Effects of habitat structure on tropical fish assemblages

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To our precious little ones,
Silas, Milla & Lola
“So long as water moves, so long as fins press against it, as long as weather changes and man is fallible, fish will remain in some measure unpredictable”

Roderick Haig-Brown
ABSTRACT

Rates of habitat alteration and degradation are increasing worldwide due to anthropogenic influence. On coral reefs, the loss of live coral reduces structural complexity while facilitating algal increase. In many coastal lagoons seagrass and corals are cleared to make room for cultivated macroalgae. This thesis deals with reef and lagoon habitat structure and how fish assemblage patterns may be related to physical and biological features of the habitat. It further examines assemblage change following habitat disturbance. Four studies on East African coral reefs concluded that both the abundance and species richness of recruit and adult coral reef fish were largely predicted by the presence of live coral cover and structural complexity (Papers I-III, VI). Typically, recruits were more selective than adults, as manifested by limited distributions to degraded sites. Paper VI compared short- and long-term responses of fish assemblages to the 1997-1998 bleaching event. The short-term response to coral mortality included the loss of coral dwelling species in favour of species which feed on algae or associated detrital resources. Counterintuitively, fish abundance and taxonomic richness increased significantly at one of two sites shortly after the bleaching. However, the initial increase was later reversed and six years after the death of the coral, only a limited number of fish remained. The influence of fleshy algae on fish assemblages was studied in algal farms (Paper IV), and examined experimentally (Paper V). The effects of algal farming in Zanzibar were significant. Meanwhile, manually clearing algal-dominated patch reefs in Belize from macroalgae resulted in short-term increases of abundance, biomass and activity of a few species, including major herbivores. The findings of this thesis demonstrate the significance of habitat as a structuring factor for tropical fish assemblages and predicts that coral death, subsequent erosion and algal overgrowth may have substantial deleterious impacts on fish assemblage composition, abundance and taxonomic richness, with recovery being slow and related to the recovery of the reef framework.
LIST OF PAPERS

This thesis is based on the following papers, which will be referred to in the text by their Roman numerals. The published papers are reprinted with the kind permission of the publishers.


* The author has since changed her surname to Garpe

My contribution to the papers in the thesis is as follows:

I-III Responsible for project design, field work, data analyses and writing
IV Participated in field work, responsible for analyses and writing
V Participated in field work, responsible for fish counts and behaviour study, assisted with fish data analyses and all fish-related parts of the paper
VI Responsible for data analyses and writing
# CONTENTS

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>ABSTRACT</td>
<td>7</td>
</tr>
<tr>
<td>LIST OF PAPERS</td>
<td>8</td>
</tr>
<tr>
<td>INTRODUCTION</td>
<td>11</td>
</tr>
<tr>
<td>Habitat structure – the arrangement of objects in space</td>
<td>11</td>
</tr>
<tr>
<td>The tropical coral reef</td>
<td>12</td>
</tr>
<tr>
<td>Habitat alteration and disturbance in the reef environment</td>
<td>13</td>
</tr>
<tr>
<td>The impacts of coral degradation on reef fish assemblages</td>
<td>14</td>
</tr>
<tr>
<td>The algal habitat</td>
<td>15</td>
</tr>
<tr>
<td>Objectives in brief</td>
<td>15</td>
</tr>
<tr>
<td>PAPERS IN BRIEF</td>
<td>16</td>
</tr>
<tr>
<td>Paper I</td>
<td>16</td>
</tr>
<tr>
<td>Paper II</td>
<td>16</td>
</tr>
<tr>
<td>Paper III</td>
<td>17</td>
</tr>
<tr>
<td>Paper IV</td>
<td>18</td>
</tr>
<tr>
<td>Paper V</td>
<td>18</td>
</tr>
<tr>
<td>Paper VI</td>
<td>19</td>
</tr>
<tr>
<td>GENERAL METHODS</td>
<td>20</td>
</tr>
<tr>
<td>Study sites</td>
<td>20</td>
</tr>
<tr>
<td>Field methods</td>
<td>21</td>
</tr>
<tr>
<td>Data analysis</td>
<td>23</td>
</tr>
<tr>
<td>GENERAL DISCUSSION</td>
<td>25</td>
</tr>
<tr>
<td>Evidence of non-random habitat use</td>
<td>25</td>
</tr>
<tr>
<td>The influence of structural complexity</td>
<td>26</td>
</tr>
<tr>
<td>Alteration in algal abundance</td>
<td>27</td>
</tr>
<tr>
<td>Reef fish communities facing habitat degradation</td>
<td>29</td>
</tr>
<tr>
<td>REFERENCES</td>
<td>31</td>
</tr>
<tr>
<td>TO ALL OF YOU WHO CONTRIBUTED…</td>
<td>40</td>
</tr>
</tbody>
</table>
INTRODUCTION

Habitat structure – the arrangement of objects in space

Habitat provides functional space for associated organisms and constitutes a fundamental concept in ecology, affecting community structure in a variety of organisms and environments. In a broad sense, habitat is defined as an area of the physical environment more or less distinct from others in a range of abiotic and biotic variables (Kramer et al. 1997). Habitats may be continuous, patchy or isolated and they may be stable, seasonal, unpredictable or temporary (Southwood 1977). Habitat has a particular structure in which resources are arranged in space and time according to changes in the physical environment and according to a range of ecological processes. The essential aspects of habitat structure have been defined as heterogeneity, complexity and scale (McCoy & Bell 1991). Heterogeneity is the relative abundance of different structural components per unit area (e.g. the proportions of coral, algae and bare rock on a coral reef). Complexity is defined as the absolute abundance of individual structural components per unit area (e.g. the degree of branching in corals or the density of macroalgae). Finally, scale is defined as the size of the area used to measure heterogeneity or complexity (e.g. size of sampling area, transect, quadrate). Microhabitat is used at higher resolution to address subdivisions of the habitat that are relatively homogenous and differ only in limited number of variables.

Most organisms exhibit non-random and predictable spatial distributions associated with the biotic and physical structure of their habitat (Bell et al. 1991). The use of any resource in disproportion to availability is described as selective resource use, while selection is the process in which an animal chooses a resource (Johnson 1980). Typical for the study of habitat selection is that the actual behaviour is rarely observed; rather it is inferred from observed patterns of non-random distributions. Species-specific habitat selection is typically related to the quality of the habitat for a particular species, in terms of e.g. prospective availability of food resources and predator shelter. The expectancy of finding a suitable habitat in which to hide, feed and breed is foremost governed by spatial habitat features such as the degree of isolation, the distance between and the size of habitat patches as well as by the dispersal or migratory range of the organism (Southwood 1977). Remaining in suboptimal habitat may affect condition and survival (Berumen et al. 2005). The degree of habitat selection and, as a consequence, habitat dependency, typically varies among taxa as well as among life stages within taxa.

This thesis pays special attention to the complexity of the habitat, which is considered a useful predictor of the abundance, distribution and diversity of various taxa including birds (MacArthur & McArthur 1961, Anderson & Shugart 1974), lizards (Pianka 1966) and invertebrates (Lawton 1983). In aquatic habitats, the positive effects of features providing structural complexity in an otherwise unstructured habitat have been repeatedly demonstrated in a range of environments and for a whole host of taxa including both invertebrates (Heck & Wetstone 1977, Kelaher 2003, Underwood 2004) and fish (Connell & Jones 1991, Pihl et al. 1994, Holbrook et al. 2002). The significance of structural complexity has many explanations including the relationship between resource availability and surface area (Heck & Wetstone 1977). In addition, it has been suggested that ecological and
life-history strategies can diversify in response to increased structural complexity, given the higher number of possible microhabitats and niches to occupy within the habitat, thus promoting coexistence and high taxonomic richness (MacArthur & McArthur 1961). Perhaps most importantly, structural complexity reduces predator efficiency (Beukers & Jones 1997) and its availability is hence directly related to predator-prey interactions.

