

Human Abuses of Coral Reefs- Adaptive Responses and Regime Transitions

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Doctoral Thesis in Marine Ecotoxicology



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Till min lilla Wilma

Som får solen att lysa fast regnet vräker ner

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Abstract

During the last few decades, coral reefs have become a disappearing feature of tropical marine environments, and those reefs that do remain are severely threatened. It is understood that humans have greatly altered the environment under which these ecosystems previously have thrived and evolved. Overharvesting of fish stocks, global warming and pollution are some of the most prominent threats, acting on coral reefs at several spatial and temporal scales. Presently, it is common that coral reefs have been degraded into alternative ecosystem regimes, such as macroalgae-dominated or sea urchin-barren. Although these ecosystems could potentially return to coral dominance in a long-term perspective, when considering current conditions, it seems likely that they will persist in their degraded states. Thus, recovery of coral reefs cannot be taken for granted on a human timescale.

Multiple stressors and disturbances, which are increasingly characteristic of coral reef environments today, are believed to act synergistically and produce ecological surprises. However, current knowledge of effects of compounded disturbance and stress is limited. Based on five papers, this thesis investigates the sublethal response of multiple stressors on coral physiology, as well as the effects of compound stress and disturbance on coral reef structure and function. Adaptive responses to stress and disturbance in relation to prior experience are highlighted. The thesis further explores how inherent characteristics (traits) of corals and macroalgae may influence regime expression when faced with altered disturbance regimes, in particular overfishing, eutrophication, elevated temperature, and enhanced substrate availability. Finally, possibilities of affecting the resilience of macroalgae-dominated reefs and shifting community composition towards a coral-dominated regime are explored.

Key Words: Coral reefs • Disturbance • Stress • Adaptive responses • Macroalgae • Ecosystem regimes • Resilience • Competition • Traits

List of papers

The following five papers are the basis of this thesis and referred to in the text by their roman numerals:

- I. Nyström M, **Nordemar I**, Tedengren M (2001) Simultaneous and Sequential Stress from Heat and Copper Exposure on the Metabolism of *Porites cylindrica*, Philippines. Mar Biol 138:1225-1231
- II. **Nordemar I**, Nyström M, Dizon R (2003) Effects of elevated seawater temperature and nitrate enrichment on the branching coral *Porites cylindrica* in the absence of particulate food. Mar Biol 142:669-677
- III. **Nordemar I**, Kautsky H (2002) Human influence and degradation of coral reefs in the Gulf of Thailand. Proc 9th Int Coral Reef Sym 2:1047-1052
- IV. McClanahan TR, McField M, Huitric M, Bergman K, Sala E, Nyström M, **Nordemar I**, Elfving T and Muthiga NA (2001) Responses of algae, corals and fish to the reduction of macro algae in fished and unfished patch reefs of Glovers Reef Atoll, Belize. Coral Reefs 19:367-379
- V. **Nordemar I**. Regime Transitions on Coral Reefs– the Roles of Substrate Availability, Competitive Traits and Altered Disturbance Regimes. *Manuscript*

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Introduction

Coral reefs develop in shallow tropical areas with suitable environmental conditions. This restricts the present range to an area of about 285 000 km² (Spalding et al. 2001). Yet, despite covering only a small part of the oceans, coral reefs are among the most diverse and productive ecosystems on this planet (Birkeland 1997), serving humans with a vast array of ecological services (Moberg and Folke, 1999). On a global scale, modern coral reefs have persisted for about 50 million years despite several large scale extinction events (Kaufmann and Fagerstrom 1993). However, during the last two decades, researchers have witnessed an alarming global degradation of coral reefs, a low coral recovery, and the invasion of durable and less desirable macroalgae (Wilkinson 2000, 2002). This threatens to cause substantial losses of ecological goods and services (Moberg and Folke 1999). It is believed that the pace of recent coral reef degradation, loss of biodiversity and the extent of macroalgae-dominated communities may be unprecedented in history. Driving forces behind these changes are growing human population and an increased demand for and unsustainable use of natural resources.

Since almost half a billion people, or 8% of the global population, live within 100 km of a coral reef (Bryant et al. 1998), the local and regional exploitative pressure on natural resources from reef ecosystems is high, and the effects of human-induced pollution, exploitation, and destruction on reefs are widespread (Bryant et al. 1998). In the mid 1990's, direct anthropogenic disturbances such as land-based pollution, sediment releases and over-exploitation were considered the most significant threats to coral reefs (Wilkinson 1999). However, due to elevated seawater temperatures in 1997-98, the world's coral reefs suffered a mass coral bleaching event (coral bleaching is the loss of symbiotic microalgae, *zooxanthellae*, and/or their photosynthetic pigments, e.g. Brown 1997), on a scale previously unrecorded. Approximately 16% of all reefs were lost (Hoegh-Guldberg 1999, Wilkinson 2000). This demonstrates that widely distributed local activities can generate global impacts on coral reefs.

Human societies depend heavily on ecological systems for their survival and well-being (Folke 1991; Daily 1997), and the continued supply of ecological goods and services from ecosystems are thus of critical importance for societal development (Folke et al. in press). This is particularly true for low income countries where people rely more directly on local natural resources. In order to restore or maintain ecosystems in desirable healthy states, sound natural resource management is required. This implies an improved understanding of the mechanisms that contribute and/or reduce coral reef resilience.

Setting the frame of the thesis

Disturbance and ecosystem regimes

In my thesis, disturbance has been defined as a discrete killing, displacement, or damaging of one or more individuals (or colonies) (Connell et al. 1997). Disturbances can be acute, i.e. a short-term pulse. They can also be chronic, such as a long-term press force or several short-term pulses with intervals too short for recovery (Connell et al. 1997). The definition of stress I use is an impaired physiological status of organisms, which may have sublethal effects on, e.g. feeding, growth, fecundity, etc. (Hughes and Connell 1999). In response to natural disturbances, such as disease, predation and hurricanes, coral reefs are constantly undergoing mortality, regeneration, and adaptation (Connell 1978; Grigg 1995). Repeated cycles of crashing and re-building are believed to be inherent features of ecosystems (Holling 1986), creating a mosaic of patches at different developmental stages within and between coral reefs (Connell 1978; Connell et al. 1997). It is thought that ecosystems adapt to and even depend on these disturbances for maintaining coexistence between competitors, a high level of biodiversity (Connell 1978) and continued renewal (Holling 1986; Grigg 1995), even though disturbance mortality can be high (Hughes and Connell 1999).

It has been suggested that coral reefs are dynamic non-linear systems with multiple alternate regimes, between which the system may shift following disturbance (e.g. Done 1992; Knowlton 1992; Nyström et al. 2000; McClanahan et al. 2002; Bellwood et al. 2004; Knowlton 2004; McManus and Polsenberg 2004) (Fig. 1). Over the last two decades many coral reefs have transgressed from a coral-dominated regime to one that is dominated by macroalgae (Hughes 1994; MacCook 1999; Wilkinson 1999; Goreau et al. 2000; McManus et al. 2000), suspension-feeders (Bell 1992; Done 1992; Hunter and Evans 1995; Glynn 1997) or other ecosystem regimes (Bellwood et al. 2004). These macroalgae-dominated reefs seem fairly stable and difficult to reverse (e.g. Goreau et al. 2000; Nyström et al. 2000; Knowlton 2001; McClanahan et al. 2001; Smith et al. 2002; Szmant 2002; Hewitt et al. 2004; Smith et al. 2004; Conklin and Smith in press; but see Edmunds and Carpenter 2001). Although the exact mechanisms still remain obscure, evidence strongly suggests that not only do human interventions contribute to these transgressions, but also that we influence the durability of these algal regimes once they have occurred.

