Habitat structure, degradation and management effects on coral reef fish communities

Saleh A.S. Yahya

Department of Zoology

Stockholm University

2011

Habitat structure, degradation and management effects on coral reef fish communities

Doctoral dissertation 2011

Saleh A.S. Yahya

Department of Zoology

Stockholm University

106 91 Stockholm

Sweden

To my parents

ABSTRACT

Coral reefs are among the most diverse and productive ecosystems on earth, and are critical to the survival of tropical marine ecosystems and sustenance of local human populations. However, coral reefs are quite vulnerable to disturbances, both natural and anthropogenic. This thesis looks at how coral reef communities have responded to climactic disturbances, particularly the 1997-98 El Niño Southern Oscillation (ENSO) and subsequent coral bleaching and mortality that affected much of the Indian Ocean, including the coastal waters of Tanzania, where the study was conducted. In particular, it investigates the effects of coral bleaching, habitat degradation and reef spatial arrangement on reef fish assemblages.

Habitat structural complexity and spatial arrangement of reefs had an effect on reef fish communities. Fish communities showed patterns in distribution among habitats and between patch and continuous reefs. Fishes preferred live to bleached/dead or eroded coral, but trophic groups reacted differently to patch and continuous reefs. There were slight changes in fish abundance and significant changes in fish diversity on experimental, bleached branching *Acropora* coral plots over a period of one year. While fish abundance on one site increased shortly after a bleaching event, 6 years later fish abundance had decreased significantly. Conversely, coral reef communities in northern Tanzania had changed little over an 8-year period, with minor changes associated with the 1997-98 ENSO and the presence or absence of fisheries management. The coral reefs in the region were found to show high variability in community structure and responses of associated fish and invertebrate communities.

The findings of this thesis indicate the importance of habitat structure and spatial arrangement of reefs, the detrimental effects of coral bleaching, and the possibility that some reefs and some (generalist) reef fish taxa may exhibit resilience to climate change.

Contents

LIST OF PAPERS

Paper I Garpe KC, Yahya SAS, Lindahl U, Öhman MC (2006) Long-term effects of the 1998 coral bleaching event on reef fish assemblages. Marine Ecology Progress Series 315: 237-247

Paper II Yahya SAS, Gullström M, Öhman MC, Jiddawi NS, Andersson MH, Mgaya YD, Lindahl U (2011) Coral bleaching and habitat effects on colonisation of reef fish assemblages: an experimental study. Estuarine, Coastal and Shelf Science 94: 16-23

Paper III Yahya SAS, Gullström M, Öhman MC, Jiddawi NS, Mgaya YD. Fish assemblages in relation to habitat quality and structure of staghorn coral at Mafia and Zanzibar islands, Tanzania. Manuscript

Paper IV Yahya SAS, Muhando C, Gullström M. Fish and sea urchin community patterns and habitat effects on Tanzanian reefs. Manuscript

Paper V McClanahan TR, Muthiga NA, Maina J, Kamukuru AT, Yahya SAS (2009) Changes in northern Tanzania coral reefs during a period of increased fisheries management and climatic disturbance. Aquatic Conservation and Freshwater Ecosystems 19: 758-771

Published papers are reprinted with kind permission from the publishers.

INTRODUCTION

Coral reefs

Coral reefs play an important role for a range of organisms. Their intricate physical structure provides an ideal setting for a system of complex ecological interactions, thus making coral reefs a good source of food and shelter. Coral reefs comprise a high diversity of organisms including hard and soft corals of various sizes and morphologies, their symbiotic dinoflagellate microalgae (zooxanthellae), coralline and other macroalgae, invertebrates and fish. The structure and position of coral reefs along tropical coastlines protect these coasts from storms, flooding and erosion, at the same time enabling formation of associated seagrass and mangrove ecosystems (Hoegh-Guldberg 1999). Coral reefs are a source of resources for many coastal communities. For instance, calcified corals are mined and processed to produce building blocks and lime for construction. Coral reefs are also major tourist attractions (Hawkins and Roberts 1994, Wilhelmsson et al. 1998), with coral reef tourism alone generating billions of dollars (Hoegh-Guldberg 1999). Coral reef fisheries are even more important (Russ 1991), yielding at least 6 million metric tonnes of fish catches worldwide annually (Munro 1996). In Tanzania, for example, over 90% of the marine fisheries are artisanal, focusing on coral reef fish (Jiddawi and Öhman 2002). Besides finfish, coral reefs are fishing grounds for cephalopods, gastropods, echinoderms and bivalves.

Climate change and bleaching of corals

Despite being very productive coral reefs are also one of the most vulnerable marine ecosystems (Hoegh-Guldberg 1999). One aspect of this sensitivity is that reef structure is affected by coral bleaching. When corals and other zooxanthellate invertebrates (i.e. invertebrates that live with symbiotic dinoflagellates or zooxanthellae in their tissues) are physiologically stressed, the critical balance that maintains their symbiotic relationship with zooxanthellae is lost (Hoegh-Guldberg 1999, Reaser et al. 2000). This leads to expulsion of zooxanthellae and/or a fall in the concentration of photosynthetic pigments within the zooxanthellae (Kleppel et al. 1989, Hoegh-Guldberg and Smith 1989, Booth and Beretta 2002). Stresses causing this loss of colour (i.e. bleaching) in corals and other invertebrate hosts include reduced salinity (Goreau, 1964), reduction or increase in light (Hoegh-Guldberg and Smith 1989, Lesser et al. 1990), sudden and extended changes in temperature (Coles and Jokiel 1978, Hoegh-Guldberg and Smith 1989, Jokiel and Coles 1999), pollution from heavy metals such as copper (Jones 1997) and agricultural chemicals and biological factors such as bacteria (Kushmaro et al. 1996, Hoegh-Guldberg 1999). However, most mass coral bleaching events are caused by environmental extremes such as high temperature or irradiance (Glynn 1993, Baker et al. 2008). Studies point to an association between elevated sea temperatures and mass coral bleaching events. This connection was reported about two decades ago (Glynn 1984, 1988) and studies since then have supported this view, more so after the severe 1997/98 El Ninǒ Southern Oscillation (ENSO) and subsequent coral bleaching events (e.g. Goreau et al. 1993, Jones 1997, Pratchett et al. 2006).

Bleached corals commonly lose 60-90% of their zooxanthellae individuals and each remaining zooxanthellae may lose 50-80% of its photosynthetic pigments (Glynn 1996). After expulsion of these symbiotic dinoflagellates the coral is usually white (bleached), and has reduced growth, calcification rate and repair capability (Goreau and Macfarlane 1990, Glynn 1993). As the rate of photosynthetic productivity decreases (Coles and Jokiel 1977) and this is the major source of energy for calcification (Muscatine 1990) the coral will be weakened in its ability to grow and compete for space with other organisms such as macroalgae (Hoegh-Guldberg 1999).

Since 1979, there have been six major bleaching events, mainly caused by higher seawater temperatures associated with global climate change and El Niño/La Niña events, and with possible synergistic effects of elevated ultraviolet and visible light (Hoegh-Guldberg 1999, Hoegh-Guldberg et al. 2005). In 1997/1998 the El Niño Southern Oscillation (ENSO) was unprecedented, with raising seawater temperatures worldwide (McPhaden 1999), resulting in up to 90% coral mortality in some places (Wilkinson 2000). The frequency and severity of bleaching incidences are likely to increase in the future (Hoegh-Guldberg 1999). Thus, there is a need to study how bleaching affects the extended coral reef community. Bleaching and natural disasters in general are unprecedented events, thus the number of studies on effects of fish communities has been relatively few. Furthermore, it has been difficult to carry out field experiments to investigate such phenomena. Typically, disturbance effects have been limited to a single site and pre-disturbance data and/or undisturbed reference sites have been missing.