Habitat alteration, or the reduction of a specific habitat or microhabitat in favour of another, will affect habitat heterogeneity and complexity with consequences for associated organisms, and those selective towards the affected habitat in particular (Swihart et al. 2003, Jones et al. 2004). In recent time, the degradation of vital habitat has caused the both local decline and global extinction of a number of taxa (Pimm & Raven 2000) and further loss is imminent (Thomas 2004) with consequences for many functional aspects of ecosystem services (Dobson et al. 2006).

The tropical coral reef

The coral reef provides an environment, which is heterogeneous and complex on a wide range of spatial and temporal scales (Jackson 1991). At a scale of centimetres there are differences between substrate components including corals, algae, rubble, sponges, bare rock and sand. On this small scale there may also be significant differences in growth forms among coral and algal taxa, as well as among other components. At a scale of metres, reefs consist of hard substrate patches with considerable structural complexity, sometimes mixed with sand, algal ridges or rubble flats. On a yet larger scale, reefs are divided into zones including fore-reef, reef crest, flat and slope, all providing quite distinct conditions in terms of substrate cover, vertical relief, depth and water movement. Reefs that are situated hundreds of metres apart may differ both in structure and in hydrodynamic conditions. Finally, the scale can be extended to include reef systems and biogeographic zones.

Reef fish assemblages are open communities (for review, see Sale 1991), in which local replenishment of the adult population is typically decoupled from local reproduction, and occurs via the settlement of dispersive larvae (but see Jones et al. 1999, Swearer et al. 1999, Jones et al. 2005). Given the variability of the environment and the active swimming behaviour of the larvae (Stobutski & Bellwood 1997), the competent larvae should theoretically be confronted with a large array of available habitats in which to settle. The settling larvae require suitable habitat in which they can maximise energy gain (growth) while minimising the risk of mortality. Early post-settlement mortality is typically high for coral-reef fishes (Almany & Webster 2006), and preferential settlement may increase the chances of post-settlement survival by escaping predation (Wellington 1992), obtaining food resources (Levin 1994) and avoiding aggression from adults (Sale 1972, Almany 2003). Differential use of habitat at settlement (Sale et al. 1984, Caselle & Warner 1996, Öhman et al. 1998) as well as habitat-specific variability in post-settlement survival (Connell & Jones 1991, Beukers & Jones 1997, Risk 1997, Lecchini et al. 2007) may in some species persist and shape adult distributions (Wellington 1992, Sponaugle & Cowen 1996, Gutiérrez 1998). Yet in other species,
ontogenetic shifts decouple the distributions of respective life stage (Sponaugle & Cowen 1996, Lecchini & Galzin 2005).

Fishes may, at least during certain life stages, be closely associated with specific habitat features, including live coral (Jones et al. 2004) distinct coral taxa (Munday et al. 1997) and potential shelter (Chabanet et al. 1997, Friedlander & Parish 1998, Gratwicke & Speight 2005a). Distinct fish assemblages may also be related to reef zone (Munday et al. 1997, Ault & Johnson 1998), depth (Wellington 1992, Srinivasan 2003), flow regimes (Breitburg et al. 1995) and connectivity among different habitats (Grober-Dunsmore et al. 2007). Several studies have demonstrated how the distribution of habitat units can explain variations in species distribution and abundance among zones and sites (Risk 1997, Tolimieri 1998, Holbrook et al. 2000), as well as among geographic locations (Holbrook et al. 2000, Munday 2002). While the temporal component of larval distribution patterns remains debated (for review, see Doherty 2002), benthic habitat is becoming increasingly recognised as a predictor of reef fish assemblage structure within as well as among sites. Understanding local recruitment patterns and the factors that contribute to their variability is critical to the comprehension of reef fish populations and hence invaluable for sound management of local fish stocks.

Habitat alteration and disturbance in the reef environment
Disturbances of different origin are frequently occurring on coral reefs. They vary in scale, intensity, duration, frequency and degree of impact on associated biota, direct or indirect (Connell 1997, Jones & Symys 1998). They are commonly limited to single reefs or at the most, to reef areas on a regional scale (Connell 1997, Halford et al. 2004). Habitat disturbance, defined as killing, displacing or damaging structural components, may result in both physical (e.g. change of flow, turbulence etc) and biological (e.g. loss of refuges or food sources) habitat alteration, and as a consequence indirectly affect associated fauna. Disturbance response is typically related to the location, the nature of the impact, as well as to the site-specific history of disturbance (Hughes 1989). Few reefs today can be considered pristine and previous impacts may for example have increased the vulnerability or resistance of both habitat and associated biota to additional disturbance. Reef recovery is generally related to the intensity of the disturbance, whether or not the original environmental conditions can be restored and whether or not there is potential for regrowth of survivors. If most structuring components (i.e. corals) are killed, regeneration is dependent on the arrival of propagules from elsewhere, in which case the location of the impact is vital. It should be noted that the reef at any time exhibits a mosaic of multiple processes including mortality and regeneration of the reef framework and that moderate disturbance regimes have been suggested to explain the exceptionally high biodiversity of reef (Connell 1978, Karlson & Hurd 1993, Connell 1997). In contrast, high frequency disturbances with no intermittent time for recovery (e.g. destructive fishing practises, sedimentation, pollution) will cause a situation of chronic disturbance (Connell et al. 1997) and continuous degradation. Recovery from acute disturbance (e.g. storm or bleaching episodes) is typically related to local levels of chronic disturbance (Connell et al. 1997).
The impacts of coral degradation on reef fish assemblages

Close association between fish and habitat should leave fish assemblages highly vulnerable to habitat disturbance while rendering studies of habitat perturbation a question of both ecological and managerial interest. Secondary effects of coral loss have previously been documented following infestations of the coral-feeding starfish, *Acanthaster planci* (Sano et al. 1987, Berumen & Pratchett 2006), storm damage (Halford et al. 2004) and experimental coral destruction (Sano et al. 1984, Lewis 1997, Syms 1998, Syms & Jones 2000). In the last decades coral bleaching, typically followed by coral death and erosion, has become a veritable menace to coral reef ecosystems (Hughes et al. 2003, Hoegh-Guldberg 2004). Recent evidence suggests that rising sea surface temperature, driven by climate change, will cause increasingly frequent and widespread bleaching in the near future, with detrimental consequences to reefs worldwide (Donner et al. 2005). Concurrently, changes in ocean chemistry are threatening to reduce coral calcification rates and rates of reef accretion, further endangering coral reef recovery (Kleypas et al. 1999). In the light of these threats, focus has shifted and the direct and indirect effects of widespread bleaching-induced coral loss with limited recovery have become a key topic in reef ecology and conservation. As a result, there is an emerging consensus among reef ecologists that major impacts of coral bleaching events on associated fish communities can be anticipated (Munday 2004, Jones et al. 2004, Pratchett et al. 2004, Sano 2004, Bellwood et al. 2006, Wilson et al. 2006, Graham et al. 2006).

