac{n}{(n-1)}\left(1 - \sum_{i=1}^{s} p_i^2\right)$$

Community similarity between habitats was conducted for fish. The species listed from incidental records were compared using Euclidean ecological distance, as this method works well with presence-absence data (Kindt and Coe 2005). The biogeographical affinity of fish found in WMNP was determined for each species, using range information found on FishBase (Froese and Pauly 2015). The percentage of Circumtropical, Indo-Pacific, Indian Ocean and western Indian Ocean-affiliated fish species are presented. The various analyses were conducted using the packages BiodiversityR and Vegan (Kindt and Coe 2005).

## 2.3 Results

### 2.3.1 Literature review

Since its creation in 1968, WMNP has been the site of many research projects, in subjects as varied as subsistence economics (Versleijin 2001) to turtle endogeny (Watson 2006). A total of 101 unique references were found (Fig. 2.3 and Appendix 1).

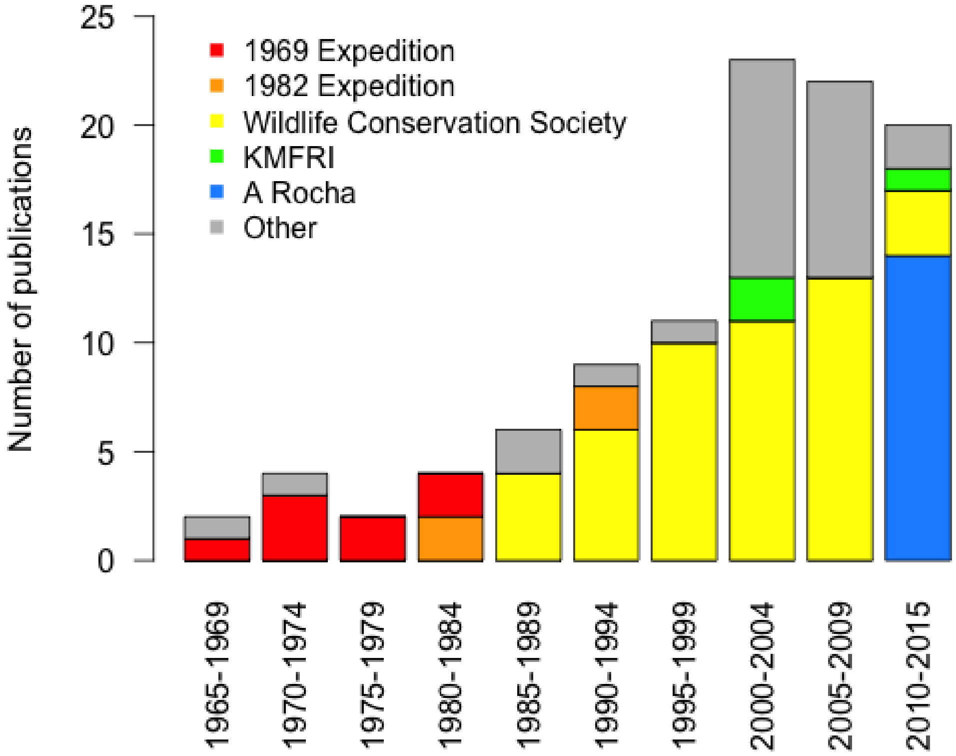


**Figure 2.3 Publication by research group in WMNP from 1968-2015, including records from the 1969 Bangor expedition, 1982 Radboud expedition, Wildlife Conservation Society, Kenya Marine and Fisheries Research Institute (KMFRI) and A Rocha Kenya**

The first publication to include data from Watamu (Isaac and Isaac 1968) reviewed marine botany for the entire Kenyan coast. Shortly afterward the Bangor expedition in 1969 collected specific information about the newly gazetted park and produced 8 publications, largely around the lead editor David

Jones' interest in isopods (Crustacea: Isopoda)(e.g. Jones 1971), but also including the first comprehensive baseline data available for the park's biodiversity and ecology (Jones 1969). Three years after being declared a UNESCO biosphere reserve in 1979, a research expedition from the University of Radboud, Njimegen in the Netherlands, carried out a second review of the park in 1982, focussing on the issues of coral health and sedimentation from terrestrial erosion (Blom *et al*. 1985, van Katwijk *et al.* 1993).

In 1987 the Kenyan Wildlife Conservation Society (WCS) group, headed by Dr. Timothy McClanahan, began regular ecological monitoring of Kenya's MPAs, including Watamu, being the first Kenyan-based research project to work in the park. To date, with nearly 30 years of annual data collection, WCS have published 45 pieces of work using data from Watamu, including some of the most widely cited and globally important coral reef ecology and conservation references in the current scientific literature (e.g. McClanahan *et al.* 2001, McClanahan *et al.* 2007a). This is especially true post-1998, when the devastating mass bleaching and mortality of corals in Watamu and across the world, spurred the study of coral reef ecology and conservation in the face of human-driven climate change.

More recently the government bodies Kenya Wildlife Services (KWS) and Kenya Marine and Fisheries Research Institute (KMFRI) began monitoring and conducting marine research. In partnership with KWS, A Rocha Kenya, a local conservation NGO began its marine programme in 2010. There have been 14 publications from this group (available online at http://kenya.arocha.org/work/scientific-research/reports/), with much of the data presented in this report being collected by the group.

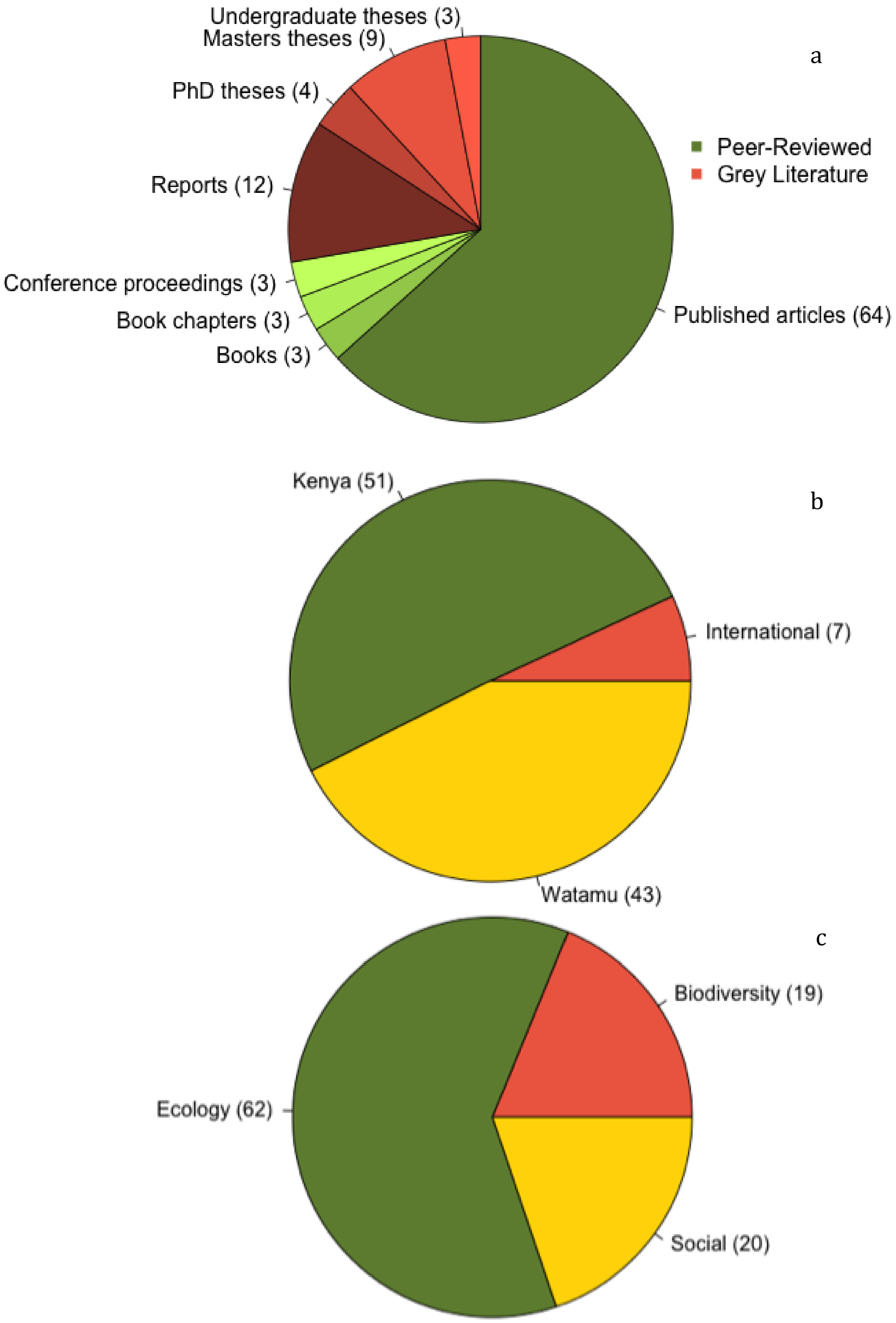


**Figure 2.4 Pie charts of WMNP references by a) type, b) geographical scope and c) thematic area.**

The majority (72%) of references found were peer-reviewed papers, with 64 published articles (Fig. 2.4a). Of the three broad thematic areas (social, biodiversity and ecology) most references, with 62 pieces of work, related to ecology (Fig. 2.4b). There were 20 references relating to social and community issues and 19 documenting biodiversity. Of the papers that present biological information gathered in WMNP, 14 include data from the intertidal zone, 14 from the lagoonal zone and the majority, with 57 references, from coral reefs. There were 43 references where data were presented only from Watamu, 51 where information from WMNP was included with other sites in Kenya, and seven references where information was presented from WMNP and internationally (Appendix 1).

### 2.3.2 Distribution of habitats in WMNP

Most of WMNP is within the reef crest, which is located 0.5-1 km offshore. Areas beyond the reef crest were not surveyed because of difficulty in accessing these rougher waters and also the greater depth, which rapidly obscures the visibility of the benthos in satellite images. The map presented covers 8.35km$^2$ (83.5% of 10km$^2$) of the park's area (Fig. 1.5).

**Table 2.2 Area covered by different habitat in WMNP in km$^2$ and percentage of the mapped area**

| Habitat | Area in km$^2$ | % of mapped area |
|---|---|---|
| Littoral | 0.418 | 5.0 |
| Coral | 0.085 | 1.0 |
| Tidepool | 0.216 | 2.6 |
| Subtidal rock | 0.144 | 1.7 |
| Beach | 0.495 | 5.9 |
| Subtidal sand | 2.185 | 26.2 |
| Intertidal seagrass | 0.359 | 4.3 |
| Subtidal seagrass | 3.292 | 39.4 |
| Mixed subtidal | 1.154 | 13.8 |

An estimated 82% of the mapped area is subtidal, 13% is intertidal and 5% is the supralittoral fringe (Table 2.2). Subtidal seagrass is the most dominant component of the park covering nearly 40% of the benthos. Coral reef was the smallest habitat covering an estimated 1%. Hard substrata (either rock or coral) cover just 5.3% of intertidal and subtidal areas. Lines of exposed Pleistocene limestone run parallel to the shore, along the beach edge forming the numerous tide-pool patches and also along the reef crest and through the lagoon forming subtidal rocky reefs (Fig. 2.5). Other areas were characterised by sandy and rubble substrata with extensive seagrass growth in shallower (<4m) depths.

Most coral reef habitat is also found in a line parallel to shore on the seaward slope of a sandy channel that stretches along the central section of the park (Fig. 2.5). This habitat consists of a chain of small lagoonal patch reefs, featuring large (>2m) *Porites* colonies, separated by sandy- or seagrass-covered channels. At the landward edge of these patch reefs, the reef rises above the ~1m deep sandy/seagrass habitat to the MLW. At the seaward edge the reef drops to ~3m deep in the northern end of the main reef chain and to ~6m at the southern end of this main reef structure (see Section 1.6). Smaller reef areas not on this main chain are found at Turtle Reef in the northern part of the park and Uyombo at the southern boundary of the park (Fig. 1.4, Fig. 2.5). These areas are similar to the main reef chain, but are slightly more exposed to oceanic conditions (although not true fore-reefs) with a seaward slope descending to a max depth of ~8-10m.

At the southern end of the park a deep (~8m), sandy, tidal channel extends from Mida Creek (Fig. 2.2). The shoreline near Uyombo village, south of this channel, has the largest extent of intertidal seagrass found in the park, as well as the largest of the park's 11 islands. The lagoon is approximately 1700 metres wide at the southern end, but narrows to just 600 metres wide in the north. The northern section of the park, known as Turtle Bay, is shallow (max ~3m) and has few patch reefs or coral growth of any kind. It is in this northern section of the park where there are the most intertidal rocky areas both adjacent to the beach and in the centre of the lagoon (Fig. 2.5).

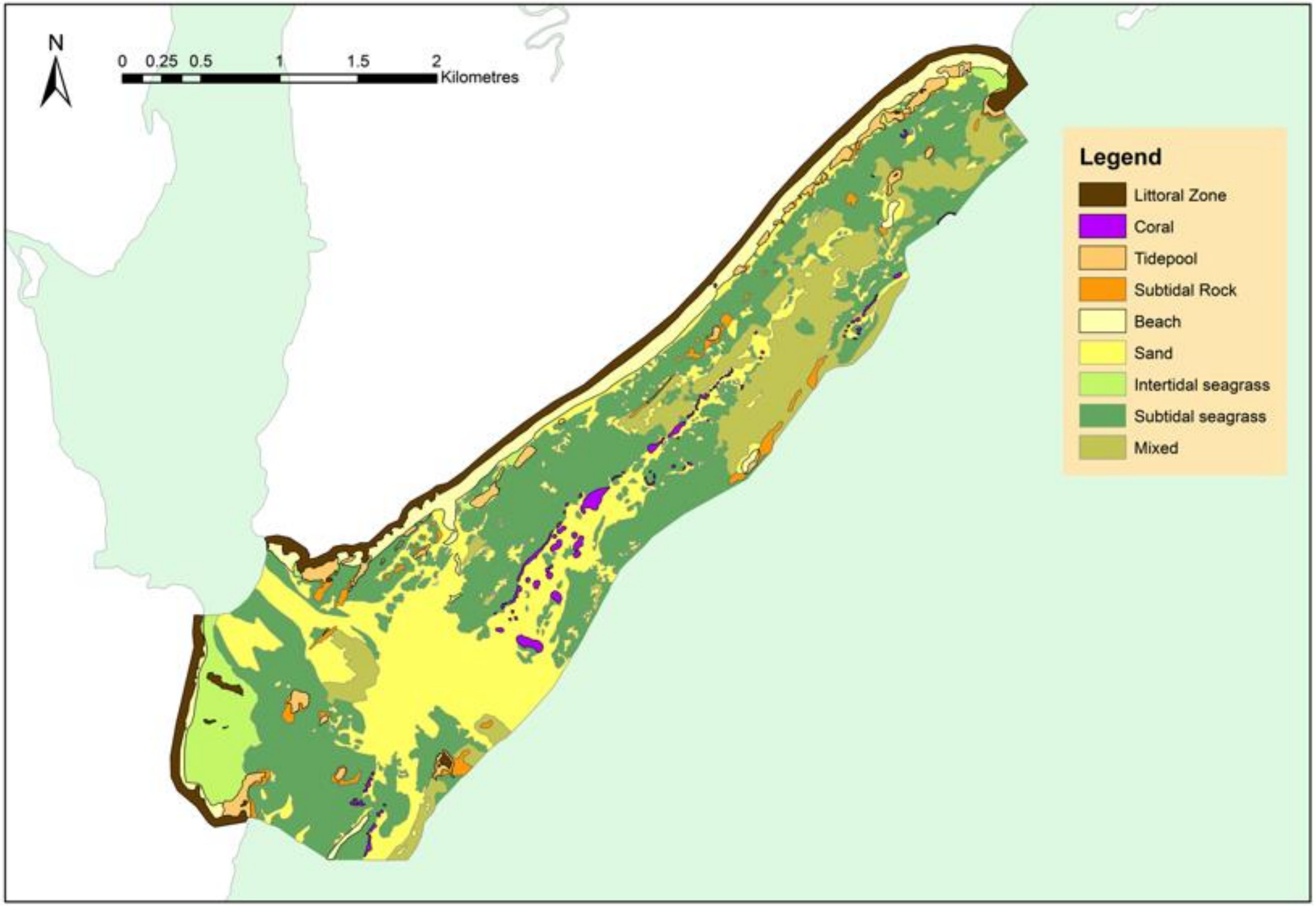


Figure 2.5 Map of habitats found between the reef crest and terrestrial boundary of WMNP.

### 2.3.3 The biodiversity of WMNP

Five major taxa were assessed to species level and one taxon, scleractinian corals, was assessed to genus level. The species richness of fish, molluscs and echinoderms was estimated using quantitative methods and incidental observations presented below (Table 3), along with incidental records of crustacean and seagrass species richness and coral genus richness. Full species lists are found in Appendix 2.

**Table 2.3 Species richness of fish, echinoderms, molluscs, crustacean and seagrass and genus richness for corals from quantitative and *incidental* data collection in different zones.**

| ***Taxon*** | | ***Zone*** | | | ***Total Richness*** |
|---|---|---|---|---|---|
| | | **Reef** | **Intertidal** | **Lagoonal** | |
| **Fish** | Quantitative | 146 | 38 | 71 | **407** |
| | *Incidental* | *266* | *89* | *157* | |
| **Echinoderms** | Quantitative | 13 | 11 | n.d. | **34** |
| | *Incidental* | *22* | *23* | *9* | |
| **Molluscs** | Quantitative | 17 | 32 | n.d. | **60** |
| | *Incidental* | *26* | *39* | *8* | |
| **Crustacea** | *Incidental* | *10* | *15* | *1* | **23** |
| **Seagrass** | *Incidental* | *n.d.* | *n.d.* | *11* | **11** |
| **Coral (genus)** | *Incidental* | *41* | *13* | *n.d.* | **43** |

Fish were the richest taxon in the park with 407 species observed from 62 families and 178 genera overall. Ten of the fish species were elasmobranchs. The most speciose teleost family was the Labridae (Wrasses) with 45 species (Appendix 2). Coral reefs had the highest richness for fish observed of all the habitats (Table 2.3). During species identification of fish an undescribed species of guitarfish (Rhinobatidae) was observed (L. Compagno, Shark Research Institute, pers. comm.) along with seven potentially un-described sweepers *(Pempheris spp.)* (J. Randall, Bishop Museum, pers. comm.).

Molluscs were the most speciose invertebrate taxon assessed, with incidental records of 60 species. A total of 55 mollusc species were gastropods, including 12 nudibranchs. The 34 echinoderms were comprised of nine starfish (Asteroidea), ten urchins (Echinodea), ten sea cucumbers (Holothuroidea) and five brittlestars (Ophiuroidea). The 43 genera of corals observed came from 11 families. Most coral genera were found on the reef, but 13 genera were observed in the rocky intertidal (tidepool) zone, with 2 of these (*Anomastrea* and *Alveopora*) being only seen in this habitat.

Considering all the taxa there were 18 species found which have an IUCN Red List status of conservation concern, with five near threatened (NT) species, 11 vulnerable (VU) species and two endangered (EN) species. Six of these species were elasmobranchs, six were bony fish (Teleosts), four sea cucumbers (Holothuroidea), one seagrass and one coral species.

- Black-tip reef shark - *Carcharhinus melanopterus* (NT)
- White-tip reef shark - *Triaenodon obesus* (NT)
- Blue-spotted stingray - *Taeniura lymma* (NT)
- Brown-marbled grouper - *Epinephelus fuscoguttatus* (NT)
- Malabar grouper - *Epinephelus malabaricus* (NT)

- Sharp-nose stingray - *Himantura gerrardi* (VU)
- Honeycomb stingray – *Himantura uarnak* (VU)
- Alfred’s manta ray - *Manta alfredi* (VU)
- Giant grouper - *Epinephelus lanceolatus* (VU)
- Saddle-back coral grouper - *Plectropomus laevis* (VU)
- Thorny seahorse - *Hippocampus hystrix* (VU)

- Hedgehog sea cucumber - *Actinopyga echinites* (VU)
- White-belly sea cucumber - *Actinopyga mauritiana* (VU)
- Military sea cucumber - *Actinopyga miliaris* (VU)
- South African eelgrass - *Zostera capensis* (VU)
- Crisp pillow coral - *Anomastraea irregularis* (VU)

- Humphead wrasse - *Cheilinus undulatus* (EN)
- Edible sea cucumber - *Holothuria scabra* (EN)

The ranges of each fish species were pooled into broad biogeographical categories. Most fish had a range extending beyond the Indian Ocean with 323 being Indo-Pacific and six species with a circumtropical range (Fig. 2.6) There were 44 species endemic to the WIO region and a further 24 species extending beyond WIO, but confined to the Indian Ocean.

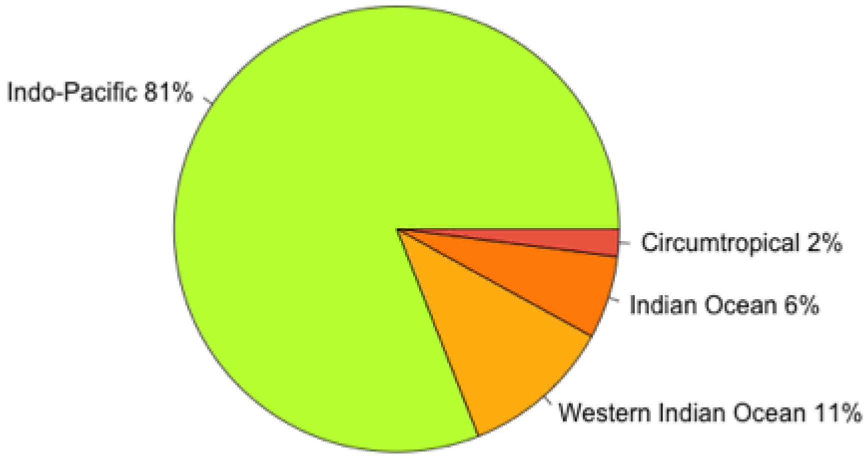


**Figure 2.6 Percentage of fish species by biogeographic affinity.**

### 2.3.4 Sampling completeness and estimating total richness

Sampling effort can be used to assess the completeness of a species list. Sampling of a community is rarely complete and undetected species make up part of the total richness. A disadvantage of incidental richness is that sampling completeness and total richness estimates are not possible and as such the results below come from quantitative records only.

**Table 2.4 Sampling effort of quantitative data collection by taxon and habitat**

| Taxon | Habitat | Area surveyed ($m^2$) | % Area of mapped habitats | Number of individuals recorded |
|---|---|---|---|---|
| Fish | Reef | 4000 | 4.7% | 2409 |
|  | Intertidal | 131 | 0.1% | 220 |
|  | Lagoonal | 14,500 | 0.2% | 1400 |
| Echinoderms | Reef | 800 | 0.9% | 565 |
|  | Intertidal | 153 | 0.1% | 772 |
| Molluscs | Reef | 1440 | 1.7% | 95 |
|  | Intertidal | 1510 | 0.7% | 622 |

The largest area covered in quantitative surveys was for fish in the lagoonal zone covering 14,500$m^2$ (Table 2.4). However, as a proportion of the total area covered by this habitat in WMNP, only 0.2% of the habitat was sampled. By contrast, the smaller area covered for fish on coral reef of 4000$m^2$ was technically a greater sampling effort as this accounted for 4.7% of this smaller habitat.

The number of individuals recorded is a useful measure of sampling effort, as well as indicating the abundance of taxa in different parts of the park. In order to assess the completeness of species lists, individual-based rarefaction curves require a minimum of 20 individuals (Gotelli and Elison 2013). The smallest sample was 95 individuals for molluscs on coral reefs, meaning that rarefaction was possible for all taxa.

**Table 2.5 Observed richness and richness estimates from quanitative data. Estimates using Jackknife1 (JK1), Jackknife2 (JK2), Chao (CH) and Bootstrap (BS).**

| Taxon | Habitat | Observed Quantitative Richness | JK1 | JK2 | CH | BS |
|---|---|---|---|---|---|---|
| Fish | Reef | 146 | 183 | 197 | 175 | 164 |
| | Intertidal | 38 | 58 | 76 | 137 | 46 |
| | Lagoonal | 71 | 99 | 116 | 108 | 83 |
| Echinoderms | Reef | 13 | 15 | 12 | 13 | 14 |
| | Intertidal | 11 | 15 | 19 | 17 | 13 |
| Molluscs | Reef | 17 | 24 | 26 | 22 | 20 |
| | Intertidal | 32 | 42 | 42 | 37 | 37 |

Rarefaction curves for reef fish and lagoonal fish approached the asymptote (Fig. 2.7), suggesting these habitats were adequately sampled for fish. Richness estimates predicted an extra 18-51 fish species on reefs, and an extra 12-40 species in lagoonal areas that had not been recorded, depending on the richness estimator used (Table 2.5). Intertidal fish appeared to have been under sampled, as the rarefaction curve showed a steep rise with no asymptote (Fig. 2.7), which means that estimates of total richness were broad, ranging from 58-137 species (Table 2.5).

Echinoderm species lists appeared to be largely complete with the rarefaction curves for both intertidal and reef species nearing the asymptote (Fig. 2.7). Richness estimates suggested that reef echinoderms had been completely sampled (actual = 13, estimate = 12-15) (Table 2.5), and that there are only 2-6 extra species in intertidal areas (Table 2.5). However, incidental records found 9 extra species of echinoderm on reefs and 12 in intertidal areas (Table 2.3). Intertidal molluscs appeared well sampled (Fig. 2.7), with 5-10 extra species predicted (Table 2.3). The rarefaction curve for reef molluscs didn’t approach an asymptote and richness estimates suggested there were only 3-9 more species undetected.

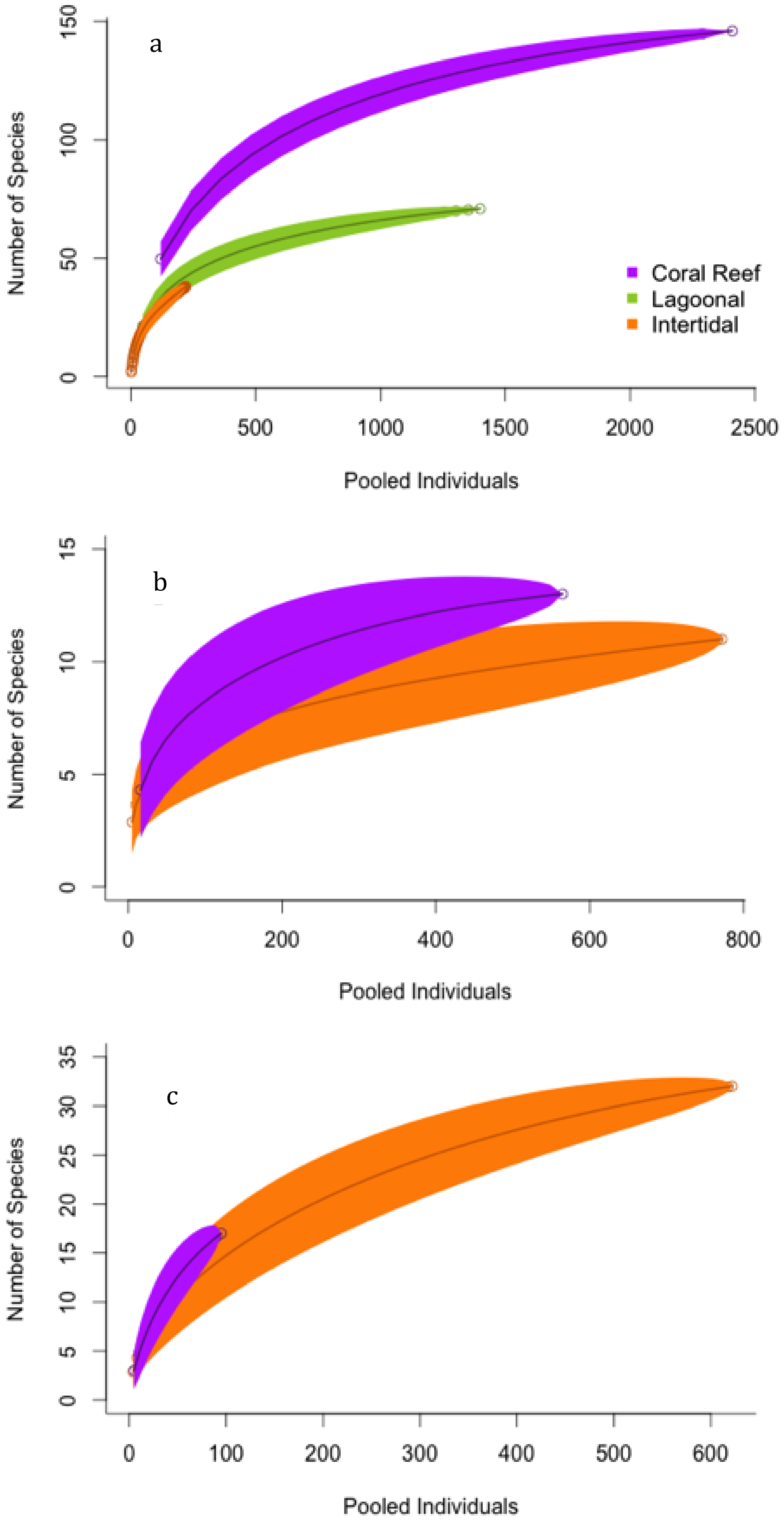


**Figure 2.7 Rarefaction curves of species richness based on individual sampling. Presented by habitat for a) fish, b) echinoderms and c) molluscs.**

### 2.3.5 Species diversity and community similarity between habitats

Fish were the most diverse taxon with PIE values ranging from 0.904 in lagoonal areas to 0.962 in coral reef areas (Fig. 2.8). Coral reef echinoderms had the lowest diversity for invertebrates with a PIE value of 0.662. The highest invertebrate diversity was for intertidal molluscs, with a PIE value of 0.762. Diversity of fish was highest on coral reefs and lowest in lagoonal habitats. The diversity of both molluscs and echinoderms was higher in intertidal areas than on reefs.

Using incidental records of species presence and absence the ecological distance was compared for fish communities between the three habitats (Table 2.6). The Euclidean distances show that coral reef was the most distinct habitat for fish. Indeed 173 species or 65% of the total incidental species richness for this habitat were only found in reefs and not other habitats. The intertidal zone had the fewest unique species, with 29 (32.6%) and the lagoonal zone had 71 (46.4%) unique species.

Table 2.6 Ecological distance between fish communities based on incidental data.

| **Habitat comparison** | **Euclidean distance** |
|---|---|
| Coral reef - Intertidal | 16.03 |
| Coral reef - Lagoonal | 16.61 |
| Intertidal - Lagoonal | 12.61 |

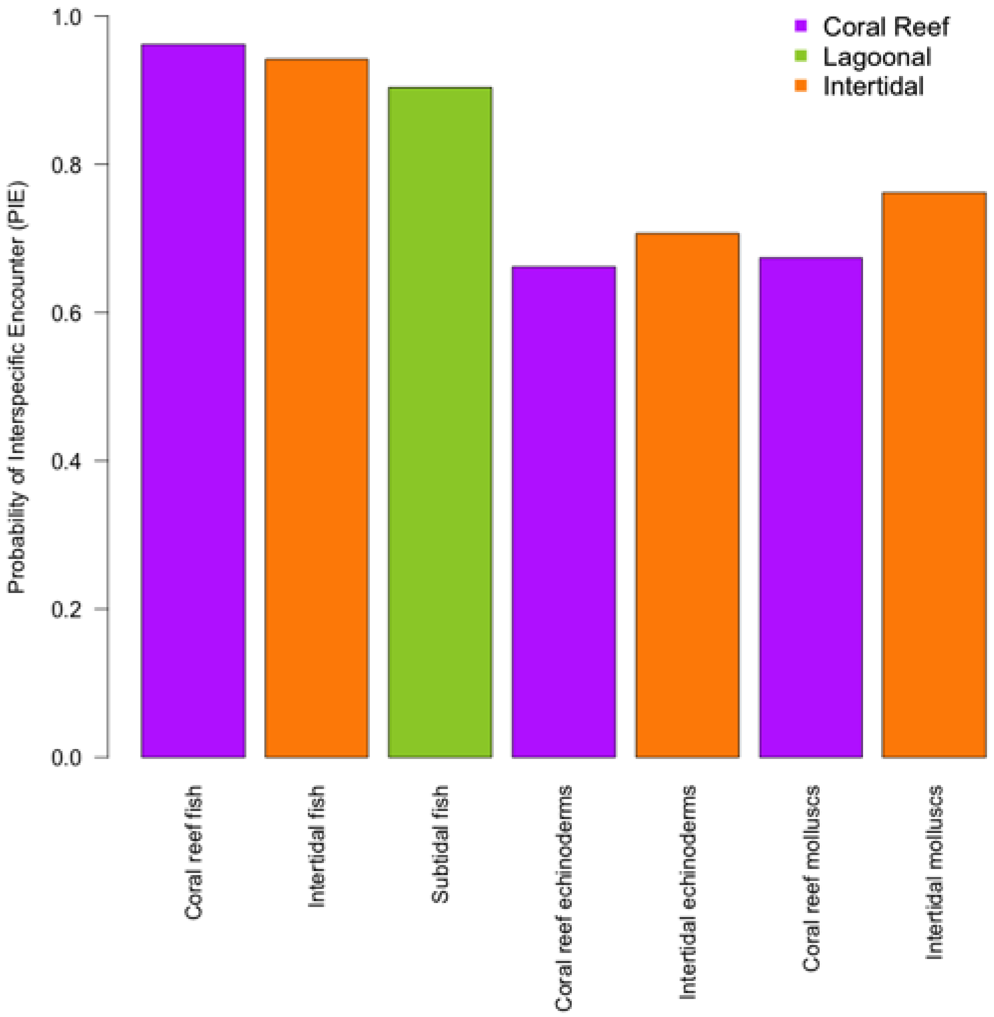


**Figure 2.8. Species diversity by taxa and zone using the Probability of Interspecific Encounter (PIE) index.**

## 2.4 Discussion

### 2.4.1 Progress towards a baseline for WMNP

The aim of this chapter was to provide a baseline of current habitat distributions and biodiversity of WMNP. The literature search found 101 unique records of published papers, reports and theses where WMNP was included as a research site (Figs 2.3 and 2.4). The majority of references related to coral reef ecology and biodiversity, illustrating a strong bias to reefs, even though they are the smallest component of the mapped park area (~1%) (Table 2.2, Fig. 2.5). The remaining 99% of the park remains under studied, but contributions from this research have begun to address this bias, with extensive sampling of the intertidal area (Table 2.4). The most understudied habitats are the seagrass beds, subtidal rocky reefs and sandy channels in the 'lagoonal zone', which cover 82% of the mapped park area (Table 2.2, Fig. 2.5).

A heavy focus on coral reefs is not unusual in tropical marine ecology because of their considerable perceived importance in terms of biodiversity (Plaisance *et al.* 2011), ecosystems services (Constanza *et al.* 1997) and aesthetic appeal. However, this focus misses key ecological processes and biodiversity found within other tropical marine habitats. This study found the intertidal zone had the most biodiverse echinoderm and mollusc communities (Fig. 2.8) and recorded 10 of the 18 IUCN red-listed species of conservation concern in non-reef habitats. Investigating the ecological importance of non-reef habitats Sindorf *et al.* (2015) noted that eroded rocky intertidal areas (~2% of WMNP) contained a high proportion juvenile reef fish species, which were using the pools as nursery grounds.

In this study fish communities were the best-sampled taxa both in terms of area covered and number of individuals recorded (Table 2.4). Rarefaction curves show that sampling was adequate for taxa in most habitats, but indicated that sampling of intertidal fish and coral-reef molluscs was incomplete (Fig. 2.7). There were 14 references published about biodiversity, with coral (Lemmens 1993), echinoderms (Humphreys 1981), seagrass (Issac and Isaac 1968) and mollusc diversity (McClanahan 1990) being assessed >20 years ago (Appendix 1). Unfortunately, the differing sampling methods and sites meant it was not possible to compare current species lists with these historical records. Fish were not assessed in any previous work in WMNP, which is surprising as this is often the best-sampled group in tropical marine studies (Plaisance *et al.* 2011).

The Bangor expedition in 1969 made the first habitat map of WMNP (Fig 2.9). The current map (Fig. 2.5) improves on this habitat information with increased accuracy made possible by modern high-resolution satellite imagery and the spatial analysis conducted with GIS software (ESRI 2011). However, the main structures in the park, such as the location of coral habitats and sandy channel is clear in Jones' (1969) map and in the current habitat distribution map. Maps can be used in MPAs for a wide range of purposes from planning fieldwork to zoning and management tasks (Ferreira *et al.* 2012, Maynard *et al.* 2010). Increasingly maps are also being used as a research tool, such as for mapping coral reef resilience (Rowlands *et al.* 2012) and predicting fish communities (Purkis *et al.* 2008). It is hoped that the current map will provide basic information about the park, which will be easily accessible to managers, community groups and NGOs, without needing to have an extensive background in science (Salm and Clark 2000, Ferreira *et al.* 2012).

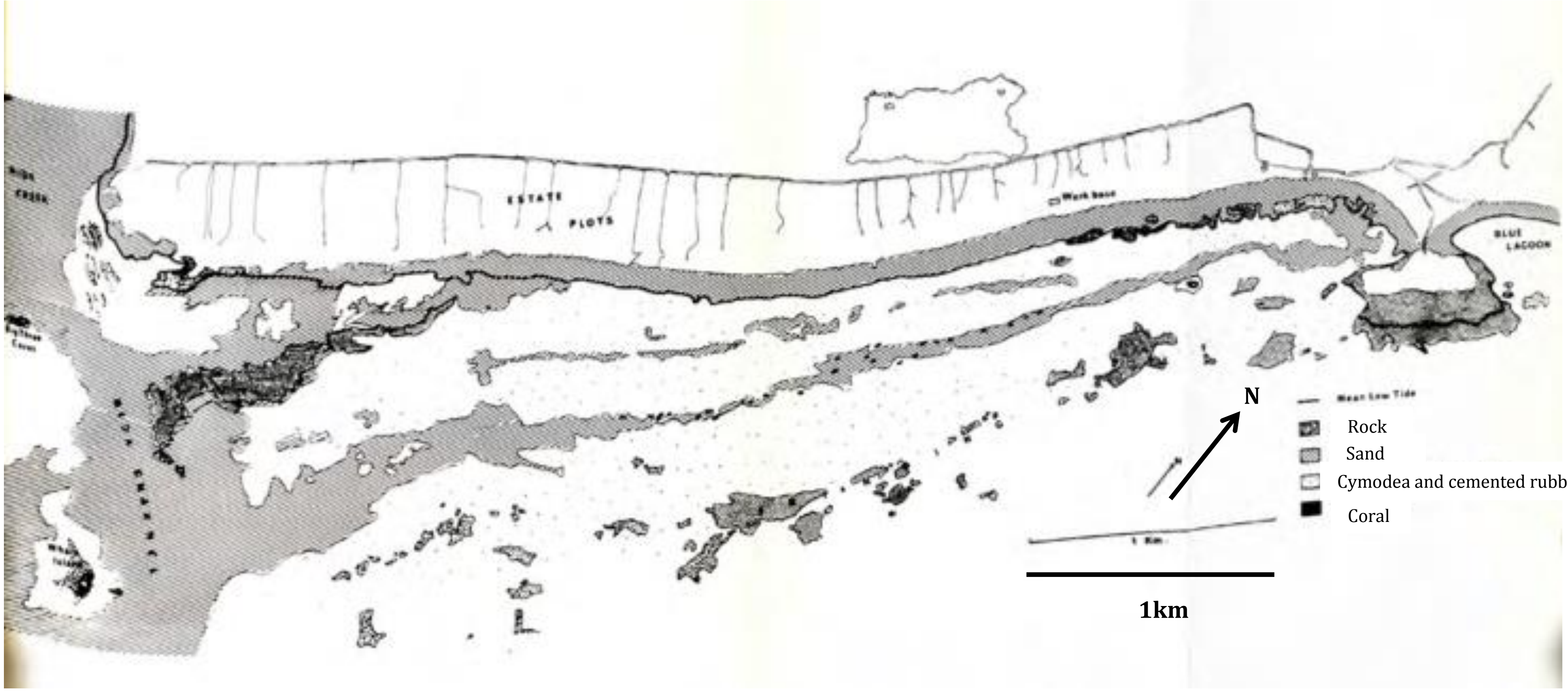


Figure 2.9 The first habitat map of WMNP produced by the Bangor Expedition 1969 (Jones 1969). Annotated by the author to show compass direction and scale and the key.

### 2.4.2 Research gaps and future work

The literature review highlights several areas where our knowledge of WMNP is relatively good. McClanahan's work on coral ecology and degradation with fishing pressure and climate change gives us a detailed understanding of the functioning and conservation pressures facing the coral reefs of WMNP (e.g. McClanahan *et al.* 2001 and McClanahan 2014a). Kaunda-Arara and Rose's (2004) work on fish movement in WMNP demonstrated that the protected area's fish community was spilling-over into adjacent areas. A more obscure field that has been well documented is the infaunal isopod taxonomy and biodiversity of the beach and subtidal sand in WMNP (e.g. Jones 1971). Having comprehensive historical records for coral reef areas is rare (Knowlton and Jackson 2008). While there is an impressive research history in WMNP, the information available is heavily biased by the interests of dominant authors and research groups (Appendix 1).

Species records from the current study were limited to well-documented and conspicuous groups that could be easily identified in the field. Identification of other taxa, such as soft corals (Octocorallia) and sponges (Porifera), which require a higher degree of taxonomic specialisation and the collection of specimens was not attempted. Cryptic and infaunal species require taking sediment cores and dead coral rock (Plaisance *et al.* 2011), which was conducted in historical studies of WMNP (Brander *et al.* 1971), but was beyond the scope of the current study. Many of the taxa not assessed contribute significantly to total biodiversity of shallow marine habitats (Taylor 1971, Richmond 2002) and play a crucial role in coral-reef ecology and functioning (Diaz and Rutzler 1999).

Future biodiversity assessments should prioritise infaunal species of mollusc, echinoderm and crustaceans and all species of soft corals, sponges, macroalgae, polychaetes and tunicates.

This study provides the most detailed and accurate information to date of habitat distribution within the lagoon, made possible through high-resolution satellite images, GIS software and extensive ground-truthing of the habitats. However, the area mapped only extends to the reef crest and the remaining 1.65km$^2$ within the boundaries of WMNP is unknown, without any information on the species found there. An additional gap in the mapping is for the supra-littoral habitats, recognising the differences in the dunes, coastal scrub, cliffs and islands found above the tideline, which are protected as part of the MPA.

There remains a large imbalance between information on the coral reef patches compared to other more extensive subtidal habitats found in the park, particularly the seagrass beds. Eleven of the 12 seagrass species found in the WIO were recorded in WMNP (Richmond 2002). Seagrass beds act as nursery grounds, feeding grounds, and efficient carbon sinks and harbour unique biodiversity (Green and Short 2003). The conservation status, importance and threats to the ~4km$^2$ of subtidal and intertidal seagrass habitat in WMNP remain largely unknown.

### 2.4.3 Anthropogenic stressors impacting WMNP

Nearly 50 years ago, when WMNP was initially gazetted, there were concerns of overexploitation in the lagoon, particularly of shells for the tourist trade (Jones 1969). By declaring the area a no-take zone it was hoped this would alleviate the pressure on the reefs and other habitats (West and Salm 2003). In the past 50 years human populations and urban development have increased dramatically in Watamu (>500%), triggered by tourism and migration into the area (Muthiga 2009). The presence of a large human population has had several impacts, the most obvious of which is the encroachment of the dune and beach areas of the park by hotels and other developments. Another potential impact of tourist development, which has never been formally assessed, is the increase in polluting substances entering the lagoon. Large numbers of pleasure vessels and tourist boats are moored in the northern part of the park, potentially releasing hydrocarbons and antifouling paint into the water.

Increasing population on the Kenyan coast has also impacted reef fisheries, with a significant reduction in fish yields during the 1990s (Kaunda-Arara *et al.* 2003). While WMNP has been moderately successful at enforcing its no-take status (McClanahan *et al.* 2010), there exists a degree of poaching of fish and other natural resources from the park (B. Cowburn pers. obs.) the extent and impacts of which are unclear. The increasingly degraded areas around the park (B. Cowburn, unpublished data), may be causing a ‘spill-in’ of negative environmental conditions (Eklof *et al.* 2009), through reduced larval supply, or reduced populations of fish which range both inside and out of the park.

The most significant impact to the park to date, was the mass-bleaching and mortality of coral in 1998 (Muthiga 2009). This extreme mass bleaching event that caused the loss of approximately 16% of reefs globally (Wilkinson 2008), saw 70% mortality of corals in WMNP (Chapter 3). Since 1998 there have been four minor bleaching events and with further increases in ocean temperatures predicted, the future of corals in WMNP is likely under threat (Hoegh-Guldberg 2014).

### 2.4.4 The conservation value of WMNP

MPAs are conserved for a wide range of purposes including promoting tourism, managing fisheries and creating sustainable livelihoods (Salm and Clark 2000, Muthiga 2009). In addition, MPAs act as refuges for threatened species, protect natural habitats and maintain key ecological processes internally and in the wider context of surrounding unprotected areas (Salm and Clark 2000). In this section, the information gathered during this study is used to assess the contribution of WMNP to species and ecological conservation.

Species lists reveal that there are 18 species that have IUCN red listed status other than 'Least Concern' or 'Data Deficient': six elasmobranchs, six teleosts, four sea cucumbers *(Holothuroidea)*, one seagrass species and one coral species. The most severe threat to the survival of most of these species is overfishing, particularly for export to the East Asian market (Warren-Rhodes *et al.* 2003, Clark 2004). WMNP has been effective at protecting a healthier fish community than surrounding areas (McClanahan 2014b), suggesting the park may be contributing to the protection of these endangered species. However, the lifecycles and home ranges of these species are unknown and may extend beyond the park. Indeed, the discovery of potentially eight un-described species, including a 2m long species of guitarfish, during this study demonstrate that much more research is needed to fully understand what WMNP is conserving.

The coral species, *Anomastrea irregularis,* is IUCN red-listed as 'vulnerable' and is also restricted to the western Indian Ocean (Obura 2012). Large numbers of the coral were found in the intertidal rocky platforms along the beach margin and near Mida Creek. The significance and health of this population of corals is not clear. In WMNP 44 (11%) of the fish species observed have ranges restricted to the western Indian Ocean (Fig 2.6). Being a poorly-studied region (Richmond 2002) it is possible there are more endemic species than this, potentially amongst the 8 un-described fish species discovered in this study.

The effective protection against unsustainable resource extraction in WMNP was displayed by the presence of several keystone species observed during fieldwork. The orange-lined triggerfish (*Balistoides undulates*) and red knobbed starfish (*Protoeaster linckii*) were common in WMNP (Appendix 2), but on unprotected reefs in the Kenya the loss of these keystone species through overfishing has been associated with the rapid increase of sea urchin populations (*Diadema spp.* and *Tripneustes gratillia* respectively) with damaging consequences for the wider ecosystem (McClanahan 2000, Eklof *et al.* 2009). Conserving keystone species and the reef community as a whole using no-take zones maintains the various ecological links that produce resilient and healthy ecosystems (West and Salm 2003, Mumby *et al.* 2007b). Despite multiple stressors impacting marine habitats in Watamu, the establishment of WMNP ~50 years ago has positively influenced the reef community (McClanahan

2014b) contributing to the conservation of valuable species and ecological processes in this area.

### 2.4.5 Protecting marine habitats in a rapidly developing tropical nation

The influence of protected areas extends beyond their impact on local habitats and biodiversity. Whether through management, income generation or resource access, MPAs have numerous consequences for those living nearby (Cinner *et al.* 2009). A full discussion of the socio-economic impacts of WMNP is outside the scope of this study and is much better addressed elsewhere (e.g. Versleijin and Hoorweg 2009, Carter 2012). However, the interactions between park and people have significant bearing on conservation in WMNP and should be outlined.

Income generation through tourism has been successful in WMNP, attracting approximately 25,000 visitors per year and generating €200,000 per year in park entrance fees (Cowburn *et al.* 2013). Watamu has seen a 900% increase in tourist infrastructure over the past forty years (Muthiga 2009). There are several undesirable sociological and ecological side effects of tourism that have been noted in Watamu. The tourists have a direct impact on reefs and intertidal areas through visiting these habitats (Cowburn *et al.* 2013, Musembi *et al.* 2014) and indirect impacts on reefs, such as increasing demand on local fisheries to provide for tourists and tourism workers (Carter 2012). Tourism has brought money and work to people living in Watamu, but it has also introduced a disturbing suite of negative influences including sex tourism, drugs and crime (Versleijin and Hoorweg 2009, Carter 2012).

Many locals feel that income from tourist activities is highly unequally distributed within the community (B. Cowburn pers. obs). KWS extract >50% of the average price paid by tourists in WMNP as park entrance fees, of which little is shared or invested in the local community, and is rather pooled into a central government fund (Versleijin and Hoorweg 2009). Immigration to the area has meant Watamu is now composed of several ethnic groups including two coastal groups, inland Kenyans and resident Europeans (Carter 2012), all of which creates a volatile environment filled with community conflicts and mistrust (B. Cowburn pers. obs).

To date there is little support for the marine park from local fishermen, either in Watamu (Versleijin and Hoorweg 2009) or in other marine parks elsewhere on the coast (Cinner *et al.* 2009). This attitude is held by the local community, despite a wide-spread knowledge of declining fish stocks and a need for fisheries management (Cinner *et al.* 2009). WMNP, like many protected areas in Africa (Neumann 1997), was established as an exclusion zone; a policy that is seen to this day in KWS. Versleijin and Hoorweg (2009) reported that the local community on the coast perceive KWS as an oppressive 'police' force as opposed to conservation managers.

The socio-economic situation of an MPA is often the least well-understood component of park management, but is essential to its success, with societal values, demographics, political stability and the economic setting of an MPA all impacting effectiveness (Fox *et al.* 2014). In a global assessment of MPAs Fox *et al.* (2014) found that Human Development Index (HDI) and Integrity of Governance are significantly correlated with MPA success. Unfortunately, on both a national level and a local level Watamu suffers from high levels of poverty and corruption. Considering the complex interaction between tourism and poor governance structures within KWS (Muthiga 2009) the continued successes of WMNP into the future looks rather bleak.

However, efforts are being made to alleviate these issues with several NGOs working in Watamu to counter poverty, social issues and the heavy reliance on natural resources. Managers within KWS are attempting to change the age-old methods employed by their rangers and adopt people-integrated management strategies (Muthiga 2009). Fishermen are forming unions through Beach Management Units (BMUs), which work with KWS and local government to ensure a healthy dialogue around fisheries. The future work for the conservation in WMNP is as much in the socio-economic field, as in the marine ecology presented in this report. Addressing the issues presented here are essential if the park is to continue protecting its incredible biodiversity and habitats for a further 50 years.

## Conclusions

Watamu Marine National Park has been subject to a range of anthropogenic changes over the past 47 years of being a no-take marine park, but sustains a range of habitats and species of conservation importance. The data presented in this chapter provide an overview of the park's current status, which can be used as a baseline in future studies. In particular, the habitats of the park are now mapped revealing the extent and distribution of different habitats, species lists are presented for six major taxa, including the first comprehensive species list for fish, and an extensive bibliography has been compiled revealing the gaps in our understanding of WMNP. Despite being a small park in a relatively poor tropical nation, WMNP is far from being a 'paper-park' and contributes to local and regional conservation efforts. However, with increasing pressure from human development and climate change, the future of the park relies on effective management, linked with scientific research and community consultation, if it is to continue to protect marine habitats and biodiversity.

Plate 3. Typical reef scene in Watamu Marine National Park. Bennett's Reef in 2013 (Photo: B. Cowburn).

