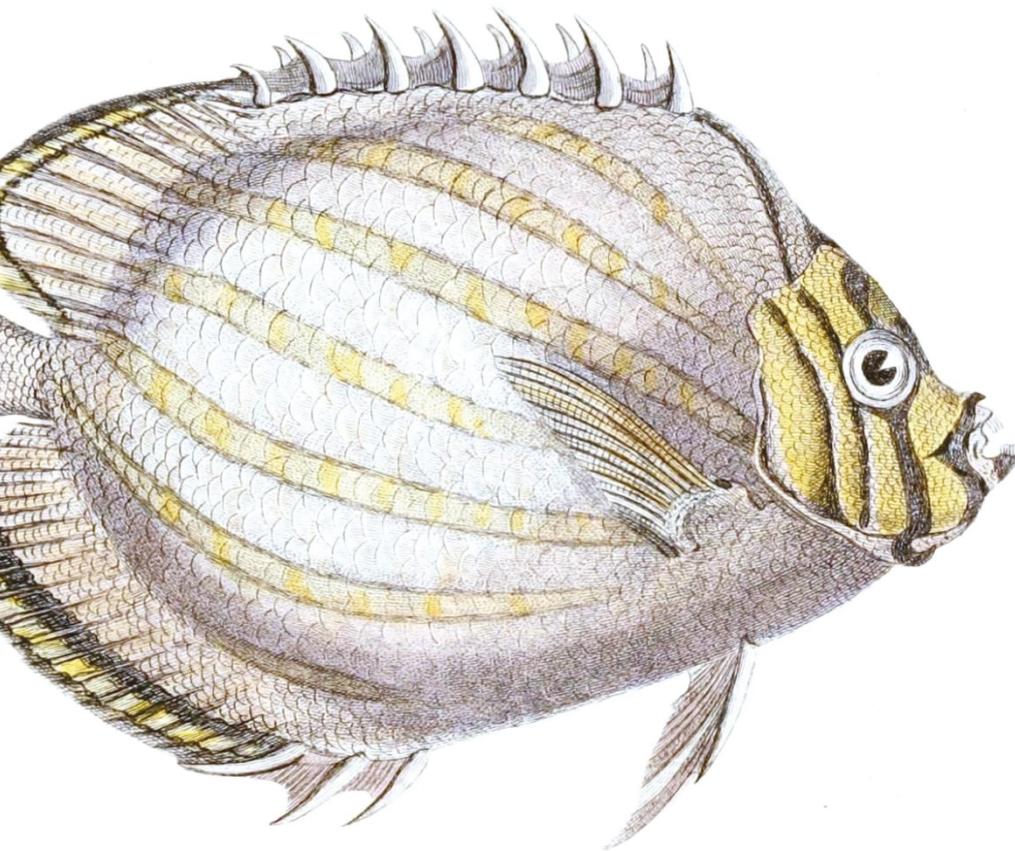


The Functioning of Coral Reef Communities
Along Environmental Gradients



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Summary

One of the primary challenges in ecology is to understand how environmental disturbance affects diversity and community structure, and what are the subsequent consequences on ecosystem functioning. Coral reefs are some of the most diverse ecosystems on the planet resulting in complex sets of interactions between benthic, habitat-forming constituents and mobile fish consumers. However, scleractinian corals, the primary habitat engineers, are dependent on high-light, low-nutrient water conditions and thus are highly responsive when the environment varies from this status. In Southeast Asia, an increase in human coastal populations centred around urban areas has resulted in extensive changes to the coastal environment such as degraded water quality and removal of fish consumers. This has resulted in highly varied abiotic and biotic conditions in relation with distance from the shore. Often, coral reefs closer to shore are much lower in benthic and fish diversity than those further from anthropogenic influences, with direct impacts on ecosystem functioning. Therefore the aim of this thesis was to explore coral reef ecosystem functioning with respect to changes in benthic community structure and fish diversity in relation to varying environmental conditions in the Spermonde Archipelago, Indonesia. A combination of observational, experimental and theoretical analyses were conducted on the functioning of coral reefs using eight islands on a transect of increasing distance from the mainland, varying from 1 to 55 km. At these eight sites, benthic and pelagic surveys identified variation in the status of coral reef communities, while recruitment and feeding assays identified variation in important ecological processes. Lastly, experimental observations were further qualified with stable isotope analysis and the application of contemporary indices of functional diversity. It was found that indeed, the coral reefs varied along a continuum of structure, assemblage and processes. Increasing distance from shore was associated with greater live coral cover and structural complexity, while sites closer to shore were dominated by turf algae and rubble. Furthermore, turf algae was observed as playing a particularly important role, as this group was dominant during recruitment and subsequent development of open benthic space as supplied by terracotta tiles. Fish diversity, along with redundancy in the important herbivore group, also increased with distance from shore, resulting in an increasingly diverse response to *Sargassum* and *Padina* assays. The functional composition of the fish assemblages became increasingly variable with loss in coral cover and structural complexity, suggesting communities become destabilised under habitat degradation. Furthermore, stable isotope analysis indicated that the trophic niche of a fish species can increase at sites with more degradation suggesting varying functional utility. However, functioning is not determined only by exposure to chronic, abiotic conditions. Outbreaks of the crown-of-thorns starfish (*Acanthaster planci*) and mechanical destruction (bomb fishing) resulted in extreme loss of live coral. At these sites, biological and functional diversity displayed some of the lowest values among all sites. Coral reefs can exist in systems with altered water condition if physiological and ecological capacity of the organisms allow for their continuation. Nevertheless, degraded water condition will select against many species, resulting not only in the observed lower biological diversity, but also in less species taking part in functional roles as reflected in higher functional variability. Combined, these results show that the functioning of coral reefs does not exist in discrete states; rather, their functioning is a result of abiotic stressors and biological feedbacks. It is becoming increasingly clear that pristine coral reefs are not a reality in many cases around the world. Thus understanding coral reef functioning at all stages of degradation will help with future management. This thesis adds to the ever-growing knowledge about disturbed coral reefs, but more importantly, it describes the changing relationship between diversity and functioning of coral reefs in relation to disturbance.

Zusammenfassung

Eine der primären Herausforderungen der Ökologie ist die Frage, inwiefern Umweltveränderungen die Diversität und Zusammensetzung von Artengemeinschaften beeinträchtigen, und welches die daraus resultierenden Auswirkungen auf die Funktionsweise von Ökosystemen sind. Korallenriffe gehören weltweit zu den artenreichsten Ökosystemen und bilden ein komplexes Beziehungsnetz zwischen habitatbildenden, benthischen Komponenten und mobilen Fischgemeinschaften als Konsumenten. Riffbildende Steinkorallen fungieren als die wichtigsten habitatbildenden Ökosystem-Ingenieure, benötigen hohe Lichtverhältnisse und sind besonders gut an die niedrigen Nährstoffbedingungen in tropischen Gewässern angepasst, weshalb sie sehr empfindlich auf Umweltveränderungen reagieren können. Marine Ökosysteme in Südostasiens leiden stark unter der stetig wachsenden Bevölkerung, die vorallem in urbanen Ballungsräumen im Küstenbereich meist eine drastische Abnahme der Wasserqualität und durch Überfischung einen Verlust an Konsumenten in der Nahrungskette mit sich bringt. Mit relativem Abstand von der Küste geht eine deutliche Veränderung in abiotischen und biotischen Wasserbedingungen einher, wodurch die benthische sowie pelagische Biodiversität küstennaher Korallenriffe oft weitaus geringer ist als die von küstenfernen Riffen. Das Ziel dieser Dissertation war daher, in dem indonesischen Spermonde-Archipel die Funktionsweise von Korallenriffen hinsichtlich der Struktur der benthischen Artengemeinschaft und der Fischbiodiversität unter verschiedenen Umweltbedingungen zu untersuchen. Dafür wurden Beobachtungsstudien sowie experimentelle und theoretische Analysen an Korallenriffen von acht verschiedenen Inseln durchgeführt, die in zunehmender Entfernung von der Küstenlinie liegen (1km bis 55km). Die benthischen und pelagischen Bestandsaufnahmen zeigten für alle acht Riffe einen unterschiedlichen Zustand der Artengemeinschaft, während Besiedlungs- und Fütterungsexperimente Unterschiede in wichtigen ökologischen Prozessen verdeutlichten. Diese experimentellen Beobachtungen wurden anhand stabiler Isotopenanalysen und der Anwendung von kürzlich entwickelten Indizes bezüglich funktioneller Diversität weiter validiert und es konnte gezeigt werden, dass die Korallenriffe tatsächlich entlang eines Kontinuums von Struktur, Zusammensetzung und Prozessen variieren. Mit größerer Entfernung von der Küste erhöhte sich die Bedeckung mit lebenden Korallen sowie die strukturelle Komplexität des Riffs, während Riffe näher an der Küste eindeutig von Aufwuchsalgen und Korallenschutt dominiert waren. Aufwuchsalgen waren die dominanten Neubesiedler im Riff und reduzierten damit die Fläche an frei besiedelbarem Substrat, was sich in Besiedlungsexperimenten mit im Riff ausgebrachten Terracotta-Platten zeigte. Fischdiversität und funktionelle Redundanz innerhalb der wichtigen Gruppe herbivorer Fische erhöhte sich mit wachsender Entfernung von der Küste und resultierte in einer zunehmend diversen Reaktion in Fraßexperimenten mit *Sargassum* und *Padina*. Die funktionelle Zusammensetzung der Fischgemeinschaft war verstärkt variabel je geringer die Korallenbedeckung und die strukturelle Komplexität des Habitats war, was eine Destabilisierung der Gemeinschaft unter Verschlechterung des Habitatzustandes anzeigt. Desweiteren zeigte die Analyse von stabilen Isotopen, dass sich mit zunehmender Degradierung der Riffe die trophische Nische von Fischarten erweitern kann, was auf eine veränderte funktionelle Rolle der Fischart schließen lässt. Die Funktionsweise von diesen Korallenriffen ist jedoch nicht nur von chronischen, abiotischen Faktoren beeinflusst. Eine Massenvermehrung von Dornenkronenseesternen (*Acanthaster planci*) und mechanische Zerstörung (durch Dynamitfischerei) führte in einigen Riffen zu einem erheblichen Rückgang der Korallenbedeckung. Diese Riffe wiesen die geringste biologische und funktionelle Diversität auf. Korallenriffe können durchaus unter sich verändernden Umweltbedingungen überleben, solange die physiologische und ökologische Belastbarkeitsgrenze von Organismen nicht überschritten wird.

Dennoch verursachen Umweltveränderungen eine Selektion vieler Arten, was zu der beobachteten Biodiversitätsabnahme führt, und da die einzelnen funktionellen Rollen folglich von weniger Arten wahrgenommen werden erhöht sich die funktionelle Variabilität des Systems. Zusammenfassend zeigen die Ergebnisse, dass die Funktionsweise von Korallenriffen keinen statischen, unabhängig existierenden Zustand darstellt, sondern dass sie vielmehr ein Resultat von abiotischen Stressoren und biologischen Reaktionen ist. Es wird immer deutlicher dass unberührte Korallenriffe weltweit eine Seltenheit geworden sind, weshalb Kenntnisse über ihre Funktionsweise in verschiedenen Stadien von Degradierung für ihr zukünftiges Management unerlässlich sind. Die vorliegende Arbeit vermittelt daher wichtige neue Erkenntnisse über degradierte Korallenriffe und darüber, inwiefern Umweltveränderungen die Beziehung zwischen Biodiversität und der Funktionsweise von Korallenriffen beeinträchtigen.

Ringkasan

Salah satu tantangan utama dalam ekologi adalah memahami bagaimana gangguan lingkungan mempengaruhi keanekaragaman, struktur masyarakat, yang kemudian berpengaruh pada fungsi ekosistem. Terumbu karang adalah salah satu ekosistem yang paling beragam di muka bumi dimana bentik, konstituen pembentuk habitat dan konsumen pergerakan ikan saling berinteraksi. Akan tetapi, karang scleractina, yang perannya adalah sebagai pembentuk utama habitat terumbu karang tergantung pada intensitas cahaya yang tinggi, kondisi air yang rendah nutrisi dan dengan demikian karang tersebut menjadi sangat peka ketika lingkungan disekitarnya berubah. Di Asia Tenggara, peningkatan populasi masyarakat pesisir yang berpusat di sekitar wilayah perkotaan, telah mengakibatkan perubahan yang sangat besar pada lingkungan pesisir, seperti penurunan kualitas air dan pergeseran konsumsi ikan. Hal ini mengakibatkan variasi kondisi abiotik dan biotik sangat tinggi, dalam kaitannya dengan jarak dari pantai. Seringkali, terumbu karang yang dekat dengan pantai memiliki keanekaragaman bentik dan ikan yang lebih rendah, dibanding dengan terumbu karang yang letaknya jauh dari pengaruh antropogenik yang berdampak langsung pada fungsi ekosistem. Oleh karena itu tesis ini bertujuan untuk mengetahui lebih dalam fungsi ekosistem terumbu karang sehubungan dengan perubahan struktur komunitas bentik dan keanekaragaman ikan serta hubungannya dengan berbagai kondisi lingkungan di Kepulauan Spermonde, Indonesia. Kombinasi pengamatan, percobaan dan analisis teori dilakukan pada uji fungsi terumbu karang dengan menggunakan transek pada delapan pulau dengan meningkatkan jarak dari daratan, yang bervariasi 1-55 km. Pada delapan lokasi tersebut, survey bentik dan ikan pelagis dilakukan untuk mengidentifikasi variasi dalam status komunitas terumbu karang, sementara itu perekrutan dan uji pemberian makanan dilakukan untuk mengidentifikasi variasi melalui beberapa proses ekologi yang penting. Terakhir, pengamatan eksperimen untuk memenuhi syarat lebih lanjut dilakukan analisis kestabilan isotop dan penerapan indeks kontemporer keanekaragaman fungsional. Ditemukan bahwa memang, terumbu karang bervariasi sepanjang rangkaian struktur, kumpulan dan proses. Semakin jauh jarak lokasi dari pantai semakin besar tutupan karang hidup dan semakin tinggi kompleksitas strukturalnya, sedangkan lokasi yang lebih dekat dengan pantai didominasi oleh mikroalga dan *rubble*. Selanjutnya, mikroalga yang diamati memainkan peran yang sangat penting, karena kelompok ini mendominasi selama perekrutan demikian pula pada pengembangan ruang bentik terbuka yang disediakan pada ubin terakota. Keanekaragaman ikan, serta redundansi pada kelompok herbivor, juga meningkat, semakin jauh jarak dari pantai, menghasilkan respon yang semakin beragam pada uji *Sargassum* dan *Padina*. Komposisi fungsional dari kumpulan ikan menjadi semakin variabel dengan hilangnya tutupan karang dan struktural kompleksitas menyarankan komunitas menjadi stabil pada habitat yang mengalami penurunan. Selanjutnya, pada analisis kestabilan isotop menunjukkan bahwa relung tropik dari spesies ikan dapat meningkatkan pada lokasi yang lebih menurun dan menunjukkan berbagai utilitas fungsional. Namun, fungsi tidak ditentukan hanya oleh paparan yang kronis, dan kondisi abiotik. Wabah mahkota dari duri bintang laut (*Acanthaster planci*) dan kerusakan secara mekanik (bom ikan) mengakibatkan hilangnya karang hidup secara ekstrim. Pada lokasi tersebut, sistem biologi dan fungsi keanekaragaman hayati menampilkan nilai terendah diantara semua lokasi. Terumbu karang dapat bertahan dalam sistem dengan kondisi air yang berubah-ubah jika kapasitas fisiologis dan ekologis organisme memungkinkan untuk keberlanjutan mereka. Namun demikian, kondisi air yang mengalami penurunan mengakibatkan banyak spesies tidak mampu bertahan, sehingga tidak hanya di keanekaragaman hayati rendah yang diamati, tetapi juga kurangnya spesies yang mengambil bagian dalam peran fungsional sebagaimana tercermin dalam variabilitas fungsional yang lebih tinggi. Gabungan dari hasil penelitian ini menunjukkan bahwa fungsi terumbu karang tidak ditemukan dalam

wilayah diskrit , sebaliknya fungsi mereka adalah hasil dari stres abiotik dan input biologis. Hal ini menjadi semakin jelas bahwa terumbu karang yang masih asli tidak nyata dalam banyak kasus di seluruh dunia. Dengan demikian memahami fungsi terumbu karang di semua tahapan penurunan dan kerusakannya akan membantu untuk pengelolaan terumbu karang dimasa depan. Tesis ini menambah pengetahuan yang terus berkembang tentang gangguan terhadap terumbu karang, tetapi yang lebih penting adalah menggambarkan perubahan hubungan antara keanekaragaman dan fungsi terumbu karang dalam kaitannya dengan gangguan terhadap terumbu karang tersebut.

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Section One

General Introduction

Coral reef functioning

Nowhere on earth does the concept of an ecosystem become more complex than when examining tropical coral reefs (Connell 1975, 1978, Connell et al. 1997). They consist of some of the highest biomass and biological diversity in the oceans of which leads to a complex hierarchy of interactions (Connell 1975). Hatcher (1997) initiates the idea of coral reef functioning through his definition of coral reefs as “a marine limestone structure built by calcium-carbonate secreting organisms which, with its associated water volume supports a diverse community of predominantly tropical affinities, at a higher density of biomass than the surrounding ocean.” This definition lacks any detail about scale or integration of ecological processes and continues with the incorporation of Odum and Odum's (1955) comparison of the coral reef ecosystem to an organism or chamber, with tight boundaries and, dominant internal dynamics of recycling and self-seeding. “Organisationally the system has high internal connectivity, is self-regulating and has high persistence stability. Materials and information are conserved, and transfers across system boundaries are small proportions of the total flux, most of which are internal.” Hatcher states that more recent studies have highlighted the connectivity of reefs (Sorokin 1995) where they are “analogous to sponges, stripping plankton and nutrients from the water column, transforming them and accumulating or exporting the resultant materials and organisms.” Essentially, these three definitions all coincide with the ever evolving definition of a coral reef system and its complexity, but their interpretation can depend on the specific processes and the spatial and temporal scale of observation. Figure I.1 provides an interpretation of coral reef ecosystem function compiled from Hatcher (1997), Odum and Odum (1955) and Sorokin (1995) where differing compartments of functioning have a high interdependence. Not all of these compartments are equal in importance, for example accretion is given highest significance because without this function, reefs cease to exist (Braithwaite et al. 2000, Hoegh-Guldberg et al. 2007, Perry et al. 2013).

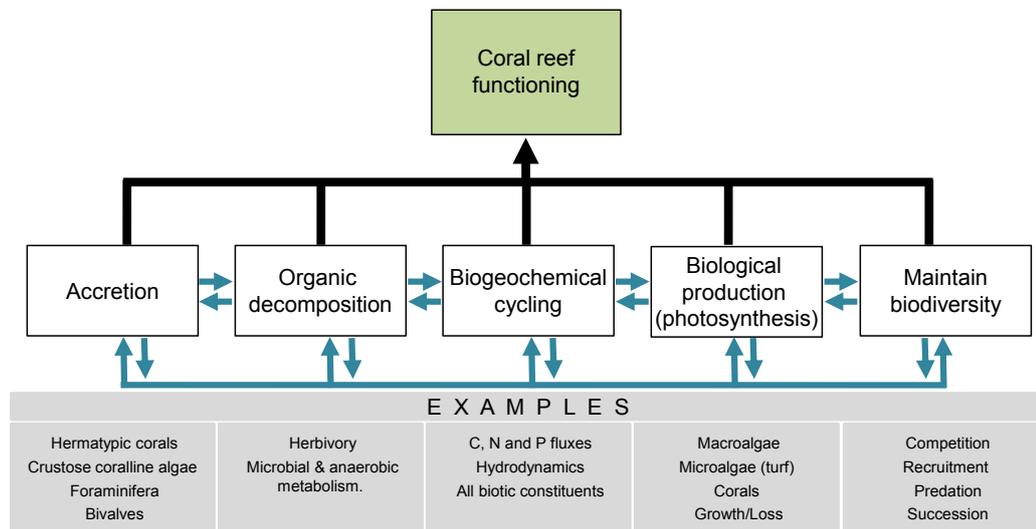


Figure 1. Visualisation of coral reef compartments and how they contribute to ecological functioning (as interpreted from Hatcher 1997, Odum and Odum 1955 and Sorokin 1995). These compartments can exist in homeostasis, but given their interdependence, change to any of the compartments results in change of the other compartments. A common example is that of a phase shift from coral dominance to that of macroalgal dominance. In this example, overfishing of herbivores (organic decomposers) results in macroalgae (biological production) increasing in abundance and overgrowing (maintenance of biodiversity) reef building, scleractinian corals. This inhibits the accretion (accretion) of the reef matrix and it can also affect the nutrient cycling (biogeochemical cycling) within the community.

Models of entire coral reef ecosystems have attempted to identify the most pertinent system functions (Polovina 1984), and most point to the importance of two broadly stated processes: constructional and decompositional processes, or the calcification by corals and algae versus erosion by biological and/or physical agents (Bellwood et al. 2003). A coral reef ecosystem can exist because of the balance between these processes, and changes can alter ecosystem feedback loops leading to systemic alteration. The scale of observation of these processes and their linkages will lead to different understanding about their connectedness. For example, small-scale variation in feedback loops of biogeochemical cycling, accretion and biological production have helped describe, at large spatial and temporal scales, the processes that lead to habitat gradients and patterns of zonation on coral reefs (Sheppard 1982, Done 1983, Harborne et al. 2006). Furthermore, these biogeochemical cycles are the direct result of growth and feeding of corals, algae and fish which can be described at a spatial scale of high resolution (McCook et al. 2001, Burkepille and Hay 2008).

Due to the importance of habitat accumulation through the accretion of carbonate material, processes affecting the net change in this material are prioritised because they determine ecosystem structure and function. These processes can be seen as a balance between constructional organisms such as scleractinian corals, other carbonate secreting invertebrates (e.g. molluscs), crustose-coraline algae, foraminifera, and decompositional organisms such as certain species of fishes, sponges and sea urchins (Hay 1984). Groupings of functionally similar species and their trophic and competitive interactions help understand the interconnectedness of processes (Polovina 1984) and, at a broad scale help to better interpret ecosystem functioning.

The substratum of coral reef system has been broken up, consolidated and rebuilt across millions of years (Braithwaite et al. 2000). The deconstruction of the benthos with subsequent benthic biotic overgrowth has increased structural complexity contributing to the diversity of lifeforms present. Coral reefs have evolved strong relationships with mobile fish constituents who often play a crucial role in maintaining decomposition and accretion related processes (Moberg and Folke 1999, Worm and Lotze 2006). Some fish feed directly from the carbonate substratum resulting in the deconstruction of the carbonate structure and its redistribution (Bellwood et al. 2003, Bellwood 2008). Similarly, other fishes feed upon those biotic groups that compete for spatial resources with individuals of the accreting functional group (Lefèvre and Bellwood 2011). Nevertheless, partitioning the many resources of the coral reef habitat has resulted in diverse differentiation of fish characteristics. Fine differences among fishes in their physiological, morphological and behavioural trait composition mean that there is often a high degree of overlap in habitat interaction; however the diverse benthic assemblage allows for some specificity in resource utilisation (Sale 2002, Wilson et al. 2009, Pratchett et al. 2011b) suggesting that a change in habitat will affect fish interactions. Thus, disturbance on the benthic habitat will limit or change resources and favour fishes that retain traits that allow them to maintain or alter their ecological niches (McGill et al. 2006). This also suggests that the role of a fish consumer may be dependent on the habitat composition resulting in varying functional roles of the species. Since fishes play an important role in the functioning of coral reefs, restructuring habitats will also rely on the feedback mechanisms provided by the fish consumer group (Villéger et al. 2010, Pratchett et al. 2011a).