Related to this is another phenomenon of increasing concern − ocean acidification. Higher CO_2 levels and sea surface temperatures will lead to increased frequency and severity of the bleaching process. Increasing CO_2 levels may contribute to dissolution of coral skeletons (after bleaching and/or mortality) and reduction in rates of reef calcification. Additionally, impacts on other physiological processes (such as calcium carbonate accretion and reproductive potential) in coral reefs and other reef-building species are likely, but little is known about these responses and their biotic consequences (Hoegh-Guldberg 1999, Hoegh-Guldberg et al. 2007, Anthony et al. 2008).

Herbivory and reef resilience

A diverse assemblage of abundant herbivorous species exists on coral reefs (Randall 1967) where they are responsible for removal of a large portion of the plant biomass; consequently herbivory is one of the major processes structuring benthic coral reef communities (Hay 1991). Herbivores on reefs have been implicated in three fundamental processes (Choat 1991). They are a link for the flow of energy between primary producers and carnivorous consumers. Secondly, herbivores influence the production, distribution, size and internal composition of reef flora (Hay 1991). Lastly, interactions among territorial herbivorous fishes have been instrumental in the development of demographic and behavioural models for reef fishes in general. Other major reef herbivores such as the sea urchins are also main consumers of algal production and they may show overlap in resource use with herbivorous fishes (Bruggemann et al. 1994).

Human disturbances and natural stressors have had increasingly significant adverse effects on coral reefs in recent times. As a result, many reefs have undergone rapid changes in the dominant biota leading to alternate phases (Hughes et al. 2007). Bleaching and other disturbances may cause corals to die and/or ultimately to lose the battle with macroalgae on the reef. Moreover, removal of herbivores by overfishing may cause algae to proliferate. The result is a change from coral dominance to macroalgae dominated communities, reported as the coral-macroalgal phase shift (Norström et al. 2009). Overgrowth of macroalgae can hinder coral growth and smother coral recruits. Grazing by herbivores can clear substrates for coral recruitment after disturbance (Hay 1997), hence halting or reversing alternate shifts (Green and Bellwood 2009) and promoting reef resilience. Resilience has been defined as the ability of an ecosystem to absorb shocks, resist phase shifts and regenerate after natural and human-induced disturbances (Nyström et al. 2000). The understanding of the role of various herbivores on reefs, and their role in reef resilience is thus of paramount importance.

Reefs as fish habitat

The fish community is a conspicuous part of the coral reef ecosystem with more than 4,000 species recorded worldwide (Sale 1980). How reef fish and other demersal fish populations are regulated has been debated extensively among fish ecologists. Various hypotheses have proposed to define the most important factor that regulates reef-fish communities. These hypotheses have concerned various processes in fish population dynamics including competition (Smith and Tyler 1972), recruitment (Doherty 1982), settlement (Sale 1974),

predation (Hixon 1991) and disturbance (Talbot et al. 1978). To date, ecologists have not reached a consensus on how reef-fish communities are regulated but these single-factor models are largely being replaced by a multifactorial approach where the composition of a given fish assemblage is the result of a variety of processes that influence fish numbers and composition (Jones 1991, Caley et al. 1996).

In a coral reef unique fish assemblages may be associated with broad zones spanning hundreds of meters (Letourneur 1996, Munday et al. 1997, Öhman et al. 1997, 1998b, Ault and Johnson 1998) or smaller patches such as monospecific stands of coral beds (Meekan et al. 1995), or even on the microhabitat scale with a specific type of coral colony (Ormond et al. 1996, Munday et al. 1997, Öhman et al. 1998a). These fish assemblages are very diverse and may harbour up to thousands of species (Ebeling and Hixon 1991). How this high diversity is maintained has been explained by four major theories, namely the competition model, the lottery hypothesis, the predation-disturbance model, and the recruitment-limitation model. The competition model maintains that the high diversity is the result of strong competitive interactions leading to high levels of specialization, resulting in narrower ecological niches (Smith and Tyler 1972, Smith 1978). The lottery hypothesis on the other hand, holds the view that chance recruitment of fishes to the reef and persistence determines species composition on the reef (Sale 1974, 1978, 1991; Sale and Dybdahl 1975). The predation-disturbance model suggests that postsettlement mortality of juveniles and adults from predation and various disturbances keeps fish populations below the level at which resources become limiting (Talbot et al. 1978, Hixon 1991, Hixon and Beets 1993). The recruitment-limitation model,

perhaps the most widely accepted model, argues that larval supply is never adequate for the adult population size to reach its full potential, thus resources on the reef are not limiting (Williams 1980, Victor 1983, Doherty and Williams 1988).

The reef habitat is an important component regulating fish communities, and correlations between fish numbers and different reef-habitat features have been described (e.g. Jennings et al. 1996, Chabanet et al. 1997, Öhman and Rajasuriya 1998, Öhman et al. 1998b). Habitat structure may mediate the operation of the above-mentioned processes such as recruitment, competition and predation (Jones and Syms 1998). If fish communities are influenced by habitat structure, then a change in habitat structure would be expected to alter fish community composition. Hence, changes in the reef environment would have an effect on the interaction between fish and reef habitat structure.

The effect of coral reef structure on fish communities has been an area of interest for a long time, with studies reaching conflicting conclusions. Studies have shown that habitat complexity has an effect on fish abundance and species richness. Habitat complexity can be examined on different levels including topographic complexity (Risk 1972, Luckhurst and Luckhurst 1978, Chabanet et al. 1997, Öhman and Rajasuriya 1998), substratum diversity (Öhman and Rajasuriya 1998), relief (Luckhurst and Luckhurst 1978, Wilhelmsson et al. 2006) and live cover (Carpenter et al. 1981, Sano et al. 1984). Apart from a positive correlation with rugosity (topographic complexity), the relationship between species richness and the other habitat variables has been inconsistent (Gratwicke and Speight 2005). Positive

correlations between fish density and live coral cover have been reported (Bell and Galzin 1984, Bouchon-Navaro and Bouchon 1989, Chabanet et al. 1997, Öhman and Rajasuriya 1998). Live coral also contributes to overall reef structure, thus influencing habitat complexity. Moreover, fish species diversity has been reported to show a positive correlation with structural complexity of coral habitat (Luckhurst and Luckhurst 1978, McClanahan, 1994; McCormick, 1994). Some studies, however, indicate little or no correlation between fish and coral growth (McManus et al. 1981, Bell et al. 1985). This variability in results indicates that it is difficult to draw any general conclusions, as investigators have used a wide variety of methods for assessing habitat complexity (Gratwicke and Speight 2005) as well as its effect on reef-fish communities.

OBJECTIVES

This thesis presents five studies generally focusing on effects of changes in habitat structure on reef fish communities. The first study examined long-term responses of fish communities in experimental coral habitats, subjected to a natural catastrophic disturbance in the form of severe coral bleaching. The second study was an experimental field study where bleaching was simulated and the resultant effects on fish assemblages examined. In the third study, fish assemblages on reefs of different quality and structure were described and assessed. The fourth study examined dynamics of the major herbivores on coral reefs in Mafia and Zanzibar (Tanzania), namely herbivorous fishes and sea urchins, with respect to habitat condition. The fifth study looked at coral reef fish communities in the Northern Tanzania,

eight years after a major bleaching event, and with respect to increased management of reefs in the area. In brief, the objectives of the studies were:

Paper I To assess the long-term effects of habitat alteration caused by coral bleaching on reef fish communities.

Paper II To assess the immediate and short-term effects of habitat alteration caused by coral bleaching on reef fish assemblages.

Paper III To assess the effects of quality, structure and spatial configuration of coral reefs on reef fish assemblages.

Paper IV To investigate the relationship between sea urchins, herbivorous fishes and habitat variables on coral reefs.