# Chapter 3. Reef health and ecosystem resilience over 30 years on a Kenyan coral reef

## Abstract

The decline of coral reefs as a result of thermal stress and mass coral bleaching is an increasingly common phenomenon globally and threatens these ecosystems irrespective of their protected status. This chapter documents the changes in the coral and benthic community of Watamu Marine National Park (WMNP), Kenya, over a 30-year period from 1983 to 2013 to understand how coral bleaching has impacted the reef. The key processes of recruitment, growth and mortality in the early life stages of corals are investigated to identify factors that may be preventing recovery. The most significant impact on the reef occurred during 1998, where 70% of coral cover was lost and the community composition was altered, with declines in *Acropora, Montipora* and branching *Porites* colonies. However, despite this change in coral community, the reef has not phase-shifted to a macro-algal dominated state. Instead, the reef is dominated by bleaching-resistant coral taxa and turf algae, which may represent a transitory state or a novel stable state. Mortality rate and growth rate of juvenile corals have not changed between 1994 and 2014, but recruitment rate has dropped from a median of 5.5 recruits per $m^2$ to just 2 per $m^2$ in 2014, which will reduce the recovery potential of the park. The lack of recovery in Watamu to its pre-1998 state, may indicate it is vulnerable to future bleaching events that could cause the reef to cross a tipping-point and phase-shift to an even less desirable ecosystem state. It is therefore recommended that water quality and

larval supply are investigated to identify management options that will aid the future of Watamu’s coral community in a warming world.

## 3.1 Introduction

The global decline in coral cover, abundance and diversity on tropical reefs is well documented (e.g. Wilkinson 2008). The causes of this decline are varied and often compounded, but increasingly mass coral bleaching and its' associated mortality caused by increasing sea surface temperatures, is becoming the dominant threat to corals (Hughes *et al.* 2003). The response of reefs and coral communities to stress and acute disturbance is often non-linear and characterised by feedback mechanisms and critical thresholds (Mumby *et al.* 2007b), which are best described through the concept of ecological resilience (Holling 1973).

The factors promoting resilience of a particular reef are numerous and have complex interactions (Nystrom *et al.* 2008). It has been noted that reefs with low anthropogenic stress can bounce back from acute disturbances, as the various ecological links that promote reef resilience remain intact (Sheppard *et al.* 2008, Diaz-Pullido *et al.* 2009). This finding has led to the theory that no-take marine protected areas (MPAs), should be able to protect reefs against climate change, because they reduce other human stressors (West and Salm 2003, Mumby *et al.* 2007b).

Evidence of MPA effectiveness is varied. On a global scale MPAs have been shown to prevent coral loss compared to unprotected areas, which are on average losing coral cover to a range of impacts (Selig and Bruno 2010). However, MPAs do not influence the amount of coral lost during a mass bleaching event (Selig *et al.* 2012) and currently there is no conclusive evidence that MPAs promote reef recovery after bleaching events. There are examples where MPAs appeared to improve recovery (e.g. Wilson *et al.* 2012) and other examples where they did not (e.g. Ledlie *et al.* 2007). In some cases, it may be that the MPA is too small or poorly managed to effectively preserve the ecological factors that promote reef resilience (Selig *et al.* 2012), which are common issues for MPA effectiveness in general (Mora and Sale 2011). However, reefs in MPAs may also be ineffective at promoting recovery because they are located in areas of high thermal stress (Maina *et al.* 2008), have poor connectivity to other reefs (Selig *et al.* 2012) or because they suffered a phase-shift to a stable low-coral cover state (Ledlie *et al.* 2007, Mumby *et al.* 2007a).

Recent literature about the management of reefs has focussed on preventing phase-shifts (Nystrom *et al.* 2008) and identifying areas with factors promoting resistance and resilience to climate change (Grimsditch and Salm 2006, Baskett *et al.* 2014). Much less attention is paid to reefs in MPAs that may have already shown a phase-shift, and identifying how to manage for recovery (Graham *et al.* 2013). However, before any management actions are taken it is important to identify the resilience capacity of a reef and determine whether ecological thresholds have been exceeded and how near the system is to these thresholds (Nystrom *et al.* 2008). Where an MPA is already established, an understanding of the resilience of the system is needed to identify and boost stabilising factors, if the reef has not undergone a phase-shift, or to promote de-stabilising factors if the reef has phase-shifted to a non-coral dominated stable state (Graham *et al.* 2013)

Operationalizing resilience theory in practical conservation has received increasing attention in recent years (Mumby *et al.* 2014, Anthony *et al.* 2015), although it has only been applied in a few cases (e.g. Maynard *et al.* 2010). Traditional reef health measures, such as coral cover may not be the most informative, as they can remain high while masking underlying degradation of key ecological processes, such as recruitment and herbivory (Nystrom *et al.* 2008). Coral demographic processes, such as recruitment, growth and mortality are more useful for understanding the trajectory of a coral community and the resilience of the overall system (Hughes and Tanner 2000, Anthony *et al.* 2015).

### 3.1.1 Investigating coral decline and recovery in a Kenyan MPA.

Coral decline and recovery, and their causes, were investigated in Watamu Marine National Park (WMNP), located on the Kenyan Coast (E40°00’00”, S3°23’00”), which is an amenable location for such a study for several reasons. It is an old MPA, being established in 1968, with relatively good enforcement (Muthiga 2009), which means exploited organisms (e.g. fish) have had time to recover (McClanahan 2014b) and the coral community has had time to respond to the benefits of being in a protected area (Selig and Bruno 2010). The area has been impacted by mass coral bleaching on several occasions, with a recorded amount of coral mortality in some cases (McClanahan 2014a). Perhaps most crucially, there are quantitative data on the coral community from as early as 1983, before the particularly severe 1998 bleaching, meaning the park has a valuable baseline to compare with, which is rare in coral reef studies (Knowlton and Jackson 2008, Bruno *et al.* 2014).

The aims of this study are:

- To determine whether a phase-shift has occurred on the coral reefs of WMNP and, if so, how and when.

- Measure the processes of coral recruitment, mortality and growth and compare them with historical data to determine how these processes may have changed over time.
- Investigate which factors may be affecting the current coral community and suggest potential options for management to improve the state of coral in the park.

## 3.2 Methods

### 3.2.1 Study sites and datasets

The data that are analysed and presented in this chapter are drawn from four main sources, which investigated the coral community at different time periods and using different methods (Table 3.1). All the data used in this study were gathered in Watamu Marine National Park (WMNP), The MPA covers 10km$^2$, predominantly of lagoon habitat, including extensive seagrass beds and small patch reefs (see Chapter 2 and Fig. 2.5). The inlet to Mida Creek mangroves is found at the southern end of the park, which causes daily tidal flushing and mixing of water from this mangrove area with lagoon waters and the open ocean. All reef areas in WMNP are lagoonal in nature, dominated by large (>2m) *Porites* colonies growing along the edge of channels running through the backreef zone (see Section 1.6). Bennett's Reef and Coral Gardens are located at the northern end of the main chain of patch reefs in WMNP, where the channel depth is just ~3m below mean low water springs (MLWS) (Figs. 1.4 and 2.5). Lambis reef is further south along this main reef chain, descending to ~6m below MLW at its base. Bara Bara is similar to Lambis, but is found in the middle of the channel, surrounded by ~6m deep water. Uyombo and Turtle Reef are found along deeper channels (8-10m deep) near to the reef crest and hence have more oceanic exposure.

In this study the datasets used include:

- **Radboud University Expedition 1983:** The earliest quantitative record of the coral communities in WMNP comes from 1983, where a number of sites around Watamu and Malindi were assessed, of which 8 sites are located in WMNP. The site locations from this study were plotted by scanning the site map from the original publication (Blom *et al.* 1985) and overlaying this image on the current map of the park (Fig. 1.4). At least one site, named Triad 36 in the original publication, corresponds with the contemporary site 'Coral Gardens'. No other matches were confirmed and there may be some inaccuracy about the exact locations of these sites (van Katwijk 2015, pers. comm., Radboud University Njimegen). Nevertheless, all the points are within 500m of known sites from later datasets and hence are considered as being part of the same ecological area of lagoonal reef. Data on coral cover, coral genus composition and colony size were reported in this chapter.

- **Wildlife Conservation Society (WCS) 1987-2010:** Data were collected annually from a 30x30m plot at Coral Gardens. This provides a detailed timeline of the coral community in the park over a period of 23 years, but restricted to this single site. The data from this dataset have been used in numerous publications alongside similar time series from other Kenyan locations (e.g. McClanahan 2014 and McClanahan *et al.* 2008). Data on benthic cover, coral genus composition and colony size are presented.
- **Obura Ph.D. Research 1992-1994:** David Obura conducted his Ph.D. research in Watamu and Malindi, collecting data from Bennett's and Lambis reefs over an 18-month period from November 1992 to April 1994. In this chapter data about recruitment rate, growth rate and mortality rate are used.

- **Cowburn D.Phil. Research 2011-2014:** The author conducted research in Watamu from September 2011 to April 2014. A range of methods were used to collect comparable information to the three sources listed above. As this is the most recent dataset, it is referred to as ‘Contemporary’ data below. It should be noted that these data were collected during and after a non-lethal mass bleaching event in April-July 2013 (Chapter 4). However, this event was largely non-deleterious for the coral community in Watamu (Chapter 4), and hence was not thought to impact the results of this study.

**Table 3.1 Data sources, methods and sites used in this study. *Benthic cover in contemporary data was obtained from single observation photoquadrats and from permanent quadrats**

| **Data Source** | **Year** | **Data used in this study** | **Sampling method (and frequency)** | **Locations (see Fig. 1.4)** |
|---|---|---|---|---|
| Radboud University Expedition | 1983 | • % Coral cover<br>• Coral colony genus composition<br>• Colony size | • Line-intercept transects (Single observation) | Coral Gardens and 7 unnamed sites |
| Wildlife Conservation Society (WCS) | 1987-2010 | • % Benthic cover<br>• Coral colony genus composition<br>• Colony size | • Line-intercept transects (Annual observations) | Coral Gardens |
| Obura Ph.D. | 1992-1994 | • Recruitment rate<br>• Growth rate<br>• Mortality rate | • Permanent quadrats (Every 3 months) | Bennetts and Lambis |
| Cowburn D.Phil. or Contemporary | 2011-2014 | • % Benthic cover*<br>• Coral colony genus composition<br>• Colony size<br>• Recruitment rate<br>• Growth rate<br>• Mortality rate | • Belt transects (Single observation)<br>• Photo quadrats (Single observation)<br>• Permanent quadrats (Every 3 months)<br>• Recruitment plates (Single observation) | 6 named sites |

### 3.2.2 Benthic cover, coral colony genus composition and colony size

Data on benthic cover and the abundance and size of coral colonies of different genera were collected by the University of Radboud expedition in 1983, WCS in 1987-2010 and in contemporary fieldwork in 2013, giving a 30-year time series. Data in 1983 were collected from 8 sites and from 6 sites in 2013 (Fig. 1.4), but only from the single site, Coral Gardens, by WCS between 1987 and 2010 (Table 3.1), which was monitored annually (except for 1998).

Monitoring by WCS investigated benthic cover using line intercept transects (LITs) whereby a 10m rope is laid across the reef. Between 9-18 LITs were recorded each year. Benthic cover was estimated as the length under the line of the major categories, hard coral, soft coral, coralline algae, calcareous algae, fleshy algae, turf algae, sand, rubble, and other sessile invertebrates. The total length of each category was summed and presented as percentage of the entire length covered by the LITs. The WCS dataset also recorded the abundance of hard corals, their genus and their longest diameter intercepting these LITs. All datasets in this study identified coral genera using older coral taxonomy (*sensu* Veron) to allow for comparison with historical datasets.

Data from the University of Radboud expedition were collected in a similar manner, using 10m long LITs. Transects were arranged in three groups of 5 transects laid parallel with 1m gap between them. In total each site or 'triad' (Blom *et al.* 1985) consisted of 150m of transect. The percentage hard coral cover, coral colony genus and longest diameter were recorded in a similar manner to the WCS data collection. Unlike the WCS data collection, the percentage cover of other benthic categories were not available from 1983.

The coral community composition and size in 2013 were recorded in belt transects. Each transect was 20m by 1m (20m$^2$) with three replicates at Bennett's Reef, Coral Gardens, Lambis and Bara Bara (60m$^2$) and four at Uyombo and Turtle Reef (80m$^2$). All corals found in these transects were identified to genus level (using older taxonomy *sensu* Veron) and the length of the long axis recorded. Contemporary benthic data were collected using photoquadrats and analysis of benthic coverage on Coral Point Count (CPCe) (Kohler and Gill 2006). Four quadrats (1m$^2$) were placed at regular intervals along the belt transects at each site, with a 5m gap between each quadrat (i.e. at 0m, 5m, 10m and 15m). Sixteen quadrats were collected at Uyombo and Turtle Reef (along the 4 belt transects) and 12 at Bennett's, Coral Gardens, Lambis and Bara Bara (3 transects).

There are several methods available for assessing benthic cover on coral reefs (Hill and Wilkinson 2004). Some of these methods have been formally compared (Leujak and Ormond 2007), including the LIT and photo quadrat methods used in this study, and found to be not significantly different from one another. This suggests that it is reasonable to draw conclusions about benthic cover from the two methods used in data sources here. Nevertheless, caution should be taken interpreting the results as the two methods have inherent biases (Leujak and Ormond 2007). Additional noise may be added to the dataset, through the effect of different researchers collecting data and examining different study sites (Table 3.1).

It was hypothesised that there would be significant changes in coral cover, genus composition and colony size in relation to the 1998 bleaching event. Changes in coral cover were investigated comparing site means between 1983

(Radboud) and 2013 (Comtemporary), as the data from the University of Radboud were only available as site level. Coral cover was assessed for normality using Shapiro-Wilkes (S-W) tests and was found to be non-normally distributed in both the 1983-2013 ($W$=0.862, $p$=0.033). The homoscedasity of linear models between coral cover and pre and post 1998 bleaching was investigated using Breuscher-Pagan (B-P) tests and found to be heteroscedastic for the 1983-2013 ($\chi^2$=6.414, $p$=0.011). The data were successfully transformed using a natural log function and a Welch's t-test was used to assess the differences between samples.

Difference in mean adult (>10cm) coral colony size was compared between 1983 (Radboud) and 2013 (Contemporary) datasets for seven common coral genera (*Acropora, Echinopora, Favia, Favites, Montipora, Pocillopora* and *Porites*). S-W tests confirmed the normality of mean colony size for all the genera, and B-P tests found the variance between 1983 and 2013 groups to be homoscedastic. As these data conform to expectations of normality and homoscedastity, the significance of differences in colony size was investigated using two-tail un-paired t-tests.

Coral genus composition between years was compared using non-metric multidimensional scaling (nMDS). The different years were classed as Pre-1998 and Post-1998, and an Analysis of Similarity (ANOSIM) was carried out to determine if these two groups were significantly different in their genus composition. Multivariate analyses were carried out in Community Analysis Package (CAP) (Henderson and Seaby 2014).

### 3.2.3 Permanent quadrats

This method was used by Obura from 1992-1994 and in contemporary data collection from 2013-2014. Quadrats, $1m^2$ in area, were haphazardly placed on the reef and marked with metal nails in the corners for finding the exact spot in future monitoring. All juvenile corals, defined as <10cm (Soong and Lang 1992), were given a unique code and marked on a diagram of the quadrat. The colonies were identified to genus, and measured along their long axis and perpendicular axis. Quadrats were monitored every three months, to see changes in colony size, note new recruits and mortality of corals.

Obura's 20 permanent quadrats were monitored from October 1992 to April 1994 (18 months) in Bennett's Reef and Lambis. However, only data from April 1993 to April 1994 were used to ensure that the observations of the coral community were over the same time frame and seasons to the contemporary permanent quadrats, which were monitored from April 2013 to April 2014. The 38 contemporary quadrats were collected from the same sites, but not in the original quadrat positions, which could not be located accurately. Although quadrats were split between two sites >1km apart, both Lambis and Bennett's reefs were found on the same chain of patch reefs along the main chain of reef habitat found in WMNP (Section 1.6 and Fig. 2.5). They were considered to be ecologically similar and hence data were pooled for 1994 and 2014.

**Table 3.2. Permanent quadrat replication at Bennett's and Lambis reefs in Obura (1995) and contemporary data.**

| Data Source | Bennetts Reef | Lambis Reef |
|---|---|---|
| Obura (1992-1994) | 10 | 10 |
| Cowburn (2013-2014) | 20 | 18 |

Recruitment rate, mortality rate and growth rate were estimated from the permanent quadrat data. Recruitment was defined as any new coral found in a quadrat during the 12 months after the initial observation of colonies. Colony mortality was recorded as any colony that was present at some point during monitoring, but not present in the final assessment of quadrats. Mortality rate was calculated as the number of colonies that died during the observation period divided by the total number of colonies observed. Mortality rate was presented as percentage mortality per quadrat.

The lengths of the long and perpendicular axis were combined to give the geometric mean of each colony. The growth rate was calculated using Equation 3.1, where the overall change in geometric mean was divided by the amount of time the colony was observed. Hence growth rate is defined as change in geometric mean per month. Each colony is considered as an independent replicate.

**Equation 3.1 Growth rate of corals from permanent quadrats**

$$Growth\ Rate = \frac{Final\ geometric\ mean - Initial\ geometric\ mean}{Number\ of\ months\ the\ colony\ was\ monitored}$$

The differences in juvenile coral abundance at the start of the observation period (1993 and 2013) and the recruitment, growth and mortality of juvenile corals after 1 year of observation were compared to investigate if there were significant changes in these variables during the two time periods. Juvenile coral abundance and recruitment rate were compared using general linear models (GLM) using the poisson distribution, which is appropriate for variables based on count data (Hector 2015). Mortality was compared between years using a

GLM with binomial distribution, appropriate for variables with proportions. Growth rate was non-normally distributed (S-W: $W$=0.834, $p$<0.001), but had homoscedastic variance between years (B-P: $\chi^2$=0.002, $p$=0.965). Comparisons of growth rate of *Acropora*, other-branching and non-branching corals were compared between 1993 and 2013 using Kruskal-Wallis with Dunn's MCP pairwise comparison.

The growth rate and mortality rate of juvenile corals may be influenced by benthic components including turf algae, macro-algae and coralline algae (Birrell et al. 2008). The benthic cover of permanent quadrats in 2013 was analysed using CPCe as described in section 3.2.2 and algal benthic components were correlated with contemporary growth and mortality rates. As recruitment and mortality were not normally distributed variables (S-W: $W$=0.814, $p$<0.001 and $W$=0.896, $p$<0.001 respectively) the comparison between recruitment and mortality did not meet the assumptions of an Ordinary Least Squares (OLS) regression and hence a Spearman's Rank Correlation was used to test these relationships. The significance values produced from these repeated tests against recruitment and mortality rate were corrected with a Bonferroni correction factor.

All statistical tests carried out on data from permanent quadrats were analysed using R.

### 3.2.4 Recruitment Plates

Recruitment plates were placed on the reef for 4 months from December 2011 until April 2012, at Bennett's and Uyombo reefs. Plates were made of dead *Porites* coral skeleton, cut into squares that were approximately 10cm x 10cm x

1cm. They were mounted at $45^0$ in a plastic mesh cage, to prevent grazing on the tiles and weighted with a cement base (Fig. 3.1). Twelve plates were placed haphazardly on each reef (24 in total) and all were retrieved in April 2012. The plates were removed from their cages and all coral spat were counted and identified to family level (Babcock *et al.* 2003).

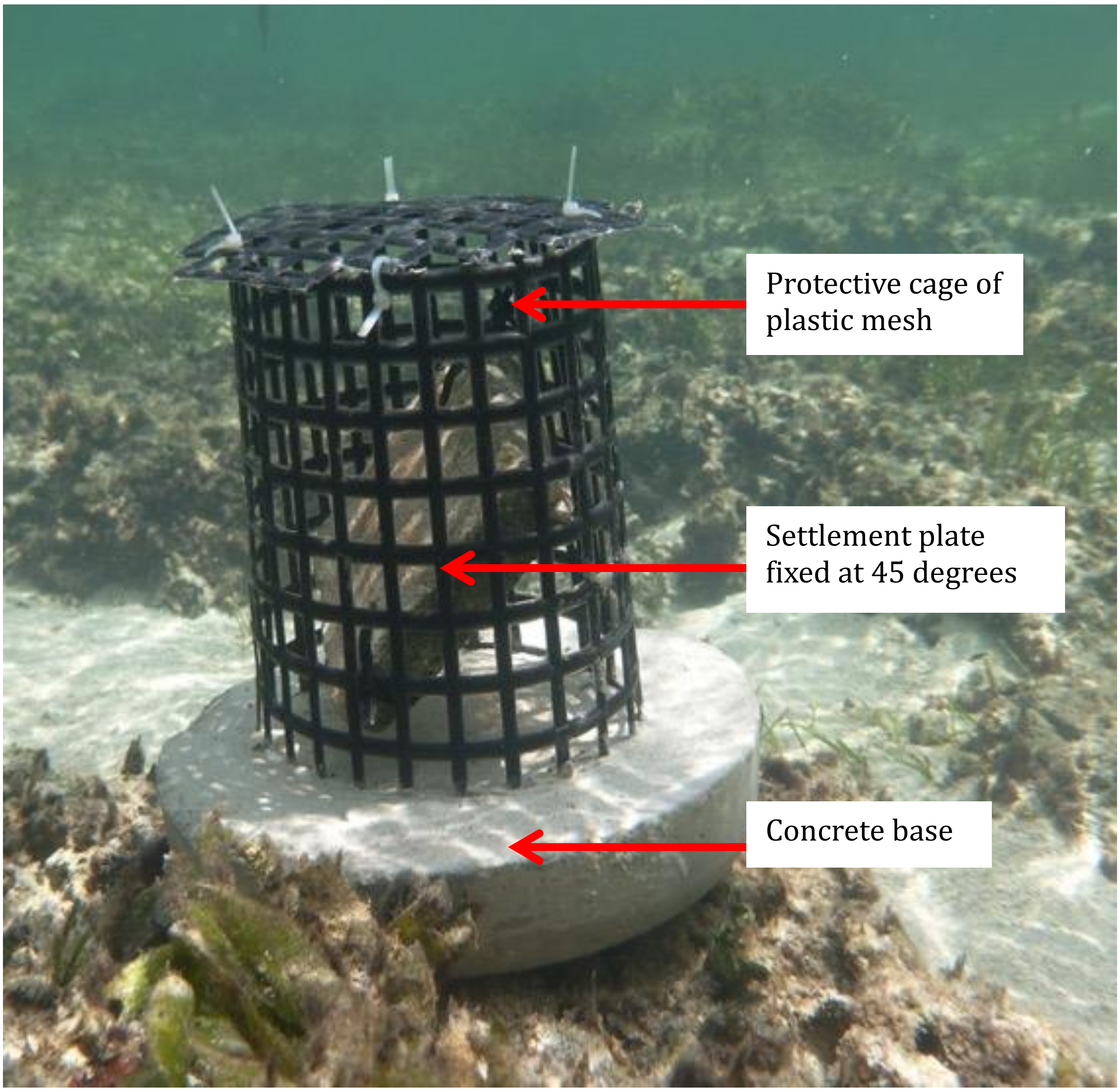


**Figure 3.1 Settlement plate and housing on the reef (Photo B. Cowburn).**

## 3.3 Results

### 3.3.1 Changes in benthic cover

Comparing coral cover across the 8 sites assessed in 1983 by the University of Radboud expedition, the median coral cover based on site means was 29.8% with an interquartile range of 20.4% - 47.2% (Fig. 3.2). In the 6 contemporary sites in 2013 median coral cover was 20.2% lower with a median cover of 9.6% and had a narrower interquartile range from 6.5% - 11.4% (Fig. 3.2). The difference in coral cover between 1983 and 2013 was significant (*t*=4.549, *DF*=13, *p*=0.001). However, as the majority of sites were not in the same location the significance of the observed decrease in coral cover should be treated with caution. Coral Gardens was the only site investigated during both periods of field work and had a cover of 46% in 1983, but had dropped to 10.4% in 2013.

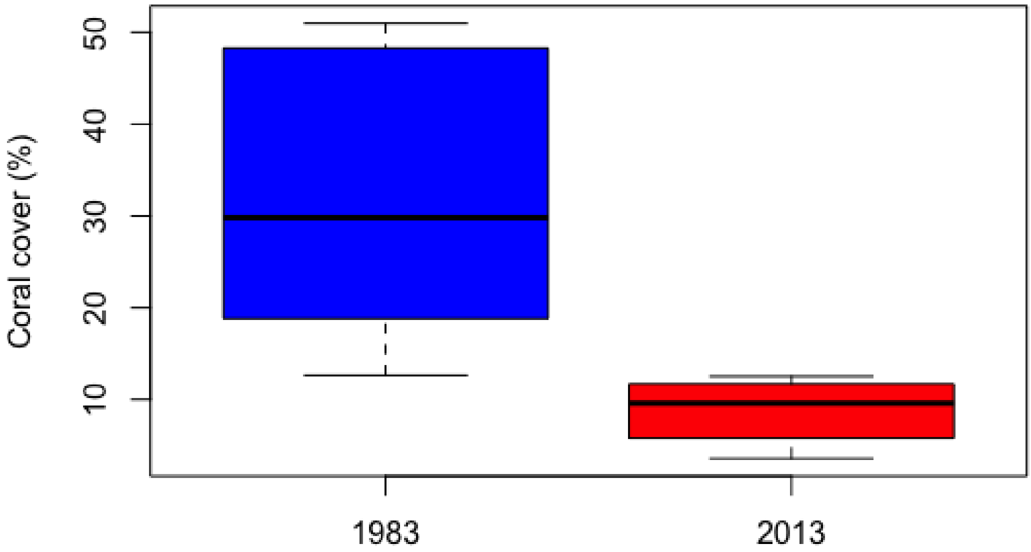


**Figure 3.2 A boxplot of mean coral cover from University of Radboud sites in 1983 and contemporary sites in 2013. The black line represents the median and the box represents the upper and lower quartiles. The whiskers respresent highest and lowest values within 1.5 x interquartile range.**

The starting coral cover for WCS long-term monitored plot in 1987 at Coral Gardens was 30% and was as high as 47% in 1996 (Fig. 3.3 and Fig. 3.4). From November 1997 to March 1999 coral cover dropped from 37.7% to 10.4%, giving an estimate of 72% mortality of coral during the 1998 mass-bleaching event. During the years post-1998 coral cover ranged between 9-13% without signs of a recovery to pre-1998 levels. Mean coral cover for pre-1998 years was 36.7% (SE±2.87) and post-1998 11.4% (SE±0.42).

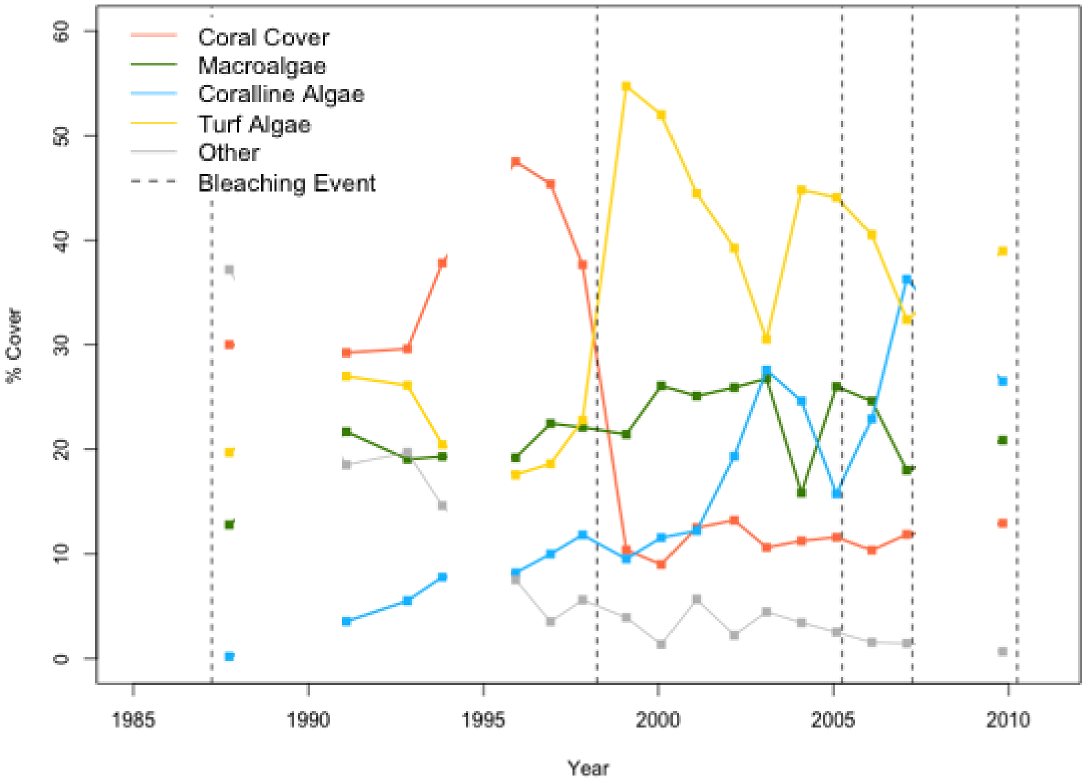


**Figure 3.3 Mean percentage cover of major benthic categories from WCS monitoring at Coral Gardens 1987-2010. Points show when surveys took place. Bleaching events are marked as dashed vertical lines. Points in the time series <2 years apart are joined by a line.**

The mean percentage macroalgal cover was slightly higher post-1998 (1999-2009) compared to pre-1998 (1987-1997), a mean of 19.5% pre-1998 to 23.1% post-1998 at Coral Gardens. Coralline algae had a mean of 6.7% pre-1998 and 20.6% post-1998 (Fig. 3.3 & Fig. 3.4). Turf algae cover had a mean of 21.8% pre-1998 and was higher with a mean of 42.2% in post-1998 sampling periods. Other benthic organisms such as soft corals (Octocorallia) and sponges (Porifera) remained below 1% during all years of observation. The high percentage (>5%) of 'Other' benthic cover from 1987-1995 consisted of seagrass and sand, perhaps as the result of a temporary deposition of sediment on this lagoonal patch reef.

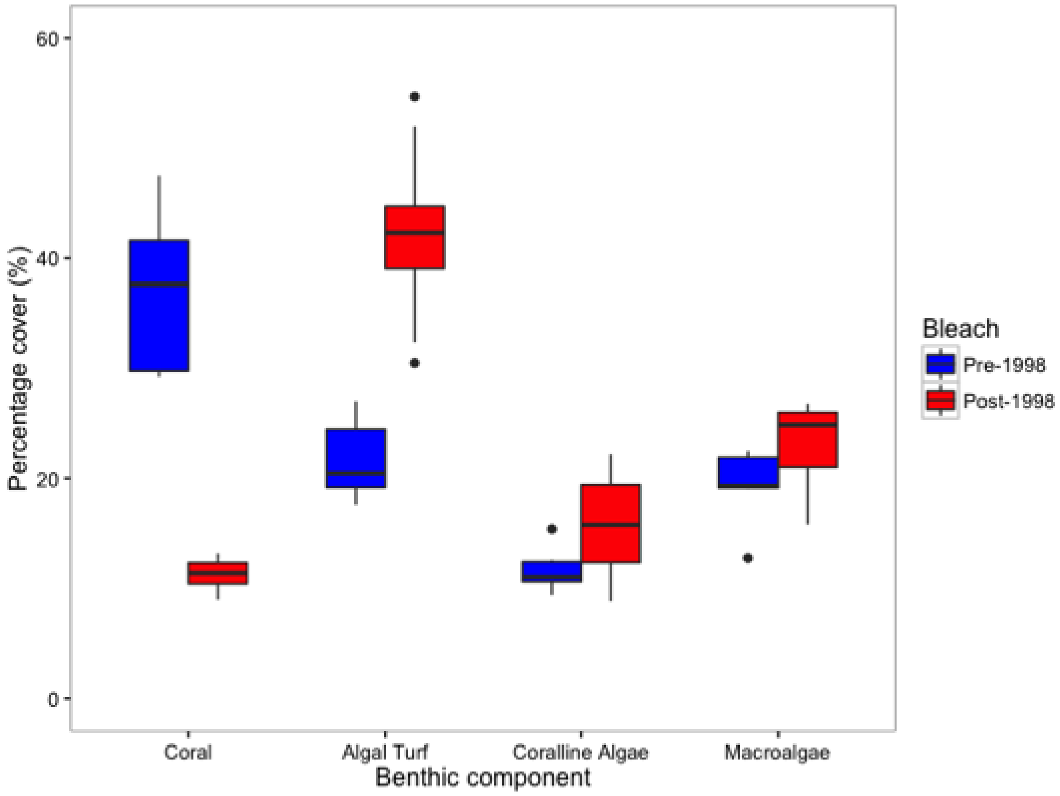


**Figure 3.4 Boxplot of the mean percentage cover of coral, algal turf, coralline algae and macroalgae in pre-1998 (1987-1997) and post-1998 (1999-2009) years from the WCS time series. The black line represents the median and the box represents the upper and lower quartiles. The whiskers respresent highest and lowest values within 1.5 x interquartile range, with value lying outside this range represented with a point.**

The percentage benthic cover of coral, crustose coralline algae (CCA), macroalgae and turf algae, from the 6 contemporary sites monitored in 2013 was assessed using the photoquadrat method (Table 3.3). The dominant benthic component was turf algae covering 49.4% (SE±2.38), followed by macroalgae 27.2% (SE±2.15). Coral cover across all sites was 9.1% (SE±1.67) and CCA was 5.4% (SE±1.00).

Table 3.3 Percentage cover of major benthic categories by site, from contemporary research in 2013.

| Site | % Coral | %CCA | % Macroalgae | %Turf Algae |
|---|---|---|---|---|
| **Bara Bara** | 3.5 (SE±1.00) | 1.5 (SE±0.72) | 31.0 (SE±4.75) | 62.3 (SE±4.73) |
| **Bennett's** | 13.5 (SE±3.82) | 6.0 (SE±2.27) | 40.6 (SE±5.55) | 32.5 (SE±4.29) |
| **Coral Gardens** | 10.4 (SE±5.44) | 5.3 (SE±2.44) | 17.3 (SE±3.67) | 58.5 (SE±5.65) |
| **Lambis** | 9.2 (SE±6.02) | 5.0 (SE±1.92) | 28.3 (SE±4.41) | 52.3 (SE±5.32) |
| **Turtle Reef** | 6.1 (SE±3.46) | 3.0 (SE±0.89) | 30.9 (SE±5.89) | 50.8 (SE±5.15) |
| **Uyombo** | 11.6 (SE±3.59) | 11.6 (SE±3.63) | 14.8 (SE±3.70) | 42.3 (SE±6.16) |
| Mean | **9.1 (SE±1.67)** | **5.4 (SE±1.00)** | **27.2 (SE±2.15)** | **49.3 (SE±2.38)** |

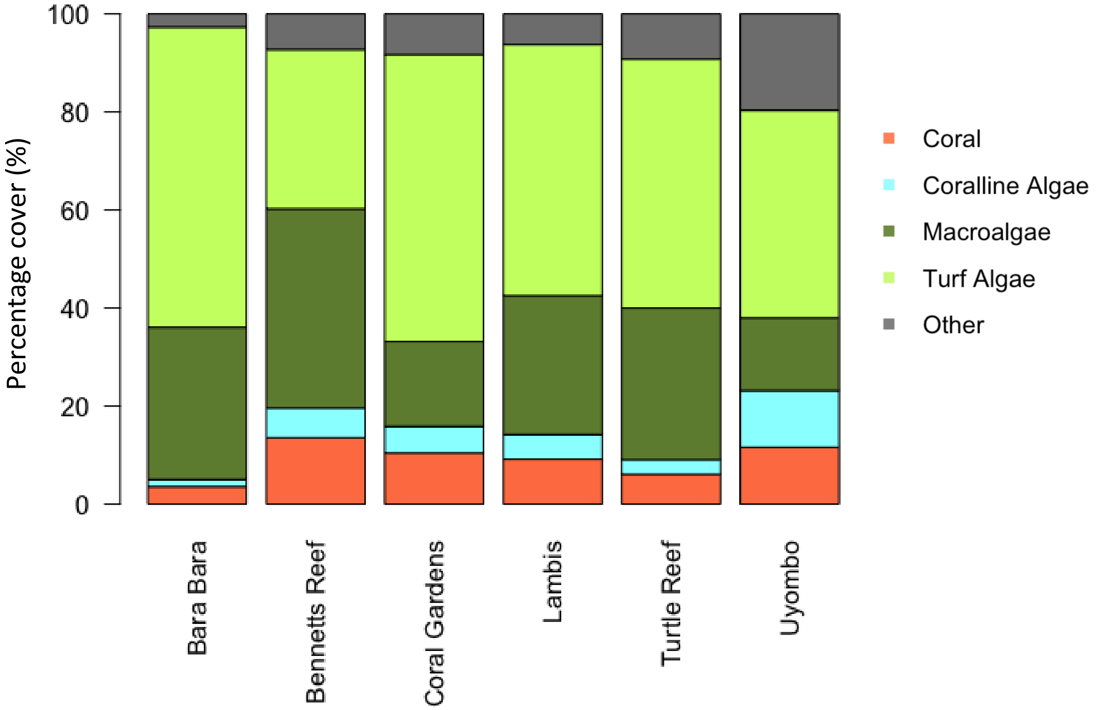


Figure 3.5 Percentage cover of major benthic categories by site, from contemporary research in 2013.

### 3.3.2 Changes in coral genus composition

The percentage cover of the nine most common coral genera from WCS time series at Coral Gardens was compared pre-1998 and post-1998 (Fig. 3.6a). The cover of *Acropora, Montipora* and branching *Porites* was lower in post-1998 years, with a 90% decrease in *Acropora* and *Montipora* mean cover value from pre-1998 levels. *Echinopora* cover appears to be slightly higher in post-1998 samples and the remaining genera, *Favia, Favites, Galaxea, Pocillopora* and massive *Porites* remained at similar levels across the 1998 bleaching event.

The percentage cover of the nine genera across University of Radboud sites in 1983 and the contemporary sites in 2013 was also compared (Fig. 3.6b). The varation in genus composition was greater between the sites than the interannual variation from the WCS series at Coral Gardens. However, in common with the WCS dataset, *Acropora*, *Montipora* and branching *Porites* have lower percentage cover in post-1998 (i.e. 2013), compared to the pre-1998 (1983) conditions.

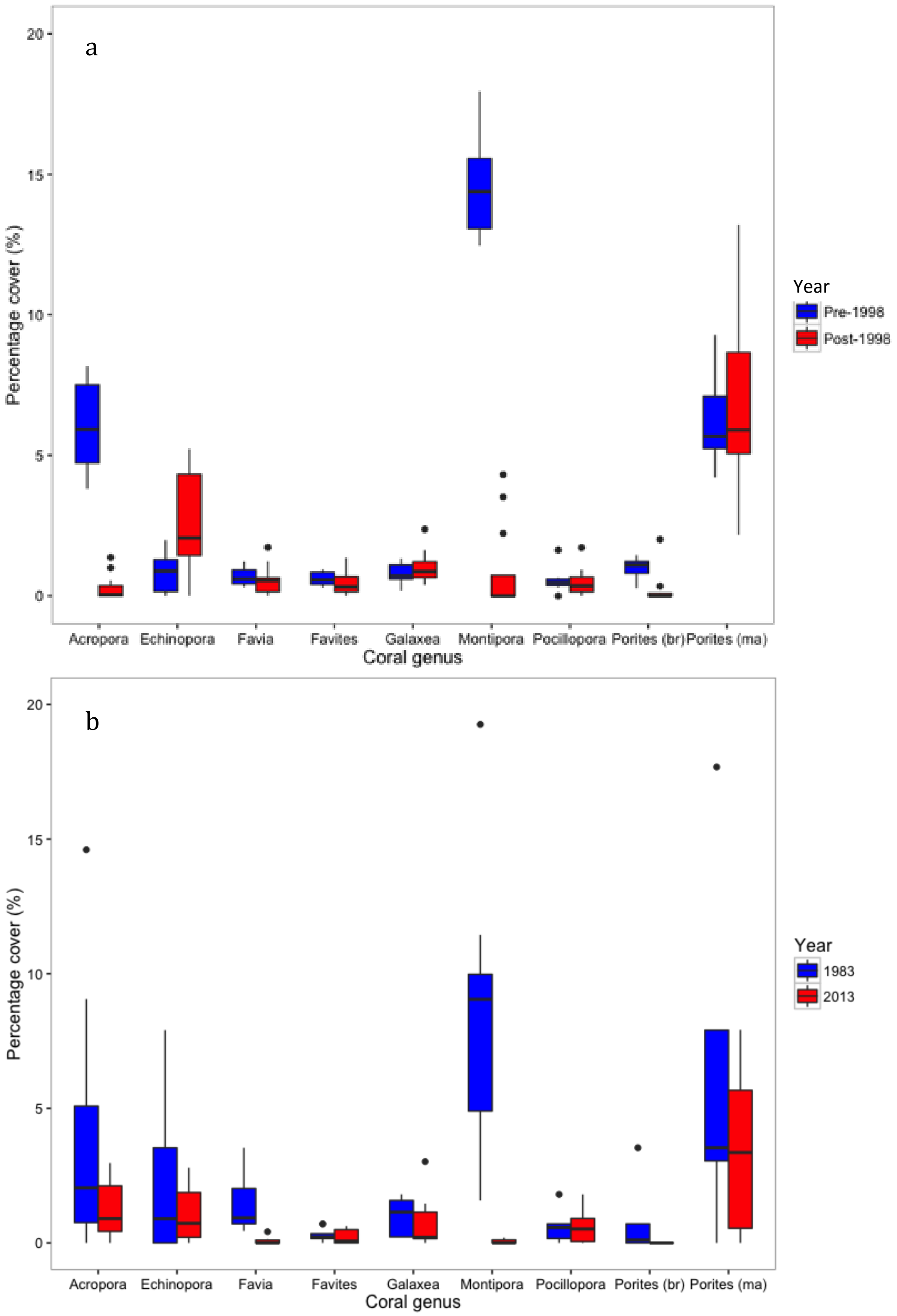


**Figure 3.6 Boxplot of coral genus cover from a) WCS time series at Coral Gardens pre-1998 (1987-1997) and post-1998 (1999-2010) and b) University of Radboud sites in 1983 and contemporary sites in 2013 for *Acropora, Echinopora, Favia, Favites, Galaxea, Montipora, Pocillopora, Porites* (br) branching, *Porites* (ma) massive. The black line represents the median and the box represents the upper and lower quartiles. The whiskers respresent highest and lowest values within 1.5 x interquartile range, with outlying values beyond this indicated with a point.**

The genus composition of the coral community at Coral Gardens, based on the WCS time series colony abundance data was plotted using multidimensional scaling (MDS), using the Bray-Curtis similarity measure (Fig. 3.7). The stress of this model was moderate (0.191), suggesting the representation is robust. Coral colony genus composition pre-1998 is tightly clustered on the left of this plot, with the point represented by the coral composition of combined sites from the University of Radboud expedition in 1983 (U1983) also loosely clustered in this group. Post-1998 coral communities, including combined genus composition from the 6 sites in 2013 (U2013) are found on the right of this plot and are more variable. An Analysis of Similarity (ANOSIM) was carried out on pre and post-1998 groupings, and was found to be highly significant ($p$=0.001) with a test statistic of 0.775.

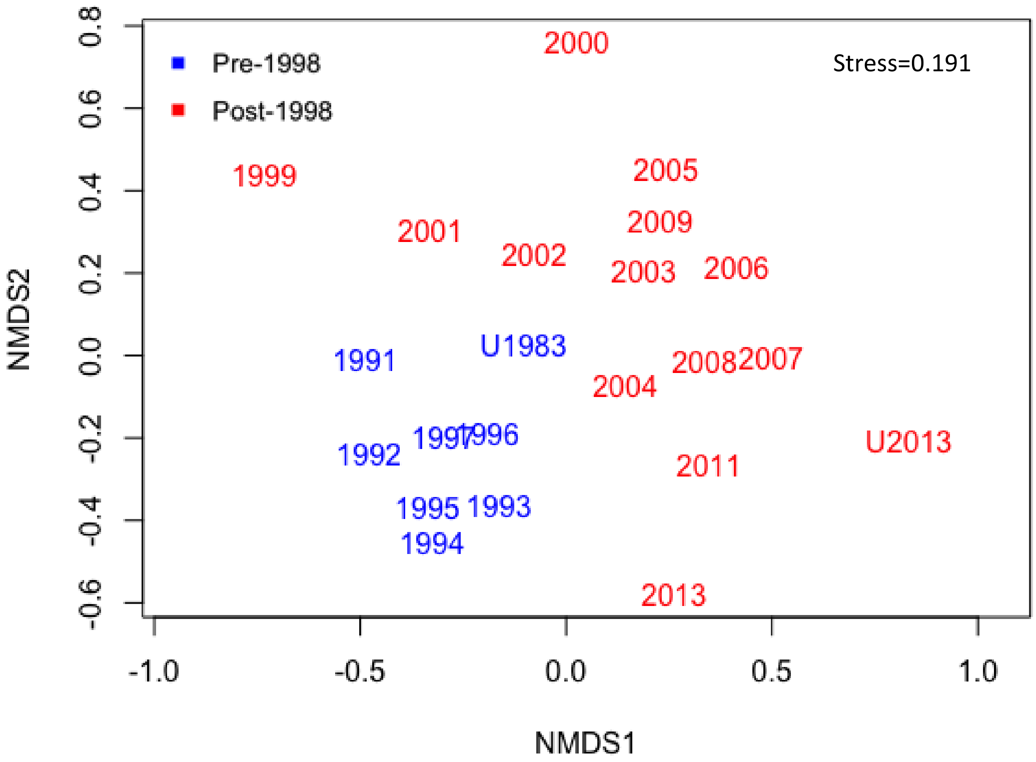


**Figure 3.7 Multidimensional scaling (MDS) plot of coral genus composition at Coral Gardens from WCS colony abundance data from 1991-1997 (pre-1998) and 1999-2013 (post-1998). Including coral genus composition from combined sites for the whole of WMNP in 1983 (U1983) and 2013 (U2013).**

### 3.3.3 Changes in adult coral colony size

The mean coral colony diameter at University of Radboud sites (1983, *n*=8) and contemporary sites (2013, *n*=6) was compared for seven genera (Fig. 3.8). Two of the genera mean sizes were lower in 2013 compared to 1983, with significant decreases for *Montipora* by 76% (*t*=3.060, *DF*=13, *p*=0.011) and massive *Porites* by 59% (*t*=2.269, *DF*=13, *p*=0.048). The average colony diameter of *Favites* increased by 42% (*t*=-2.586, *DF*=13, *p*=0.024). There was no significant change in size for *Acropora, Echinopora, Favia* or *Pocillopora.*

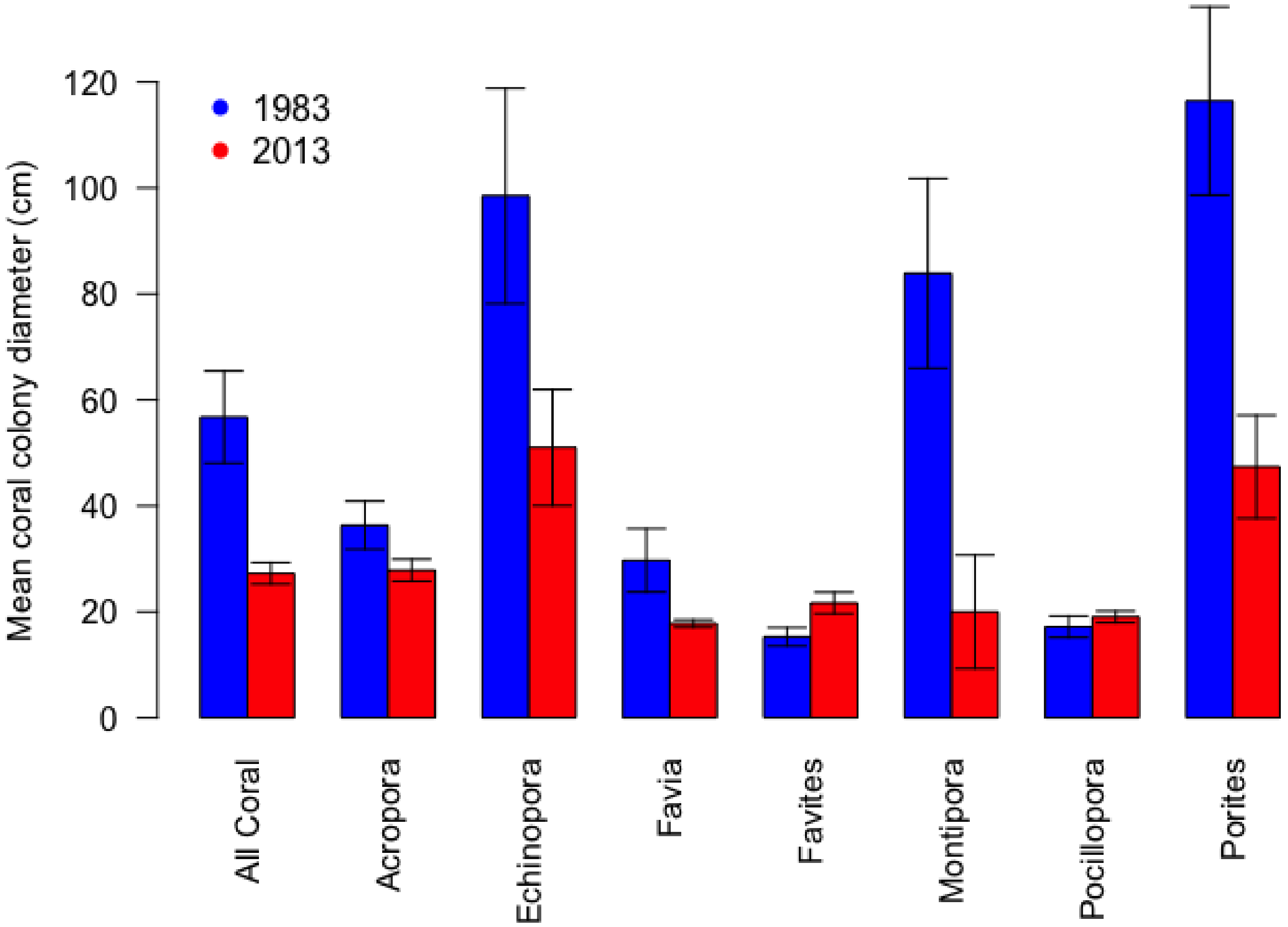


**Figure 3.8 Mean coral colony diameter (cm) from the University of Radboud sites from 1983 (*n*=8) and contemporary data collection sites in 2013 (*n*=6) all corals combined, *Acropora, Echinopora, Favia, Favites, Montipora, Pocillopora* and *Porites*. Bars represent the standard error of the site means.**

### 3.3.4 Permanent Quadrats

From the 20 permanent quadrats laid out at Bennett's and Lambis reefs 1992-1994 there were 222 juvenile colonies observed. From the 38 quadrats in 2014 there were 137 juvenile colonies. The mean number of colonies per quadrat ($1m^2$) was lower in 2014 at 2.1 per $m^2$ (SE±0.25), compared to a mean abundance of 6.35 per $m^2$ (SE±0.89) in 1994. This difference was highly significant (GLM: $\chi^2= 88.64$, $DF=57$, $p<0.001$) (Fig. 3.9).

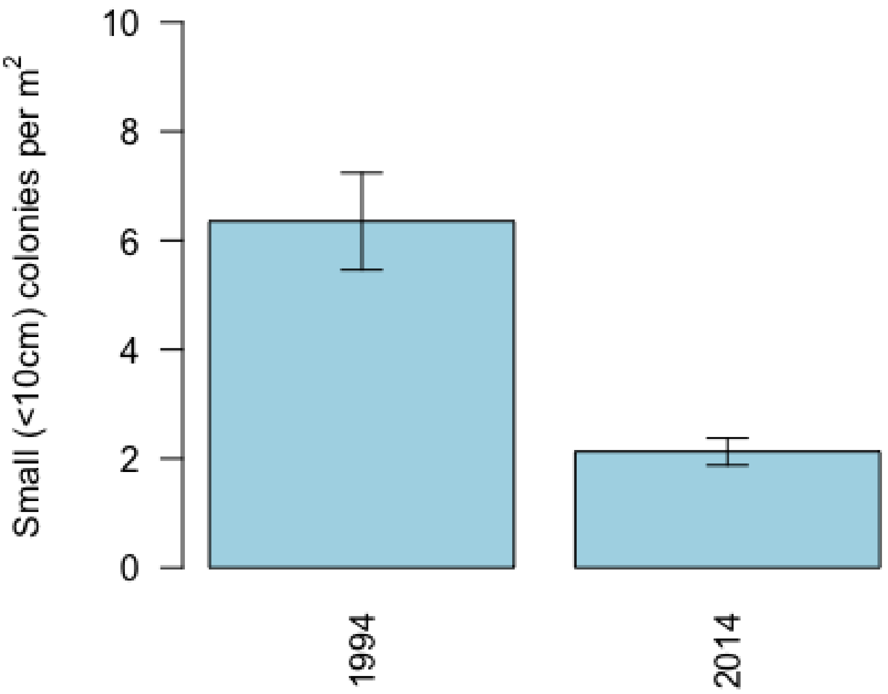


**Figure 3.9 Barplot of mean juvenile (<10cm) coral colony abundance per quadrat in 1994 and 2014 at Bennett's and Lambis reefs. The bars represent the standard error of the mean.**

Recruitment rate decreased significantly from a mean of 4.8 per m$^2$ per year (SE±0.71) in 1994 to 1.5 per m$^2$ per year (SE±0.22) in 2014 (GLM: $\chi^2$=88.72 *DF*=57, $p$<0.001) (Fig. 3.10).