Fish species diversity

Despite disturbance, there is a positive relationship between fish diversity, especially herbivores, and ecosystem resilience within coral reefs (Elmqvist et al. 2003, Hooper et al. 2005) where healthy systems generally display high functional diversity and functional redundancy leading to an increase in

the diversity of responses during disturbance (Nyström 2006). Many studies have focused on the role of fish species diversity within functional redundancy and response diversity because measuring the absolute differences between species is not informative without information about the contextual role within an assemblage (Luiz et al. 2012, Parravicini et al. 2014, Mouillot et al. 2014). For instance, the significance of species loss within a functional group that has five species will be greater compared to one with twenty species. Furthermore, interactions become more complex with an increase in species number making it difficult to predict the effect of the loss of an individual species. Thus, there is considerable interest in the capacity of species' to compensate for each other when any one species is lost (Nyström 2006). Given the extent of environmental change within coral reef systems, identifying the capacity of species to expand beyond their normal functional role will reveal potential for functional compensation. Understanding species' ecological differences within functional groups will increase our ability to assess ecological insurance and understand the potential consequences of the loss of biodiversity (Haddad et al. 2008, Mora and Sale 2011, Pavoine and Bonsall 2011).

It is only of recent that ecologists have begun to systematically identify the role of species in the creation, destruction, modification and maintenance of habitats (Lawton 1994, Chapin et al. 1997). Increased impacts on communities from natural and anthropogenic perturbations have motivated researchers to ask whether the extent of species functional variability does influence the properties and performance of the systems (Walker 1992, Schulze 1995, Schlöpfer and Schmid 1999, Elmqvist et al. 2003). An emphasis on relationships among quantifiable functional variables of species allows the identification of general patterns and hence, predictions about system maintenance (Flynn et al. 2011). To understand interactions among species, concentration must first be on the variation of functional roles within and between species. In the development of understanding system functioning, it is important to demonstrate that variations in individual species' functions are likely to have consequences for the functioning of the community and ecosystem. This is especially important in changing systems where the dynamics of a given set of species can vary depending on the species present, and their interspecific interactions with the environment (Naeem and Li 1997, Lavorel et al. 2014).

Herbivory

Primary consumers, or herbivores, are of critical importance in ecological systems because they are responsible for the transfer of primary production to higher trophic levels. Through their feeding behaviour, primary consumers affect the physical structure and productivity of vegetated habitats. Termed "top-down" control, this implies that consumers can control prey populations lending importance to the understanding of mechanisms of consumers and producers that cause variation in their interactive strengths of their relationships. Differences in individual grazer traits (feeding efficiency, metabolism, size, mobility), grazer community composition (abundance, taxonomy, diversity) or predator regulation can affect rates of productivity, its removal or its standing crop (Borer et al. 2005, Poore et al. 2012). In coral reefs, it has been repeatedly shown, both experimentally and *in situ*, that the removal of herbivores from the ecosystem results in algae taking over benthic communities (Hughes 1994, Hughes et al. 2007, Jessen and Wild 2013). This can be further facilitated when the normally oligotrophic water conditions change and are no longer limited in nutrients, resulting in expedited algal growth (Littler and Littler 2007, Burkepille and Hay 2009) and light reduction and sedimentation that impede coral accretion (Fabricius 2005). Feeding by herbivores maintains benthic algae community development at a 'mature' state (Zanini et al. 2006), one

dominated by calcifying and encrusting algae, that allows for the recruitment and development of corals (Lapointe et al. 2004, Littler et al. 2006, Ritson-Williams et al. 2009).

To prevent coral reefs from changing to altered states, herbivorous coral reef fishes must limit both the establishment and growth of algae (Green and Bellwood 2009) through direct consumption and dislodgment. Because algae occur on coral reefs in many different forms and have differing predator deterrents, inhibition of algal growth is greatest when species richness, and functional richness, is high among algal consuming fishes (Burkepile and Hay 2008, 2010). On healthy coral reefs, differing groups of herbivorous fishes feed from standing fleshy macroalgae and from the closely associated benthic turf algal matrix. Thus, the maintenance of high species diversity contributes to high functional redundancy within these differing groups and guarantees the continuation of the functions despite impacts. Furthermore, the maintenance of high species diversity also contributes to response diversity within functional groups when disturbance occurs because not all species play exactly the same role (Nyström 2006).

Glossary of terms used within this thesis

Biological diversity	The variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems
Bottom-up vs. Top-down	Bottom-up refers to ecosystem controls via nutrient supply and productivity. Top-down refers to predation or physical determinates that structure population dynamics of an ecosystem (Menge 2000).
Constructional and decompositional processes	Within the context of a coral reef, constructional processes are generally biotic taxa that lay carbonate structure contributing to reef accretion. Decomposition processes refer to biotic (fish) or abiotic (wave energy) that result in the break-down of the carbonate structure of the reef.
Ecosystem function	The collective processes of an ecosystem driven by its constituent biota (Naeem et al. 1999)
Ecosystem resilience	The ability of an ecosystem to absorb natural and human-induced disturbance events and still be retained with the same ecosystem state (Nyström et al. 2000).
Eutrophication	Excessive richness of nutrients in a lake or other body of water, frequently due to runoff from the land, which causes a dense growth of plant life and death of animal life from lack of oxygen.
Functional compensation	When a particular species increases its functional efficiency at providing a ecological service when conditions become stressed, maintaining net stability of the ecosystem (Frost et al. 1995).
Functional diversity	The extent of functional differences among species in a community (Filman 2001)
Functional group	Sets of species that perform similar ecological roles (Nyström 2006)
Functional redundancy	The capacity of on species to functionally compensate for the loss of another species (Steneck and Dethier 2011).
Response diversity	The diversity of ecological responses to environmental change among species within functional groups (Nyström et al. 2012)
Species richness	The number of different species represented in an ecological community, landscape or region.
Traits	Any morphological, physiological, or phenological feature measurable at the individual level (Mouillot et al. 2013b).

Disturbances in communities

In opposition to top-down controls, much of the world's primary production is limited by the supply of biologically available nitrogen and phosphorous (Zak and Pregitzer 1988, McLendon and Redente 1991, Galloway et al. 1995). "Bottom-up" control is determined by the amount and form of nitrogen and phosphorous driving variation in producer communities (Westman 1981, Smith and Rice 1983, Thorne and Hamburg 1985, Zak and Pregitzer 1988). Increases in availability can increase productivity and biomass accumulation significantly, because indigenous producer species are often adapted to low nutrient conditions (Vitousek and Howarth 1991).

Extensive anthropogenic modification to global biogeochemical cycles and consumer trophic structures has confounded our understanding of processes affecting primary production and food web structure, and how ecosystems function. However, global inputs of nitrogen, phosphorous and iron into natural systems has more than doubled in the last decade due to anthropogenic factors (Falkowski et al. 1984, Jeffries and Maron 1997, Calbet and Landry 2004) causing widespread eutrophication within aquatic systems (Carpenter et al. 1998). Furthermore, in marine aquatic systems, humans have changed heterotrophic consumption through the removal of top predators (Dulvy et al. 2004) and primary consumers (Hughes 1994). Alterations in ecosystem nutrient supplies can lead to a loss in community diversity (Aerts and Berendse 1988, Arai 2001, Petchey et al. 2004) and changed pathways of nitrogen (Tilman 1987) and carbon cycling (Falkowski et al. 2000). Changes in primary production can change patterns and interaction among primary consumers with strong consequences on food webs and consequently, community and ecosystem stability (Yodzis 1981, McCann and Hastings 1997, Neutel et al. 2002). Variable compositions within and among producers and consumers suggests communities will respond in a dynamic fashion to any level of habitat modification because this will alter resource availability, habitat use, predator-prey relationships and ultimately, niche utilisation.

Carbonate accreting organisms, especially corals, grow relatively slow when compared with other sessile benthic biota. Even the fastest growing corals extend at a rate of no more than 20 cm per year, indicating coral dominance can be impeded if faster growing groups are facilitated (Shinn 1966). In particular, the replacement of corals by algae is considered to be highly important because on contemporary coral reefs, this is a critical step during reef degradation (Miller and Hay 1998, McCook 1999, McCook et al. 2001). This can be further facilitated when the normally oligotrophic water conditions change and are no longer limited in nutrients, resulting in expedited algal growth (Littler and Littler 2007, Burkepile and Hay 2009) and light reduction and sedimentation that impede coral accretion (Fabricius 2005). In extreme examples, the benthic composition can be represented by a complete alternate assemblage dominated by either algae or other invertebrates (Norström et al. 2009) and, hence, providing fewer ecosystem services (Brock and Carpenter 2006). Likewise, altered ecological feedbacks destabilise top-down and bottom-up processes in the coral reef habitat and this can lead to alternate ecological states. For example, high coral cover and feeding by herbivores promotes the production and successful recruitment of juvenile corals, which helps to maintain coral dominance (Hughes 1994, Carpenter and Edmunds 2006). Alternatively, if herbivores are lost, increases in macroalgal stands overgrow and shade benthic areas which restrict juvenile coral recruitment.

Most coral reefs of the world occur within a geographical range that is impacted by direct anthropogenic influences (Burke et al. 2011). Here, reefs are exposed to resource use and terrestrial effluents changing both their biotic composition and the abiotic environment to which they are exposed. Furthermore, exposure to these disturbances may vary depending on local management and relative distance to humans and to the mainland, resulting in gradients of disturbance. Increased

inorganic nutrients and particulate matter have been noted to change coral reef benthic communities from nutrient-recycling symbiotic organisms hosting diverse assemblages to increasing proportion of algae and heterotrophs and an overall lower diversity (Fabricius 2005). Coral reef benthic organisms live within a range of acceptable abiotic conditions, generally driven by physiological capacity (Montgomery 2011). These limitations on physiological capacity can act as filters on communities where change in benthic composition alters the habitat for other mobile constituents, resulting in altered or lost niche utilisation (Bellard et al. 2012). Thus, studying coral reefs along disturbance gradients will help elucidate community interactions whereby benthic communities change in a systematic way to disturbance. This is reflected in the greater reef community, resulting in mechanistic understanding about changes in coral reef functioning.

Study site

The Southeast Asia region of the Indo-Pacific is one of the most biologically diverse regions in the world. The Coral Triangle is the heart of the coral reef ecosystem, and this area, spanning Indonesia, Malaysia, Papua New Guinea, the Philippines, the Solomon Islands and East Timor accounts for 75 % of all known coral species and more than 3000 fish species (Veron et al. 2009, Burke et al. 2012). Marine resources of the Coral Triangle support ~130 million people locally, with tens of millions more when considering exports (Burke et al. 2011). Within this area, localised, human-derived pressure to coral reefs is considered to be of greater immediate concern than large scale global pressures. A recent report has rated 85 % of the reefs within the Coral Triangle as threatened with overfishing, including destructive techniques, as the most pervasive and damaging threat (Burke et al. 2012). Furthermore, the effects of coastal development and watershed pollution are also major contributors to the decline of coral reefs in the region. Overfishing and destructive resource use, in part because of increased coastal populations, has resulted in increased resource use on >50 % of the coral reefs since 1998 (Burke et al. 2012). It should not be overlooked that localised disturbances deteriorate the capacity for coral reefs to respond positively to global disturbances (Carilli et al. 2009, Ateweberhan et al. 2013).

Within the Coral triangle, an area of particular concern is the Spermonde Archipelago (119°15'E, 5°00'S) of Southwest Sulawesi, Indonesia. This archipelago of roughly 100 populated islands lies adjacent to the sixth largest city of Indonesia; Makassar, home to approximately 1.5 million people and contributing to high demand of marine resources both locally and for export (Erdman and Pet-Soede 1997, Schwerdtner-Mañez and Ferse 2010, Ferse et al. 2012), and the city has the second largest commercial port in the country contributing greatly to supplies for the east of the country. The archipelago consists of small coral atolls offering residents few employment alternatives to fishing (Ferrol-Schulte et al. 2013). Thus, the livelihoods of the Spermonde fisherfolk are deeply dependent on the coral reef resources. Since the 1970's, access to alternative, more productive fishing techniques such as explosives and cyanide have increased negative pressure on the ecosystem (Pet-Soede and Erdmann 1998a, 1998b).

The coral reefs of the Spermonde Archipelago are subjected to a wide range of disturbances, both derived regionally from the main land and locally from the islands (for a detailed description, see Chapter I). Spatially and temporally varying impacts indicate that the coral reef system persists at differing ecological states. Indeed, previous studies have identified spatial gradients in coral (Edinger et al. 2000b, Hoeksema 2012), sponge (de Voogd et al. 2006) and foraminifera diversity (Cleary and Renema 2007) and also beta diversity of the benthic assemblages (Becking et al. 2006). Likewise, the scleractinian coral *Styolophora subseriata* displayed high physiological plasticity across the land-derived

water gradient (Sawall et al. 2011), and coral recruitment persists even at the most degraded sites (Sawall et al. 2013). All of these studies indicate ecosystem functioning to varying degrees, even in a heavily degraded state, however, no work has examined the fish assemblages and their role in maintaining ecosystem function. Varying stages of habitat degradation and differences in coral reef ecosystem functioning may reflect reefs of the greater Southeast Asian region, a region with a high dependency on coral reef resources. Furthermore, most coral reefs of the world are of a threatened status, and it is predicted that most reefs will decline in health (Bellwood et al. 2004, Hughes et al. 2007, Burke et al. 2011). Thus, understanding fish and changes in benthic communities of coral reefs in the Spermonde Archipelago will help elucidate patterns and processes on coral reefs of the region, but also, understanding these reefs may contribute to knowledge about the potential development of other, currently less disturbed coral reef systems found around the world (Graham et al. 2014).

Objectives

The conservation of ecological communities depends on identifying general principles of environmental feedback loops among abiotic conditions, producers and consumers and allows for the management and maintenance of ecological resilience (Connor and Simberloff 1979, Lawton 1999). Thus, importance should be given to understanding the specific mechanisms and/or ecological processes that maintain ecosystem functioning of diverse species assemblages. Specifically, response of ecosystem functioning to environmental gradients allows for greater predictability because abiotic parameters often control between-site variation allowing for the evaluation of incrementally differing community structures. For each species, there is a multivariate relationship between species' traits, abiotic conditions and species-species interactions (Cornwell and Ackerly 2009). For instance, when environmental disturbance excludes, or reduces a specie's abundance, differences in trait composition among species can drive interspecific differences in response to the disturbance (Haddad et al. 2008). This means disturbances can restrict, or filter, the range of morphological, physiological, behavioural or phenotypic traits (Diaz et al. 1998, Weiher et al. 1998, Diaz and Cabido 2001) suggesting that the performance of species will be a function of the abiotic gradient leading each species to prefer and perform optimally in a distinct region of niche space along the gradient (Colwell and Fuentes 1975, Pulliam 2000, McGill et al. 2006). There has been increased interest in how communities' biological diversity and trait assemblages vary along gradients because, combined, they may provide a more thorough understanding about systems that are undergoing environmental changes (McGill et al. 2006).

In coral reefs, the variation in community assemblage along environmental gradients has long been recognised, however, focus is generally on the change in benthic communities (Fabricius et al. 2005, Fabricius 2005, Lirman and Fong 2007). When included, analyses of fish communities are generally restricted to the evaluation of biodiversity indices (Fabricius et al. 2005, Wismer et al. 2009, Andréfouët and Wantiez 2010) presenting information only on the status of the communities overlooking the important contribution this group plays in coral reef functioning and how this can change given habitat gradients. Moreover, recent advances in ecological analyses have identified novel methods linking species traits and the functioning of ecosystems (Mouillot et al. 2013a) allowing greater evaluation of ecosystem processes. This thesis, therefore, uses a coral reef archipelago along an environmental gradient to examine relationships between benthic and fish communities with varying disturbance. Because of the ecological importance of fish herbivory, special attention is given to this functional group in its role shaping benthic communities. However, knowing that fish communities are also determined by the benthic habitat, fish are examined for trait-based links to the

environment at both the community and the individual specie levels. Within this context five specific questions were addressed:

- 1) What are the relationships between the reefs' water quality and benthic condition and the associated fish assemblages?
- 2) How do changes in environmental condition affect herbivorous fish community composition and functioning?
- 3) How do algal communities react to changes in herbivore pressure and variation in environmental condition?
- 4) Do individual herbivore species have the capacity to change habitat use in response to changes in habitat condition?
- 5) Does the functional composition of fish communities react to changes in habitat condition?

The different components of this study are addressed in a series of nine chapters outlined below. There are, however, five primary chapters (Chapters I, V, VI, VIII and IX) coinciding directly with the above questions, while other chapters contribute to peripheral observations and or subjects. Furthermore, the structure of this thesis coincides with the scientific process (observation, experimentation and theoretical work). This structure not only provides a logical progression of question construction and answering, but also represents the progression necessitated in my three year study. Although previous work existed from the Spermonde Archipelago, review of the literature identified major gaps of research (Section 1), while it was initial observations (Section 2) during the first trip in 2012 that provided knowledge of the system to return with probing questions to be answered experimentally (Section 3). Finally, experimental dissemination allowed for conceptualisation of ecosystem processes explored in Section 4. Section 5, or the General Discussion, provides synthesis of sections 2-4 in relation to Section 1.

Publication Outline

Section Two. Observations of a disturbed coral reef system

Chapter I – A coral reef system and a cross-shelf, environmental gradient

Publication title – Water quality and local disturbances drive spatial differences in coral reef benthic and fish communities of the Spermonde Archipelago, Indonesia

Plass-Johnson JG, Bednarz VN, Schwieder H, Heiden J, Weiland L, Wild C, Lukman M, Ferse SCA, Teichberg M

In preparation for *Ecosystems*

In Chapter I ‘The effect of a water quality gradient and local disturbances on benthic and fish coral reef communities’, we conducted annual surveys of the water quality, and benthic communities and fish communities of eight islands of the Spermonde Archipelago. These eight islands were located along a spatial gradient away from Makassar, effectively creating a gradient of stress caused by variation in water quality derived from effluents of the city. However, variation in local resource use and management can result in disturbance effects on community structure beyond regional drivers. Thus, we examine coral reef community structure in relation to both land-based and locally derived disturbances. All subsequent studies were based on these initial observations.

Contributions: This project was initiated by J.G. Plass-Johnson, M. Teichberg, C. Wild and S.C.A. Ferse. The experimental design for this study was developed by J.G. Plass-Johnson, M. Teichberg and S.C.A. Ferse. Sampling was conducted by J.G. Plass-Johnson, J. Heiden, H. Schwieder, L. Weiland, V.N. Bednarz, and S.C.A. Ferse. Data analysis was conducted by J.G. Plass-Johnson and the manuscript was written by J.G. Plass-Johnson with improvements from all contributing authors.

Chapter II – *Acanthaster planci* outbreak

Publication title – A recent *Acanthaster planci* outbreak in the Spermonde Archipelago, Indonesia

Plass-Johnson JG, Schwieder H, Heiden JP, Weiland L, Wild C, Ferse SCA, Jompa J, Teichberg M

Accepted in *Regional Environmental Change*: doi: 10.1007/s10113-015-0821-2

Chapter II, ‘*Acanthaster planci* outbreak in the Spermonde Archipelago, Indonesia’ records the onset and impact of an important live coral predator, the crown-of-thorns starfish. Little is known about the onset of outbreaks of this organism in Indonesia, and this observation provides further information linking it to water quality.

Contributions: This project was initiated by J.G. Plass-Johnson, M. Teichberg, and S.C.A. Ferse. The experimental design for this study was developed by J.G. Plass-Johnson, M. Teichberg and S.C.A. Ferse. Sampling was conducted by J.G. Plass-Johnson, J. Heiden, H. Schwieder, L. Weiland, V.N. Bednarz, and S.C.A. Ferse. Data analysis was conducted by J.G. Plass-Johnson and the manuscript was written by J.G. Plass-Johnson with improvements from all contributing authors.

Chapter III – Sponge take-over of a reef

Publication title - The takeover of a benthic coral reef community by the sponge *Ircinia* sp.

Plass-Johnson JG, Meyer A, Wild C, de Voogd N, Ferse SCA, Teichberg M

In preparation for *Bulletin of Marine Science*

Chapter III ‘The takeover of a benthic coral reef community by the sponge *Ircinia* sp.’ continues with the identification and repercussions of anthropogenic impacts in the archipelago. At Karang Kassi, a reef heavily impacted by bomb fishing, the sponge *Ircinia* sp. is observed overgrowing the highly disturbed benthic communities over three years. This provides one of the few observations of community regime shifts to a sponge in the Indo-Pacific region. Furthermore, genetic identification is incomplete because an exact match was not made suggesting either an invasive or new species. This project will be extended in collaboration with a sponge specialist (N. de Voogd) from the *Naturalis Biodiversity Center*, Leiden.

Contributions: This project was initiated by J.G. Plass-Johnson, M. Teichberg and S.C.A. Ferse. The experimental design for this study was developed by J.G. Plass-Johnson, M. Teichberg and S.C.A. Ferse. Sampling was conducted by J.G. Plass-Johnson, J. Heiden, H. Schwieder, L. Weiland, and V.N. Bednarz. Sample analyses were performed by A. Meyer and N. de Voogd. Data analysis was conducted by J.G. Plass-Johnson and the manuscript was written by J.G. Plass-Johnson with improvements from all contributing authors.

Chapter IV – Observation of potential change in fish functional role

Publication title - Observation of macroalgal browsing in juvenile humphead parrotfish, *Bolbometopon muricatum*, in the Spermonde Archipelago, Indonesia

Plass-Johnson JG, Ferse SCA, Wild C, Teichberg M

Published in *Bulletin of Marine Science* (2014) 90: 763-764. doi: 10.5343/bms.2014.1006

In Chapter IV, a chance observation during the sample collection for publication VI resulted in the first recording of macroalgal feeding of one of the most important coral reef excavators. Thus, this paper provides evidence that the concept of coral reef functioning can continuously evolve as more observations reveal unknown processes.

Contributions: Contributions for this chapter follows those of publication VI where J.G. Plass-Johnson, S.C.A. Ferse, and M. Teichberg initiated the study. The experimental design was developed by J.G. Plass-Johnson, S.C.A. Ferse, and M. Teichberg. Field sampling was conducted by J.G. Plass-Johnson and L. Weiland. Data analysis was conducted J.G. Plass-Johnson and the manuscript was written by J.G. Plass-Johnson with contributions from all co-authors.