Modifying the coral reef environment

Disturbance dynamics of coral reefs are increasingly influenced by human activities (Nyström et al. 2000; Jackson et al. 2001; Hughes et al. 2003). It is now widely agreed that global warming has a profound effect on the world's coral reefs (e.g. Hoegh-Guldberg 1999; Watson et al. 1999; Wilkinson 2002). Predictions suggest that reef-building corals (hereafter referred to as 'corals') at a

global scale will experience stressful temperatures, beyond upper tolerance limits, more frequently and during longer periods over the next decades (Hoegh-Guldberg 1999; Wilkinson 2000, 2002; Hughes et al. 2003). Concurrently, coastal development and land-uses changes have resulted in increased, and sometimes even chronic, levels of nutrients and sediments on coral reefs (e.g. Szmant 2002; McCulloch et al. 2003; Lapoint et al. 2004; Schaffelke pers com). An emerging problem is also the increasing diversity and distribution of coral diseases around the world (Peters 1997; Harvell et al. 1999). These have largely contributed to the reef decline in Belize and other areas in the Caribbean (Aronson et al. 2004).

The global assessment of the status of coral reefs carried out in 1997 and 1998, showed that most reefs were severely overfished and that most high-value organisms were missing (Wilkinson et al. 1999). World fisheries have already overly exploited fish stocks and as a result must presently target organisms at lower trophic levels than they did only two to three decades ago (Pauly et al. 1998; Myers and Worm 2003; Bellwood et al. 2004). Overfishing affects more than just harvestable stocks. As marine food-webs are altered (Jackson et al. 2001; Pauly et al. 2002; Meyers and Worm 2003) ecological functions (e.g. grazing of algae) and thus coral reef resilience are threatened (Nyström et al. 2000; Hughes et al. 2003; Bellwood et al. 2004; Nyström, manuscript in review). The scale of abuse has increased as the fisheries industry and demand have become global (Hughes et al. 2003). Today, many scientists are convinced that global warming (Wilkinson 1999; Pockley 2000; Wilkinson 2000), as well as global trade (Hughes et al. 2003; Bellwood et al. 2004), exert equal or perhaps even greater threats to reefs compared to direct local anthropogenic disturbances.

Considering the alarming rate of coral reef degradation and low rate (sometimes lack) of recovery, it has been suggested that coral reefs are more vulnerable to anthropogenic impacts compared to natural disturbances (Johannes 1975; Loya 1976; Richmond 1993; Connell 1997). This has been attributed to the introduction of new stressors, such as pesticides, heavy metals and oil residues, that organisms have not previously encountered (e.g. Johannes 1975; Loya 1976), and the more chronic nature of anthropogenic disturbances, e.g. sedimentation or nutrient pollution in coastal areas (e.g. Connell 1997). It was recently proposed that deteriorating reefs may also be the product of altered natural disturbance regimes in combination with reduced ecosystem resilience (Nyström et al. 2000). The diversity, magnitude, duration and frequency of disturbance events (such as extreme temperatures, pest or predator attacks) seem to have increased, while recovery intervals between events have been shortened (Connell et al. 1997; Done 1999; Nyström et al. 2000; Hughes et al. 2003). In consequence, compounded disturbances are more likely to occur on coral reefs and may represent the norm for the next decades (Brown 1997). At the same time, overharvesting suppress or remove essential natural disturbances that coral reefs depend on, such as grazing and predation (Nyström et al. 2000).

Compounded disturbances

Interacting disturbances are considered to be especially detrimental to coral reefs (e.g. Hughes 1994; Done et al. 1996; Connell 1997; Hughes and Connell 1999; Pittock 1999; Wilkinson 1999; Goreau et al. 2000; McManus et al. 2000; Nyström et al. 2000). Disturbances may not only interact in simultaneous combination, but also in sequence and if recovery intervals are inadequate, this can compromise organisms' abilities to cope with future disturbance (Peters 1997; Harvell et al. 1999; Nyström et al. 2000). For example, coral reefs on the Great Barrier Reef in Australia, with a recent history of low salinity exposure, were more severely affected by elevated temperature than other reefs (Berkelmans and Oliver 1999). It has also been observed that corals already stressed by sediment, sewage, pesticides, heavy metals and elevated temperature are more prone to bacterial attacks, and have tumors more often (Peters 1997; Harvell et al. 1999). Some coral diseases have been shown to be promoted by elevated temperature and nutrients (Rosenberg and Ben-Haim 2002; Bruno et al. 2003), which may partly explain the observed dramatic increase of both new coral diseases and disease-affected corals (Rosenberg and Ben-Haim 2002).

Effects of compounded disturbances are often more than additive, which can generate ecological surprises such as "phase shifts" (Paine et al. 1998). Several investigations have theoretically demonstrated how compounded disturbances on coral reefs such as overfishing, eutrophication, hurricanes, mass coral bleaching, epidemic diseases, and/or coral predator outbreaks may have resulted in regime transitions to fleshy macroalgal dominance (e.g. Hughes 1994; Done et al. 1996; McCook 1999; Goreau et al. 2000; McManus et al. 2000). Compounded disturbances also seem especially detrimental to the regeneration of coral reefs (Hughes and Connell 1999; Goreau et al. 2000). For example, Loya (1976) showed that recovery after an extreme low tide event in Eilat was prolonged on reefs subjected to chronic oil pollution compared to nearby unpolluted reefs. Connell (1997) concluded that chronic man-made pollution often inhibits recovery as opposed to natural pulse disturbances.

Ecosystem resilience and response diversity

"Ecosystem resilience" is defined herein as the amount of disturbance a system can absorb and still remain in a particular ecosystem regime (Holling 1973). Subtle interactions of a number of factors can lead to loss of resilience, which is difficult to detect until a reef fails to reorganize and instead shifts to an alternate regime, following a disturbance that previously could be absorbed (e.g. Nyström and Folke 2001). Although a diversity of events can trigger such shifts, loss of ecosystem resilience paves the way for a shift to occur (Scheffer et al. 2001; Folke et al. in press) (Fig. 1).

The role of biodiversity has been debated, and although the emerging consensus suggests that biodiversity contributes to resilience (Naeem et al. 1995; McGrady-Steed et al. 1997), it has been proposed that resilience is also related to the ability of organisms to overlap in function (e.g. Peterson et al. 1998; Walker

et al. 1999). Elmqvist et al. (2003) suggested that functional groups with a high functional redundancy may still be vulnerable to change, if species within the group respond in a similar manner to disturbance (Elmqvist et al. 2003; Bellwood et al. 2004; Nyström manuscript in review). They concluded that variation in responses among species within functional groups to environmental change, i.e. response diversity, can be critical for continued ecosystem functioning and resilience. To illustrate this concept on coral reefs Elmqvist et al. (2003) used an example where diversity and abundance of herbivorous fish and sea urchins have eroded. This reduced ecosystem resilience and increased the probability of a regime transition to occur. Moreover, response diversity and ecosystem resilience is also affected by reduced health and resistance of the remaining organisms (Elmqvist et al. 2003).