Paper V To investigate the effect of climatic disturbance and management of reefs on coral reef communities.

STUDY SITES

Study sites extended over three regions on the Tanzanian coastline (Fig. 1). The first study region comprises Mafia and Zanzibar islands, off the mainland coast. Mafia Island Marine Park (MIMP) is located in southern Tanzania (Papers I–III). The park is situated about 120 km south of Dar es Salaam and 20 km offshore from the Rufiji Delta. It was gazetted in 1995 and covers an area of 822 km^2. Kitutia reef (Papers I–III) and Chole Bay (Paper III) are reef areas located within the non-extractive zone of MIMP, and are thus protected from fishing. Bawe (Papers III and IV), Murogo (Paper III), Changuu (Papers IV and V) and Chapwani

(Paper V) reefs lie off Zanzibar town (Unguja Island), which in turn lies 40 km from the Tanzanian mainland. These sites currently experience moderate levels of fishing and dive tourism. The fifth site in Zanzibar, Chumbe Island Coral Park (CHICOP, Papers IV and V) is also located off Zanzibar town. CHICOP has actively managed its reef system since it was established in 1991, prohibiting all extractive activities. The second study region was situated in the area of Dar es Salaam, more specifically in Mbudya and Bongoyo, two islands within the Dar es Salaam Marine Reserves (Paper V). The reserves have been effectively managed since 2002 and allow restricted gear use. The northern Tanzanian reefs near Tanga municipality comprise the third study region (Paper V). The final (fourth) region was the reefs in Kisite Marine National Park in Kenya (Paper V), which were considered geographically associated with Tanga in terms of close distance, coral morphology and coral taxonomic composition (McClanahan et al. 2007). Tanga reefs have been managed in collaboration with the community since 1994. This management has involved enforcement of laws against destructive fishing, and the establishment of small and temporary closures (Horrill et al. 2000, Wells et al. 2007)
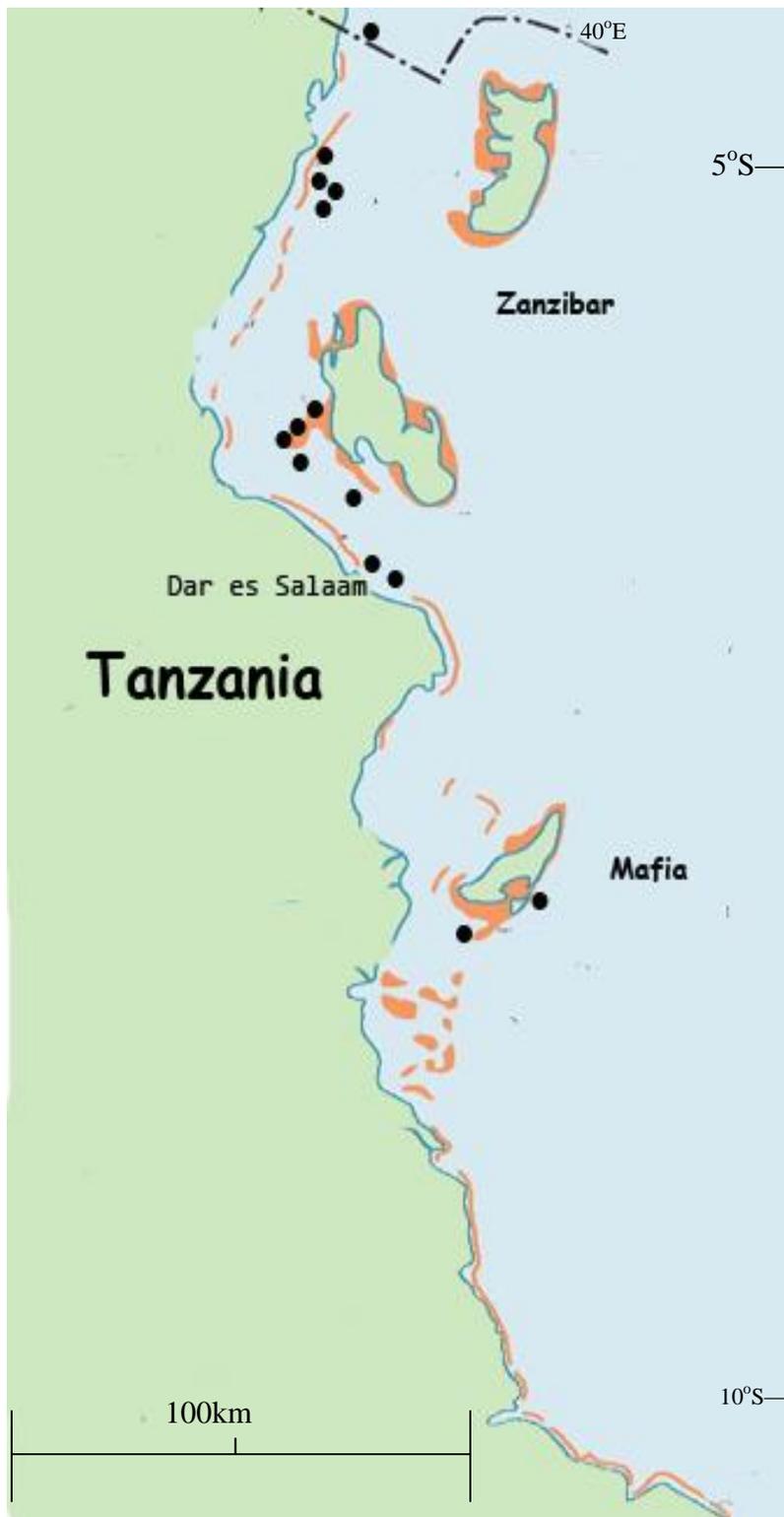
Fig. 1. Map of Tanzanian coastline showing the study area.

Depth of all reefs surveyed ranged from 4 to 10 m at low tide. The mean tidal range was 3.3 m with a maximum of about 4 m. The entire study area is influenced by monsoon weather patterns, with southerly winds and rough seas during the south-east monsoon (April to September), and higher air temperatures and weaker winds during the north-east monsoon (November to February) (McClanahan 1988, Jiddawi and Öhman 2002).

In 1997/1998, a coral bleaching event, the most geographically extensive and severe on record (Strong et al. 1998, Hoegh-Guldberg 1999, Wilkinson et al. 1999), caused extensive coral mortality on the four study sites of this thesis as well as many other sites in the region (Wilkinson et al. 1999).

FIELD METHODS

Methods used in the different studies are described here in summarized form. More comprehensive descriptions of experimental design and methods are given in the individual papers.

Coral transplantation

Studies in papers I and II were experimental field surveys using transplanted colonies of the staghorn coral *Acropora muricata* (formerly *A. formosa*). In Study I, *A. muricata* colonies were transplanted in 1995 to 32 quadrate plots measuring 2.5 x 2.5 m each (Lindahl 1998).

These coral colonies were placed loosely in the plots or tied together with string for increased stability. The coral fragments were collected from naturally growing thickets close to the study site. Sixteen experimental plots were positioned in each of the two sites situated 200 m apart.

In Study II, colonies of *A. muricata* were transplanted from a nearby coral reef to a rubble-dominated experimental area (approximately 2000 m^2). Branches of corals from natural thickets growing in the area were carefully stripped of algae before they were transplanted to the experimental site, where they were tied to reinforcement bars buried in the seafloor. Half of the branches were transported straight from the source to the experimental site, while the remainder half were first exposed to sunlight above the water surface until they were bleached. Quadrate plots in this study were of the size 0.5 x 0.5 m. The final, balanced design had a total of 60 coral plots in three treatments, including live coral (n = 2 x 12), bleached coral (n = 2 x 12) and eroded coral rubble (n = 12).

Although Study III investigated fish assemblages on branching *Acropora*, it was not based on transplanted coral plots but was a study describing distribution patterns. Study IV and V, however, were more concerned with whole reef systems, rather than monospecific coral stands.