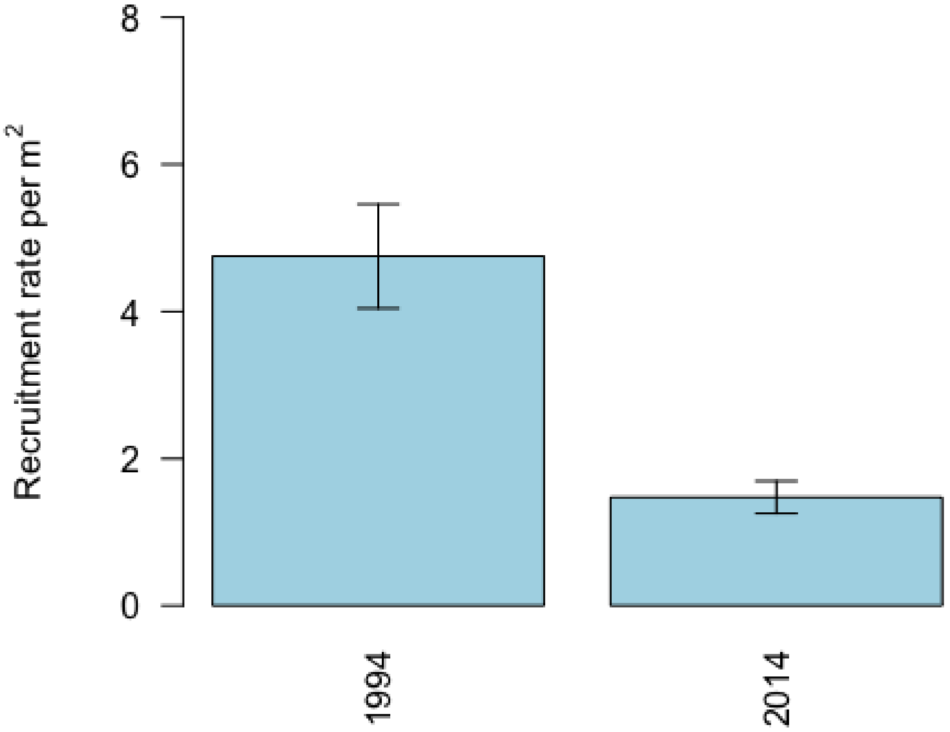


**Figure 3.10 Barplot of new recruits detected per quadrat during one year in permanent quadrats in 1994 and 2014 at Bennett's and Lambis reef. The bars represent the standard error of the mean.**

Growth rate was highly variable with the change in geometric mean varying from a maximum of 41mm per month increase seen in one *Acropora* colony and a maximum decrease of -15mm per month from one *Pocillopora* colony (Fig. 3.11). Colonies of *Acropora* and 'other branching' genera (e.g. *Pocillopora, Stylophora* and branching *Porites*) were separated from 'non-branching' genera to account for the faster growth rate of branching corals.. The median growth rate of all corals was 1.23mm per month, with a median rate of 1.11mm per month for non-branching corals, 2.18mm for *Acropora* colonies and a rate of 1.47mm per month for other branching corals. The differences in growth rate between coral types were significant (Kruskal-Wallis: $\chi^2$=8.10, *DF*=264, *p*=0.017). *Acropora* had a significantly higher growth than non-branching corals (Dunn MCP: *Z*=2.75, *p*=0.018), but the growth rate of other branching corals was not significantly different to *Acropora* (Dunn MCP: *Z*=1.42, *p*=0.456) or non-branching corals (Dunn MCP: *Z*=1.28, *p*=0.597). The median rate of growth for all corals in 1994 was 1.12mm per month and in 2014 it was 1.47mm. The difference in growth rate beween 1994 and 2014 was not significant between any of the coral types (Wilcoxon rank sum: non-branching: *W*=3369, *DF*=174, *p*=0.329; *Acropora*: *W*=138, *DF*=35, *p*=0.856; other branching: *W*=307, *DF*=55, *p*=0.401).

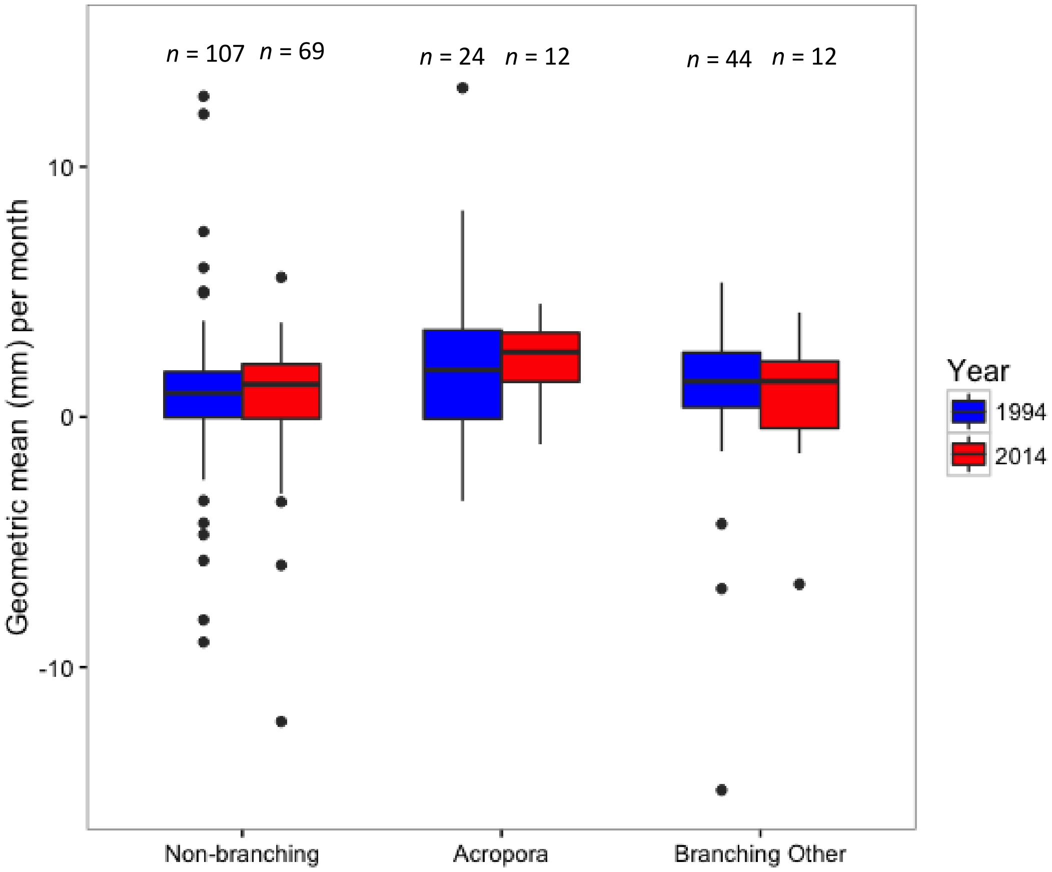


**Figure 3.11 Boxplot of growth rate, as the change in geometric mean (mm) per colony per month, in 1994 and 2014 at Bennett's and Lambis reefs for 'non-branching' corals, *Acropora* and 'other branching' corals. The scale of the plot is limited to -15 - +15mm excluding the most extreme outliers. The sample size (*n*) is provided for each treatment of coral group and year. The black line represents the median and the box represents the upper and lower quartiles. The whiskers respresent highest and lowest values within 1.5 x interquartile range, with outlying values beyond this indicated with a point.**

Mortality rate was expressed as the proportion of colonies found in a quadrat that died before the end of the observation period. Mean mortality of corals during the 12 months of observation was 44% (SE±5.44) in 2014 and 36.6% (SE±3.66) in 1994 (Fig. 3.12). The difference in mortality rate between years was not significant (GLM: $\chi^2$= 24.77 *DF*=57, *p*=0.581). There were no significant relationships between recruitment rate and any of the benthic variables (Fig. 3.13) or between mortality rate and the benthic variables (Fig. 3.14).

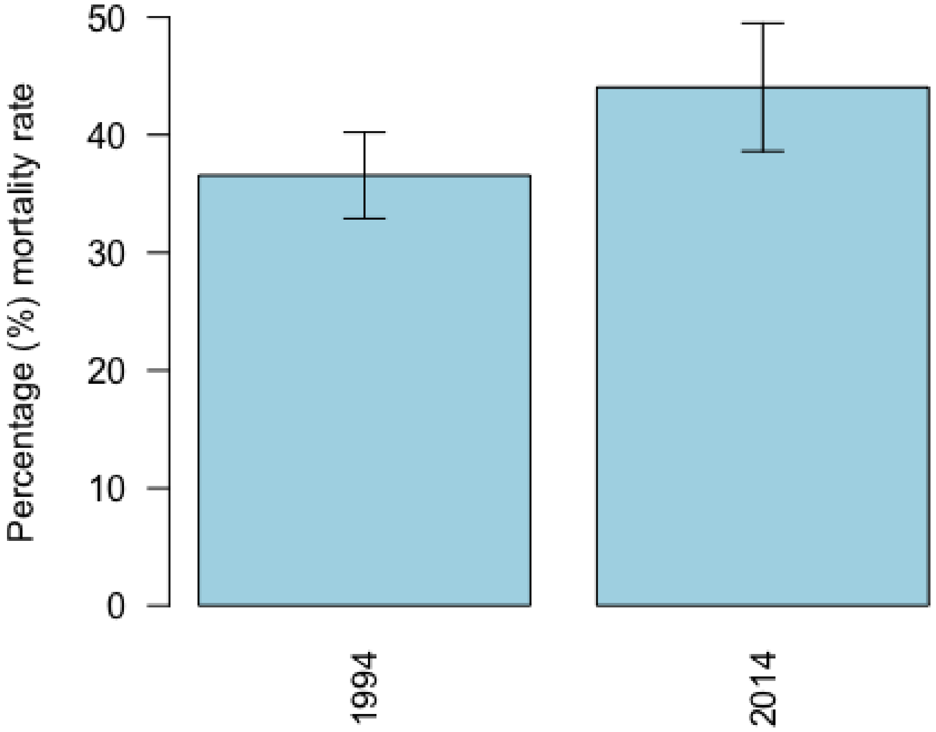


**Figure 3.12 Barplot of mortality rate, as the proportion of colonies per quadrat that died during one year in 1994 and 2014 at Bennett's and Lambis reefs. The bars represent the standard error of the mean.**

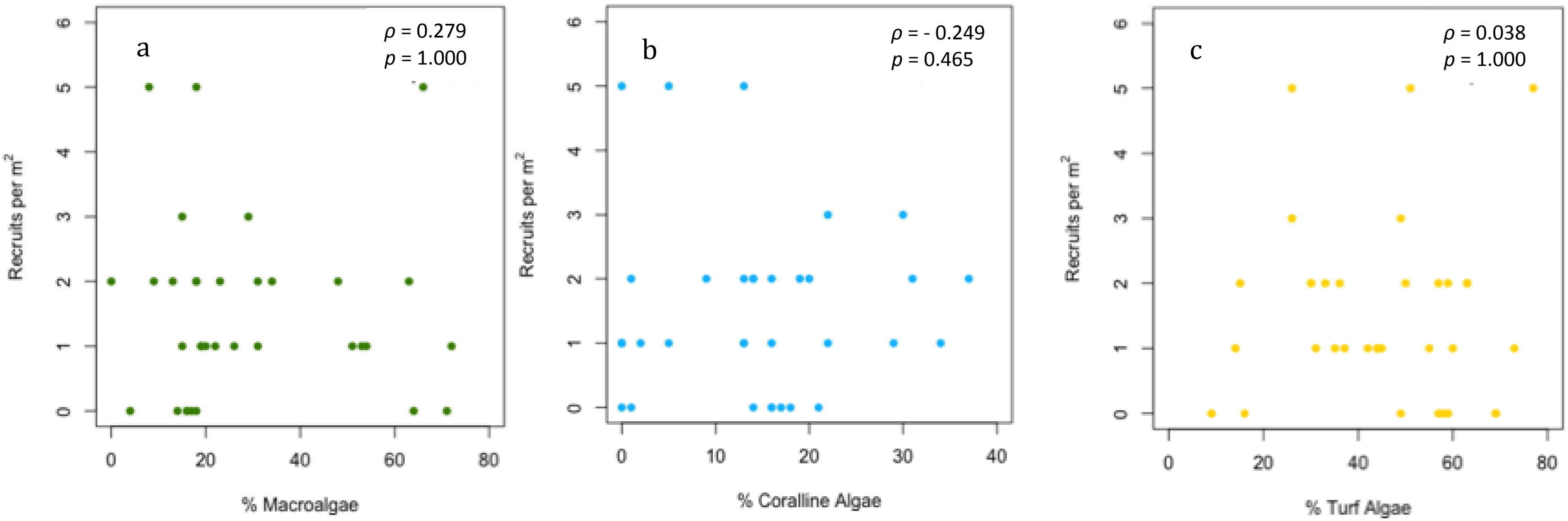


**Figure 3.13 Recruitment rate for new corals settling in permanent quadrats in Bennett's and Lambis reef during one year from April 2013 - April 2014 plotted against a) Macroalgae, b) Coralline algae and c) Turf algae cover. A Spearmans rank correlation coefficient ($\rho$) and Bonferroni corrected $p$-value are presented for these associations.**

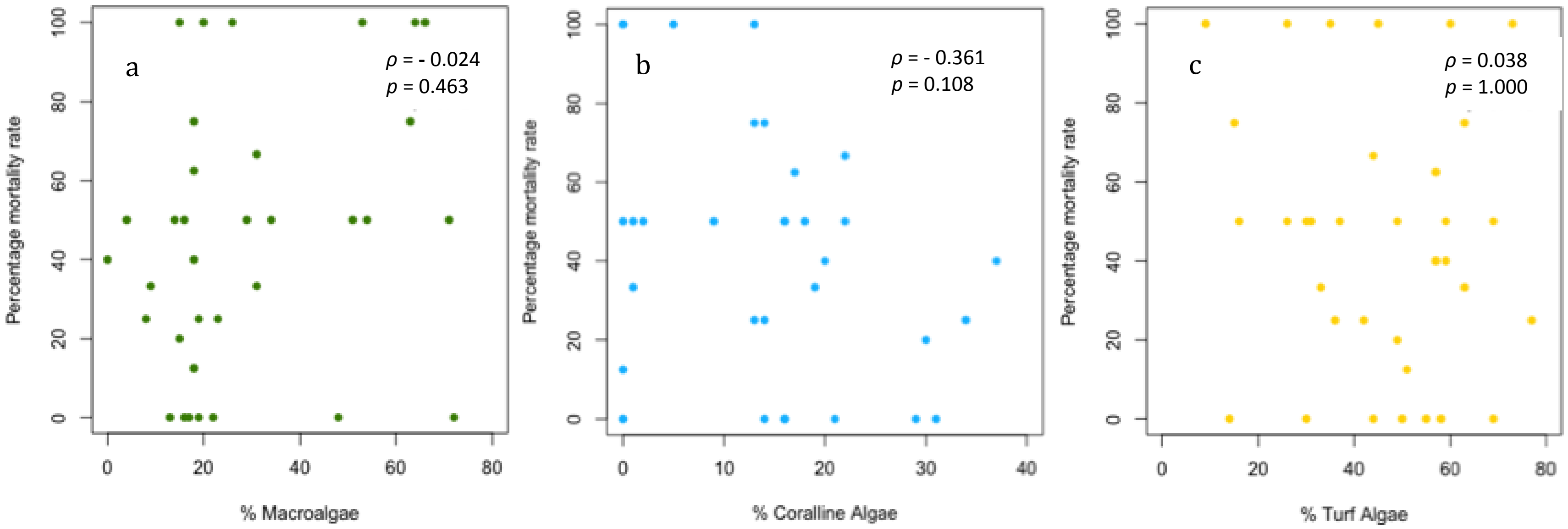


**Figure 3.14 Mortality rate as the percentage of small colonies (<10cm) found in permanent quadrats at Bennett's and Lambis in April 2013 that were dead by April 2014 plotted against a) macroalgae, b) coralline algae and c) turf algae cover. A Spearmans rank correlation coefficient and Bonferroni corrected *p*-value are presented for these associations.**

### 3.3.5 Coral settlement plates

Coral settlement tiles at Bennett's Reef and Uyombo were removed in April 2012 after four months in the water; a total of 65 spat were found (Fig. 3.15). All the spat were found on plates from Uyombo, with not one spat on the 12 plates from Bennett's Reef. The mean number of spat in Uyombo was 5.42 (SE±2.01). All of the spat were Pocilloporidae, hence presumably *Pocillopora*, as no other members of this family are found in WMNP.

**Figure 3.15 Newly settled *Pocillopora* coral spat on settlement plate (Photo C. Raker).**

## 3.4 Discussion

### 3.4.1 Evidence of stable states and phase-shift in WMNP

Since the earliest record from WMNP in 1983 there have been 6 known mass bleaching events along the Kenyan Coast, with an event of unknown impact in 1987, a major event in 1998 and four minor events in 2005, 2007, 2010 and 2013 (McClanahan *et al.* 2014 & Chapter 4). Before 1998 the reef in Watamu had coral cover at similar levels to other sites in Kenya (McClanahan *et al.* 2001) and the wider Indian Ocean (Ateweberhan *et al.* 2011) with a community dominated by *Acropora, Montipora* and massive *Porites* colonies (Fig. 3.6). Watamu experienced thermal stress in 1987, but maintained moderate coral cover of 30% and 47% over the period 1992-1997 (Figs. 3.3). The data from Coral Gardens collected by the University of Radboud expedition in 1983 showed that coral cover was 46% and the genus composition of corals was similar to after the 1987 event (Fig. 3.6b, Fig. 3.7). This suggests that the reef was resilient to the 1987 bleaching event, and maintained a relatively stable coral community for at least 16 years prior to 1998.

Based on the data from Coral Gardens, it can be seen that in 1998 this reef lost 72% of its coral cover overall and up to 90% of its *Acropora* and *Montipora* cover, which had dominated before the mass-bleaching (Fig. 3.6a). Coral cover at Coral Gardens dropped to 10.4% immediately after the bleaching (Fig. 3.3) which is the level to which coral cover dropped across Kenya's marine parks and unprotected areas post-bleaching irrespective of initial coral cover or protected status (McClanahan *et al.* 2001). The loss of *Acropora* and *Montipora* is also concordant with trends seen in Kenya (McClanahan *et al.* 2001), the Great

Barrier Reef (Berkelmans *et al.* 2002) and much of the rest of the Indo-Pacific (e.g. Loya *et al.* 2001).

The three lines of evidence for Watamu's coral community change used in this study come from different datasets and sites and were collected using different methods (Table 3.1), which will have introduced extra variability into the data. Nevertheless, the results show that the loss of coral cover (Figs. 3.2, 3.3, 3.4) and shift in genus composition (Figs. 3.6 & 3.7) after the 1998 bleaching event is the most important change to the coral community across the three decades of observation, both at Coral Gardens and across the wider park.

At Coral Gardens macroalgal cover increased by just 3.6% between pre-1998 levels and post-1998 (Fig. 3.3) with the majority of the non-coral benthic space post-1998 being dominated by turf algae and coralline algae. Data collection by the University of Radboud expedition in 1983 of coral cover across 8 sites, did not record information on other benthic components, such as algal cover. Obura (1995) presents algal cover for Lambis and Turtle Reef in 1993, and from the WCS dataset there is benthic cover information available for Coral Gardens from 1993, hence there are three sites with which to compare algal change (Table 3.4). Estimates for crustose coralline algae (CCA) in 2013 (Fig. 3.5, Table 3.5) are much lower than those for post-1998 years from the WCS time series, and decreased in all sites from 1993. The reason for the discrepancy between CCA trends in the WCS time series (Fig. 3.3) and estimates from 2013 (Fig. 3.5) is not clear. One possible reason is that the WCS monitoring plot was located on an area of large *Porites* bommies, which are more likely to encourage CCA growth when coral tissue is lost (Obura pers. comm, CORDIO East Africa). The increase in macroalgal cover is greater in Lambis and Turtle reef than seen in Coral Gardens (Table 3.4), suggesting that in other parts of the park the increase in macroalgae was greater. However, the component with the greatest increase for all three sites is turf algae, which makes up the largest proportion of the benthic component in contemporary sites (Fig. 3.5).

**Table 3.4. Algal cover change at three sites in WMNP between 1993 and 2013**

| **Site** | **Historical Source** | **Macroalgae (%)** | **CCA (%)** | **Turf Algae (%)** |
|---|---|---|---|---|
| Coral Gardens | WCS | 16.1->17.3 | 11.1->5.4 | 20.5->58.4 |
| Lambis | Obura | 20.2->28.3 | 16.7->5.0 | 39.4->51.3 |
| Turtle Reef | Obura | 15.1->30.9 | 3.5->3.0 | 19.3->50.8 |

Without being able to perform formal statistics on the apparent increase in macroalgal cover in Watamu, any conclusions based on visual comparison of the data should be treated with caution. Nevertheless, it could be argued that given the data available, even though there has been an increase of macroalgae, turf algae has played a more significant role in occupying the benthic space vacated by corals post-1998. Evidence from this study suggests that turf algae are not affecting recruitment or mortality rates in Watamu as this benthic component was not correlated with either of these variables (Figs. 3.13 and 3.14). There are ecological mechanisms by which turf-algae can reinforce a coral-poor state, by reducing coral recruitment and survival if the turf layer becomes too thick and/or entraps a layer of sediement (Birrell *et al.* 2008, Penin *et al.* 2010), but there is little evidence to suggest it creates a strong phase-shift effect on reefs (Nystrom *et al.* 2008). Jouffray *et al.* (2015), also noted that reefs can be found in a turf-dominated state, and interpreted this as either a transitory state or a novel stable state.

Although the 1998 bleaching event had a catastrophic and long-lasting impact on the coral community in Watamu, the system appears to have been resilient to a macroalgal phase-shift, maintaining some coral cover and suitable substrata for coral settlement and growth. However, the relatively stable benthic community post-1998, across years (Fig. 3.3) and sites (Table 3.3), between coral dominance and macroalgae dominance may suggest a novel stable state in Watamu (Bruno *et al.* 2009). The low coral cover (<10%) and altered community composition suggest there may be environmental conditions preventing the recovery to a pre-bleaching state. The next section will compare coral recruitment, growth and mortality between 1994 and twenty years later in 2014 to investigate the potential factors limiting coral recovery.

### 3.4.2 Identifying changes in coral demography pre and post-1998

The processes of recruitment, growth and mortality are key to understanding the demography of a coral community (Artzy-Randup *et al.* 2007). In this investigation these processes were studied in the smallest coral colonies (<10cm diameter), because this is the period of a coral's post-settlement life where it is most vulnerable to mortality (Vermeij and Sandin 2008), and growth rate is important to 'escape' this demographic bottleneck (Edmunds 2007).

Between 1994 and 2014 the monthly growth rate of corals in Bennett's and Lambis reefs did not change significantly and was approximately 1-2mm per month. Growth of corals in the Great Barrier Reef and French Polynesia were very similar to Watamu with the rate of linear coral increase of approximately 1.5mm per month (Trapon *et al.* 2013), but was reported at much lower levels of 0.4mm per month in the Red Sea (Glassom and Chadwick 2006) and 0.25-0.6mm in the Caribbean (Edmunds 2007). The observations from this study suggest that Watamu has maintained its coral growth rate over the past 20 years at a rate that is comparable to other Indo-Pacific sites.

Growth rate of corals can be measured in different ways, including calcification rate, skeletal density and linear extension (Risk and Sammarco 1991, Lough and Barnes 2000). In this study growth was measured using linear extension. While this is the easiest method in the field, it has the disadvantage that it is influenced by any partial mortality the colony may undergo, as well as any growth. By only investigating growth rate in the smallest corals, it was possible to minimise the influence of partial mortality, as small corals are much more likely to experience entire colony mortality or survive (Madin *et al.* 2014). However, at this small scale, errors in measurement would have proportionally more impact on the results.

Mortality rate was expressed as a proportion of colonies that died from the total colony count for a quadrat. The rate was not significantly different between 1994 and 2014 (Fig. 3.12). There are relatively few studies that specifically look at the mortality rates of juvenile corals, but there are comparisons available from French Polynesia in Penin *et al.* (2010) and Trapon *et al.* (2013) and the Red Sea from Glassom and Chadwick (2006). A comparison between the current study and these references suggest a similar juvenile mortality rate of 30-50% per year.

The number of small corals <10cm in diameter was 6.4 per m$^2$ in 1994, but dropped significantly to 2.1 per m$^2$ in 2014 (Fig. 3.9). Overall the number of small colonies per m$^2$ was low in Watamu compared to other reefs globally. At the near-pristine Kingman Reef in the Northern Line Islands, the number of juvenile corals (>5cm) was 40 per $m^2$ (Sandin *et al.* 2008), which was similar to levels reported by Glassom and Chadwick (2006) in the Red Sea. In other areas of the Indian Ocean, the Seychelles and the Maldives, that have also experienced severe mass-bleaching, the number of juveniles (<5cm) was 17 per $m^2$ (Chong-Seng *et al.* 2014) and 18 per $m^2$ (Cardini *et al.* 2012). In Watamu the number of colonies (<5cm) was much lower with 3.2 colonies per $m^2$ in 1994 main study sites and just 1.2 per $m^2$ in 2014. Watamu is located near the northern limit of the fringing reef formation along the East African coast (McClanahan 1988), which may suggest that either conditions are marginal or few recruits disperse to this area (Souter et al. 2009). The abundance of juveniles is comparable to the number of juveniles seen in Biscayne Bay, Florida in 1994 (Miller *et al.* 2000), which is at the northern edge of reef development in the Caribbean basin. Lower juvenile abundances in back-reef and lagoonal areas were reported from the Northern Line Islands of 13 per $m^2$ (Roth and Knowlton 2009) and the Maldives of 6 per $m^2$ (Cardini *et al.* 2012). All patch reefs studied in Watamu were lagoonal, which partly explains the low juvenile densities observed, but even so the number of small colonies is lower than expected for an Indo-Pacific reef.

In addition to juvenile coral density, recruitment rate, as the number of new colonies appearing in quadrats, was compared (Fig. 3.10). In 1994 there was a mean of 4.8 new colonies appearing in each quadrat ($1m^2$) per year, which had declined significantly to 1.5 colonies in 2014. The settlement rate of polyps onto plates was 5.4 per plate in Uyombo and 0 for Bennett's Reef. Comparing these findings to other studies has not been possible because measuring recruitment as the 'rate of new colonies appearing over time' has not been found in any other work and the variation in settlement plate material, orientation, placement and caging creates too much variation between settlement plate studies (Mundy 2000).

Recruitment is the hardest life stage of a coral to investigate because the small size and cryptic settlement of newly recruiting corals (Vermeij and Sandin 2008). In this study it is likely that the smallest corals (<1cm), were underestimated in the visual censuses conducted. Other studies have used enhanced detection methods such as UV light (Harris 2010) and a magnifying lens (Chadwick and Glassom 2006), which found recruit numbers two to three times higher than in unaided visual censuses. At the point of visual detection corals may be several months old and by 5cm in diameter could be three years old (Trapon *et al.* 2013), meaning the first 3-6 months of a corals life, where mortality rate is the highest, is unrecorded (Vermeij and Sandin 2008).

Settlement plates are a useful alternative method of measuring recruitment because they allow the detection of corals as small as one polyp (1-5mm) and theoretically eliminate variation in recruitment as a result of differences on natural surfaces in settlement cues, light, and water flow (O'Leary *et al.* 2011). Settlement plates therefore give a better idea of larval supply to a reef, but may not reflect true settlement patterns at a particular site. For example, in this study, and others (e.g. O'Leary *et al.* 2011), *Pocillopora* is the dominant coral settling on plates, despite the plates being placed among diverse coral communities, indicating there may be a selectivity bias as a settlement substratum. In this study both visual census of juvenile corals (<10cm) on natural substrata and settlement plates were used to estimate the recruitment rates in Watamu.

In the current study, using evidence from juvenile densities and the number of new recruits appearing, it can be concluded that either coral settlement has decreased between 1994 and 2014 or post-settlement mortality has increased. Without settlement plate information available for 1994 it is not possible to separate these processes, but data from plates in Uyombo and Bennett's suggest that larval supply has a part to play, as Bennett's saw no larval settlement during the same four-month period whereas Uyombo did.

### 3.4.3 Identifying the causes for reduced recruitment and lack of coral recovery

Based on the data from this study it can be concluded that recruitment and/or the survival of the smallest colonies has declined between 1994 and 2014. It should be noted, however, that recruitment is highly variable between years (Hughes *et al.* 1999) and since this conclusion is based on only two individual years of observation, it may not represent the real trend across time. For example, it should also be noted that during contemporary data collection (April 2013), there was a minor bleaching event, which resulted in 10% mortality (Chapter 4). However, since growth and mortality rates have remained at similar levels to 1994 in contemporary observations (Figs. 3.11 and 3.12), during what could be considered a bad year, it would seem recruitment is the reason for the lower density of small corals observed, and the overall reduced coral cover.

The benthic cover and recruitment rate from each permanent quadrat were compared to investigate whether major benthic components in a quadrat were associated with recruitment rate observed (Fig. 3.13). Turf algae, coralline algae and macroalgae were not correlated with recruitment. This suggests that these benthic organisms are not limiting the recruitment process in Watamu, as seen in other places (e.g. Kuffner *et al.* 2006, O'Leary *et al.* 2012).

Post-settlement mortality of newly-settled corals is commonly caused by grazing and predation by fish and urchins (Penin *et al.* 2010, O'Leary *et al.* 2013). Being a no-take MPA for over 40 years means that Watamu has a healthy fish community (McClanahan 2014b) that maintains keystone ecological species such as triggerfish, which prey on sea urchins that commonly graze on coral recruits (McClanahan 1994, O'Leary *et al.* 2013). Abundance of fish has been relatively consistent over the 20 years between 1994 and 2014 (McClanahan 2014), suggesting that predation and grazing on recruits has not changed.

Sedimentation and eutrophication are potential causes for the reduction in abundance of the juvenile corals, affecting both settlement and post-settlement mortality (Birrell *et al.* 2008, Fabricius 2005). Unfortunately, these parameters were not measured during this study, and there is a need to investigate the potential impacts of water quality in Watamu. A source of natural sedimentation and nutrient rich outflow comes from Mida Creek, a nearby mangrove area (Kitheka *et al.* 1999). During the study period, the area has maintained its mangrove cover (Kirui *et al.* 2013), but has seen large increases in human population around the creek (Muthiga 2009) with an unknown impact on water quality. A trend of heavily-sedimented reefs just to the north of the mouths of creeks has been observed along the Kenyan fringing reef, where the dominant southern currents push nutrient and sediment rich waters north (Obura, pers. comm.). Anthropogenic drivers of declining water quality in Watamu could be caused by the increasing human population in the area, driven by tourism

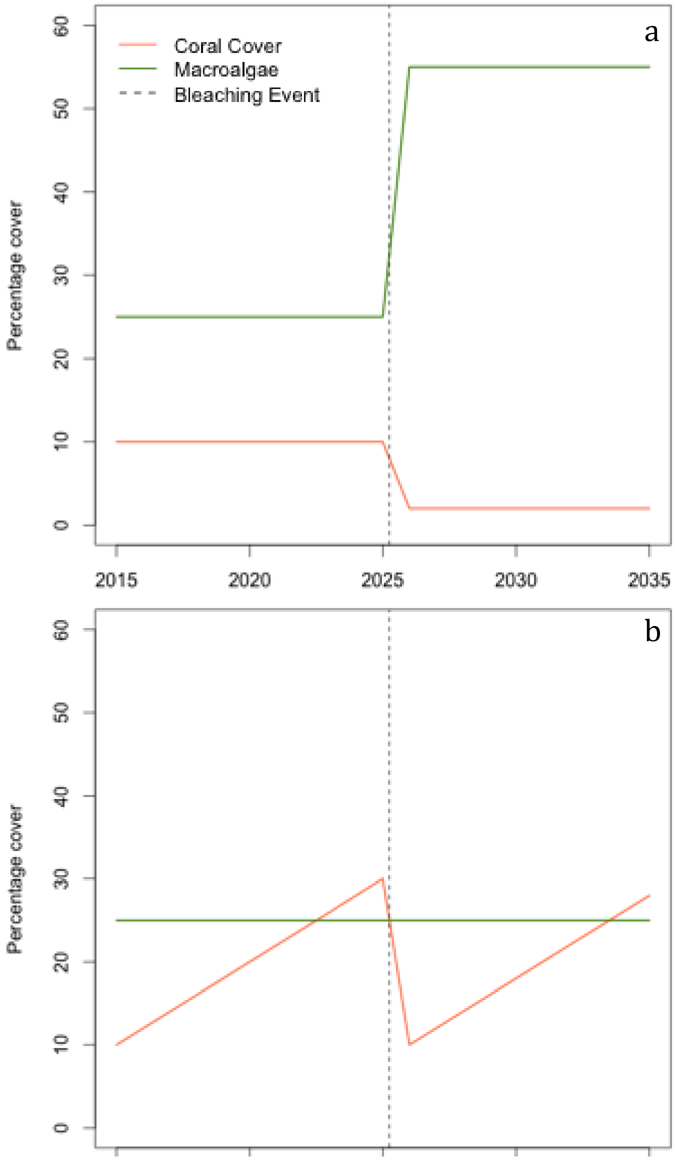
(Muthiga 2009). Sewage-enriched groundwater flow and pollutants from boats are not monitored, but are likely to have increased over the years (Chapter 2).

Adult coral reproductive capacity is controlled by the number of colonies and how large these colonies are (Soong and Lang 1992). Both coral cover (as a rough proxy for number of colonies) and average colony size of two genera have declined over the study period (Figs. 3.3 and 3.7), suggesting that the larval supply from local corals may have declined. Levels of connectivity and larval supply from outside WMNP may also be preventing recovery. Genetic divergence along the East African coastline for two species of coral was found to be higher in Malindi compared to populations >100km further south in Mombasa and Tanzania. (Souter and Grahn 2008, Souter *et al.* 2009), suggesting that this area is more isolated. Assuming this pattern is also true for Watamu (20km south of Malindi), this would suggest that either source areas of larvae have become degraded or the area is naturally genetically isolated. It is possible that Watamu is naturally genetically isolated to an extent, because it is near the northern limits of the East African Coastal Current and the end of the dispersal chain this current brings from the south (McClanahan 1988, Obura 2012). However, in addition to WMNPs marginal location, areas to the south outside the MPA have been degraded (McClanahan *et al.* 2001), with the next nearest marine park located 100km away in Mombasa. This is much farther than the average larval dispersal distance in corals (Ayre and Hughes 2004, Palumbi 2003), which may have reduced the larval supply to WMNP. To conclusively test these different assertions would require population genetic data from Watamu and different source areas (Ayre and Hughes 2004), which is beyond the scope of this study.

### 3.4.4 Conclusions and future management options

The reefs in WMNP have maintained some coral cover and suitable substrata for recruitment since 1998, but were significantly altered by the 1998 bleaching compared to their pre-1998 state, with lower coral cover, altered coral community and lower recruitment. Resilience in Watamu's main reef sites, north of Mida Creek outflow may be naturally low, as a result of sediment and nutrient flow from the creek. In addition, being located in a lagoon may have also decreased recovery rate and increased thermal stress as a result of longer water retention and localised warming (Obura and Mangubhai 2011). Hence Watamu could be described as a 'vulnerable' site (Mumby *et al.* 2014), with high sensitivity to stressors and poor capacity to recover. However, lagoons and thermally stressful environments are also associated with higher resistance to future bleaching (McClanahan *et al.* 2007a, Oliver and Palumbi 2011), which may confer some resistance to WMNP's coral community.

The future trajectory of the reefs is unclear. It is possible that the reef has reached a novel stable state dominated by turf algae (Jouffray et al. 2015). However, it may be that recovery is slower than other reefs, but with the continued protection of key functional groups and management of other anthropogenic stressors through Watamu's no-take MPA status, the coral may return. However, without recovery the reef resilience could also be teetering on the brink of a significant threshold and may phase-shift to a less favourable stable state in the near future. For example, below coral cover of 10% it has been shown that fish communities are significantly altered (Beldade *et al.* 2015). If Watamu suffers another drop in coral cover the reef may not support the herbivourous fish community currently keeping macroalgae in check and may decline and a phase-shift occur. This is depicted in (Fig. 3.16), to illustrate Watamu's current situation.



**Current recruitment and post-settlement survival**

- Coral cover remains close to 10%.
- During a future bleaching event coral cover is lost, crossing a threshold and leading to an increase in macroalgae.
- The macroalgal state is stable and prevents coral recovery

**Increased recruitment and post-settlement survival**

- Coral cover increases over time
- Macroalgal cover is constant
- During a future bleaching event coral cover is lost, but the reef remains resilient and coral cover begins to increase again

Figure 3.16 Theorised model of Watamu's future after an extreme bleaching event with a) current recruitment and post-settlement survival and b) increased recruitment and post-settlement survival.

A phase-shift is a highly undesirable outcome, as any management for the reef to recover would have to overcome the hysteresis effect caused by the factors maintaining a macro-algal state (Fig. 1.2) (Mumby *et al.* 2007a, Graham *et al.* 2013). Actions to increase the resilience of the current stable state are needed to allow the reefs to be more robust to potential future climate stress (Mumby *et al.* 2014, Anthony *et al.* 2015).

An initial step may be to investigate the water quality in Watamu and determine whether land-based activities and boats are impacting the health of corals in the lagoon. If water quality is not an issue, or could be improved, then management should focus its attention on coral recovery, specifically through recruitment. Connectivity to the south is expected to improve over coming years, as a network of small, Locally Managed Marine Reserves (LMMAs), are being established along the coast between official National Parks (Rocliffe *et al.* 2014). These no-take areas have seen increases in fish and coral populations locally (Rocliffe *et al.* 2014) and, given time, will presumably act as stepping-stones for larval dispersal along the coast. Locally, the coral community and the local larval supply might benefit from restorative coral planting, which has been effective in areas hit by acute disturbances (e.g. Mbije *et al.* 2013). Coral transplants will avoid the recruitment stage, which is currently depressed in Watamu, and with similar levels of growth and mortality to 20 years ago, will be likely to survive.

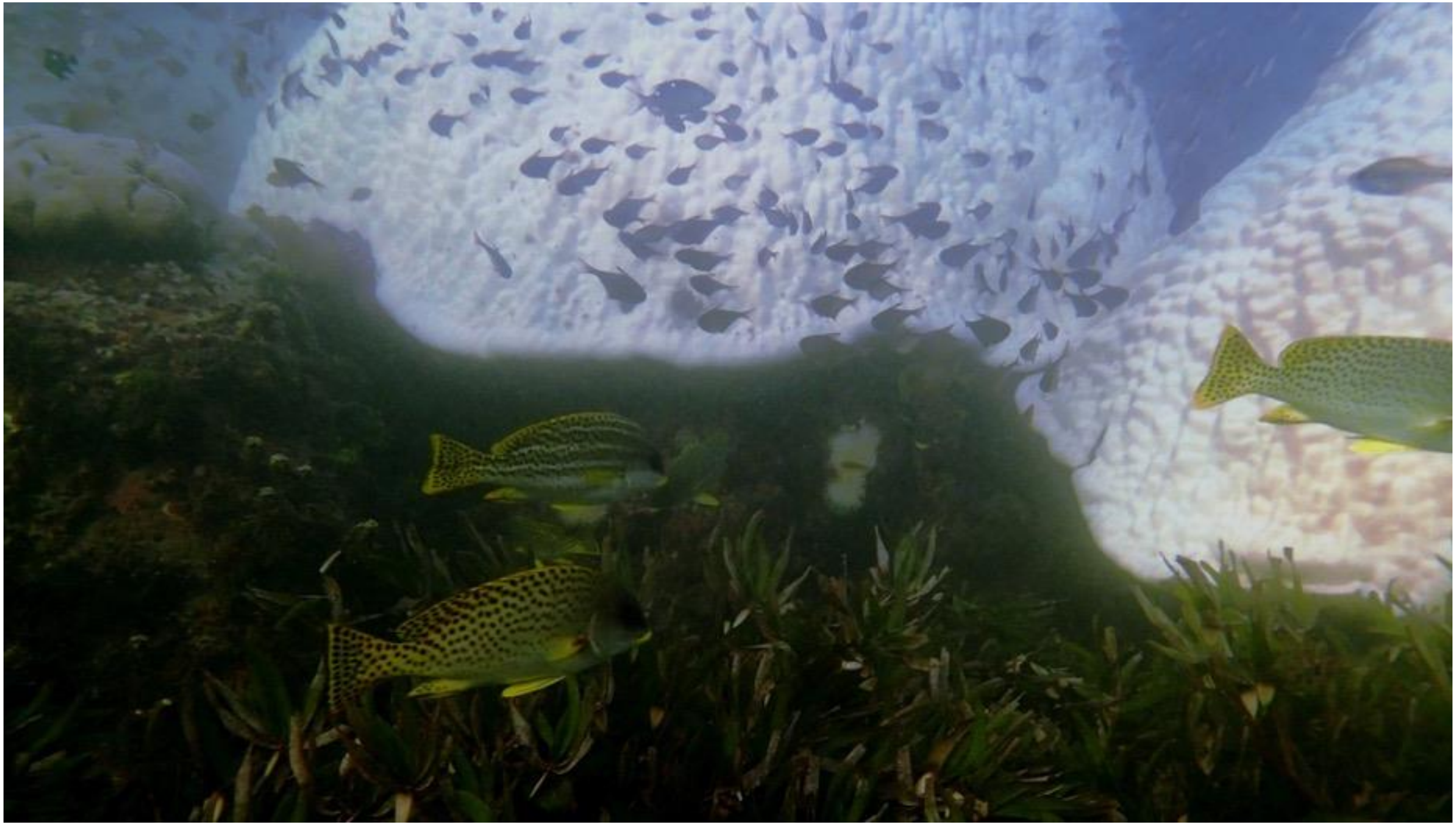


Plate 4. Bleached *Porites* colonies in Watamu during a bleaching event in April 2013 (Photo: B. Cowburn).

# Chapter 4. Assessing the impact of repeated thermal stress and coral bleaching on a Kenyan coral reef

## Abstract

In this chapter the temperature profile and thermal stress experienced by reefs in Watamu Marine National Park (WMNP) over the past 3 decades are presented. This includes a detailed study of the response and recovery of corals from a minor bleaching event in 2013. The most significant deleterious impact of coral bleaching during the time examined occurred in 1998, where widespread coral mortality was observed. Although other bleaching events have occurred since 1998, it does not appear that these events caused extensive mortality, and it was observed that the majority of corals recovered from the 2013 event, which was the most significant thermal stress experienced by reefs in WMNP since 1998. In addition, there was little evidence to suggest bleaching had sub-lethal negative impacts on corals in 2013, suggesting that the bleaching observed was a regulatory response to thermal stress in most corals. The only coral genus that sustained deleterious impacts of bleaching was *Pocillopora*, in which branching colonies suffered approximately 50% mortality. Branching *Acropora* corals, which are normally highly susceptible to thermal stress, showed low bleaching response and very high survival in 2013, suggesting either community-level adaptation or colony level acclimatisation of these dominant Indo-Pacific reef builders. The future bleaching impacts in WMNP will depend on the degree of thermal resistance the coral community has accumulated through its past bleaching experience and the frequency and severity of future bleaching events.

## 4.1 Introduction

### 4.1.1 Predicting the future of coral reefs with climate change and mass-bleaching

The rise of mass coral reef bleaching around the world is being met with great concern by the scientific and conservation communities. The frequency of mass coral bleaching events has been increasing over the past 150 years (Glynn 1993; Baker *et al.* 2008) and the impacts of bleaching events are dramatically altering the ecology of reefs in shallow tropical waters around the world (Goreau *et al.* 2000). Increasing scientific attention to bleaching is at least partially responsible for this increase in bleaching observations (Baker *et al.* 2008), but the link between increased bleaching and increasing thermal stress, caused by anthropogenic climate change, appears robust (Brown 1987, Glynn 1993, Oliver *et al.* 2009). Tropical seas have warmed by an average of 0.4°C over the past 100 years (Eakin *et al.* 2009). Under the best case scenario proposed by the International Panel on Climate Change (IPCC), where global average temperature rise is maintained under 2°C, tropical waters are committed to at least a further ~1°C warming by 2100 (Gattuso et al. 2015). In a 'business as usual' scenario corals will experience temperatures ~3°C higher than current sea surface temperatures by 2100 (Donner *et al.* 2009, Gattuso et al. 2015).

Corals live close to their thermal upper limits (Glynn and D'Croz 1990) and a modest increase of 1°C of sea temperatures above normal summer conditions can trigger lethal mass bleaching events (Coles *et al.* 1978, Hughes *et al.* 2003). These conditions have mostly been experienced during El Niño Southern Oscillation (ENSO) years (Brown 1987, Glynn 1993), with major mass coral bleaching events impacting reefs around the globe occurring in 1982, 1987, 1998, 2005, 2010 (Oliver *et al.* 2009, McClanahan 2014, Kleypas *et al.* 2015) and 2015 (NOAA 2015). The worst event globally was in 1998, where up to 16% world's coral reefs were lost (Wilkinson 2008) and many localities suffered over 90% mortality (Obura 2005). It has been estimated that mass coral bleaching events like the one that occurred in 1998 may be commonplace by 2020-2030 (Hoegh-Guldberg 1999, Donner 2009). If reefs experience 1998 intensities of bleaching and mortality every 5 years, it has been suggested coral would not be able to recover fast enough between events and the reefs would become functionally 'extinct' (Sheppard 2003).

Accurately predicting future bleaching and mortality of corals is fraught with a range of issues. Projections of global climate are constructed using different emission scenarios (IPCC 2014), which has the fundamental difficulty that emissions do not predict $CO_2$ concentrations perfectly because of uncertainty with the planet's natural ability to store and release carbon under future scenarios (Donner *et al.* 2009). These projections must also contend with modelling complex natural climatic oscillations, such as ENSO and the Indian Ocean Dipole (IOD), in order to understand how often 'extreme' events are likely to occur (Donner *et al.* 2009, McLeod *et al.* 2010). At a finer spatial scale, hydrodynamic features such as depth, tidal movement, currents and upwelling will create a range of local conditions with local thermal profiles (McClanahan *et al.* 2007a, Palumbi *et al.* 2014). A final major source of uncertainty is the degree to which an area's thermal profile and prior bleaching experience influence the impact of thermal events on the corals (Rowan *et al.* 1997, Thompson and Woesik 2009). It is this final source of uncertainty where there may lie the most hope for corals in future projections of climate change and bleaching (Pandolfi *et al.* 2011).

### 4.1.2 The impacts of bleaching on the coral organism and coral populations

At the cellular level coral bleaching is observable as a decrease in the concentration of symbiotic zooxanthellae in the cells of the coral polyps, usually in response to light and temperature (Coles and Jokiel 1978). The impact of this process has repercussions on coral physiology, coral populations and the wider reef ecosystem (Baker *et al.* 2008). The links between physical conditions, mass coral bleaching and eventual mortality are complex (Fitt *et al.* 2001, Anthony *et al.* 2007), but the main three factors determining the severity of a mass bleaching event are water temperature, and the amount of time thermal stress is applied (Berkelmans 2002, Liu *et al.* 2003) and light intensity (Drollet *et al.* 1994). The impact on the wider reef ecosystem is determined by the severity of individual mass bleaching events, the ability of the reef to recover (i.e. its resilience) and the time until the next bleaching event (i.e. bleaching frequency) (Sheppard 2003).

The reduction or loss of symbiotic zooxanthellae leads to decline in food stores and nutrients in the coral organism (Porter *et al.* 1989). This can produce a range of negative impacts in corals including reduced growth rate (Porter *et al.* 1989), reduction in reproductive output (Baird and Marshall 2002) and disease (McClanahan *et al.* 2004b). When bleaching is extreme the stress on the organism causes mortality, either of the whole coral colony or parts of the colony (Glynn 1984). In bleaching events with high coral mortality the impacts on the wider ecosystem can be devastating, leading to reduction in coral cover (Glynn

1993), changes in coral community composition (McClanahan *et al.* 2007b), changes in species composition and diversity in non-coral organisms (Graham 2007, Pratchett *et al.* 2008), phase-shifts to macroalgal state (Diaz-Pulido and McCook 2002), and without coral recovery, eventual collapse of the reef structure under physical and biological erosion (Glynn 1997 and Pratchett *et al*. 2009). In this degraded state, reefs are no longer able to provide the wealth of beneficial ecosystems services they do (Costanza 1997).

As a result of the catastrophic changes associated with bleaching, the term has become synonymous with mortality in some cases (Suggett and Smith 2011). However, it has been noted that the bleaching response can also have some positive impacts on corals and reefs as a whole through mechanisms described in the Adaptive Bleaching Hypothesis (ABH) (Buddemeier and Fautin 1993, Ware *et al.* 1996). This theory posits that a variety of symbiont-host combinations with different thermal tolerances exist, and that bleaching allows the coral to be repopulated with a more favourable symbiont community in response to environmental stress (Buddemeier and Fautin 1993).

Acclimatisation of corals to increased thermal stress has been observed over time (Maynard *et al.* 2008), at different spatial scales (McClanahan *et al.* 2007a, Thompson and van Woesik 2009) and even in different parts of the same colony (Rowan *et al.* 1997, Brown *et al.* 2002). Acclimatisation is in part conferred through physiological changes in the coral organism (Brown *et al.* 2002), regulation of symbiont concentration (Fitt *et al.* 2001) and changes in symbiont composition to zooxanthellae clades with higher thermal thresholds (Buddemeier and Fautin 1993, Baker *et al.* 2004).

In addition to acclimatisation, coral community adaptation is another important outcome of bleaching. In more extreme events with high levels of mortality, mass bleaching may apply a selective pressure against thermally sensitive colonies and species, leading to community level adaptation to thermal stress (Maynard *et al.* 2008).

Corals have existed in periods of geological time with much higher concentrations of $CO_2$ and global temperatures than today (Pandolfi *et al.* 2011). Their ability to acclimatise and/or adapt to extreme thermal stress is demonstrated in areas such as the Arabian Gulf, where corals can experience a thermal range from 14-36°C (Coles and Reigl 2013). The key question is therefore not, can coral survive predicted temperatures, but rather will they be able to acclimatise and adapt at the rate that tropical oceans are warming (Sheppard 2003, Donner 2009). If thermal stress and bleaching become too intense, the negative impacts on coral communities will lead to significant reductions in reef functioning and extent (Glynn 1993, Baker *et al.* 2008). However, if adaptation and acclimatisation can keep in step with climate change, there may be hope for corals into the future (Pandolfi *et al.* 2011).

### 4.1.3 Understanding thermal stress and bleaching impact on a vulnerable reef in Kenya

This study investigates thermal stress and bleaching impact in a lagoonal coral reef system in Watamu Marine National Park (WMNP), Kenya (Fig. 1.5). The park is a 10km$^2$ no-take area of back reef and lagoon containing seagrass beds and patch reefs located on the Kenyan coast (40°00’00”E, 3°23’00”S). Sea temperatures were reconstructed for the area over the past 30 years to investigate past thermal stress. These thermal trends were compared with known bleaching events during this time period to understand bleaching thresholds in Watamu. In addition to investigating past thermal stress, a recent bleaching event was recorded in 2013 between April to July. Data were collected on the bleaching intensity, mortality, and post-bleaching impacts on the coral community. The aim of this study is to explore a range of potential bleaching impacts on a reef and understand how accumulated thermal stress is affecting corals in their natural ecological setting.

There have been at least six mass bleaching events recorded in Kenya over the past three decades, with an event of unknown magnitude in 1987, the highly damaging 1998 event, and four relatively minor events in 2005, 2007, 2010 (McClanahan 2014) and 2013. The 1998 event was the most significant impact experienced by the coral community in Watamu, resulting in 70% decline in coral cover (Chapter 3). The recovery of corals has been limited, with coral cover remaining around 10% with an altered coral community structure of bleaching-resistant coral genera (Chapter 3). Nevertheless, the reef has not phase-shifted to an algal-dominated state and minor bleaching events post-1998 appear to have been non-lethal (Chapter 3, McClanahan 2014).