General objectives of the thesis

In this thesis, I have studied the effects of altered environmental conditions and modified disturbance regimes on coral reefs (**Paper III-V**) and corals in particular (**Paper I, II and V**). Although organisms are naturally exposed to combinations of disturbances (Brown 1997), experimental studies on environmental stressors are traditionally investigated individually (Folt et al. 1999). Thus, we still have limited knowledge of how different disturbances interact and what their impacts might be (Folt et al. 1999). Due to this lack of information, we are restricted in our interpretation of ecosystem changes in the field. Consequently, we often correlate reef stress and degradation to only one factor such as eutrophication (e.g. Bell and Elmetri 1995; Hunter and Evans 1995; Lapoint 1997), overfishing (e.g. McClanahan et al. 1994; Russ and Alcala 1998), or elevated temperature (e.g. Hoegh-Guldberg 1999; Wilkinson et al. 1999). We have only recently begun to elaborate on more complex disturbance patterns (e.g. Done et al. 1996; Berkelmans and Oliver 1998; Paine et al. 1998; McCook 1999; McManus 2000; Nyström et al. 2000; Szmant 2002).

The overall aim of this thesis is to investigate effects of altered disturbance regimes, and to specifically contribute to the understanding of compounded disturbances. This thesis focuses on the effects of overfishing (**Paper III-V**), elevated temperature (**Paper I-II and V**), eutrophication (**Paper III**), nutrient enrichment (**Paper II and V**) and heavy metal pollution (**Paper I**), in various combinations. The thesis also explores effects of Marine Protected Areas MPAs and macroalgae reductions as management tools to restore coral-dominated reefs (**Paper IV**). I specifically address adaptive responses (**Paper I-II and V**) and response diversity (**Paper III-V**), which influence ecosystem resilience. The context of the thesis is depicted in figure 1.

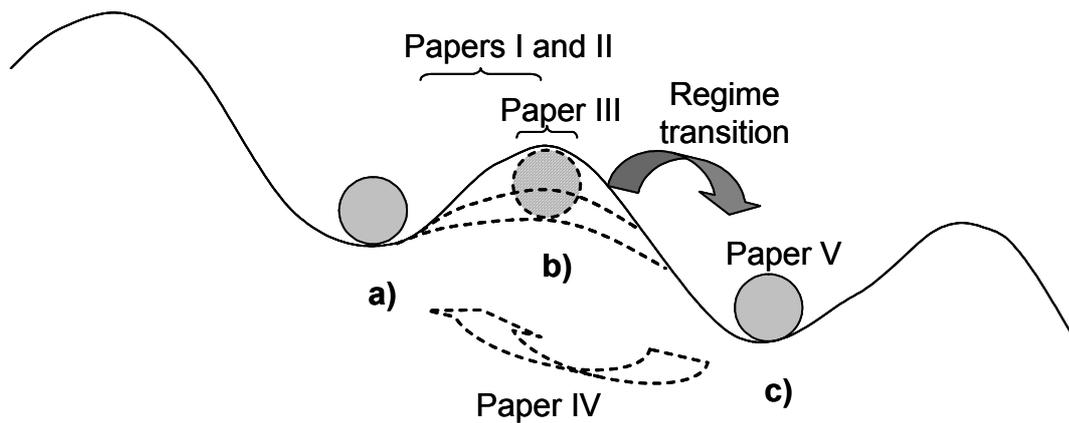


Fig. 1. This figure depicts the “ball and cup analogy” (Holling et al. 1995) in relation to the thesis. Phase **a**, illustrates a “healthy” coral-dominated regime characterized by high diversity and abundance of species (exhibiting a high response diversity). In phase **b**, the coral reef is under increasing stress conditions, such as pollution, excess nutrients and reduced herbivory, challenging the resilience of the ecosystem (Papers I and II). Although the reef may still seem “healthy” (i.e. coral-dominated) it has suffered cryptic loss of resilience (reduced species diversity, -abundance and health), and has become progressively more vulnerable to external shocks, such as hurricanes, pathogens etc. (Paper III). In phase **c**, an ecosystem transition has occurred and the coral reef is dominated by an alternative regime, e.g. macroalgae. Management to restore algal reefs back to coral dominance (Paper IV) needs to consider mechanisms that contribute to the resilience of the algae dominated regime (Paper V).

Papers in brief

Effects of increasing seawater temperatures on corals – a short background to Papers I and II

Elevated temperature is generally predicted as the single most deadly stressor to corals (e.g. Hoegh-Guldberg 1999; Wilkinson 1999, 2000; Hughes et al. 2003), and since the severe mass bleaching event in 1997/98 much research has focus on this topic. It is believed that corals are presently living close to their upper thermal tolerance limit (Jokiel and Coles 1990; Hoegh-Guldberg 1999). A temperature elevation of just 1-2°C above the normal temperature is known to evoke a bleaching response (loss of symbiotic *zooxanthellae* and/or their pigments) within weeks, while the stress response seems much faster (within days) if temperature increases more (3-4°C) (Brown 1997). Several investigations have confirmed that anomalously high seawater temperatures often cause bleaching (Hoegh-Guldberg 1999; Warner et al. 1999; Jones et al. 2000; Fitt et al. 2001). Furthermore, studies have shown that elevated temperature may damage photosystem II of *zooxanthellae* (Iglesias-Prieto et al. 1992; Warner et al. 1996; Salih et al. 1998; Warner et al. 1999; Jones et al. 2000; Fitt et al. 2001), reduce

primary production (Porter et al. 1999), alter respiration (Porter et al. 1999; Fitt et al. 2001) and reduce tissue biomass (Fitt et al. 2001). Of concern is that bleached corals have reduced chances of survival (Hoegh-Guldberg 1999; Baird and Marshall 2002; but see Gates and Edmunds 1999; Knowlton 2001), and if they do survive, their fecundity (Szmant and Gassman 1990; Michalek-Wagner and Willis 2000; Baird and Marshall 2002), rate of calcification and growth (Abramovitch-Gottlieb et al. 2002; Baird and Marshall 2002), and ability to withstand pathogens (Rosenberg and Ben-Haim 2003; Bruno et al. 2004) and further stress may seriously decline.

After the severe global mass bleaching event in 1997-98, it was confirmed that “both human influenced and more ‘pristine’ areas had been affected to the same extent” (Hoegh-Guldberg 1999). Since there is no protection against elevated temperature, bleaching may strike any coral reef, irrespective of management efforts such as MPAs. However, studies have highlighted that elevated temperature may interact with other conditions on regional and local scales, which enhance or mitigate the bleaching response. For example, coral reefs on the Great Barrier Reef in Australia, with a recent history of low salinity exposure, were shown to be more severely affected by elevated temperature than other reefs (Berkelmans and Oliver 1999). In my thesis, I wanted to elucidate if other stressors, in this case copper pollution (**Paper I**) and nitrate enrichment (**Paper II**), may influence the physiological response of elevated temperature in corals, and how elevated temperature, in turn, may influence their susceptibility to these stressors.