The 1997/1998 El Niño Southern Oscillation (ENSO) was unprecedented, affecting seawater temperatures worldwide (McPhaden 1999). As a result, extensive bleaching occurred on nearly all coral reefs, followed by as much as 90% coral mortality at some localities (Wilkinson 2000). Given the structural properties of corals, bleaching and subsequent coral death may dramatically change the reef framework. Immediate effects of coral death include the reduction or loss of coral tissue followed by rapid colonisation of turf algae (Diaz-Pulido & McCook 2002), with consequences for the re-colonisation by coral larvae (Birrell et al. 2005). With time, dead corals typically break into pieces and coral rubble may, hence, become the dominant substratum (Sano et al. 1987, Riegl 2001). Subsequently, other sessile organisms such as macroalgae may take over, which further interfere with recruitment and subsequent recovery of the coral community (McCook et al. 2001).

Although live coral and branching taxa in particular, are considered to provide favourable habitats for a number of demersal fishes (Bell & Galzin 1984, Chabanet et al. 1997), there are only a few species that are known to be entirely dependent on live coral for food (Reese 1981, McIlwain & Jones 1997), while the majority of associations are due to shelter-dependence. Consequently, erosion may be more dramatic to fish assemblages than the initial coral death. In addition, the longevity of the typical adult reef fish (Choat and Robertson 2002), as well as their mobility compared to conspecific recruits, make responses among them less likely to be manifested in short-term studies. Hence, consideration of long-term impacts of reef fish assemblages to coral death is crucial.
The algal habitat

Evidence from temperate regions show that submerged vegetation has the potential to impact distribution patterns of both marine and freshwater fish (DeMartini & Roberts 1990, Jones 1992, Pihl et al. 1994, Duffy & Balz 1998) in particular by increasing the amount of available refuge and altering the availability of food resources (Rozas & Odum 1988) for herbivores, invertebrate feeders and omnivores, which predate on associated epifauna. Although herbivory is widespread among fishes in the tropics, macroalgae is of minor importance as a direct food resource for herbivorous fish (Choat et al. 2004). Late successional algae typically have lower photosynthetic rates and net production, as well as a reduced nutritive content and increased chemical defences resulting in lower palatability than early successional and opportunistic turf algae (Hay 1997). Consequently, most herbivorous fish, with the exception of a small guild of macrophyte browsers, forage in turf algae (Choat et al. 2004), and the overgrowth of turf algae and encrusting corallines by fleshy algae is likely to restrict foraging among herbivorous fish (McClanahan et al. 1999, Williams & Polunin 2001, but see Ceccarelli et al. 2005). Meanwhile, herbivory has on many reefs has been hampered by intense fishing (Hughes 1994, Jackson et al. 2001) and the lack of this function may affect the balance between the coral and algae community, potentially causing advantages for algal proliferation (Hughes 1994). Combined with chronic disturbances, such as nutrient loading, coral disease and systematic overfishing, acute disturbances such as bleaching-induced coral mortality may cause the reef environment to shift from coral to algae dominance (for review, see McManus & Polsenberg 2004).

Concurrently, lagoon environments in the Indo-Pacific are cleared from coral and seagrass to provide for the cultivation of macroalgae, which is harvested for the production of food, agar and carageenan (Jensen 1993). While the effects of this mariculture on associated plant and invertebrate communities have been documented (Johnstone & Ólafsson 1995, Ólafsson et al. 1995, Eklöf et al. 2005, 2006a) there is still limited information on how algal farming may influence fish assemblages (but see Eklöf et al. 2006b).

Objectives in brief

The overall aim of this thesis was to understand in which ways spatial variation in fish assemblage composition is related to habitat structure, and subsequently to explore the effects of alterations in habitat structure on associated fish assemblages.

**Paper I** To assess the influence of habitat structure on the distribution and abundance of *Pomacentrus sulfureus*, a western Indian Ocean damselfish.

**Paper II** To examine reef fish assemblage patterns over a range of sites in relation to spatially variable habitat structure, largely influenced by a recent bleaching event.

**Paper III** To describe habitat use and distribution patterns by reef fish recruits in relation to adult habitat use and distribution patterns, at a number of sites which vary in their degree of degradation due to recent bleaching.

**Paper IV** To assess the influence of habitat alteration related to algal farming (*Eucheuma* spp) on shallow lagoon fish assemblages.
Paper V To assess the influence of habitat alteration caused by extensive macroalgal reduction on reef fish assemblages.

Paper VI To assess the influence of habitat alteration caused by coral bleaching on reef fish assemblages.

PAPERS IN BRIEF

Paper I. Linking the abundance of one species to habitat variables, while comparing two measures of structural complexity

The first study explored the spatial variation of *P. sulfureus* among sites situated around Zanzibar Island, Tanzania. The ecology of this damselfish, which is relatively common on many reefs in the western Indian Ocean, had not been previously described. Damselfishes (Pomacentridae) constitute a diversified family of conspicuous fishes that are found in shallow habitats throughout the tropical seas. Densities of juvenile and adult *P. sulfureus* were examined in relation to both taxonomic and structural features of the habitat, on a scale relevant to the study species. With the hypothesis that fine-scale structural complexity may be important to this damsel, the percent cover of all branching structures (potentially providing shelter to small fish) was included as a measure of structural complexity, in addition to the commonly used contour measure (Risk 1972). Quantitative surveys of *P. sulfureus* revealed that this species was distributed in an uneven pattern around Zanzibar Island and that the distribution reflected local and regional differences in habitat structure, which in turn may have been related to variations in flow and exposure regimes. The multiple regression models, which identified relationships between juvenile and adult *P. sulfureus* abundance and specific habitat features, revealed that the majority of the variation in juvenile numbers was attributed to percent cover of branching structures, the high-resolution measure. In contrast, the low-resolution measure of structural complexity (rugosity) did not influence neither adult nor juvenile abundance and may not have been a relevant measure for this small reef fish. The best predictor of adult abundance was substrate diversity (inverse relationship). The results indicated that *P. sulfureus* exhibit an ontogenetic shift in habitat use and that the limited habitat use of juvenile *P. sulfureus* is contained within that of conspecific adults, and that juveniles are likely to adopt more general habitat associations as they grow.

Paper II. A study of whole-fish assemblages in a locality affected by recent coral bleaching

The second paper moves on from the investigation of a single species (Paper I) to the study of whole-fish assemblages at a number of sites within the Mafia Island Marine Park (MIMP), Tanzania. Given that coral cover in MIMP had been severely impacted by the 1998 bleaching event (Souter et al. 2000, Lindahl et al. 2001), this study aimed to explore fish-habitat associations with special attention given to the potential effects of live coral, dead coral and structural complexity. Although the effects of coral cover on fish abundance and diversity have been rigorously explored (e.g. Bell & Galzin 1984, Chabanet et al. 1997), reports on how dead coral influences fish assemblages are limited (but see Sano et al. 1984, Lewis 1997). This
study was further intended as a framework for a comparison of pre- and post-disturbance fish assemblages (Paper VI) conducted in a more limited area (included among the sites of Paper II), as well as a study of habitat use among recruits (Paper III). Paper II constitutes one of few comprehensive quantitative descriptions of coral reefs and associated fish assemblages in Tanzania. In total, 395 species belonging to 56 families were recorded. Multivariate ordinations, based on the data from 11 sites demonstrated that reef communities in MIMP differed among reefs and in relation to depth, exposure and geographic location, and that fish assemblage composition varied among sites in concordance with the habitats provided. In all, mean live coral cover in the park was 14 %, while dead coral cover comprised close to 50 % of the substrate. Sites with highest proportion of dead coral exhibited highest degree of among-transect variability. Stepwise multiple regressions showed that habitat variables explained a large part of the variation in species numbers and in total, and taxon-specific, abundance. Live coral cover was the foremost predictor of both numerical and species abundance, as well as of corallivores, invertivores, planktivores and of the families Pomacentridae, Chaetodontidae and Pomacanthidae. In contrast, the proportion of branching substrates, the foremost predictor of P. sulfurus (Paper I), did not explain any of variation in the fish descriptors. Given the demonstrated influence of live coral cover, as well as the large proportion of dead coral recorded in the area, it is likely that the recent coral mortality had had an influence on the distribution and abundance of reef-associated fish in MIMP.