Section Three. Experiments in coral reef processes

Chapter V – Herbivory on macroalgae

Publication title - Fish herbivory as key ecological function in a heavily degraded coral reef system

Plass-Johnson JG, Ferse SCA, Jompa J, Wild C, Teichberg M

Published in *Limnology and Oceanography*. doi: 10.1002/lno.10105

In Chapter V, we examine the capacity to maintain a critical function of coral reefs, herbivory, in a heavily degraded system. We transplanted two species of macroalgae from the back-reef to the reef slope to see how herbivore communities would vary along five islands of the water gradient. With this experiment, we show that despite heavy anthropogenic impacts to the coral reef habitat, herbivorous fish communities are able to completely remove the algal crop within 24 h, and this is done through variation in those fish communities among sites.

Contributions: J.G. Plass-Johnson, S.C.A. Ferse, and M. Teichberg initiated the study. The experimental design was developed by J.G. Plass-Johnson S.C.A. Ferse, and M. Teichberg. Field

sampling was conducted by J.G. Plass-Johnson and L. Weiland. Data analysis was conducted J.G. Plass-Johnson and the manuscript was written by J.G. Plass-Johnson with contributions from all co-authors.

Chapter VI – Recruitment and succession in the face of herbivory

Publication title - Experimental analysis of the effects of herbivory on recruitment and succession of a coral reef system along a water quality gradient: the Spermonde Archipelago, Indonesia

Plass-Johnson JG, Heiden JP, Abu N, Lukman M, Teichberg M

In revision with *Coral Reefs*

In Chapter VI, we conduct a four month long experiment examining benthic community recruitment and succession, accompanied by herbivore exclusion, along three islands of the water gradient. Open benthic space is extremely limited on coral reefs, and colonisation is often determined at the earliest moments after being cleared. With this experiment we provide insight on how recruitment and succession can change in relation to changing water quality and changing herbivore communities. This study is one of the first using ambient environmental conditions to examine variation in benthic community recruitment and succession, while experimentally altering herbivory.

Contributions: This project was initiated by J.G. Plass-Johnson, J. Heiden and M. Teichberg. The experimental design was developed by J.G. Plass-Johnson and J. Heiden. Sampling was conducted by J.G. Plass-Johnson, J. Heiden and N. Abu. Data analysis was completed by J.G. Plass-Johnson and J. Heiden and the manuscript was written by J.G. Plass-Johnson with improvements from all contributing authors.

Section Four. Theoretical links in the coral reef system

Chapter VII – Coral bleaching

Publication title - Coral Bleaching

Plass-Johnson JG, Cardini U, Hoytema N, Bayraktarov E, Burghardt I, Naumann M, Wild C

Published in *Environmental Indicators* (2015)(eds Armon R, Hanninen O). Pp. 117-146. Springer, Heidelberg, New York. doi: 10.1007/978-94-017-9499-2_9

Coral bleaching is a major cause of coral reef decline at the global scale, and this phenomenon also impacts the regenerative capacity of coral reefs experiencing heavy local scale degradation. In Chapter VII we examine both the indicators that signify the onset of coral bleaching and also indicators that might allow for the elucidation of past bleaching events. This is the first review of indicators associated with coral bleaching, providing a comprehensive overview of impacts from the level of the organism to the system.

Contributions: C. Wild, R. Armon and R. Hanninen initiated this review. The initial composition of the manuscript was decided by J.G. Plass-Johnson and C. Wild while subsequent management and editing of content was handled by J.G. Plass-Johnson. Individual authors were responsible for subsections and J.G. Plass-Johnson was responsible for the subsection “Coral susceptibility and resilience to bleaching and subsequent reef degradation”.

Chapter VIII – Niche utilisation

Publication title - Cross-shelf variation in the trophic niche of two important herbivorous coral reef fishes, *Chlorurus bleekeri* and *Dischistodus prosopotaenia*

Plass-Johnson JG, Bednarz VN, Ferse SCA, Teichberg M

In preparation for *Coral Reefs*

Variation in the coral reef habitat at islands along the on-shore off-shore gradient indicates that the associated fish community must vary their habitat use in order to persist. In Chapter VIII we examine the trophic niche of two herbivorous fishes that were observed to be present at most of the examined sites. Here we show, under changing habitat and competitors, that these two species may change their food source, however their net trophic niche, and thus habitat use, does not change. This is the first study to examine the isotopic trophic niche of coral reef fishes along a spatial gradient of a changing habitat.

Contributions: This study was initiated by J.G. Plass-Johnson. The experimental design was conceived by J.G. Plass-Johnson and V.N. Bednarz. Field sampling was conducted by J.G. Plass-Johnson and V.N. Bednarz. Data analysis was completed by J.G. Plass-Johnson and the manuscript with completed by J.G. Plass-Johnson with contributions from all co-authors.

Chapter IX – Environmental impact and the functional composition of fish communities

Publication title - Non-random variability in the functional composition of coral reef fish communities along an environmental gradient

Plass-Johnson JG, Teichberg M, Husain AAA, Taylor M, Ferse SCA

In review with *Ecology*

Variability in the composition of an assemblage has been recognised as a symptom of environmental stress. However, changes to a habitat would act upon traits of the organisms of the community and not just their species identity. In Chapter IX we examine the variability of the trait-based functional composition of fish communities at seven islands along the environmental gradient. This study provides insight into the mechanisms that drive change in fish communities. Furthermore, this is the first study examining variability in the trait-based functional composition of a community in relation to environmental degradation.

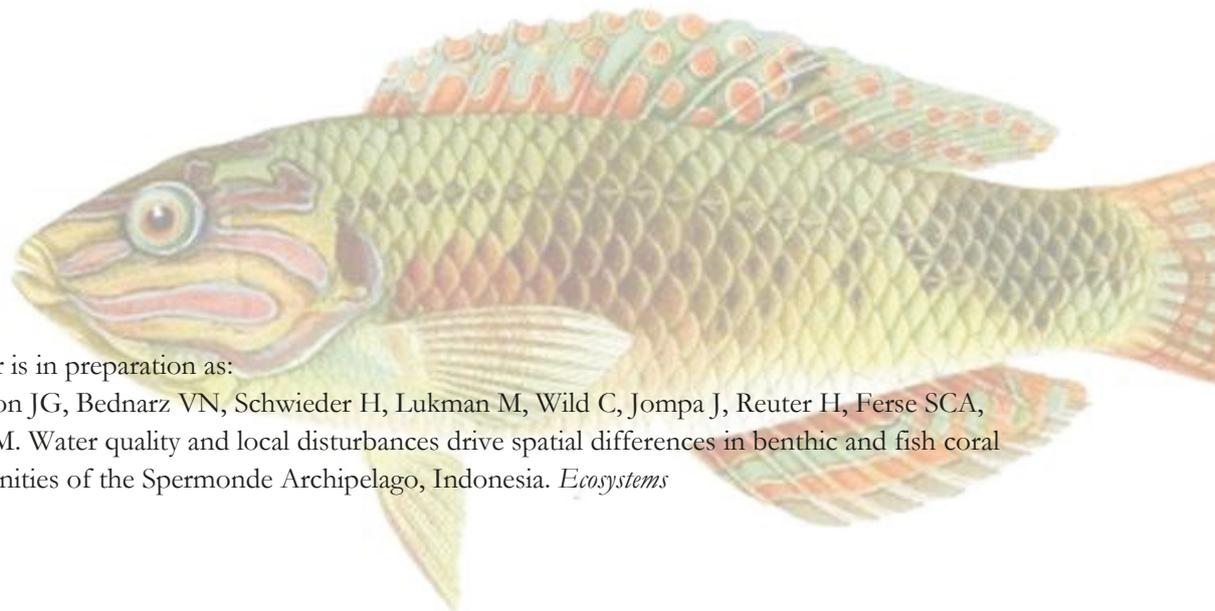
Contributions: This study was initiated by J.G. Plass-Johnson and S.C.A. Ferse. The experimental design was conceived by J.G. Plass-Johnson and S.C.A. Ferse. Field sampling was conducted by J.G. Plass-Johnson. Data analysis was done by J.G. Plass-Johnson, S.C.A. Ferse and M. Taylor. The manuscript was written by J.G. Plass-Johnson with contributions from all co-authors.

Section Two

Observations of a disturbed coral reef system

Chapter I

A coral reef system and a cross-shelf, environmental gradient



This chapter is in preparation as:

Plass-Johnson JG, Bednarz VN, Schwieder H, Lukman M, Wild C, Jompa J, Reuter H, Ferse SCA, Teichberg M. Water quality and local disturbances drive spatial differences in benthic and fish coral reef communities of the Spermonde Archipelago, Indonesia. *Ecosystems*

Introduction

The functioning of oligotrophic coral reefs is based on the tight recycling of nutrients because the surrounding waters are depleted (Hatcher 1990, Cardini et al. 2014, Bednarz et al. 2015), and offer minimal import of new energy. Scleractinian corals are partially reliant on photosynthetic products from their zooxanthellae symbionts (Muscatine and Porter 1977). Subsequent accretion of carbonate by the host polyp results in the development of reef habitat for which all other coral reef organisms rely upon. These conditions are susceptible to change when abiotic conditions are altered. Coastal coral reef systems within close geographical range to highly populated urban areas are often highly impacted by land-based activities, resulting in increased nutrient inputs, sedimentation rates, and fishing pressure (Burke et al. 2011). Depending on the spatial distance of a coral reef to the coastal line, terrestrial effluents can act as a point source where reefs closest to shore receive most of the export and those further away receive the least (Fabricius 2005). Terrestrial effluents can increase near-shore nutrient levels and this reduces nutrient limitations of primary producers (Jessen et al. 2015). However, the production of particulate organic matter (POM) is also often increased which affects light attenuation due to suspended material (Fabricius 2005). The effects of terrestrial derived gradients in coastal marine waters across coral reefs have been noted in many parts of the world (Edinger et al. 1998, Fabricius et al. 2005, Lirman and Fong 2007). Their effects are generally related to reduced scleractinian coral fitness and greater competition of benthic space between corals and other organisms (Fabricius 2005). Coral reefs closer to shore are generally characterised by less hard coral abundance, an increase in fleshy algae, and a decrease in coral and fish species diversity or even complete shifts in the sets of species (Fabricius et al. 2005).

Spatial gradients of water quality do not affect reefs in a discrete fashion, rather gradual changes in water dynamics along a gradient will expose reef organisms to gradually changing abiotic conditions. This increased stress which may act as a filter on benthic communities, as only organisms with the physiological capacity to adapt may persist within the community, resulting in a gradual taxonomic change (Smith et al. 1981, Edinger et al. 1998, Fabricius 2005). The relationship between water quality and benthic composition may become confounded in areas where people have a heavy reliance, and thus impact, on coral reef resources. For instance, dynamite fishing may result in reduced coral cover beyond the impacts of the terrestrial derived effluents (Pet-Soede and Erdmann 1998a). This in turn could impact the fish species that rely on live coral cover (Alvarez-Filip et al. 2011), while other species may benefit from the new habitat structure (Öhman et al. 1997). Additionally, locally derived waste from a populated island may increase nutrient levels on the local reef, and result in increased algal abundances which in turn, may attract more herbivorous fish species (Nash et al. 2015). Similarly, patchy fishing practices would also decrease fish abundance and species diversity despite the habitat status or structure.

This has become a common issue in the Southeast Asian region where densely populated urban areas result in lowered coastal water quality and sometimes extreme coral reef resource extraction (Burke et al. 2012). Hook-and-line, gill nets, trawling, dynamite and cyanide fishing techniques can have varying consequences to the coral reef system, however the stress on the ecosystems can be facilitated if human communities also occur on reef derived islands. In the Spermonde Archipelago of Southwest Sulawesi, Indonesia, island human populations also rely on nearby coral reefs for housing material leading to the mining of coral and sand from the local coral reef systems (De Voogd and Cleary 2007). Also, these small populations, ranging from a few to 1000s of inhabitants, generally have minimal waste management facilities, resulting in vast dumping of waste materials into surrounding waters (JPJ, SCAF pers. obs.).

Mitigating the impacts that affect coral reefs can only be accomplished once the source of the impact has been identified. Thus, discerning the effects on coral reefs based on land derived water quality changes or from locally based marine resource use, may help in the management of these perturbations. In the current study, we use a populated archipelago off the city of Makassar, Indonesia to explore variations in coral reef habitats in relation to differing stressors. The city of Makassar has a population of 1.5 million people and effluents originating from the city have been shown to affect the archipelago to varying degrees. Near shore islands (up to 7 km off shore) are exposed to high sedimentation, aquaculture outflow and wastewater from fluvial discharge of the nearby rivers, while midshelf (7-13 km off shore) reef are impacted by effluents during the onset of the monsoons (Moll 1983a, Renema and Troelstra 2001). Finally, offshore islands (> 13 km) are exposed to effluents only during the strongest rains or not at all. Benthic communities (Becking et al. 2006), and sponge and corals have shown strong on-shore to off-shore patterns in diversity (Edinger et al. 2000c, Cleary et al. 2005, Cleary and de Voogd 2007). The importance of other non-water quality based impacts are often noted for causing excessive loss in diversity (Edinger et al. 2000c, 2000b) while bomb fishing has caused excessive, yet patchy impacts in live coral and fish density loss (Pet-Soede et al. 1999, 2001b, Sawall et al. 2013).

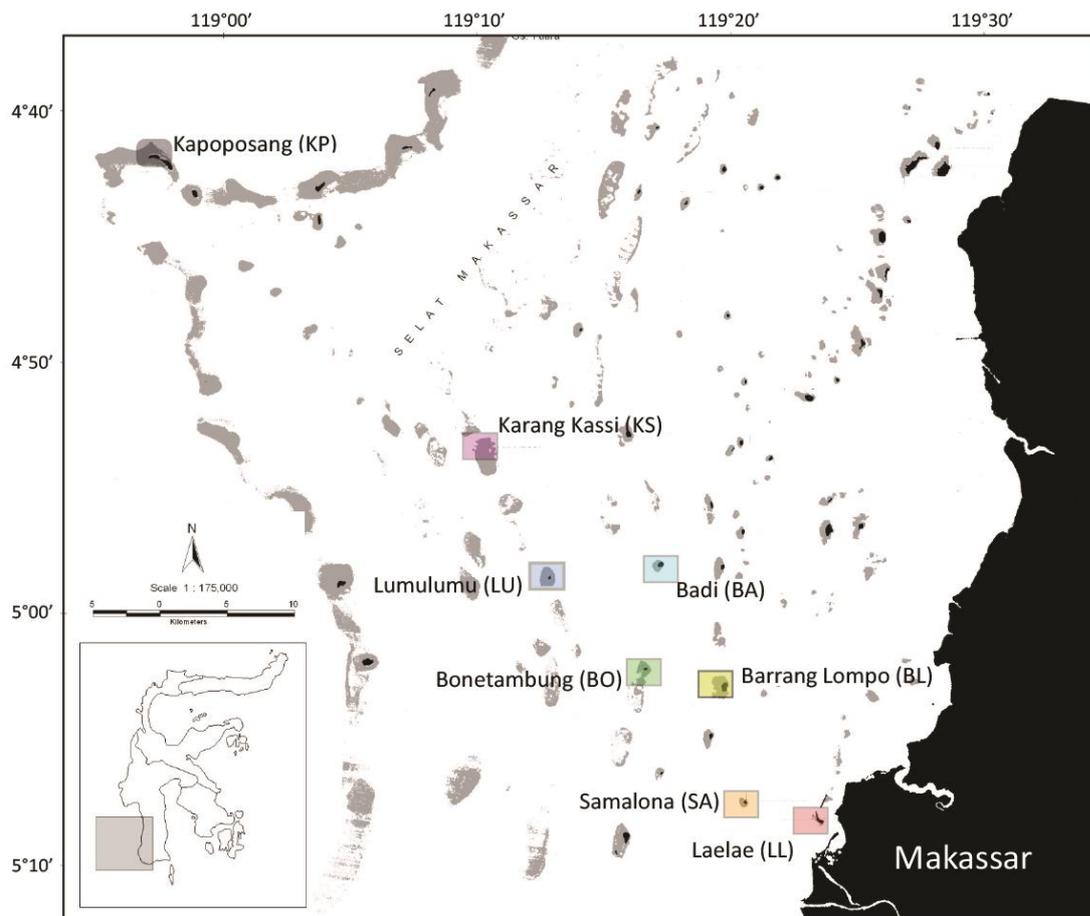


Figure 1.1. Map of the Spermonde Archipelago, Indonesia indicating the sampling sites. Colours correspond with subsequent figures.

In this study, we use a two-step process to identify variation in coral reef benthic and pelagic communities of the Spermonde Archipelago in relation to a spatial gradient in distance from shore. We assume that some of the observed patterns in the communities are a result of differences in water quality, while further variation can be accounted for by other non-water quality based disturbances (e.g. local fishing practices, anchoring, island derived nutrients). Firstly, we test if water quality is associated with distance from shore, and if a decrease in water quality is associated with a decrease in live coral and structural complexity. We hypothesise that variation in benthic attributes not explained by water quality may be linked to other sources of perturbations such as coral mining and bomb fishing. Secondly, we test if a decrease in live coral and structural complexity coincides with a decrease in fish species diversity or abundances. As benthic composition and complexity provide habitat for fish, we also test for changes in fish trophic composition associated with benthic composition. With this two-step approach, we first identify the dominant source of impact on the benthic communities, and then see if this impact is carried through to their associated fish assemblages.

Methods and Materials

Study Sites

This study was conducted across three consecutive years during the same annual dry season of the Spermonde Archipelago, Indonesia. The first sampling campaign occurred between the 20th of September and the 11th of October, 2012. The second sampling was between the September 22nd October 1st, 2013, and the third sampling was between the 16th and 29th of November, 2014. Eight islands were chosen with increasing distance from the city of Makassar (Fig. 1.1). In order of increasing distance from shore, with distance in brackets, the islands included Laelae (LL; 05°08S, 119°23E, 1 km), Samalona (SA; 05°07S, 119°20E, 7 km), Barrang Lompo (BL; 05°02S, 119°19E, 11 km), Bonetambung (BO; 05°01S, 119°16E, 14 km), Badi (BA; 04°57S, 119°16E, 19 km), Lumu Lumu (LU; 04°58S, 119°12E, 22 km), Karang Kassi (KS; 04°53S, 119°09E, 27 km) and Kapoposang (KP; 04°41S, 118°57E, 55 km distance) (Fig. 1.1).

All islands are located on the continental shelf and, apart from KP, all islands experience similar oceanographic conditions with respect to wave exposure and currents. KP was the only site which differed; located on the edge of the continental shelf, this site is exposed to deep oceanic waters, and stronger waves and currents. The northwest corner of each island (except KP) was used to standardise the sampling sites among reefs. The western coast of the islands generally features a well-developed, carbonate fore-reef and a sandy back-reef and flat. The reef crest was shallow (~3 m) and the slope reaches down to 15 m. The last study site, KP, was located on the reef edge above the outer continental shelf wall (Fig. 1.1). Work at KP was conducted at the northeast side of the island at the edge of the carbonate shelf because this area displays the highest level of reef accretion.

At each site, three 50 m permanent transects were installed where all subsequent water, benthic and fish data were collected. Transects were standardised at 2 m below the reef crest, which for each site fell between 4 and 5 m depth at low tide. Transects were separated by 10 m, and the beginning and end of the transects were marked with steel rebar to provide attachment points for the transect tapes. All work, including water samples, and benthic and fish surveys were conducted during one day at each site. Work was started at a standardised time each day (08:00h); weather was always sunny and dry with minimal wave energy.

Chapter I

Water parameters

All water quality parameters including particulate organic matter (POM), ammonium (NH₄⁺), nitrate + nitrite (NO_x), phosphorus (PO₄³⁻), chlorophyll-a (Chl-a), dissolved organic carbon (DOC), dissolved oxygen (HDO), salinity and light attenuation (K_d) were collected during the three primary sampling campaigns (see *study sites*), however two complimentary samplings occurred during the first week of February 2013 and the first week of June 2014. This data helped to identify differences in water conditions among the islands during the wet season providing a better representation of water quality dynamics among sites. Water samples were collected in six replicates from the same depth at the permanent transects. Salinity and Chl-a data were logged with a Eureka Manta logger (GEO Scientific Ltd.) recording at two minute intervals. K_d was calculated from underwater light profiles taken with a light meter (LiCor Li-192SA, Lincoln, USA), where:

$$K_d = \ln [Ed_{(z_2)}/Ed_{(z_1)}] * (z_1 - z_2)^{-1}$$

Ed_(z₂) and Ed_(z₁) are measurements at 0.05 m (z₁) and 4 m (z₂) below the surface (Kirk 1994).

Benthic community assessment

Benthic communities were quantified with 50 photographic quadrats per 50 m transect. Photographs were taken at 1 m (standardised with a measuring pole) above the substratum, every 2 m along each transect. At every second metre, a photograph was taken on both sides of the transect tape, with a section of the tape within the picture, to identify total area of the picture. Analysis of the pictures was conducted with Coral Point Count with Excel extensions (CPCE; Kohler and Gill, 2006) analysed with fifty randomised points (based on results from power analysis) per photograph for the following biotic groups: ascidians, sponges, soft corals, crustose coralline algae (CCA), other invertebrates, cyanobacteria, macroalgae, turf algae, live hard coral. To compliment this, surface structures was also quantified despite the biotic growth. These groups included sand, rubble and pavement, with the latter defined as any hard surface. Rugosity was the last measurement of the benthic habitat, and this was assessed with the linear distance-fitted chain method (Risk 1972). The chain length used was 20 m, and measurement was conducted once per transect, starting at the first 10 m point. Lastly, morphology of the live coral was also recorded. The selection of benthic groups and coral morphologies was based on English et al. (1997).

Fish surveys

Visual surveys of fish species were conducted within 2.5 m either side of the permanent transects. All fish species >3 cm were counted and their size estimated to the nearest cm. Cryptic fishes were not recorded because accurate counts and identification could not be guaranteed. Subsequent analyses of fish were based on trophic groups where each species was allocated based on the dominant constituent of its diet. Species identification and diets followed Allen & Erdmann (2012) and FishBase.org (Froese and Pauly 2011). Biomass of fishes was calculated from individual size observations using length-weight relationships obtained from Kulbicki et al. (2005).

Data analysis

Data were analysed in several steps to determine 1) the relationship between water parameters and distance from shore, 2) the direct effects of water quality on the status of the benthic communities, and 3) the relationships between the benthic and fish groups. Water parameters were correlated to distance from shore, and the parameters that significantly correlated with distance, based on a

significant Pearson's correlation coefficient, were subsequently normalised and reduced to one-dimension with a principal component analysis (PCA). Principle component one (PC1) then represented an artificial gradient of water quality based on distance from shore. Although all parameters retained for PC1 were collinear, the remaining variation helped to better define relative distances between the islands according to water condition.

Benthic data for each transect were collected each year over three years. We chose to focus our data analysis only on spatial differences across the Archipelago, therefore, benthic data for each transect were averaged across years. In order to relate the individual benthic (biotic and structural) groups to PC1 we used generalised additive models (GAMs). The fit of the models were checked with residual plots. These analyses identified specific benthic groups that varied spatially with the water gradient.