Bleaching impacts from minor and repeated events, such as experienced by corals in WMNP post-1998, are under-represented in the literature, but are probably key to understanding the processes of acclimatisation and adaptation (Suggett and Smith 2010, Pratchett *et al.* 2013). From a conservation point of view, investigating bleaching in WMNP is important, because the reef would currently fall into Global Coral Reef Monitoring Network (GCRMN) “Critical Stage”, where 50-90% of coral has already been lost and is threatened with entering the most degraded GCRMN category, 'Effectively Lost' in the next 10-20 years (Wilkinson 2008). Hence WMNP represents a site that may hang in the balance between climate-driven collapse and potential acclimatisation. This study will investigate the balance of these two possibilities.

## 4.2 Methods

In this chapter the trends in temperature and thermal stress are examined in Watamu from 1982-2014 using data derived from satellites and data-loggers. A bleaching event was observed in 2013 and the bleaching response, mortality and other impacts on the coral community were observed in three shallow (<10m) patch reefs, separated by 1.0-2.5km.

### 4.2.1 Temperature and thermal stress

Sea surface temperatures (SSTs) for Watamu were derived from the Advanced Very High Resolution Radiometer (AVHRR) pixel nearest to Watamu centred at 3.375°S, 40.375°E (approximately 40km offshore) from January 1982 to December 2013. The AVHRR is the satellite most commonly used by National Oceanographic and Atmospheric Administration (NOAA) to monitor tropical temperature anomalies and predict bleaching. The data were accessed from http://las.incois.gov.in/las. Lagoon water temperature was measured using a Hobo U22-001 temperature logger (Onset Corporation, Poccasset, MA, USA) placed at 1m below mean low water spring (MLWS) under a coral head at Coral Gardens, from June 2002 until June 2014 (McClanahan, Wildlife Conservation Society). Hobo estimates the accuracy of these loggers to 0.35°C, which was confirmed by calibration of the loggers before deployment (McClanahan, pers. comm.).

The central tendency of temperature data were expressed as mean, minimum (min) and maximum (max) temperatures annually, where min and max refer to the average temperature in the coolest or hottest month, respectively. Variation in temperature is expressed inter-annually by taking the standard deviation (σ) of the mean and max temperatures for the years in question (Donner *et al.* 2011). Seasonal variation is defined as the difference between the SSTmax and SSTmin (i.e. hottest month – coolest month) (Donner *et al.* 2011).

Thermal stress in the temperature profiles was revealed by converting the raw data into the NOAA's standard coral bleaching products. These bleaching products were first used during a mass bleaching event on the Great Barrier Reef in 2002 (Liu *et al.* 2003) and are currently used to predict mass bleaching events and produce bleaching warnings around the world (Eakin *et al.* 2009). The methods below are described in more detail by Eakin *et al.* (2009) and also on NOAA's website http://www.ospo.noaa.gov/Products/ocean/.

- Climatological SSTmax: A temperature threshold is defined from the average hottest month (SSTmax) for the years 1985-1990 and 1993 (Eakin *et al.* 2009). This is used to describe the normal upper thermal limits for the area in question and the climatological SSTmax + 1°C is considered the threshold above which bleaching becomes likely (Eakin *et al.* 2009). For the temperature logger where data are only available from 2002, the climatological SSTmax is calculated as the satellite threshold plus/minus the average difference in between weekly temperature readings between 2003-2013.
- Hotspot: Is defined as a period of time where the temperature is above the climatological SSTmax. In this study, 'hotspot' for each year was calculated as sum of the positive thermal anomalies (or weekly temperature above climatological SSTmax). For example, during one year

with two weeks with anomalies of 1.5°C in both weeks, the number of hotspot weeks is 2 and the cumulative hotspot is 3°C.

- Degree heating weeks (DHW): Defined as when temperatures are above the climatological SSTmax + 1°C threshold for 1 week. Hence a hotspot of 1°C above climatological SSTmax for 2 weeks equals 2 DHWs, as does a hotspot of 2°C for 1 week. NOAA issues 'Bleaching Alert 1' indicating bleaching is likely if an area experiences 4 DHWs and 'Bleaching Alert 2' indicating mortality is likely if there are 8 DHWs.

Past thermal stress and the timing of bleaching events were compared for Watamu. Bleaching events have been monitored in 1998 and 2005 (McClanahan 2014) and observed in 1987, 2007 and 2010, without monitoring of bleaching intensity (T. McClanahan, Wildlife Conservation Society, pers. comm.)

Satellite information was assumed to be an accurate record of the oceanic sea temperature just offshore from Watamu and the *in situ* data logger as a record of the lagoonal temperature. The differences in mean value and variation between temperature in the lagoon and open ocean were assessed by comparing the temperature profiles of the data sources during the periods where both were available (i.e. 2002-2014). A regression analysis of the average monthly temperature between the two datasets was carried out. The intercept from the regression equation was used as the conversion factor to derive the climatological SSTmax for the lagoon, as this is the average difference in temperature between the satellite SSTs and logger recordings. With this lagoon-adjusted climatological SSTmax the degree of thermal stress between the lagoon and nearby oceanic waters was compared.

### 4.2.2 Estimating coral bleaching response using transects

The peak lagoon water temperature was recorded on the 20th of March, 2013 and the first bleaching response of corals was investigated three weeks later on the 12th of April. Three subsequent surveys were conducted at roughly monthly intervals on the 25th of May, 18th of June and 25th of July 2013.

Coral bleaching response was investigated using 10m x 1m (10m$^2$) belt transects at Bennett's, Lambis and Uyombo reefs in the lagoon of WMNP (Fig. 1.4). Each month 20-30 transects were laid haphazardly across the reef and all the hard coral colonies (Scleractinia) were counted, with their genus and bleaching response recorded. Visual censuses of bleaching response based on coral colour have been demonstrated to reliably detect decreases in zooxanthellae concentrations in corals (Siebeck *et al.* 2006). In Siebeck *et al.*'s study 5 categories of colouration were tested. In this study loss of colouration is simplified to 3 categories; 'normal' for colonies with no colouration loss or very limited colouration loss (80-100% normal hue), 'pale' for any significant colour loss, but not white (20-80% normal hue) and 'bleached' for corals with near total or total colour loss (0-20% normal hue) (Fig. 4.1). Categories of 'partially pale' and 'partially bleached' were used where colonies had portions of their tissue that were pale or fully bleached (20-80% tissue affected), but the rest of the colony maintained normal colouration. A similar classification and ranking of bleaching cateogories has been used by the Wildlife Conservation Society to monitor bleaching in the Western Indian Ocean (e.g. McClanahan *et al.* 2004).

A bleaching index was produced from bleaching responses by assigning a numerical weighting between 0 and 1 to each bleaching category and taking the weighted average of the whole coral community and separate genera (Equation

4.1). Normal colouration was weighted as 0 and bleached as 1, meaning that a completely normal coral community (or genus) would score a bleaching index of 0, whereas a community where 100% colonies were completely bleached would score 1. The bleaching index was used to compare between months and genera, because it summarised bleaching response into a single numerical value, which was comparable between different sample sizes and different years.

Live coral colony abundance in transects was hypothesised to decrease over the months from April to July as coral mortality occurred. A Shapiro-Wilks (S-W) test showed that the variable 'abundance' was non-normal ($W$=0.960, $p$=0.003) and Breush-Pagan (B-P) test showed that the variance of abundance in each month was homoscedastic ($\chi^2$=6.378, $p$=0.095). Hence, a Spearman's rank correlation was used to investigate the change in colony abundance during the bleaching event.

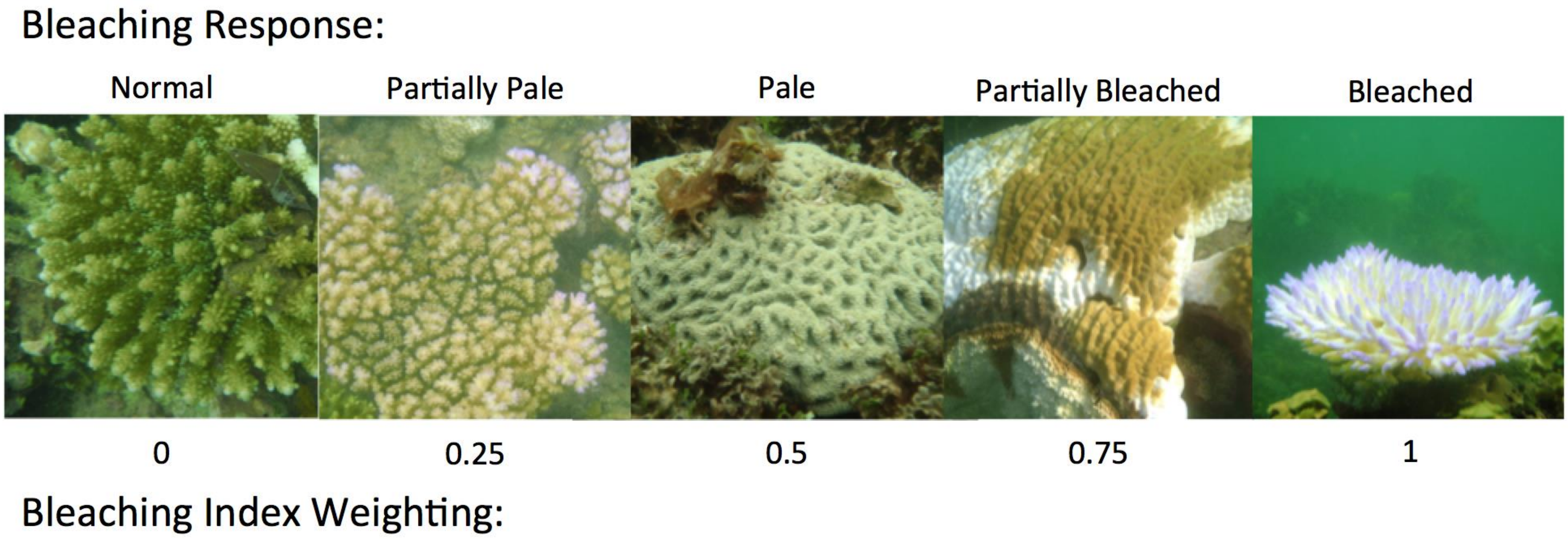


**Figure 4.1. Bleaching response categories and index weighting with exemplary photos (Photos by B. Cowburn).**

$$\boldsymbol{Bleaching\ Index} = \frac{(\sum Normal * 0 + \sum Partially\ Pale * 0.25 + \sum Pale * 0.5 + \sum Partially\ Bleached * 0.75 + \sum Bleached * 1)}{Number\ of\ colonies\ (n)}$$

**Equation 4.1: Weighted average equation for bleaching index.**

### 4.2.3 Investigating bleaching response and post-bleaching mortality in permanent quadrats

The bleaching response and post-bleaching mortality of individual colonies was investigated using marked corals in permanent quadrats that were assessed on the 12th of April at peak bleaching and again on the 25th of July. Forty-four 1m$^2$ quadrats were placed haphazardly on the same three patch reefs as investigated using belt transects. During the initial assessment in April the corners of each quadrat were marked using stainless steel nails with colourful plastic wire attached. The location and genus of each coral colony within the quadrat was drawn on a diagram of the quadrat *in situ* and was also recorded with a photograph of the quadrat taken at 90° to the substratum (Fig. 4.2).

The bleaching responses of colonies were recorded in April in the same manner as in belt transects (see above). Colonies in July were classified as 'No mortality', where no tissue loss occurred, 'Total mortality' where the entire colony died and 'Partial mortality' where some but not all of the coral tissue died. The size of each colony was estimated by analysing images on CPCe (Kohler and Gill 2006). The length of longest axis and the perpendicular axis were measured and combined to give a geometric mean length of each coral (Equation 4.2).

**Equation 4.2. Geometric mean length of a coral colony**

$$Geometric\ mean = \sqrt{Long\ axis\ \times\ Perpendicular\ axis}$$

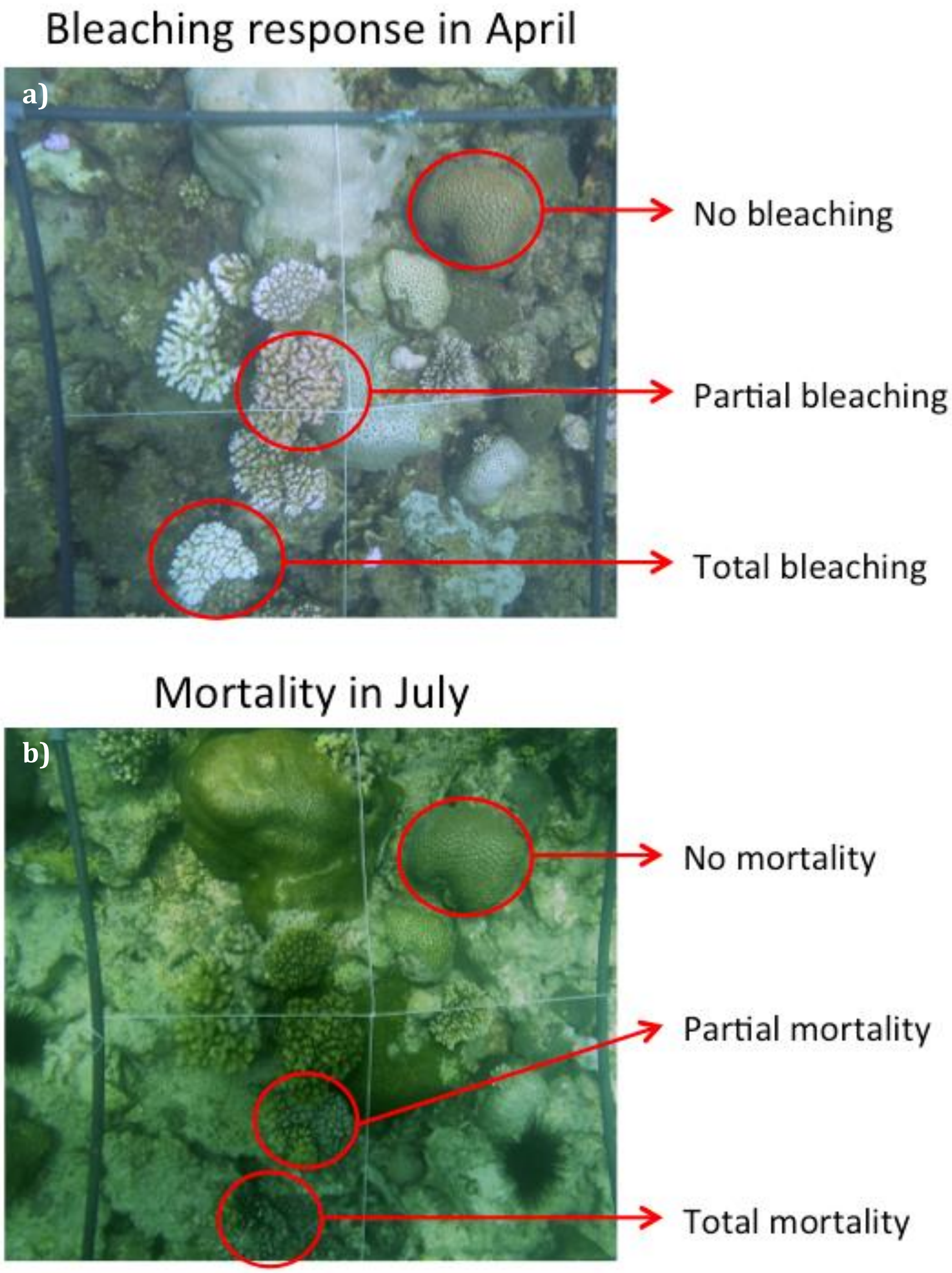


**Figure 4.2. A permanent quadrat showing examples of bleaching response in a) April and b) post-bleaching mortality responses in July 2013.**

Mortality was compared with initial bleaching response of each colony, colony size and the family of the coral. In this analysis bleaching response (Fig. 4.1) was simplified to ‘No bleaching’ (normal), ‘Partial bleaching’ (partially pale, pale and partially bleached) and ‘Total bleaching’ (bleached), because of the smaller sample size available when using marked corals. This is also the reason why different corals were pooled at the family level and not to genus level as in the analysis of the transect data. A McNemar’s paired test was used to test the hypothesis that a higher bleaching response would lead to greater mortality in marked corals.

### 4.2.4 Post-bleaching growth

Fifty-four juvenile corals, defined as being <10cm at their long axis, were located in permanent quadrats, mentioned above. Each coral was identified to genus level (Table 4.1) and its long axis and perpendicular axis were measured using callipers. These colonies were measured every 3 months for 1 year after peak bleaching in April 2013 until April 2014. Growth rate was expressed as the average net change in geometric mean (Equation 4.2) of each colony per month.

**Table 4.1 Genus composition of marked juvenile corals monitored for growth rate**

| Genus | Number of Colonies |
|---|---|
| *Acanthastrea* | 1 |
| *Acropora* | 17 |
| *Dipsastraea* | 5 |
| *Favites* | 4 |
| *Gardineroseris* | 1 |
| *Hydnophora* | 2 |
| *Montipora* | 1 |
| *Pavona* | 6 |
| *Platygyra* | 1 |
| *Pocillopora* | 8 |
| *Porites* | 8 |
| **Total** | **54** |

The bleaching response of marked corals was compared with their post-bleaching growth rate, to investigate whether higher bleaching response reduced growth rate as a sub-lethal impact of bleaching. A S-W test showed that the growth rate was normally distributed ($W$=0.976, $p$=0.337) and a B-P test showed the varience between the bleaching response groups was homoscedastic ($\chi^2$=0.634, $p$=0.729). An ANOVA was therefore used to test if there were significant differences in growth rate between different bleaching responses of the colonies.

## 4.3 Results

### 4.3.1 Climatology of Watamu

Mean annual sea surface temperature (SSTmean) was 27.04°C (SE±0.044) and varied from a minimum of 26.57°C in 1984 to a maximum of 27.64°C in 1998 (Fig. 4.3), based on the AVHRR satellite data. The average seasonal range was 3.68°C with an average coolest month (SSTmin) of 25.19°C (SE±0.085) and average warmest month (SSTmax) of 28.87°C (SE±0.080). SSTmax ranged from 28.13°C in 1985 to 30.31°C in 1998. The climatological SSTmax calculated as the mean temperature of the hottest months for the years 1985-1990 and 1993 (Liu *et al.* 2003, Eakin *et al.* 2009) was 28.83°C and hence the +1°C threshold was 29.83°C. The relationship between time and SSTmax was not significant based on a Pearson's product moment correlation ($R^2$=0.289, $DF$=29, $p$=0.115).

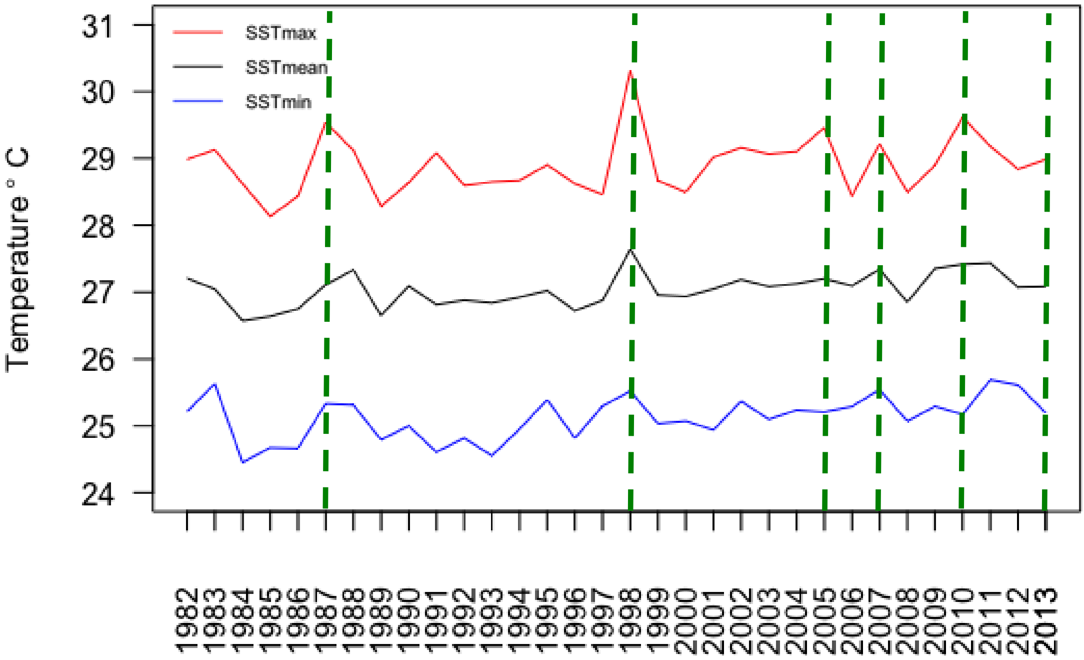


**Figure 4.3. Annual SSTmax, SSTmean and SSTmin for Watamu, based on AVHRR satellite data from January 1982 – December 2013. Bleaching years in 1987, 1998, 2005, 2007, 2010 and 2013 are indicated by the green dashed line.**

### 4.3.2 Past thermal stress and bleaching in Watamu

The average SSTmax in each year was plotted (Fig. 4.3). Previous bleaching events in Watamu in 1987, 1998, 2005, 2007 and 2010 coincided with the five hottest months of this time series, with 1998 having the highest SSTmax of 30.3°C, or 1.5°C above climatological SSTmax. The thermal anomaly experienced during all weeks that exceeded the climatological SSTmax (hotspot conditions) were summed to give an 'annual cumulative hotspot' or positive thermal anomaly for that year. The annual cumulative hotspot was >3°C in the five bleaching years and in 1998 reached an annual hotspot of 12.9°C (Fig. 4.4), with SSTmax >+1°C recorded in 14 weeks. In 2013 the SSTmax was only +0.13°C above the climatological SSTmax and had an annual hotspot value of only +1.3°C. This positive thermal anomaly for 2013 is less than the cumulative hotspot conditions observed in years where no bleaching occurred, such as 2011 which had a hotspot value of +1.7°C.

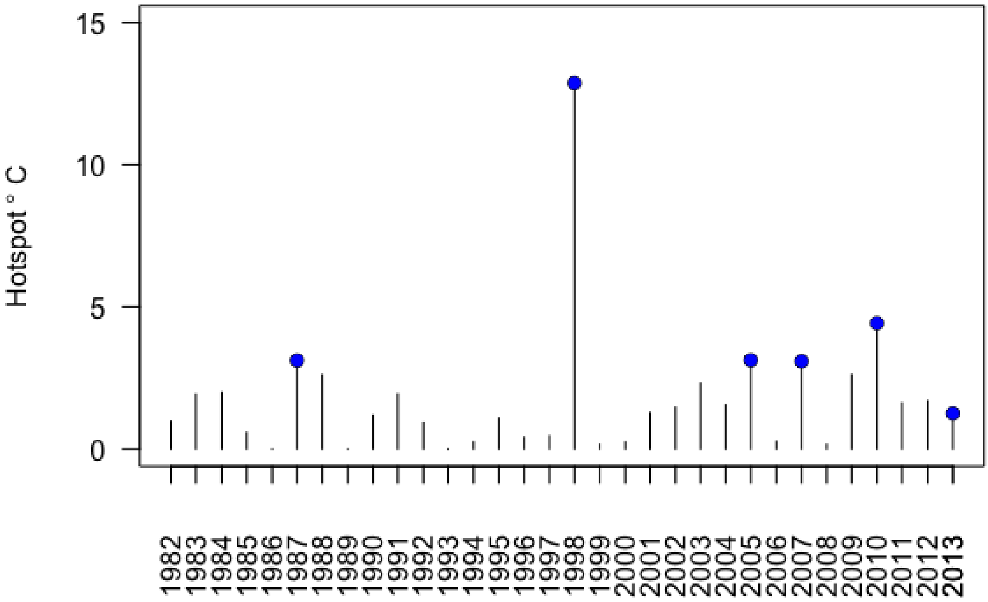


Figure 4.4 Total cumulative hotspot conditions annually in 1982-2013 from the AVHRR satellite data. Bleaching years are indicated with a point.

The number of degree heating weeks (DHWs) was calculated (Fig. 4.5). In 1998 there were 10.5 DHWs, which placed Watamu in NOAA's Alert Level 2, where the level of thermal stress is expected to cause mortality (NOAA 2015), which did occur extensively in Watamu during this year (McClanahan *et al.* 2001). There are far fewer DHWs in 1987 and 2005 with just 1.3 and 1.1 respectively, which does not cross NOAA's bleaching alert level 1, where bleaching would normally be expected (NOAA 2015). During the 2007, 2010 and 2013 bleaching events no DHWs were recorded at all based on satellite data.

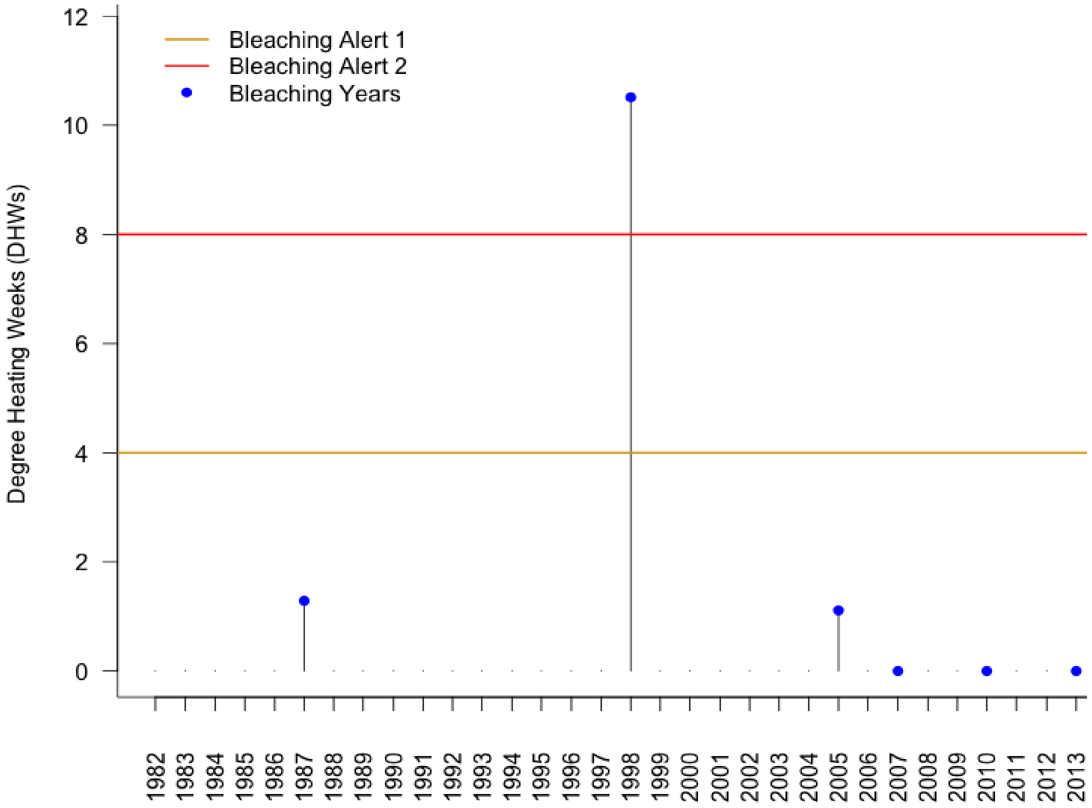


**Figure 4.5 Annual DHWs from 1982-2013 from AVHRR satellite data with NOAA bleaching alert 1 and 2 overlaid and bleaching years indicated**

### 4.3.3 Comparing satellite SST and data logger temperature

The SSTs each month from the AVHRR satellite data were compared with the temperature recorded by the logger for the time period between 2003 and 2013 (Figs. 4.6 & 4.7). A Pearson's product moment correlation was performed, which showed that the two temperature readings were closely matched ($\rho$=0.951, $DF$=117, $p$<0.001). The fitted line equation of the correlation between the two readings was derived from a linear model of the data (Equation 4.3).

**Equation 4.3 Line equation of the relationship between satellite and logger temperatures from 2003-2013, based on a linear model**

$$Logger\ \ temperature = (1.018\ \times\ Satellite\ temperature) + 0.259$$

The intercept of the regression equation indicates that the logger records slightly warmer temperature in the lagoon than the satellite pixel located offshore, by 0.26°C. The average SSTmean was higher based on the logger with a mean of 27.32°C (SE±0.054) compared to 27.19°C (SE±0.098) from the satellite, but this difference was not significant in a paired t-test ($t$=-1.644, $DF$=123, $p$=-0.139). The standard errors from these annual means show that the inter-annual variation is nearly double from the logger (SE±0.098) compared to the satellite (SE±0.054). The seasonal variation (SSTmax-SSTmin) recorded by the satellite was 3.72°C (SE±0.111). The logger recorded a slightly larger range of 3.81°C (SE±0.166), but this difference was not significant ($t$=0.392, $DF$=10, $p$=0.705).

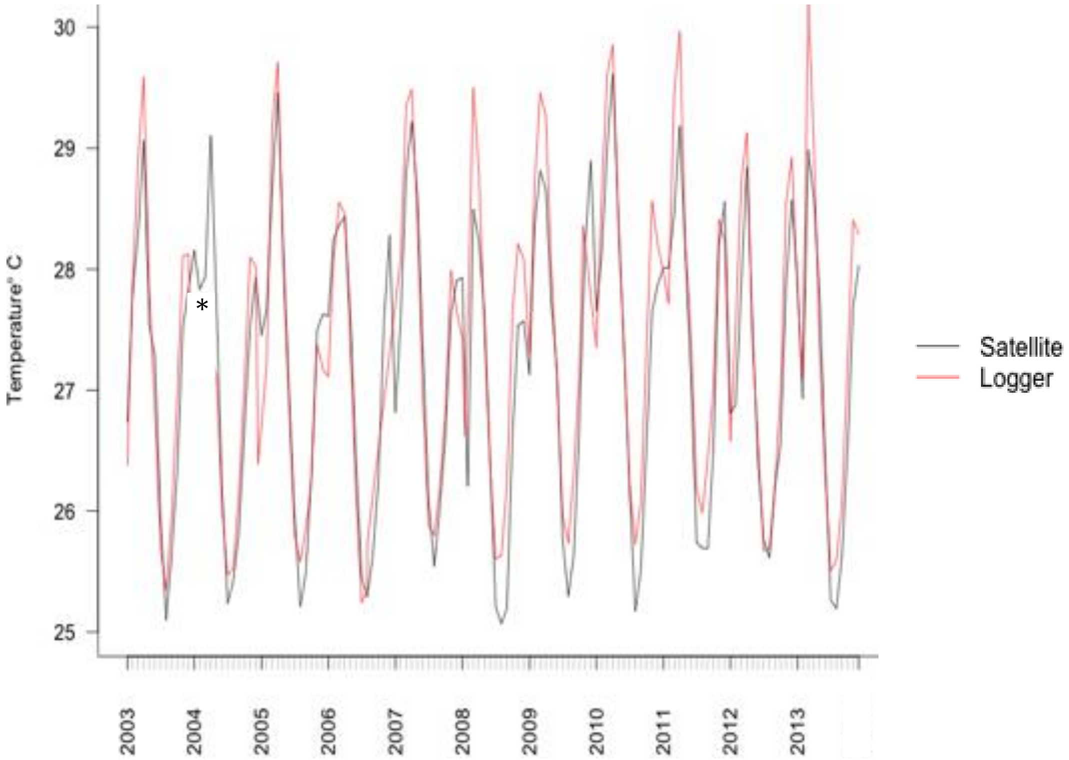


Figure 4.6 Monthly temperature measured by AVHRR satellite and *in situ* logger from 2003-2013. *Data from January – May 2004 are missing from the logger time series.

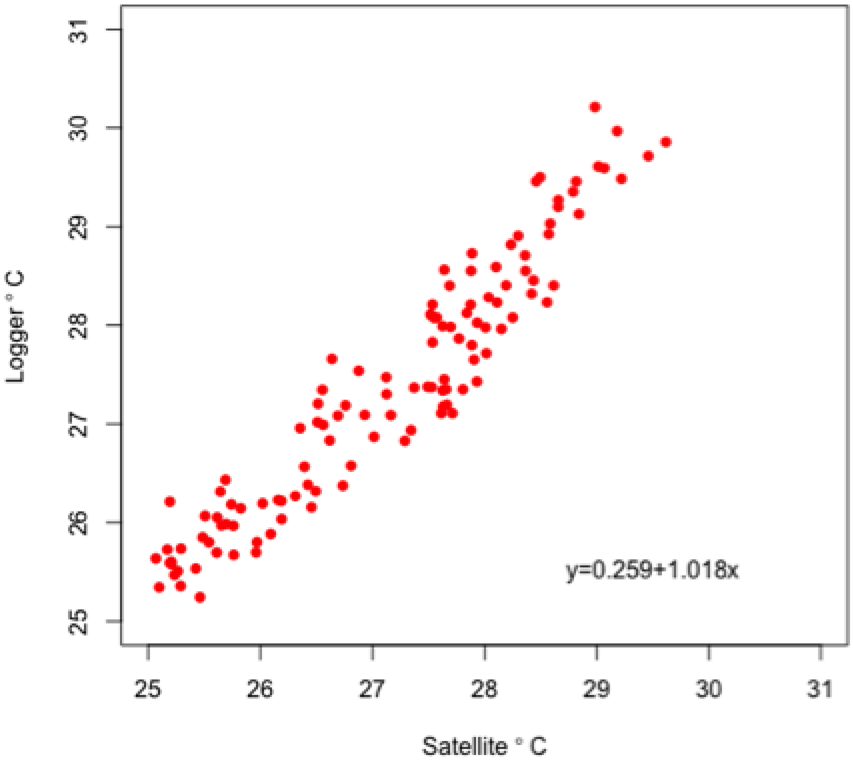


Figure 4.7 Regression plot of monthly SSTmean from AVHRR satellite and *in situ* logger from 2003-2013. The fitted line equation derived from the linear model is given.

The slope coefficient (Equation 4.3) of 1.018 suggests the difference between logger and satellite is greater at hotter temperatures. SSTmax also demonstrated this, with a greater difference between logger and satellite SSTmax compared to SSTmean. There was a difference of 0.57°C between the average satellite SSTmax of 28.99°C (SE±0.111) and the mean SSTmax for the logger 29.56°C (SE±0.133). This difference was significant based on a paired t-test ($t$=-5.455, $DF$=10, $p$<0.001). The climatological SSTmax for the lagoon was therefore calculated as 0.57°C above the value from satellite data, at 29.4°C and was used to calculate DHWs based on logger data.

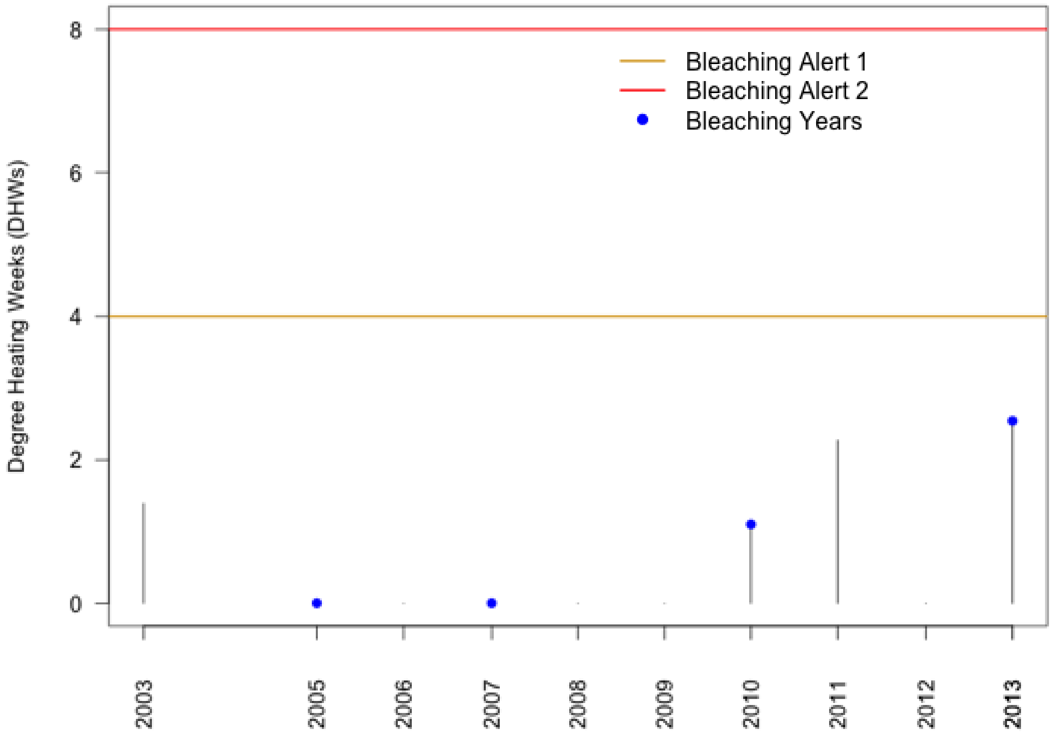


**Figure 4.8 Annual DHWs based on *in situ* temperature logger from 2003-2013**

Unlike the DHWs calculated from satellite data (Fig. 4.6) there were 4 years with periods where the lagoon temperature exceeded the 1°C threshold for a week or more, based on the temperature logger (Fig. 4.9). 2013 had the most DHWs with 2.5, followed by 2.3 DHWs in 2011, which was not a bleaching year.

In 2005, which was the only year with any recorded DHWs based on satellite data (Fig. 4.8), the logger recorded no anomaly. None of the DHWs reached the NOAA Alert 1 with 4 DHWs where bleaching is to be expected, but nevertheless bleaching occurred four times during the period the logger was in place.

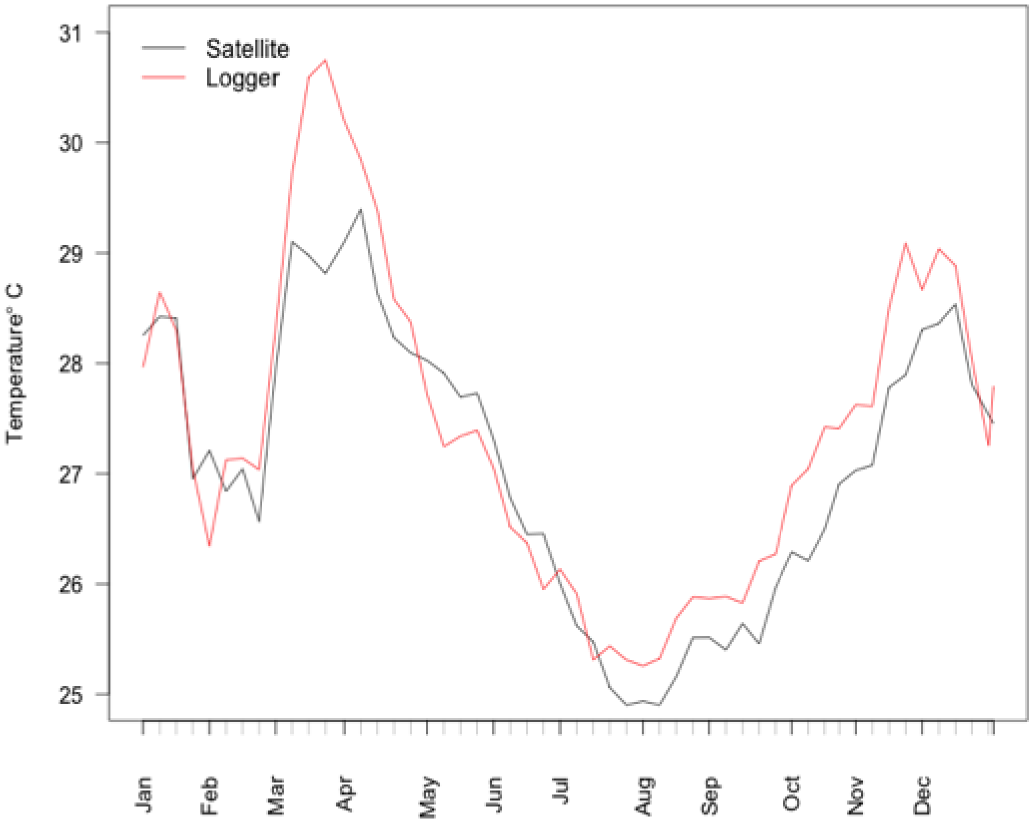


**Figure 4.9 Mean weekly water temperature measured by AVHRR satellite and *in situ* temperature logger from January to December 2013.**

The discrepancy between the temperature logger and satellite was compared for 2013, when bleaching was recorded for this study. The general pattern is for temperatures to be quite close, but in March and April 2013 the temperature recorded by the logger in the lagoon was nearly 2°C warmer than the satellite pixel offshore (Figs. 4.6 and 4.9). The peak temperature around the 20th of March 2013 registered 30.7°C, which, based on the estimate for the lagoon climatological SSTmax, means the Hotspot was 1.3°C. This was the warmest period in the lagoon recorded since the logger was installed in June 2002 (Fig. 4.6).

### 4.3.4 Bleaching response in 2013

A total of 2218 coral colonies from 24 genera were observed across all transects, with between 400 to 700 colonies being recorded each month. In April 2013 59.4% of all colonies showed signs of bleaching, with 17.2% showing complete colony bleaching (Fig. 4.10). In May the number of colonies displaying bleaching had nearly halved to 35.3% with just 2.2% being completely bleached. In June and July over 90% of colonies showed normal colouration and there were no fully bleached colonies observed.

The bleaching response and colony counts were converted into a bleaching index. The index of all colonies combined and the ten most common genera were plotted (Fig. 4.11). The combined bleaching index in April was 0.425. The genus with the highest bleaching index in April was *Pocillopora* with a value of 0.733, followed by the merulinids (previously the favids): *Dipsastraea (Favia), Favites* and *Platygyra*. The genus *Acropora* ranked 6th of the 10 genera in April (Table 4.2), below the three Merulinidae and *Porites,* with a bleaching index of 0.349. The genus with the lowest bleaching index was *Galaxea,* with a value of 0.105.

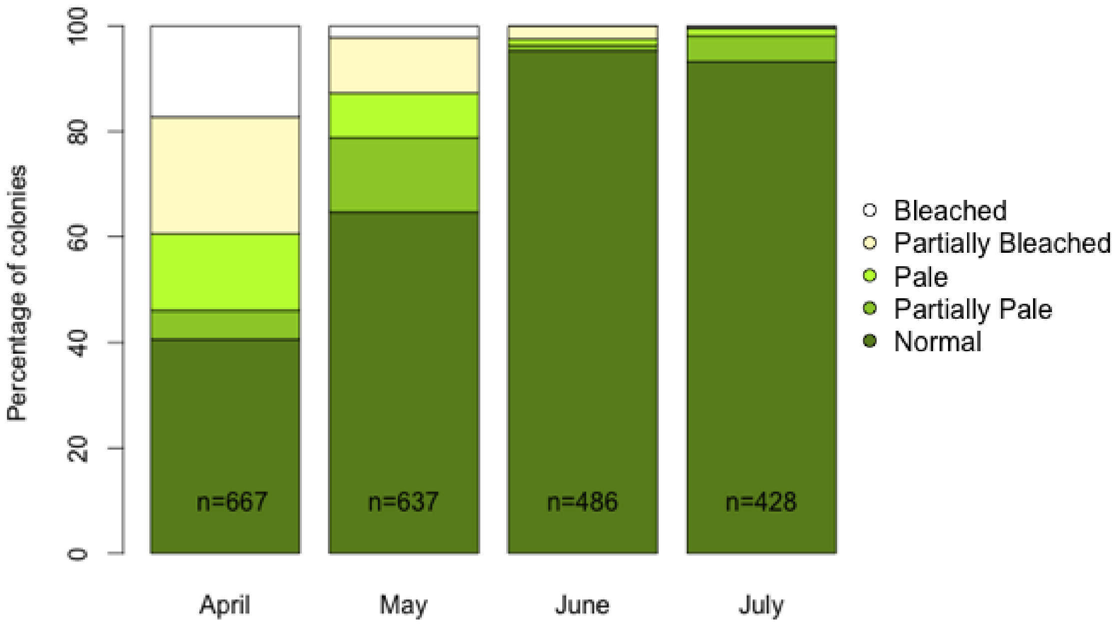


**Figure 4.10 Bleaching response of all coral colonies based on transects in April to July 2013.**

**Table 4.2. The bleaching index of the 10 most common coral genera in 2013, ranked from strongest bleaching response to least. The percentage abundance of each genus before bleaching in April is presented.**

| Genus | Rank | Bleaching index in April | % Abundance in April |
|---|---|---|---|
| *Pocillopora* | 1 | 0.733 | 20.3% |
| *Dipsastraea* | 2 | 0.636 | 6.6% |
| *Favites* | 3 | 0.605 | 5.7% |
| *Platygyra* | 4 | 0.536 | 2.1% |
| *Porites* | 5 | 0.419 | 12.0% |
| *Acropora* | 6 | 0.349 | 17.8% |
| *Pavona* | 7 | 0.300 | 2.2% |
| *Acanthastrea* | 8 | 0.271 | 1.8% |
| *Echinopora* | 9 | 0.224 | 4.3% |
| *Galaxea* | 10 | 0.105 | 18.3% |

The bleaching index values (Equation 4.1) for the entire coral community and the majority of genera were below 0.05 by June, indicating most colonies had returned to normal colouration or died (Fig. 4.11). The genus *Dipsastraea* showed the highest level of bleaching in June and July with an index value of 0.103 and 0.067 respectively, followed by *Platygyra and Favites*, which still showed a degree of bleaching towards the end of the study period.

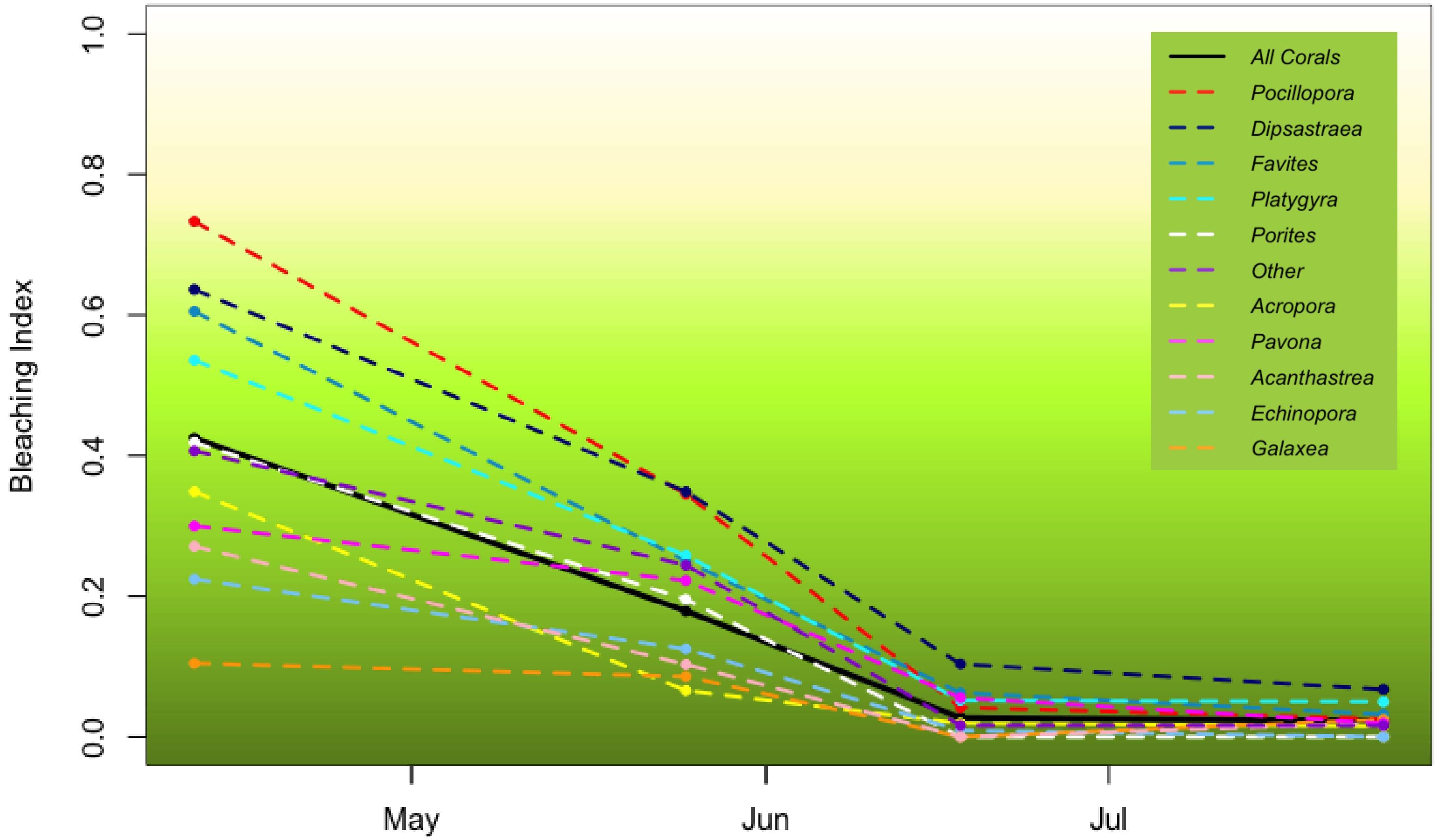


**Figure 4.11 Bleaching index of all corals (solid black line) and the 10 most common genera from transect surveys on the 12th April, 25th May, 18th June and 25th July 2013.**

### 4.3.5 Post-bleaching mortality

The abundance of live corals in transects were compared each month to infer whether post-bleaching mortality had led to a reduction in coral colonies (Fig. 4.12). In April the median colony abundance per $10m^2$ transect was 19.5 compared to a median of 12.5 colonies in July. The variation around average abundance was high (Fig. 4.12) and a Spearman's rank correlation found the abundance variation over bleaching months to be not significant ($\rho$=-0.084, $DF$=107, $p$=0.390).

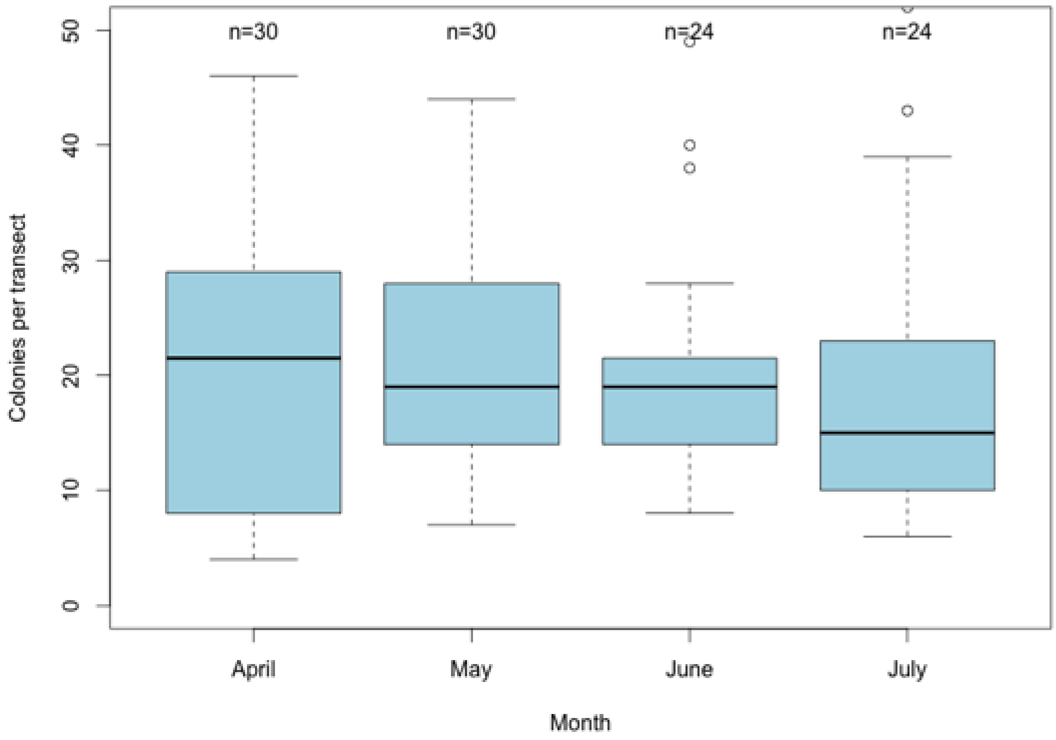


**Figure 4.12 Coral colonies per transect ($10m^2$) from April to July 2013, with '*n*' of transects in each month indicated. The black line represents the median and the box represents the upper and lower quartiles. The whiskers respresent highest and lowest values within 1.5 x interquartile range, with outlying values beyond this indicated with a point.**

In the 44 permanent quadrats there were 170 colonies from 14 genera that were observed and marked in April. When colonies were revisited in July 132 (78%) had survived the bleaching event with just 22 (13%) that had died completely and 16 (9%) that had suffered partial mortality. The colonies were pooled to family level to compare mortality. Acroporidae had the highest whole colony survival rate with 94% of colonies completely unaffected by mortality in July, followed closely by Merulinidae (90%) and Poritidae (85%) (Fig. 4.13). Only the genus *Pocillopora*, the sole representative of the family Pocilloporidae, suffered high levels of mortality, with 49% of colonies dying and a further 15% suffering partial mortality, leaving only 37% of colonies unaffected in July.