Copper as a combining stressor with elevated temperature (Paper I)

Although the heavy metal copper is an essential element for all organisms in low concentrations (Depledge and Rainbow 1990), it is also one of the most common marine pollutants – originating from coastal run-offs coastal and offshore mining, anti-fouling paint, and industrial outlets (Jones 1997). Metal uptake in corals may be direct (soluble fraction) or through feeding activities (particulate fraction) (Howard and Brown 1984). A concentration of 10 $\mu\text{g Cu l}^{-1}$ or even less is known to affect corals (Evans 1977 cf Howard and Brown 1984). Copper is known to inhibit electron transport in photosystem II (Samson et al. 1988), affect *Symbiodinium* photosynthesis (Alutain et al. 2001) and may cause coral bleaching (Jones 1997). Copper has also been shown to affect fertilization success of coral gametes (Reichelt-Brushett and Harrison 1999) and reduce larval settlement (Reichelt-Brushett and Harrison 2000). However, studies on effects of copper and other heavy metals on coral physiology are still relatively few (Wilkinson 1999; but see Harland and Brown 1989; Alutain et al. 2001), and this was the first investigation to study the interactive effect of elevated temperature and copper pollution on coral metabolism.

In this paper, corals were short-term (24h) exposed to elevated temperature (+4°C above ambient temperature) and copper (11 $\mu\text{g l}^{-1}$), alone and in

simultaneous and sequential combination (Fig. 1 in **Paper I**). The sublethal responses were investigated under controlled lab conditions on the branching coral *Porites cylindrica*. The results showed no additive or synergistic effects of elevated temperature and copper. Corals exposed to elevated temperature, both alone and in combination with copper, reduced photosynthetic rates to almost the same extent (Fig. 2 in **Paper I**). However, the corals also seemed to acclimate to some extent, as suggested by the reduced respiration rate (Fig. 3 in **Paper I**). Copper exposure, as a single stressor, did not significantly affect the production rate, although respiration was reduced (Fig. 2 and 3 in **Paper I**). On the other hand, the sequential stress of elevated temperature and copper enrichment, with a 5 days recovery interval, produced a slightly more detrimental response (than the simultaneous combination), since coral respiration was not significantly reduced (indicating a larger cost to acclimate) (Tab. 1 in **Paper I**). Hence, short-term (24h) copper exposure seems not to be a major problem for the corals unless they have been previously exposed to elevated temperature (sequential stress). The recovery interval between the stress pulses was probably too short to allow full recovery, as was also indicated by the enhanced production and respiration rates in the pre-heated corals still recovering from previous temperature exposure (Fig. 2 and 3 in **Paper I**). The response of sequential stress may thus have been prolonged and more detrimental, compared to stressors arriving simultaneously. The results in this paper are mainly consistent with other results of temperature stress (e.g. Porter et al. 1999) and copper exposure (Alutain et al. 2001) on coral metabolism.

Although corals appeared to bleach in all experimental treatments, an examination revealed that chlorophyll concentration was not affected. It is still possible that *zooxanthellae* may have been lost during the experiment, but this could not be determined since the density was not measured. However, in this paper, we speculate that the corals appeared paler by retracting tissue, thereby exposing more of the white skeleton, which is a common coral response to alleviate stress temporarily (e.g. Brown et al. 1994; Warner et al. 1996; Jones 1997; Brown et al. 2002), especially in *Porites* spp. (Jones et al. 2000; Piller and Reigl 2001). Visual inspection showed that once heat stress was removed, corals regained their coloration within days. This paper also demonstrated that corals may increase production rate above "normal" when relieved of stress (Fig. 1 in **Paper I**), and suggested that surplus energy may be used for repairing physiological damages, which may also explain the increased respiration rate (Fig. 2 in **Paper I**).

Nitrate and starvation as combining stressors with elevated temperature (Paper II)

Corals are generally considered to be adapted to low external concentrations of nutrients (Odum and Odum 1955; Johannes 1975), but due to anthropogenic influence, eutrophication of coral reefs seems to have increased world-wide,

particularly in coastal areas (Berner and Izhaki 1994; Stambler et al. 1994; Wilkinson 1999). Nitrate in particular has been suggested to be the major external source of nitrogen for corals (Bythell 1990), particularly in eutrophic areas (Marubini and Davies 1996). Previous investigations have shown that elevated nitrogen (NO_3 and NH_4) concentrations can increase *zooxanthellae* population growth rate and/or their density (Hoegh-Guldberg and Smith 1989; Dubinsky et al. 1990; Stambler et al. 1991, 1994, Stimson and Kinzie 1991; Hoegh-Guldberg 1994; Marubini and Davies 1996; Takabayashi 1996; Muller-Parker and D'Elia 1997). Despite increased gross primary production (Dubinsky et al. 1990; Takabayashi 1996; Ferrier-Pagés et al. 2000), energy is increasingly spent on *zooxanthellae* population growth, which seems to divert allocation of energy from being transferred to the coral host (Falkowski et al. 1993; Muller-Parker and D'Elia 1997). In response, the host may have to limit energy expenditure on, e.g. reproduction and growth (Ward and Harrison 2000; Cox and Ward 2002; but see Atkinson et al. 1995; Bongiorni et al. 2003). Since both elevated temperature and nitrogen enrichment can lead to a destabilized coral symbiosis, there may be potential interacting mechanisms, which was the focus of this paper. Only one previous study has investigated effects of the interaction between elevated temperature and nutrients (NO_3 and PO_4) with respect to coral growth rate, *zooxanthellae* and chlorophyll concentrations (Maté 1997). However, in this study, effects were hard to follow and inconsistent among species, which highlights that there may very well be species specific responses.

In **Paper II**, the branching coral *Porites cylindrica* was exposed to nitrate enrichment (+15 μM NaNO_3 for 14 days) and/or elevated temperature (+2°C above ambient temperature during the last 2 days of the nutrient exposure) in absence of particulate food. The results showed that primary production rate was significantly reduced in all exposed treatments, and there was a significant additive effect of combining elevated temperature and nitrate enrichment (Fig. 5a and b in **Paper II**). However, there were no effect on Chl *a* or *c* concentrations, *zooxanthellae* density or colony coloration (Fig. 1-3 in **Paper II**), although the *zooxanthellae* appeared (not quantified) to be smaller in the nutrient enriched treatments. Thus, our results on effects of nitrate enrichment contradict previous investigations on effects of nutrient enrichment. We speculate that reduced photosynthesis in response of nitrate enrichment may be the result of smaller and thus less productive *zooxanthellae* (shading pigments). We further suggest that nitrate enrichment in our study could have increased the population growth rate of *zooxanthellae*, which made them smaller, as has been reported in giant clams (which also have symbiotic microalgae) (Ambariyanto and Hoegh-Guldberg 1996; Koop et al. 2001). It is hypothesized that surplus algae were expelled from the coral due to lack of space in the starved (tissue thinning) coral host (Fig. 4 in **Paper II**). Previous investigations have not studied the effect of nitrogen enrichment under starved conditions, which may explain our contradicting results.

Since respiration rate remained unaffected by all treatments (Fig. 6a and b in **Paper II**), this implies that the corals were unable to acclimate to any impaired photosynthesis, which is then likely to affect, e.g. coral tissue biomass, fecundity, and/or growth rate. However, 14 days of exposure in this study may not have been enough time to produce a significant effect on tissue biomass, which remained similar among all treatments (Fig. 4 in **Paper II**). Nevertheless, coral tissue biomass was significantly reduced in all experimental treatments (including controls), which implies stressful lab conditions. We suggested that elevated concentration of dissolved inorganic nitrogen, utilized by the symbiotic microalgae, were not translocated to the coral host in sufficient amount to substitute particulate food as a nitrogen source, as implied by others (Bythell 1990; Marubini and Davies 1996). Several previous studies have also suggested the importance of particulate food for corals (Szmant-Froelich and Pilson 1980; Bythell 1988; Dubinsky and Jokiel 1994; Fitt and Cook 2001), although its role may vary among coral species (Moberg et al. 1997; Tomascik et al. 1997). Anthony and Fabricius (2000) stated that *Porites cylindrica* has a low heterotrophic capacity (implied low requirement for heterotrophic food), which the results of **Paper II** do not support.