Paper III. Exploring microhabitat use by reef fish recruits, comparing sites subjected to varying degree of coral degradation

While Paper II demonstrated that habitat structure is an important regulator for adult reef fish and that live coral may be particularly important, Paper III explored the habitat use of recruits. The study examined the habitat use by almost 3000 recruits comprising 56 taxa at seven sites in MIMP. In the light of ongoing habitat degradation, the presence of both recruit- and adult habitat has been suggested as a requirement for the local persistence of habitat-dependent reef fishes (Jones et al. 2004). Among coral reef fish, selective habitat use has been recorded in one or more life-stages for a number of species and identified at various scales from among microhabitats to across shelf (Williams 1982, Sale et al. 1984, Fowler et al. 1992). The study compared both species-specific densities and habitat use among sites and in relation to adult distribution patterns. The quantitative estimates revealed that recruit densities ranged between 0·10 (± 0·03 SE) m⁻² and 0·69 (± 0·23 SE) m⁻². Although live coral represented only 15 % of the overall measured substrate composition, almost half of all observed recruits were found in this substrate. Pooled across all sites, 46 % of the recruits used live coral cover in disproportion to availability. Among the 11 most common recruit taxa 10 exhibited non-random habitat use and six associated with live coral in disproportion to availability. Among adults, four of these showed significant relationships with live coral. In contrast, the abundance of both recruits and adults was inversely related to that of dead coral in MIMP. Only 25% of all recruit recordings were made in dead coral, despite dead coral and rubble being the dominating substrate at all but one site in MIMP. According to predictions, the lack of recruitment habitat at the most degraded site was manifested as a discrepancy between recruit and adult community composition. Paper III demonstrated that reef fish recruits used habitats non-randomly and that a
substantial proportion was selective towards live coral. Close associations between fish and habitat for both recruits and adults are likely to result in substantial impacts of habitat degradation.

**Paper IV. Investigating the effects of algal farming on fish assemblages in shallow lagoons**

In the same way coral cover and structural complexity exerts a major influence in the reef environment (Papers I-III), the influence of submerged vegetation on associated fish distribution and abundance has repeatedly been demonstrated (DeMartini & Roberts 1990, Jones 1992, Duffy & Balz 1998). **Paper IV** ventured away from the reef and into the shallow coastal lagoons. This environment shares a number of species with the reefs and has been identified as a potential nursery area for some of the fishes that in later stages enter the reef habitat (Nagelkerken et al. 2001, Adams & Ebersole 2004). Macroalgae are cultivated and harvested in a number of tropical countries, including Tanzania (Lirasan & Twide 1993), where shallow lagoons along the eastern coast of Zanzibar Island constitute favourable environments for algal farming. The farms consist of numerous ropes called monolines, to which the thalli of the red algae, *Eucheuma*, are attached. With these dense rows of algae, a different habitat is introduced in an environment where earlier there was only sand, seagrass and the occasional coral thicket. Fish assemblages in two lagoons where *Eucheuma* was farmed were investigated and compared to those at control sites situated within the same lagoons. Visual belt transect counts identified 101 species of fish belonging to 31 families. Only 15 of the species were present at both locations. Multivariate analyses revealed that fish community composition was related to the nature of the substrate in respective lagoon. Algal farms hosted distinct fish assemblages in terms of abundance, species richness and trophic identity. At one of the locations, where farming was intense and had a longer history, and where non-farmed habitats exhibited low structural complexity and diversity, algal farms hosted a more abundant and diverse fish fauna than controls. At the other location, where farming started more recently and remained less intense, and where the surrounding lagoon provided more varied and structurally complex substrates, overall fish abundance was lower in farms than at control sites. The results indicate that the impact of habitat alteration is related to the history of disturbance as well as to the pre-disturbance species composition and the characteristics of the pre-disturbance habitat.

**Paper V. A study of reef fish assemblages subjected to experimental algae reduction**

The relationship between macroalgae and fish was further explored in **Paper V**, which described a large-scale algae removal experiment on Glovers Reef, Belize, to understand the consequences of large-scale macroalgal overgrowth for coral reef fish. In this study macroalgae was manually reduced on eight patch reefs (average size ~1000 m²), among which half were situated in a new no-fishing zone and half in an unrestricted fishing zone. Another eight reefs were left as non-manipulated controls in each respective zone. The immediate response of fishes to the algal reduction were examined with particular focus on the response of species feeding on algae or in the epilithic algal matrix (EAM) such as surgeon (Acanthuridae), damsels...
(Pomacentridae) and parrotfishes (Scaridae). A similar study had recently been carried out in Kenya (McClanahan et al. 1999) and an additional objective was to test the generality of the obtained results by using this West Atlantic site as a comparison. Multivariate ordination of fish assemblage data indicated that the algal removal had marginal effect on whole-fish assemblages but that the effect was highly significant on the biomass of common grazers. In addition, increased activity was recorded for major grazing fish following the algal reduction. The results of this experiment supported the Kenyan study (McClanahan et al. 1999) suggesting that overgrowth of turf algae and encrusting corallines by fleshy algae could suppress foraging and limit distributions grazers and EAM feeders. Following the reduction of macroalgae, increased accessibility and net production of early successional turf were likely to have accounted for the increase in numbers, biomass and feeding rates of the dominant grazers.

Paper VI. Exploring the response of fish assemblages on small patch reefs to bleaching-induced coral mortality

While Papers I-V demonstrated that fish assemblages vary with habitat structure and particularly implicated the importance of live coral, Paper VI was following fish assemblages on patches of transplanted coral over time, recording immediate and long-term impacts of bleaching-induced coral mortality. In this study the coral plots were re-investigated six years after the 1997-1998 bleaching event and fish assemblage composition was compared to that recorded by Lindahl et al. (2001) six months after the disturbance. Given the poor post-bleaching recovery on these reefs (Papers II-III), we predicted a long-term response in fish community composition related to the reduction of structural complexity in the habitat. Multivariate ordination of fish community data demonstrated significant changes in composition related to the habitat alteration. Within-site variability increased with disturbance, the increase being most apparent following substrate erosion. The discrepancies between long-term and short-term responses were striking and underline the importance of long-term monitoring of fish assemblages following habitat alteration. Six years after the impact, the initial post-disturbance increase in fish abundance observed in 1998 (Lindahl et al. 2001) was reversed and more variable fish assemblages with comparatively less individuals and taxa than both before and shortly after the 1998 bleaching were recorded in the resulting low-relief environment. Functional groups, with documented affiliations with coral, were particularly influenced by the habitat alteration and most eventually disappeared altogether. The abundance of species feeding on algae or associated detrital resources increased as an immediate response to bleaching, but was subsequently decimated in the eroded habitat. In conclusion, it was evident that widespread catastrophic bleaching may have long-term effects on associated fish fauna.
GENERAL METHODS

Study sites

Western Indian Ocean

The majority of the work displayed in this thesis (Papers I-IV, VI) was conducted in the western Indian Ocean. Historically most reef fish ecologists have conducted their research in the Indo-west Pacific as well as in the Caribbean. In the light of this geographic imbalance, the recent interest in reef fish ecology in the western Indian Ocean reef is much welcomed (e.g. Graham et al. 2006, Graham et al. 2007).