The last part of the analysis related benthic groups to the fish assemblages. Similar to the benthic data, fish data were averaged across years. Fish community indices (species richness, total abundances, and the slope and y-intercepts of the length distribution) and trophic groups were related to the benthic composition with hierarchical partitioning. Slope and y-intercept are community-aggregated data describing the fish size distribution and change depending on mortality rates (Graham et al. 2005). Steepening of the slope indicates a decreased number of large fishes or an increase in the number of small fishes while the y-intercept is relative to the abundance of the entire community (Trenkel and Rochet 2003). Benthic groups were included only if they accounted for

Table 1.1. Mean (\pm SE, below mean) water parameters at each of the sampling sites. Sampling sites (with acronyms) and distance to shore can be seen in Fig. 1.1. Parameters selected for PCA (Fig. 1.4) are highlighted in **bold** at their name. A significant correlation coefficient was interpreted at $p < 0.05$ (pearson's correlation coefficient (R) for $df = 6$: >0.70) and this is indicated in a **bold** R value. Water parameters include dissolved organic carbon (DOC), particulate organic matter (POM), chlorophyll-a (Chl-a), dissolved oxygen (DO), light attenuation coefficient (K_d), nitrite + nitrate (NO_x), phosphate (PO_4^{3-}), nitrogen to phosphate ratio (N:P), silicate (Si), temperature (Temp), pH and salinity.

Site		LL	SA	BL	BO	BA	LU	KS	KP
Distance (km)	R	1	7	11	14	19	22	27	55
DOC ($\mu\text{g/l}$)	-0.74	93.16	95.19	88.74	88.89	82.35	86.76	87.36	80.50
		4.72	4.61	3.20	2.36	2.67	1.50	2.07	2.22
POM (mg/l)	-0.71	11.84	5.19	5.04	4.89	5.09	4.80	4.48	4.20
		2.18	0.82	0.82	0.66	0.76	0.75	0.88	0.85
Chl-a ($\mu\text{g/l}$)	-0.73	1.47	0.43	0.52	0.34	0.44	0.42	0.29	0.26
		0.26	0.08	0.13	0.04	0.08	0.06	0.05	0.05
DO (mg/l)	0.59	5.94	6.04	6.51	6.57	6.28	6.52	6.32	6.80
		0.06	0.17	0.09	0.05	0.07	0.03	0.07	0.05
K_d	-0.76	0.36	0.19	0.27	0.23	0.20	0.20	0.17	0.08
		0.02	0.03	0.04	0.05	0.03	0.02	0.02	0.02
N:P	0.75	1.82	1.83	2.50	2.60	2.45	4.34	5.99	1.31
		0.43	0.40	0.43	0.57	0.37	0.87	0.76	0.26
NO_x ($\mu\text{g/l}$)	0.52	0.22	0.15	0.22	0.14	0.10	0.26	0.43	0.12
		0.05	0.03	0.04	0.03	0.02	0.04	0.05	0.02
PO_4^{3-} ($\mu\text{g/l}$)	-0.21	0.12	0.11	0.08	0.07	0.07	0.08	0.12	0.09
		0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01
Si ($\mu\text{g/l}$)	0.31	2.17	2.38	2.38	1.74	2.02	2.09	2.94	4.04
		0.23	0.48	0.38	0.15	0.19	0.18	0.35	0.93
Temp ($^{\circ}\text{C}$)	-0.85	30.31	29.99	29.96	29.23	29.84	29.12	29.08	29.71
		0.22	0.23	0.24	0.24	0.23	0.24	0.22	0.14
pH	0.03	8.16	8.17	8.18	8.19	8.19	8.18	8.15	8.20
		0.00	0.01	0.01	0.01	0.00	0.01	0.01	0.00
Salinity (ppt)	-0.18	33.72	33.41	33.66	33.60	33.50	33.62	33.57	33.22
		0.23	0.24	0.21	0.18	0.19	0.18	0.20	0.22

more than 5 % of the benthic composition with the assumption that most of the change observed in fish groups would be associated with the more dominant benthic groups. Analysis was restricted to only the dominant trophic groups to guarantee statistical applicability. The fish-benthic relationship was conducted in two stages with the first relationship based on primary biotic groups and the structural index rugosity. If live coral was a significant contributor to the variance of a fish assemblage, a second hierarchical clustering was performed on the fish group with the live coral subgroups describing coral morphology. These groups were mushroom, foliose, branching (including digitate and tablet) and massive (including encrusting) corals. Digitate and tablet corals were extremely rare and therefore were added to the branching group. Only encrusting coral growing on pavement was added to the massive group. When rugosity was significant, the fish group was then related to subgroups of structural complexity; sand, rubble, pavement. If both live coral and rugosity were significant, the fish group was then related to all subgroups. This two-step process provided greater clarity on the relationship between the fish and benthos than the basic one-step process. Statistical significance of hierarchical partitioning models was validated at the 5 % level via 1000 permutations of the data matrix.

All analyses were conducted in the R environment (Team 2013). GAMs were performed with the *mgcv* package (Wood 2011), hierarchical partitioning was performed with *hier.part* package (Walsh and MacNally 2008) and PCA was conducted with the *vegan* package (Oksanen et al. 2007).

Results

Description of spatial gradients in water quality, benthic and fish communities

There was a clear spatial gradient in many of the measured water quality parameters (Table 1.1). DOC, POM, chl-a, K_d , and temperature decreased with greater distance from shore (shown by significant Pearson correlation coefficients, Table 1). Although inorganic nitrogen and phosphorous concentrations were low in all sites and did not show a clear gradient with distance, the N:P significantly increased further from shore. DO was slightly lower in nearshore sites, but not significant.

A majority of the benthic groups were directly influenced by spatial gradients according to distance from shore (Fig. 1.2). The benthic community at many of the islands was largely dominated by turf algae with SA, BL and BO composing of ~50 % and then decreasing away from shore. At many of the islands, the second most abundant group was live coral. This group was lower in the first four islands and increased in the outermost four islands besides for KS. BO was particularly low only slightly higher than LL, the closest islands. The branching and massive coral groups were the most dominant morphologies however the spatial gradient by morphology was not as clear as overall live coral. Of the other benthic groups, macroalgae, CCA, sponge and cyanobacteria were generally low (<10 %), however general spatial trends could be seen with a decrease in macroalgae, and an increase in all the other groups with increasing distance from shore (Fig. 1.2). Spatial changes in the structural components of the sites, such as rugosity, sand, pavement and rubble, were also clear. Rugosity and pavement increased while sand and rubble decreased with increasing distance from shore (Fig. 1.2).

For fish, the most abundant trophic group was the planktivores (Fig. 1.3) with a clear trend of increasing total abundance with distance from shore. Greater species richness and lower slope greater was also associated with distance from shore indicating a more even distribution of size classes (slope, Fig. 1.3).

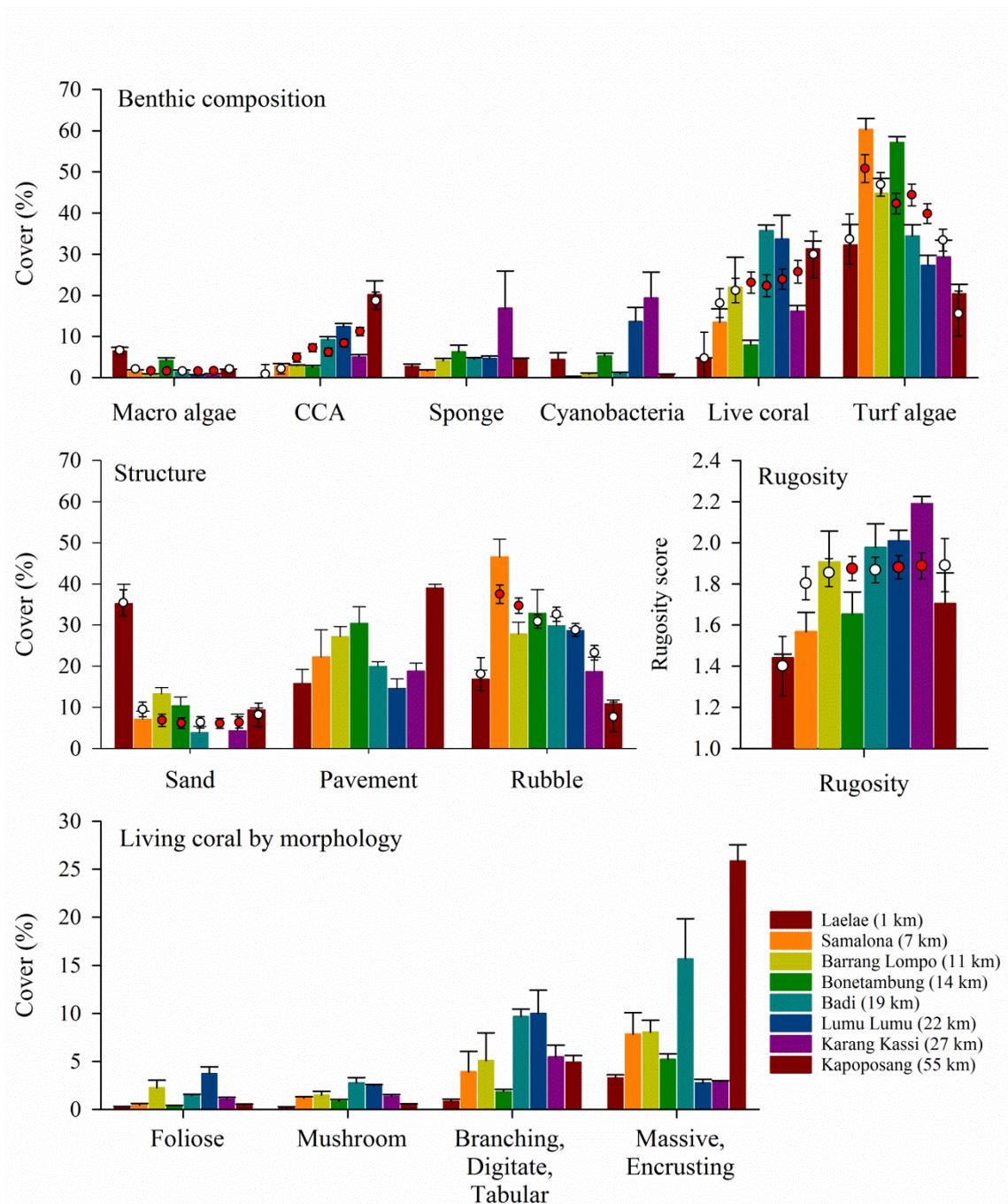


Figure 1.2. Mean (\pm SE) percent cover of primary benthic biotic groups, structural groups and coral morphologies. Circles represent the predicted values (\pm SE) of significant generalised additive models performed on the given benthic group and PC1 (Table 2). Red circles indicate a difference between the model and the observed value at that site based on differences in standard errors. GAMs were not performed on the coral morphological groups. Sites are ordered from left to right increasing in distance from the mainland.

Benthic group	Edf	Rdf	F	p	Dev. Expl
<i>Biota</i>					
Macroalgae	2	2	14.85	<0.001	58.6 %
CCA	2	2	20.05	<0.001	65.6 %
Sponge	2	2	1.03	0.38	8.9 %
Cyanobacteria	2	2	0.37	0.70	3.4 %
Live coral	2	2	4.87	0.02	31.7 %
Turf	2	2	11.35	<0.001	52.0 %
<i>Structure</i>					
Rugosity	2	2	4.64	0.02	30.6 %
Sand	2	2	34.64	<0.001	76.7 %
Pave	2	2	4.05	0.33	27.8 %
Rubble	2	2	21.14	<0.001	66.8 %

Table 1.2. Results from generalised additive models (GAMs) of relationship between PC1 of the environmental variables and benthic groups. Visualisations of the models are represented in Fig. 1.1 where red circles indicate significant differences between a site and the predicted model. Estimated (Edf) and residual (Rdf) degrees of freedom include a smoothing function. Significance, indicated in **bold**, was interpreted at alpha < 0.05. Dev. Expl. is deviance explained by the GAM.

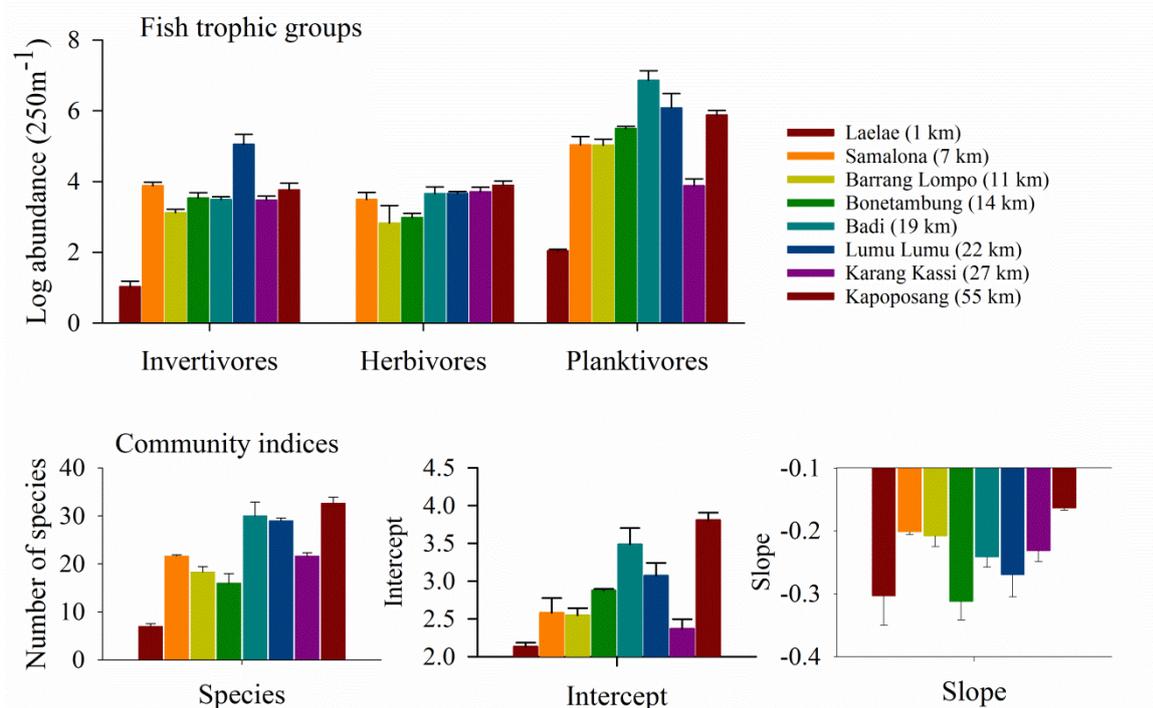


Figure 1.3. Mean (\pm SE) values of major fish trophic groups and community indices. Sites are ordered from left to right increasing in distance from the mainland.

Relationship between water quality and benthic composition

All water variables that correlated with distance from shore were used to determine the influence of water quality on the benthos using a PCA. This included DOC, POM, chl-a, K_d , and N:P. Although variation in temperature across the gradient was strong, its link to other water parameters was not clear and, thus, was dropped from the PCA analysis. Alternatively, although DO did not correlate significantly with distance, it was added to the PCA because it can be a parameter indicative of productivity in the water column and systemic eutrophication (Fabricius 2005). PC1 separated sites largely based on distance from shore (Fig. 1.4). However, LL separated much more from the other sites than what is indicated by distance alone (Fig. 1.1). Furthermore, BO and BA swapped in their order while KP was closer to the other islands compared to its spatial distance. Nevertheless, PC1 was used to represent a change in water quality where LL was the lowest and KP was the highest. A transition along PC1 from LL to KP, from low to high water quality was associated with a strong

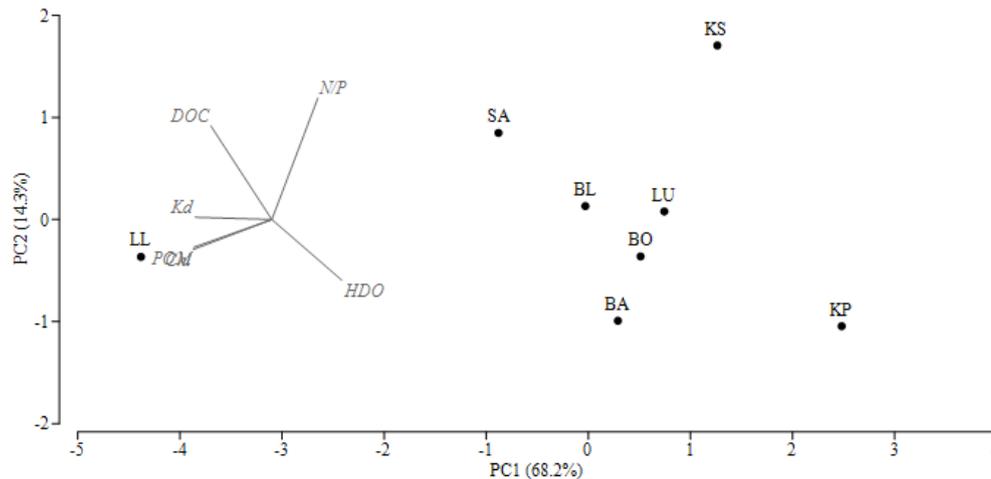


Figure 1.4. Principle component analysis performed on the water quality parameters that correlated with distance from shore (Table 1.1).

decrease in macroalgae and turf algae ($p < 0.001$), and a strong increase in CCA and moderate increase in live coral ($p < 0.02$) (Table 1.2 & Fig. 1.5). Increasing water quality was also associated with a moderate increase in rugosity and a strong decrease in sand and rubble (Table 1.2 & Fig. 1.5). Some of the primary trends were only realised after LL. For instance, turf algal cover was much lower at LL then increased significantly at the next site, SA, where it was the highest among the sites (Fig. 1.2 & Fig. 1.5). This was similar for rubble where LL had some of the lowest percentages among all sites (Fig. 1.2 & Fig. 1.5). Likewise, there was a clear relationship between turf algae and rubble after LL (Fig. 1.2)

Predicted (\pm SE) values were generated from GAM output for each benthic group, and these were compared with observed (\pm SE) values from individual sites (Fig. 1.2). A difference between the SE of the predicted and site values identified benthic groups of an island that did not fall within the predicted water gradient. Among sites, LL had a benthic composition and structure that was much different than the other sites. It had the highest macroalgal cover and the lowest CCA and live coral. Also, sand was the highest here while rugosity was lowest among all sites (Fig. 1.2). The next site increasing in distance from shore, SA, had more turf algae and rubble then was expected by the model and at BL rubble and macroalgae were lower than expected while sand was higher (Fig. 1.2). BO, the next site in order of increasing distance, had one of the most different benthic compositions (Fig. 1.2). Macroalgae and turf were higher than the expected while CCA and live coral were lower (Fig. 1.2). It also had more sand and lower rugosity than expected (Fig. 1.2). BA had lower than expected macro- and turf algae, high CCA and one of the highest live coral covers. Like BA, LU had low macro- and turf algae, high CCA and live coral, but the live coral consisted mostly of branching and foliose coral, but very low massive corals (Fig. 1.2). KS had much lower CCA and coral cover than the expected GAM model, and this space was in-turn occupied by cyanobacteria and sponge (Fig. 1.2). It had a rugosity that was higher than the expected model. KP had no benthic groups that were outside the expected, it did however have the highest CCA and live coral cover, along with the lowest turf algae and rubble, but a middle score in rugosity (Fig. 1.2).

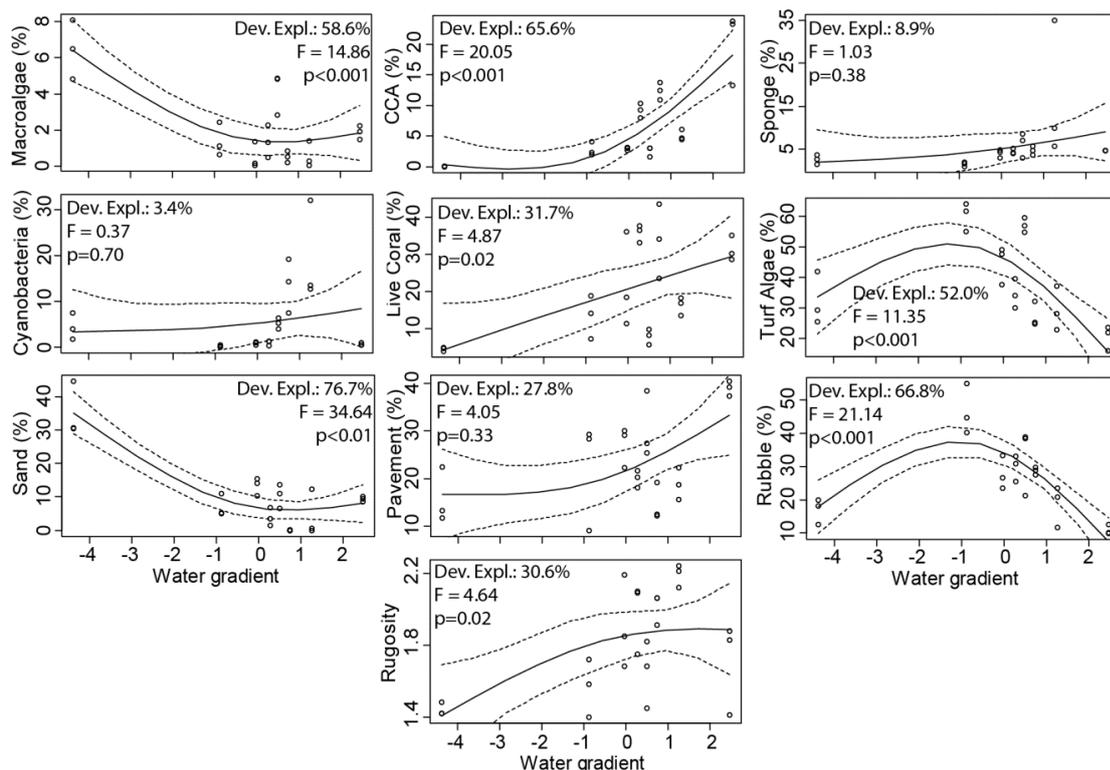


Figure 1.5. Results of generalized additive models based on the relationship between benthic groups and PC1 (Fig. 1.4). Significance was interpreted at $\alpha < 0.05$. Relationship of model output and benthic groups of individual islands can be seen in Figure 1.2.

Table 1.3. Effects determining the local status of reefs of the Spermonde Archipelago. Population are best estimates provided by JPJ, SCAF and J. Jompa.

Site	Pop.	Impacts	Year	Reference
Laelae	700	Harbour, sewage, sedimentation, industry	Continuous decades	for Edinger et al. 1998 Jompa 1996 Moll 1983 This study
Samalona	50	<i>Acanthaster planci</i> outbreak	2003	Baird et al. 2013
		<i>Acanthaster planci</i> outbreak	2003	Baird et al. 2013
		Pollution from the city	Continuous	See Lae Lae
Barrang	5000	<i>Acanthaster planci</i> outbreak	2012	Plass-Johnson et al.
Lompo		Intermediate bombing	Continuous	Pet-Soede and Erdmann 1998
		Coral mining	Continuous	JPJ pers. obs
		Localised pollution	Continuous	Moll 1983 JPJ pers. obs.
Bonetambung	2000	<i>Acanthaster planci</i> outbreak	2012	Plass-Johnson et al.
		Intermediate-high bombing	2010	Sawall et al. 2013
Badi	1000	No destructive fishing	2003	Jompa pers. com.
Lumulumu	1000	<i>Acanthaster planci</i> outbreak	2012	Plass-Johnson et al.
		Extensive bombing	Continuous	Pet-Soede and Erdmann 1998
Karang Kassi	0	Extensive bombing	Continuous	JPJ Pers.obs
		Sponge overgrowth	2012	JPJ unpub. data
Kapoposang	300	Partial reserve	2005	Jompa pers. com.