Human pollution and overexploitation in a marginal reef environment (Paper III)

An estimated 88% of Southeast Asia's coral reefs are threatened by overexploitation and degradation, mainly due to overfishing, destructive fishing practices, sedimentation and pollution from land-based sources (Bryant et al. 1998). This field study was carried out in the Gulf of Thailand in three areas (Sichang, Samet and Man), where the fringing reefs are naturally exposed to low salinity, high sedimentation and low light conditions in a gradient (Piyakarnachana 1981; Yamazoto and Menasveta 1986; Moberg et al. 1997; Kleypas 1999) (Fig. 1 in **Paper III**). In addition to the marginal conditions (Kleypas et al. 1999), these reefs are also feared to be increasingly threatened by human pollution and overexploitation (Sudara 1981; Menasveta and Hongskul 1988; Suvavepun 1991). The objective of this paper was to investigate the extent of recent degradation, and how the natural setting (disturbance history) has affected the ecosystem's ability to handle anthropogenic disturbances. Changes in the relative substrate cover of living and dead corals, rock, algae and abundance of suspension-feeders, burrowing or boring into the dominant reef-building coral *Porites lutea*, were used as indicators of reef status. We assumed the entire Gulf to be overfished (Suvavepun 1991) and consequently that herbivorous fish would largely be lacking on reefs in all investigated areas. In accordance with other investigations regarding effects of nutrient- and sediment pollution and reduced salinity on coral reefs (e.g. Grigg and Dollar 1990; Bell 1992; Glynn 1997; Lapoint 1997; Moberg et al. 1997; Nyström et al. 1997; Hoegh-Guldberg and Williamson 1999), we expected the marginal reefs in the inner Gulf to have: a lower coral cover, higher benthic algae cover, increased

coral mortality, and more abundant cryptofaunal suspension-feeders than reefs further out.

As expected, the cover of bare rock was highest on the reefs in the Sichang area (Fig. 3 in **Paper III**), and these reefs were also less developed in terms of reef framework extension (Fig. 2 in **Paper III**). These results indicate that reef development in the marginal inner Gulf may have been limited for decades or centuries (perhaps even longer), which has also been suggested by others (Piyakarnachana 1981; Yamazoto and Menasveta 1986). However, recent degradation seems limited in the Sichang area, as we found few dead corals, compared to the more offshore reefs (Fig. 2 and 3 in **Paper III**), where the reefs seem to have been devastated by dynamite fishing, construction building, increased sedimentation and eutrophication, despite regulations. The results suggest that selection, due to limitations in the natural environment may already have removed stress sensitive species in the upper Gulf, and that these coral communities are now composed of more robust species that also better tolerates anthropogenic disturbances (Moberg et al. 1997). However, despite many interacting natural and man-made disturbances (including overfishing), and apparent coral mortality and vacant space, no large fleshy macroalgae were observed on any of the investigated reefs (only inconspicuous short turf was observed). Thus, compounded disturbances have not generated a regime transition from coral to macroalgae dominance on these reefs, as have been demonstrated in other regions. The study suggests this mainly to be due to efficient grazing by the very abundant sea urchin *Diadema setosum*. Previous investigations have also witnessed a lack of conspicuous large macroalgae in the innermost area (Kamura 1989). However, Kamura (1989) stated that most of the algal species in the area were naturally inconspicuous and seldom grow beyond the microscopic stage, despite lack of grazing, and attributed this to the low salinities. Nevertheless, sea urchins likely maintain parts of these reefs in a shortly cropped 'barren state'. Macroalgae have clearly not invaded any of the reefs surveyed in this field study. However, coral regeneration seems impaired by other factors. It is proposed that both poor water quality and intense grazing from sea urchins limit coral recruitment success and thus prevent regeneration of corals.

The density of selected suspension-feeding cryptofauna was highest in the innermost eutrophied and freshwater influenced area, but also surprisingly abundant in the Man area (Fig. 4H in **Paper III**). Since suspension-feeding cryptofauna were used as indicators of stress and pollution, their unexpectedly high abundance in the Man area suggests local pollution (possibly from a turtle farm nearby). Hence, this study highlighted how previously relatively well developed fringing reefs in the outer Gulf have recently deteriorated to a large extent. Although the surveyed reefs have not yet been overgrown by macroalgae, the relatively abundant suspension-feeding cryptofauna embedding or boring into the corals suggests that reefs may be changing to an alternate

“heterotrophic” or filter-feeding regime (Bell 1992; Done 1992; Hunter and Evans 1995; Glynn 1997; Bellwood et al. 2004).

Management of macroalgae-dominated reefs in the Caribbean (Paper IV)

Regime transitions to macroalgae dominance are increasingly common features of tropical reefs around the world, especially in the Caribbean, and corals show little sign of recovery. The aim of **Paper IV** was to explore the potential for shifting reefs back to an earlier algal successional stage of turf dominance, to allow for increased coral recruitment, by manual macroalgal reduction. We also wanted to investigate to what extent MPAs, which may attain more abundant and diverse fish populations (increased herbivory), might help sustain the achieved low algal biomass. The roles of MPAs, direct macroalgae reduction and their interaction were investigated on patch reefs of Glovers Reef Atoll in Belize. Macroalgae were experimentally reduced on 8 similar-sized patch reefs; 4 within a protected “no-take” zone (gazetted 3 years earlier) and 4 within a “general use” (open access) zone. 8 adjacent reefs (4 in each management zone) were studied as controls. Responses in terms of fish abundance of various species, herbivory (algal assays), and benthic cover of corals, macroalgae etc. were surveyed on the 16 patch reefs, sampled 5 times over a 1-year period.

We found that reefs in the protected zone had higher abundances of about half of the fish species, including some herbivores (Tab. 4 in **Paper IV**), but lower abundance of sea urchins. Total and fish herbivory were higher in the protected zone (Tab. 5 in **Paper IV**). On the other hand, sea urchin grazing was higher in the unprotected zone (Tab 5. in **Paper IV**). However, macroalgal cover was not significantly affected by management (protection). Nevertheless, coral cover was initially lower and calcareous algae higher on patch reefs in the protected zone (Tab 1. in **Paper IV**). We attribute differences in benthic cover to better physical and chemical conditions for corals in the unprotected zone.

The algal reduction decimated macroalgal cover, from approximately 22% to 4%, and thus initially exposed more corals and increasing the cover of turf substantially. The reduction immediately increased the abundance (aggregation) of some fish species (Tab 4. in **Paper IV**) and the *Labridae* and *Acanthuridae* fish families (species pooled into families) (Tab 4. in **Paper IV**), which are predominantly herbivorous. However, macroalgal cover quickly recovered from the reductions in both management zones, and species community composition was restored after 1 year (Tab 1. in **Paper IV**). Fish abundance of the *Labridae* and *Acanthuridae* families concurrently declined (Tab 4. in **Paper IV**). The experimental reduction did not reduce macroalgae cover more than temporarily, not even in combination with management (fishing protection) (Tab. 1 and 2 in **Paper IV**). Thus, current management seems unable to influence competition between fleshy macroalgae, turf and corals.