Fish surveys

In the studies of this thesis, fish were surveyed using various methodologies including stationary visual census technique (Papers I and II), roving diver technique (Paper III) and belt transects (Papers IV and V). In the stationary visual census technique fishes were identified and counted by a SCUBA diver using a method modified from Bohnsack and Bannerot (1986). Specifically, a diver slowly approached a plot and stopped at a distance of 2 m away from the plot to count all fish observed for two minutes. The diver then moved closer and recorded any unseen cryptic species for an additional two minutes. This period of time was considered sufficient for contemporary plot size, and minimized the risk of multiple counts of individuals. Only fish occurring up to 1.5 m above the plots were recorded. Density and diversity of fish on the plots was then monitored. In Paper I fish were surveyed six months before, six months after and six years after the 1997/98 El Niño and its subsequent coral bleaching event. For Study II, initial fish counts were carried out in December 2004, within 24 hours after the plots were in place, and then repeated daily for three consecutive days. The sampling procedure was carried out another three times over the next 13 months.

A modified roving diver technique (Schmitt and Sullivan 1996) was adopted in Study III. Using this technique, the diver sampled the first appropriately-sized (3 m^2) *Acropora* patch encountered, and identified and counted all fish on the plot and then continued swimming for a minimum of two minutes before sampling the next available coral patch. The sampling design of Study III was therefore, to some extent, determined by availability of these branching *Acropora* plots. This was not aided by the fact that there has been a great reduction

in the coverage of *Acropora* in the region (Lindahl et al. 2001, Garpe and Öhman 2003, 2007).

The benthic community composition of reefs in Study IV was assessed by placing random 20 m-line transects (following the line intercept method by English et al. 1997) where all substrate directly under the draped line was measured and recorded using SCUBA. Hard corals were identified to genus level while other organisms were pooled into crustose coralline algae, soft corals, sponges, algal assemblages, macroalgae, turf algae, seagrass, zoanthids and corallimorpharians. However, for analyses, we considered cover of scleratinian corals and their health (whether live, bleached or eroded) as well as the cover of some functionally different algal groups including macroalgae, turf algae and crustose coralline algae.

Two belt transect methods were used in Study V. The first one, the discrete group sampling (DGS) method, involved sampling of a limited number of species and families of fish, each during a single pass of the transect (McClanahan 1994). Four passes were made and groups were counted as follows: 1 – Scaridae and Acanthuridae; 2 – Balistidae, Chaetodontidae, Diodontidae and Pomacanthidae; 3 – Labridae; and 4 – Pomacentridae. In the second method a single pass of the belt was made, where fish were recorded and categorized into family groups and size classes.

Trophic groups considered in Study II and III were corallivores, herbivores, planktivores, invertivores, omnivores and piscivores. It is sometimes difficult to distinguish whether fish attachment to habitat is for the purpose of feeding or for other reasons, especially in coral reef ecosystems. In Paper I fishes have been grouped into more specialised categories according to both their feeding habits and affiliation with habitats.

Habitat and reef characteristics

In Papers I and II, coral fragments were transplanted onto plots of known size. The nature of the substratum was determined by point-sampling on projections of slide photographs taken at several random positions in each plot. Substratum was classified into live coral, dead coral, coral rubble and sand. Coral relief was estimated by taking 10 readings of the highest branches in each plot lying under two transect tapes. The average of these readings represented the relief of each plot. Coral transplant plots in Paper II were of relatively uniform size and volume. Unlike in Papers I and II, plot sizes in Paper III corresponded to the size of the transplants (i.e. coral cover was higher than 90%), thus there was no need for estimations of coral cover in this study. Sixteen randomly placed 20 m transects were laid in Paper IV for estimations of substrate cover. Nine randomly placed 10 m transects were laid in the fifth study (Paper V), and all benthic organisms 3 cm or larger were encountered and size-measured using the line intercept method. Substratum types recorded were classified as coral and frondose algae (to genus level), turf algae, sponge and soft coral.

Other investigations

Study V also looked at corals, algae and sea urchins (besides fish) using two ecological process assays: herbivory on seagrass and predation on sea urchins. For herbivory assays 30 blades of the seagrass *Thalassia hemprichii* were clipped to a nylon line at 2 m intervals (according to Hay 1981, McClanahan et al. 1994) and left for 24 h before retrieving to record bite rates, amounts and whether bitten by fish or sea urchins. Sea urchins were sampled in nine random 10 m^2 circular quadrates at each site, and all individuals were identified to species level and counted. Wet weights of twenty urchins of each species were measured for converting population densities to biomass estimates. Predation on sea urchins was estimated by threading 30 individual *Echinometra mathaei* to monofilament lines randomly placed on the reef and left for 24h, after which mortality from predation was recorded and a predation index calculated.

Data analyses

Variations in time, habitat (Paper II), location (Paper V), and the interactions of these factors were analysed using repeated measures ANOVA models. In Paper II, two-way ANOVA models were used to compare fish data among sites (4 levels) and among habitats (3 levels), using both variables as fixed factors. Reef types were assessed using one-factor ANOVA models. A hierarchical cluster analysis using Ward similarity was performed on the coral genera data to investigate similarities in coral community distribution patterns (Paper V). Additionally, cumulative numbers of coral genera and fish species were plotted against the sampling effort.

Mann-Whitney *U*-tests were used to compare site differences within sampling occasions (Paper I) and between protected and unprotected sites (Paper IV). In Paper I, *t*-tests for matched pairs and Wilcoxon signed ranks were utilised in comparing between sampling occasions. The data in Paper IV did not approximate homogeneity and normality, thus fish abundances, biomass and diversity as well as sea urchin biomass were tested for variation between sites using the Kruskal-Wallis test. *A posteriori* multiple mean comparisons were performed with Bonferroni corrected Mann-Whitney *U*-tests. Relationships between components of the benthic community were analysed using Spearman's correlation coefficient.

The multivariate non-metric multi-dimensional scaling (nMDS) ordinations (Papers I–IV) gave graphic visualizations of fish assemblage patterns, which were based on the Bray-Curtis similarity measure and density data (Clarke 1993). Using this multivariate technique, each point within an ordination denotes the assemblage structure in a sample in comparison to other samples. Thus, the proximity of points indicates the similarity in structure of their associated assemblages. A stress value indicates how precise the configuration of points is. Analysis of similarity (ANOSIM; Clarke and Green 1988) was used to analyse differences in fish assemblage structure among sites, habitats, reef-types and time periods, respectively (Papers I–III). ANOSIM confirms differences observed in nMDS ordinations, giving a measure and test of level of separation between samples. Where nMDS and ANOSIM indicated that there were differences in fish assemblages between sites and sampling periods,

the similarity percentage of analysis (SIMPER) procedure was used to identify the proportional contribution of individual species to among-sample dissimilarity (Clarke 1993). In other words, SIMPER identified taxa whose change in abundance had the most significant effect on the fish assemblage structure.

RESULTS AND DISCUSSION

This thesis includes studies focusing on fish response to changes in habitat, specifically bleaching and degradation of coral reefs. Of particular emphasis were the short- (Paper II) and long-term (Papers I and V) effects on coral reef communities of the El Niño Southern Oscillation (ENSO) of 1997/98. This event caused elevated temperatures worldwide and led to coral bleaching and mortality of up to 90% in East African reefs (Linden and Sporrong 1999, Linden et al. 2002). The first study (Paper I) examined whole fish assemblages in plots of transplanted coral in Mafia Island Marine Park, Tanzania, before and after the 1997/1998 bleaching episode. In Paper III, the effects of habitat quality, habitat structure and spatial arrangement of reefs on fish assemblages were investigated, while Paper IV focused on how aspects of herbivory differed between fished reefs and reefs within closures.