Zanzibar, Tanzania

Two studies were conducted in the waters surrounding Zanzibar Island (Unguja), Tanzania (Papers I, IV). The island is situated 35 km from the African mainland in the western Indian Ocean. Narrow reefs situated close to shore, fringe most of the eastern coast of Zanzibar, while on the western coast, reefs of limited extent circumscribe rock island and sandbanks (for details, see Nsajigwa et al. 2002). The western reefs are generally more protected in terms of waves and currents than the eastern reefs. The study of Pomacentrus sulfureus (Paper I) included 11 reef sites around Zanzibar with substantial among-site differences in hydrodynamic conditions and habitat structure. The degree of anthropogenic disturbance is likely to have varied among sites, with western sites likely to be more impacted than eastern sites. Western reefs were situated at different distances to Zanzibar Town, from where sewage was discharged untreated into the sea, with consequential elevations of e.g. nutrient levels (Björk et al. 1995) and water turbidity (Muhando et al. 2002). Degree of protection against resource use also varied among reef sites at the time of the survey. The study of algal farming (Paper IV) was conducted in two shallow lagoons on the eastern coast of Zanzibar. In Kiwengwa, the fringing reef was situated approximately 800 – 900 m offshore, and along the coast large sandy flats with minor patches of algal turf and seagrass were interspersed with seagrass beds. In Matemwe, the distance from the shore to the reef was only 400 – 500 m and the natural substrate in the coastal back-reef lagoon was heterogeneous, including a mixture of sand, soft corals, small colonies of scleractinian coral (< 1 m²), rubble and small patches of algae and seagrass.

Mafia Island Marine Park, Tanzania

Three studies (Papers II-III, VI) were conducted in the waters of Mafia Island Marine Park (MIMP), situated ~120 km south of Zanzibar, 60 km south of Dar es Salaam and 21 km east of the Rufiji delta, at the edge of the continental shelf of the African mainland. The marine park, which was declared in 1995, covers an area of 822 km². Within the park, there are restrictions on resource usage, and although fishing is conducted within the park, destructive fishing practices and coral mining are prohibited. In total 11 sites within the park have been investigated (all presented in Paper II). Typically, the reefs surveyed were not uniform in structure, nor did they exhibit similar and predictable zonation patterns, as those described in other geographical regions (e.g. Done 1982). Tanzanian reefs are subjected to the East African Coastal Current, which flows north along the coast of Tanzania and Kenya. Currents are locally modified by prevailing monsoon and tidal patterns causing a complex and multidirectional current system. Further, the reefs experience mixed semidiurnal tides with mean spring amplitude of 3.3 m. From November to March,
the northeast monsoon blows with moderate force whereas the stronger southeast
monsoon prevails from May to October.

Caribbean
Coral reefs in the Caribbean have experienced repeated disturbance over the past
few decades, resulting in the loss of hard coral cover and reefs dominated by various
2003). This ecological change has been associated with disease-induced coral
mortality (Aronson & Precht 2001), loss of the important grazing sea urchin
(*Diadema antillarum*, Carpenter 1990), cyclones (Mumby 1999), increased fishing
pressure (Hughes 1994, Jackson et al. 2001), coral bleaching (Ostrander et al. 2000,
but see Mumby 1999) and seawater nutrient concentrations (LaPointe 1999).

Glovers Reef, Belize
Glovers Reef is a 260 km² atoll located approximately 15 km east of the Belizean
Barrier reef. The atoll is a nearly continuous reef with three large tidal channels and
~ 850 patch reefs within the lagoon. The outer edge of the atoll drops into deep
water (> 500 m) while the central lagoon seldom exceeds 20 m in depth. Patch reefs,
the focus of the study, occurred in the lagoon and varied in size from ~25 m² to
~10,000 m² and were separated by sand and seagrass beds with the distance between
the nearest-neighbour patch reef seldom exceeding 30 m. The Belizean Fisheries
Department zoned the atoll into four fisheries management zones and began
management in June 1996. The southern half of the atoll is divided into Wilderness,
Conservation and General Use Zones. The Wilderness and Conservation Zones
exclude virtually all forms of fishing. The General Use Zone allows the controlled
continuation of existing fisheries practices while the fourth zone is a seasonal
closure area of a grouper spawning ground on the north-east end of the atoll. Algae
removal and subsequent fish surveys were carried out in the Wilderness and the
General Use Zones.

Field methods

Fish sampling
For the purpose of this thesis, fish have been surveyed in various ways including
simultaneous belt transects (*Papers I-III, IV*), timed counts on whole patch reefs
(*Paper V*), timed counts in quadrates of limited size (*Paper VI*) and non-
quantitative sampling of habitat use by recruits within a set site (*Paper III*). In the
belt transect method a 20 (*Papers I, IV*) or 25 m (*Papers II-III*) transect was laid
out parallel to the reef slope while simultaneously counting large, fast-swimming
and shy species within 4 (*Papers I, IV*) or 5 m (*Papers II-III*) width. After waiting
10 minutes, the investigator returned along the transect, while recording site attached
fish larger than 10 cm. The diver then swam the transect once more while counting
recruits, cryptic species and pomacentrids within a width of 1 m. The investigators
(KCG in *Papers I, III*, SS in *Paper IV*) spent a set amount of time on each count
and replicates ranged between five (Paper I) and 10 (Papers II-IV). Fishes were
identified to lowest taxa and the abundance of schooling fish and fishes occurring in
higher densities were estimated using abundance categories in a log3 scale (1, 2 - 3, 4
- 9, 10 - 27, 28 - 81, 82 - 243, etc.).
The timed counts used on Belizean patch reefs sampled a limited number of species during each single search-sampling period of 5 min. In **Paper V** seven such distinct groups were sampled during the total sampling period, during which the investigator (KCG) swam haphazardly over each patch reef. The counts were restricted to individuals > 3 cm and fishes of special interest were assigned to different size classes. The 35 min sampling period was repeated twice.

When examining the response of fish assemblages to coral death and erosion in plots of transplanted coral (**Paper VI**), a stationary survey method modified from Bohnsack & Bannerot (1986) was used. During the census, the diver rested at the seabed approximately 1 m from the edge of the plot and counted all fishes in the plot, including transient as well as stationary fishes, for a period of 10 minutes on each occasion. Only fish occurring up to 1.5 m above the seabed were counted. Each count was replicated three times on different days.

In order to identify patterns of microhabitat use by recruits (**Paper III**) at seven of the MIMP sites, the investigator (KCG) spent on average 160 min per site, while recording the depth and microhabitat of each recruit encountered. Many fishes exhibit gregarious settlement and while each group of individuals was recorded as an independent observation, the number of individuals in each group was also documented. As with the transect counts, the number of individuals in larger groups, were estimated applying abundance categories in log_3 scale. The microhabitats used by recruits were typified using the same categories as in point-base surveys of the transect substrate (**Papers I-III**). In addition, depth and the occurrence of overhangs near the recruits were recorded. Recruits were identified by morphology, colour and size (typically < 2.5 cm although depending on taxon).

In order to estimate the potential effects of the algal reduction on herbivorous fish feeding and aggression patterns (**Paper V**), direct observations on bite rates and aggression were carried out on a few dominant grazers. The observer (KCG) followed each haphazardly selected individual for a 1 min observation period during which all bites on substrate were recorded, as well as all interactions with other fish (McClanahan et al. 1999).