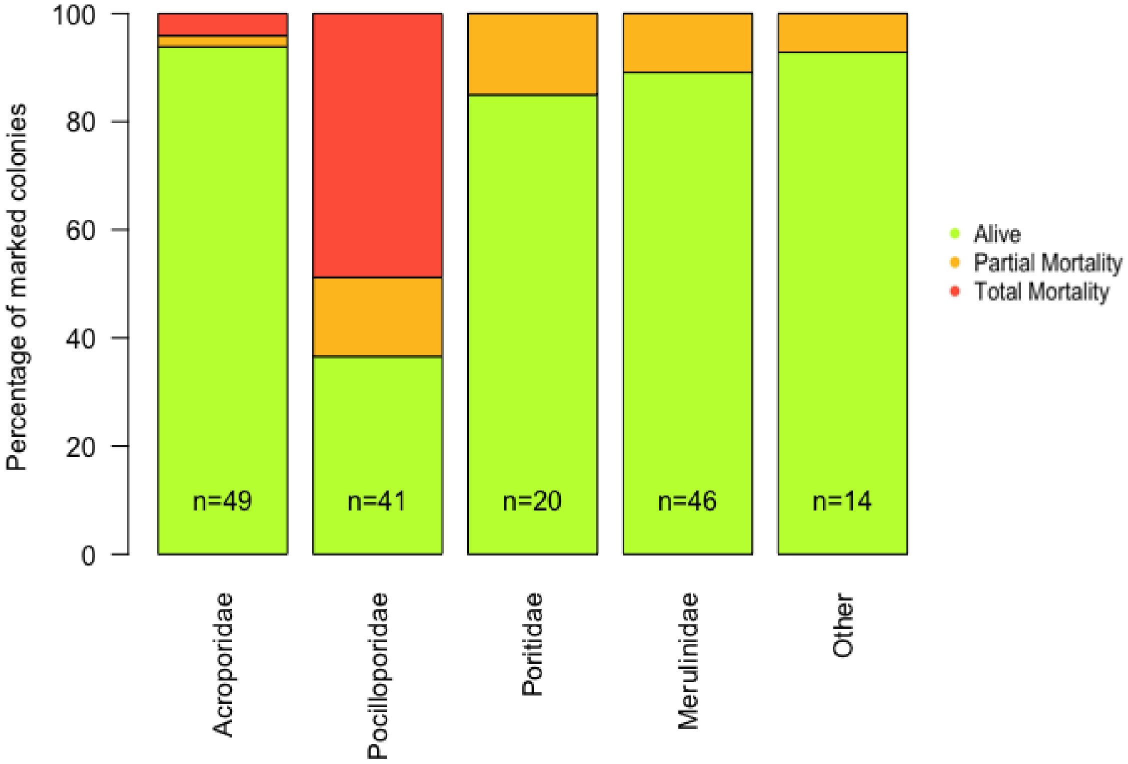


**Figure 4.13 Mortality response of marked colonies by family.**

The bleaching response of the marked colonies in April was compared with the eventual mortality in July (Fig. 4.14a). The majority of colonies with no bleaching response (normal colouration) in April were alive in July, with just 7% (4 colonies) showing partial or total mortality at the end of the study. The mortality of colonies with a partial bleaching response in April (i.e. partially pale, pale and partially bleached) was very similar to colonies with no bleaching response, with 9% (5 colonies) showing a degree of mortality, and 91% (52 colonies) that were unaffected. By contrast, colonies that show total colony bleaching in April were more likely to show mortality by July with 16% (9 colonies) showing partial mortality and 36% (20 colonies) showing whole colony mortality. The association between initial bleaching response and eventual mortality was significant based on McNemar's paired test (McNemar's $\chi^2=73.20$, $p<0.001$). However, this conclusion should be treated with caution, as approximately half of the fully bleached colonies in April were *Pocillopora*, suggesting this finding may be confounded by unequal taxonomic composition in each bleaching category.

To investigate the influence of *Pocillopora* on this result the bleaching response and mortality were compared between all colonies except *Pocillopora* (Fig. 4.14b) and *Pocillopora* by itself (Fig. 4.14c). With non-*Pocillopora* corals the mortality rate of colonies that were totally bleached in April was slightly higher than colonies that experience no bleaching or partial bleaching, but the effect was not as extreme as when *Pocillopora* was included. Correspondingly, when the relationship between initial bleaching and eventual mortality is compared for *Pocillopora* alone it can be seen that initially bleached corals experienced much higher mortality. Because of the low frequencies (<5) in the contingency table, comparing initial bleaching response and eventual mortality for other genera and *Pocillopora* by itself could not be compared using a McNemar's test.

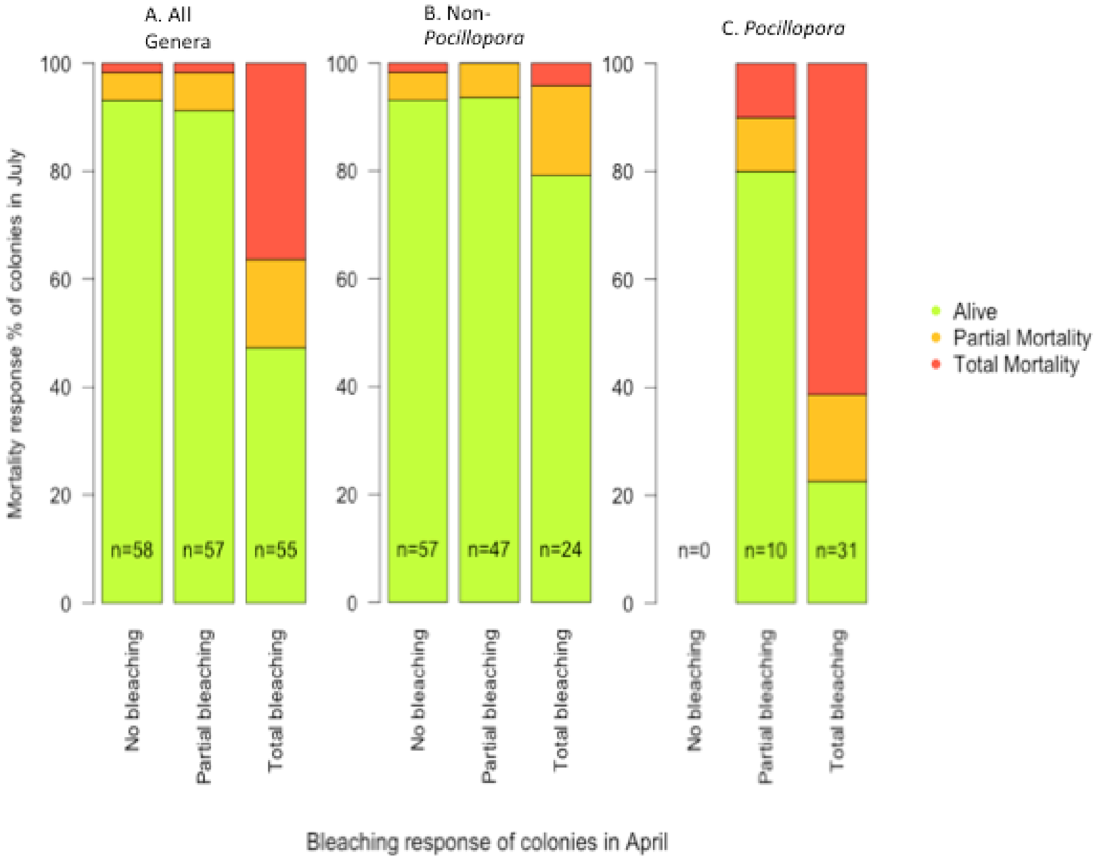


**Figure 4.14 Bleaching response and subsequent mortality of marked colonies of a) all genera, b) all non-*Pocillopora* genera and c) *Pocillopora.***

### 4.3.6 Impact of bleaching on growth rate

The growth rate of 52 juvenile colonies was investigated for 1 year after the bleaching event, until April 2014 (Fig. 4.15). The mean growth rate for all colonies was 1.58mm per month (SE±0.250). Colonies with no bleaching response (i.e. 'Normal') in April grew at a slightly higher rate of 1.70mm per month (SE±0.383). Colonies with a partial bleaching response (i.e. 'Partially pale', 'Pale' or 'Partially bleached') had a slightly lower growth rate of 1.24mm per month (SE±0.423) and completely bleached corals had a slightly higher growth rate of 1.95mm per month (SE±0.503). An Analysis of Variance (ANOVA) showed that the differences of growth rate between the different bleaching responses were not significant (*F*=0.573, *DF*=51, *p*=0.568).

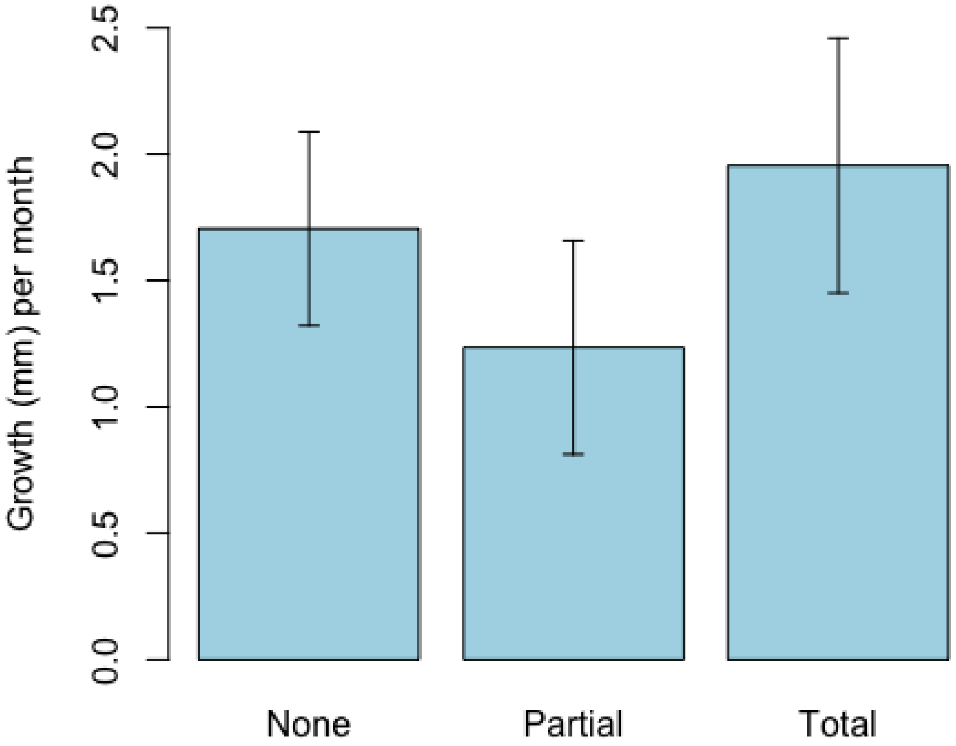


Figure 4.15 Post-bleaching growth rate as the monthly change in diameter (mm) of marked colonies with different bleaching responses in April. The error bar shows the standard error around the mean.

## 4.4 Discussion

### 4.4.1 Climate and bleaching history of Watamu

Satellite data show that the ocean climate off Watamu is close to mean global values for a coral reef area, with an average annual temperature of 27.0°C (SE±0.04) compared to a global average of 27.6°C (Kleypas *et al*. 1999). The most significant thermal stress and coral bleaching in this area took place in 1998 (Figs. 4.4, 4.5), as was the case for much of the western Indian Ocean, and globally (Ateweberhan *et al.* 2011, Eakin *et al.* 2009). The hottest month (SSTmax) in Watamu in 1998 was 30.3°C, similar to a global average in 1998 from 47 sites of 30.4°C (Lough 2000). Four of the other five known bleaching events occurred during the last decade (2003-2013) (Fig. 4.8), suggesting that bleaching frequency has increased over time. However, thermal stress, measured as either annual cumulative hotspot anomaly (Fig. 4.4) or SSTmax (Fig. 4.3), did not increase over time. Globally, both thermal stress and bleaching frequency have increased (Barton and Casey 2005, Eakin *et al.* 2009), but the western Indian Ocean has seen lower levels of thermal stress compared to other reef regions (Selig *et al.* 2010). The bleaching events in 2005, 2007, 2010, were minor, with little mortality (McClanahan, Wildlife Conservation Society, pers. comm.) and such minor bleaching during summer months were also observed in Kenya before 1998, but rarely recorded (Obura, CORDIO East Africa, pers. comm.). Hence it seems that 1998 was the most significant bleaching and thermal stress event experienced by sites in Watamu during the past 30 years and that other stress has been occasional, but minimal.

Remotely sensed Sea Surface Temperatures (SSTs) on reefs have allowed coral reef scientists to understand more about how thermal stress results in bleaching (Liu *et al.* 2003). Based on the nearest satellite data for Watamu, the Degree Heating Weeks (DHWs), which are the main indicator used to predict bleaching events (Liu *et al.* 2003, Eakin *et al.* 2009), do not match with historical bleaching events other than 1998 (Fig. 4.5). To investigate this discrepancy, the available *in situ* temperature logger data were compared to the satellite information. The weekly temperatures recorded by logger and satellite were well correlated (Figs. 4.6 and 4.7), but certain features were not matched between the two water temperature recordings. The logger recorded slightly higher temperatures than the satellite, but the difference was not significant and was within the 0.35°C margin of recording error reported by the manufacturer (Section 4.2.1). Two key features of the thermal profile relating to coral bleaching, which were not accurately predicted by the satellite, were the SSTmax and seasonal variation, both of which were higher based on the logger. These parameters are important for predicting bleaching (Donner 2011) and estimating the degree of thermal acclimatisation the corals have experienced (McClanahan *et al.* 2007a). In 2013, the difference between the temperature recorded in the lagoon by the logger and the off-shore satellite was nearly 2°C, which explains why the satellite did not record any DHWs for 2013. This observation highlights how localised some thermal stress and bleaching can be (Selig *et al.* 2010), and during 2013, although extensive bleaching was recorded in Watamu, there was little bleaching elsewhere in Kenya (B. Cowburn, pers. obs).

Bleaching events in Watamu were not explained well by DHWs from either the satellite or the logger (Figs. 4.5 and 4.8). Assuming the logger is recording accurately, this temperature profile should describe the temperatures the corals in the lagoon are experiencing. However, no DHWs were recorded in 2005 and 2007 when bleaching was observed and DHWs in 2003 and 2011 occurred without any bleaching occurring. None of the annual DHWs recorded post-1998 reached the threshold of 4 DHWs, which is the level that NOAA release bleaching warnings (Eakin *et al.* 2009). It could be that the bleaching events were triggered by other factors, such as light intensity or pollution (Fitt et al. 2001, Baker et al. 2008), although Berkelmans (2009) found the main factors explaining variation in bleaching intensity are elevated temperature and the time exposed to elevated temperature (Berkelmans 2009). Alternatively, it could be that the climatology used to predict the bleaching threshold is inaccurate (Lough 2000). The climatology used in this study, and by NOAA, is based on the late 1980s and early 1990s, by which time there had already been an increase in tropical SSTs (Eakin *et al.* 2009) and a major bleaching event for many areas in 1987 (Glynn 1993). This may explain why corals bleached at DHWs below the expected threshold of 4 and in some cases without any DHWs, because the climatological baseline was artificially increased (Obura and Mangubhai 2011). A final explanation could be that the bleaching threshold itself is not static, as assumed, but changes based on the acclimatisation and adaptation of the coral community (Ware *et al.* 1996, Fitt *et al.* 2001).

### 4.4.2 Bleaching impact on the coral community in 2013

In April 2013, approximately three weeks after the peak water temperature (Fig. 4.9), 59% of corals showed some degree of bleaching response (Fig. 4.10). Bleaching was observed in the majority of coral genera, and in different patch reefs across the lagoon. Despite widespread bleaching, the mortality of corals was limited, with the majority of corals recovering normal colouration by June, three months after the peak thermal stress. Most of the corals that died, belonged to the genus *Pocillopora,* with other coral families having less than 10% mortality (Fig. 4.13). Minor non-lethal bleaching events such as this are not uncommon (Obura 2009), but are not reported on as often as major bleaching events with high levels of mortality (Suggett and Smith 2010). As such, observations from this event provide a useful insight into the impacts of minor bleaching.

Detecting mortality after a bleaching event is an important feature of any bleaching monitoring programme or study of bleaching impact, as this is the most severe outcome for the corals (McClanahan *et al.* 2009). In this study two methods were used, direct observation of mortality rates of marked corals (Fig. 4.13) and inference through decreases in coral colony abundance in random transects (Fig. 4.12). Both methods suggested a similar mortality rate, with 13% mortality based on marked corals and 16% based on coral abundance in transects. However, despite a step-wise reduction in mean abundance as the bleaching events progressed, when analysed statistically the reduction in colony abundance was not significant because of the variation in abundance between transects. Other studies (e.g. McClanahan *et al.* 2001) have estimated mortality through counting dead colonies after a bleaching event, however, this tends to underestimate true mortality rates, as dead corals are quickly overgrown by turf algae making them less easy to visually detect (Obura 2001, McClanahan et al. 2004a). Random transects to compare coral abundance or coral cover before and after bleaching can detect significant trends in major events (e.g. Zahir 2000), but may not perform as well when mortality is less severe, as in this study. The 16% mortality value may not be statistically significant, but it may be biologically significant, especially if such events occur frequently (Sheppard 2003). Using marked corals allows confident estimation of mortality rate, as well as being able to more reliably estimate partial tissue-loss and any sub-lethal impacts of bleaching on the colony as well.

The initial bleaching response in *Pocillopora* was linked with the eventual survival of the coral, with the most severely bleached colonies being more likely to die (Fig. 4.14b). However, in other genera this trend was not as clear, with only marginally higher mortality rates for colonies that totally bleached in April compared to those that showed no signs of bleaching, suggesting that bleaching may not negatively affect the survival of these corals in the short term. In other bleaching events sub-lethal impacts of coral bleaching have been observed; this includes reduced reproduction (Baird and Marshall 2002), growth (Porter *et al.* 1989), and increased susceptibility to disease (McClanahan *et al.* 2004b). The impact of bleaching on reproduction was not tested for in the corals in Watamu, but growth rate was found to be similar in corals that had bleached compared to those that had not (Fig. 4.15) and no disease was observed. This suggests that corals (except for *Pocillopora*) sustained very little negative impact from the bleaching event in 2013.

Bleaching without mortality is a well-recognised phenomenon, with mortality thresholds for corals reported as 0.2-2°C above bleaching thresholds (Berklemans *et al.* 2009). Because of the link between bleaching, stress and mortality, bleaching has been considered by some as a pathological condition (e.g. Douglas 2003). However, others have noted that bleaching may allow normal function of the coral organism to continue near their upper thermal limits, and that mortality and other deleterious impacts are the result of 'extraordinary bleaching', beyond the mitigation capacity of bleaching and is distinct from regulatory bleaching (Fitt *et al.* 2001, Obura 2009). The lack of obvious negative impacts on the majority of corals that bleached in 2013 supports the idea that bleached corals are not necessarily unhealthy.

Interestingly the *Acropora* colonies did not bleach or suffer mortality as severely as several merulinid (favid) genera or *Porites* (Table 4.2, Figure 4.11), which contradicts the widely observed tendency of *Acropora* to be one of the most sensitive genera to thermal stress, along with *Pocillopora* (Loya *et al.* 2001). The 'standard' pattern of bleaching intensity, where branching corals are considered sensitive and massive corals are more resistant, was widely observed in 1998, and other major bleaching events (e.g. Brown and Suharsono 1990, McClanahan *et al.* 2007b). However, more recently there have been examples where repeated bleaching can alter the bleaching response of *Acropora* (Guest *et al.* 2012) and the suggestion that these branching corals can acclimatise faster than massive corals (Maynard *et al.* 2008). There is evidence to suggest these changes in bleaching sensitivity for corals occur at a physiological level (Grottoli *et al.* 2014), but it is important to note that it may also be the result of the selective mortality of all sensitive species or colonies within the genus

(Berklemans *et al.* 2009), hence changing the overall sensitivity of the genus (Donner *et al.* 2009).

### 4.4.3 Conclusions and future considerations

The thermal history of Watamu over the past 30 years shows that 1998 was the most significant acute thermal stress event for this area. Since 1998 minor non-lethal bleaching events have occurred, with the most severe thermal stress, based on temperature logger data, occurring in 2013. The negative impacts of thermal stress on the coral community in 2013 appear to be minimal, suggesting that the majority of bleaching observed on the reef was regulatory, not pathological (Obura 2009). In other areas, it has been noted that past bleaching can allow corals to acclimatise to thermal stress (e.g. Rowan *et al.* 1997). Evidence of acclimatisation and/or adaptation of corals in Watamu is suggested by the low susceptibility of *Acropora* to bleaching in 2013. The several minor bleaching events after 1998 may have conferred corals in Watamu with a degree of resistance to future bleaching (Ware *et al.* 1996). To test this theory, the bleaching and mortality response of corals would need to be investigated during the next major bleaching event, by comparing the mortality rate and thermal stress to the 1998 event, in order to determine the degree of adaptation and acclimatisation the corals have undergone (Maynard *et al.* 2008).

Predicting the future of coral reefs in the light of increasing thermal stress requires an understanding of how quickly corals can cope with rising temperatures through adaptation and acclimatisation (Donner *et al.* 2009b). However, the long-term trajectory of reef communities will largely depend on the frequency and severity of future lethal bleaching events and the ability of reefs to recover between events (Sheppard 2003). Post-1998 many reefs around the Indian Ocean saw encouraging recovery of coral cover and diversity (Ateweberhan *et al.* 2011), with recovery to pre-1998 coral cover in 5 years in some parts of the Maldives (Zahir *et al.* 2005). In Watamu, the recovery has been non-existant; with significantly lower coral cover during the 15 years after the mass bleaching in 1998, when compared to pre-1998 levels (Chapter 3). Slow recovery of reefs, such as Watamu, may result from either human or natural factors depressing the resilience of these systems (as discussed in Chapter 3), and highlights the importance of identifying and protecting naturally resilient reefs and protecting less resilient reefs from other anthropogenic stressors (Pandolfi 2015). Further loss of coral for Watamu in the imminent future may lead to a phase-shift and severe degradation of the ecosystem's function (Graham *et al.* 2008, Beldade *et al.* 2015). Ultimately, the future bleaching impacts on reefs will be determined by the earth's unpredictable climatological response to higher concentrations of greenhouse gases and society's ability to control emissions over the next century (Donner *et al.* 2009, Gattuso et al. 2015).

**Plate 5. Measuring resilience indicators on a reef on Pulau Enggano, Sumatra (Photo: B. Cowburn)**

# Chapter 5. Predicting coral reef resilience to bleaching and understanding the drivers of resilience in six Indian Ocean locations

## Abstract

Predicting the impacts of future thermal stress on coral reefs is needed in order to plan conservation objectives for a century with increased mass coral bleaching and climate change.  Coral reef research has identified a range of factors that influence a reef's resilience to future mass bleaching events, which are used as indicators in assessments to inform conservation management. However, with the complexity of resilience as an ecological process and limited application of the assessment in the field, it is not clear how well the current model can inform decision-making. This study presents data from resilience assessments carried out in six locations across the Indian Ocean; Watamu and Kisite (Kenya), Vamizi (Mozambique), Kuramathi (Maldives) and Tikus and Enggano (Sumatra). Eight resilience indicators were compared between sites and locations to identify the components of resilience found/lacking on the different reefs. The variation in resilience, resistance and recovery scores between different reefs is explored and explanatory variables are used to investigate which overarching factors drive these patterns. There was no relationship between resistance and recovery, suggesting that these resilience components should be considered separately when interpreting resilience assessments. Several explanatory variables showed significant relationships with resistance and recovery, providing useful insights into how resilience of

these is influenced by past climate, natural conditions and human pressures. Secondary information gathered about the different locations, including findings in this thesis from Watamu, matched resilience patterns observed during these snapshot assessments, indicating that the current resilience model has a degree of explanatory power. However, more research is needed into specific ecological processes to refine the model to reflect interactions and thresholds that exist within reef resilience.

## 5.1 Introduction

### 5.1.1 Resilience theory and coral reefs

Resilience theory in ecology is based on observations of stable states within ecosystems (Holling 1973). Holling (1973) noticed predictable community structures in freshwater systems that would rapidly switch between 'stable states' along disturbance gradients. This led to the idea of phase-shifts between stable states, and the definition of resilience being the ability of an ecosystem to maintain and/or return to its original stable state after disturbance (Holling 1973, Nyström *et al.* 2008). Resilience theory was first used in coral reef ecology to describe the failure of Jamaican reefs to recover from storm damage and the evolution of a new macroalgae-dominated stable state on these reefs (Hughes 1994). Taking a global view of different reef states, Bruno *et al.* (2009) claimed that reefs cover a continuum of conditions with no obvious coral-dominated or macroalgal-dominated stable states. However, Nyström *et al.* (2008) argued that such changes take time and that a phase-shift can occur before there is an observable regime shift (see also Mumby *et al.* 2014 & Spalding and Brown 2015). Direct evidence for resilience theory operating on coral reefs comes from Mumby *et al.*'s (2007b) work where they were able to demonstrate critical thresholds in herbivorous fish biomass for predicting a trajectory towards either coral- or macroalgal-dominated states.

After the global mass-bleaching and mortality of corals associated with the 1998 El-Nino Southern Oscillation (ENSO), reef scientists began to use resilience theory to explain differences in mortality and recovery of reefs in response to this dramatic disturbance (West and Salm 2003). A wide variety of factors were observed to be associated with reef resilience (Obura 2005), such as variation in bleaching susceptibility of corals (Loya *et al.* 2001) and recruitment (Edwards *et al.* 2001). Hence in 2009, the International Union for the Conservation of Nature (IUCN) compiled a list of potentially important resilience indicators and a methodology for assessing reef resilience to better predict the impacts of climate stress and coral bleaching on reefs in the future (Obura and Grimsditch 2009).

### 5.1.2 Application of resilience theory in reef research and management

The resilience assessment protocol produced by the IUCN was intended to be used by managers to inform conservation decision-making for future climate disturbance (Obura and Grimsditch 2009), but to date has had little application in real life scenarios (Maynard *et al.* 2015). There are a number of challenges in carrying out resilience assessments and making accurate resilience predictions based on these, including: collecting and interpreting multiple indicators (Maynard *et al.* 2012); uncertainty of the relationship between indicators and resilience (Nyström *et al.* 2008); limited snapshot view of reef condition in the wider dynamic trajectories of coral reefs (Knowlton and Jackson 2008); and uncertainty of where significant thresholds for resilience lie (Anthony *et al.* 2015).

Using the IUCN resilience assessment across a wide range of sites in Indonesia, Maynard *et al.* (2012), found some indicators were better at predicting response to bleaching in 2010 and eliminated indicators that had less explanatory power. McClanahan *et al.* (2012) took this work further by prioritising just 11 indicators based on expert opinion, scientific evidence and the feasibility of data collection. In addition to this, they weighted the indicators according to perceived importance, recognising that different factors have more influence on reef resilience and ability to cope with acute thermal stress than others (McClanahan *et al.* 2012).

There is a growing need to 'operationalize' resilience theory so that it can be used by non-scientists in conservation planning and management (Maynard *et al.* 2015, Anthony *et al.* 2015). Despite the improvements to the original IUCN protocol mentioned above, there are still relatively few frameworks available for interpreting resilience indicators (Maynard *et al.* 2012). In addition, the current assessment does not reveal the underlying causes or drivers of different resilience potential observed between reefs (Jouffray *et al.* 2015). For this chapter, resilience assessments were carried out with the aim of providing an interpretation framework for understanding the patterns and underlying drivers of reef resilience, and hence suggest potential management solutions.

### 5.1.3 Objectives of this study

In this study, resilience indicators were collected using the most up to date refinements and improvements to the original IUCN protocol (McClanahan *et al.* 2012, Maynard *et al.* 2015). The data were collected in six locations stretching >7000km across the Indian Ocean from Mozambique to Sumatra. Such a wide geographical range probably does not reflect a normal management scenario where resilience would be assessed in a single location or across a region (e.g. Maynard *et al.* 2012). Rather, this ocean-wide assessment aimed to encompass a wide range of reefs under different climatological (see Section 1.7), biogeographical, physical and human scenarios to understand the broad patterns of resilience variation in a diverse sample of Indian Ocean reefs. The specific objectives of this chapter include:

- Estimating the resilience of different reefs using the current protocol and refinements;
- Investigating how different components of resilience (resistance and recovery) are related;
- Interpreting resilience assessments using the relationships between different resilience indicators and the explanatory power of individual resilience indicators;
- Explore how broad-scale human, natural and climatic features of reef sites drive variation in the estimated resilience;
- Recommend improvements and refinements to current resilience assessments and their interpretation.

## 5.2 Methods

In this study data were collected on the ecological and environmental parameters relating to the condition of reefs found in six locations, in four tropical Indian Ocean nations; Kenya, Mozambique, Maldives and Indonesia (Sumatra) (Fig. 5.1). Data were collected either in the field or through remote sensing (Table 5.1). Some of the data collected were used to produce resilience indicators (response variables) and other data were converted into potential drivers of resilience (explanatory variables).

Table 5.1: Summary of variables by data collection method

| | **Field data** | **Remotely sensed data** |
|---|---|---|
| **Response variables** | - Herbivore biomass<br>- Resistant corals<br>- Coral diversity<br>- Juvenile coral abundance<br>- Macroalgae cover<br>- Sediment cover | - Nutrients<br>- Chronic thermal stress |
| **Explanatory variables** | - Reef zone<br>- Rugosity<br>- Depth<br>- Protected status | - Human population<br>- Acute thermal stress<br>- Distance to mainland |

Each location differed in its reef structure, oceanography and human pressure, and was at least 150km away from the next nearest location. A brief description of each location based on field notes and local knowledge is given here;

- Watamu (Kenya) (see also Chapters 2, 3 and 4): A section of continental fringing reef near the northern end of Kenya's 200km long reef system. Although all the reefs are either fully protected in Watamu Marine National Park (MNP) or partially protected by the wider Watamu-Malindi Marine National Reserve (MNR), there is high human pressure on marine resources and habitats generally in this area. In addition to the 6 lagoonal reefs discussed in earlier chapters of this thesis, 4 additional fore-reef sites exposed to oceanic conditions were surveyed and included for this location. The sites in Watamu were visited at least once every month between 2011-2014 and data for this chapter were collected over 2 weeks in August 2013.

- Kisite (Kenya): Sites in Kisite were located on reefs fringing small islands (<10km$^2$) in an archipelago at the southern end of Kenya's continental reef. Sedimentation and outflow from a nearby river was apparent in sites in the north and west of the area, but the southern offshore site had good water quality. Four sites are fully protected by Kisite MNP, and two are partially protected by Mpunguti MNR. The two northern sites, located near the largest and the only inhabited island in the archipelago are unprotected. Human pressures in Kisite are similar to Watamu, but the area is less densely populated. This site was visted by the author 2-3 times annually between 2011 and 2014, with data collection taking place between the 11-18th February 2014
- Vamizi (Mozambique): Vamizi is a low island (i.e. of coral origin) with extensive fringing reef, in the Quirimbas Archipelago, which stretches 200km along Mozambique's northern coastline. Terrestrial and human pressure increases nearer the mainland. Most sites were located on the leeward slope or a back-reef habitat on the northeast of the island. There is hardly any human impact on Vamizi Island itself, being managed by an eco-resort, who also set up the local community no-take reef conservation

area, which contained six of the eight sites in this location. This site was only visited during data collection between 13-20th of April 2014.

- Kuramathi (Maldives): The Maldives consists of a double chain of atolls rising from a submarine plateau, located in the central Indian Ocean >500km from the Indian sub-continent. Sites at Kuramathi were located on the reef slope, flat and lagoon near two inhabitated coral cays on the southern edge of a small (10km wide) atoll structure on the western chain of atolls just to the north of Ari atoll. Reef sites on the slope were exposed to rough conditions, especially during the west monsoon winds from May until October. Reefs at this location were near an inhabited island called Rasdhoo and a resort island called Kuramathi. Fishing was permitted around Rasdhoo, but banned around the resort. This site was only visited during data collection between the 15-30th of October 2014.
- Tikus (Sumatra): Located on and around an uninhabited coral cay 3km offshore from the Sumatran mainland and the city of Bengkulu. The reefs surveyed at Tikus were located on the sheltered leeward slope of the reef structure. Terrestrial influences and high human impact were obvious, with fishing, pollution from the mainland and physical damage to the reef being observed during fieldwork. This site was only visited during data collection between the 10-15th of September 2013.

- Enggano (Sumatra): Enggano is a high island (i.e. has terrestrial geology) located 100km South-West of the Sumatran mainland. The reefs at Enggano were located in sheltered locations in predominately lagoonal and leeward conditions. Although it is a large island (~400km$^2$), it is sparsely populated, with much of it being covered in rainforest. The low population on Enggano and its isolation from the mainland mean human impact on reefs is low, although the area has no formal protection. This site was only visited during data collection between the 5th-9th of September 2013.

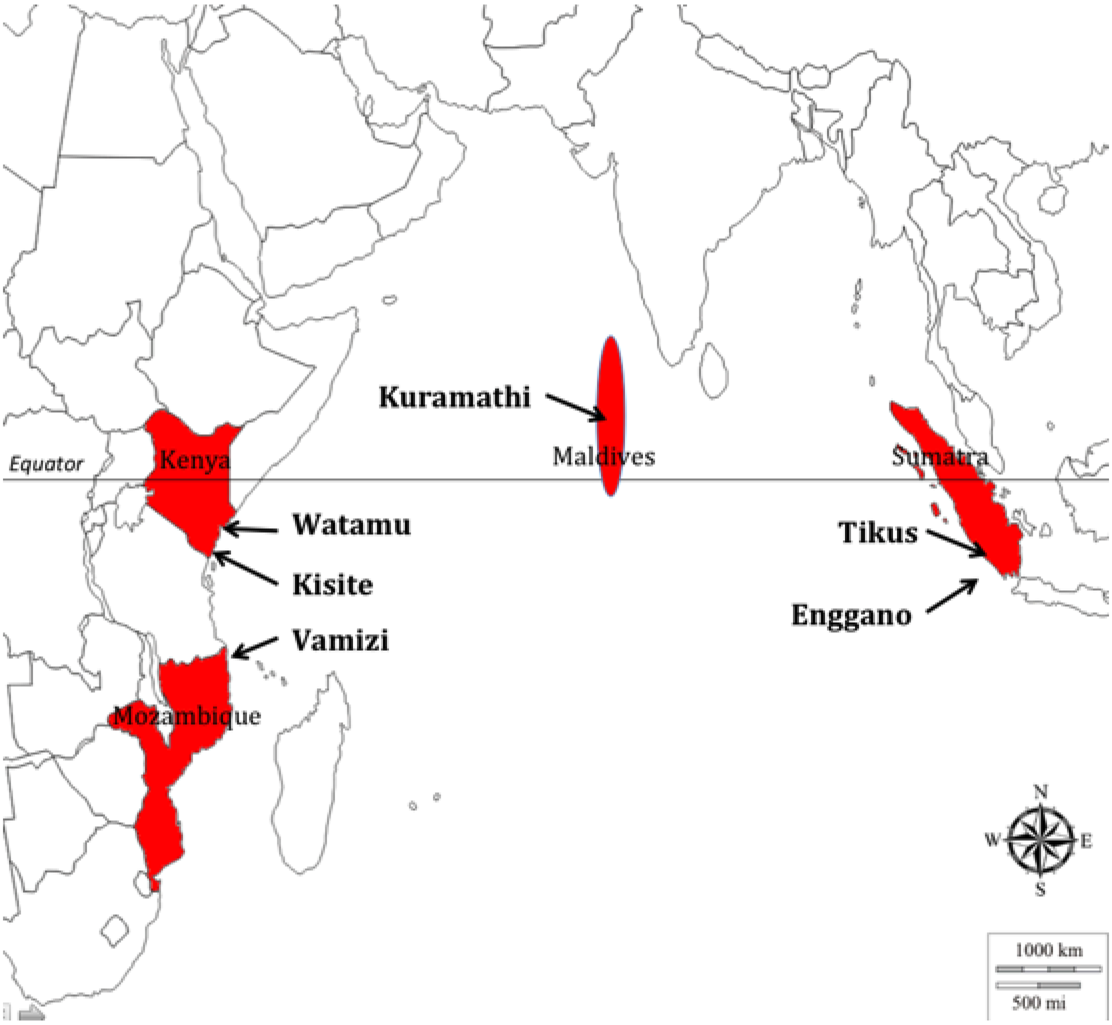


**Figure 5.1. Map of the Indian Ocean with the six locations indicated where data were collected for this study; Watamu and Kisite (Kenya), Vamizi (Mozambique), Kuramathi (Maldives) and Tikus and Enggano (Sumatra).**

### 5.2.1 Field methods

Field methods to collect resilience indicators on the reef were adapted from the IUCN's resilience assessments for coral reefs (Obura and Grimsditch 2009). Assessments were carried out in a spatially structured hierarchy with transects being clustered into sites and sites being clustered into a location (Location>Site>Transect). There were six locations containing 40 reef sites (Fig. 5.2 & Table 5.2). At each site all parameters were collected in 3 or 4 transects, with a total of 129 transects from the 6 locations (except for 1 site at Kuramathi and 1 at Vamizi where only 2 transects were collected).

For each transect the following parameters were collected on repeated passes over the transect line in the field; fish biomass, adult coral community and benthic structure. All fish longer than 10cm were counted and identified to species level in a 40m by 5m (200m$^2$) area. Each fish's length was estimated and placed into 10cm wide size-classes (i.e. 10-20cm, 20-30cm…). All adult corals (>10cm) were identified to genus level in a 20m by 1m (20m$^2$) belt transect. Four quadrats were placed at regular intervals along the 20m$^2$ belt transect, in which all juvenile corals (<10cm) were counted and identified to genus level. Benthic cover was recorded by photographing the quadrats and analysing the images using CPCe (Kohler and Gill 2006). Coral cover was not considered as a resilience indicator in this study, but was recorded from the photo-quadrats, and compared with the final resilience scores for each site.

Raw data were converted into resilience indicators using methods similar to those used in other resilience studies (e.g. Maynard *et al.* 2015). The methods below describe how a value is reached for each replicate (i.e. transect or quadrat). During the analysis of these variables the site mean of each is used.

- **Herbivore biomass**: Each fish counted in transects was identified to species and the length estimated to the nearest 10cm. Length estimates were converted to biomass using Equation 5.1 and 'a' and 'b' coefficients were obtained for each species from Fishbase (Froese *et al.* 2014). Species were classified to guild (Samoilys and Carlos 2000, Green and Bellwood 2009) and the biomass for all herbivorous guilds was combined for each transect. Length estimates were converted from kg per transect to kg per 1000m$^2$.

**Equation 5.1. Converting fish length estimate to biomass**

$$Weight = a \times Length^{b}$$

- **Resistant corals:** Coral genera considered susceptible to thermal stress are *Acropora, Montipora, Seriatopora, Stylophora, Pocillopora* and branching *Porites* (Loya *et al.* 2001). All other genera were defined as resistant to bleaching (Maynard *et al.* 2012). The percentage of adult (>10cm) resistant coral colonies was used as the resilience indicator.
- **Coral diversity:** Simpson's index of genus diversity was calculated for all adult (>10cm) corals in each transect (Maynard *et al.* 2015).

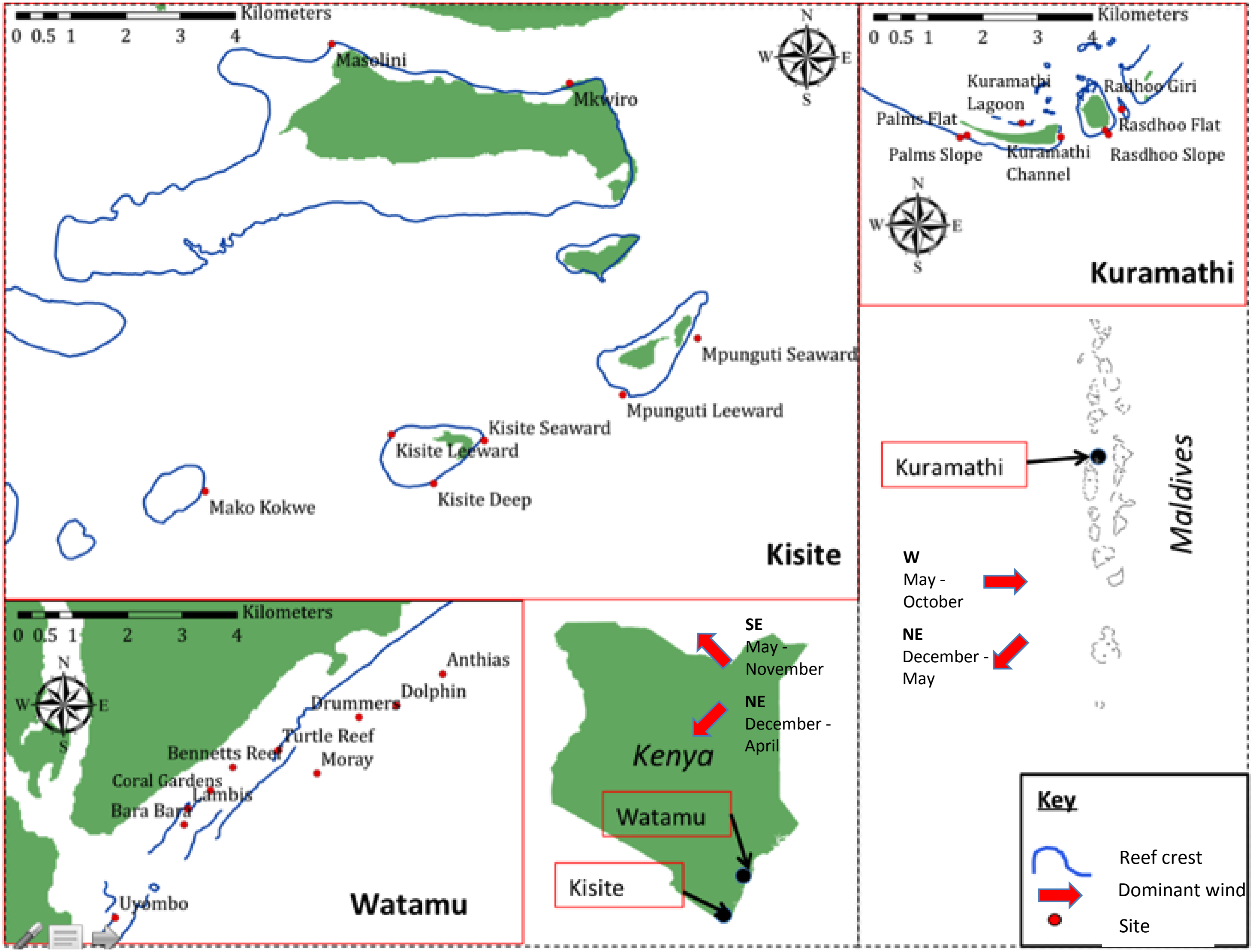
**Equation 5.2. Simpson's index of coral genus diversity**

$$Simpson's\ index = \frac{Total\ coral\ abundance\ \times\ (Total\ coral\ abundance - 1)}{\sum Abundance\ of\ each\ genus\ \times\ (Abundance\ of\ each\ genus - 1)}$$

- **Juvenile coral abundance (Recruitment):** The average number of juvenile corals (<10cm) counted in quadrats along each transect was used as a proxy for recruitment (Obura and Grimsditch 2009). Juvenile abundance was expressed as colonies per m$^2$.

- **Macroalgae cover:** The percentage of fleshy macroalgae covering the benthos was estimated from $1m^2$ photoquadrats using CPCe (Kohler and Gill 2006).
- **Sediment cover:** The percentage of loose substrata (sand and rubble) covering the sea floor was estimated from photoquadrats using CPCe. Note this variable may not represent all sedimentation impacts on the reef. Sedimentation, in the sense that was used by McClanahan et al. (2012), includes the rate of sediment being deposited on live benthos, which could not be assessed in the timeframe available for fieldwork.

**Figure 5.2** ***(cont. overleaf)*****. Maps of each location with sites marked. The position of the crests of major reef formations and the dominant wind direction(s) are indicated for each location. Insets of Kenya, Maldives, Sumatra and Mozambique with locations indicated.**



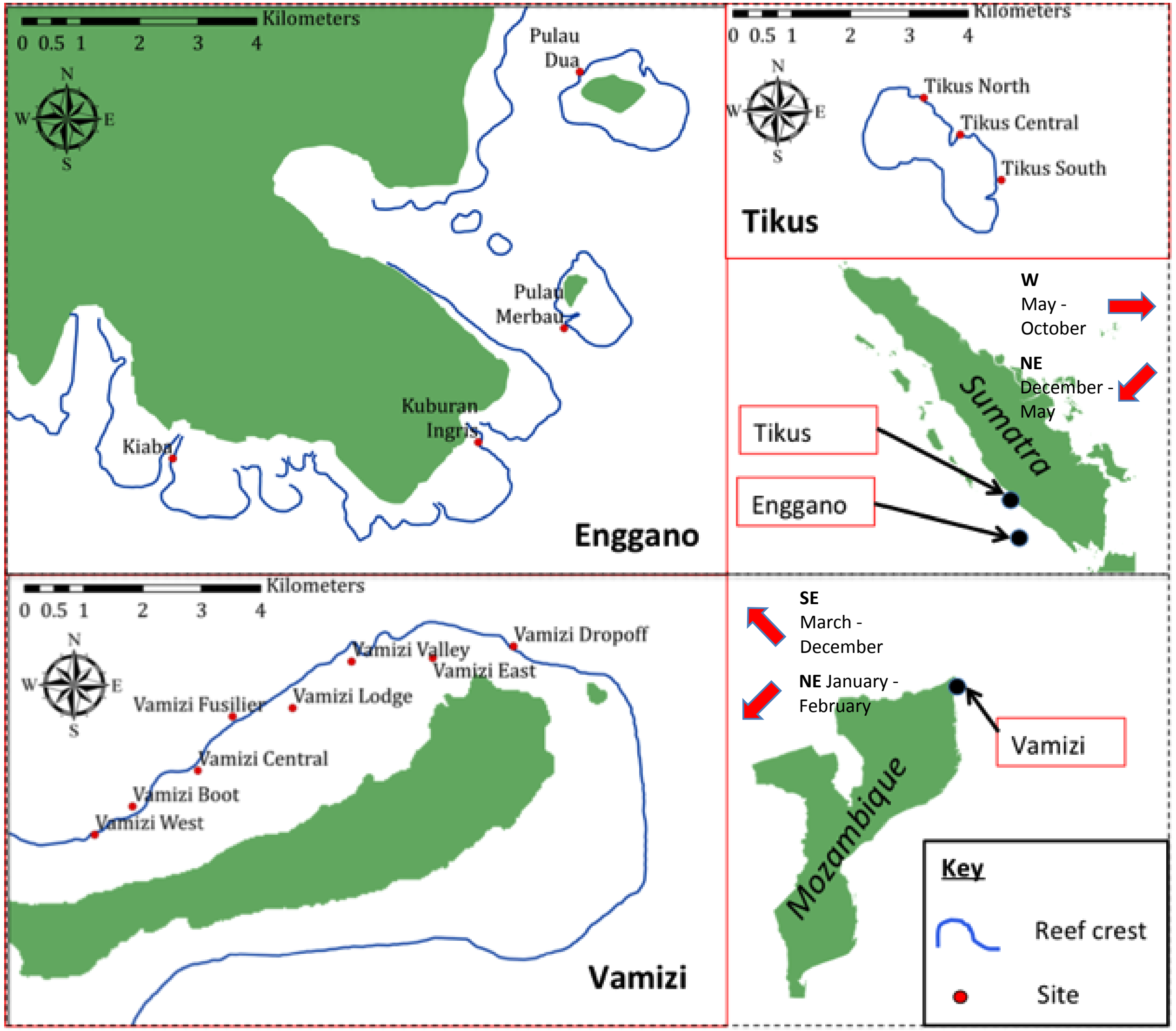

Kilometers
0 0.5 1 2 3 4
N
W
E
S
Pulau Dua
Pulau Merbau
Kuburan Ingris
Kiaba
Enggano
Kilometers
0 0.5 1 2 3 4
Tikus North
Tikus Central
Tikus South
Tikus
W
May - October
NE
December - May
Sumatra
Tikus
Enggano
Kilometers
0 0.5 1 2 3 4
Vamizi Dropoff
Vamizi Valley
Vamizi East
Vamizi Fusilier
Vamizi Lodge
Vamizi Central
Vamizi Boot
Vamizi West
Vamizi
SE
March - December
NE January - February
Vamizi
Mozambique
Key
Reef crest
Site

Table 5.2. Locations by country with number of sites and transects

| Country | Location | Coordinates | No. of sites | No. of transects |
|---|---|---|---|---|
| Kenya | Watamu | 3°23’30”S, 40°00’00”E | 10 | 32 |
| Kenya | Kisite | 5°40’30”S, 39°20’30”E | 8 | 27 |
| Mozambique | Vamizi | 11°00’00”S, 40°40’00”E | 8 | 23 |
| Maldives | Kuramathi | 4°15’45”N 73°00’00”E | 7 | 20 |
| Sumatra | Tikus | 3°50’00”S, 102°10’40”E | 3 | 12 |
| Sumatra | Enggano | 5°29’00”S, 102°23’00”E | 4 | 15 |

Potential drivers of resilience were collected in the field and included depth, rugosity, protected status and zone (Table 5.1). Rugosity was visually scored from 1-5 using a scale described by Polunin and Roberts (1993). Protected status was defined as being ‘open’ or ‘closed’ to fishing. Closed status refers to any reef with a no-take policy for the extraction of fish and other marine life, found within the boundaries of a government-designated marine protected area (MPA) or community reserve. Open status refers to any reef found within an area where resource harvesting is permitted or partially permitted. Twenty reefs were open to fishing and twenty were closed (Table 5.3).

Zone was classified into five categories based on the reef’s location relative to the reef crest and predominant wind and wave exposure (Fig. 5.3). ‘Lagoon’ and ‘Flat’ zones were located on the sheltered landward side of the reef crest, with lagoon reefs being found in water deeper than 2m, whereas a flat was defined as being shallower than this (<2m). ‘Channels’ were defined where a deeper section of water cut across the reef crest, often associated with strong currents. A ‘Leeward’ slope was defined as a reef slope protected from dominant wave and wind exposure, whereas a 'Seaward' slope was facing oceanic conditions and exposure. When testing for multicollinearity between explanatory factors using repeated ANOVAs and regressions (for numeric variables), Zone was significantly correlated with Rugosity ($F$=5.47, $DF$=39, $p$=0.002) and Depth ($F$=12.62, $DF$=39, $p$<0.001), so these variables were not used in further analyses. Zone was therefore assumed to explain a degree of the variation in resilience driven by rugosity, depth and other variables not measured in this study such as light, current, local nutrient flows (Mumby *et al.* 2012, Houk *et al.* 2014) and local temperature regime (Oliver and Palumbi 2011).