Bleaching effects: the influence of structural complexity

The long- (Paper I) and short-term (Paper II) effects of bleaching on reef fish communities were investigated by studying fish assemblages on transplanted coral plots with habitat types

representing a simple bleaching gradient from live coral to bleached (dead) and eroded/degraded coral (Paper II). The transplants were examined shortly before, 6 months after and 6 years after the major bleaching episode of 1997/98. The results revealed no observed differences between fish abundances on live corals and freshly bleached corals, while they both had greater fish densities than eroded corals (Paper II). This suggests that the coral bleaching itself did not generate any corresponding changes in fish assemblage structure. However, with time bleaching may lead to death of corals. This in turn weakens the corals and makes them more vulnerable to environmental forces and ultimately the coral structure breaks down. The effects of coral bleaching may not always be instantly evident, as, for example, the reduction in availability of coral polyps for fish species that feed on corals may lead to significant but sub-lethal effects on the fishes (Kokita and Nakazono 2001, Pratchett et al. 2004, Berumen et al. 2005). In fact the effect of coral bleaching may sometimes be an increase in fish densities, such as found by Lindahl et al. (2001). In Paper I, six months after coral death, the total abundance and taxonomic richness had increased at one of the two sites, whereas six years later the two measures had decreased significantly at both sites. Such responses would be expected as turf algae colonize the dead coral substrates, possibly resulting in increase in herbivores on the reef. With subsequent degradation of the dead corals and lowering of habitat structural complexity the fish abundance and diversity would drop again.

Fish diversity was lower in eroded plots than in plots of live and bleached coral. This is an indication of a positive relationship between fish diversity and habitat complexity (Papers I–

III). Some fish species are generalists and associated with corals during some parts of their life cycle (Wilson et al. 2010), while others are specialists strictly dependent on corals for food (e.g. Pratchett et al. 2006) and/or shelter only when threatened (Holbrook et al. 2002). Specialists are more likely to be affected by coral loss than are generalists. Other factors affecting fish diversity are the extent of original coral cover, magnitude of disturbance and the strength of the relationship between fish and corals at the time of disturbance (Paper I).

Among-sample variability increased with disturbance and was most apparent following substrate erosion (Papers I and II, Fig 2). Functional groups with documented habitat-associations were also significantly influenced by habitat alteration. For instance, the abundance of coral dwellers decreased following coral death and erosion. All herbivores increased as an immediate response to bleaching, but were subsequently uncommon in eroded plots. Although coral feeders were rare throughout the study, they were – as predicted – absent from the eroded reefs.
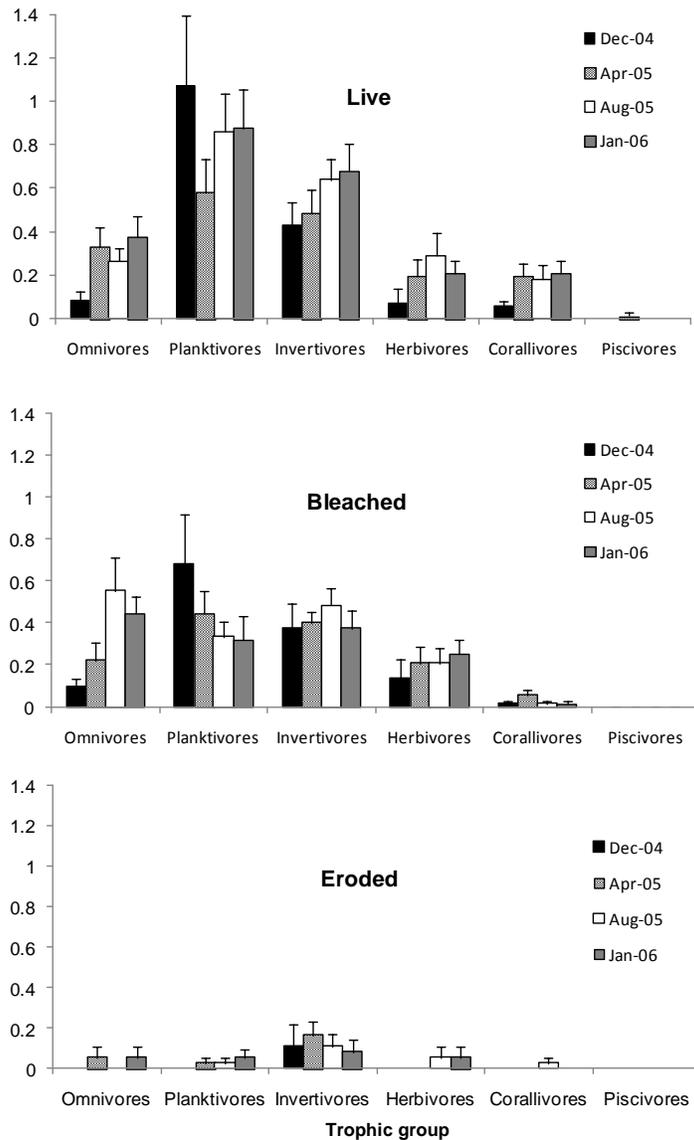
Fig 2. Mean number of fish per plot at live, bleached and eroded coral habitat types, recorded on four occasions over a period of one year. Error bars denote standard error.

In the second study (Paper II), there was a clear effect of structural complexity and relief on fish abundance and diversity, as evidenced by the differences in fish composition on eroded

coral (rubble) plots compared to the live and bleached coral treatments. Differences between live and bleached habitats were less obvious and not statistically significant. After the first survey (December 2004), time influenced fish diversity but not abundance. When assemblage patterns were examined, however, a shift with habitat structure and time was shown. Planktivores and corallivores showed preferences for living corals. Planktivores and invertivores dominated the fish assemblages initially, but their influence decreased with time. There was no significant difference in fish diversity between live and bleached coral habitats, but the eroded coral plots had significantly lower fish diversity and abundance when compared to live and bleached coral plots. This is in contrast to study III where bleached and eroded plots did not differ in fish abundance or diversity. The contrasting results in study III may partly be due to different spatial configurations of the reefs studied. The combined effect of habitat quality and spatial arrangement on fish-habitat relationships is not yet well understood (Moore et al. 2011). Studies II and III were similar considering the interaction of fish trophic groups and reef habitat.

The importance of structural complexity implies that long-term impacts of bleaching might be more dramatic to fish assemblages than the initial loss of live coral cover, as dead coral typically erodes to rubble. This was illustrated by the higher resilience of fish assemblages in the short-term study (Paper II), when compared to the response on fish community-level six years after a major bleaching event (Paper I). Similarly, in Paper I the assemblage structure of fish on the four plots that survived the 1997/1998 bleaching event eventually became similar to that of the dead plots as the corals gradually bleached and died. Species with close

association to the substrate were most affected by bleaching in both studies (i.e. Papers I and II), especially fish that feed exclusively on corals (i.e. corallivores). Obligate corallivores are especially vulnerable to loss of live coral (Munday 2004, Wilson et al. 2006, Pratchett et al. 2008) and have been identified as the most vulnerable functional group to climate disturbances (Graham et al 2011a). Another group similarly affected was the planktivores, but only in the second study (Paper II). This effect on planktivores may be explained by the large number of juveniles recorded as some non-coral specializing fish species have been reported to show strong associations with live coral as juveniles (Booth and Beretta 1994, Feary et al. 2007b).