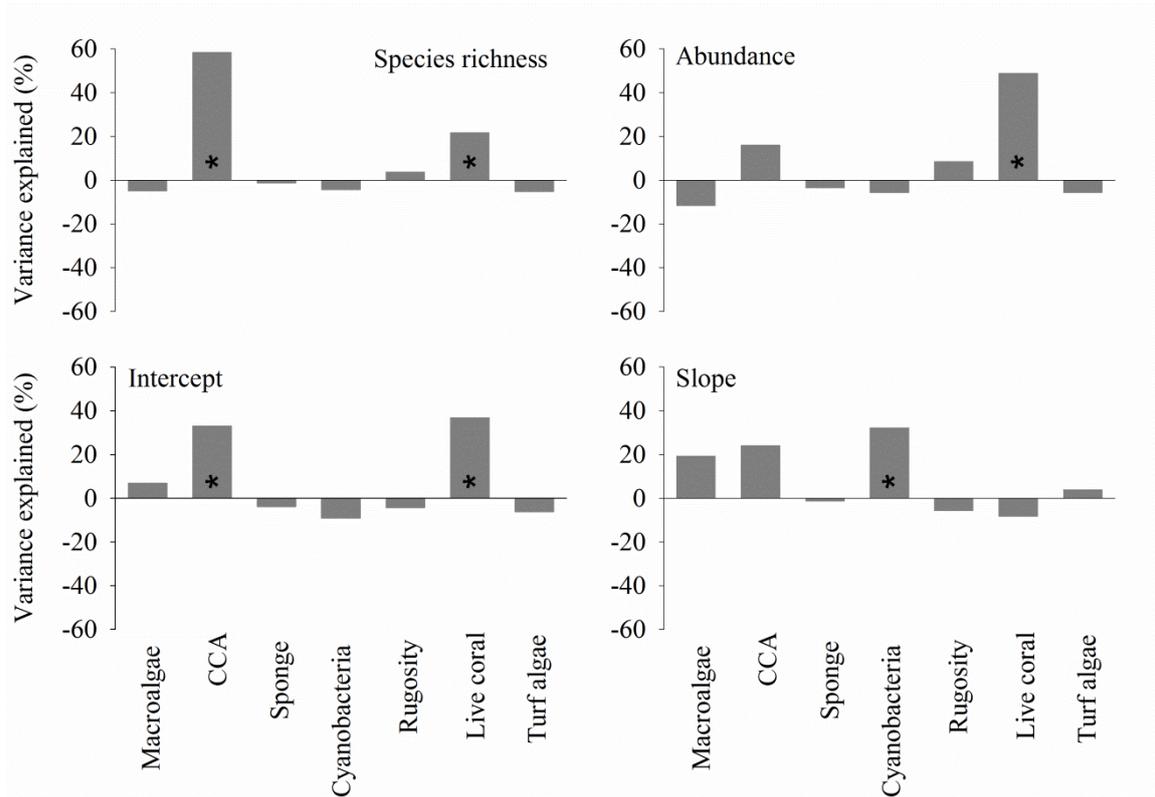


Figure 1.6. Results of the hierarchical partitioning analysis of the percent contribution of primary benthic biota on fish community indices. The direction of the bars indicate the direction of the relationship between the benthic and fish group as ascertained from draftsman plots. Significant relationships ($p < 0.05$) are indicated with an asterisk (*). When live coral was significant, the fish group was then related to coral morphologies (Fig. 1.7).

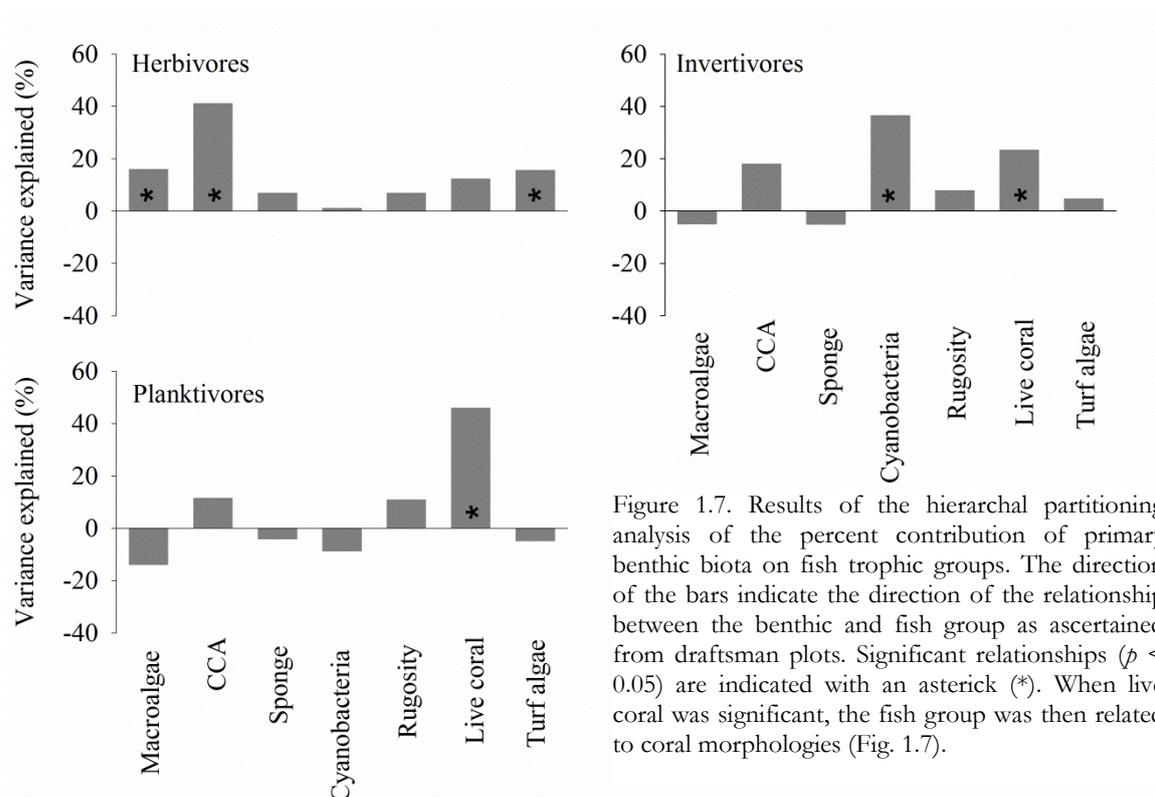


Figure 1.7. Results of the hierarchical partitioning analysis of the percent contribution of primary benthic biota on fish trophic groups. The direction of the bars indicate the direction of the relationship between the benthic and fish group as ascertained from draftsman plots. Significant relationships ($p < 0.05$) are indicated with an asterisk (*). When live coral was significant, the fish group was then related to coral morphologies (Fig. 1.7).

Relationship between benthic and fish communities

Fish communities were dominated by three trophic groups (planktivores, herbivores and invertivores) with piscivores and carnivores being nearly absent. All fish community indices apart from size structure slope were positively associated with live coral cover (Fig. 1.6). Species richness and intercept were also positively associated with CCA while slope was strongly, negatively associated with cyanobacteria (Fig. 1.6). Live coral cover was positively associated with planktivores and invertivores while the former was also positively associated with cyanobacteria (Fig. 7). Herbivores were significantly, positively, associated with both algal groups (turf and macroalgae) and CCA (Fig. 1.7). Surprisingly, no fish community indices or trophic groups were significantly associated with rugosity.

Species richness, abundance, intercept, planktivores and invertivores were all significantly associated with live coral, so subsequent analyses were performed on their association with coral morphological structure. In this, the massive morphology had the strongest influence on fishes with a significant association with all groups besides invertivores (Fig. 1.8). This was similar with the branching group where there were significant associations with all fish indices and trophic groups except for species richness (Fig. 1.8). The effect, however, was about half that of the massive group where the deviance explained was around 50 % and 25 % for branching. The other coral morphology groups were not significantly associated with fishes apart from the foliose group having a slight effect on species richness (Fig. 1.8).

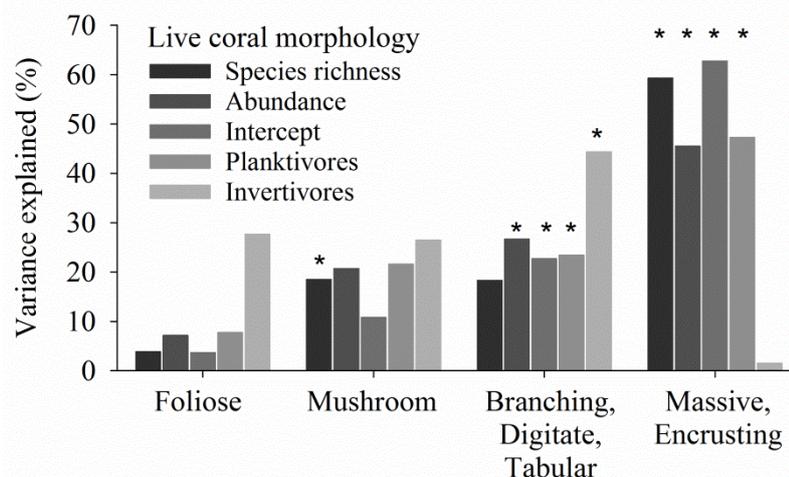


Figure 1.8. Results of the hierarchical partitioning analysis of the percent contribution of coral morphologies on fish indices and trophic groups. Fish indices and trophic groups were only analysed if live coral was significant in the first analysis. The direction of the bars indicate the direction of the relationship between the benthic and fish group as ascertained from draftsman plots. Significant relationships ($p < 0.05$) are indicated with an asterick (*).

Discussion*Relationships with the spatial gradient and between groups*

In the Spermonde Archipelago, evidence for a near-shore to off-shore gradient in water quality and subsequent effects on the benthic and pelagic communities were strong. Near shore benthic communities were characterised by proportionally much less live coral, higher amounts of sand, higher proportions of turf algae and lower structural complexity. Many of the factors changed predictably along the spatial gradient although variation of individual sites from the model estimates occurred in all benthic groups. Significant relationships between the water quality gradient (PC1) and

benthic groups indicate a strong influence of water quality; however, variations in cover of benthic groups at individual islands suggest additional impacts may also be playing a role in driving community structure. Furthermore, the benthic community, in particular live coral cover and crustose coralline algae had a strong effect on fish communities. These benthic groups varied with distance from shore but they also affected the species richness, abundance and trophic composition of the associated fish communities, indicating that fish communities are also indirectly impacted by changes in water quality related to distance from shore.

Water quality

Despite low inorganic nutrient concentrations and no clear spatial pattern among our sites, there was an indication of N limitation in nearshore reefs. It is hard to explain N:P ratios given that there was no clear pattern with actual nutrient levels, however water bodies near land masses used for agriculture, receiving P enriched fertilizers, generally show lower ratios (Bennett et al. 2001). Low nutrient concentrations may have been a result of up-take by both benthic and pelagic primary producers (Fabricius 2005). Chl-a has been used as a proxy for nutrient status in shallow reef waters with relatively low nutrient concentrations (Fabricius et al. 2005, Fabricius 2005). In our study, Chl-a concentrations were nearly two-times higher than near shore sites of the Great Barrier Reef (Fabricius et al. 2005) and five-times higher than the Florida Keys (Lirman and Fong 2007). These measurements were consistent with those taken from 1997 (Edinger et al. 1998) and 2010 (Sawall et al. 2011) indicating decades of exposure of the coral reef communities with contributions from fluvial export and intense urbanisation of the area (Erftemeier 1993). Furthermore, spatial gradients were also displayed in high DOC, POM and reduced water clarity (high K_d), all signifying eutrophic conditions at near shore sites; however the extremely high levels were only apparent at LL with SA, the next site, reflecting half the values in almost all water parameters. Our findings are consistent with previous suggestions that only the near shore sites are continuously exposed to terrestrial exports (Moll 1983a, Renema and Troelstra 2001). The next four islands (BL to LU) had intermediate Chl-a levels while the two outermost islands had levels five-times lower than LL. This was also reflected in the light attenuation where KS and KP had the lowest K_d values (high transparency).

Live coral and structural complexity

With the exception of two islands, live coral cover and structural complexity (rugosity) increased with distance from shore. With the former, there was no clear trend in the change of morphological composition of the corals with distance, although the branching group and the massive group were the most abundant groups. The early life stages of corals are particularly affected by water quality where settlement and growth is strongly impacted by organically enriched sediments (Babcock and Smith 2000, Fabricius et al. 2003). Furthermore, high sediment loads can smother, and stress established coral colonies (Stafford-Smith 1993). Coral recruitment at nearshore sites in Spermonde is low (Sawall et al. 2013) and established colonies must show a high level of trophic plasticity to survive at these sites (Sawall et al. 2011) dealing with the high levels of POM. Reaction of juvenile and established corals to decreased water quality conditions would suggest spatial gradients in coral species composition resulting in changing live coral cover. Moreover, at similar sites (Kanyangan 1 km from shore, SA, BL and KP, Edinger et al. 1998) a strong relationship of coral diversity and coral cover has been found with distance from shore. Scleractinian corals are the primary reef builders, and

given the strong correlation between live coral and rugosity in this study, it can be assumed that the amount of live coral at the sites contributed to spatial variation in rugosity.

Algae

One of the most cited phase changes on coral reefs is that from a coral-dominated state to a macroalgal-dominated state (Norström et al. 2009), which may occur after macroalgae are released from nutrient limitation and herbivores are overharvested (McCook et al. 2001, Hughes et al. 2007). In Spermonde, however, all islands were low in their relative cover of macroalgae. LL, the closest site to shore and most impacted site had the highest abundance of macroalgae, however this was still low relative to other sites where phase changes have been recorded (Bruno et al. 2009). Given the low herbivore biomass at LL, macroalgae may be controlled in-part by water conditions where high particulate matter both smothers algae and reduce light access. Abundances of herbivores were higher at the other sites and previous studies have shown adequate herbivore response to macroalgal transplantation (Plass-Johnson et al. 2015b, Chapter V) and further limitations occurring at the recruitment stage (Chapter VI).

Like many reefs around the world (McCook 2001, Vermeij et al. 2010b, 2012), turf algae are the most dominant benthic group of Spermonde. Except for LL, turf algae were highest close to shore and its relative abundance gave way to live coral with greater distance. From this data it is hard to discern the causality of the relationship between the two groups. Previous studies have shown that scleractinian corals are generally competitively superior for space to turf algae (McCook 2001, Vermeij et al. 2010b) however this seems to be species dependent (Vermeij et al. 2010a) when water conditions become eutrophic. McCook et al. (2001) found that *Porites lobata* took space from turf algae even at sites with the lowest water quality. *Porites* spp. was the most dominant taxa of the massive live coral group in Spermonde (JPJ pers. obs., Edinger et al. 1998) suggesting that live coral cover may react more to changes in water condition rather than directly to turf algae. If this proves true, this study along, with other previous studies showing robust macroalgal removal by herbivores may indicate a high level of resilience within the Spermonde ecosystem. Alternatively, Littler and Littler (2007) found an increase in turf algae when both nutrients and herbivory were low. Although Chl-a was high at near shore sites suggesting high nutrient input, the use of nutrients by phytoplankton would reduce N availability to benthic groups such as fleshy macroalgae. This, combined with low herbivory rates because of impacted herbivore communities may result in increased turf growth at near shore sites.

Near-shore sites of the Spermonde Archipelago are composed of higher proportions of rubble. Previous work has shown that reefs with high proportions of live, branching coral subjected to disturbance can result in the accumulation of rubble (Chong-Seng et al. 2014). However, percent cover of live coral in 2012-2014 were within a similar range of 20 years previous (Edinger et al. 1998) suggesting a continuous level of live coral however short temporal variation between these periods in live coral cover cannot be determined. The onset of acute disturbances are not rare in the Spermonde Archipelago (Chapter II & III, Baird et al. 2013) and may contribute to the accumulation of rubble, however the strong relationship between rubble and water conditions (Chapter I) suggest a water related cause. Nevertheless, rubble creates unsuitable substrate for settlement of most organisms perhaps favouring turf algae, thus providing the clear positive relationship seen between rubble and algae (Fig. 1.2 & 1.5) in Spermonde.

Fish

In the Spermonde Archipelago, live coral cover has strong effects on the fish assemblages. Higher abundances of massive and branching corals provide more habitat hosting more species and individuals. Interestingly, the length distribution (slope) of the fish assemblages was related to cyanobacteria and not live coral cover. This can be explained by greater chances of stochastic events during sampling at the more degraded sites (or those sites with more cyanobacteria). At these sites, an impacted habitat results in less small bodied, site-attached species but more mobile, larger individuals such as the wrasses (Chapter IX). Wrasses tend to be invertebrate feeding and this group was also related to cyanobacteria. The link between planktivores and branching coral seems intuitive with damselfishes relying on the high structure complexity of this coral group for habitat (Alvarez-Filip et al. 2011). The effect of crustose coralline algae (CCA) and fish may be best explained within the context of the positive association that this benthic group on reef structure. For example, CCA is the primary biotic group consolidating reef rubble and subsequently creating habitat for fishes (Rasser and Riegl 2002). The herbivore group was related to both algal groups (macro- and turf algae) indicating a higher reliance of the fish group on food resources than on habitat. This, however, should be seen within context of human resource use in Spermonde. Carnivores and piscivores were rarely seen in the surveys probably because of the high level of fishing pressure in the region. The removal of these groups would allow fishes of lower trophic groups to spend less time on predator avoidance and increase resource acquisition (Dulvy et al. 2004).

Site specific effects

Beyond the water gradient occurring from the mainland, the Spermonde Archipelago is subjected to a multitude of environmental stressors due to subsequent effects from water quality (e.g. *Acanthaster planci* outbreak) or from resource use supplying both local populated islands and for export. Many of the islands are populated (Table 3) with fishing as the primary employment (Pet-Soede and Erdmann 1998a, Ferse et al. 2012). Cyanide and bomb fishing have been practiced within the archipelago for decades (Pet-Soede et al. 1999) and continue through the current work (JPJ pers. obs.). Although these disturbances can target fish communities, often benthic communities are also impacted reducing habitat quality for new recruitment of fish communities. Here, we discuss differences in benthic and fish composition from the expected model across sites (Table 1.3) and link them to possible localised disturbances within the Spermonde Archipelago. Little historical quantitative data exists on the exact sites, but where available, we draw comparisons providing information on the direction of change in the coral reef communities.

Laelae

None of the benthic categories of Laelae fell outside of the expected model, however its highly degraded state resulted in its status being very different from the other islands. Subsequently, the benthic status of Laelae was one of the primary reasons that nonlinear models were used. Laelae's near-shore location results in continuous exposure to raw sewage and riverine effluents (Moll 1983b). Visibility was often less than a couple of meters and this is reflected in the high POM and K_d values. As such, the benthic community has been reduced to only those groups and species that are able to sustain with low light and high sedimentation. Laelae displays a high level of barnacle recruitment (Chapter VI), common for harbour substrates (Jones 1990). Also, this site had the highest

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composition of sand reflected export from the river but also the deposition of organic production in the water column. *A. planici* was recorded at this site in 2003 (Baird et al. 2013), however its impacts were not measured. Lastly, Laelae had the lowest fish abundance statistics in all community indices and trophic groups; more indications of the highly degraded state of this site.

Samalona

Samalona is only six kilometres from Laelae, and consists of a very different benthic composition compared to Laelae. Samalona has a small population that work at a resort hosting both Indonesian and international holiday makers. The resort restricts destructive fishing practices around the island (J Jompa Pers com). Nonetheless, its position near shore subjects it to relatively poor water quality conditions, particularly during the onset of the monsoon season where flooding of the rivers results in large amounts of pollution being introduced into the surrounding water (Moll 1983b, Renema and Troelstra 2001). As a result, benthic cover of sand is much lower than Laelae however rubble is much higher here than expected. This might be explained by a recent crown-of-thorns (*A. planici*; COTS) outbreak (Baird et al. 2013), however impact on the live coral community was not quantified. Further contributions to rubble development are probably caused by continuous exposure to low water quality resulting in increased coral mortality. The potential impact of COTS is serious (Chapter II), and differences in live coral cover since a previous measurement in 1997 suggest significant losses (Edinger et al. 1998). Given the poor water quality of the area of Samalona, recovery of the coral reefs may have been restricted to increases in turf algae. Nevertheless, restrictions on fishing around Samalona have helped fish communities here, as this site had relatively high abundances of herbivores and invertivores, and also, it had one of the highest average slopes (Fig. 4) indicating more large bodied fishes than other sites in the area.

Barrang Lompo

Barrang Lompo has one of the highest human populations of the Spermonde Archipelago with a dependence on fishing (Pet-Soede et al. 2001a) and also hosts a research station. Barrang Lompo falls outside the predicted models only slightly higher in sand and lower in rubble. A COTS outbreak was recorded here in 2012 (Chapter II) but most damage was seen on the reef crest. Coral mining is common with *Porites* sp. commonly used in the construction of buildings (JPJ pers. obs.). This would not be recorded with a low rugosity because often, larger *Porites* colonies are broken into smaller parts with pieces left behind. This maintains structural complexity despite the loss of live coral cover. Live coral cover was within the range of the model but it also had a high SE probably a result of patchy use of live coral as building resource (JPJ pers. obs.). Furthermore, live coral cover was between 40-50% in 1997 (Edinger et al. 1998) suggesting significant changes in the benthic community. Fish abundances and species richness at Barrang Lompo were relatively low, however a high population increases both benthic and pelagic resource use making the relationship between benthic and fish assemblages unclear.

Bonetambung

Bonetambung is 14 km from the mainland and perhaps one of the most impacted islands from other perturbations outside of the water gradient. Bonetambung has one of the lowest cover in live

coral, high abundance of turf algae and low rugosity. It is hard to entirely account for its degraded status, but its geographical position between two islands hosting high levels of bomb fishermen (BL and LU, SCAF and J. Jompa pers. comp.) indicate that it could experience a high frequency of bomb. Along with BL, BO also experienced a COTS outbreak in 2012 (Chapter II). BO experiences relatively high coral recruitment (Sawall et al. 2013) indicating that coral growth is restricted after successful recruitment. Fish communities are dominated by a few, small planktivore species suggesting depletion of the fish communities.

Badi

Badi has a small population composing mostly of hook and line fishers. Badi has been the focus of multiple projects marine management projects, both ecological of social, from the University of Hasanuddin (UNHAS). This has influenced a higher level of ecological awareness within the local community and as such, they have restricted destructive marine resource use for many years. Badi has one of the highest live coral covers of the islands, rich both in the massive and branching groups. This has affected the fish communities where species richness and abundances remain high. Furthermore, although piscivores were dropped from the analysis because of their very low occurrences, Badi was one of two sites (also KP) where they were regularly seen (JPJ pers obs). Previous studies displayed a rich and varied herbivore community during experimental transplantations of *Padina* and *Sargassum* (Plass-Johnson et al. 2015b) however, experimental exclusion of herbivores resulted in little differences in benthic recruitment between treatments and controls (Chapter IV), suggesting differing capacity between browsing and scraping herbivorous fish groups.