**Table 5.3. The number of reef sites by location in different categories of the two explanatory variables of resilience fieldwork, open or closed to fishing, and the reef zone**

| **Explanatory Variable (Category)** | **Watamu (Kenya)** | **Kisite (Kenya)** | **Vamizi (Mozambique)** | **Kuramathi (Maldives)** | **Tikus (Sumatra)** | **Enggano (Sumatra)** | ***Total*** |
|---|---|---|---|---|---|---|---|
| ***Fishing*** | | | | | | | |
| Closed | 6 | 4 | 6 | 4 | 0 | 0 | *20* |
| Open | 4 | 4 | 2 | 3 | 4 | 4 | *20* |
| ***Zone*** | | | | | | | |
| Seaward | 4 | 3 | 1 | 2 | 0 | 1 | *11* |
| Leeward | 1 | 2 | 2 | 0 | 2 | 1 | *8* |
| Lagoon | 5 | 1 | 0 | 1 | 0 | 1 | *8* |
| Flat | 0 | 1 | 4 | 2 | 0 | 0 | *7* |
| Channel | 0 | 1 | 1 | 2 | 1 | 1 | *6* |

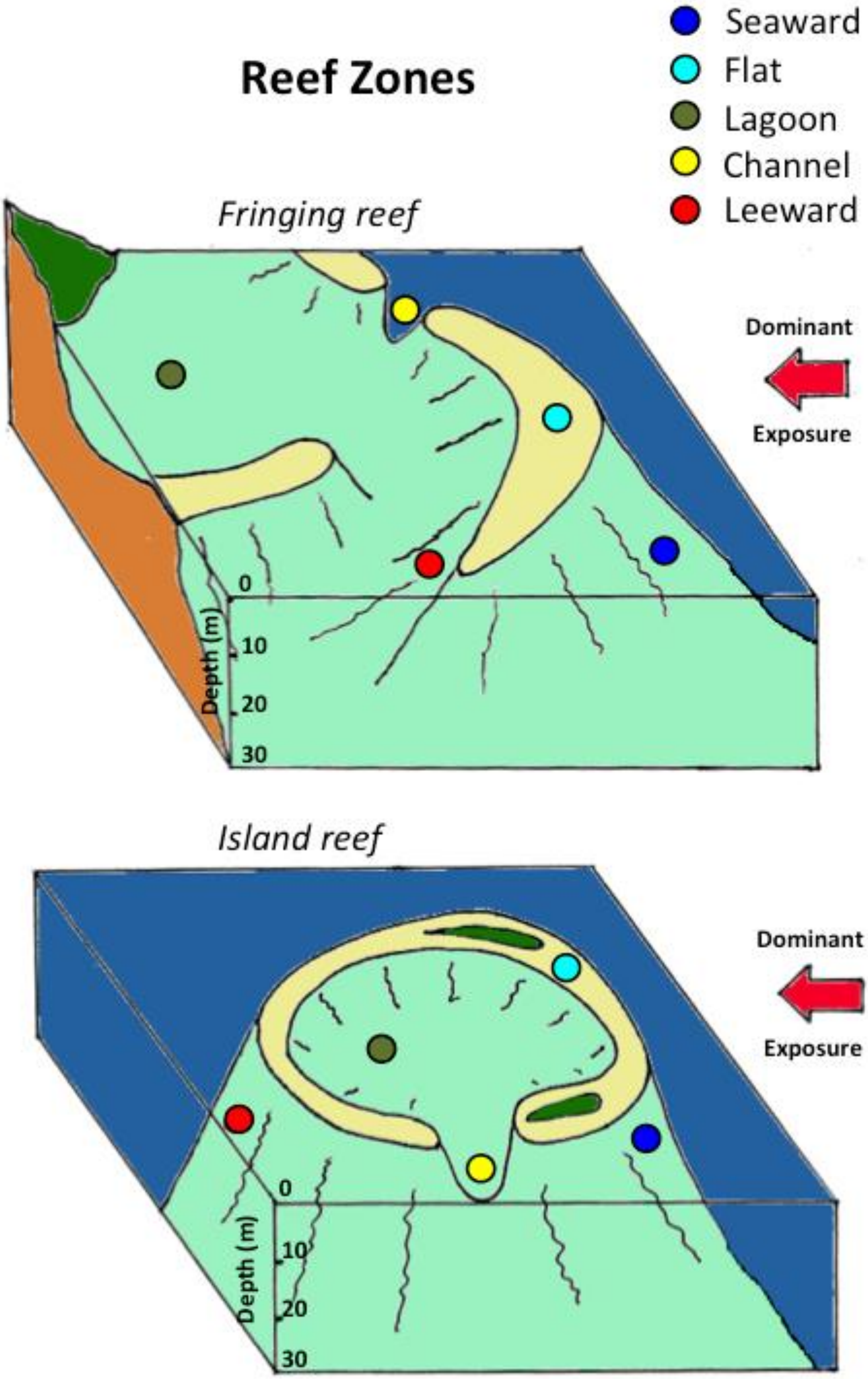


Figure 5.3. Diagrams of typical fringing reef and island reef formations showing the location of the five categories of reef zones used in this study.

### 5.2.2 Remote sensing

Five remotely-sensed parameters were used. Chronic and acute thermal stress were acquired from satellite derived Sea Surface Temperatures (SSTs) (Eakin *et al.* 2009)(Chapter 4). Chlorophyll *a* concentrations, also derived from satellite data, were used as a proxy for nutrient regime (Acker *et al.* 2008). Data on local human population was accessed from the LandScan geographic information systems (GIS) data layer (Bright *et al.* 2012).

Sea surface temperatures (SSTs) for each location were derived from the nearest Advanced Very High Resolution Radiometer (AVHRR) pixel, from January 1982 to December 2013 (Table 5.4). The data were accessed from http://las.incois.gov.in/las. The resolution of the AVHRR was 40km, and hence was not enough to extract temperature profiles for each site, hence acute and chronic thermal stress were collected at the location scale ($n$=6). Each location's climatology was calculated as the mean temperature during the hottest month (SSTmax) in 1985-1990 and in 1993 (Eakin *et al.* 2009). Chronic thermal stress was calculated as the standard deviation ($\sigma$) of the annual SSTmax from 1982-2013 (Donner 2011). Acute thermal stress was defined as the number of degree heating weeks (DHWs) in the El-Nino Southern Oscillation (ENSO) of 1998 (McClanahan *et al.* 2007a) (Table 5.5). A degree heating week was defined as when SSTs were over the climatological SSTmax by 2.45 $\sigma$ °C for one week (Donner 2011). A threshold for acute thermal stress based on the location's variability ( $\sigma$ ) was used, as thermal variability influences coral bleaching and mortality thresholds (McClanahan *et al.* 2007a).

Table 5.4. AVHRR pixel locations for each location

| Location | Nearest AVHRR pixel centre |
|---|---|
| Watamu (Kenya) | 3° 22’ 30”S, 40° 22’ 30”E |
| Kisite (Kenya) | 4° 37’ 30”S, 39° 22’ 30”E |
| Vamizi (Mozambique) | 11° 7’ 30”S, 40° 37’ 30”E |
| Kuramathi (Maldives) | 4° 7’ 30”N, 72° 39’ 30”E |
| Tikus (Sumatra) | 3° 39’ 30”S, 102° 7’ 30”E |
| Enggano (Sumatra) | 5° 22’ 30”S, 102° 22’ 30”E |

Chlorophyll *a* concentrations were derived from the Aqua MODIS monthly 4km resolution satellite data. The data were downloaded using the Goddard Earth Sciences Data and Information Services Centre’s online data analysis system “Giovanni” (http://giovanni.gsfc.nasa.gov/giovanni/) as a grid of average values across each location from 2003-2013. These values were interpolated on ARC-GIS (ESRI 2011) to estimate average chlorophyll *a* concentration at each reef site.

Human population data were derived from LandScan’s 2011 1km resolution data (Bright *et al.* 2012). Population for each site was calculated as the total number of people living within 20km of the site’s coordinates (Mora *et al.* 2011) (Table 5.5). Distance to the mainland was measured as the linear distance from each site to the nearest major (>100,000km$^2$) landmass (Obura and Grimsditch 2009) (Table 5.5).

Table 5.5. Explanatory variables by location from remote sensing

| Location | Population (20km radius) | Acute stress (DHW 1998) | Distance to mainland (km) |
|---|---|---|---|
| Watamu (Kenya) | 7350 (SE±934.2) | 11.5 | 0.9 (SE±0.13) |
| Kisite (Kenya) | 2301 (SE±547.1) | 5.8 | 5.9 (SE±1.10) |
| Vamizi (Mozambique) | 1497 (SE±351.1) | 4.8 | 12.7 (SE±0.91) |
| Kuramathi (Maldives) | 1864 (SE±0) | 7.5 | 650 (SE±0) |
| Tikus (Sumatra) | 60843 (SE±129.4) | 2.3 | 8.8 (SE±0.15) |
| Enggano (Sumatra) | 1470 (SE±100.6) | 3.8 | 125 (SE±0) |

### 5.2.3 Calculating resilience, resistance and recovery potential

Resilience indicators were combined into a relative weighted score of resilience, resistance and recovery potential by site using the same method carried out by Maynard *et al.* (2015). The original IUCN resilience assessments contain 61 indicators (Obura and Grimsditch 2009), which were prioritised to 11 indicators based on expert opinion and scientific evidence by McClanahan *et al.* (2012). Of these 11 indicators, 'physical human impact', 'coral disease' and 'fishing pressure' were not collected, leaving eight remaining resilience indicators (Table 5.1 and 5.6). Two key processes within resilience are the ability of corals to resist thermally-induced bleaching and mortality (resistance) and the ability of the reef community to bounce back from acute disturbances (recovery) (West and Salm 2003, Nyström *et al.* 2008). The resistance and recovery potential at each site was estimated using five indicators for each of these resilience components (McClanahan *et al.* 2012) (Table 5.6). Two of the indicators, 'Nutrients' and 'Sediment cover', were used to calculate both resilience and recovery.

Raw values of resilience indicators were combined into a single score by site. Indicators where high values suggest low resilience included Macroalgal Cover, Sediment Cover and Nutrients. These variables were inverted so that in each weighted indicator a larger number increases the overall resilience score. The normalised relative score of each indicator was calculated by dividing each site value by the highest value of that indicator, to give a value between 0 and 1. These normalised scores were weighted by 'perceived importance scores' from McClanahan *et al.* (2012) (Table 5.6). Finally, the weighted scores of each indicator were summed and divided by the maximum possible score for resilience (8.97), resistance (6.18) and recovery (5.28) (Equation 5.3).

**Table 5.6. Perceived importance weightings of resilience indicators used to calculate resilience, resistance and recovery, based on McClanahan *et al.* (2012).**

| Indicator | Resilience | Resistance | Recovery |
|---|---|---|---|
| Resistant corals | 1.36 | 1.56 | - |
| Chronic stress | 1.22 | 1.46 | - |
| Nutrients | 1.16 | 1.08 | 1.02 |
| Sediment cover | 1.10 | 1 | 1 |
| Coral diversity | 1.09 | 1.08 | - |
| Herbivore biomass | 1.02 | - | 1.06 |
| Macroalgae cover | 1 | - | 1.07 |
| Juvenile coral abundance | 1 | - | 1.13 |
| *Maximum possible score* | *8.97* | *6.18* | *5.28* |

**Equation 5.3: Calculating site scores for potential resilience, resistance and recovery**

$$Site\ score = \frac{\sum\ (normalised\ indicator\ score\ \times\ importance\ weighting)}{maximum\ possible\ score}$$

### 5.2.4 Exploring resilience using multidimensional scaling (MDS)

The weighted resilience indicators for each site were displayed using a multidimensional scaling (MDS) plot. Clustering and the distribution of reef sites indicate the similarity in resilience based on Bray-Curtis similarity and the stress of the model is indicated (Henderson and Seaby 2008). The centroids of each weighted resilience indicator are displayed on the MDS. The indicators' distance from the ordination plot's origin indicates how much variation in site arrangement is caused by this variable. Finally contours of combined resilience were plotted onto the ordination using the R-package 'Vegan' (Oksanen 2015). Resistance and recovery scores were also plotted onto the same MDS produced from the eight resilience indicators, to display how these components of resilience were distributed relative to the sites and indicator centroids, as well as overall resilience score.

### 5.2.5 Investigating the drivers of resistance and recovery

It was hypothesised that resistance and recovery scores of reefs were influenced by the explanatory variables reef zone, protected status, human population, distance to mainland and past acute thermal stress. Resistance and recovery scores were both normally distributed based on Shapiro-Wilkes (S-W) tests ($W$=0.949, $p$=0.069 and $W$=0.967, $p$=0.128 respectively). The variance in resistance and recovery scores were homogenously distributed within different 'zone' categories based on Breush-Pagan (B-P) tests ($\chi^2$=5.439, $p$=0.784 and $\chi^2$=5.111, $p$=0.276 respectively). These data therefore meet parametric assumptions and hence a 1-way ANOVA (aov) with Tukey post-hoc test is used to investigate differences in resistance and recovery score between zones. The variance of resistance and recovery scores was also homogenous protected status categories 'open' and 'closed' to fishing ($\chi^2$=2.149, $p$=0.143 and $\chi^2$=0.214, $p$=0.644 respectively), hence a t-test is used to compare the differences between these two groups. The continuous variables 'human populations', 'distance to mainland' and 'acute thermal stress' were non-normally distributed (S-W: $W$=0.787, $p$<0.001; $W$=0.539, $p$<0.001 and $W$=0.861, $p$<0.001 respectively) and could not be adequately transformed to conform to normality. As these variables did not meet the assumptions of a parametric correlation, the relationship with resistance and recovery score is investigated using a Spearman's rank correlation (Sr). Resistance, recovery and overall resilience score were also compared with coral cover at sites to investigate if there were correlations between these variables. Coral cover and overall resilience score were both normally distributed (S-W: $W$=0.974, $p$=0.673, and $W$=0.983, $p$=0.784 respectively), hence the significance of these associations was investigated using Pearson's product moment correlations.

## 5.3 Results

### 5.3.1 Potential resilience, resistance and recovery scores

The resilience, resistance and recovery scores for each site are given in Appendix 3. The resilience scores for sites ranged from a high of 0.85 in Palms Flat, Kuramathi (Maldives), to a low of 0.51 in Masolini, Kisite (Kenya). The locations with highest mean resilience score were Watamu (Kenya) and Kuramathi with a score of 0.69 (SE±0.014 and 0.031 respectively) (Fig. 5.4a). Tikus (Sumatra) had the lowest mean resilience score of 0.58 (SE±0.019). The location with the biggest variation in resilience was Kisite with a range of 0.21.

The resistance of sites varied from a maximum of 0.93 in Lambis, Watamu, to a minimum score of 0.57 in Tikus North, Tikus. As with resilience, the location with the lowest resistance was Tikus with a mean resistance of 0.62 (SE±0.038) (Fig. 5b). Watamu had the highest mean resistance score of 0.85 (SE±0.021), which was 0.11 higher than the next highest mean score from Enggano (Sumatra) at 0.74 (SE±0.035).

Recovery score ranged from 0.33 to 0.94, with the minimum and maximum values recorded in the same locations as the min and max of resilience score, Masolini and Palms Flat respectively. Kuramathi had the highest mean recovery with a score of 0.66 (SE±0.048), closely followed by Enggano with a score of 0.65 (SE±0.008) (Fig. 5c). As with resilience and resistance, Tikus had the lowest mean recovery value of 0.49 (SE±0.024). Interestingly, three of the sites from Watamu with some of the highest resistance, Lambis, Bennett's and Turtle Reef, had very low recovery scores (Appendix 3, Fig. 5b & 5c).

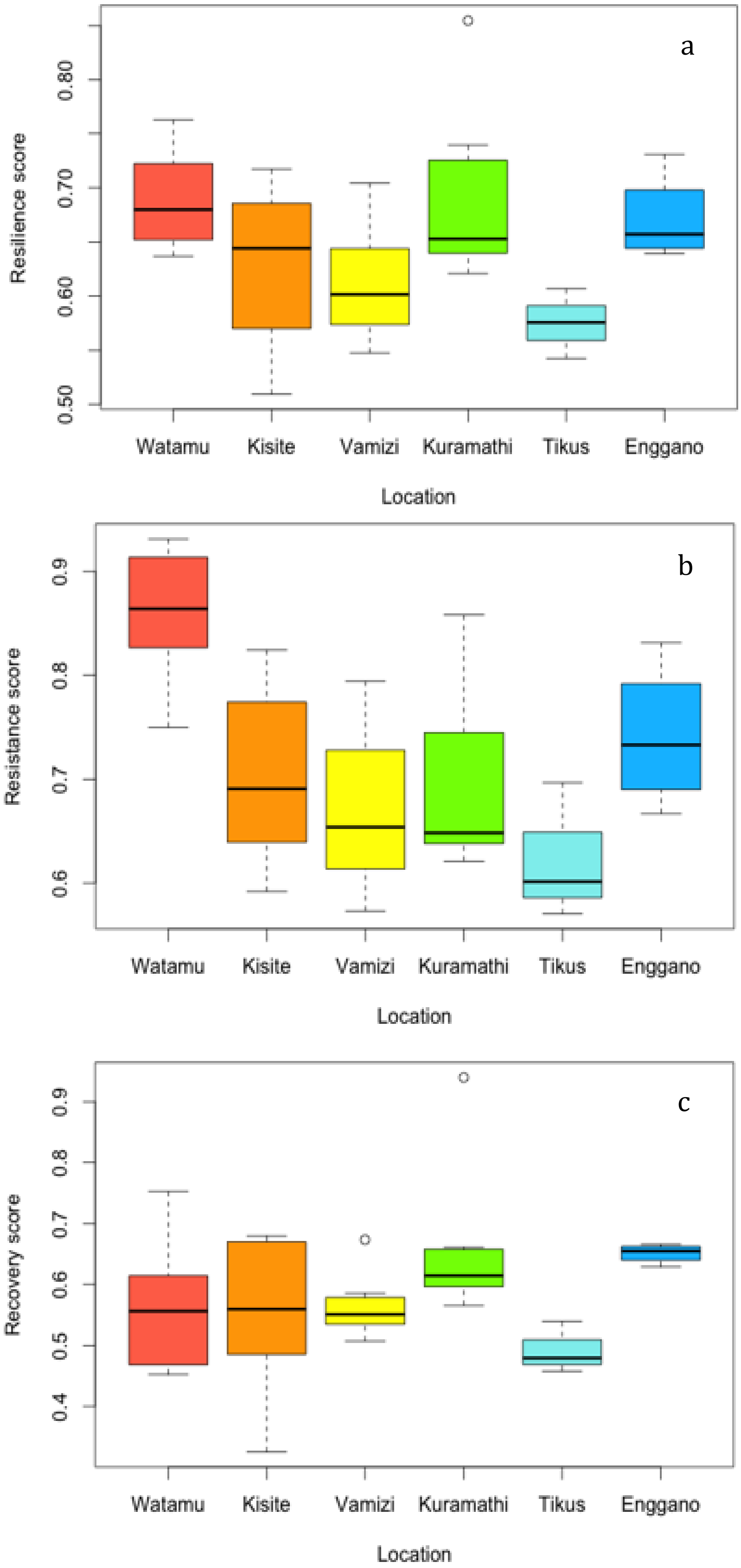


**Figure 5.4. Boxplot of the a) resilience, b) resistance and c) recovery score by location; Watamu (Kenya), Kisite (Kenya), Vamizi (Mozambique), Kuramathi (Maldives), Tikus (Sumatra), Enggano (Sumatra). The black line represents the median and the box represents the upper and lower quartiles. The whiskers respresent highest and lowest values within 1.5 x interquartile range, with outlying values beyond this indicated with a point.**

### 5.3.2 Relationships between resilience, resistance and recovery indicators and scores

Sites were plotted in multidimensional space based on the Bray-Curtis dissimilarity of their eight resilience indicator values. The MDS plot produced had a moderate level of stress with a stress value of 0.18 (Fig. 5.5a). Indicator centroids were plotted to show the relationship between indicators and between sites and indicators. Note that values of sediment cover, macroalgal cover and nutrients were inverted so that all variables were theoretically positively correlated with resilience, hence the sites located near the centroid for 'Nutrient' have low nutrients. Contour lines of resilience, resistance and recovery score were overlaid onto the MDS plot to show how the distribution of sites and resilience indicators are related to the scores.

The distribution of sites on the MDS plot shows that there are no distinct clusters, suggesting that the reefs sampled represent a continuous distribution of resilience attributes (Fig. 5.5a). Tikus is the most distinct location, with its three sites being clustered in the bottom right of the MDS plot, and low resilience values (Fig. 5.5a). Watamu and Kuramathi sites are also relatively clustered on the left and top of the plot, respectively and are predominately located in regions of the plot with higher resilience values (Fig. 5.5a also see Fig. 5.4 and Table 5.7). Contours of resistance show a gradient along axis 1 with higher resistance on the left of the plot, where sites from Watamu are placed (Fig. 5.5b). Contours of recovery show a gradient along axis 2, suggesting Kuramathi has the highest recovery potential (Fig. 5.5c). This orthogonal relationship suggests that resistance and recovery score are not correlated, despite sharing two variables, Nutrients and Sediment. A scatter plot of recovery score and resistance score did not show a relationship between these two components of resilience (Fig. 5.6) and an ANOVA showed they were not significantly correlated ($F$=0.45, $DF$=39, $p$=0.507).

On the MDS plot the indicator centroids for ‘Coral diversity’ and ‘Chronic stress’ are located near the origin, suggesting these variables do not explain much variation between sites. Juvenile coral abundance, herbivore fish biomass, and sediment cover were located furthest from the origin, showing these indicators vary the most between sites. ‘Nutrients’, ‘Herbivore biomass’ and ‘Juvenile abundance’ are located towards the top of the diagram and are associated with high recovery (Fig. 5.5c). ‘Resistant coral’ and ‘Sediment cover’ are located on the left of the plot and hence are linked with high resistance potential (Fig. 5.5b). Interestingly ‘Macroalgae’ is located on the right of the diagram, suggesting that low macroalgal cover is associated with low resistance scores (Fig. 5.5b).

**Table 5.7. Mean and standard error of resilience indicator values by location.**

| Location | Resistant Corals (%) | Coral Diversity (Simpson's Index) | Juvenile Abd. (per $m^2$) | Macroalgae cover (%) | Sediment cover (%) | Herbivore Biomass (kg per $1000m^2$) | Nutrients (m per $m^3$ of Chlorophyll a) | Chronic stress ( σ SSTmax)* |
|---|---|---|---|---|---|---|---|---|
| Watamu (Kenya) | 62.8 (SE±6.3) | 0.80 (SE±0.017) | 3.1 (SE±0.61) | 19.4 (SE±3.96) | 5.2 (SE±0.82) | 24.1 (SE±4.85) | 0.41 (SE±0.008) | 0.444 |
| Kisite (Kenya) | 40.0 (SE±4.4) | 0.76 (SE±0.022) | 3.7 (SE±0.69) | 1.1 (SE±0.52) | 28.1 (SE±7.35) | 18.8 (SE±4.88) | 0.48 (SE±0.067) | 0.412 |
| Vamizi (Mozambique) | 31.2 (SE±3.5) | 0.70 (SE±0.032) | 5.9 (SE±0.62) | 0.0 (SE±0.03) | 26.3 (SE±4.34) | 15.0 (SE±1.72) | 0.51 (SE±0.037) | 0.419 |
| Kuramathi (Maldives) | 54.5 (SE±8.6) | 0.75 (SE±0.026) | 14.7 (SE±2.84) | 0.1 (SE±0.05) | 40.8 (SE±7.78) | 30.6 (SE±4.78) | 0.43 (SE±0.009) | 0.369 |
| Tikus (Sumatra) | 53.3 (SE±13.2) | 0.56 (SE±0.121) | 6.1 (SE±1.70) | 0.3 (SE±0.26) | 17.8 (SE±5.40) | 16.9 (SE±4.17) | 1.10 (SE±0.013) | 0.395 |
| Enganno (Sumatra) | 24.7 (SE±7.4) | 0.70 (SE±0.054) | 7.3 (SE±2.36) | 0.9 (SE±0.74) | 17.7 (SE±4.77) | 17.4 (SE±2.83) | 0.22 (SE±0.024) | 0.466 |

** No standard error is presented for chronic thermal stress as these values were collected by location, not by site as with other indicators*

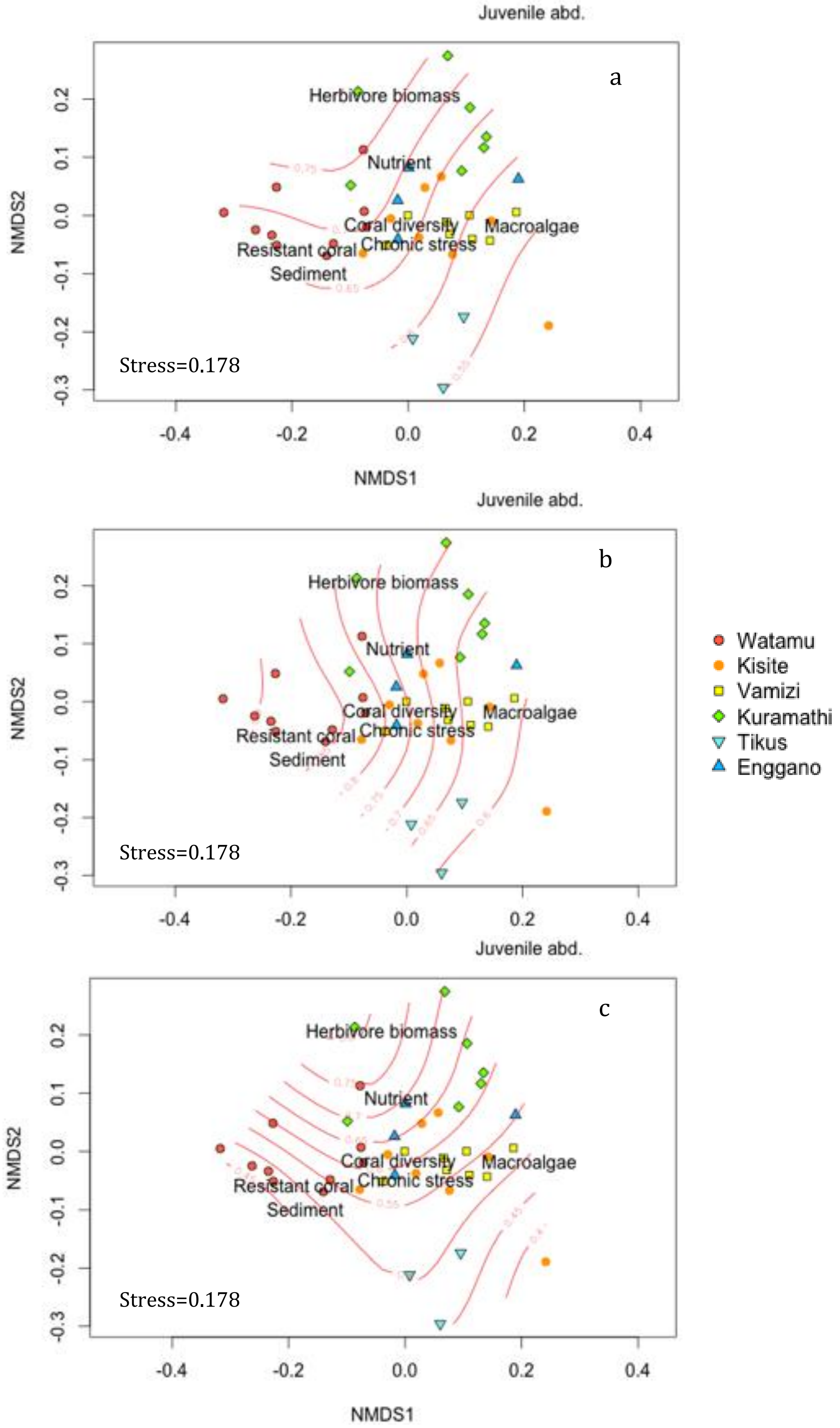


**Figure 5.5. Multi-dimensional scale (MDS) plots of weighted resilience indicators with sites and variable centroids indicated. Contour lines of a) resilience, b) resistance and c) recovery are drawn based on the scores of each site.**

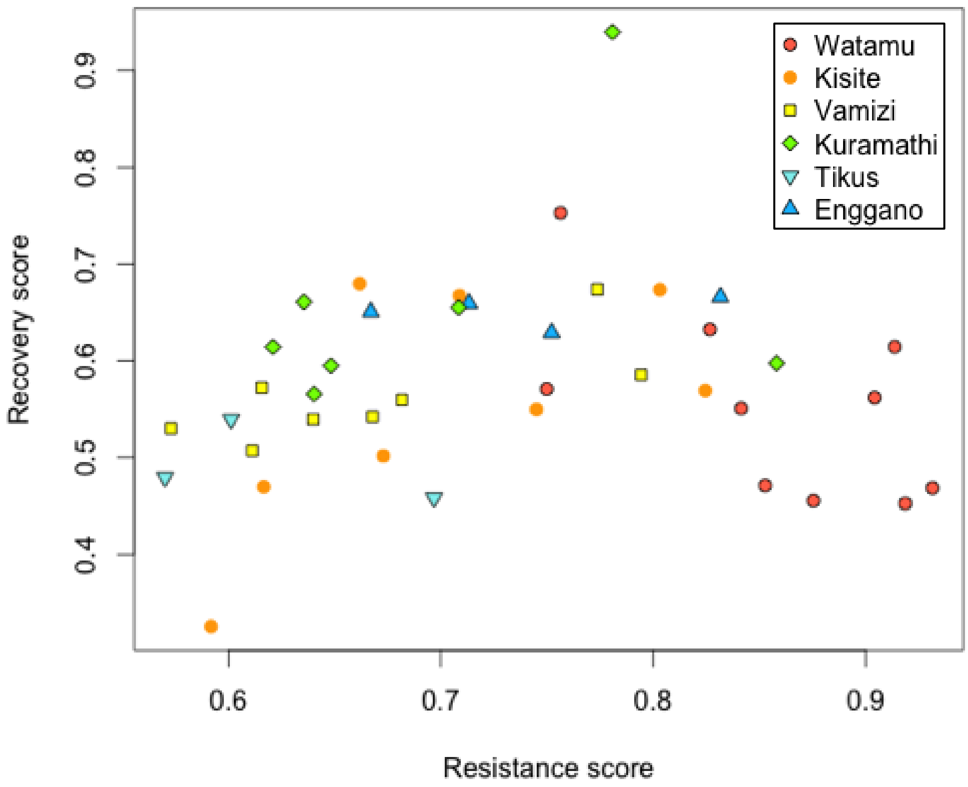


**Figure 5.6 Scatterplot of recovery and resistance score for all sites by location.**

### 5.3.3 Correlations between scores of resistance and recovery and potential drivers

Five explanatory variables were analysed with resistance and recovery scores to investigate the drivers behind the resistance and recovery potential of different sites (Table 5.8). Categorical variables, 'Zone' and 'Protected status' met parametric assumptions and were compared to scores using 1-way analysis of variance (ANOVA). Distance to mainland and human population were continuous variables with highly non-normal distributions, hence Spearman's rank correlation was used for the statistical comparison and driver values were square-root transformed for visual comparison (Figs. 5.8 and 5.9).

The relationship between zone and resistance and recovery score were explored (Fig. 5.7). Mean resistance was highest in lagoons with a mean score of 0.83 (SE±0.042) and lowest on reef flats with a mean of 0.66 (SE±0.029) (Fig. 5.7a). Leeward slopes had the most variation in resistance score with an interquartile range of 0.19 resistance points. Recovery score was highest on seaward slopes with a mean score of 0.65 (SE±0.018) and lowest in lagoon sites with a mean of 0.52 (SE±0.038)(Fig. 5.7b), although channel, flat, and leeward slope had a similar recovery level to lagoons with majorty of sites having a score of between 0.5-0.6 (Fig. 5.7b & Appendix 3). The differences in resistance and recovery between zones were significant (aov: $F$=4.27, $DF$=39 $p$=0.006 and $F$=3.04, $DF$=39, $p$=0.030 respectively). A Tukey's post-hoc test showed that resistance scores of lagoon sites were significantly higher than flats, leeward slopes and channels ($p<0.05$). Lagoon resistance score was not significantly different to seaward slopes and the scores of other zones were not significantly different to each other. The Tukey's test for recovery scores showed that the only significant difference in recovery between zones was the higher score in seaward slopes versus lagoons ($p$=0.043) (Fig 5.7b).

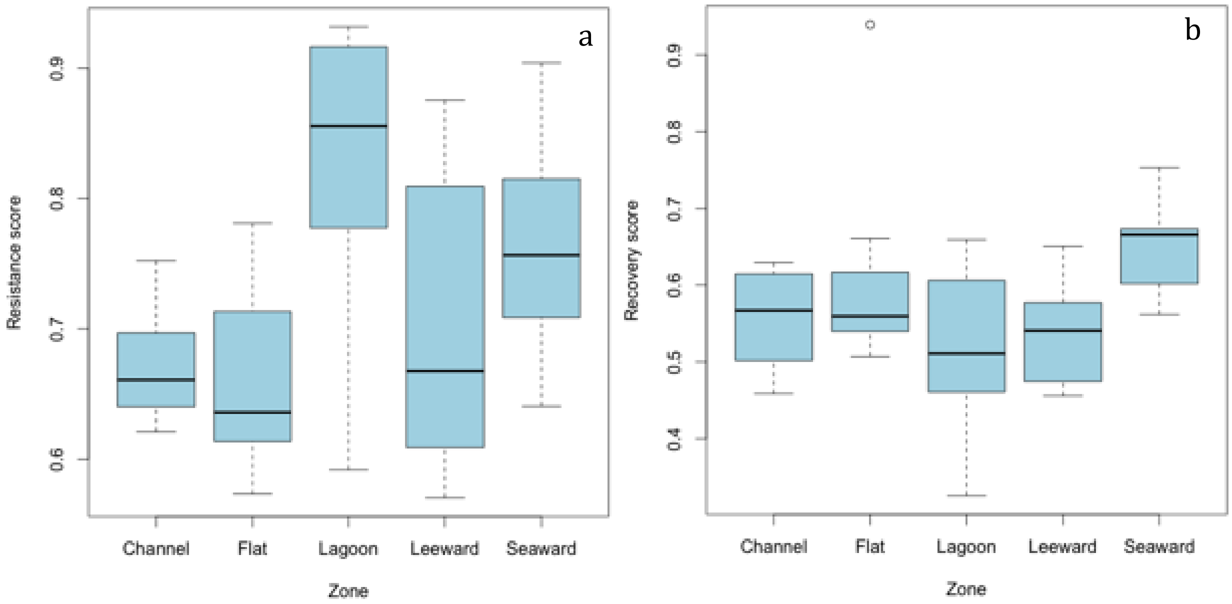


**Figure 5.7 Boxplot of a) resistance score and b) recovery score in different reef zones. The black line represents the median and the box represents the upper and lower quartiles. The whiskers respresent highest and lowest values within 1.5 x interquartile range, with outlying values beyond this indicated with a point.**

The resistance and recovery scores of reef sites either open or closed to fishing (protected status) were compared (Fig. 5.8). Resistance scores were similar in both management types with mean resistance of 0.74 (SE±0.027) in closed sites and 0.72 (SE±0.021) in open sites. Recovery score was also similar, with a mean recovery score of 0.58 (SE±0.026) at closed sites and a score of 0.58 (SE±0.021) at sites open to fishing. The differences between resistance and recovery score and protected status were not significant ($F$=0.51, $DF$=39, $p$=0480 and $F$=0.06, $DF$=39 $p$=0.806 respectively).

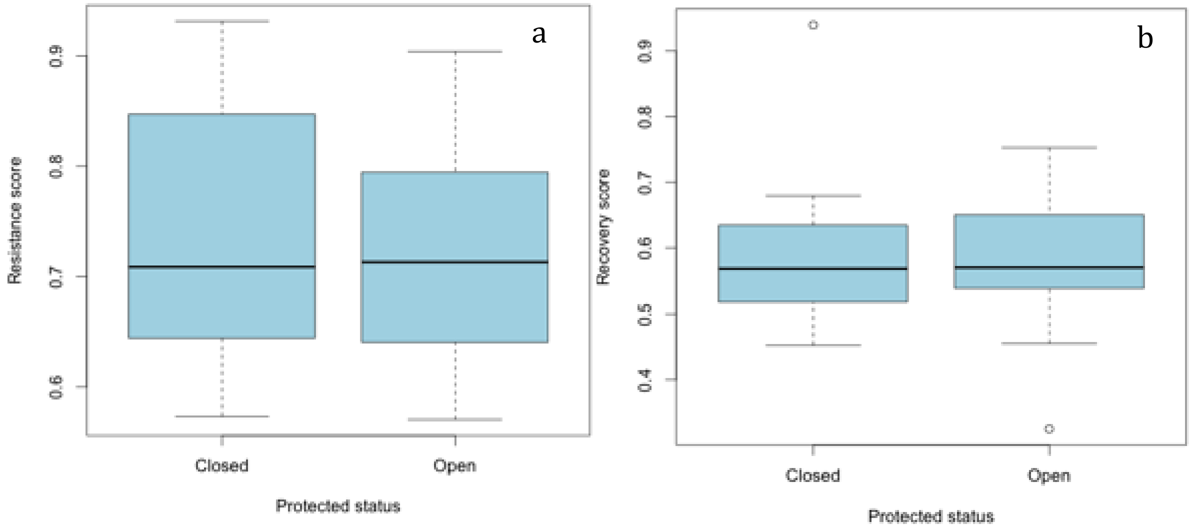


**Figure 5.8 Boxplot of a) resistance score and b) recovery score and protected status. The black line represents the median and the box represents the upper and lower quartiles. The whiskers respresent highest and lowest values within 1.5 x interquartile range, with outlying values beyond this indicated with a point.**

The human population within a 20km radius of each site was significantly negatively correlated with recovery score, based on a Spearman's Rank Correlation of these two variables ($\rho$=-0.493, $p$=0.03) (Fig. 5.9). There was no significant correlation between human population and resistance score ($\rho$=0.213, $p$=0.561). The distance of reef sites to a continental mainland was significantly negatively correlated with resistance score ($\rho$=-0.414, $p$=0.024) and was significantly positively correlated with recovery score ($\rho$=0.459, $p$=0.006).

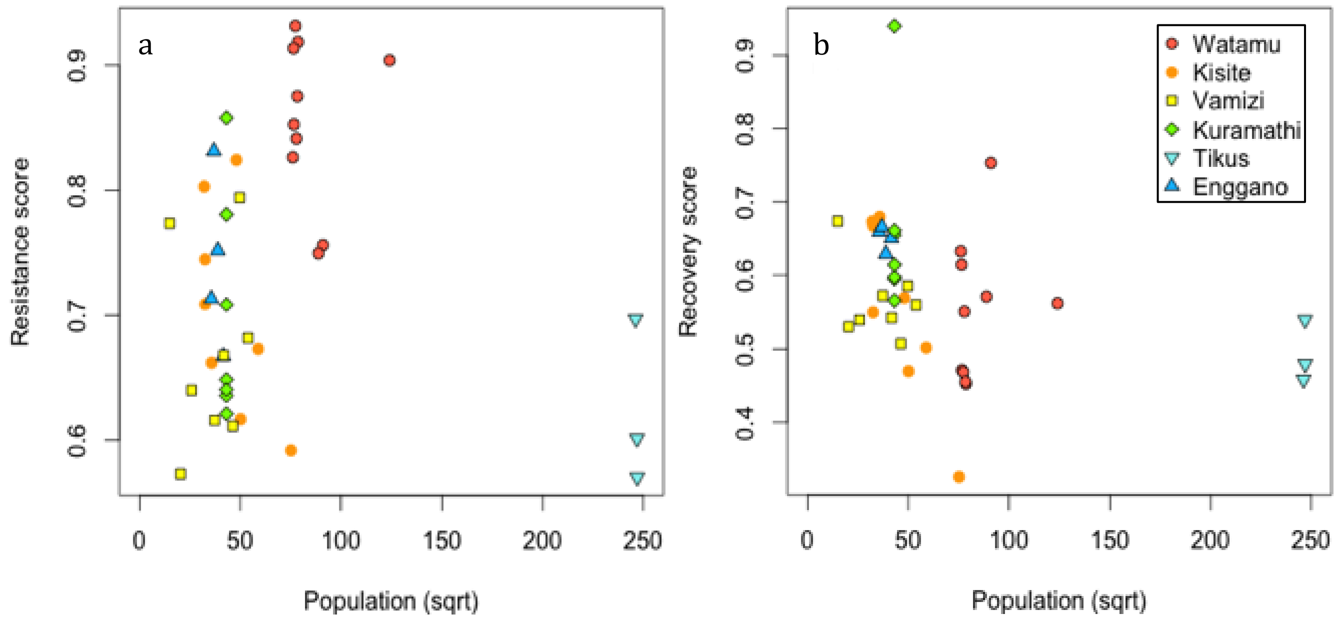


**Figure 5.9 Scatterplot of a) resistance score and b) recovery score versus transformed human population for each site with location indicated.**

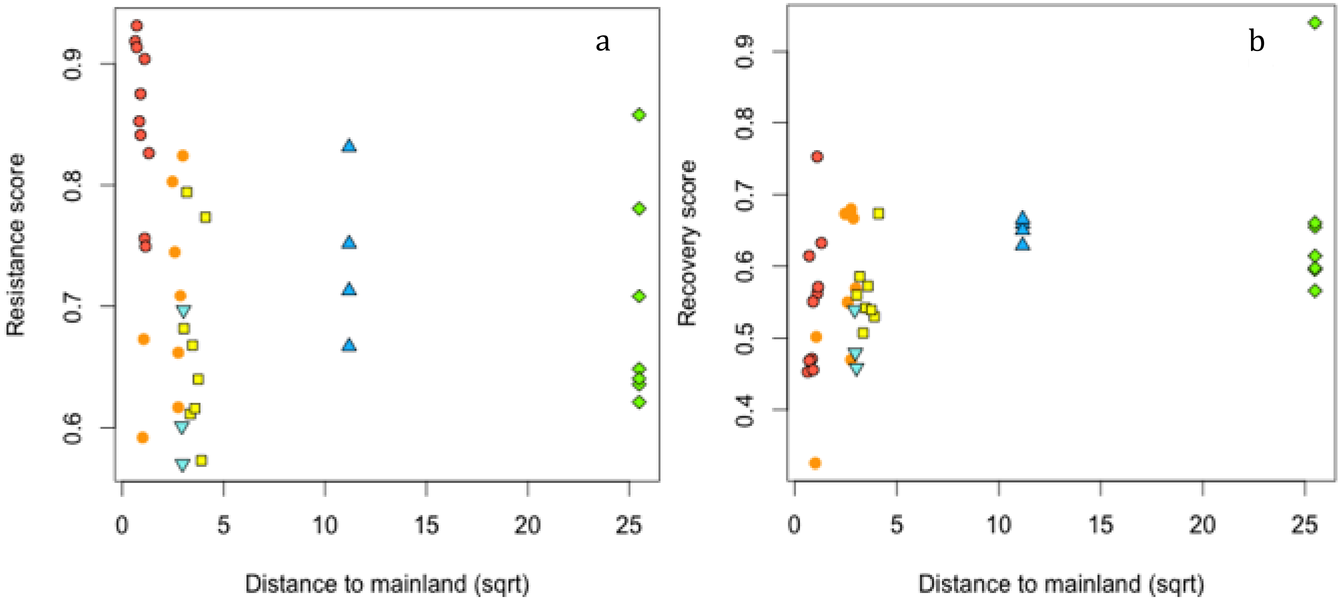


**Figure 5.10 Scatterplot of a) resistance score and b) recovery score and transformed distance to mainland for each site with the location indicated. Colour code for location as in Fig. 5.9.**

The scatter plot of acute thermal stress and resistance score appears to be positively correlated (Fig. 5.11). However, the AVHRR satellite data used to derive the metric of acute thermal stress was only available at a spatial resolution of 4km and hence the acute thermal stress was only available at the location level (*n*=6) meaning that statistical strength of this correlation could not be tested.

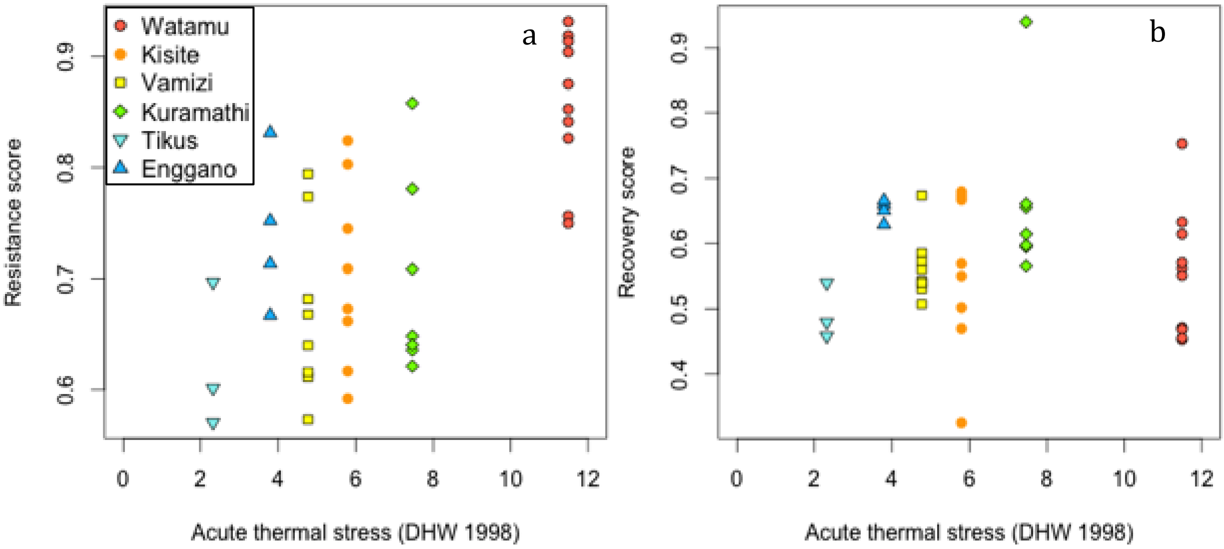


**Figure 5.11 Scatterplot of a) resistance score and b) recovery score and acute thermal stress for each site with the location indicated.**

### 5.3.4 Coral cover and resilience, resistance and recovery scores

Hard coral cover ranged from a minimum of 3.5% in Bara Bara, Watamu to 48% in Pulau Merbau, Enggano. The location with the highest coral cover was Vamizi, with an average cover of 42.0% (SE±2.70) and the lowest was Watamu with an average of 8.7% (SE±1.20) (Fig 5.12). Coral cover was significantly negatively correlated with resistance ($\rho$=-0.410, $p$=0.027) (Fig. 5.13b), but was not significantly correlated with either resilience ($\rho$=-0.233, $p$=0.444) (Fig. 5.13a) or recovery ($\rho$=0.104, $p$=1.000) (Fig 5.13c).

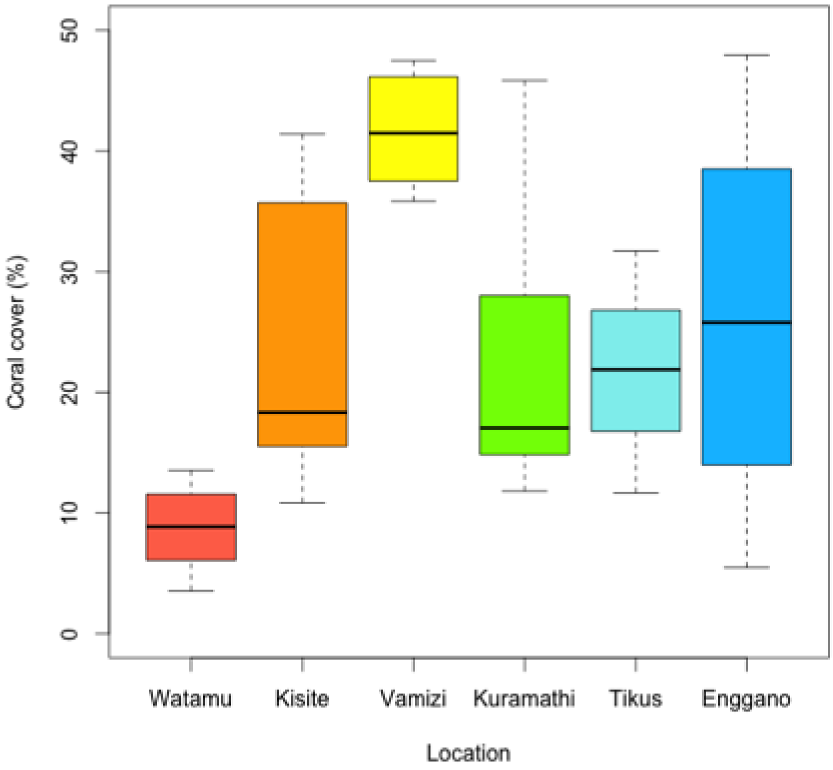


**Figure 5.12. Coral cover by location; Watamu (Kenya), Kisite (Kenya), Vamizi (Mozambique), Kuramathi (Maldives), Tikus (Sumatra), Enggano (Sumatra). The black line represents the median and the box represents the upper and lower quartiles. The whiskers respresent highest and lowest values within 1.5 x interquartile range, with outlying values beyond this indicated with a point.**

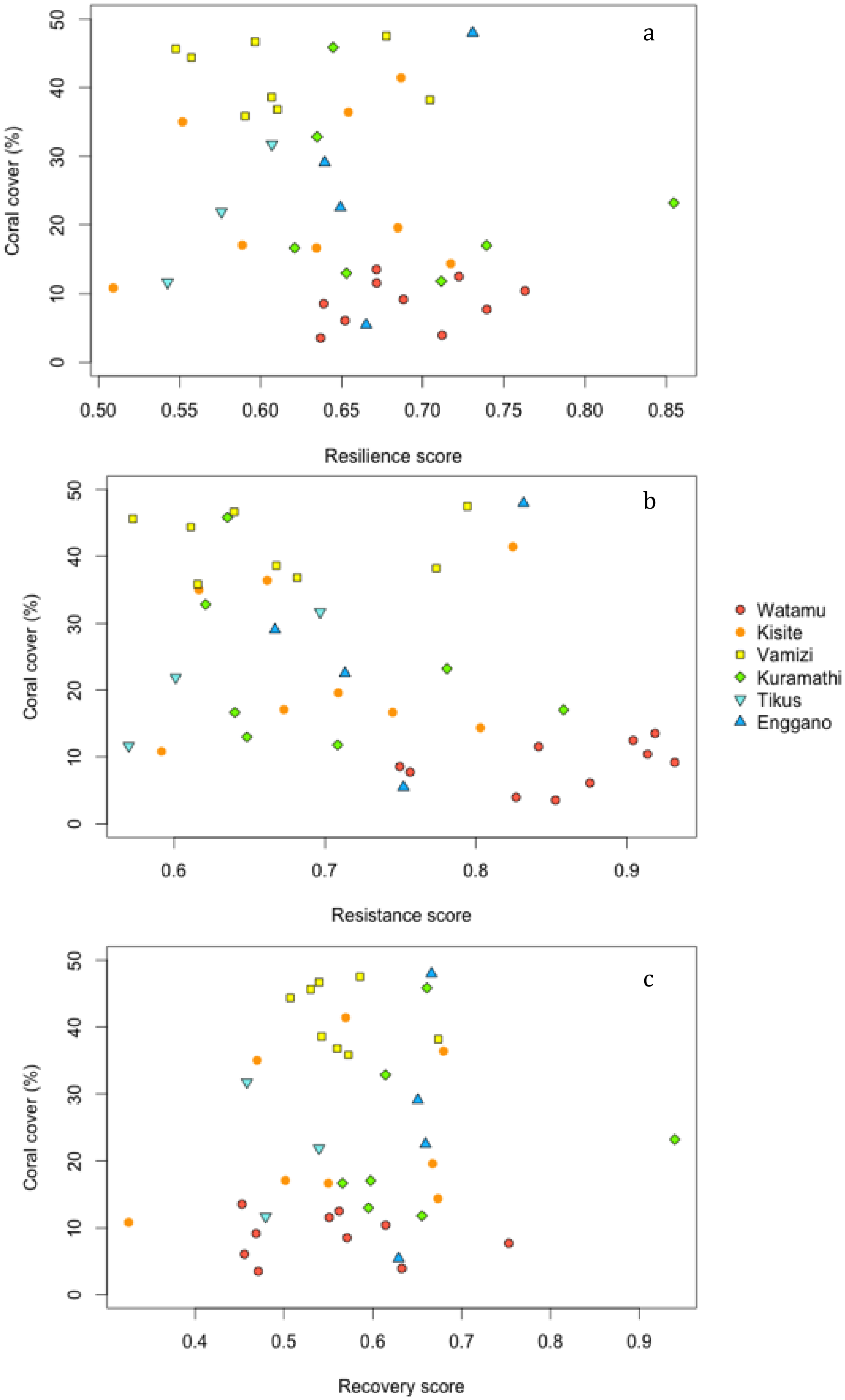


**Figure 5.13 Scatterplot of coral cover versus a) resilience, b) resistance and c) recovery score for all sites with location indicated.**

## 5.4 Discussion

### 5.4.1 Interpreting resilience assessments

The locations with the highest resilience were Watamu (Kenya) and Kuramathi (Maldives) (Fig. 5.4a). Considering the processes of resistance and recovery separately, it can be seen that Watamu is ‘resilient’ because of its high resistance while Kuramathi is ‘resilient’ because of its recovery potential (Fig. 5.4b and 5.4c). The MDS ordination of sites, indicators and scores (Fig. 5.5) shows that resistance and recovery are arranged orthogonally to one another, suggesting that these processes operate independently. This finding is concordant with the general scientific consensus on resilience theory for coral reefs, where these processes are viewed as distinct components of overall resilience (Obura 2005, Nyström *et al.* 2008) and also have differing implications for conservation objectives (West and Salm 2003). The lack of correlation between these two components (Fig. 5.6) allows for the independent testing of relationships between resistance, recovery and drivers (Table 5.8).