Effect of management and protection of reefs

Management of reefs in Tanzania has been carried out by means of Marine Protected Areas (Papers II, IV and V). The most common method of enforcement is the introduction of no-take areas, i.e. closures from fishing and other extractive activities. Increased abundance of fish as a result of management may have consequences for coral reef communities. A return of larger-bodied fish to the reefs (which are targeted by fishers) can lead to better grazed reefs with higher coral cover and less frondose algae cover (Paper IV, V, McClanahan and Arthur 2001). High densities of sea urchins in fished reefs such as Changuu, attributed to a decline of sea urchin predators (McClanahan 2000), was contrasted in protected reefs where sea urchin predators and grazing competitors were found to increase in numbers. Patch reefs in the protected Chole Bay (Mafia Island Marine Park) had the highest abundance and diversity of patch and continuous reefs in four areas in Tanzania (Paper III). Ecological

theory predicts that populations of specialist species are likely to be constrained by the abundance of specific resources. Under protection therefore, the increase in available resources should favour abundance of both generalist and specialist fish species. With time, protection may therefore lead to pronounced differences in fish assemblage structure on coral reefs (Paper IV, V, Fig 3).
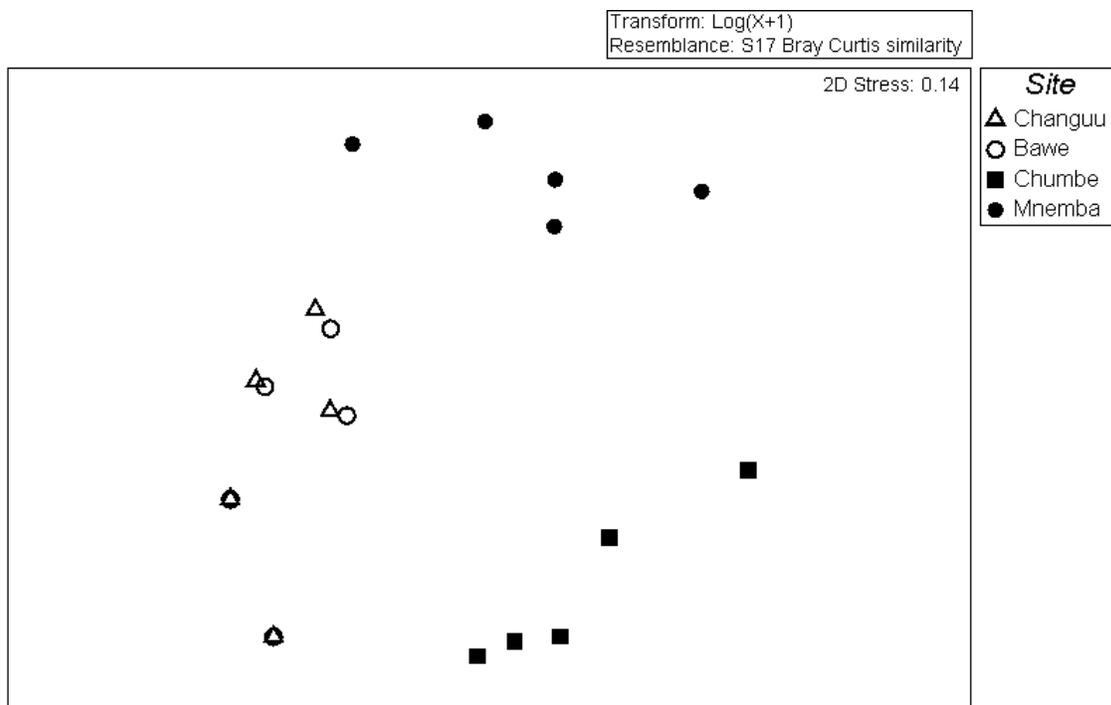

Fig. 3. Non-metric multidimensional scaling (MDS) ordinations of fish assemblage structure on 2 protected (dark symbols) and 2 fished reefs.

Although in the long term crustose coralline algae is expected to thrive where sea urchin numbers are low (O'Leary and McClanahan 2011), we found abundance of the two to be positively correlated. Neither was there a strong negative relationship between herbivore

abundance and that of the other two functional groups of algae, the macroalgae and turf algae. In addition, algal abundance was highest in the fisheries closures. This departure from the traditional view of macroalgal-reef herbivore dynamics and could be due to the influence of several factors operating over different spatial scales (Hoey and Bellwood, 2010). Possibly the effect of habitat is a factor in the complex herbivore dynamics, as well as are the presence/absence of a few key fish species (Cheal et al. 2011) and the influence of bottom-up processes.

CONCLUDING REMARKS

Despite methodological differences, the results from these five studies indicate some general patterns and conclusions. Structural complexity was shown to influence coral reef fish diversity and abundance. The effects of a disturbance event such as bleaching are more apparent in the long term (years) than in the short term (weeks to months). This is because the physical framework of the reef remains intact in the short term. With time, however, the reef erodes and the structural complexity is lost, with severe consequences for associated fish assemblages. The 'slow' response of fish assemblages to bleaching of corals could indicate that reef fish are more resilient than previously thought. Many species did not discriminate between live and bleached or partially degraded colonies. This could signify that settlement patterns are resilient to the initial stages of declining coral health (Feary et al. 2007; Paper II). Generalist fish species in general are more resilient to habitat degradation than coral specialists (see Pratchett et al. 2004, 2008). Similarly, the general stability of reefs in the Western Indian Ocean 6 years after the massive ENSO of 1997/98 indicates that some coral

reefs are relatively ecologically stable and resilient to climate change, and possibly of regional or global conservation importance (Paper V, West and Salm 2003). A better understanding of the driving role of processes, structural complexity and diversity on recovery is needed (Graham et al 2011b). At local level, at least, priorities should include identification and management of these high-diversity, resilient reefs (Mclanahan et al. 2011) so as to minimise effects of future climate change impacts. This discovery of stable, fairly intact reefs indicates that descriptive and monitoring studies are essential, despite the current shift towards experimental studies of coral reefs. Patch reefs (even small ones) have the potential to support juvenile fish and should not be sidelined in management plans. While the role of herbivory is significant in maintaining reef resilience, the specific roles of individual herbivorous species remain uncertain. In addition, reefs have different biological and oceanographic conditions, and hence explanations of community structure should be taken in context. Those and other aspects described in this thesis deserve further investigation.

ACKNOWLEDGEMENTS

REFERENCES

Anthony KRN, Kline DI, Diaz-Pulido G, Dove S, Hoegh-Guldberg O (2008) Ocean acidification causes bleaching and productivity loss in coral reef builders. PNAS 105:17442-17446

Ault TR, Johnson CR (1998) Spatially and temporally predictable fish communities on coral reefs. Ecological Monographs 68:25-50

Baker AC, Glynn PW, Riegl B (2008) Climate change and coral reef bleaching: An ecological assessment of long-term impacts, recovery trends and future outlook. Estuarine, Coastal and Shelf Science 80:435-471

Bell JD, Craik GJS, Pollard DA, Russell BC (1985) Estimating length frequency distributions of large reef fish under water. Coral Reefs 4: 41-44

Bell JD, Galzin R (1984) Influence of live coral on coral reef fish communities. Marine Ecology Progress Series 15:265-274

Berumen ML, Pratchett MS, McCormick MI (2005). Within-reef differences in diet and body condition of coral-feeding butterflyfishes (Chaetodontidae). Marine Ecology Progress Series 287:217-227

Bohnsack JA, Bannerot SP (1986) A stationary visual census technique for quantitatively assessing community structure of coral reef fishes. NOAA Technical Reports NMFS 41:1-15

Booth DJ, Beretta GA (1994) Seasonal recruitment, habitat associations and survival of pomacentrid reef fish in the US Virgin Islands. Coral Reefs 13:81-89

Booth DJ, Beretta GA (2002) Changes in a fish assemblage after a coral bleaching event. Marine Ecology Progress Series 245:205-212

Bouchon-Navaro Y, Bouchon C (1989) Correlations between chaetodontid fishes and coral communities of the Gulf of Aquaba (Red Sea). Environmental Biology of Fishes 25:47-60