**Substrate sampling**

In five of the six studies substrate was examined by a either a point-base method (Wiens & Rotenberry 1981, **Papers I-III**) or line intercept method (LIT, English et al. 1994, **Papers IV-V**). The point-base method included a rope which at 1-m intervals, and perpendicular to the transect line was positioned, stretching out on alternating sides of the main transect tape. The nature of the substrate was recorded at five random points along this 1 m rope. The method yielded a number of sampling points within the transect area, which were then used to calculate the proportional cover of different substrates. At each point, the substrate was characterised according to both taxonomic and structural properties. Within each site, transects were separated by a minimum distance of 45 m and replicated five (**Paper I**) to 10 times (**Papers II-III**). The LIT method records the exact substrate composition underneath the transect line. The fractional lengths of the components intercepting the transect were measured to the nearest centimetre.
In the sixth study dealing with coral degradation due to bleaching (Paper VI) live coral fragments were transplanted to 2.5 x 2.5 m² plots. The character of the substratum, including live and dead coral, coral rubble and sand, was estimated in 1997 and 1998 by point-sampling on projections of slide photographs taken at several random positions in each plot. In addition, coral relief was estimated in 1998 and 2004 by placing two transect tapes, each with five regularly spaced 10 cm sections, across each plot. The height above the substrate of the tallest coral branch under each of the 10 cm sections was recorded, and the average of 10 such readings was used to represent the relief of each plot.

Data analysis

In Papers II and IV fishes were divided into groups according to their feeding ecology: corallivores, piscivores, invertebrate feeders, omnivores, herbivores and planktivores, based on published material (Randall et al. 1990, Burgess et al. 1990, Smith & Heemstra 1991) supplemented by field observations. Fishes typically categorised as ‘herbivores’ constitute a heterogeneous group exhibiting various feeding behaviours, such as browsing, scraping and excavating (Bellwood & Choat 1990). Some species commonly seen foraging on turf-covered substrates do not even feed on vegetative material but on detritus caught in algae (epilithic algal matrix or EAM, Choat et al. 2004). However, throughout this thesis, ‘herbivores’ is commonly used to denominate all species foraging in algal habitat. In Paper V size-frequency data was converted to biomass, using length-weight relationships (Bohnsack & Harper 1998). Estimates of fish and substrate diversity (Papers I-II, IV) were calculated using the Shannon-Wiener index (H’), using log base e. Finally, structural complexity was described by the index R (Papers I-II), calculated as the average of bottom contour to transect ratio (Risk 1972) as well as by the proportion of branching structures (Papers I-III), calculated by adding the percentages of all branching substrates, live or dead.

Given the objective of understanding patterns in of multi-species assemblages in relation to among-site variability in habitat structure, multivariate techniques provided valuable tools (Papers I-VI). Statistical differences among sites, depths and exposure were typically analysed using analysis of similarity (ANOSIM, Papers II-VI), which is an analogue of the analysis of variance (ANOVA) with a randomisation test for significance. The analysis generates a measure of the degree of separation among sites, R, which is close to zero when similarities between and within sites are, on average, the same. An R value of one indicates that all replicates within sites are more similar to each other than any replicate from different sites.

For valuable graphic display, the multivariate non-metric multi-dimensional scaling ordination (MDS, Papers II-IV) provides a representation of community patterns generated from a ranked similarity matrix based on the Bray-Curtis similarity measure (Clarke 1993). Each point within the configuration represents the community composition (e.g. fish or substrate) in one sample, in relation to other samples. The closer two points are, the more similar are the associated communities. The degree to which the distances between all points in the plot accurately represent the similarity between them is quantified by the stress value, which shall remain
small for accurate interpretation. In **Papers II** and **IV** the RELATE procedure (Clarke & Ainsworth 1993) examined the degree of agreement between two multivariate scaling ordinations, using a modified form of Spearman rank correlation called the weighted Spearman rank correlation, with a coefficient, $\rho_w$ (Global rho), which always lies between $-1$ and $1$.

Similarity percentage analysis (SIMPER) was used in **Papers IV-VI** to identify $\delta_i$ %, which is the proportional contribution of individual species (i), to the average among-site dissimilarity (Warwick et al. 1990). The Bray-Curtis measure of dissimilarity $\delta$ takes on values in the range of 0 to 100 with $\delta = 100$ representing the case of no species in common and $\delta = 0$ being two samples with identical species patterns. SIMPER hence enables the identification of taxa to which specific clustering of the MDS is attributable.

PCA is another exploratory ordination technique, which reduces data into fewer dimensions. Variables are projected onto new axes or principal components (PC), which account for a certain amount of variance of the sample. In **Paper III** correlation-based PCA ordinations was carried out on square-root transformed proportional substrate use by common recruits. PCA was further used to determine taxon-specific among-site flexibility in microhabitat use.

Variability within communities has been suggested to be a symptom of disturbance (Warwick & Clarke 1993). Comparing variability among sites (**Paper II**, **VI**) and over time (**Paper VI**) was carried out by using the program MVDISP. To down-weight large numbers and account for variation, all variables have been square root or double square-root transformed prior to multivariate analyses.

Multivariate tools were complemented by several univariate tests including one-way and two-way analysis of variance (**Papers IV-V** respectively), Kruskal-Wallis test (**Papers I, V**), Spearman rank correlations (**Paper III**), t-tests (**Papers V-VI**), Wilcoxon Signed Ranks, Mann Whitney U-tests and randomisation test (**Paper VI**). When more than one statistical test is performed, the risk of incorrectly declaring significance increases. In order to ensure that this risk remained at the commonly applied limit of 5 %, a downwards adjustment of the alpha value of each individual test may be used. In **Papers III-V** the Bonferroni correction method was chosen, which divides the alpha value by the number of tests performed (Holm 1979).

In an attempt to reveal potential relationships between fish abundance data and habitat characteristics in **Papers I-II**, forward stepwise multiple regression analyses were performed (Sokal & Rohlf 1995). Among a set of independent variables (habitat characteristics), the forward selection procedure identifies the minimum set of predictors, which together explains the maximum total variance accounted for by the regression, and consequently represent the most plausible causal links to the dependent variables, which in our case included site averages of fish abundance, species richness, diversity and abundance of the major fish families and feeding categories.
GENERAL DISCUSSION

Evidence of non-random habitat use

This thesis provides evidence that coral reef fish, like many other organisms, exhibit non-random and predictable spatial distribution associated with habitat structure. The results comply with previous work, clearly pointing out the significance of live coral and structural complexity for both the abundance and richness of fish communities (Paper I-III, VI). Three life stages of reef fish were studied: recruits (Paper III), juveniles (Paper I) and adults (Paper I-VI), and while preferences or use may differ among life stages, non-random habitat use was demonstrated in all of them.

Non-random habitat use at one or more life-stage has been recorded in a number of taxa and identified at various scales from among microhabitats (Sale et al.1984, Ault & Johnson 1998) to across continental shelf (Williams 1982, Fowler et al. 1992). Among newly recruited coral reef fish in Mafia Island Marine Park, only a small fraction used microhabitat in proportion to availability while the rest appeared selective. Approximately half of the encountered recruits (species and individuals) were selective towards live coral and two thirds of all recorded individuals were observed in structurally complex substrates (Paper III). These results can be compared with those of Jones et al. (2004), who in a study from Papua New Guinea found 65 % of all recruits to use live coral cover in disproportion to availability. Corresponding to a decline in coral cover, Jones et al. (2004) further documented a decrease in the abundance of species with coral-selective recruits. Thus, it appears that the presence of recruitment habitat is vital in order to maintain adult population size. Similarly, results from MIMP demonstrated that species, which as recruits exhibited high selectivity towards coral, were limited in number or even absent from sites suffering severe degradation and lack of live coral cover (Papers II-III).