Lumu Lumu

Contrary to Badi, the reefs of Lumu Lumu have suffered from little management and a resident population consisting of many bomb fishermen. Live coral cover and rugosity remain relatively high here, however these measurements are deceiving as most coral is new growth on top of bombed, branching *Acropora*. The true status of the reef may be more reflected in the high level of cyanobacteria that has slowly increased through the years. Furthermore, some sites at LU lost > 30% of its live coral to COTS outbreak in 2012 (Chapter II). The fish community consists of large proportion of small bodied damselfishes, and wandering wrasses, but herbivores were rarely seen.

Karang Kassi

Karang Kassi is the only unpopulated site in this study. Without a population to oversee management of the reefs, this site suffers from wide spread bomb fishing (JPJ pers obs). Live coral cover is one of the lowest among all the sites and this has been replaced with cyanobacteria and encrusting sponge (Chapter III) with reports of the latter becoming the dominant benthic taxa at some sites (Chapter III). Rugosity remains relatively high, however similar to Lumu Lumu, this is reflected in the large composition of remnant *Acropora* rubble. Rubble does not come out proportionally high in our data due to the quantification technique where selection for sponge and cyanobacteria resulted in not identifying the underlying benthic structure. Fish species richness and

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abundances were low, however the slope was relatively high reflecting the proportionally high number of wrasses.

Kapoposang

Kapoposang was the site furthest site from shore and its location on the edge of the continental shelf suggests that water conditions are more representative of oceanic conditions rather than being impacted from Makassar. Kapoposang along with Badi retains a marine reserve which in practical terms results in reduced bomb and cyanide fishing, and not a dismissal of all fishing. Nonetheless, these restrictions have most likely helped the site retain one of the healthiest statuses, with high live coral cover and CCA, low turf algae and a lot of hard substrate for recruitment. The coral community is dominated by the massive group and this probably resulted in a relatively low rugosity score where rubble and branching corals would contribute greatly to distances laid in the chain. Fish species diversity and abundances are high at this site for the Spermonde Archipelago and a previous study showed a diverse and healthy herbivore community in response to algal transplantations (Plass-Johnson et al. 2014, 2015b). Moreover, restrictions on fishing have benefited the over-all length distributions of the community with Kapoposang having one of the highest slopes among all the sites.

Summary

Our study showed that terrestrial effluents can have a strong impact on the coral reef communities of the Spermonde Archipelago, but localised impacts such as fishing can further escalate habitat modification. Changes in the benthic composition resulted in changes in the fish communities. Generally, there was a proportional change in benthic composition with distance from shore, changing from live coral cover off-shore to greater turf algae near shore. Changes in the benthic community were consistent in direction with other studies (decreasing corals and increasing algae closer to shore) suggesting that the status of today's reefs are a product of decades of exposure to poor water quality and resource use. Furthermore, characterisation of the benthic and fish communities provides baseline information for future studies however it is clear that minimal levels of management can result in significantly benefit the coral reef communities. Analysing benefits to the fishing community is beyond the scope of this study but the status of Badi and Kapoposang suggest positive influences.

Chapter II

Acanthaster planci outbreak

This chapter has been accepted as:

Plass-Johnson JG, Schwieder H, Haiden JP, Weiand L, Wild C, Jompa J, Ferse SCA, Teichberg M. (2015) A recent outbreak of crown-of-thorns starfish (*Acanthaster planci*) in the Spermonde Archipelago, Indonesia. *Regional Environmental Change*. doi: 10.1007/s10113-015-0821-2

Abstract

A recent review of crown-of-thorns starfish (*Acanthaster planci*; COTS) in Indonesia has suggested their impacts have gone under-reported. In 2012-2013, we surveyed COTS at permanent transects within 12 sites of the Spermonde Archipelago, Indonesia, a coastal region close to two rivers and the heavily urbanised city of Makassar. Evidence of COTS was apparent at 8 of 12 sites surveyed with highest densities (37 starfish per 250m² at Barrang Lompo) comparable to those reported in the Indonesian historical literature. At Barrang Lompo and Bonetambung, the COTS outbreak resulted in the loss of half the live coral. Terrestrial effluents have reduced water quality in the Spermonde Archipelago, which further supports recent work linking water quality and COTS outbreaks, and thus providing a warning of future outbreaks to Indonesian coastal managers given the countries increased urbanisation.

Introduction

Acanthaster planci, or the crown-of-thorns starfish (COTS), is a significant threat to coral reefs in the Indian and Pacific oceans. Generally, COTS occur naturally in low abundances (<1 starfish ha⁻¹), however population outbreaks of COTS can occur rapidly and be devastating, possibly resulting in up to 80 % mortality of corals (Pratchett et al. 2014). Damage by COTS can result in the loss of structural complexity, biodiversity, and productivity of corals and the greater reef community (Kayal et al. 2012). Despite the destructive potential of COTS, a lack of observations on the development and progression of population outbreaks impede our understanding surrounding the ecological processes of these events.

A recent review by Baird et al. (2013) of COTS occurrences in Indonesia suggests a paucity of information for the Indonesian archipelago, the region with the highest marine biodiversity in the world. However, surveys in 2007 and a review of non-primary literature by Baird and colleagues indicate that COTS outbreaks have been substantial, at times causing more than 50 % loss of live coral. Due to a lack of awareness of the damage caused by COTS, their damage can be attributed to other destructive causes (e.g. bomb fishing, coral bleaching). Given this lack of information, greater reporting of COTS occurrences, and their contribution to coral loss, will assist stakeholders on the management of Indonesian reefs.

The aim of this study was to describe the temporal and spatial patterns of a recent COTS outbreak in the Spermonde Archipelago of Southwest Sulawesi, Indonesia in 2012-2013 with further discussion linking these observations to outbreak patterns described in the literature.

Methods and Materials

Abundance data for COTS were collected during three benthic surveys of the Spermonde Archipelago (4° 52' S, 119° 06' E), across one year. Permanent transects were installed on the reef crest and slope (parallel to crest transects) of 12 islands (Fig. 2.1), and they were visited in September 2012, March 2013 and September 2013. Transects were 50 m long and replicated three times at each site and depth. Initially, the transects were installed for monitoring benthic community condition. Survey location was standardised at the northwest corner of the islands because this region generally displays the greatest reef accretion (Moll 1983). Moreover, survey locations were decided *a priori* to the installation of permanent transects based on a site selection survey conducted in November 2011 by two of the authors (HS and SCAF). Observation of high abundances of COTS during the first survey resulted in the inclusion of counts of COTS and fresh feeding scars in the surveys. Live coral

composition was assessed with 50 photographic quadrats per transect, where 20 random points were identified per photograph. Live coral cover was defined as healthy coral showing no necrosis. COTS and scars were counted in an area of ± 2.5 m either side of the transect tape. Identified COTS feeding scars were only counted when freshly removed tissue, revealing white skeleton, was apparent. Furthermore, scars could be identified by their size and shape. Surveys were conducted using SCUBA which allowed for a thorough search for COTS, including the underside of overhangs and within coral thickets.

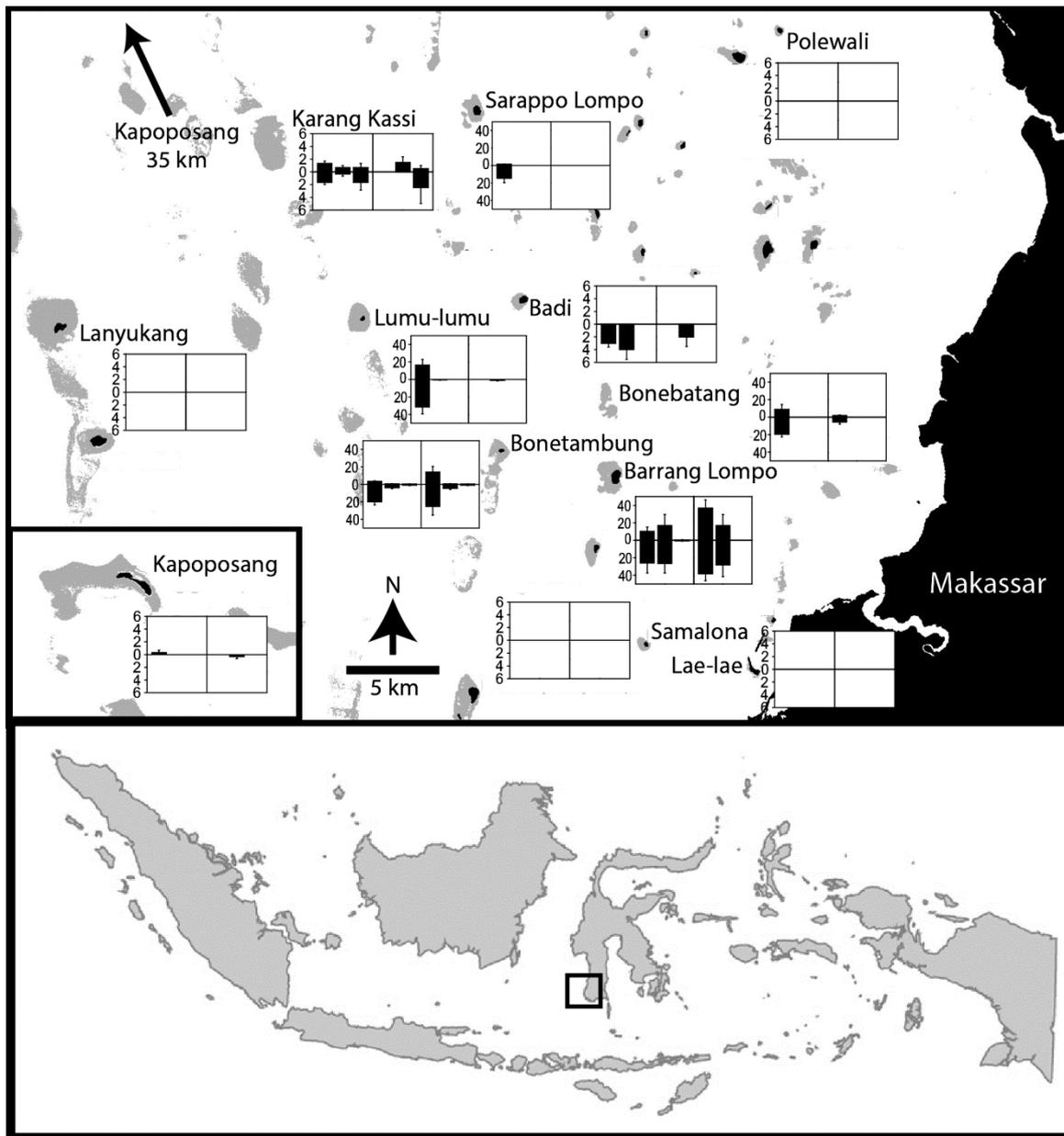


Figure 2.1. Map of the Spermonde Archipelago (top) and its location within Indonesia (bottom). Data represent the mean starfish abundance (\pm SE) per survey (top boxes) and number of feeding scars (bottom boxes) on the slope (left boxes) and crest (right boxes). The three bars within a box indicate sampling time starting with the earliest on the left (September 2012) and latest on the right (September 2013). The absence of data for some sites of surveys indicates that there were no COTS present during the surveyed period. Note the different scales on the y-axis (mean starfish abundance).

The impact of COTS on live coral cover was calculated at the individual transect, where the percent loss of coral cover between each survey period, calculated as rate per month, was correlated with the observed COTS abundance of the previous survey. They were also related to the initial coral cover of each period to identify whether COTS abundances were affected by the availability of food resources. Data points represent only sets of transects with an average observed COTS abundances greater than five 250m² because this corresponds to the density of an outbreak (Pratchett et al. 2014). The relationship between COTS and the lost coral cover can help to identify the potential impact of COTS on coral communities in the Spermonde Archipelago. Survey results for COTS densities are presented at our scale of measurement at the transect level (250m²), but further discussion is scaled to 200m² for ease of comparison with other studies.

Results

Evidence of COTS activity was recorded at 8 of the 12 sites, with live COTS documented at 5 sites (Fig. 2.1). All of the sites with evidence of COTS, besides for Kapoposang, were located in the central region of the archipelago (Fig. 2.1). There were generally more live COTS and scars during the first and second survey. With the exception of Barrang Lompo, Bonetambung and Karang Kassi, evidence of their presence had completely disappeared by the third survey (Fig. 2.1). Differences between the slope and the crest were minimal; however, Sarappo Lompo showed 14.7 ± 5 (mean \pm SE 250m²) scars on the slope in the first sampling, with no evidence of COTS presence on the crest.

The highest COTS density was found at the reef crest in Barrang Lompo during the September 2012 survey (36.7 ± 9.5 starfish). Barrang Lompo also exhibited the highest abundances during the second sampling (slope 17.0 ± 11.5 ; crest 17.2 ± 12.5 starfish). The slope at Lumu-lumu had $16.3 (\pm 6.3)$ starfish during the first survey and Bonetambung had $14.3 (\pm 5.3)$ starfish on the crest during the second survey. Anecdotal evidence suggests that coral predation was not species-specific (Fig. 2.2A-F), and COTS abundances could be extremely high within a relatively small area (Fig. 2.2F).

The sets of transects where more than an average of five COTS were observed included the crest of Bonetambung in 2012, the crest and slope of Barrang Lompo in 2012 and early 2013 ($n = 6$) and the slope of Lumu-lumu in 2012. There was a general correlation between coral cover, starfish abundance, and coral mortality (Fig. 2.3), with the latter reaching 10-20% per month. Fewer than 12 individuals of COTS resulted in less than 7 % coral loss per month while coral mortality with > 12 individuals was highly variable resulting in 7 to 20 % loss of coral per month (Fig. 2.3). No COTS were seen in the final survey even though some transects still retained 15% coral cover. Because our observations were confined to the fixed plots, we cannot exclude movement of the starfish to patches of higher coral cover.

Discussion

Baird et al. (2013) recently brought to attention the under-reporting of *Acanthaster planci* outbreaks in Indonesia, despite the severe impact on live coral that they can have. The surveys of Baird and colleagues found abundances from one to 5.2 individuals 200m², and their supporting review of historical Indonesian literature revealed outbreaks of ≤ 26 individuals 200m². Direct comparison of the present data with that of Baird et al. (2013) is difficult due to differing survey methods, however standardisation of data from Barrang Lompo during the peak observed outbreak (29.4 ± 5.1 starfish 200m²) indicates COTS densities in the range of the worst historical outbreaks. Furthermore, these numbers are similar to those reported for Moorea, French Polynesia (30.3 ± 6.1 starfish 200m²,

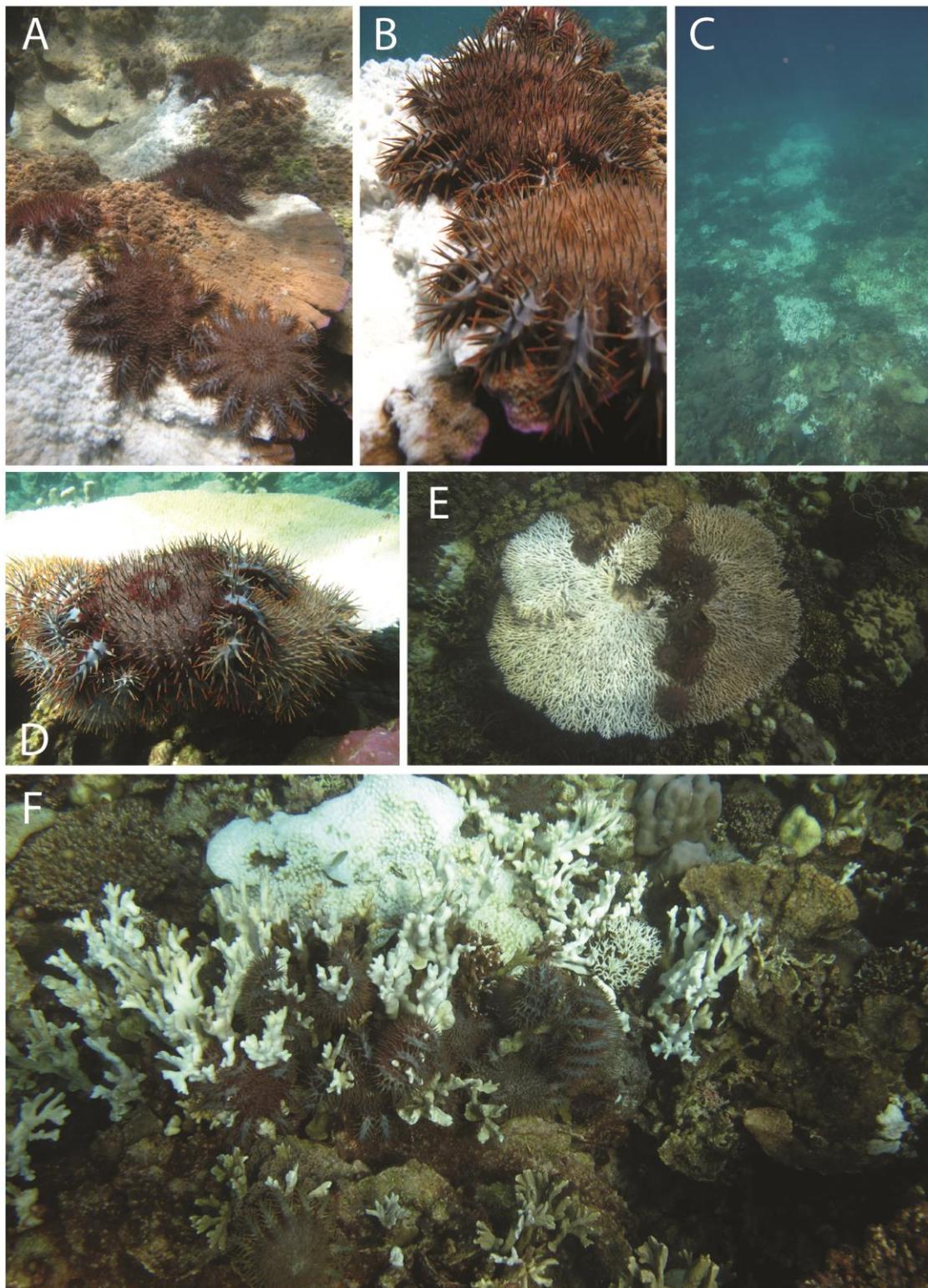


Figure 2.2. Crown-of-thorns activity at Barrang Lompo (A, D and F), Bonetambung (B and E), and Lumulumu (C) recorded during the September 2012 survey. At Barrang Lompo, COTS were observed feeding on multiple genera of coral in very high densities. Eighteen starfish were observed feeding in roughly 2 m² at Barrang Lompo (F). C shows a track, approximately 20 m long, of fresh feeding scars left by COTS in September 2012.

Kayal et al. 2012) between 2004 and 2010, an outbreak recorded as the most intense disturbance of that reef in 40 years of monitoring, and one of the largest reported outbreaks in the last decade. Furthermore, this outbreak resulted in > 90 % live coral loss.

It is important to note that the outbreak in our study had all but completely disappeared within one year. During the first survey, Barrang Lompo, Bonetambung, Lumu-lumu, Karang Kassi and Bonebatang all had COTS present, but by the second survey this was reduced to only two sites. By the third survey, all indications of COTS, including scars, were completely absent with the exception of a few starfish and scars at Karang Kassi. Previous observations have identified outbreak durations of roughly one year (Pratchett et al. 2009), while at other locations outbreaks have lasted for years (Kayal et al. 2012), even occurring cyclically (Pratchett 2005). In a survey of 180 m² of reef at Barrang Lompo in late 2011 (Muller et al. 2012) and a coarse but extensive (over 1 km length) survey by two of the authors (HS and SCAF) at the same time, no observations of COTS were reported, suggesting that our surveys may have identified the beginning of the outbreak, although individual animals in other sections of the reef may have remained undetected by the earlier survey. Anecdotal observation by the lead author (JPJ) of a considerable number of starfish at Barrang Caddi, an island 4 km from Barrang Lompo, during the last survey (September 2013) suggests that COTS continued to persist in the archipelago.

The damage caused to live coral by the starfish was considerable, and this was apparent at both Barrang Lompo and Bonetambung. Individual transects on both islands lost up to half their coral cover between the first and last survey. Unfortunately, our surveys were spatially confined to the permanent transect so we could not track further movements of COTS to areas retaining high levels of coral cover. Although there are many potential drivers affecting coral reef degradation in Indonesian, careful observation indicates that the damage observed in this study was most likely caused by COTS. Similarly, Baird et al. (2013) found > 50 % mortality of acroporids in seven of their 16 sites where COTS were present. Two of their sites, Samalona and Lae-lae (referred to as P. Semolina and P. Lele in Baird et al 2013) were included in our study. Baird et al. (2013) observed COTS activity at both islands, and they report that more than half of Samalona was affected. During our study and an earlier visit in late 2011, COTS were never present, nor was there evidence of their feeding at either site. However, both of these sites have the lowest live coral cover of the surveyed archipelago (JPJ unpublished data) suggesting unsuitable conditions for the starfish. It is not clear whether the current status of Samalona and Lae-lae is a product of the outbreak observed by Baird

and colleagues or due to other confounding factors such as high sediment loads and nutrients coming from nearby rivers and the city (Edinger et al. 2000) impeding coral growth.

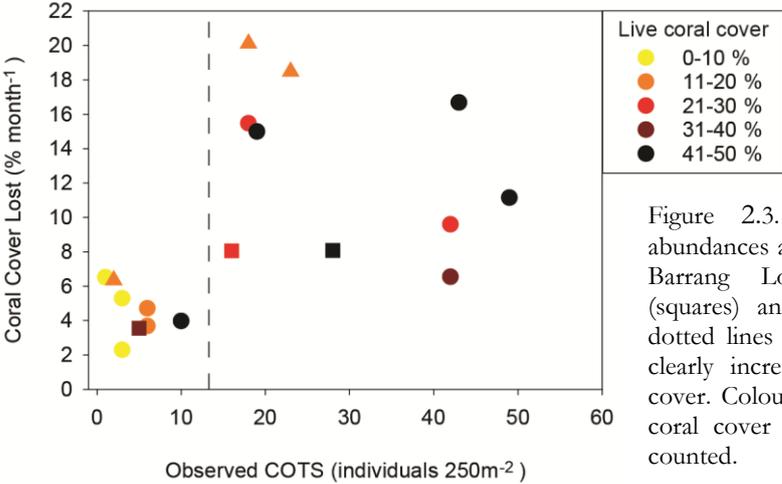


Figure 2.3. Relationship between COTS abundances and the loss of live coral cover at Barrang Lompo (circles), Lumu Lumu (squares) and Bonetambung (triangles). The dotted lines denote abundances where COTS clearly increased their impact on live coral cover. Colour relates to the percentage of live coral cover observed when the COTS were counted.

Nonetheless, our study provides support for this phenomenon and information about the spatial and temporal patterns and impact of COTS in the Spermonde Archipelago.