Bruggemann JH, Kuyper MWM, Breeman AM (1994) Comparative analysis of foraging and habitat use by the sympatric Caribbean parrotfish *Scarus vetula* and *Sparisoma viride* (Scaridae). Marine Ecology Progress Series 112:51-66

Caley MJ, Carr MA, Hixon TP, Hughes TP, Jones GP, Menge BA. (1996) Recruitment and the local dynamics of open marine populations. Annual Review of Ecology, Evolution and Systematics 27:477-500

Carpenter KE, Miclat RI, Albaladejo VD, Corpuz VT (1981) The influence of substrate structure on the local abundance and diversity of Philippine reef fishes. Proceedings of the 4th International Coral Reef Symposium 2:497-502

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

Cheal AJ, Aaron MacNeil, M, Cripps E, Emslie MJ, Jonker M, Schaffelke B, Sweatman H (2010) Coral–macroalgal phase shifts or reef resilience: links with diversity and functional roles of herbivorous fishes on the Great Barrier Reef. Coral reefs 29:1005-1015

Choat JH (1991) The biology of herbivorous fishes on coral reefs. Pgs 120-155 in P. F. Sale, ed. The Ecology of Fishes on Coral Reefs. Academic Press, San Diego, CA, 92101, 754 pp.

Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology 18:117-143

Coles SL, Jokiel PL (1977) Effects of temperature on photosynthesis and respiration in hermatypic corals. Marine Biology 43:209-216

Doherty PJ (1982) Coral reef fishes: recruitment limited assemblages? In E. D. Gomez et al. (eds) Proceedings of the 4th International Coral Reef Symposium 2:465-470

Doherty PJ, Williams D McB (1988) The replenishment of coral reef fish populations. Oceanography and Marine Biology 26:487-551.

Ebeling AW, Hixon MA (1991). Tropical and temperate reef fishes: comparison of community structures. In P. F. Sale, ed. The Ecology of Fishes on Coral Reefs. Academic Press, San Diego, CA. pp 509-563.

Feary DA, Almany GR, McCormick MI, Jones GP (2007) Habitat choice, recruitment and the response of coral reef fishes to coral degradation. Oecologia 153:727-737

Green AL, Bellwood DR (2009) Monitoring functional groups of herbivorous reef fishes as indicators of coral reef resilience – A practical guide for coral reef managers in the Asia Pacific region. IUCN working group on Climate Change and Coral Reefs. IUCN, Gland, Switzerland. 70 pp.

Hay ME (1997) The ecology and evolution of seaweed-herbivore interactions on coral reefs. Coral Reefs 16, Supplement: S67-S76. (also published in the Proceedings of the 8th International Coral Reef Symposium Vol. I: 23-32. 1997)

Hixon MA (1991) Predation as a process structuring coral reef fish communities. In P. F. Sale (ed) The Ecology of Fishes on Coral Reefs. Academic Press, San Diego. p 475-508.

Hixon MA, Beets JP (1993). Predation, prey refuges, and the structure of coral-reef fish assemblages. Ecological Monographs 63:77-101.

Hughes TP, Rodrigues MJ, Bellwood DR, Ceccarelli D, Hoegh-Guldberg O, McCook L, Moltschaniwskyj N, Pratchett MS, Steneck RS, Willis B (2007) Phase shifts, herbivory, and the resilience of coral reefs to climate change. Current Biology 17: 1-6.

Garpe KC, Öhman MC (2003) Coral and fish distribution patterns in Mafia Island Marine Park, Tanzania: fish–habitat interactions. Hydrobiologia 498:191-211

Garpe KC, Öhman MC (2007) Non-random habitat use by coral reef fish recruits in Mafia Island Marine Park, Tanzania. African Journal of Marine Science 29: 187-199

Glynn PW (1993) Coral reef bleaching ecological perspectives. Coral Reefs 12:1-17

Glynn PW (1996) Coral reef bleaching: facts, hypotheses and implications. Global Change Biology 2:495–509

Goreau TJ, MacFarlane AH (1990). Reduced growth rate of Montastrea annularis following the 1987/1988 coral-bleaching event. Coral Reefs 8:211-215

Graham NAJ, Nash KL, Kool JT (2011b) Coral reef recovery dynamics in a changing world Coral Reefs 30:283–294

Graham NAJ, Chabanet P, Evans RD, Jennings S, Letourneur Y, MacNeil MA, McClanahan TR, Ohman M, Polunin NVC, Wilson SK (2011a). Extinction vulnerability of coral reef fishes. Ecology Letters 14, pp. 341–348

Gratwicke B, Speight MR (2005) The relationship between fish species richness, abundance and habitat complexity in a range of shallow tropical marine habitats. Journal of Fish Biology 66:650-667

Hawkins JP, Roberts CM (1994) The growth of coastal tourism in the Red Sea: present and possible future effects on coral reefs. Ambio 23:503-508

Hay ME (1991) Fish-seaweed interactions on coral reefs: effects of herbivorous fishes and adaptations of their prey. In: Sale PF (ed) The ecology of fishes on coral reefs Academic Press, San Diego, p 96-119

Hixon MA (1991) Predation as a process structuring coral reef fish communities. In: Sale PF (ed) The ecology of fishes on coral reefs Academic Press, San Diego, p 475-508

Hixon MA, Beets JP (1993) Predation, prey refuges and the structure of coral-reef fish assemblages. Ecological Monographs 63:77-101

Hoegh-Guldberg O, Smith GJ (1989) The effects of sudden changes in temperature, light and salinity on the population density and export of zooxanthellae from the reef corals *Stylophora pistillata* Esper and *Seriatopora hystrix* Dana. Journal of Experimental Marine Biology and Ecology 129, 279–303.

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

Hoegh-Guldberg O, Fine M, Skirving W, Johnstone R, Dove S, Strong A (2005) Coral bleaching following wintry weather. Limnology and Oceanography 50:265–271

Hoegh-Guldberg O, Mumby PJ, Hooten AJ, Steneck RS, Greenfield P, et al. (2007) Coral reefs under rapid climate change and ocean acidification. Science 318: 1737–1742.

Hoey AS, Bellwood DR (2010) Cross-shelf variation in browsing intensity on the Great Barrier Reef. Coral Reefs 29:499–508.

Holbrook SJ, Brooks AJ, Schmitt RJ (2002) Variation in structural attributes of patch-forming corals and patterns of abundance of associated fishes. Marine and Freshwater Research 53:1045-1053.

Jiddawi NS, Öhman M (2002) Marine Fisheries in Tanzania: Status and Potential. Ambio 31: 518-536.

Jokiel P, Coles SL (1990) Response of Hawaiian and other Indo-Pacific reef corals to elevated temperature. Coral Reefs 8, 155–162.

Jones GP (1991) Post recruitment processes in the ecology of coral reef fish populations: a multifactorial perspective. In: Sale PF (ed) The ecology of fishes on coral reefs. Academic Press, San Diego. p 294-328

Jones GP, Syms C (1998) Disturbance, habitat structure and the ecology of fishes on coral reefs. Australian Journal of Ecology 23:287-297

Kokita T, Nakazono A (2001) Rapid response of an obligately corallivorous filefish *Oxymonacanthus longirostris* (Monacanthidae) to a mass coral bleaching event. Coral Reefs 20:155-158

Lindahl U (1998) Low-tech rehabilitation of degraded coral reefs through transplantation of staghorn corals. Ambio 27:645-650

Lindahl U, Öhman, MC, Schelten CK (2001) The 1997/1998 mass mortality of corals: effects on fish communities on a Tanzanian coral reef. Marine Pollution Bulletin 42:127-131

Linden O, Sporrong N (eds.) 1999. Coral Reef Degradation in the Indian Ocean. Status report 1999. CORDIO.

Lindén O, Souter D, Wilhelmsson D, Obura D (eds.) (2002) Coral Reef Degradation in the Indian Ocean. Status report 2002. CORDIO 284 pp.