The protected area had only been in effect for a few years, and implementation was apparently insufficient as poaching still occurred. Moreover,

the experiment was likely confounded by two large-scale disturbances. First, an unprecedented bleaching event was initiated at the onset of the study and lasted for 3.5 months (Mumby 1999), which probably affected coral recruitment success (McField 1999) and likely explain the slight reduction of coral cover on the patch reefs over the following year (Tab. 1 in **Paper IV**). Second, hurricane Mitch arrived shortly after the algal reduction, but did not cause much physical damage to the patch reefs. Nevertheless, water run-off and mixing from the hurricane probably increased nutrient enrichment (indicated by an extensive regional phytoplankton bloom; Andréfouët et al. unpublished data), which may have promoted macroalgae growth on these patch reefs. We speculate if this could explain why brown fleshy macroalgae increased by 66% on control reefs during the first two months of this experiment.

Regime transitions- expanding perspectives and elucidating the mechanisms (Paper V)

Well before the reports of large-scale ecosystem transitions started to appear in the literature, it was known that intense herbivory keep macroalgae growth in check on coral reefs (Birkeland 1977; Hay 1984) and that nutrients sometimes promote algal growth (Odum and Odum 1955; Kinsey 1974; Lapoint 1985; Lapointe 1987). Thus, the prevalent explanations in literature for gradual ecosystem changes as well as abrupt regime shifts (or “regime transitions”, when not making a distinction between the two) to algal dominance have for the last two decades been either reduced top-down (herbivory) and/or increased bottom-up (nutrients) control (Hughes 1994; Done et al. 1996; McCook 1999; Goreau et al. 2000; McManus et al. 2000; Szmant 2002; **Paper IV**). Previous conceptual models have largely ignored competitive interactions between corals and macroalgae (but see Jompa and McCook 2002; Diaz-Pulido and McCook 2003; Jompa and McCook 2003; Diaz-Pulido and McCook 2004), and explanations only recently became more complex and included release of substrate (from mass coral bleaching, coral diseases, hurricanes, increased sedimentation etc.) as an important initiating factor (Hughes 1994; Done et al. 1996; Ostrander et al. 2000; Aronson and Precht 2001; Diaz-Pulido and McCook 2002; Szmant 2002). Large substrate availability was probably perceived as infrequent events in the past, and competition was mainly considered limited to direct interference. Today, corals face mass mortality events on a scale previously unrecorded, and the patterns of substrate availability have thus been altered. Hence, the previous conceptual models assuming low substrate availability needs to be re-evaluated. However, despite recent suggestions that large substrate release, following perturbations, may play an important role in regime transitions on coral reefs, no studies have investigated the effects of enhanced substrate availability in detail. Nor have any studies explored the mechanisms behind indirect exploitative competition for space between corals and macroalgae (or other reef biota), which tentatively can lead to regime transitions.

In this paper, traits involved in exploitative competition between the two functional groups, corals and macroalgae are examined based on a literature survey. The selected traits were primarily those involved in tissue healing, growth, reproduction, dispersal and recruitment. This literature survey also scrutinizes how the selected traits may influence regime expressions, when faced with altered disturbance regimes, in particular overfishing, eutrophication, elevated temperature, and enhanced substrate availability. Traits involved in direct interference are only briefly included.

The results generated from this review suggest that macroalgae have the potential to exploit released space more quickly than corals. This finding is based on differences in reproductive frequency and mode of reproduction between the two functional groups. The shorter generation times (life-histories with multiple generations), and the more scattered release, longer dispersal and successful recruitment of asexual propagules (fragments and spores) in macroalgae, increase their chances of recruiting onto available substrate before corals. Corals, on the other hand, are largely limited to sexual propagules for exploiting newly available space (asexual fragments cannot disperse far beyond their origin), and sexual reproduction in many corals is restricted to a relatively narrow time-period, sometimes as seldom as one night a year. Considering the increasing frequency and magnitude of substrate release, at the expense of corals (Wilkinson 1999, 2000), the competitive balance between the two functional groups is likely to favor macroalgae. Moreover, this investigation suggested that changes in the environment such as reduced herbivory and nutrient enrichment may not only express macroalgal biomass, and sometimes stimulate their growth rate, but may also promote algal fecundity (Nordemar unpublished data). This is likely to support their ability to exploit newly available space, and thus their competitiveness to corals, which concurrently face reduced calcification, growth and fecundity due to degraded environmental conditions (Szmant and Gassman 1990; Michalek-Wagner and Willis 2000; Ward and Harrison 2000; Abramovitch-Gottlieb et al. 2002; Baird and Marshall 2002; Cox and Ward 2002; but see Atkinson et al. 1995; Bongiorni et al. 2003). Once the first algae have colonized a newly available area, they can often spread quite readily from asexual propagation and/or rapid growth (Kinlan and Gaines 2003).

Furthermore, **Paper V** reveals that the capacity for dispersal of various coral and algal recruits remains somewhat obscure. Evidence to date suggests that sexually produced propagules of broadcast spawning corals may disperse farther than algal zygote propagules, which seem to disperse on the same scale as brooded coral larvae. On the other hand, asexual algal recruits (fragments and spores) are likely to disperse farther (or much further) than coral fragments. Due to altered disturbance regimes and ecosystem changes, the coral habitat is getting more fragmented, while the algal habitat is increasingly more connected, which is likely to impact on ecosystem resilience on a larger spatial scale, i.e. spatial resilience (Nyström and Folke 2001).

Findings gathered in the review strengthened the previously recognized high resilience of the macroalgae-dominated regime (Hughes 1994; McClanahan and Muthiga 1998; McCook 1999; Goreau et al. 2000; McManus et al. 2000; Knowlton 2001; Smith et al. 2002; Szmant 2002; Hewitt et al. 2004; Smith et al. 2004; Conklin and Smith in press; **Paper IV**). Despite frequent disturbance and algal removal, macroalgae have a large capacity to regenerate individual plants as well as entire populations (patches) (McClanahan 1997; **Paper IV**; Vroom 2001; Smith et al. 2002; Vroom et al. 2003; Smith et al. 2004; Walters et al. 2004; Conklin and Smith in press). In contrast, corals have a very limited capacity to regenerate colony lesions, and gaps in the reef framework are often re-colonized over decades or even longer (Connell et al. 1997). Various feed-back mechanisms were elucidated in **Paper V**, such as regenerating basal attachment points (e.g. holdfasts), apical hooks, and fragments, as well as rapid sprouting of dormant propagules, which sustain self-regeneration of the algal regime. Findings show that macroalgae possess traits, which make them strong competitors for space, but that this expression on coral reefs is normally suppressed under intense herbivory. This supports the previously recognized importance of herbivory for controlling macroalgae, thus facilitating the expression of the coral-dominated regime.