Although a relationship between availability of required microhabitat and recruitment have been demonstrated for many specialised taxa (Caselle & Warner 1996, Light & Jones 1997, Schmitt & Holbrook 2000, Holbrook et al. 2000), spatial stochasticity in larval supply and/or post settlement mortality (Ault & Johnson 1998) could potentially weaken it. It should further be noted, that contrary to one of the early theories of reef fish distribution patterns (Smith & Tyler 1972), near-pristine coral reefs (if they exist) are typically not filled with fish; in other words, recruitment may be insufficient to fill available habitat and create observable correlations between abundance and habitat availability (Ault & Johnson 1998). Even when habitat is filled, it is typically difficult to evaluate whether a species is constrained by the availability of suitable habitat or by larval supply. However, given the current rate of reef degradation, the significance of habitat as a limiting factor could be increasing, resulting in species-specific alterations in distribution patterns and assemblage change due to short supply of e.g. live branching coral.

Reef fish recruits are typically sedentary and their microhabitat use is rather easy to assess. Having survived the critical first period on the reef, they commonly go through one or more ontogenetic shifts in habitat use (Light & Jones 1997, Lecchini & Galzin 2005) often accompanied by changes in resource use (McIwain & Jones 1997). Whether similar in habitat features, or entirely distinct from those of
conspecific recruits, home ranges typically expand with individual size (Alimov 2003, *Paper I*). Among *Pomacentrus sulfureus*, the focal species of *Paper I*, juveniles were rarely found far from adults and it was suggested that the habitat preferences of juveniles may have been contained within the larger home ranges of adult conspecifics. In terms of habitat requirements, it should be noted that adults may be more versatile due to their need not only of foraging habitat and potential shelter, but of habitat in which successful reproduction can be achieved.

For many species in MIMP, habitat patterns of adult fish corresponded to those observed at recruitment and hence live coral cover was the foremost habitat variable explaining spatial variation in overall adult abundance and species richness (*Paper II*). At least for specialised species, adult distribution patterns may also be related to habitat availability (Munday et al. 1997, Holbrook et al. 2000). Besides, the density of species undergoing ontogenic shifts in habitat use may be directly related the local availability of nursery habitat (Adams & Ebersole 2004). However, distribution over larger scales, like among reefs, lagoons, around islands and across continental shelves, will always have to take many more features than microhabitat and substrate into account. Hydrodynamic conditions are likely to differ among reefs, typically affecting local habitat structure as well as fish recruitment and adult distribution. Further, it is possible that the suitability of a given microhabitat is context-specific, which means it will only be used if it occurs in a particular reef area (Doherty et al. 1996). While distribution patterns appear related to habitat variables (substrate, microhabitat), they may instead be responding to co-varying environmental variables (e.g. hydrodynamic features) rather than the substrate features. For example, in *Paper I*, we found juvenile *P. sulfureus* to be associating with structurally complex substrates. Accordingly, they were common on the sheltered site of the island where structurally complex habitat was dominating while almost absent at exposed sites which were devoid of structurally complex habitat. Yet, it would have been necessary to manipulate the structural features of the habitat, offering similar substrate at all sites, in order to single out the potential effect of location and specific environmental conditions associated with it, on species distribution. This example clearly illustrates the difficulties of interpreting single factor approaches for such complex organisms as reef fish. Although desirable to simultaneously assess all habitat variables on all scales, it is for obvious reasons not practical, and thus full understanding of these communities can only be approached in small steps, ideally including both descriptive and experimental work. Then, hopefully, together these pieces of information will provide an increasingly more comprehensive understanding of fish distribution patterns.

The influence of structural complexity

Generally, the response of fish to habitat characteristics and particular substrates may differ at different scales of spatial resolution as well as with taxonomic identity and life stage. For instance, reef fishes range in adult body size over two orders of magnitude, and they occupy home ranges from as small as a coral head to as large as a reef. To facilitate interpretation, the scale at which the study object might perceive the environment, should dictate the method used. However, although multiple-species studies reduce the chances of targeting all taxon-specific habitat-relations, in reality the practicality of different techniques often dictate the choice. Structural
complexity has been recorded using various techniques, including chain: link measurements (Risk 1972), visual qualitative assessment (Caselle & Warner 1996, Gratwicke & Speight 2005b), remote sensing (Kuffner et al. 2007) and detailed measurements of variations in substrate height and angle (McCormick 1994). This thesis includes several measures of structural complexity. For example, and as a complement to the commonly used rugosity measure, the proportion of branching structures, was introduced as a high resolution measure and correctly assumed more relevant to small demersal reef fish, juveniles (Papers I) and recruits (Paper III). In contrast, this measure had no effect on the broad taxonomic and trophic groups examined in MIMP.

Despite the different methods used, there is a large body of evidence that structural complexity plays a major role in shaping patterns of distribution and abundance of tropical demersal fish (Chabanet et al. 1997, Friedlander & Parish 1998, Gratwicke & Speight 2005a, Lingo & Szedlmayer 2006, Graham et al. 2006, Papers I, III, VI). Although high structural complexity on a reef is commonly associated with high live coral cover, live coral cover may decline without significantly reducing structural complexity, as is typically the case shortly after coral mortality due to bleaching or crown of thorn damage (Papers II-III, VI). In due course internal and external erosion take their toll and colonies are reduced to rubble. However, shortly following a major bleaching event, dead coral colonies may largely dominate. With recurrent bleaching episodes, this ephemeral habitat may become increasingly widespread, yet how fish relate to it has rarely been investigated. Papers II-III are based on data recorded two years after the 1997-1998 bleaching event. At this time, the loss of structural complexity was not as obvious as the loss of coral cover. Yet, the fish fauna appeared already affected, as evidenced by distinct community composition, low abundance, species richness and impoverished recruitment to impacted sites (c.f. Bellwood et al. 2006, Wilson et al. 2006). Paper III reports that 25 % of all encountered recruits were observed in dead coral, and among those more than half in dead coral with its structural complexity still retained, a highly ephemeral habitat. Although community change was significant already six months after coral death (Paper VI), the major loss of all species except a few generalists occurred only after the erosion of the corals, which supports the fact that fish assemblages are more affected by disturbances resulting in loss of habitat complexity than those that cause coral mortality without reducing the reef framework (Wilson et al. 2006, Paper VI). Extrapolating these results to all sites in MIMP (Paper II), and considering that dead coral, consisting mainly of branching and tabular corals, constituted almost half of examined substrate in 2000, the erosion that since then inevitably has followed is likely to have had severe consequences for associated fish assemblages.

Alteration in algal abundance

As a result of coral degradation many coral-dominated reefs have shifted towards algal dominance (Hughes 1994, Bellwood et al. 2004), with potential consequences for all reef-associated fauna, including fish (Paper V). Although the relationship between coral death, algal increase, eutrophication and herbivory remains debated (Williams & Polunin 2001, Burklepille & Hay 2006, Aronson & Precht 2006, Mumby 2006, Hughes et al. 2007), reduced herbivory due to the mass mortality of Diadema...
and overfishing is believed to have facilitate algal increase (Hughes 1994, McClanahan & Muthiga 1998, Jackson et al. 2001), which in turn may have suppressed coral settlement and survival (Hughes 1989, McCook et al. 2001) with consequences for coral recovery. Although potential for coral recruitment following the restoration of Diadema populations was documented by Carpenter & Edmunds (2006), there is generally little optimism about the future of Caribbean coral reefs (Aronson & Precht 2006, Mumby 2006). With current levels of anthropogenic disturbance, the algal dominance appears practically irreversible and according to Aronson & Precht (2006), only major reef protection schemes in conjunction with the reduction of green house gas emissions, could possibly promote coral recovery in the Caribbean.