Lastly, previous work has shown links between COTS outbreaks and water quality (Fabricius et al. 2010; Pratchett et al. 2014) where increased phytoplankton greatly increases the probability of COTS larvae completing development (Fabricius et al. 2010). Anthropogenic and riverine export from the Makassar area contribute to high particulate organic matter and chlorophyll-*a* concentrations of coastal waters of the Spermonde Archipelago (Fabricius 2005; Sawall et al. 2011) suggesting possible causation for previous and current COTS observations. Although the exact cause of COTS outbreaks remains undetermined (Pratchett et al. 2014), deteriorating water quality caused by urbanisation should forewarn managers of Indonesian coral reefs that the potential for more COTS outbreaks will be high. The effects of the COTS outbreak in Spermonde show that, within one year, damage to live coral cover can be severe with up to 20 % loss month⁻¹, and therefore future outbreaks should be monitored closely.

Chapter III

Sponge take-over of a reef

This chapter is in preparation as:

Plass-Johnson JG, Meyer A, Wild, C., Ferse SCA, de Voogd N, Teichberg M. The overtake of a benthic community by the sponge *Ircinia* sp. *Bulletin of Marine Science*

The change of coral reefs to alternative states, termed phase shift, has become an increasing occurrence in the last 30 years. Overfishing of herbivores and the increase of nutrient input into coastal marine systems has resulted in the main reef building constituent, the scleractinian corals, becoming outcompeted for space by other benthic organisms. Traditional perception of phase shifts on coral reefs is that from one of coral dominance to macroalgal dominance because generally, the loss of herbivores allows the faster growing algae to overtake corals. However, phase shifts can result in alternative states consisting of other dominant organisms. This includes corallimorpharians, soft corals, ascidians, sea anemones and sponges (reviewed in: Norström, Nyström, Lokrantz, & Folke, 2009).

Although the potential of sponges to overgrow reefs, particularly in the context of disturbance, has long been suggested (Plucer-Rosario 1987), changes to a sponge-dominated alternative state have only been reported four times in the literature (Norström et al. 2009). Despite a few reports of sponge proliferation in acute instances (Coles and Bolick 2007, Fujii et al. 2011 de Voogd et al. 2013), all reports of a phase shift to sponge come from the Caribbean and sponge proliferation occurred after large scale scleractinian die-off from disease, bleaching or hurricanes. In the most extreme example, the sponge *Chondrilla nucula* occupied ~40 % of the substratum after a severe bleaching event (Aronson et al. 2002). Given the paucity on information on the occurrence of sponge dominated alternative states, the current observation reports the first sponge alternative state (i.e. where sponges constitute the largest single benthic category) in the Indo-Pacific region, and it establishes the spreading rate of a sponge takeover of a reef benthic community in Indonesia.

During four benthic surveys through two years (September 2012 – September 2014), the spread of the sponge *Ircinia* sp. was observed at the Karang Kassi reef complex in the Spermonde Archipelago, Southwest Sulawesi. Methods included the survey of three-50 m transects at two sites of the reef. One site was heavily impacted by bomb fishing while the other remained mostly undisturbed. Analysis of the benthic composition using photographic quadrats indicated that, at the impacted site, *Ircinia* sp. increased in mean benthic cover from 9.0 (\pm 2.1 SE) % in September 2012 (left column, Fig. 3.1), to 16.4 (\pm 3.6) % in February 2013 (centre column, Fig. 3.1), to 36.7 (\pm 6.5) % in September 2013 (right column, Fig. 3.1) to 48.1 (\pm 5.5) % in September 2014. At the impacted and undisturbed sites, live coral cover remained constant at ~10 % and ~25 %, respectively, while *Ircinia* sp. was never present at the undisturbed site. Wider observations of the impacted area by the lead author suggest that the spread of the sponge reaches much further than the surveyed transects facilitated by the degraded habitat. Taxonomic identification has been confirmed by comparing the COI of *Ircinia* sp. (Accession Nr. LN828727-LN828730) with the published *Ircinia* sp. voucher BA10-21 (Accession Nr. JX306085).

It would seem that our observation of the proliferation of the sponge *Ircinia* sp. is consistent with previous observations in the Caribbean. The site at Karang Kassi receives regular exposure to destructive fishing practices (JPJ pers. obs.) which has caused extensive damage to the live coral community. Subsequently, there remained ample open space for the sponge to take over. A critical question for the functioning of the coral reef system is whether the observed change constitutes a temporal phenomenon that is reversible, or whether the new state becomes stable over time (i.e. a regime shift occurs). Therefore, determination of a regime shift at this site of Kassi will depend on *Ircinia* sp.'s capacity to maintain benthic dominance. Nonetheless, observations of the take-over and dominance of coral reef benthic communities by sponges are absent in the literature from the Indo-Pacific region. Our observations indicate that the proliferation of sponges can be substantial once a reef becomes highly impacted, confirming Plucer-Rosario's (1987) prediction of 30 years ago.

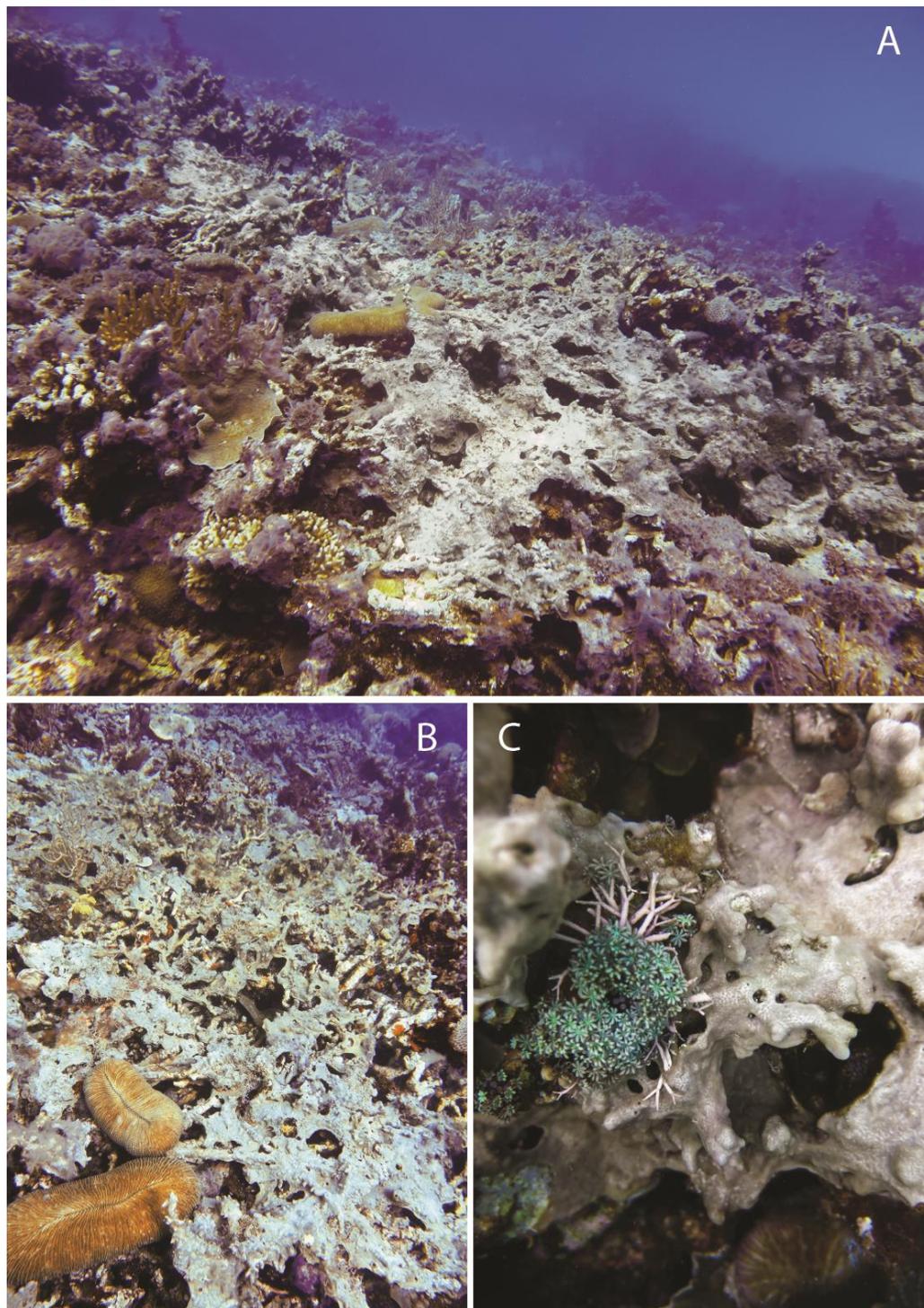


Figure 3.1. Benthic pictures demonstrating the progression of *Iridia* sp. at Karang Kassi reef.

Chapter IV

Observation of potential change in fish functional role

This chapter has been published as:

Plass-Johnson JG, Ferse SCA, Wild C, Teichberg M. (2104) Observation of macroalgal browsing in juvenile humphead parrotfish, *Bolbometopon muricatum*, in the Spermonde Archipelago, Indonesia.

Bulletin of Marine Science 90(3): 13-15. doi: 10.5343/bms.2014.1006

In the Indo-Pacific, the humphead parrotfish (*Bolbometopon muricatum* (Valenciennes 1840)) is among the most important and charismatic fishes in coral reefs. It is one of the largest and oldest growing fishes with adults reaching 45 kg and 130 cm at 40 years of age (Bellwood and Choat 2011). Generally, they are found in groups of up to 30 individuals, and like most parrotfishes, they feed from the reef's carbonate substratum. However, *B. muricatum* is unique in its mode of feeding, which includes predation on live coral and the excavation of large amounts of carbonate substrate. In the Australian Great Barrier Reef, *B. muricatum* contributes disproportionately to bioerosion processes, with the capacity of one individual to ingest 5 tonnes of carbonate per year (Bellwood et al. 2003). This feeding redistributes approximately 32.3 kg m⁻² of sediment year⁻¹, clearing space for new recruitment and reshaping benthic community composition (Bellwood et al. 2003). Nearly half of the ingested sediment consists of live coral (Hoey and Bellwood 2008), suggesting coral predation as another important functional role for the species.

Unfortunately, *B. muricatum*'s large size makes it a target species for fisheries and its late maturation makes it susceptible to overfishing. As a result, it has been greatly overharvested throughout most of its geographical range (Bellwood et al. 2012). Currently it remains in good numbers at only a few places (Bellwood and Choat 2011). However, even in places where it receives the greatest protection (e.g. Great Barrier Reef), the species' size distribution is heavily truncated, with only ~5% below 45 cm in length, indicating low recruitment (Bellwood and Choat 2011). Generally, because of *B. muricatum*'s scarcity, studies of its biology and ecology are anecdotal and based on the more conspicuous adults. There is a paucity of information concerning early life stages, and given their low numbers, a greater understanding may help in their conservation.

On October 2nd, 2013, at Kapoposang Reef, South Sulawesi, Indonesia, *B. muricatum*, displaying juvenile colouration (~40 cm), was observed feeding on the macroalgae genus *Padina* during a remote underwater video transplant assay (Fig. 4.1). These assays included the provision of one *Padina* sp. and one *Sargassum* sp., simultaneously, however *B. muricatum* fed upon *Padina* sp. exclusively. *B. muricatum*'s entry and exit from the camera's field of view resulted in the observation of intermittent feeding for a total of 7.5 min through 63 min of video. During this time, 102 bites were taken, equating to 14 bites min⁻¹. The average foraging time (time between first and last bite before exiting from camera view) was 20.5 (SE: ±1.8) seconds. Furthermore, 12 algal (*Padina*) assays without video were deployed at that site on this day, of which eight showed large bite marks suggestive of feeding from *B. muricatum*. The same bite marks were observed in three non-video assays on the following day, indicating that feeding on *Padina* by *B. muricatum* was not limited to a single event.

Due to the nature of the observation (stationary underwater video camera), it cannot be confirmed whether the recording shows the same or several individuals. However, given *B. muricatum*'s limited juvenile populations, the additional information of *Padina* feeding may provide valuable insight on their trophic biology. Herbivorous feeding on epilithic turfing algae has been reported for this size of *B. muricatum* (Bellwood and Choat 1990). However, observations of macroalgal browsing are rare and this example suggests ontogenetic variation in *B. muricatum*'s diet, which is common in the parrotfishes (Plass-Johnson et al. 2013), yet so far not described for this species. Furthermore, such observations of opportunistic feeding indicate that this species may play a role in herbivory that has largely been overlooked to date. Given the ongoing deterioration of coral reefs, *B. muricatum*'s primary habitat, and the ongoing overexploitation of this species, this aspect of its ecology may warrant further attention.

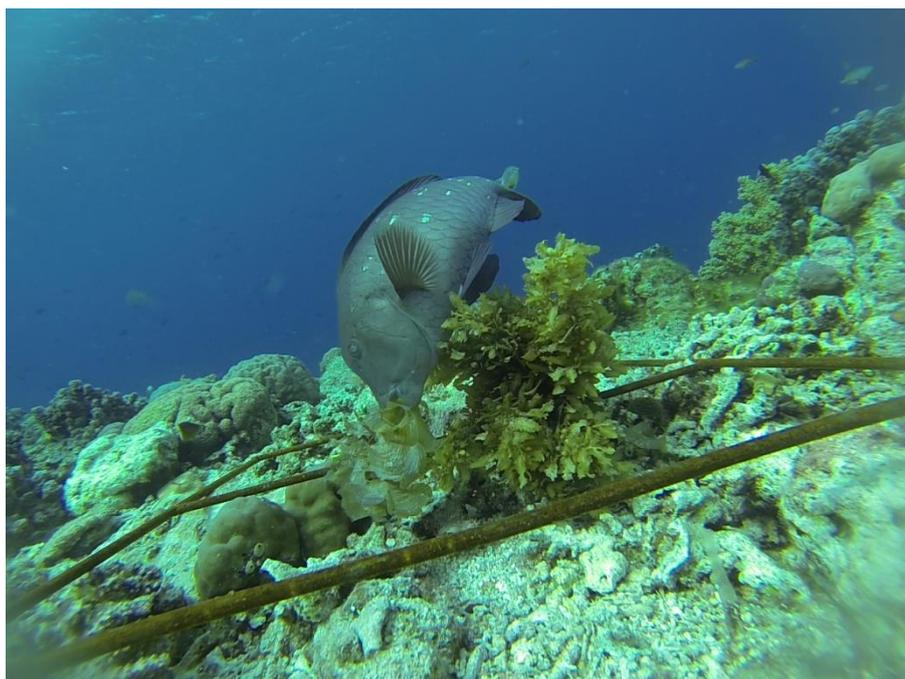


Figure 4.1. (Above) Selective feeding by *Bolbometopon muricatum* on *Padina* sp. even (Below) reaching over the *Sargassum* sp. sample.

Section Three

Experiments in coral reef processes

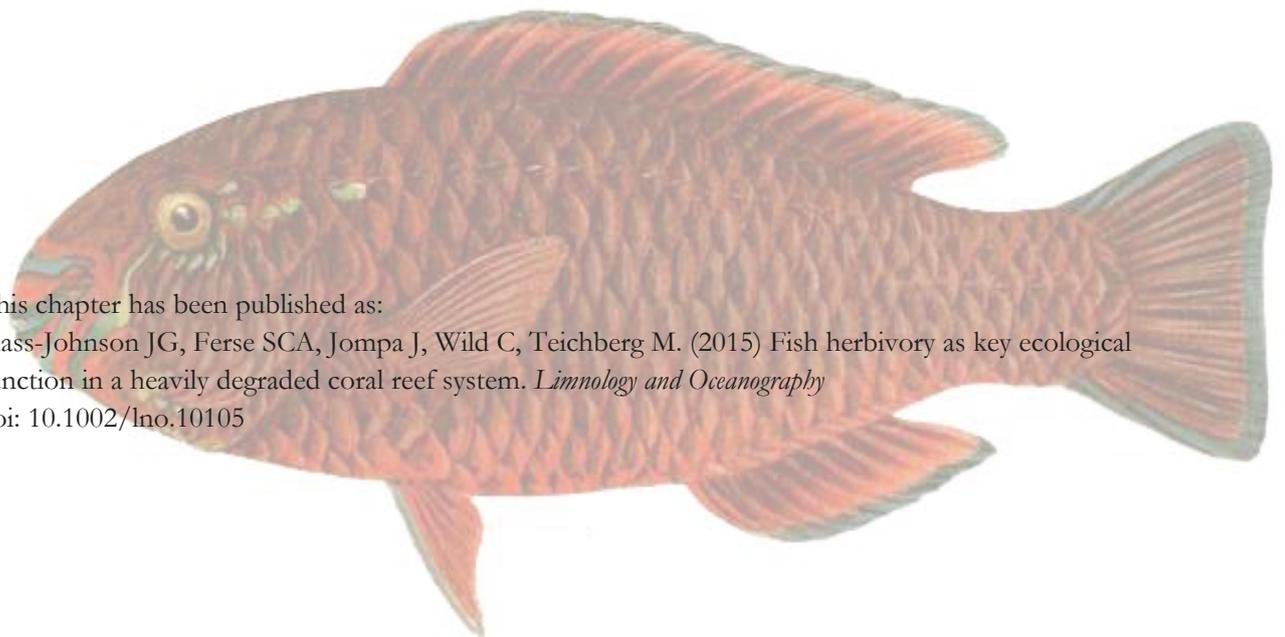
Chapter V

Herbivory on macroalgae

This chapter has been published as:

Plass-Johnson JG, Ferse SCA, Jompa J, Wild C, Teichberg M. (2015) Fish herbivory as key ecological function in a heavily degraded coral reef system. *Limnology and Oceanography*

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Abstract

Localised impacts, such as eutrophication and overfishing, have been identified as major threats to reefs worldwide, resulting in changes in coral reef community composition, from coral-dominance to algal-dominance. Herbivory by fishes is frequently cited as a key process structuring benthic community response to stressors. Here, we experimentally tested the capacity of herbivorous fishes to remove macroalgae along an onshore-offshore spatial gradient in the Spermonde Archipelago, Indonesia; a coral reef system exposed to long-term anthropogenic disturbances. Bioassays of *Sargassum* and *Padina* spp. were collected from the reef flat and transplanted onto the reef slope at five islands varying in distance (1-55 km) from the coastline and city of Makassar, South Sulawesi. Supplementary underwater video deployment and fish surveys were used to identify species-specific differences in herbivore communities and rates of algal removal. Over a 24 h period, *Padina* was almost completely removed from the two outermost islands, but removal declined toward shore. With the exception of the site closest to Makassar, more than 50 % of all transplanted macroalgae were removed. Species diversity of algal-consuming fishes and total bites increased towards off-shore, with only one species, *Siganus virgatus* (Siganidae), feeding at all sites. These changes in herbivore communities underline the capacity for functional resilience under varying levels of reef degradation. Our results exemplify the complexities of ecological functioning along environmental gradients.

Introduction

The process of herbivory is crucial for sustaining coral reef health (Hughes et al. 2003, 2007a; Mumby 2006; Burkepile and Hay 2006) by either directly or fortuitously removing benthic primary producers, particularly macro- and microalgae (Hughes et al. 2003; Littler et al. 2009). Fish and urchins which feed from the substratum can remove algae at early life stages or in established forms (Bellwood et al. 2004). It has been repeatedly shown through experimentation that, without herbivory, it is possible for algae to outgrow corals, thereby gradually changing reefs to a state of algal dominance (Hughes et al. 2007b; Smith et al. 2010). This is enhanced when increased nutrients and the removal of algae-consuming species occurs together, allowing algae to grow faster and to establish standing stocks that are able to outcompete corals for access to light and space. Given the continuous decline in the health of coral reefs around the world (Burke et al. 2011), ecological importance has been given to those fish species which are able to remove established algal communities, and return a reef to a state of coral dominance (Hughes et al. 2007b).

Fish communities on coral reefs are not constant in space or time (Warwick and Clarke 1993), and their structure can be a response to multiple biotic and abiotic factors (Warwick and Clarke 1993; Genner et al. 2010). However, fishing has been identified as particularly important, because it can remove traits, species and/or functions from a community, such as large predators (Jennings et al. 1995). Similarly, macroalgal communities can respond to changing water conditions (i.e. nutrients, sedimentation, temperature) and consumer communities (McCook 1999; Teichberg et al. 2010), altering their morphology and chemical composition. Unfortunately, for many reefs around the world, fishing and eutrophication, driven in particular by increasing coastal populations, are identified as the most common threats (Burke et al. 2011). Projections of further population growth suggest that these local stressors will become even more pressing in coming decades, with negative consequences for coral reef ecosystem integrity (Burke et al. 2011; Mora 2014). Herbivorous fishes on most reefs around the world are heavily impacted both directly and indirectly by overfishing (Edwards et al. 2014), suggesting that within these systems species richness and herbivore functioning may be increasingly diminished. Assessing how the composition of herbivorous fish communities and

their ability to remove algae change in response to varying levels of reef degradation will help to understand the capacity of coral reefs to respond to projected impacts (Burkepile and Hay 2006).

Studies on Australia's Great Barrier Reef (GBR) have suggested that fish species capable of removing the brown macroalga *Sargassum* are of particular importance (Bellwood et al. 2006a) because this alga was dominant after long-term herbivore exclusion (Hughes et al. 2003). However, the dominant herbivorous fish species can change among seasons (Lefèvre and Bellwood 2011) and with differing spatial scales (Cvitanovic and Bellwood 2008; Hoey and Bellwood 2010; Bennett and Bellwood 2011; Vergés et al. 2012). Generally, species of the families Acanthuridae, Kyphosidae, Labridae (parrotfishes) and Siganidae are considered to be the most important herbivores, but the specific impact and role of the species can vary dramatically. Cross-continent comparison indicated that less than five species contributed to the greatest proportion of macroalgae removal on the GBR, while ~15 species were responsible at Ningaloo Reef (Vergés et al. 2012). These examples show that herbivory can be site- and time-specific and, furthermore, they also suggest a high level of ecological resilience within the herbivore functional group.

In the Indo-Pacific region, most studies examining macroalgal removal through the use of transplants have been conducted on the GBR. These studies have proven invaluable in understanding the potential processes that determine herbivory; however, their application for similar processes in other areas realising greater levels of fishing may be limited. The cultural, political and geographical setting of the GBR results in this reef being more impacted by large-scale processes (e.g. ocean acidification and temperature anomalies) than local fishing perturbations (Burke et al. 2011). Likewise, most reefs of the Indo-Pacific exhibit lower herbivore biomass than the GBR (Edwards et al. 2014) partly because of differences in fishing practices driven by local socio-economic and governance conditions.

Indonesia's coral reefs, for example, are heavily impacted by changes in land and resource use. Agriculture, aquaculture, destructive coral reef resource use, ineffective law enforcement, and a large coastal population which heavily relies on coral reefs for food result in localised impacts being more pronounced than global processes (Burke et al. 2011, 2012). Given the location-specific threats which occur in the Southeast Asian region, and the high spatial and temporal variability of herbivory, it is of particular importance to examine the capacity for algal removal in coral reefs with high levels of localised impacts, such as that found in the Spermonde Archipelago, Southwest Sulawesi, Indonesia.