Discussion

Adaptive responses and history of stress exposure

Although compounded stress is generally believed to cause additive (due to cumulative stress) or synergistic effects on corals (Berkelmans and Oliver 1999; Brown et al. 2000), few studies have demonstrated this experimentally (but see **Paper I** and **II**). Previous experiments have to my knowledge only been able to show mitigating effects on coral metabolism of stressors in combination, e.g. reduced salinity and copper exposure (Alutain et al. 2001) and elevated temperature and salinity (Porter et al. 1999). This is not all that surprising as field studies have also shown mitigating effects of potential stressors (e.g. Dunne and Brown 2001; Fine et al. 2002). Adaptive responses seem to be a key explanation. Corals have the ability to respond to stress by a set of physiological mechanisms to reduce the stress and uphold homeostasis. For example, in response to low-light conditions in corals, the *zooxanthellae* can maintain photosynthetic production by enhancing their efficiency, e.g. increasing the chlorophyll content of the cells (Masuda et al. 1993). The coral host, in turn, may enhance the rate and extend periods of heterotrophic feeding (Anthony and Fabricius 2000). In **Paper I**, we suggested that the acute stress response to elevated temperature and copper exposure in *Porites cylindrica* involved the retraction of tissue into the skeleton, thereby reducing both the exposure and the respiration rate (Fig. 3 in **Paper I**). Once relieved of heat stress, the corals seem to acclimate, perhaps to an accumulated energy debt and need to repair physiological damages, by enhancing

the production rate (Fig. 2 in **Paper I**). However, at this point *P. cylindrica* seems more sensitive and could not acclimate as much to a second stress (Cu exposure). In **Paper II**, the corals seemed least able to acclimate to the combination of both elevated temperature and nitrate enrichment, as the production rate declined below that of the other treatments (Fig. 5a and b in **Paper II**). It is speculated that each of the stressors affected *zooxanthellae* photosynthesis by separate mechanisms, i.e. photosystem damage and less efficient shaded photosystems. It is possible that food limitation in this experiment may have enhanced or elucidated the underlying stress response (Koehn and Bayne 1989), which the corals could have compensated for otherwise.

Sometimes environmental cues can trigger adaptive responses ahead of changes to pre-adapt organisms to rapid changes. For example, increased solar radiation, which normally precedes elevated sea water temperature, may increase concentrations of photoprotective and fluorescent pigments, and up-regulate the production of Heat Shock Proteins (HSPs), which can protect the coral symbionts from heat stress (Dunne and Brown 2001). This could explain why coral reefs with different histories of irradiance exhibited contrasting responses, when exposed to elevated temperature (Dunne and Brown 2001). Because corals do not have unlimited combinations of adaptive responses, it is likely that they use general mechanisms to acclimate to different stressors such as the induction of stress proteins and retraction of tissue. Thus, compounded stress may not always be more detrimental. Prior exposure to heat stress could potentially pre-adapt corals to subsequent heavy metal stress by inducing HSPs, as seen in bivalves (Tedengren et al. 1999) and crustaceans (Bond and Bradley 1995). However, *P. cylindrica* in **Paper I** was more severely affected by elevated temperature and Cu exposure in sequential combination. It is possible that HSPs were not induced during this short-term heat exposure. Clearly, the stress response depends on the specific interacting stressors, their sequence, the recovery intervals etc.

Can nutrient enrichment mitigate stress effects of elevated temperature?

A few investigations have suggested that corals (visually) appear to benefit from nutrient enrichment, when they are exposed to elevated temperatures (e.g. McClanahan et al. 2003). There are many potential underlying mechanisms behind this. It is common that N enrichment increases the *zooxanthellae* population growth rate (under normal food conditions), which could potentially counteract increased rate of *zooxanthellae* degradation in response to elevated temperature. An alternative, or additional, mechanism may be that N fertilization facilitates an increased production of HSPs (which are rich in nitrogen), which may increase thermal tolerance and photosynthesis, as seen in higher plants (Heckathorn et al. 1996). However, the results in **Paper II** do not support these suggestions. Although the corals appeared unaffected by the combined exposure,

with respect to bleaching (i.e. *zooxanthellae* density and concentration of chlorophyll), the metabolic measurements showed impaired photosynthesis (Fig. 5a and b in **Paper II**). Thus, **Paper II** suggests that nitrate enrichment may aggravate effects of elevated temperature on *zooxanthellae*, and nutrient-exposed coral reefs may be more susceptible to stress during periods of elevated temperature compared to more “pristine” areas, at least when particulate food is lacking. However, **Paper II** demonstrated no effect of nitrogen and elevated temperature (alone or in combination) on the coral host after 14 days of exposure. This remains to be explored further. Unless the underlying stress responses in the host and the symbionts are clearly disclosed, reports of field observations implying that nutrient enrichment may be beneficial to heat stressed corals (e.g. McClanahan et al. 2003) could initiate fatal management plans.

Loss of functional redundancy, response diversity and ecosystem resilience

As the adaptive response to stress is increasingly energy demanding, corals may have to use lipid reserves (Falkowski et al. 1993; Glynn 1993), reduce growth rate and fecundity (Szmant and Gassman 1990; Ward and Harrison 2000; Michalek-Wagner and Willis 2000; Baird and Marshall 2002; Cox and Ward 2002; Bongiorno et al. 2003; but see Atkinson et al. 1995), before the stress ultimately results in mortality. Hence, less stress tolerant individuals will be removed more or less gradually (depending on the stress, species specific adaptive responses and tolerance limits), and the coral community will become increasingly dominated by resistant individuals or species. Stress adaptation in corals, e.g. to high temperature and coral disease, may also involve re-shuffling and/or mortality of susceptible *zooxanthellae* clades followed by acquisition of new types from the environment, which can lead to a more temperature tolerant clade composition (Buddemeier and Fautin 1993; Rowan et al. 1997; Baker 2001; Toller et al. 2001; Baker 2003; Baker et al. 2004; Rowan 2004).

Disturbance can thus be buffered in the reef ecosystem through species compensation among functional groups, provided that they have varying responses to disturbance (i.e. response diversity) (Elmqvist et al. 2003) and overlap in function (i.e. functional redundancy) (Lawton and Brown 1993; Steneck and Dethier 1994). However, redundancy is not endless, which may be particularly obvious at environmental limits. For example, reef-building corals share a similar, relatively narrow, temperature range (Veron 1986; Achituv and Dubinsky 1991; Veron and Minchin 1992; Kleypas et al. 1999; but see Hughes et al. 2003). In an era of global warming, corals move closer to their upper tolerance limits (Jokiel and Coles 1990; Hoegh-Guldberg 1999), and an increasing number are killed during bleaching events, although it is likely that various other human induced sources of stress and disturbance have added to this decline (Bryant et al. 1998; Wilkinson 1999, 2000). Today’s disturbance panorama primarily remove stress sensitive branching corals and thus favor

stress tolerant massive coral species (Done 1999; Gates and Edmunds 1999), which have become the dominant reef-builders in many areas (Wilkinson 1999, 2000; **Paper III**). By filtering species that exhibit varying traits, response diversity will be reduced (Norberg 2004; **Paper V**). In other words, ecosystem functions may still be maintained (at least to some extent) through species substitution, but ecosystem resilience may nevertheless decline (Elmqvist et al. 2003; Bellwood et al. 2004), and the community is likely to be more vulnerable to unexpected disturbance events or changing environmental conditions. For example, stress tolerant massive corals will probably be less able to keep up with the predicted sea level rise due to their slow growth (Done 1999), especially if the rate of calcification is reduced due to an altered carbonate budget in the sea (Gattuso et al. 1999; Kleypas et al. 1999; Langdon et al. 2000; but see Iso et al. 2000; Bessat and Buigues 2001) or if environmental stress affects growth rates. Enhanced bioerosion, from dense sea urchin populations and boring cryptofauna, can also threaten slow-growing reefs (**Paper III**), especially when coral recruitment is also affected (e.g. Sammarco 1980; McClanahan and Shafir 1990). Consequently, the future existence of reefs that are almost exclusively composed of massive slow-growing corals, e.g. in the inner Gulf of Thailand (**Paper III**), seems ominous, and it is possible that they may be on the verge of regime transitions to alternate reef communities. In **Paper III** part of the reefs were already in a sea urchin barren state, while it is suggested that the remaining coral community may also face a transition to a suspension- or filter-feeding (heterotrophic) community.