Luckhurst BE, Luckhurst K (1978) Analysis of the influence of substrate variables on coral reef fish communities. Marine Biology 49:317-323

McClanahan TR (1988) Seasonality in East Africa's coastal waters. Marine Ecology Progress Series 44: 191-199

McClanahan TR (1994) Kenyan coral reef lagoon fish: associations with reef management, substrate complexity, and sea urchins. Coral Reefs 13:231-241

McClanahan TR (2000) Recovery of a coral reef keystone predator, *Balistapus undulatus*, in East African marine parks. Biological Conservation 94: 191-198

McClanahan TR, Arthur R (2001) The effect of marine reserves and habitat on populations of East African coral reef fishes. Ecological Applications 11: 559-569

McClanahan, TR, Graham NAJ, Calnan JM, MacNeil MA (2007) Towards pristine biomass: reef fish recovery in coral reef marine protected areas in Kenya. Ecological Applications 17:1055-1067.

McClanahan TR., Maina JM, Muthiga NA. (2011) Associations between climate stress and coral reef diversity in the western Indian Ocean. Global Change Biology 17, 2023–2032.

McCormick MI (1994) Variability in age and size at settlement of the tropical goatfish *Upeneus tragula* (Mullidae) in the northern Great Barrier Reef lagoon. Marine Ecology Progress Seres 103:1-15

McManus JW, Midat RI, Palaganas VP (1981) Coral and fish community structure of Sombrero Island, Batangas, Philippines. Proceedings of the 4th International Coral Reef Symposium 2:271-280

McPhaden MJ (1999) El Niño: The child prodigy of 1997-98. Nature 398:559-562

Moore CH, Van Niel K, Harvey ES (2011) The effect of landscape composition and configuration on the spatial distribution of temperate demersal fish. Ecography 34: 425-435.

Munday PL, Jones GP, Caley MJ (1997) Habitat specialisation and the distribution and abundance of coral-dwelling gobies. Marine Ecology Progress Series 152: 227-239.

Munday PL (2004) Habitat loss, resource specialization, and extinction on coral reefs. Global Change Biology 10:1642-1647

Muscatine L (1990) The role of symbiotic algae in carbon and energy flux in reef corals. Coral Reefs 25:1-29

Nyström M, Folke C, Moberg F (2000) Coral reef disturbance and resilience in a human-dominated environment. Trends in Ecology and Evolution 15: 413-417.

O'Leary JK, McClanahan TR (2010) Trophic cascades result in large-scale coralline algae loss through differential grazer effects. Ecology 91:3584–359

Öhman MC, Rajasuriya A (1998) Relationships between habitat structure and fish communities on coral and sandstone reefs. Environmental Biology of Fishes 53:19-31

Öhman MC (1999) Coral bleaching effects on reef fish assemblages and fisheries. In: Linden O, Sporrong N (eds) Coral reef degradation in the Indian Ocean CORDIO, Stockholm. p 71-77

Öhman MC, Munday PL, Jones GP (1998b) Settlement strategies distribution patterns of coral-reef fishes. Journal of Experimental Marine Biology and Ecology 225:219-238

Öhman MC, Rajasuriya A, Olafsson E (1997) Reef fish assemblages in north-western Sri Lanka: distribution patterns and influences of fishing practises. Environmental Biology of Fishes 49:45-61

Öhman MC, Rajasuriya A, Svensson S (1998a) The use of butterflyfishes (Chaetodontidae) as bioindicators of habitat structure and human disturbance. Ambio 27:708-716

Pratchet MS, Wilson SK, Berumen ML, McCormick MI (2004) Sublethal effects of coral bleaching on an obligate coral feeding butterflyfish. Coral Reefs 23: 352 - 356

Pratchett MS, Munday MS, Wilson SK, Graham NAJ, Cinner JE, Bellwood DR, Jones GP, Polunin NVC, McClanahan TR (2008) Effects of climate-induced coral bleaching on coral-reef fishes: ecological and economic consequences. Oceanography and Marine Biology: An Annual Review 46: 251-296

Pratchett MS, Wilson SK, Baird AH (2006) Declines in the abundance of Chaetodon butterflyfishes (Chaetodontidae) following extensive coral depletion. Journal of Fish Biology 69: 1269-1280.

Randall JE (1967) Food habits of reef fishes of the West Indies. Studies in Tropical Oceanography 5:665-847.

Reaser JK., Pomerance R, Thomas PO. (2000) Coral bleaching and global climate change: scientific findings and policy recommendations. Conservation Biology 14:1500-1511

Risk MJ (1972) Fish diversity on a coral reef in the Virgin Islands. Atoll Res Bull 153:1-6

Russ GR (1991) Coral reef fisheries. In Sale PF (ed) The ecology of fishes on coral reefs. Academic Press: San Diego pp 601-635

Sale PF (1974) Mechanisms of coexistence in a guild of territorial fishes at Heron Island. Proceedings of the 2nd International Coral Reef Symposium 1:193-206

Sale PF (1978). Coexistence of coral reef fishes - A lottery for living space. Environmental Biology of Fishes 3:85-102.

Sale PF (1980) The ecology of fishes on coral reefs. Oceanography and Marine Biology: An Annual Review 18:367-421

Sale PF. (1991). Reef fish communities: open nonequilibrial systems. In P. F. Sale, ed. The Ecology of Fishes on Coral Reefs. Academic Press, San Diego p 564-598.

Sale PF, Dybdahl R (1975). Determinants of community structure for coral reef fishes in an experimental habitat. Ecology 56:1343-1355.

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

Schmitt EF, Sullivan KM (1996). Analysis of a volunteer method for collecting fish presence and abundance data in the Florida Keys. Bulletin of Marine Science 59: 404-416.

Smith CL, Tyler JC (1972) Space resource sharing in a coral reef fish community. Natural History Museum of Los Angeles County Science Bulletin 14:125-170

Smith SV (1978). Coral-reef area and the contribution of reefs to processes and resources of the world's oceans. Nature 273:225-226.

Strong AE, Goreau TJ, Hayes RL (1998) Ocean hot spots and coral reef bleaching. Reef Encounters 24:20-22

Talbot FH, Russell BD, Anderson GRV (1978) Coral reef fish communities: unstable, high-diversity systems? Ecological Monographs 48:425-440

Victor BC (1983) Recruitment and population dynamics of a coral reef fish. Science 219:419-420.

Williams, D. McB. 1980. Dynamics of the pomacentrid community on small patch reefs in One Tree Lagoon (Great Barrier Reef). Bulletin of Marine Science 30:159-170.

Wells S, Samoilys M, Anderson J, Kalombo H, Makoloweka S (2007) Collaborative fisheries management in Tanga, Northern Tanzania. In Fisheries Management: Progress Towards Sustainability, McClanahan TR, Castilla JC (eds). Blackwell Scientific: London; 139–165.

West JM, Salm RV (2003) Resistance and resilience to coral bleaching: implications for coral reef conservation and management. Conservation Biology 17: 956–967.

Wilhelmsson D, Öhman MC, Ståhl H, Shlesinger Y (1998) Artificial reefs and dive tourism in Eilat, Israel. Ambio 27:764-766

Wilhelmsson D, Yahya SAS, Öhman MC (2006) Effects of high-relief structures on cold temperate fish assemblages: a field experiment. Marine Biology Research 2:136-147

Wilkinson C (2000) Status of coral reefs of the world: 2000. Global Coral Reef Monitoring Network and Australian Institute of Marine Science, Townsville, Australia 281 pp

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

Wilson SK, Graham NAJ, Pratchett MS, Jones GP, Polunin NVC, 2006. Multiple disturbances and the global degradation of coral reefs: are reef fishes at risk or resilient? Global Change Biology 12:2220-2234