Given the previously limited spread of macroalgae on tropical reefs, this habitat has received little attention, particularly among fish ecologist. With current rates of coral degradation and subsequent algal increase, attention has increased, but the response of associated fish assemblages to alterations in algal distribution and abundance remain poorly understood (but see McClanahan et al. 1999, Sano 2001, Paper IV-V). Sano (2001) reported increased species richness and densities in fish assemblages following macroalgal overgrowth on a rubble reef in Iriomote Island, Japan. Similar results were obtained following the transplantation of Sargassum to sand, rock and rubble habitats on Cousin Island, Seychelles (Garpe, unpublished data). Preliminary results indicated that fish assemblage alteration, in part the result of recruitment, was dependent on the underlying substrate, as well as on macroalgal height and density (c.f. Paper IV-VI). It should be noted, however, that although increased macroalgal abundance on a non-complex substrate (e.g. rubble) can contribute to increased structural complexity with positive effects on associated fish, it probably cannot be compared to coral recovery. Sano (2001) compared fish assemblages on reefs where habitat had shifted towards macroalgae (dense Sargassum) to those where coral had fully recovered, and found that although the two habitats had many species in common, species richness was three times higher, and density eight times higher in live coral than in algae.

The reverse process was explored in Paper V, in which fish abundance, biomass and behaviour were analysed following experimental reduction of late successional algae. The short-term (Paper V) and longer-term effects (McClanahan et al. 2001) of algae removal on Glovers Reef, Belize, were limited. The increase in abundance of a few species was interpreted as relocation from nearby reefs and related to the increased accessibility of food resources, in terms of turf algae and associated resources.

Where algae are cultivated, effects on the habitat include alteration in terms of macrophyte abundance, macrobenthos, meiobenthos and sediment organic matter (Olafsson et al. 1995, Eklöf et al. 2005, Eklöf et al. 2006a). The farmed algae typically increase the structural complexity while reducing the diversity of lagoon habitats including sand, coral thickets and seagrass. Although far from conclusive, significant influences on fish assemblage composition have been documented visually (Paper IV) as well as inferred from local fishery catches (Eklöf et al. 2006b).
Reef fish communities facing habitat degradation

The influence of altered and/or degraded habitat structure on fish is typically species-specific with versatility and vagility being important determinants of species response (Swihart et al. 2003, Bellwood et al. 2006). Immediate assemblage change is likely to be the result of species redistribution due to alterations in resource patterns (Paper V, VI). In contrast, long-term change can be the result of processes such as recruitment failure and increased post-settlement mortality. At first, coral death is likely to deter coral associated species while favouring species foraging on turf algae or associated resources (Paper VI). Given only partial mortality and/or the persistence of structural complexity, the response may be minor or delayed (Wilson et al. 2006, Feary et al. 2007). However, macroalgal overgrowth and/or erosion will almost inevitably reduce the reef framework and alter habitat structure with increasingly severe consequences for the associated fish assemblage (Feary et al. 2007, Paper VI). A recent meta-analysis demonstrated that 62 % of examined species (34 of 55) exhibited significant declines in abundance following ≥ 10 % coral mortality (Wilson et al. 2006). The full long-term effects of major and recurrent disturbances on fish assemblages have not yet been fully understood (but see Halford et al. 2004, Bellwood et al. 2006, Berumen & Pratchett 2006) but from other ecosystems the result of habitat degradation has typically included the decline of specialists, leaving diminished communities dominated by mobile and widespread habitat generalists (Swihart et al. 2003, Warren et al. 2001). While habitat generalists may remain unaffected and perceive the fragmented coral reef habitat simply as more heterogeneous, the loss of habitat may severely limit the distribution of habitat specialists, which may be particularly true for coral feeders (Pratchett et al. 2006) and dwellers (Munday 2004, Schmitt & Holbrook 2000, Feary et al. 2007, Paper VI). Given evidence of high specialisation among reef fish recruits (Lecchini & Galzin 2005, Jones et al. 2004, Paper III), the lack of suitable recruitment habitat may effectively limit the distribution of species (Adams & Ebersole 2004, Jones et al. 2004).

If habitat loss limits the settlement of certain species or if post-settlement survival is reduced due to inferior habitat conditions (Booth & Beretta 2004), the response to altered and/or degraded habitat would be discernable in the recruit community first. Comparing recruit and adult communities among sites, Paper III revealed that differences between proportional adult and recruit abundances of some of the most common species were greatest at the most degraded reef. Although adults are generally more mobile and hence potentially able to expand their home ranges or relocate within sites, this pattern could also suggest that sublethal effects in adult physical condition (from e.g. increased competition, reduced resources and increased predation due to crowding) had not yet been manifested as a decline in population size (Pratchett et al. 2004). Evidence from assemblages of small-bodied cryptic fauna with limited life spans, has shown that the impacts of extensive bleaching are still manifested in assemblage composition 5-35 generations following the impact (Bellwood et al. 2006).

It should be noted that temporal patterns of assemblage change cannot automatically be related to e.g. bleaching or other major disturbances. Assemblages may naturally change over time, due to temporal variability in recruitment (Doherty 2002), fishing pressure (Hawkins et al. 2006) and/or minor disturbance regimes (Graham et al.
Due to natural variation, the lack of pre-disturbance data, long time series and undisturbed control sites, may confound results where habitat disturbance is widespread. In Paper VI the survival of four coral plots enabled a comparison over time and allowed the identification of bleaching-induced coral mortality and subsequent erosion of the reef framework as the factor foremost responsible for assemblage change.

Coral reefs are among the most diverse ecosystems on earth (Reaka-Kudla 1996) and throughout the tropics people are dependent on them for food, income and coastal protection (Moberg & Folke 1999). As the frequency and magnitude of reef disturbance increase, due to human activities and climate change, live coral is declining worldwide (Wilkinson 2004, Gardner et al. 2003, Hughes et al. 2003, Hoegh-Guldberg 2004). There is reason to believe that the impact of coral loss will be significant, and almost certainly cause the decline of numerous reef species, with recovery being slow and directly related to coral recovery (Halford et al. 2004, Sano 2000) and/or degree of protection (Hawkins et al. 2006). While there is evidence of resilient reefs regaining almost full resemblance to pre-perturbation states (Halford et al. 2004, Sano 2000), reefs experiencing widespread, multiple and/or recurrent disturbance and reefs with limited connectivity to non-disturbed habitat face diminished chances of recovery (Berumen & Pratchett 2006, Graham et al. 2006). Although substantial dispersal ability generally reduces vulnerability to local habitat degradation (Ford et al. 2001), global threats diminish the chances of restocking depleted fish populations from unaffected source reefs. Consequently, fish distributions may be altered and/or limited, potentially resulting in distorted food webs and ultimately loss of ecosystem functions. Whether post-disturbance alteration of fish assemblage composition will affect future resistance to disturbance remains to be seen. There is much to learn about synergistic and sequential effects of multiple disturbances on fish distribution and abundance patterns, but by now it is clear that an increasing number of reef habitats, and their associated fish assemblages, are being forced into alternative states and structures, the stability of which remains to be evaluated.
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