Regime transitions and the persistence of macroalgae-dominated reefs

Regime transitions from coral to macroalgae-dominated reefs are clearly the product of several interacting factors. While reduced herbivory has since long been accepted as the main driving force, the contribution from nutrient enrichment still remains an issue under debate (McCook 1999; Szmant 2002). **Paper V** explored a newly suggested driving force behind regime transitions, i.e. the increasing availability of substrate (more frequent and larger patches or gaps), also in combination with altered disturbance regimes, on the exploitative competition between corals and macroalgae. Based on findings in **Paper V**, it is suggested that inherent traits of corals and macroalgae differ in their capacity for exploitative competition, and altered patterns of substrate availability is thus likely to contribute to regime transitions. Macroalgal traits seem to make them extremely well adapted to exploit newly released substrate in competition with corals (**Paper V**). Corals have a window of opportunity to colonize available substrate shortly after reproduction, which is more or less restricted to a specific season (**Paper V**). A minority of all corals, reproduces more frequently and are thus regarded as opportunistic and adapted to frequent disturbance (Szmant 1986). Furthermore, **Paper V** highlights how altered disturbance regimes, e.g. overfishing, elevated sea water temperature and nutrient enrichment, can inhibit

coral traits and promote macroalgal traits involved in exploitative competition, and thus further contribute to regime transitions, when faced with increasing substrate availability. Hence, the conceptual model of regime shifts is getting increasingly more complex as more factors are added.

Predictions suggest that macroalgae reefs will become more common in the future (Wilkinson 2000; **Paper V**), and in order to avoid this weedy world, management must preferably intercept the predicted pathway before ecosystem transitions occur. Experimental algal reductions suggest that physical removal of macroalgae has no long-term effects; macroalgae communities often re-establish in a few months up to a year (McClanahan 1997; **Paper IV**; Conklin and Smith in press; but see McClanahan et al. 2002). In **Paper IV**, algal clearings were even performed in protected “no-take” areas, without success. It is possible that macroalgae clearings may be more successful on other reefs, where herbivory has been more amply restored. Management of the protected area in **Paper IV** was poorly implemented, and herbivory was likely not sufficiently enhanced. A relatively minor increase in fish biomass, although significant, may not have an impact on algal biomass (Lirman and Biber 2000; **Paper IV**); the composition of macroalgae may just shift (McClanahan et al. 2002; **Paper V**). Furthermore, as highlighted in **Paper V**, macroalgae communities can be very resilient, due to various feed-back mechanisms that sustain self-regeneration. Although, hedge-clippers and wire brushes removed most of the plants in the algal reduction in **Paper IV**, the enormous amounts of fragments generated in the process, likely contributed to their quick return. Furthermore, the capacity for regeneration of holdfasts and other basal attachment points (Smith et al. 2002; Smith et al. 2004; **Paper IV**) may have been substantial in some macroalgae, which secured their recovery. Thus, inherent traits of macroalgae can create self-sustaining durable states, and human interventions can be too risky. If algal reductions are further explored, their timing in relation to coral reproductive seasons must be considered more in detail, as well as reproductive characteristics of macroalgae. As a management tool, manual macroalgae clearings seem pointless unless herbivory has been restored, and for obvious reasons, this is not a management option for wide-spread use.

Concluding remarks

Predictions suggest that the diversity, frequency and intensity of disturbances affecting coral reefs will continue increase (Wilkinson 1999; Nyström et al. 2000; Hughes et al. 2003). For example, due to global warming the frequency of mass coral bleaching events is predicted to increase and occur almost annually in 20 to 30 years (Hoegh-Guldberg 1999). Current coral reef degradations worldwide suggest that corals may be unable to respond to environmental changes as rapidly as needed over the next century (Buddemeier and Smith 1999; but see Hughes et al. 2003). In consequence, Wilkinson (2000) suggests that 40% of the reefs may be lost by the year 2010. Although coral reefs have recovered from large catastrophic events in the past, recovery can no longer be taken for

granted considering the accelerating environmental change, altered disturbance regimes and compounded perturbations. This is manifested by the increasing number of coral reefs that fail to reorganize after disturbance events that previously could have been absorbed and instead shift to alternate regimes. Thus, coral reefs are in desperate need of management.

To enhance coral reef resilience, it is of primary concern to promote critical processes and functions that promote coral-dominated reefs. Management needs to uphold sufficient diversity and abundance of herbivores, which reduce the competitiveness of macroalgae and open up substratum for coral colonization (**Paper V**). However, other management strategies that support coral fecundity and recruitment also need to be implemented, e.g. by reducing pollution and dense sea urchin populations (**Paper V**). Likewise, macroalgal fecundity and growth should not be facilitated by nutrient enrichment, nor should we facilitate the spread of non-native macroalgae to new areas (e.g. by farming of exotic species), where the control from herbivores may be less efficient (**Paper V**). Thus, seaweed farming must be strictly regulated to prevent spreading of plant fragments, spores or sexual propagules. Before attempts to restore regimes by more direct interventions, like manual algal reductions (**Paper IV**), mechanisms that underpin algal dominance and suppress coral expression need to be understood (**Paper V**).

From a coral perspective, the seascape has become progressively more fragmented due to pollution barriers, habitat destruction, and reproductive failure in corals. The reduced connectivity between reefs can erode spatial resilience, which may impact on the reorganization capacity of perturbed reefs on a regional scale (Nyström and Folke 2001). Thus, management must promote the external flow of biota (including gametes, larvae, juveniles and mobile adults) between areas (**Paper III**), since re-colonization of perturbed reefs may be largely supported by recruitment from outside source reefs (Nyström and Folke 2001). If coral reefs are open, inter-linked systems (Hughes 1989; Jackson 1991), reef endurance on larger and longer time-scales are likely to depend on the spatial resilience of coral reefs. However, since coral dispersal have been shown to be relatively limited in space, at least under present conditions, spatial resilience cannot guarantee a quick regeneration of perturbed reefs, but is still likely to be an important process in the long-term. To properly address management of coral reefs, especially spatial resilience, environmental stressors and disturbances operating on larger spatial scales, e.g. global warming and world trade, must also be attended to (Hughes et al. 2003).

Knowledge of how compounded disturbances affect coral reefs seems to be an important but largely unexplored field of research. It is also important to further investigate the properties of acclimatization and adaptation, as they may be the key to coral survival over the next century of global changes (Buddemeier and Smith 1999; Gates and Edmunds 1999). Moreover, we must learn to what extent continued ecosystem performance can rely on substitution of species, i.e. the redundancy of the system (Norberg et al. 2001; Norberg 2004). In my thesis,

I may not offer any easy solutions to the many problems coral reefs face today. The future looks alarming. However, I've realized how unbelievable clever Nature is, and my gut feeling tells me that there may be something up the sleeve for future generations of us to see! Nevertheless, we must urgently start working together to mitigate the mass extinction event that we all seem to have contributed to. Even countries like Sweden are responsible for part of the degradation of coral reefs, due to our emission of greenhouse gases and global trade of reef fish and corals. At present, the existence of many people in poor areas of the world depends on the current status of our coral reefs.

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