In this study the indicators with the most variation between sites were juvenile coral abundance, herbivore fish biomass, and sediment cover, with the least variation driven by coral diversity and chronic thermal stress (Table 5.7, Fig. 5.5). The wide variation in juvenile coral abundance between locations and sites (Table 5.7) may be driven by ocean-wide biogeographical patterns (Harris 2010), or by local connectivity and currents (Sammarco and Andrews 1988) and habitat suitability (O’Leary and Potts 2011,). The variation in herbivore fish biomass may be driven by factors such as local oceanography (Mumby *et al.* 2012) or protected status (McClanahan 2014b). By identifying the dominant indicators within a resilience assessment it is possible to focus management objectives to influence these specific factors and boost the overall resilience of the system. In the case of recruitment, management options would include, identifying and protecting source populations of larvae (West and Salm 2003) and improving water quality (Fabricius 2005).

The lack of correlation between recovery and resistance score in this study was observed despite the fact that two indicators (Nutrients and Sediment) were included in the calculation of both resilience components (Table 5.6). It has been noted that some factors on a reef affect recovery or resistance in different ways (Nyström *et al.* 2008). For example, 'Resistant corals' that are important for resisting bleaching tend to be massive colonies, such as merulinids (favids) and poritids (Loya *et al.* 2001) and hence may reduce recovery potential through slow growth rates (McClanahan *et al.* 2012). Similarly, sedimentation and nutrients in the water, which are generally considered deleterious for reef health and recovery potential (e.g. Jouffray *et al.* 2015), may actually provide some protective benefit to reefs during bleaching events (Fabricius 2005).

In this study the location with highest coral cover and healthiest looking (diverse and structurally complex) coral community was Vamizi, Mozambique (Figs. 5.12 & 5.15b). However, the sites in this location had low resistance and recovery potential (Figs. 5.4 and 5.5), suggesting that the healthy coral belies degraded ecological processes and low resilience to future bleaching impacts (e.g. Vamizi had the lowest herbivore biomass of all locations (Table 5.7)). Coral cover is not usually considered important for resilience assessments, because of the lag-time that exists between coral cover and some chronic stressors (Mumby *et al.* 2012), and hence the decoupling of trajectories of resilience and the dominant ecological regime (Hughes 1994, Nyström *et al.* 2008). However, coral cover does affect resilience of a reef through its ecological influence on other indicators, such as fish communities (Graham *et al.* 2015), which have been shown to decline when coral cover is below 10% (Beldade *et al.* 2015). Watamu scored highly for resilience because of its resistance potential, having the best score for 3 of the 5 resistance indicators (Table 5.7), but had the lowest coral cover with an average of 8.7% (Fig. 5.12 & Fig. 5.15a). It also was the only location with a mean macroalgal cover >2% with an average of 19.4% (Table 5.7). These observations suggest that while Watamu may be resistant to future bleaching impacts (Chapter 4), it has poor recovery ability (Chapter 3) and hence is vulnerable to further coral loss and habitat degradation.

There are numerous factors that influence resilience in different reef systems (Obura 2005), but certain indicators were found to be generally more important and relevant to understanding resilience patterns (Maynard *et al.* 2012, McClanahan *et al.* 2012). While this has helped simplify the analyses and interpretation of resilience assessments, there are still gaps in our understanding of the importance of indicators at different spatial and temporal scales (Nystrom *et al.* 2008) and the presence of thresholds within indicators (Mumby *et al.* 2007b, Anthony *et al.* 2015). Currently different indicators are scored on a relative linear scale, operating in one direction with resilience (i.e. either a positive or negative effect). This does not reflect some relationships where a resilience factor has natural thresholds (Fig. 5.14a), beyond which the indicator increases in importance, such as low coral cover (>10%) that negatively affects the fish community and hence the reef's overall resilience (Beldade *et al.* 2015). Other indicators may operate in different directions for resistance and recovery and hence an optimum value for overall resilience is trade-off between these two effects (e.g. nutrient concentration; Fabricius 2005) (Fig. 5.14b). More research is needed into the relationships between indicators and resilience potential in order to refine the current model (Anthony *et al.* 2015).

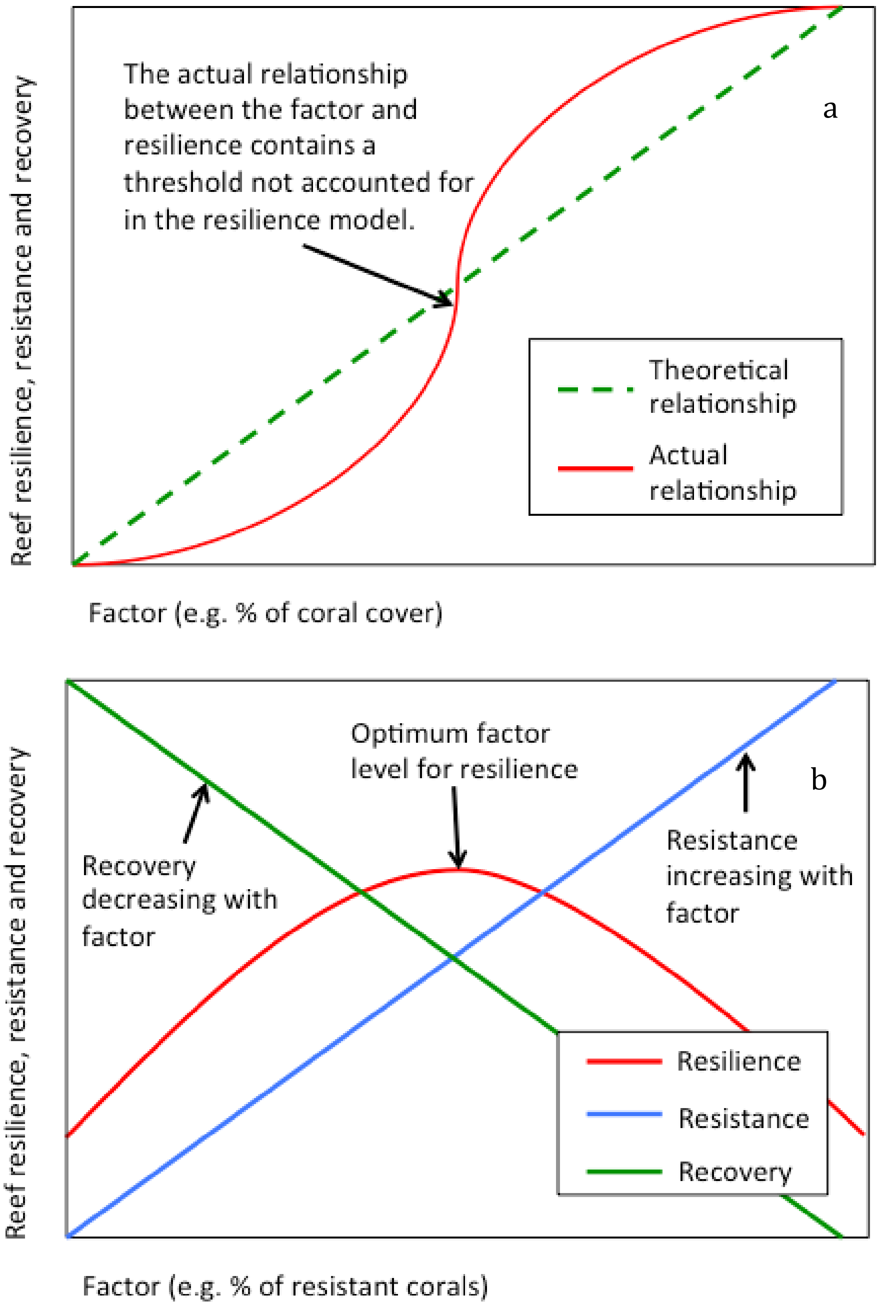


**Figure 5.14 Possible theoretical relationships between a single resilience factor and the influence on overall resilience, resistance and recovery potential of the reef with a) a non-linear relationship and b) an opposing relationships with resistance and recovery.**

### 5.4.2 Understanding the drivers of resilience to suggest conservation options

There have been increasing calls to operationalize resilience theories for managers (Nyström *et al.* 2008, Anthony *et al.* 2015, Maynard *et al.* 2015). The findings from this study, such as the high resistant potential in Watamu and low overall resilience score for Vamizi (Fig. 5.4), need to be understood in the context of environmental drivers to identify conservation options (Houk *et al.* 2014, Jouffrey *et al.* 2015). For the purposes of the discussion here, management options are classed as either conservation 'prioritisation', i.e. establishing new MPAs, or conservation 'intervention', e.g. managing fisheries or managing land-based sources of pollution (Maynard *et al.* 2015).

Recovery potential was significantly correlated with zone, distance to the mainland and human population (Table 5.8). Exposed seaward slopes had the highest recovery potential (Fig. 5.7b) along with the offshore locations Kuramathi and Enggano (Fig. 5.10b). Seaward reefs tend to have less land-based influence (Obura 2011), as do reefs further from the mainland, which suggests that terrestrial run-off and sediment from human and/or natural sources reduces reef recovery potential (Houk *et al.* 2014). In this study human population was used as a proxy for a range of human impacts, such as fishing and land-based sources of pollution (Mora *et al.* 2011), and was also found negatively correlated with recovery potential (Table 5.8, Fig. 5.9b). Human impacts on water quality and over-fishing promote factors that negatively impact resilience, through loss of herbivore biomass (Mumby *et al.* 2007a), increasing macroalgal cover (Fabricius 2005) and reduced coral recruitment and growth (Bak and Meesters 1998). Hence, these chronic human disturbances reduce the resilience of reefs to both climate impacts and other acute stressors (Houk *et al.* 2014).

High resistance scores were associated with lagoon sites (Fig. 5.7a) and negatively correlated with distance from the mainland (Fig. 5.10a). Higher resistance in lagoons and terrestrially-influenced reefs has been observed elsewhere (Obura 2009, Fabricius *et al.* 2013). The relationship between past acute thermal stress and resistance of sites could not be tested statistically because of the small numer (*n*=6) of data points available for this variable. Other studies have found a positive relationship between past bleaching experience and resistance potential (Brown *et al.* 2002, Maynard *et al.* 2008) through the selective mortality of thermally-sensitive corals (Berkelmans 2009) or colony level acclimatisation (Buddemeier and Fautin 1993).

The sites with the lowest acute thermal stress in this study were Enggano and Tikus. Both of these sites received <4DHWs of thermal stress in 1998 (Table 5), as a result of cool upwelling associated with Indian Ocean Dipole conditions in the Eastern Indian Ocean (Webster *et al.* 1999), which probably prevented these reefs experiencing mass-bleaching or mortality (Liu *et al.* 2003). Vamizi also experienced low DHWs in 1998 (Table 5.5) and is thought to have escaped bleaching through cool upwelling from adjacent deep waters in the Mozambique Channel (Garnier *et al.* 2008). The reefs in these locations represent examples of bleaching ‘avoidance’, and the conservation significance of this will be related to how reliable these avoidance factors (i.e. upwelling) are during future thermal stress events (West and Salm 2003, Obura 2005). These examples also demonstrate the importance of understanding past disturbances on reefs to understand their current state and trajectory. In the case of Vamizi, the lack of severe bleacing has allowed the reef to maintain high coral cover (Figs. 5.12 and 5.15b), but as discussed above, this shouldn’t be interpreted as higher resilience.

Past disturbances also include non-bleaching impacts such as cyclones and crown-of-thorn outbreaks, which can regularly impact reefs (Connell *et al.* 1997). In this study, bleaching, and specifically the event in 1998, was the only acute disturbance known from these locations. However, it should be noted that reefs further north in Sumatra were affected by a 'red-tide' in 1997 which killed many corals in the Mentawai Islands (Abram *et al.* 2003) and by the impacts of the Indian Ocean tsunami in 2004 (Campbell *et al.* 2007). It is unclear whether these disturbances also affected Enggano or Tikus.

If the thermal protection experienced by Enggano is reliable, it would be a good location to prioritise conservation efforts, with high recovery potential conferred by the low human population densities and an offshore location (Table 5.5) and high chronic thermal stress increasing resistance potential (Table 5.7). Tikus represents a site that could be improved with conservation intervention activities, as the resilience of this reef is reduced by heavy fishing pressure and physical human impacts from the large city of Bengkulu 3km away (B. Cowburn pers. obs). Being located near to the Sumatran mainland with high nutrients and turbidity (Spalding *et al.* 2001), might confer some resistance to this reef during future bleaching events (Fabricius *et al.* 2013). However, the lack of fringing reef along the main coastline of Sumatra (Spalding *et al.* 2001) and the low coral diversity found on Tikus (Table 5.7 and Fig. 5.15d) suggests the natural conditions are near the physiological limits of coral growth and reef formation (Kleypas *et al.* 1999). Tikus has maintained a mean coral cover of over 20% (Fig. 5.12), because of the low acute thermal stress it has experienced in the past. However, with high human pressure and unfavourable natural conditions this location is highly vulnerable to future acute disturbances (Mumby *et al.* 2014).

Like many other locations in the Central and Western Indian Ocean, Kuramathi and Watamu suffered high acute thermal stress in 1998 (Table 5.5), which caused widespread bleaching and mortality in both Kenya (McClanahan *et al.* 2001) and the Maldives (Rajasuriya *et al.* 1999). Resilience assessments showed that Kuramathi had the highest recovery potential (Fig. 5.4c and 5.5c) with the highest juvenile coral abundance and highest herbivore biomass (Table 7). In the Maldives, extensive reef systems support relatively low human population densities and a fishery that focuses on tuna (Risk and Sluka 2000), leaving keystone fish groups, such as herbivores, on the reef (Table 5.7). With low anthropogenic stress and little terrestrial influence from the Indian mainland >500km away, many reefs in the Maldives and nearby Chagos Archipelago recovered well from bleaching mortality (Edwards *et al.* 2001, Sheppard *et al.* 2008) (Fig. 5.15c). This past observation from the Maldives increases the confidence that the high recovery score for Kuramathi is probably correct and reefs here will recover well from future disturbance. The low human pressure and ability to recover from acute thermal stress indicate these Central Indian Ocean reefs are good candidates for conservation prioritisation. Indeed, the recently established Chagos Marine Reserve, containing 60,000km$^2$ of fully-protected reef, may be a significant refuge for coral during this century's continued warming and habitat destruction (Sheppard *et al.* 2012).

The past acute thermal stress in Watamu appears to have selected for a more thermally-tolerant coral assemblage (Table 5.7, Fig. 5.15a), with a dominance of merulinids and poritids (Chapter 3). This coral community, along with low sedimentation and high chronic thermal stress (Table 5.7), indicates these reefs will be resistant to future bleaching (see also Chapter 5.3). However, pre-1998 data from lagoonal sites show that Watamu has experienced significant declines in coral cover and recruitment (Chapter 5.2). It is possible the reef is in a transitory state (Jouffray *et al.* 2015), but with 15 years of similar benthic structure it appears the reef is in an alternate stable state (Chapter 3) (Bruno *et al.* 2009). The current state of the reef may be resilient to future acute thermal stress, but its resilience to other acute stressors is probably low, indicated by the low recovery ability of these reefs (Fig 5.4c). Reefs in Watamu are in need of conservation interventions to improve its recovery ability and more research is needed to understand the factors preventing Watamu returning to its pre-1998 state (Chapter 4) (Anthony *et al.* 2015).

Protected status had no relationship with either resistance or recovery potential. Six of the 10 sites in Watamu have been protected from fishing for >40years (Muthiga 2009), but some of these sites had the lowest recovery potential of all reefs assessed during this study. Six of the 8 sites in Vamizi were also protected, but the location had low resilience and resistance (Figs 5.4 and 5.5). Protected status does not appear to confer any extra resistance potential when a bleaching event occurs (Selig *et al.* 2012), but by reducing other human stressors it should theoretically increase recovery potential (West and Salm 2003). Some studies have shown positive effects of protection on reef recovery (e.g. Wilson *et al.* 2012), but others have not (McClanahan *et al.* 2014, Graham *et al.* 2015). Protected status as a metric could be improved with more information about the age, size and effectiveness of the MPA (Mora and Sale 2011, Edgar *et al.* 2014). For example, the community reserve in Vamizi was only established 8-years before resilience data in this study were collected and hence these reefs could still be recovering from past human pressure (McClanahan 2014).

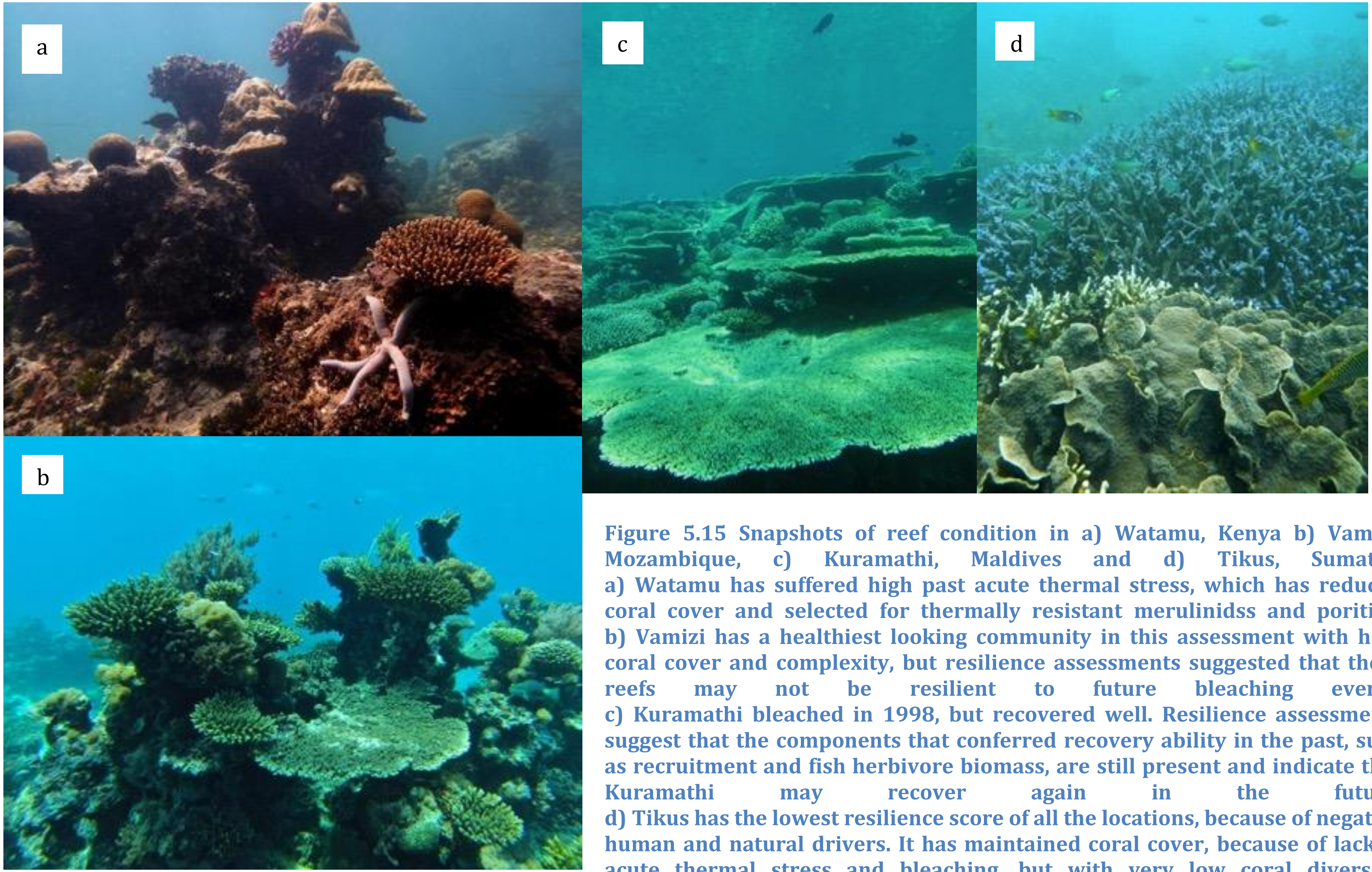


Figure 5.15 Snapshots of reef condition in a) Watamu, Kenya b) Vamizi, Mozambique, c) Kuramathi, Maldives and d) Tikus, Sumatra. a) Watamu has suffered high past acute thermal stress, which has reduced coral cover and selected for thermally resistant merulinidss and poritids. b) Vamizi has a healthiest looking community in this assessment with high coral cover and complexity, but resilience assessments suggested that these reefs may not be resilient to future bleaching events. c) Kuramathi bleached in 1998, but recovered well. Resilience assessments suggest that the components that conferred recovery ability in the past, such as recruitment and fish herbivore biomass, are still present and indicate that Kuramathi may recover again in the future. d) Tikus has the lowest resilience score of all the locations, because of negative human and natural drivers. It has maintained coral cover, because of lack of acute thermal stress and bleaching, but with very low coral diversity.

### 5.4.3 Recommendations for future resilience assessments and research

The purposes of resilience assessments and the metrics used will vary with the geographic extent of the study system and resource availability (Salm and West 2003, Obura and Grimsditch 2009). This study has presented the drivers and variation of resilience patterns across a broad geographical range using limited resources (Table 5.8). The interpretation of these patterns also drew on historical references and local information from reef sites, as well as comparisons with other assessments of reef resilience and health (Section 5.4.2) (Obura and Grimsditch 2009). Sites in Watamu had a large amount of historical information (Chapter 2), which allows for more confidence in the findings from these sites, compared to those for South-West Sumatra, where no historical coral reef records were found. Indicator selection, data collection method, historical information and variation between reef systems will influence the interpretation of resilience assessments (Obura and Grimsditch 2009, Maynard *et al.* 2012, Mumby *et al.* 2013) and should be considered before designing a resilience assessment.

**Table 5.8 Explanatory variables to contextualise resilience assessments and potential data sources based on limited or extensive resource availability for research.**

| Drivers of resilience | Limited data and resources (this study) | Extensive data and resources |
|---|---|---|
| **Climate**<br>*Acute stress,*<br>*Chronic stress* | AVHRR dataset. Reference and local information about past bleaching and mortality. | Dataloggers installed at different depths and zones over several years. Detailed records of past bleaching intensity and pre-bleaching conditions of reefs. |
| **Human**<br>*Fishing,*<br>*Land-based pollution and sedimentation,*<br>*Physical human impact* | Local population from census or remote sensing. Protected status (consider age, size and effectiveness). Local knowledge. | Monitor fisheries impact on the reef. Water quality testing for land-based pollution and sedimentation. Monitor physical human impact through dynamite fishing, coral mining, dredging etc. |
| **Natural**<br>*Light, Depth, Rugosity, Upwelling, Current, Zone etc (see Obura and Grimsditch 2009)* | Visually assigned Likhert or categorical classification. Maps, free GIS layers, papers and reports. Local knowledge. | Measurments of physical parameters in situ, connectivity to other habitats, local water flow and retention dynamics, upwelling. |

The five explanatory drivers of resilience variation selected in the study were chosen because of their relevance to reef ecology in general and evidence from other studies of their importance (Mora *et al.* 2011, Houk *et al.* 2014, Jouffray *et al.* 2015). Drivers can be refined for particular study systems, e.g. Houk *et al.* (2014) considered zone as a driver of recovery potential, as in this study, but tailored their zone classification to reef types found in the Mariana Islands, where the study was conducted. It is also justifiable to remove drivers and/or resilience indicators before analysis and interpretation, where these factors do not appear to be relevant. For example, coral disease is one of the 11 resilience indicators indicated as having high importance by McClanahan *et al.* (2012), but in this study and that of Maynard *et al.* (2015) no coral disease was observed and hence was not included.

Often time and money limit assessments to a narrow temporal window and require indirect or secondary sources of information to contextualise findings from these studies (Table 5.8). In this study locations outside of Kenya were visited only once for a period of 1-2 weeks at different times of the year (see Section 5.2). Snapshots of reef condition have been criticised because the state of a reef at a particular moment in time does not reveal the underlying trajectories and processes influencing the resilience of reef (Spalding and Brown 2015, Anthony *et al.* 2015) (Fig. 5.15b). For example, recruitment is highly variable between years (Connell *et al.* 1997), and therefore a single observation is unlikely to reflect the true recruitment rate for that site. It should also be noted that macroalgae cover and biomass changes seasonally (Ateweberhan *et al.* 2006), and hence the macroalgae cover recorded in this study may not reflect the average macroalgal cover for the sites. Monitoring reef condition over longer periods can increase confidence in the reliability of resilience assessments and, where available, information about past reef states can be used to understand past acute disturbances and general reef trajectory (Houk *et al.* 2014, Graham *et al.* 2015) (Table 5.8).

Both acute and chronic thermal stress play a major role in understanding reef condition and resilience (McClanahan *et al.* 2007a, Donner *et al.* 2009), but in this study were only available for sites at a ~50km resolution set by the satellite data used (Eakin *et al.* 2009), which greatly reduced the explanatory power of this variable (section 5.4.2). With more resources, data loggers could reveal site-level variation in thermal stress, which is known to vary greatly over small spatial scales (Selig *et al.* 2010) and reef zones (Oliver and Palumbi 2011). Proxies for underlying processes, such as nearby human population and distance to the mainland are useful because they encompass a range of influences on reefs (Mora *et al.* 2011). However, direct observations of specific processes, such as monitoring fishing pressure or terrestrial run-off can give a more refined understanding of drivers or reef condition and conservation options (Jouffray *et al.* 2015).

Despite being limited to a snap-shot view of reefs and having limited data and resources, the interpretation of this resilience assessment produced several useful findings. The independent nature of resilience and resistance potential on reefs was observed (Figs. 5.5 and 5.6), which is concordant with current resilience theory (Nyström *et al.* 2008) and management frameworks (West and Salm 2003, McClanahan *et al.* 2012). Three of the five explanatories variables were significantly correlated with resistance and recovery scores, displaying relationships similar to other studies (Section 5.4.2). The current resilience model needs to incorporate thresholds and non-linear processes (Fig. 5.14), to reflect the existence of stable states within reef systems (Hughes 1994, Jouffray *et al.* 2015) to improve the predictive ability of resilience assessments.

**Plate 6. Healthy coral growth on Uyombo reef, Watamu, in October 2015 (Photo: B. Cowburn). This reef is predicted to experience severe thermal stress in April 2016.**

# Chapter 6. Overall Conclusions

This thesis began by discussing the crisis facing coral reefs in a world with rising human pressures and climatic stress (Chapter 1). Watamu Marine National Park (WMNP) in Kenya was used as a case study to investigate a range of ecological and conservation issues facing coral reefs in the 21st century (Chapters 2-4). The park is a useful example of marine conservation, as the area has been protected for a long time (>45 years), with active conservation management and extensive research occurring in the area (Chapter 2). Nevertheless, the reef has experienced significant changes in the reef state during this time (Chapter 3) and has suffered repeated thermal stress (Chapter 4). The findings from Watamu are compared with observations of reef health and resilience from selected sites across the Indian Ocean (Chapter 5), to explore the range of reef conditions found on modern reefs and discuss general conservation options in a warming world.

## 6.1 WMNP, a long-term case study in marine conservation and reef health

Watamu's reefs are a small component of the wider matrix of habitats found in the area, including extensive seagrass beds, intertidal habitats and mangrove forest. Coral-dominated substrata make up just 1% of the lagoon area with other habitats harbouring diverse marine communities and unique species (Chapter 2). However, the concentration of life is greatest around the carbonate reef structures, with half of the fish and invertebrate richness and 95% of the coral genera recorded in WMNP found on reefs (Chapter 2). The reefs are also the most important habitats for income generation, with the majority of WMNP's revenue coming from snorkelling tourism on patch reefs in the park (Cowburn *et al.* 2013).

The impacts of mass coral bleaching in the Western Indian Ocean (WIO) during the 1998 El-Nino Southern Oscillation (ENSO), were well-documented (Obura 2005, McClanahan 2014) showing dramatic declines of coral in many locations (McClanahan *et al.* 2001). It was also noted that many reefs showed good recovery in the past 17 years (Ateweberhan *et al.* 2011). Unfortunately, this was not the case in WMNP, where the coral cover and community structure has shown little recovery from post-bleaching conditions in 1999 (Chapter 3). Comparing estimates of coral recruitment, growth and mortality between Obura (1995)'s Ph.D. research in Watamu pre-1998 and the data presented in this thesis suggest that one reason for this lack of recovery is that main northern reefs have seen a decline in recruitment (Chapter 3), although Uyombo, a small reef in the south of WMNP (Fig. 1.5), has maintained recruitment rates similar to pre-1998 levels (Chapter 3).

Local anthropogenic stressors may have a role to play as there has been a 900% increase in population in the area within 5km of the reefs over the past 40 years (Muthiga 2009). WMNP has been effective at preventing the majority of fishing in the no-take zone (B. Cowburn pers. obs.), but would be unable to protect against the effects of wastewater, pollution and run-off that come from the land. No research relating to water quality in WMNP was found during a literature search (Appendix 1) and hence a research priority for the park would be to investigate the influence of Watamu's human population on the lagoon. The situation of reefs in WMNP illustrates that marine protected areas (MPAs) can still experience multiple stressors despite being formally protected (Chapter

2). Extra conservation measures are needed, if WMNP is to continue providing ecosystem services and protecting important biodiversity (Chapter 2).

An alternative hypothesis for the decline in recruitment is that WMNP is isolated from dispersal pathways as a result of its location at the end of the East African Coastal Current (Obura 2012). Recovery rates may be naturally slow because of the reefs are found in a lagoon that receives outflow from a tidal mangrove creek (Fig. 1.4). In addition to this, poor circulation of lagoonal waters can lead to reduced recruitment (O'Leary and Potts 2011) and increased thermal stress in these areas (Chapter 4) (Oliver and Palumbi 2011). Whether these natural factors are affecting WMNP's recovery is unsubstantiated, but evidence from other locations highlights the importance of considering natural drivers that affect the overall resilience of reef ecosystems (Chapter 5) (Houk *et al.* 2014, Jouffray *et al.* 2015). Because environmental factors operate simulataneously on reefs it is not possible to determine the relative importance of human and natural drivers on Watamu's marine community. However, the past trajectories and current reef states provide useful insights in to the future for corals in WMNP.

## 6.2 The current reef state and resilience of WMNP

In the 1980s and early 1990s the coral cover on Watamu's reefs was approximately 30% and dominated by *Acropora* and *Montipora* (Chapter 3). Of the six known bleaching events during the past three decades, 1998 was the only event to cause significant mortality (Chapter 3). The post-1998 reef state is dominated by turf algae, with a quarter of the benthos covered by macroalgae and just 10% coral cover (Chapter 3). Long term monitoring of Coral Gardens and the current data on reef state across different sites in WMNP (Fig. 1.5), show that this reef condition is relatively consistent spatially and over time since 1998 (Chapter 3). Stable states are predicted by theoretical ecology (Holling 1973) and have been observed in coral reef ecology (Hughes 1994, Mumby *et al.* 2007b). The current state in WMNP is unusual in that it is neither coral dominated nor macroalgal dominated, as seen on many reefs in the Caribbean (Gardner *et al.* 2003). It is possible that the reef is in a transitory stage, as has been suggested for turf algae-dominated reefs elsewhere (Jouffray *et al.* 2015). However, the consistency of reef state in Watamu since 1998, suggests this may be a new stable state.

Environmental variability and disturbance can improve the resilience of ecosystems (Holling 1973) and in reef ecology past-bleaching experience has been shown to improve the resistance of certain coral species to further thermal stress (e.g. Brown *et al.* 2002). *Acropora* and *Montipora* suffered >90% mortality in 1998, leaving a coral community dominated by more thermally-resistant corals, such as massive *Porites* and merulnid colonies (Chapters 3 and 5). This selection against thermally sensitive genera may represent a significant adaptation of the coral community in WMNP to increasing temperatures (Chapter 5). Past bleaching experience can also lead to improved resistance through the acclimatisation of individual corals, through altered polyp physiology or more thermally-tolerant zooxanthellae symbionts (Buddemeier and Fautin 1993). In this thesis acclimatisation of WMNP's coral community was not directly tested, but observations of bleaching susceptibility during a minor bleaching event in 2013 showed that some corals, including branching *Acropora* colonies, were tolerant to bleaching and returned to normal colouration without any obvious negative impacts (Chapter 4). During the non-lethal bleaching in 2013 and three other minor events since 1998, it is likely that WMNP's corals will have acclimatised to higher thermal stress over recent time (Obura 2009, Berklemans *et al.* 2009). However, the thermal stress in 2013 was not nearly as extreme as 1998, and it will take another event of similar magnitude to determine how much adaptation and acclimatisation has occurred on WMNP's reefs (Chapter 4) (Maynard *et al.* 2008).

Based on the recent trajectory of Watamu's coral cover, reefs in WMNP would be classed as being a 'Reef at a critical stage' based on Wilkinson (2008)'s global status of reefs categories, where it has managed to maintain some coral cover and typical reef function, but is vulnerable to further threats and coral decline. At the time of writing in December 2015, a major ENSO event has already caused mass bleaching in parts of the Caribbean and Pacific this year (NOAA 2015) (Fig. 6.1) and is expected to bring thermal stress and coral bleaching to coral reefs in the WIO by April and May 2016. It appears that the current coral community and lagoonal nature of Watamu's reefs mean that reefs would be resistant to bleaching (Chapters 4 and 5). However, if significant mortality took place, recovery of the coral community would be slow (Chapters 3 and 5). It is unclear whether its resistance to thermal stress will also confer resilience to other disturbances. Fifteen percent of reefs globally are estimated to be at a 'critical stage' (Wilkinson 2008), illustrating the need to improve the resilience of these reefs, if they are not to phase-shift to even less desirable states (Anthony *et al.* 2015).

## 6.3 Using resilience theory for the conservation of coral reefs

How typical is WMNP's resilience compared to reefs worldwide? In contrast to other coral regions, reefs in the Indian Ocean recovered well from 1998 bleaching (Ateweberhan *et al.* 2011) and when compared to reefs in the Caribbean and other locations it can be seen that WMNP is a healthier and a more resilient reef system (Gardner *et al.* 2003, Ledlie *et al.* 2007). Resilience assessments were used to compare Watamu with five other locations across the Indian Ocean (Chapter 5). Watamu and Kuramathi in the Maldives were found to be the most resilient locations. Both sites experienced extensive bleaching and mortality in 1998, but were resilient for different reasons. Assessments in Kuramathi showed these reefs had very high recovery potential with good levels of coral recruitment and high herbivorous fish biomass. Hence, conservation efforts to protect Kuramathi against future bleaching impacts would mean *maintaining* factors that facilitate the rapid recovery of its reefs and investigating measures to *improve* the resistance of the area. In Watamu the opposite would be required, because of its high resistance and low recovery potential (Chapter 3). The contrasting conclusions demonstrate the importance of applying resilience as a framework for conservation decision-making.

Enggano (Sumatra) and Vamizi (Mozambique) had lower resilience scores than Watamu and Kuramathi, but had healthier coral communities (Chapter 5). Past thermal stress in these locations had not reached levels high enough to cause extensive mortality (Liu *et al.* 2003) and it appears these locations are examples of reefs that have avoided past bleaching (Obura 2005). In Enggano this was because of cooler upwellings in 1998 that occurred as a result of the Indian Ocean Dipole (IOD) that coincided with the ENSO that year

(Webster *et al.* 1999). It is not clear whether Enggano's avoidance of thermal stress is a reliable factor for all future bleaching events, but based on Sea Surface Temperatures (SSTs) in September 2015 (Fig. 6.1) it appears the cooler upwelling has occurred during this current ENSO event and may protect corals in Sumatra once more. Avoidance is not a component of resilience, but is an equally important consideration for conservation planning (West and Salm 2003). Enggano is a priority site for conservation and further research because it has low anthropogenic stress, moderately-high resilience and resistance and has demonstrated past avoidance to thermal stress (Knowlton and Jackson 2008).

Chapter 5 showed the variation in resilience of reefs across the Indian Ocean. Relationships between the resilience indicators and environmental drivers, such as human pressure and past climate influence, helped interpret the conservation options in these locations. Research into reef ecology is producing new findings that are relevant to building a model of resilience and interpreting observations of resilience in the field (Chapter 5) (see also Graham *et al.* 2013, Mumby *et al.* 2014, Anthony *et al.* 2015). The application of resilience theory in current conservation efforts will help refine the current model with the future responses of these reefs (Emslie *et al.* 2015). Hopefully with the growing political will to prevent global climate change and increasing awareness of the plight of coral reefs in the general public, reefs will face a more positive future in the long-term. The immediate future for coral reefs will depend on the intensity and frequency of future bleaching events as a result of committed warming (Donner *et al.* 2009) and our ability to improve the resilience of reefs to survive these impacts.

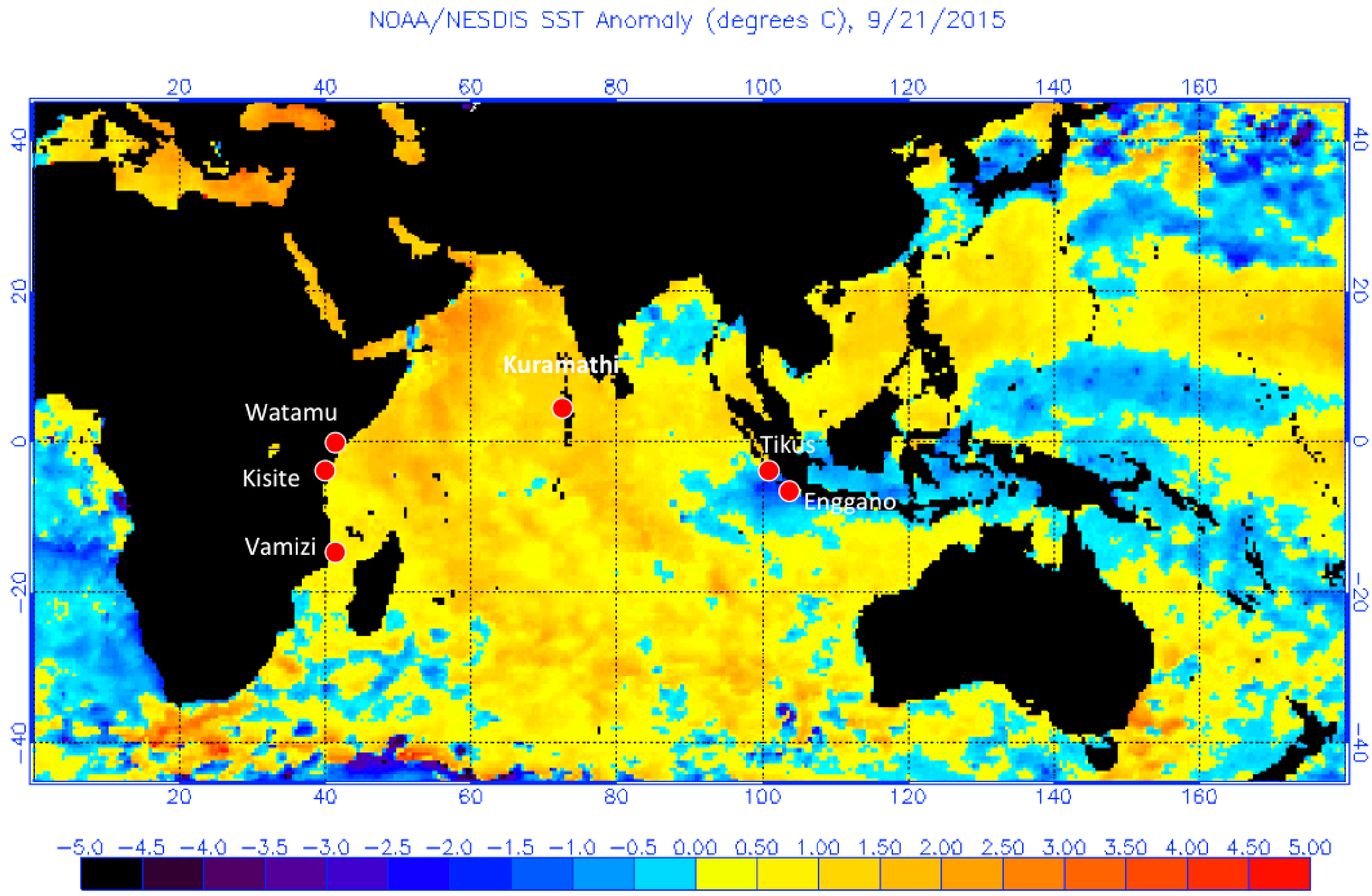


**Figure 6.1 A map of the Indian Ocean and Western Pacific, showing the Sea Surface Temperature (SST) anomaly on the 21st of September 2015, with locations from Chapter 5 indicated. Current El-Nino Southern Oscillation (ENSO) conditions are pooling warmer water in the Central and Western Indian Ocean, while cooler waters well to the surface off Sumatra.**

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*Research group:* Other

# Appendix 2: Species lists

☐☐Incidental record

34 Abundance from quantitative surveys

## Appendix 2a: Fish

| Family | Genus | Species | Common Name | Reef | Intertidal | Seagrass-Sand |
|---|---|---|---|---|---|---|
| Acanthuridae | *Acanthurus* | *dussemieri* | Eyestripe surgeonfish | ☐ | | 2 |
| Acanthuridae | *Acanthurus* | *leucosternon* | Powderblue surgeonfish | 279 | | 1 |
| Acanthuridae | *Acanthurus* | *lineatus* | Lined surgeonfish | | | ☐ |
| Acanthuridae | *Acanthurus* | *nigricauda* | Blackstreak surgeonfish | 38 | | 8 |
| Acanthuridae | *Acanthurus* | *nigrofuscus* | Dusky surgeonfish | 34 | ☐ | 65 |
| Acanthuridae | *Acanthurus* | *tennentii* | Lieutenant surgeonfish | 8 | | ☐ |
| Acanthuridae | *Acanthurus* | *triostegus* | Convict surgeonfish | 2 | 2 | 28 |
| Acanthuridae | *Acanthurus* | *xanthopterus* | Yellowfin surgeonfish | 10 | ☐ | ☐ |
| Acanthuridae | *Ctenochaetus* | *binotatus* | Twospot Bristletooth | ☐ | | |
| Acanthuridae | *Ctenochaetus* | *striatus* | Striped Bristletooth | 253 | | |
| Acanthuridae | *Ctenochaetus* | *truncatus* | Goldring Bristletooth | 18 | | |
| Acanthuridae | *Naso* | *annulatus* | Whitemargin unicornfish | ☐ | | |
| Acanthuridae | *Naso* | *brachycentron* | Humpback unicornfish | 1 | | |
| Acanthuridae | *Naso* | *brevirostris* | Spotted unicornfish | 17 | | |
| Acanthuridae | *Naso* | *elegans* | Orangespine unicornfish | 7 | | |
| Acanthuridae | *Naso* | *fageni* | Horse-face unicornfish | ☐ | | |
| Acanthuridae | *Naso* | *unicornis* | Bluespine unicornfish | 26 | | |
| Acanthuridae | *Naso* | *vlamingi* | Bignose unicornfish | ☐ | | |
| Acanthuridae | *Zebrasoma* | *desjardinii* | Desjardin's sailfin tang | 2 | | |
| Acanthuridae | *Zebrasoma* | *scopas* | Brown tang | 24 | | |
| Antennariidae | *Histrio* | *histrio* | Sargassumfish | | | |
| Apogonidae | *Apogon* | *nigripes* | Blackfoot cardinalfish | | | 102 |
| Apogonidae | *Apogon* | *semiornatus* | Obliquebanded cardinalfish | | | |
| Apogonidae | *Apogonichthyoides* | *taeniatus* | Twobelt cardinalfish | | ☐ | |
| Apogonidae | *Archamia* | *fucata* | Orange-lined Cardinalfish | ☐ | | |
| Apogonidae | *Cheilodipterus* | *arabicus* | Tiger Cardinalfish | ☐ | | 7 |
| Apogonidae | *Cheilodipterus* | *artus* | Wolf cardinalfish | ☐ | | |
| Apogonidae | *Cheilodipterus* | *macrodon* | Large-tooth cardinalfish | ☐ | | |
| Apogonidae | *Cheilodipterus* | *quinquelineatus* | Five-lined cardinalfish | ☐ | ☐ | |
| Apogonidae | *Ostorhinchus* | *angustatus* | Broad-striped cardinalfish | ☐ | | |
| Apogonidae | *Ostorhinchus* | *aureus* | Ring-tailed Cardinalfish | ☐ | | |
| Apogonidae | *Ostorhinchus* | *cookii* | Cook's Cardinalfish | ☐ | 17 | 6 |
| Apogonidae | *Ostorhinchus* | *cyanosoma* | Yellow-striped Cardinalfish | ☐ | | 2 |
| Apogonidae | *Ostorhinchus* | *flagellifera* | Coachwhip cardinalfish | ☐ | | |
| Apogonidae | *Ostorhinchus* | *nigrofasciatus* | Black-stripe cardinalfish | ☐ | | |
| Apogonidae | *Ostorhinchus* | *taeniophorus* | Reef-flat cardinalfish | | 5 | 104 |
| Apogonidae | *Pristapogon* | *kallopterus* | Iridescent cardinalfish | ☐ | 1 | |
| Atherinidae | *Atherinomorus* | *lacunosus* | Hardy silverhead | | ☐ | ☐ |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Aulostomidae | *Aulostomus* | *chinensus* | Trumpetfish | 5 | | | | |
| Balistidae | *Balistoides* | *undulatus* | Orange-strip triggerfish | 4 | | | | |
| Balistidae | *Balistoides* | *viridescens* | Giant triggerfish | ☐ | | | | |
| Balistidae | *Pseudobalistes* | *flavimarginatus* | Yellowmargin triggerfish | | ☐ | | | |
| Balistidae | *Pseudobalistes* | *fuscus* | Blue triggerfish | ☐ | | | | |
| Balistidae | *Rhinecanthus* | *assasi* | Picassofish | 1 | ☐ | | | 20 |
| Balistidae | *Rhinecanthus* | *rectangulus* | Wedge picassofish | | ☐ | | | 1 |
| Balistidae | *Sufflamen* | *chrysopterus* | Halfmoon triggerfish | 10 | | | | 1 |
| Balistidae | *Sufflamen* | *fraenatus* | Bridled triggerfish | 3 | | | | 1 |
| Blenniidae | *Antennablennius* | *variopunctatus* | Orange-spot blenny | | | 21 | | |
| Blennidae | *Aspidontus* | *taeniatus* | Cleanerfish mimic | | | | | |
| Blenniidae | *Blenniella* | *chrysospilos* | Red-spotted blenny | | ☐ | | | |
| Blenniidae | *Blenniella* | *cyanostigma* | Striped rockskipper | | | 19 | | |
| Blenniidae | *Cirripectes* | *castaneus* | Chestnut Blenny | 3 | | | | |
| Blenniidae | *Cirripectes* | *stigmaticus* | Redstreaked blenny | ☐ | | | | |
| Blenniidae | *Entomacrodus* | *striatus* | Blackspotted rockskipper | | ☐ | | | |
| Blenniidae | *Exallias* | *brevis* | Leopard blenny | 1 | | | | |
| Blenniidae | *Hirculops* | *cornifer* | Highbrow rockskipper | | | 1 | | |
| Blenniidae | *Istiblennius* | *lineatus* | Lined rockskipper | | ☐ | | | |
| Blenniidae | *Istiblennius* | *unicolor* | Pallid rockskipper | | | 1 | | |
| Blenniidae | *Meiacanthus* | *mossambicus* | Mocambique fangblenny | 3 | | | | |
| Blenniidae | *Plagiotremus* | *rhinorhynchos* | Bluestriped fangblenny | 1 | ☐ | | | |
| Blenniidae | *Plagiotremus* | *tapeinosoma* | Scale-eating fangblenny | 1 | | | ☐ | |
| Blenniidae | *Salarias* | *fasciatus* | Jeweled blenny | | | 1 | | |
| Caesionidae | *Caesio* | *caerulaurea* | Scissor-tailed fusilier | ☐ | | | | |
| Caesionidae | *Caesio* | *lunaris* | Lunar fusilier | 6 | | | | |
| Caesionidae | *Caesio* | *teres* | Yellowback fusilier | ☐ | | | | |
| Caesionidae | *Caesio* | *xanthonota* | Yellowtop fusilier | ☐ | | | | |
| Caesionidae | *Dipterygonotus* | *balteatus* | Mottled fusilier | ☐ | | | | |
| Caesionidae | *Pterocaesio* | *chrysozona* | Goldband fusilier | 30 | | | | |
| Callionymidae | *Synichiropus* | *stellatus* | Starry dragonet | ☐ | | | | |
| Caracanthidae | *Caracanthus* | *madagascariensis* | Spotted coral croucher | ☐ | | | | |
| Caracanthidae | *Caracanthus* | *unipinna* | Pygmy coral croucher | ☐ | | | | |
| Carangidae | *Alectis* | *inidicus* | Indian threadfin | | | | ☐ | |
| Carangidae | *Carangoides* | *ferdau* | Bar jack | ☐ | | | | |
| Carangidae | *Carangoides* | *fulvoguttatus* | Yellow-dotted trevally | ☐ | | | | |
| Carangidae | *Caranx* | *herberi* | Black-tip trevally | ☐ | | | | |
| Carangidae | *Caranx* | *ignobilis* | Giant trevally | | | | ☐ | |
| Carangidae | *Caranx* | *melampygus* | Bluefin trevally | 1 | | | | |
| Carangidae | *Caranx* | *papuensis* | Brassy trevally | ☐ | | | | |
| Carangidae | *Caranx* | *sexfasciatus* | Bigeye trevally | ☐ | | | | |
| Carangidae | *Gnathanodon* | *speciosus* | Golden trevally | | | | ☐ | |
| Carangidae | *Scomberoides* | *lysan* | Doublespot Queenfish | ☐ | | | | |
| Carangidae | *Trachinostus* | *blochii* | Silver pompano | | | | ☐ | |
| Carcharhinidae | *Carcharhinus* | *melanopterus* | Reef blacktip shark | | | | ☐ | |
| Carcharhinidae | *Triaenodon* | *obesus* | Reef whitetip shark | ☐ | | | | |

| | | | | | | |
|---|---|---|---|---|---|---|
| Centriscidae | *Aeoliscus* | *punctulatus* | Speckled shrimpfish | | | ☐ |
| Chaetodontidae | *Chaetodon* | *auriga* | Threadfin butterflyfish | 13 | ☐ | 4 |
| Chaetodontidae | *Chaetodon* | *falcula* | Saddleback butterflyfish | ☐ | | |
| Chaetodontidae | *Chaetodon* | *guttatissimus* | Spotted butterflyfish | 2 | | |
| Chaetodontidae | *Chaetodon* | *kleinii* | Klein's butterflyfish | ☐ | | 1 |
| Chaetodontidae | *Chaetodon* | *lineolatus* | Lined butterflyfish | ☐ | | |
| Chaetodontidae | *Chaetodon* | *leucopleura* | Somali butterflyfish | | | ☐ |
| Chaetodontidae | *Chaetodon* | *lunula* | Raccoon butterflyfish | 14 | ☐ | 5 |
| Chaetodontidae | *Chaetodon* | *meyeri* | Meyer's butterflyfish | 4 | | |
| Chaetodontidae | *Chaetodon* | *trifascialis* | Chevroned butterflyfish | 4 | | |
| Chaetodontidae | *Chaetodon* | *trifasciatus* | Redfin butterflyfish | 7 | | |
| Chaetodontidae | *Chaetodon* | *vagabundus* | Vagabond butterflyfish | | | ☐ |
| Chaetodontidae | *Chaetodon* | *xanthocephalus* | Yellowhead butterflyfish | 1 | | |
| Chaetodontidae | *Forcipiger* | *flavissimus* | Long-nose butterflyfish | ☐ | | |
| Chaetodontidae | *Heniochus* | *acuminatus* | Longfin bannerfish | ☐ | | |
| Chaetodontidae | *Heniochus* | *monoceros* | Masked bannerfish | 2 | | |
| Cirrihitidae | *Amblycirrihitus* | *bimacula* | Two-spotted hawkfish | ☐ | | |
| Cirrihitidae | *Paracirrhites* | *arcatus* | Monocle Hawkfish | 2 | | |
| Cirrihitidae | *Paracirrhites* | *forsteri* | Freckled Hawkfish | 7 | | |
| Cirrihitidae | *Cirrhitichthys* | *oxycephalus* | Pixy Hawkfish | ☐ | | |
| Cirrihitidae | *Cirrhitus* | *pinnulatus* | Stocky Hawkfish | | | ☐ |
| Clupeidae | *Herklotsichthys* | *quadrimaculatus* | Gold spot herring | | ☐ | ☐ |
| Clupeidae | *Spratelloides* | *gracilis* | Blue lateral sprat | | | ☐ |
| Congridae | *Conger* | *cinereus* | Moustache conger | | | |
| Dasyatidae | *Himantura* | *gerrardi* | Sharpnose stingray | | | ☐ |
| Dasyatidae | *Himantura* | *uarnak* | Honeycomb stingray | | | ☐ |
| Dasyatidae | *Neotrygon* | *kuhlii* | Bluespotted stingray (grey) | | | ☐ |
| Dasyatidae | *Taeniura* | *lymma* | Bluespotted Stingray | 1 | | ☐ |
| Diodontidae | *Diodon* | *hystrix* | Porcupinefish | ☐ | ☐ | 1 |
| Diodontidae | *Diodon* | *liturosus* | Black-blotched porcupinefish | ☐ | ☐ | ☐ |
| Echeneidae | *Echeneis* | *naucrates* | Sharksucker | ☐ | | |
| Ephippidae | *Platax* | *orbicularis* | Batfish | 7 | | |
| Ephippidae | *Platax* | *teira* | Longfin spadefish | | ☐ | |
| Ephippidae | *Tripterodon* | *orbis* | African spadefish | | | |
| Fistulariidae | *Fistularia* | *commersonii* | Cornetfish | 6 | | |
| Gerreidae | *Gerres* | *longirostris* | Smallscale mojarra | | ☐ | |
| Gerreidae | *Gerres* | *oyena* | Blacktip mojarra | | ☐ | ☐ |
| Gobiidae | *Amblyeleotris* | *wheeleri* | Gorgeous prawn-goby | | | ☐ |
| Gobiidae | *Cryptocentrus* | *fasciastus* | Barred prawn-goby | | | ☐ |
| Gobiidae | *Cryptocentrus* | *lutheri* | Luther's prawn-goby | | | ☐ |
| Gobiidae | *Cryptocentrus* | *strigilliceps* | Target prawn-goby | | | ☐ |
| Gobiidae | *Ctenogobiops* | *feroculus* | Sandy prawn-goby | | | ☐ |
| Gobiidae | *Gnatholepis* | *cauerensis* | Eye-bar goby | | 7 | |
| Gobiidae | *Gnatholepis* | *scapulostigma* | Shoulder-spot goby | | ☐ | |
| Gobiidae | *Istigobius* | *ornatus* | Ornate goby | | 4 | |
| Gobiidae | *Paragobiodon* | *modestus* | Modest goby | ☐ | | |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Gobiidae | *Pleurosicya* | *micheli* | Michels ghost goby | ☐ | | | | |
| Gobiidae | *Valenciennea* | *strigata* | Blue-streak goby | ☐ | | | ☐ | |
| Haemulidae | *Plectorhinchus* | *albovittatus* | Giant sweetlips | | | | ☐ | |
| Haemulidae | *Plectorhinchus* | *chubbi* | Dusky sweetlips | ☐ | | | | |
| Haemulidae | *Plectorhinchus* | *flavomaculatus* | Gold-spotted sweetlips | 38 | | | | 20 |
| Haemulidae | *Plectorhinchus* | *gaterinus* | Black-spotted sweetlips | 29 | | | | |
| Haemulidae | *Plectorhinchus* | *gibbosus* | Gibbus sweetlips | | | | ☐ | |
| Haemulidae | *Plectorhinchus* | *paulayi* | Diagonal-lined sweetlips | | | | ☐ | |
| Haemulidae | *Plectorhinchus* | *plagiodesmus* | Red-lined sweetlips | | | | ☐ | |
| Haemulidae | *Plectorhinchus* | *playfairi* | Whitebarred sweetlips | 6 | | | | |
| Haemulidae | *Plectorhinchus* | *schotaf* | Somber sweetlips | 1 | | | ☐ | |
| Haemulidae | *Plectorhinchus* | *sordidus* | Black sweetlips | | | | ☐ | |
| Haemulidae | *Plectorhinchus* | *vittatus* | Oriental sweetlips | ☐ | | | | |
| Hemiramphidae | *Hyporhamphus* | *affinis* | Insular halfbeak | | | | ☐ | |
| Hemiramphidae | *Hemiramphus* | *far* | Spotted halfbeak | | | | | 5 |
| Holocentridae | *Myripristis* | *adusta* | Bronze soldierfish | | | | | |
| Holocentridae | *Myripristis* | *hexagona* | Doubletoothed soldierfish | 4 | | | | |
| Holocentridae | *Myripristis* | *murdjan* | Red soldierfish | | | | ☐ | |
| Holocentridae | *Myripristis* | *pralinia* | Scarlet soldierfish | | | | ☐ | |
| Holocentridae | *Myripristis* | *violacea* | Violet soldierfish | 3 | | | | |
| Holocentridae | *Neoniphon* | *argenteus* | Clearfin soldierfish | | | | | |
| Holocentridae | *Neoniphon* | *sammara* | Bloodspot soldierfish | ☐ | | | | |
| Holocentridae | *Plectrypops* | *lima* | Cardinal soldierfish | | ☐ | | | |
| Holocentridae | *Sargocentron* | *caudimaculatum* | Tailspot squirrelfish | ☐ | | | | |
| Holocentridae | *Sargocentron* | *diadema* | Crown squirrelfish | 2 | | | | 7 |
| Kuhliidae | *Kuhlia* | *mugil* | Barred flagtail | | ☐ | | | |
| Kyphosidae | *Kyphosus* | *cinerascens* | Highfin rudderfish | ☐ | | | | |
| Kyphosidae | *Kyphosus* | *vaigiensis* | Brassy rudderfish | 65 | | | | |
| Labridae | *Anampses* | *caeruleopunctatus* | Blue-spotted wrasse | 3 | | | | |
| Labridae | *Anampses* | *melanurus* | White-spotted wrasse | ☐ | | | | |
| Labridae | *Anampses* | *meleagrides* | Yellowtail wrasse | 1 | | | | |
| Labridae | *Anampses* | *twistii* | Yellow-breasted wrasse | 5 | | | | |
| Labridae | *Bodianus* | *axillaris* | Axilspot hogfish | 9 | | | | |
| Labridae | *Bodianus* | *diana* | Diana's hogfish | ☐ | | | | |
| Labridae | *Cheilinus* | *chlorourus* | Floral wrasse | ☐ | | | ☐ | |
| Labridae | *Cheilinus* | *oxycephalus* | Snooty wrasse | 4 | | | | |
| Labridae | *Cheilinus* | *trilobatus* | Tripletail wrasse | 23 | | | | 14 |
| Labridae | *Cheilio* | *inermis* | Cigar wrasse | 2 | ☐ | | | 27 |
| Labridae | *Coris* | *aygula* | Clown Coris | 2 | | | | |
| Labridae | *Coris* | *caudimacula* | Spottail Coris | 3 | | 1 | | 24 |
| Labridae | *Coris* | *cuvieri* | African Coris | 1 | | | | 2 |
| Labridae | *Coris* | *formosa* | Queen Coris | 1 | ☐ | | | 9 |
| Labridae | *Epibulus* | *insidiator* | Slingjaw wrasse | 2 | | | | |
| Labridae | *Gomphosus* | *caeruleus* | Indian bird wrasse | 15 | | | | |
| Labridae | *Halichoeres* | *hortulanus* | Checkerboard wrasse | 26 | | 2 | | 3 |
| Labridae | *Halichoeres* | *marginatus* | Dusky wrasse | 6 | | | | |

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|---|---|---|---|---|---|---|
| Labridae | *Halichoeres* | *nebulosus* | Nebulous wrasse | | | 45 |
| Labridae | *Halichoeres* | *scapularis* | Zigzag wrasse | 2 | 1 | 3 |
| Labridae | *Hemigymnus* | *fasciastus* | Barred thicklip wrasse | 6 | | |
| Labridae | *Hemigymnus* | *melapterus* | Blackedge thicklip wrasse | ☐ | | |
| Labridae | *Hologymnosus* | *annulatus* | Ring wrasse | 2 | | 2 |
| Labridae | *Iniistius* | *pavo* | Blue razorfish | | | ☐ |
| Labridae | *Iniistius* | *pentadactylus* | Fivefinger razorfish | | | ☐ |
| Labridae | *Labrichthys* | *unilineatus* | Tubelip wrasse | 5 | | |
| Labridae | *Labroides* | *bicolor* | Bicolour cleaner wrasse | 3 | | |
| Labridae | *Labroides* | *dimidiatus* | Bluestreak cleaner wrasse | 32 | 6 | 17 |
| Labridae | *Macropharyngodon* | *bipartitus* | Vermiculate wrasse | ☐ | | 5 |
| Labridae | *Novaculichthys* | *macrolepidotus* | Seagrass wrasse | | | 19 |
| Labridae | *Novaculichthys* | *taeniourus* | Dragon wrasse | 2 | | |
| Labridae | *Oxycheilinus* | *bimaculatus* | Twospot wrasse | ☐ | | |
| Labridae | *Oxycheilinus* | *digrammus* | Bandcheek wrasse | 6 | | |
| Labridae | *Pseudocheilinus* | *evanidus* | Disappearing wrasse | ☐ | | |
| Labridae | *Pseudocheilinus* | *hexataenia* | Six-line wrasse | 17 | | |
| Labridae | *Pteragogus* | *flagellifera* | Flagfin wrasse | ☐ | | |
| Labridae | *Stethojulis* | *albovittata* | Bluelined wrasse | ☐ | ☐ | 28 |
| Labridae | *Stethojulis* | *strigiventer* | Three-line wrasse | ☐ | ☐ | |
| Labridae | *Thalassoma* | *amblycephalum* | Two tone wrasse | 58 | 1 | ☐ |
| Labridae | *Thalassoma* | *hardwicke* | Six-bar wrasse | 19 | | 2 |
| Labridae | *Thalassoma* | *hebraicum* | Goldbar wrasse | 62 | 11 | 5 |
| Labridae | *Thalassoma* | *lunare* | Crescent wrasse | 5 | | 3 |
| Labridae | *Thalassoma* | *purpureum* | Surge wrasse | | | ☐ |
| Labridae | *Thalassoma* | *quinquevittatum* | Five-stripe wrasse | | | ☐ |
| Labridae | *Thalassoma* | *trilobatum* | Christmas wrasse | ☐ | | |
| Lethrinidae | *Gnathodentex* | *aurolineatus* | Yellowspot emperor | ☐ | | |
| Lethrinidae | *Lethrinus* | *harak* | Blackspot Emperor | 1 | ☐ | 45 |
| Lethrinidae | *Lethrinus* | *lentjan* | Pink-ear emperor | | | ☐ |
| Lethrinidae | *Lethrinus* | *mehsena* | Sky Emperor | 7 | | ☐ |
| Lethrinidae | *Lethrinus* | *microdon* | Smalltooth Emperor | 1 | | |
| Lethrinidae | *Lethrinus* | *obsoletus* | Orange-stripe emperor | ☐ | | |
| Lethrinidae | *Monotaxis* | *grandoculis* | Big-eye Emperor | 4 | | |
| Lutjanidae | *Lutjanus* | *argentimaculatus* | River Snapper | 11 | | ☐ |
| Lutjanidae | *Lutjanus* | *bohar* | Red Snapper | 17 | | |
| Lutjanidae | *Lutjanus* | *coeruleolineatus* | Blueline snapper | | | |
| Lutjanidae | *Lutjanus* | *ehrenbergi* | Ehrenberg's Snapper | | | ☐ |
| Lutjanidae | *Lutjanus* | *fluvus* | Flametail Snapper | ☐ | | |
| Lutjanidae | *Lutjanus* | *fulviflamma* | Blackspot Snapper | 42 | 1 | 2 |
| Lutjanidae | *Lutjanus* | *gibbus* | Humpback Snapper | 3 | | |
| Lutjanidae | *Lutjanus* | *kasmira* | Blue-lined Snapper | 1 | 1 | |
| Lutjanidae | *Lutjanus* | *monostigma* | One-spot Snapper | ☐ | | |
| Lutjanidae | *Lutjanus* | *rivulatus* | Scribbled Snapper | ☐ | | |
| Lutjanidae | *Macolor* | *niger* | Black and white Snapper | 4 | | |
| Microdesmidae | *Ptereleotris* | *evides* | Blackfin dartfish | 50 | | |

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|---|---|---|---|---|---|---|
| Microdesmidae | *Ptereleotris* | *microlepis* | Pearly dartfish | | | ☐ |
| Mobulidae | *Manta* | *alfredi* | Alfred manta | | | ☐ |
| Monacanthidae | *Acreichthys* | *tomentosus* | Seagrass filefish | | | |
| Monacanthidae | *Aluterus* | *scriptus* | Scribbled filefish | 1 | | |
| Monacanthidae | *Cantherhines* | *fronticinctus* | Spectacled filefish | ☐ | ☐ | |
| Monacanthidae | *Cantherhines* | *pardalis* | Wire-net filefish | 4 | | ☐ |
| Monacanthidae | *Oxymonacanthus* | *longirostris* | Longnose filefish | 2 | | |
| Monacanthidae | *Paraluteres* | *prionurus* | Saddleback mimic | | | |
| Monacanthidae | *Pervagor* | *janthinosoma* | Blackbar filefish | 2 | | |
| Monodactylidae | *Monodactylus* | *argenteus* | Silver batfish | | | 10 |
| Mugilidae | *Oedalechilus* | *labiosus* | Foldlip mullet | | ☐ | |
| Mugilidae | *Valamugil* | *seheli* | Bluespot mullet | | | ☐ |
| Mullidae | *Mulloidichthys* | *flavolineatus* | Yellowstripe goatfish | 2 | | |
| Mullidae | *Mulloidichthys* | *vanicolensis* | Yellowfin goatfish | ☐ | | |
| Mullidae | *Parupeneus* | *bifasciatus* | Two-barred goatfish | | | ☐ |
| Mullidae | *Parupeneus* | *barberinus* | Dash and dot goatfish | 55 | ☐ | 11 |
| Mullidae | *Parupeneus* | *ciliatus* | Whitesaddle goatfish | ☐ | | |
| Mullidae | *Parupeneus* | *cyclostomus* | Yellow-saddle goatfish | 1 | | |
| Mullidae | *Parupeneus* | *indicus* | Indian goatfish | 2 | | 10 |
| Mullidae | *Parupeneus* | *macronema* | Longbarbel goatfish | ☐ | | 2 |
| Mullidae | *Parupeneus* | *rubescens* | Rosy goatfish | ☐ | | ☐ |
| Mullidae | *Upeneus* | *tragula* | Blackstriped goatfish | | | ☐ |
| Muraenidae | *Echidna* | *leucotaenia* | Whiteface moray | ☐ | 1 | |
| Muraenidae | *Echidna* | *nebulosa* | Snowflake moray | ☐ | 1 | |
| Muraenidae | *Gymnomuraena* | *zebra* | Zebra moray | | ☐ | |
| Muraenidae | *Gymnothorax* | *chilospilos* | Lipspot moray | | | |
| Muraenidae | *Gymnothorax* | *favagineus* | Honeycomb moray | | | ☐ |
| Muraenidae | *Gymnothorax* | *flavimarginatus* | Yellow-margined moray | ☐ | | |
| Muraenidae | *Gymnothorax* | *grisea* | Geometric moray | ☐ | | |
| Muraenidae | *Gymnothorax* | *pictus* | Peppered moray | | ☐ | |
| Muraenidae | *Gymnothorax* | *undulatus* | Undulated moray | | | |
| Muraenidae | *Scuticaria* | *tigrinus* | Tiger snake moray | ☐ | | |
| Muraenidae | *Uropterygius* | *marmoratus* | Marbled snake moray | | | |
| Myliobatidae | *Aetobatus* | *ocellatus* | Spotted eagle ray | | | ☐ |
| Nemipteridae | *Scolopsis* | *ghanam* | Arabian spinecheek | 2 | ☐ | |
| Ophichthidae | *Callechelys* | *marmorata* | Marbled snake eel | | | ☐ |
| Ophichthidae | *Myrichthys* | *colubrinus* | Harlequin snake eel | ☐ | | |
| Ophichthidae | *Myrichthys* | *maculosus* | Spotted snake eel | ☐ | | |
| Ostraciidae | *Lactoria* | *cornuta* | Longhorn cowfish | | ☐ | |
| Ostraciidae | *Lactoria* | *fornasini* | Thornback cowfish | | ☐ | |
| Ostraciidae | *Ostracion* | *cubicus* | Yellow boxfish | ☐ | | |
| Ostraciidae | *Ostracion* | *meleagris* | Whitespotted boxfish | ☐ | | 1 |
| Pegasidae | *Eurypegasus* | *draconis* | Short dragonfish | | | |
| Pempheridae | *Pempheris* | *bexillion* | | ☐ | | |
| Pempheridae | *Pempheris* | *flavicycla* | | 76 | 20 | |
| Pempheridae | *Pempheris* | *spp.* | | | | |

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|---|---|---|---|---|---|---|
| Pempheridae | *Pempheris* | *spp.* | | | | |
| Pempheridae | *Pempheris* | *spp.* | | | | |
| Pempheridae | *Pempheris* | *spp.* | | | | |
| Pempheridae | *Pempheris* | *spp.* | | | | |
| Pempheridae | *Pempheris* | *spp.* | | | | |
| Pempheridae | *Pempheris* | *spp.* | | | | |
| Pinguipedidae | *Parapercis* | *hexophthalma* | Speckled sandperch | 2 | | |
| Platycephalidae | *Papilloculiceps* | *longiceps* | Indian Ocean crocodilefish | | | ☐ |
| Platycephalidae | *Sunagocia* | *arenicola* | Broadhead flathead | | | ☐ |
| Platycephalidae | *Thysanophrys* | *chiltonae* | Longsnout flathead | | | ☐ |
| Plotosidae | *Plotosus* | *limbatus* | Darkfin catfish | | | ☐ |
| Plotosidae | *Plotosus* | *lineatus* | Striped catfish | | ☐ | ☐ |
| Pomacanthidae | *Centropyge* | *multipinis* | Brown dwarf-angelfish | 10 | | |
| Pomacanthidae | *Pomacanthus* | *chrysurus* | African angelfish | 1 | ☐ | ☐ |
| Pomacanthidae | *Pomacanthus* | *imperator* | Emperor angelfish | ☐ | | ☐ |
| Pomacanthidae | *Pomacanthus* | *semicirculatus* | Semicircle angelfish | 5 | ☐ | 5 |
| Pomacanthidae | *Pygoplites* | *diacanthus* | Regal angelfish | ☐ | | |
| Pomacentridae | *Abudefduf* | *notatus* | Yellow-tail sergeant | | ☐ | |
| Pomacentridae | *Abudefduf* | *septemfasciastus* | Banded sergeant | | | ☐ |
| Pomacentridae | *Abudefduf* | *sexfasciatus* | Scissor sergeant | 77 | ☐ | ☐ |
| Pomacentridae | *Abudefduf* | *sordidus* | Black-spot sergeant | | ☐ | 5 |
| Pomacentridae | *Abudefduf* | *sparoides* | False-eye sergeant | 23 | ☐ | 2 |
| Pomacentridae | *Abudefduf* | *vaigiensis* | Indo-Pacific sergeant | 4 | 21 | 29 |
| Pomacentridae | *Amphiprion* | *akallopisos* | Skunk anemonefish | 1 | | |
| Pomacentridae | *Amphiprion* | *allardi* | Allard's anemonefish | ☐ | | 3 |
| Pomacentridae | *Chromis* | *dimidiata* | Half and half chromis | 100 | | 30 |
| Pomacentridae | *Chromis* | *nigura* | Blacktail chromis | 6 | | |
| Pomacentridae | *Chromis* | *ternatensis* | Ternate chromis | ☐ | | |
| Pomacentridae | *Chromis* | *viridis* | Blue-green chromis | 40 | | |
| Pomacentridae | *Chromis* | *weberi* | Weber's chromis | 15 | | |
| Pomacentridae | *Chrysiptera* | *annulata* | Blackbarred demoiselle | | ☐ | 15 |
| Pomacentridae | *Chrysiptera* | *biocellata* | Twospot damsel | | 1 | |
| Pomacentridae | *Chrysiptera* | *brownriggi* | Surge demoiselle | | 7 | 36 |
| Pomacentridae | *Chrysiptera* | *glauca* | Grey demoiselle | | 1 | |
| Pomacentridae | *Chrysiptera* | *unimaculata* | One spot demoiselle | | ☐ | |
| Pomacentridae | *Dascyllus* | *aruanus* | Humbug dascyllus | 2 | | |
| Pomacentridae | *Dascyllus* | *carneus* | Indian dascyllus | 5 | | |
| Pomacentridae | *Dascyllus* | *trimaculatus* | Three-spot dascyllus | 8 | ☐ | 48 |
| Pomacentridae | *Neoglyphidodon* | *melas* | Black damsel | ☐ | | |
| Pomacentridae | *Neopomacentrus* | *azysron* | Yellowtail demoiselle | 33 | | |
| Pomacentridae | *Neopomacentrus* | *cyanomos* | Regal demoiselle | ☐ | | |
| Pomacentridae | *Plectroglyphidodon* | *dickii* | Dick's damsel | 6 | | |
| Pomacentridae | *Plectroglyphidodon* | *imparipennis* | Brighteye damsel | | ☐ | |
| Pomacentridae | *Plectroglyphidodon* | *johnstonianus* | Johnston damsel | 7 | | |
| Pomacentridae | *Plectroglyphidodon* | *lacrymatus* | Jewel damsel | 103 | | |
| Pomacentridae | *Pomacentrus* | *aquilus* | Dark damsel | 3 | 5 | 58 |

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|---|---|---|---|---|---|---|---|
| Pomacentridae | *Pomacentrus* | *baenschi* | Baensch's damsel | 4 | | | 1 |
| Pomacentridae | *Pomacentrus* | *caeruleus* | Blue-yellow damsel | 2 | ☐ | | 3 |
| Pomacentridae | *Pomacentrus* | *pavo* | Blue damsel | ☐ | ☐ | | |
| Pomacentridae | *Pomacentrus* | *sulfureus* | Sulphur damsel | 15 | | | |
| Pomacentridae | *Pomacentrus* | *trichrous* | Pailtail damsel | ☐ | | | |
| Pomacentridae | *Pomacentrus* | *trilineatus* | Three-line damsel | | ☐ | | ☐ |
| Pomacentridae | *Stegastes* | *fasciolatus* | Pacific gregory | 2 | | | |
| Priacanthidae | *Heteropriacanthus* | *cruentatus* | Glasseye | ☐ | | | |
| Priacanthidae | *Priacanthus* | *hamrur* | Goggle-eye | 2 | | | |
| Pseudochromidae | *Pseudochromis* | *leucorhynchus* | White-nose dottyback | | | | ☐ |
| Rhinobatidae | *Glaucostegus* | *cf. typus* | Giant guitarfish | | | | ☐ |
| Scaridae | *Calotomus* | *carolinus* | Stareye parrotfish | 39 | | | |
| Scaridae | *Cetoscarus* | *bicolor* | Bicolour parrotfish | ☐ | | | |
| Scaridae | *Chlorurus* | *atrilunula* | Black crescent parrotfish | 7 | | | |
| Scaridae | *Chlorurus* | *capistratoides* | Pale bullethead parrotfish | 1 | | | |
| Scaridae | *Chlorurus* | *sordidus* | Bullethead parrotfish | 67 | | | 12 |
| Scaridae | *Chlorurus* | *strongylocephalus* | Indian Ocean steephead parrotfish | ☐ | | | |
| Scaridae | *Hipposcarus* | *harid* | Indian Ocean longnose parrotfish | 1 | | | |
| Scaridae | *Leptoscarus* | *vaigiensis* | Seagrass parrotfish | 2 | ☐ | | 47 |
| Scaridae | *Scarus* | *frenatus* | Bridled parrotfish | 16 | | | |
| Scaridae | *Scarus* | *ghobban* | Bluebarred parrotfish | 11 | | | 1 |
| Scaridae | *Scarus* | *niger* | Swarthy parrotfish | 8 | | | |
| Scaridae | *Scarus* | *psittacus* | Palenose parrotfish | 6 | | | |
| Scaridae | *Scarus* | *rubroviolaceus* | Redlip parrotfish | 12 | | | |
| Scaridae | *Scarus* | *scaber* | Dusky-capped parrotfish | ☐ | | | |
| Scombridae | *Rastrelliger* | *kanagurta* | Striped mackerel | | | | |
| Scorpaenidae | *Dendochirus* | *zebra* | Zebra lionfish | | | | |
| Scorpaenidae | *Parascorpaena* | *mossambica* | Mozambique scorpionfish | | | | ☐ |
| Scorpaenidae | *Pterois* | *antennata* | Spotfin lionfish | ☐ | | | |
| Scorpaenidae | *Pterois* | *miles* | Common lionfish | 1 | ☐ | | |
| Scorpaenidae | *Pterois* | *mombasae* | Mombasa lionfish | ☐ | | | |
| Scorpaenidae | *Pterois* | *radiata* | Clearfin lionfish | ☐ | ☐ | | |
| Scorpaenidae | *Scorpaenopsis* | *oxycephala* | Tassled scorpionfish | ☐ | | 6 | |
| Scorpaenidae | *Scorpaenopsis* | *venosa* | Raggy scorpionfish | ☐ | | | |
| Scorpaenidae | *Sebastapistes* | *cyanostigma* | Yellowspotted scorpionfish | 12 | | | |
| Scorpaenidae | *Sebastapistes* | *strongia* | Barchin scorpionfish | | | | ☐ |
| Scorpaenidae | *Synanceia* | *verrucosa* | Stonefish | | | | |
| Scorpaenidae | *Taenianotus* | *triacanthus* | Leaf scorpionfish | ☐ | | | |
| Serranidae | *Aethaloperca* | *rogaa* | Redmouth grouper | ☐ | | | |
| Serranidae | *Cephalopholis* | *argus* | Peacock grouper | 2 | | | ☐ |
| Serranidae | *Cephalopholis* | *leopardus* | Leopard hind | ☐ | | | |
| Serranidae | *Cephalopholis* | *miniata* | Coral hind | ☐ | | | |
| Serranidae | *Cephalopholis* | *sonnerati* | Tomato grouper | ☐ | | | |
| Serranidae | *Dermatolepis* | *striolata* | Smooth grouper | ☐ | | | |
| Serranidae | *Epinephelus* | *areolatus* | Areolate grouper | ☐ | | | |
| Serranidae | *Epinephelus* | *caeruleopunctatus* | Whitespotted grouper | | | | |

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|---|---|---|---|---|---|---|---|---|
| Serranidae | *Epinephelus* | *fasciatus* | Blacktip grouper | 1 |  |  |  |  |
| Serranidae | *Epinephelus* | *fuscoguttatus* | Brown-marbled grouper | ☐ |  |  |  |  |
| Serranidae | *Epinephelus* | *lanceolatus* | Giant grouper |  |  |  | ☐ |  |
| Serranidae | *Epinephelus* | *longispinis* | Longspine grouper |  |  |  |  |  |
| Serranidae | *Epinephelus* | *macrospilos* | Snubnose grouper |  |  |  | ☐ |  |
| Serranidae | *Epinephelus* | *malabaricus* | Malabar grouper | ☐ |  |  |  |  |
| Serranidae | *Epinephelus* | *merra* | Honeycomb grouper | ☐ |  |  |  | 2 |
| Serranidae | *Epinephelus* | *ongus* | Specklefin grouper | ☐ |  |  |  |  |
| Serranidae | *Epinephelus* | *spilotoceps* | Foursaddle grouper | ☐ |  |  |  |  |
| Serranidae | *Epinephelus* | *tauvina* | Greasy grouper |  |  |  | ☐ |  |
| Serranidae | *Epinephelus* | *tukula* | Potato grouper |  |  |  | ☐ |  |
| Serranidae | *Grammistes* | *sexlineatus* | Six-striped soapfish |  |  | 1 | ☐ |  |
| Serranidae | *Plectropomus* | *laevis* | Saddleback coralgrouper | ☐ |  |  |  |  |
| Serranidae | *Plectropomus* | *punctatus* | Marbled coralgrouper | 1 |  |  |  |  |
| Serranidae | *Pseudanthias* | *squamipinnis* | Lyretail anthias | ☐ |  |  |  |  |
| Serranidae | *Variola* | *louti* | Lyretail grouper | ☐ |  |  |  |  |
| Signidae | *Siganus* | *argenteus* | Forktail rabbitfish | ☐ |  |  | ☐ |  |
| Signidae | *Siganus* | *luridus* | Squaretail rabbitfish |  |  |  |  |  |
| Signidae | *Siganus* | *stellatus* | Stellate rabbitfish | 3 |  |  |  | 2 |
| Signidae | *Siganus* | *sutor* | African whitespotted rabbitfish | 75 | ☐ |  |  | 379 |
| Soleidae | *Pardachirus* | *marmoratus* | Moses sole |  |  |  |  | 2 |
| Solenostomidae | *Solenostomus* | *cyanopterus* | Ghost pipefish |  |  |  |  |  |
| Sphyraenidae | *Sphyraena* | *barracuda* | Great barracuda |  |  |  | ☐ |  |
| Sphyraenidae | *Sphyraena* | *flavicauda* | Yellowtail barracuda |  |  |  | ☐ |  |
| Sphyraenidae | *Sphyraena* | *forsteri* | Blackspot barracuda |  |  |  |  | 10 |
| Sphyraenidae | *Sphyraena* | *jello* | Pickhandle barracuda |  |  |  | ☐ |  |
| Sphyraenidae | *Sphyraena* | *putnamiae* | Sawtooth barracuda |  |  |  | ☐ |  |
| Sphyraenidae | *Sphyraena* | *qenie* | Blackfin barracuda |  |  |  | ☐ |  |
| Sygnathidae | *Corythoichthys* | *schultzi* | Guilded pipefish | ☐ |  |  |  |  |
| Sygnathidae | *Doryhamphus* | *excisus* | Bluestripe pipefish |  |  |  |  |  |
| Sygnathidae | *Hippocampus* | *hystrix* | Thorny seahorse |  |  |  |  |  |
| Sygnathidae | *Micrognathus* | *andersonii* | Short-nose pipefish |  | ☐ |  |  |  |
| Synodontidae | *Synodus* | *dermatogenys* | Sand lizardfish | ☐ |  |  |  | 1 |
| Synodontidae | *Saurida* | *gracilis* | Graceful lizardfish | ☐ |  | 1 |  |  |
| Tetraodontidae | *Arothron* | *hispidus* | Whitespotted puffer |  |  |  |  | 2 |
| Tetraodontidae | *Arothron* | *immaculatus* | Immaculate puffer |  |  |  | ☐ |  |
| Tetraodontidae | *Arothron* | *mappa* | Globe puffer |  |  |  | ☐ |  |
| Tetraodontidae | *Arothron* | *meleagris* | Guineafowl puffer |  |  |  | ☐ |  |
| Tetraodontidae | *Arothron* | *nigropunctatus* | Blackspotted puffer | 4 |  |  |  |  |
| Tetraodontidae | *Arothron* | *stellatus* | Star puffer |  |  |  |  | 1 |
| Tetraodontidae | *Canthigaster* | *amboinensis* | Ambon toby |  |  |  | ☐ |  |
| Tetraodontidae | *Canthigaster* | *bennetti* | Bennett's toby | 6 | ☐ |  |  | 20 |
| Tetraodontidae | *Canthigaster* | *janthinopera* | Honeycomb toby | ☐ |  |  |  |  |
| Tetraodontidae | *Canthigaster* | *petersii* | Peters toby | 5 |  | 1 |  |  |
| Tetraodontidae | *Canthigaster* | *valentini* | Blacksaddle toby | 9 | ☐ |  |  | 1 |
| Theraponidae | *Terapon* | *jarbua* | Crescent-banded grunter |  | ☐ |  |  |  |

|  |  |  |  |  |  |
|---|---|---|---|---|---|
| Torpedinidae | *Torpedo* | *sinuspersici* | Marbled electric ray | ☐ |  |
| Zanclidae | *Zanclus* | *cornutus* | Moorish Idol | 19 | 1 |

## Appendix 2b – Species lists for Echinoderms, Molluscs and Crustacea

| Phylum | Class | Genus | Species | English | Reef | Intertidal | Seagrass-Sand |
|---|---|---|---|---|---|---|---|
| Echinodermata | Asteroidea | *Culcita* | *schmideliana* | Cake star | ☐ | ☐ | ☐ |
| Echinodermata | Asteroidea | *Dactylosaster* | *cylindricus* | | 1 | | |
| Echinodermata | Asteroidea | *Euretaster* | *cribrosus* | Dimple star | | | ☐ |
| Echinodermata | Asteroidea | *Leiaster* | *coriaceus* | Mottled star | | ☐ | ☐ |
| Echinodermata | Asteroidea | *Linckia* | *laevigata* | Blue star | 3 | ☐ | |
| Echinodermata | Asteroidea | *Linckia* | *multifora* | Irregular arm star | | ☐ | |
| Echinodermata | Asteroidea | *Monachaster* | *sanderi* | Pygmy plate star | ☐ | 1 | |
| Echinodermata | Asteroidea | *Nardoa* | *variolata* | Red dot star | ☐ | ☐ | |
| Echinodermata | Asteroidea | *Protoeaster* | *lincki* | Red crown star | ☐ | ☐ | |
| Echinodermata | Echinoidea | *Astropyga* | *radiata* | Radiant urchin | ☐ | ☐ | ☐ |
| Echinodermata | Echinoidea | *Diadema* | *savingyi* | Blue star urchin | 23 | 1 | |
| Echinodermata | Echinoidea | *Diadema* | *setosum* | Anal spot urchin | 5 | ☐ | |
| Echinodermata | Echinoidea | *Echinometra* | *matthaei* | Rockpool urchin | 44 | 275 | |
| Echinodermata | Echinoidea | *Echinostrephus* | *molaris* | Burrowing urchin | 198 | | |
| Echinodermata | Echinoidea | *Echinothrix* | *calamaris* | Black and white urchin | 18 | ☐ | |
| Echinodermata | Echinoidea | *Echinothrix* | *diadema* | Reef urchin | 257 | 161 | |
| Echinodermata | Echinoidea | *Eucidaris* | *metularia* | Rough pencil urchin | | | ☐ |
| Echinodermata | Echinoidea | *Toxopneustes* | *pileolus* | Flower urchin | 2 | ☐ | ☐ |
| Echinodermata | Echinoidea | *Tripneustes* | *gratillia* | Seagrass urchin | ☐ | 11 | ☐ |
| Echinodermata | Holothurioidea | *Actinopyga* | *echinites* | Hedgehog cucumber | | ☐ | |
| Echinodermata | Holothurioidea | *Actinopyga* | *mauritiana* | White belly cucumber | ☐ | 1 | |
| Echinodermata | Holothuroidea | *Actinopyga* | *miliaris* | Military cucumber | | ☐ | |
| Echinodermata | Holothuroidea | *Bohadschia* | *sp.* | Red dot cucumber | | ☐ | |
| Echinodermata | Holothuroidea | *Bohadschia* | *subrubra* | Patch cucumber | ☐ | | |
| Echinodermata | Holothuroidea | *Holothuria* | *atra* | Common black cucumber | 1 | | |
| Echinodermata | Holothuroidea | *Holothuria* | *scabra* | Tasty cucumber | | | ☐ |
| Echinodermata | Holothuroidea | *Patinapta* | *crosslandi* | Worm cucumber | | ☐ | |
| Echinodermata | Holothuroidea | *Pearsonothuria* | *graeffei* | Black palp cucumber | ☐ | | |
| Echinodermata | Holothuroidea | *Synapta* | *maculata* | Seagrass cucumber | | | ☐ |
| Echinodermata | Ophiuroidea | *Amphiura* | *dejectoides* | Brittlestar | | 41 | |
| Echinodermata | Ophiuroidea | *Ophiocentrus* | *dilalatus* | Brittlestar | ☐ | | |
| Echinodermata | Ophiuroidea | *Ophiocoma* | *erinaceus* | Brittlestar | 2 | | |
| Echinodermata | Ophiuroidea | *Ophiocoma* | *scolopendrina* | Brittlestar | 8 | 268 | |
| Echinodermata | Ophiuroidea | *Ophiomastix* | *venosa* | Brittlestar | | 7 | |
| | | | | | | | |
| Mollusca | Bivalvia | *Chione* | *toreuma* | | | 1 | |
| Mollusca | Bivalvia | *Tridacna* | *maxima* | Burrowing giant clam | 2 | 1 | |
| Mollusca | Bivalvia | *Tridacna* | *sqaumosa* | Fluted giant clam | 53 | ☐ | |
| Mollusca | Cephalopoda | *Octopus* | *cyanea* | Common reef octopus | 1 | ☐ | ☐ |
| Mollusca | Gastropoda | *Asteronotus* | *cespitosus* | | | ☐ | |
| Mollusca | Gastropoda | *Ceritium* | *nodulosum* | | | 3 | |
| Mollusca | Gastropoda | *Charonia* | *tritonis* | Giant triton | ☐ | | |
| Mollusca | Gastropoda | *Conus* | *arenatus* | Sand dusted coneshell | | 10 | |
| Mollusca | Gastropoda | *Conus* | *catus* | Cat coneshell | 1 | 2 | |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Mollusca | Gastropoda | *Conus* | *coronatus* | Crowned coneshell | | | | 1 | |
| Mollusca | Gastropoda | *Conus* | *ebraeus* | Black and white coneshell | | | | 88 | |
| Mollusca | Gastropoda | *Conus* | *litteratus* | Lettered coneshell | | | | 4 | |
| Mollusca | Gastropoda | *Conus* | *lividis* | Livid coneshell | | 2 | | 18 | |
| Mollusca | Gastropoda | *Conus* | *rattus* | Rat coneshell | | | | 3 | |
| Mollusca | Gastropoda | *Conus* | *striatellus* | Coneshell | | | | 2 | |
| Mollusca | Gastropoda | *Chromodoris* | *spp.* | Nudibranch | ☐ | | | | |
| Mollusca | Gastropoda | *Clypeomorus* | *bifasciatus* | | | | | 3 | |
| Mollusca | Gastropoda | *Cypraea* | *tigris* | Leopard cowrie | | | ☐ | | ☐ |
| Mollusca | Gastropoda | *Cypraecassis* | *rufa* | Bullmouth helmetshell | | | ☐ | | ☐ |
| Mollusca | Gastropoda | *Dolabella* | *auricularia* | Wedge seahare | | | ☐ | | |
| Mollusca | Gastropoda | *Drupa* | *fusconigra* | | | | ☐ | | |
| Mollusca | Gastropoda | *Drupella* | *rugosa* | Rugose drupe | | | | 58 | |
| Mollusca | Gastropoda | *Engina* | *mendicaria* | Bumblebee shell | | 1 | | 261 | |
| Mollusca | Gastropoda | *Flabellina* | *exoptata* | Desirable flabellina | | 2 | | | |
| Mollusca | Gastropoda | *Giberellus* | *giberellus* | Humpback conch | | | | 2 | |
| Mollusca | Gastropoda | *Glossodoris* | *hikuerensis* | Nudibranch | ☐ | | | | |
| Mollusca | Gastropoda | *Halgerda* | *formosa* | Nudibranch | | 9 | | | |
| Mollusca | Gastropoda | *Halgerda* | *tessellata* | Nudibranch | ☐ | | | | |
| Mollusca | Gastropoda | *Halgerda* | *wasinensis* | Nudibranch | ☐ | | | | |
| Mollusca | Gastropoda | *Hastula* | *lanceata* | | | | | 2 | |
| Mollusca | Gastropoda | *Hypselodoris* | *regina* | Nudibranch | | | | | ☐ |
| Mollusca | Gastropoda | *Jorunna* | *rubsecens* | Nudibranch | ☐ | | | | |
| Mollusca | Gastropoda | *Lambis* | *chiragra* (*arthritica*) | Arthritic spider conch | | 5 | | | |
| Mollusca | Gastropoda | *Lambis* | *lambis* | Spider conch | | 1 | | | |
| Mollusca | Gastropoda | *Lambis* | *truncata* | Giant spider conch | ☐ | | | | |
| Mollusca | Gastropoda | *Littoraria* | *scabra* | Mangrove periwinkle | | | | 2 | |
| Mollusca | Gastropoda | *Littoraria* | *undulata* | Periwinkle | | 1 | | 1 | |
| Mollusca | Gastropoda | *Mauritia* | *histrio* | Harlequin cowrie | | | | 2 | |
| Mollusca | Gastropoda | *Mirta* | *paupercula* | Miter shell | | | | | |
| Mollusca | Gastropoda | *Monetaria* | *annulus* | Goldring cowrie | | | | 5 | |
| Mollusca | Gastropoda | *Morula* | *granulata* | Mulberry shell | | 2 | | | |
| Mollusca | Gastropoda | *Nerita* | *albicilla* | Blotched nerite | | | | 111 | |
| Mollusca | Gastropoda | *Ovula* | *ovum* | Common egg cowrie | ☐ | | | | |
| Mollusca | Gastropoda | *Phyllidia* | *varicosa* | Nudibranch | | 3 | ☐ | | |
| Mollusca | Gastropoda | *Phyllidiella* | *meandrina* | Nudibranch | ☐ | | ☐ | | |
| Mollusca | Gastropoda | *Phyllidiella* | *zeylonica* | Nudibranch | | 7 | ☐ | | |
| Mollusca | Gastropoda | *Phyllidiopsis* | *striata* | Nudibranch | ☐ | | | | ☐ |
| Mollusca | Gastropoda | *Pleuroploca* | *trapezium* | Tulip shell | | | | | ☐ |
| Mollusca | Gastropoda | *Pollia* | *fumosus* | Smoky goblet | | | | 9 | |
| Mollusca | Gastropoda | *Pollia* | *undodsus* | Waved goblet | | | | 1 | |
| Mollusca | Gastropoda | *Pteraeolidea* | *ianthina* | Blue dragon school | ☐ | | | | |
| Mollusca | Gastropoda | *Rhinoclaris* | *sinensis* | Chinese cerith | | 1 | | | |
| Mollusca | Gastropoda | *Terebra* | *dimidiata* | Giraffe screwshell | | | | | ☐ |
| Mollusca | Gastropoda | *Thuridilla* | *indopacifica* | Nudibranch | ☐ | | | | |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Mollusca | Gastropoda | *Vasum* | *ceramicum* | Ceramic vaseshell | | | 1 | |
| Mollusca | Gastropoda | *Vasum* | *rhinocerus* | Rhinocerus vaseshell | | | 2 | |
| Mollusca | Gastropoda | *Vasum* | *turbinellus* | Black and white vaseshell | 3 | | 4 | |
| Mollusca | Gastropoda | *Vexillium* | *rugosum* | Ribbed miter | | | 2 | |
| Mollusca | Gastropoda | *Volema* | *paradisiaca* | Pear melongena | | | 1 | |
| Mollusca | Polyplacophora | *Acanthopleura* | *gemmata* | Splashzone chiton | | | 5 | |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Crustacea | Anomura | *Dardanus* | *deformis* | Anemone hermit crab | | ☐ | | |
| Crustacea | Anomura | *Dardanus* | *lagopodes* | Hairy hermit crab | ☐ | | | |
| Crustacea | Anomura | *Dardanus* | *megistos* | Bluespot hermit crab | ☐ | ☐ | | |
| Crustacea | Anomura | *Neopetrolisthes* | *maculatus* | Anemone crab | | ☐ | | |
| Crustacea | Brachyura | *Calappa* | *hepatica* | Box crab | | | | ☐ |
| Crustacea | Brachyura | *Cardisoma* | *carnifex* | Red land crab | | ☐ | | |
| Crustacea | Brachyura | *Eriphia* | *smithi* | Redeye rockpool crab | | ☐ | | |
| Crustacea | Brachyura | *Estisus* | *slendidus* | Red crab | ☐ | | | |
| Crustacea | Brachyura | *Graspus* | *tenuicrustatus* | Surge crab | | ☐ | | |
| Crustacea | Brachyura | *Lydia* | *annulipes* | Striped stone crab | | ☐ | | |
| Crustacea | Brachyura | *Ocypode* | *ceratophthalmus* | Horny eyed ghostcrab | | ☐ | | |
| Crustacea | Brachyura | *Ocypode* | *cordimanus* | Smooth handed ghostcrab | | ☐ | | |
| Crustacea | Brachyura | *Ocypode* | *ryderi* | Pink ghostcrab | | ☐ | | |
| Crustacea | Brachyura | *Percnon* | *planissium* | Flat coral crab | ☐ | | | |
| Crustacea | Brachyura | *Tetralia* | *glaberrima* | Acropora coral crab | ☐ | | | |
| Crustacea | Brachyura | *Trapezia* | *rufopunctata* | Spotted coral crab | ☐ | | | |
| Crustacea | Caridea | *Hymenocera* | *picta* | Harlequin shrimp | | ☐ | | |
| Crustacea | Caridea | *Rhynchocinetes* | *durbanensis* | Jagged shrimp | ☐ | | | |
| Crustacea | Caridea | *Stenopus* | *hispidus* | Banded cleaner shrimp | ☐ | ☐ | | |
| Crustacea | Palinura | *Panulirus* | *versicolor* | Painted spiny lobster | ☐ | ☐ | | |
| Crustacea | Stomatopoda | *Gonodactylus* | *chiragar* | Sandy mantis shrimp | | ☐ | | |
| Crustacea | Stomatopoda | *Gonodactylus* | *platysoma* | Spotted mantis shrimp | | ☐ | | |
| Crustacea | Stomatopoda | *Odontodactylus* | *scyllarus* | Peacock mantis shrimp | ☐ | | | |

## Appendix 2c – Genus list for Scleractinian corals

| **Family** | **Genus** | **Reef** | **Intertidal** |
|---|---|---|---|
| Acroporidae | *Acropora* | ¢ | ¢ |
| | *Alveopora* | | ¢ |
| | *Astreopora* | ¢ | ¢ |
| | *Isopora* | ¢ | |
| | *Montipora* | ¢ | |
| Agarciidae | *Gardineroseris* | ¢ | |
| | *Leptoseris* | ¢ | |
| | *Pavona* | ¢ | ¢ |
| Coscinaraeaidae | *Anomastrea* | | ¢ |
| | *Coscinaraea* | ¢ | ¢ |
| Dendrophyllidae | *Turbinaria* | ¢ | |
| Euphyllidae | *Galaxea* | ¢ | |
| Fungiidae | *Ctenactis* | ¢ | |
| | *Fungia* | ¢ | |
| | *Herpolitha* | ¢ | |
| | *Podabacia* | ¢ | |
| Lobophyllidae | *Acanthastrea* | ¢ | |
| | *Echinophyllia* | ¢ | |
| | *Lobophyllia* | ¢ | |
| | *Oxypora* | ¢ | |
| | *Symphyllia* | ¢ | |
| Merulinidae | *Coelastrea* | ¢ | ¢ |
| | *Cyphastrea* | ¢ | |
| | *Dipsastrea* | ¢ | ¢ |
| | *Echinopora* | ¢ | |
| | *Favites* | ¢ | ¢ |
| | *Goniastrea* | ¢ | |
| | *Hydnophora* | ¢ | ¢ |
| | *Leptoria* | ¢ | |
| | *Merulina* | ¢ | |
| | *Mycedium* | ¢ | |
| | *Oulophyllia* | ¢ | |
| | *Paramontastrea* | ¢ | |
| | *Pectinia* | ¢ | |
| | *Platygyra* | ¢ | ¢ |
| Pocilloporidae | *Pocillopora* | ¢ | |
| Poritidae | *Goniopora* | ¢ | |
| | *Porites* | ¢ | ¢ |
| Psammaocoridae | *Psammocora* | ¢ | |
| *Insertae sedis* | *Plesiastrea* | ¢ | |
| | *Blastomussa* | ¢ | |
| | *Leptastrea* | ¢ | ¢ |
| | *Plerogyra* | ¢ | |

## Appendix 3 – Resilience, resistance and recovery scores by site

| Location | Site | Zone | Resilience | Resistance | Recovery |
|---|---|---|---|---|---|
| Enggano | Kiaba | Channel | 0.67 | 0.75 | 0.63 |
| | Kuburan Ingris | Lagoon | 0.65 | 0.71 | 0.66 |
| | Pulau Dua | Leeward | 0.64 | 0.67 | 0.65 |
| | Pulau Merbau | Seaward | 0.73 | 0.83 | 0.67 |
| Kisite | Kisite Deep | Seaward | 0.68 | 0.71 | 0.67 |
| | Kisite Leeward | Leeward | 0.55 | 0.62 | 0.47 |
| | Kisite Seaward | Seaward | 0.65 | 0.66 | 0.68 |
| | Mako Kokwe | Leeward | 0.69 | 0.82 | 0.57 |
| | Masolini | Lagoon | 0.51 | 0.59 | 0.33 |
| | Mkwiro | Channel | 0.59 | 0.67 | 0.50 |
| | Mpunguti Leeward | Flat | 0.63 | 0.74 | 0.55 |
| | Mpunguti Seaward | Seaward | 0.72 | 0.80 | 0.67 |
| Kuramathi | Kuramathi Channel | Channel | 0.65 | 0.65 | 0.60 |
| | Kuramathi Lagoon | Lagoon | 0.74 | 0.86 | 0.60 |
| | Palms Flat | Flat | 0.85 | 0.78 | 0.94 |
| | Palms Fore | Seaward | 0.71 | 0.71 | 0.66 |
| | Rasdhoo Flat | Flat | 0.64 | 0.64 | 0.66 |
| | Rasdhoo Fore | Seaward | 0.62 | 0.64 | 0.57 |
| | Rasdhoo Giri | Channel | 0.63 | 0.62 | 0.61 |
| Tikus | Tikus Central | Channel | 0.61 | 0.70 | 0.46 |
| | Tikus North | Leeward | 0.54 | 0.57 | 0.48 |
| | Tikus South | Leeward | 0.58 | 0.60 | 0.54 |
| Vamizi | Vamizi Boot | Leeward | 0.68 | 0.79 | 0.59 |
| | Vamizi Central | Flat | 0.56 | 0.61 | 0.51 |
| | Vamizi Dropoff | Seaward | 0.70 | 0.77 | 0.67 |
| | Vamizi East | Flat | 0.55 | 0.57 | 0.53 |
| | Vamizi Fusilier | Leeward | 0.61 | 0.67 | 0.54 |
| | Vamizi Lodge | Flat | 0.59 | 0.62 | 0.57 |
| | Vamizi Valley | Channel | 0.60 | 0.64 | 0.54 |
| | Vamizi West | Flat | 0.61 | 0.68 | 0.56 |
| Watamu | Anthias | Seaward | 0.72 | 0.90 | 0.56 |
| | Bara Bara | Lagoon | 0.64 | 0.85 | 0.47 |
| | Bennetts Reef | Lagoon | 0.67 | 0.92 | 0.45 |
| | Coral Gardens | Lagoon | 0.76 | 0.91 | 0.61 |
| | Dolphin | Seaward | 0.74 | 0.76 | 0.75 |
| | Drummers | Seaward | 0.64 | 0.75 | 0.57 |
| | Lambis | Lagoon | 0.69 | 0.93 | 0.47 |
| | Moray | Seaward | 0.71 | 0.83 | 0.63 |
| | Turtle Reef | Leeward | 0.65 | 0.88 | 0.46 |
| | Uyombo | Lagoon | 0.67 | 0.84 | 0.55 |

| Score | Range | Lower Tercile | Middle Tercile | Upper Tercile |
|---|---|---|---|---|
| *Resilience* | 0.51-0.85 | 0.51-0.62 | 0.63-0.73 | 0.74-0.85 |
| *Resistance* | 0.57-0.93 | 0.57-0.69 | 0.70-0.81 | 0.82-0.93 |
| *Recovery* | 0.46-0.75* | 0.46-0.55 | 0.56-0.65 | 0.66-0.75 |

*Excluding extreme values for Masolini (0.33) and Palms Flat (0.93)