The Spermonde Archipelago is located within the Coral Triangle, an area which contains one of the most diverse assemblages of marine organisms in the world (Veron et al. 2009). This region also supports one of the largest reef fisheries in Indonesia. Furthermore, Spermonde features the second-largest port of the country, located at the city of Makassar (population: 1.4 million). The reefs of the area are exposed to heavy development of the coastal region, where land run-off and destructive fishing practices have existed for decades, resulting in poor water quality, and reef community and habitat degradation (Edinger et al. 1998; Pet-Soede and Erdmann 1998; Pet-Soede et al. 2001a; b). Related studies have found links with localised eutrophication and fishing impacts (Edinger et al. 1998, 2000; Pet-Soede et al. 2001a; b; Cleary et al. 2005; Becking et al. 2006; Cleary and Renema 2007; Knittweis et al. 2009; Sawall et al. 2011, 2013), the former being associated with increases in live coral with distance from Makassar (Edinger et al. 1998; Renema and Troelstra 2001). The direct effect of fishing practices on herbivores is unstudied, thus unclear, however unselective fishing is intense (Pet-Soede et al. 2001a; b). This suggests possible impacts on herbivore communities and/or their preferred habitat, while near-shore water nutrient levels are high (Edinger et al. 1998; Sawall et al. 2011, 2012) for coral reefs. Despite a situation which would be expected to facilitate a change to algal dominance, macroalgal density is relatively low on the reef slope, and live coral cover is maintained

even at the most impacted, near-shore sites (Sawall et al. 2013, Jompa unpub. data). No work has explored the role of herbivory in maintaining this dynamic system.

Therefore, this study aimed to experimentally and systematically assess *in-situ* macroalgal removal rates and herbivore species composition across the Spermonde Archipelago. Transplanted macroalgal assays, underwater video, and underwater transect surveys were used to quantify the relative importance of herbivorous fish species in reducing macroalgae on the reefs and how these communities can change under severe ecological impacts, thereby aiming to provide insights on the importance of this key ecological function on impacted coral reefs.

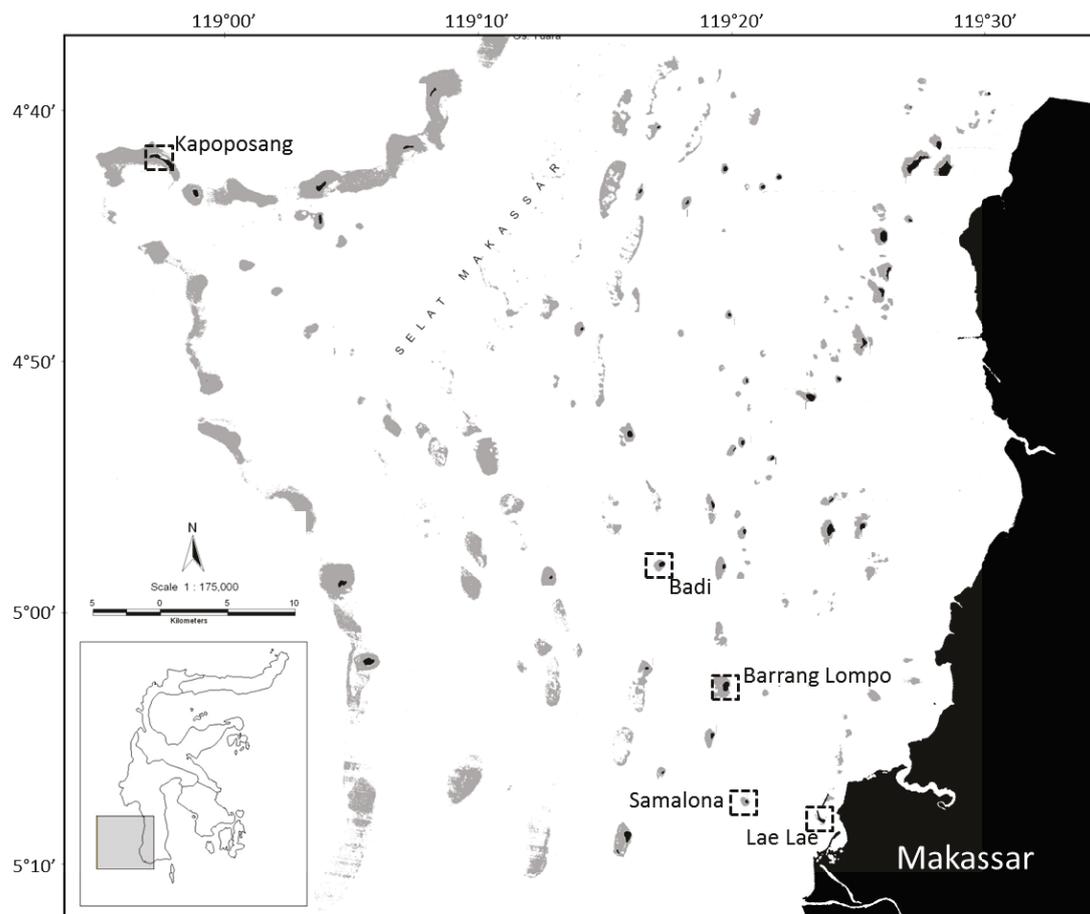


Figure 5.1. Map of the Spermonde Archipelago. Dashed lines indicate study sites where bioassay experiments and surveys were conducted. Black indicates dry land and grey is reef.

Methods and Materials

Study Sites

This study was conducted between the 8th and 25th of September, 2013, on five islands of the Spermonde Archipelago, Indonesia, along a transect of increasing distance from the city of Makassar (Fig. 5.1). Near-shore islands are affected by effluents from the city's harbour, sediments, aquaculture outflow and wastewater from the fluvial discharge of nearby rivers (Renema and Troelstra 2001). Coral cover and diversity increases with distance from the mainland (Edinger et al. 1998), and the islands for this study were chosen to reflect these patterns along a cross-shelf gradient. Lae Lae (LL; 05°08S, 119°23E) was the closest (1 km distance) to the mainland, followed by Samalona (SA;

05°07S, 119°20E, 7 km distance), Barrang Lompo (BL; 05°02S, 119°19E, 11 km distance), Badi (BA; 04°57S, 119°16E, 19 km distance) and Kapoposang (KA; 04°41S, 118°57E, 55 km distance) (Fig. 5.1).

All islands are located on the continental shelf except KA, which was the only site located on the edge of the continental shelf. Sampling was conducted during the dry season and there were little to no differences in weather conditions among days. The northwest corner of each island (except KA) was used to standardise the sampling sites among reefs. The western coast of the islands generally features a well-developed, carbonate fore-reef and a sandy back-reef and flat. The reef crest was shallow (~3 m) and the slope reaches down to 15 m. The last study site, KA, was located on the reef

edge above the outer continental shelf wall (Figure 5.1). Work at KA was conducted at the northeast site of the island at the edge of the carbonate shelf because this area displays the highest level of reef accretion.

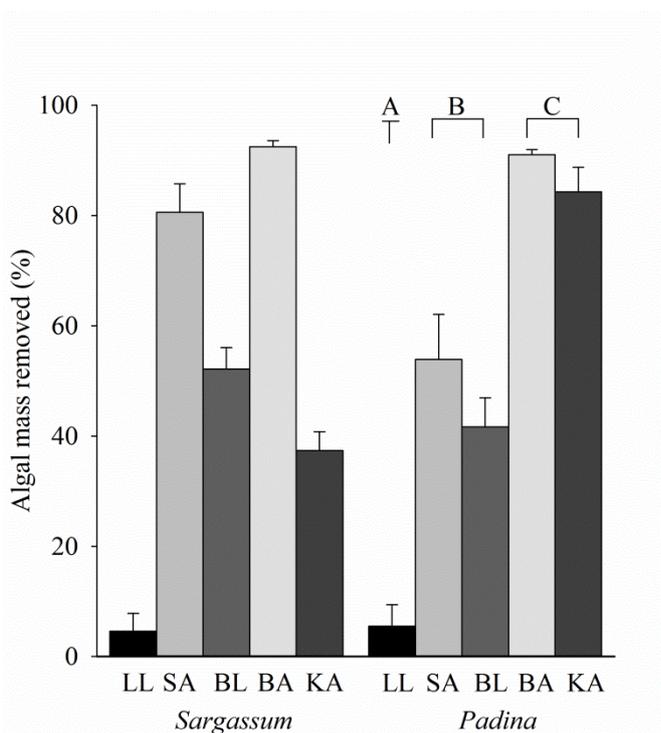


Figure 5.2. Average (\pm SE) amount of *Sargassum* and *Padina* removed per 24 h period for consumer exposed treatment. Islands are in order from closest to furthest from Makassar (LL: Lae Lae, SA: Samalona, BL: Barrang Lompo, BA: Badi, KA: Kapoposang). Data represents total mass loss after the correction for controls. Data from Day One are not included. Lettering above *Padina* indicates islands that were not significantly different in the PERMANOVA pair-wise post hoc test. There is not lettering above *Sargassum* because all islands were significantly different from each other.

Macroalgal transplants

Transplant bioassays and video cameras were used to assess species-specific rates of feeding on the macroalgae *Sargassum* sp. and *Padina pavonica*. *Padina* was selected as it represents one of the most abundant macroalgae on reef flats (Plass-Johnson unpub. data), while *Sargassum* is important in other comparatively similar areas (McClanahan et al. 2001; Hoey and Bellwood 2009), with the capacity to dominate coral reef communities after experimental phase shifts (Bellwood et al. 2006a; Hughes et al. 2007b).

All *Sargassum* and *Padina* transplants were collected from the same area of reef flat of BA throughout the experiment to control for among-reef differences in algae which may affect herbivore feeding (e.g. nutritional composition or secondary metabolites). Throughout the experiment all samples were assumed to be the same species based on area of collection and similarity of morphology, however species identification of *Sargassum* sp. was not feasible due to their poorly understood taxonomy (Kilar et al. 1992). Samples along with their holdfasts were chosen to represent their naturally occurring conditions (between 25 – 118 g). Samples were collected daily and held in outdoor flow-through raceways at the field station on BL. Samples were spun for 10 s in a salad spinner and weighed to the nearest 1 g, labelled with a small cable tie, and then immediately returned

to raceways. All samples were used for the experiment on the subsequent day after collection to minimise their deterioration.

At each reef for each day, six assays of each species were haphazardly deployed within a 200×2 m area on the reef slope at approximately 6 m depth. Five assays were attached with cable ties to artificial 60×60 cm steel anchors. The additional assay was placed in a $60 \times 60 \times 60$ cm cage with 1 cm mesh to control for change in weight not due to herbivory (e.g. handling or in-water physical damage). Assays were deployed early in the morning (~ 0700 hrs) and collected 24 h later. After collection, samples were again weighed after spinning to calculate weight loss due to herbivory. Transplants were conducted at each reef for four successive days at two concurrent reefs. BA and SA were completed first, followed by BL and LL, and lastly KA.

Video analysis

Video cameras (GoPro Hero3 in underwater housing) were mounted on steel rebar approximately 50 cm from one haphazardly chosen, uncaged, algal assay of each species at each reef on each day. The assays were filmed for approximately a 4 h period immediately after deployment (~ 0730 until 1130 hrs). The steel anchors that assays were attached to allowed for reference of fish size. Video recording was repeated daily, however data from Day One was excluded (see Statistical analyses), totalling 12 h of video footage recorded per macroalga and island.

For each video, fish size (total length), number of bites and species were recorded for each individual. Forays where it was not possible to discern between bites were recorded conservatively as a single bite. All fish observed feeding were recorded in size classes (2.5 cm for individuals < 10 cm, 5 cm for individuals > 10 cm, i.e. bin: 0.1-2.5 cm, 2.6-5.0 cm etc.) and then converted to kg based on published length-weight relationships (Kulbicki et al. 2005). To account for differences in fish sizes, the fish length was taken as the midpoint of each size class (Lefèvre and Bellwood 2011). To standardise for the impact of fish size, bite impact was calculated by multiplying fish size by bites (body mass in kg \times bites) (Cvitanovic and Bellwood 2008; Hoey and Bellwood 2010; Lefèvre and Bellwood 2011; Bennett and Bellwood 2011).

Herbivore survey

To evaluate differences in herbivore community composition, abundances and total biomass among islands, surveys (on SCUBA) were conducted two days prior to the start of and post each experiment. Roving herbivorous fishes of the families Acanthuridae, Kyphosidae, Labridae (parrotfishes) and Siganidae were counted and assigned to size classes (see Video analysis) using three 5×50 m transects. These fish families were selected because they have the greatest impact on benthic macroalgal communities (Ceccarelli et al. 2005). Similar to the transplants, fish survey transects were deployed 1-2 metres below the reef crest. Swimming speed was constant and slow, with each transect taking approximately 15 min. Counts were restricted to individuals > 3 cm to ensure identification was possible. Fish survey data were converted to biomass estimates based on published length-weight estimates.

Statistical analyses.

For most of the islands, permutational analysis of variance (PERMANOVA) identified differences in tissue loss that were significantly less on Day One than successive days for both species of macroalgae (*Sargassum* PERMANOVA: Pseudo- $F_{15,80} = 8.58$, $p < 0.001$; *Padina* Pseudo- $F_{15,80} = 5.96$, p

< 0.001), indicating that there was a period of time needed for herbivorous fishes to find and accept the assays during the experiment. Because of this, Day One was omitted from both the transplant and video analyses for all islands. There was no statistical difference among days after the removal of Day One (*Sargassum* PERMANOVA: Pseudo- $F_{10,60} = 0.45$, $p = 0.917$; *Padina* Pseudo- $F_{10,60} = 1.263$, $p < 0.284$), subsequently day was treated as the replicate ($n = 3$) for further analysis.

Weight loss for each alga was calculated similar to Bennett and Bellwood (2011). The mean proportional loss of mass (g) from the caged controls was used to estimate non-herbivore loss from assays. Therefore, mass loss was calculated as:

$$T_{\text{loss}} = 1 - H_a / (H_i \times [1 - C_a]),$$

where T_{loss} is the proportion of algae consumed, H_a is the algal mass (g) after 24 h exposure to herbivory, H_i is the initial algal mass, and C_a is the mean percentage lost from the controls (Table 5.2) of the associated island. Differences in consumed algae were analysed among islands using a one-way PERMANOVA with site as a fixed factor. A Euclidean distance measure was calculated based on square-root transformed data (for normalisation). Differences among islands were identified with pairwise comparisons using PERMANOVA. PERMANOVA was chosen because it is robust when the assumptions of normality and homogeneity of variance are not met (Anderson et al. 2008). This was the case given differences in macroalgae consumption among and within some reefs (e.g. BL), and high rates of removal (e.g. BA), leading to a highly negative skew. PERMDISP was used to test the assumption of homogeneity of variance (dispersion) (Anderson et al. 2008), and in one case of significance (i.e. *Padina*, BA \times LL, $p = 0.32$), interpretation was conservative. PERMANOVA with pair-wise comparisons was used to identify difference in algal removal among islands.

The total contribution to mass-standardised bites, with a threshold of > 3 % of total standardised bites at any given island, was used to identify species which had the greatest impact on macroalgae (*Sargassum* and *Padina* analysed separately). Although a threshold of 3 % is arbitrary, a similar threshold has been previously applied (Vergés et al. 2012) with the assumption that the impact of species which contributed to ≤ 3 % was negligible. Data from these fish species were then used to characterise trends in herbivory across islands. Differences in herbivore biomass from underwater transect fish surveys were calculated with a one-way ANOVA with island as a fixed factor. Data were $\log(x+1)$ transformed and checked for homogeneity of variance (Bartlett's test) and normality (using scatter plots).

All statistical analyses were performed using Primer-E v6 software (Clarke and Gorley 2006) with the PERMANOVA+ add-on package (Anderson et al. 2008). Fish species identification was based on Allen and Erdmann (2012).

Table 5.1. PERMANOVA for test of Island after Day one was removed. All other days were pooled because they were not different from each other. Significant differences are indicated with bold.

	df	SS	MS	Pseudo-F	P(perm)	Uniq. Per.
<i>Sargassum</i>						
Island	4	1.22	0.31	250.09	<0.001	9917
Res	10	00.01	0.01			
<i>Padina</i>						
Island	4	1.19	0.30	39.30	<0.001	9929
Res	10	0.08	0.01			

Results

Algae removal

Removal of *Sargassum* was variable among islands, while the removal of *Padina* increased with distance from Makassar (Fig. 5.2). For *Sargassum*, removal was significantly different among islands (Table 5.1), with highest rates at BA and SA (Fig 5.2). *Padina* removal was highest at the two outermost islands (BA and KA), intermediate at SA and BL, and lowest at LL (Fig. 5.2). Likewise,

Padina removal was not significantly different between KA and BA, and between SA and BL (Table 5.1). Algal loss due to handling ranged from 2.3 % to 6.7 % (Table 5.2).

Video analysis

Across the islands, there was an increase in the total number of fish feeding on both macroalgae with increasing distance from Makassar, with the exception of a slight decrease from SA to BL for *Padina* (Table 5.3). This pattern was the same for the species which had the greatest impact in terms of standardised mass total bites (Table 5.3), with the total number of important herbivores being relatively low (≤ 5 species). Interestingly, through 24 h of video, there was not a single observation of feeding on either macroalga at LL. The average number of bites on *Sargassum* and *Padina* increased with distance from Makassar, except for a decrease in bites on *Padina*, again at BL (Table 5.3). The proportional contribution of the species that accounted for $> 3\%$ of total standardised bites was always above 94 %, and above 99 % for most islands (Table 5.3).

There were few fish species (contributing $> 3\%$ of mass-standardised bites) that overlapped among islands, and only one was found at all four (*Siganus virgatus*; Fig. 5.3A). *S. virgatus* fed on both macroalgae at all islands except for *Padina* at KK; it had more bites on *Sargassum* and was the most important consumer of *Sargassum* at SA and BL (Fig. 5.3). *S. margaritifera* was the biggest consumer of both macroalgae at SA, but it did not occur in the videos at any of the other islands. Two acanthurids, *Naso unicornis* and *N. lituratus*, were disproportionately important on the outer two reefs (Fig. 5.3). At BA, the former accounted for 83 % and 95 % of the standardised bites taken on *Sargassum* and *Padina*, respectively. At KA, *N. lituratus* accounted for 64 % and 53 % of the standardised bites on *Sargassum* and *Padina*, respectively.

Herbivore communities

From the visual surveys, herbivore biomass increased with increasing distance from Makassar, with the outer two islands (BA and KA) being different from the middle islands (SA and BL; ANOVA, $F_{4,1} = 320.4$, $p < 0.05$; Fig. 5.4). LL had significantly lower herbivore biomass than all other islands (Fig. 5.4). The parrotfishes were always proportionally the largest group of herbivores. The siganids (*Siganus*) were present at all islands, while the acanthurids (*Naso*, *Ctenochaetus*, *Zebrasoma* and *Acanthurus*) became more abundant on the outer two islands (Fig. 5.4). In general, there were more fishes surveyed than those that fed on the assays, yet, there was little overlap in species (Table 5.4). Many of the important species in the video assay, for example *N. unicornis* and *N. lituratus*, were never observed in the visual surveys. *S. virgatus* was the only important species which occurred in both sets of data. Other universal species included *Scarus flavipectoralis* and *Siganus corallinus*, however their contribution was not important in the videos.

Table 5.2. Percentage ($\% \pm$ SE) loss of algae from control assays. Any loss represents loss attributed to other disturbances than herbivory.

Island	Sargassum	Padina
Lae Lae	5.3%	6.7%
SE	(0.9%)	(0.7%)
Samalona	5.7%	8.0%
SE	(1.2%)	(1.2%)
Barrang Lompo	4.0%	6.0%
SE	(0.6%)	(1.5%)
Badi	2.7%	4.0%
SE	(1.3%)	(1.5%)
Kapoposang	2.3%	2.3%
SE	(1.3%)	(1.9%)

Table 5.3. Total number of herbivore species feeding on transplanted *Sargassum* and *Padina* at each island with the number of species contributing >3% of total mass-standardised bites indicated within brackets. Total mass-standardised bites of all herbivore species and those which contributed to >3% of the total are given for each island. The proportion of total contribution of those species contributing to >3% of total mass-standardised bites is indicated in brackets. Islands are in order from closest to furthest from Makassar (LL: Lae Lae, SA: Samalona, BL: Barrang Lompo, BA: Badi, KA: Kapoposang).

Island	Number of spp.		Total mass-standardised bites				Effect of algae
	<i>Sarg.</i>	<i>Padina</i>	All species		Spp. contributing >3%		
			<i>Sarg.</i>	<i>Padina</i>	<i>Sargassum</i>	<i>Padina</i>	
LL	0	0	0	0	0	0	
SA	5(2)	4(3)	265.9	37.2	263.9 (99%)	37.0 (99%)	0.671
BL	6(2)	3(2)	297.1	2.5	296.1 (99%)	2.4 (96%)	0.034
BA	6(3)	7(4)	599.6	721.4	598.5 (99%)	719.4 (99%)	0.793
KA	17(5)	11(4)	413.3	596.1	387.9 (94%)	592.8 (99%)	0.487

Discussion

Our results indicate that in a heavily populated area with terrestrial influences, the coral reefs of the Spermonde Archipelago, the fundamental ecological function of herbivory is maintained by a few key, consumer fish species. These differences in algal removal across sites were reflected in distinct differences in the fish species involved in herbivory. The two furthest sites, BA and KA, exhibited more species feeding and more bites on the macroalgae than the sites closer to the mainland. The fish species at two of the three closest sites, SA and BL, had much less impact on the macroalgae during the time of video. At SA and BL, algae-consuming species were solely from the genus *Siganus*. Further off-shore (BA and KA), the role of *Siganus* spp. was strongly overshadowed by the feeding of two *Naso* species (*Naso unicornis* and *N. lituratus*) and one parrotfish, *Bolbometopon muricatum*.

Patterns in algal removal, particularly for *Padina*, showed marked spatial differences, increasing in relation to distance from shore. Patterns for *Sargassum* were more complex, feeding was more variable among sites, even with a decrease in its removal at the farthest site. Interestingly, at the site closest to Makassar (LL), there was no evidence of herbivory on either macroalga suggesting that herbivory in the Spermonde Archipelago is not maintained in an area with high human population densities.

Although the biomass (Wismer et al. 2009) and species diversity (Risk 1972) of macroalgal-consuming fishes has been correlated with live coral cover and rugosity (Wilson et al. 2006), discerning the specific cause of these relationships has been hard. Generally, near-shore reefs are exposed to higher levels of terrestrial effluents and fishing. Both can cause degradation of coral reef systems, but the relationship between the two, and their impacts on the benthos and fish communities can be ambiguous. Nonetheless, data from our transect surveys support the observations that herbivore diversity and biomass increase with an increase in distance from shore. Similar studies have linked on-shore to off-shore spatial gradients to herbivore biomass (Wismer et al. 2009) and theoretical functional metrics (Johansson et al. 2013), and our assay study supports these with evidence of actual herbivory processes. This pattern is also described by Hoey et al. (2010) and Mantyka and Bellwood (2007), where herbivory was related to distance from shore on the GBR.

Browsing herbivorous fishes can vary in their ecological role both within and among species due to food preferences (Plass-Johnson et al. 2013) and behaviours (Fox and Bellwood 2011). Recent studies have found the siganids to be important herbivores (Fox and Bellwood 2008, 2011, 2012) with strong ecological differences within the group (Hoey et al. 2013). Hoey et al. (2013) identified dietary preferences in the group, with many species preferring brown foliose macroalgae over leathery

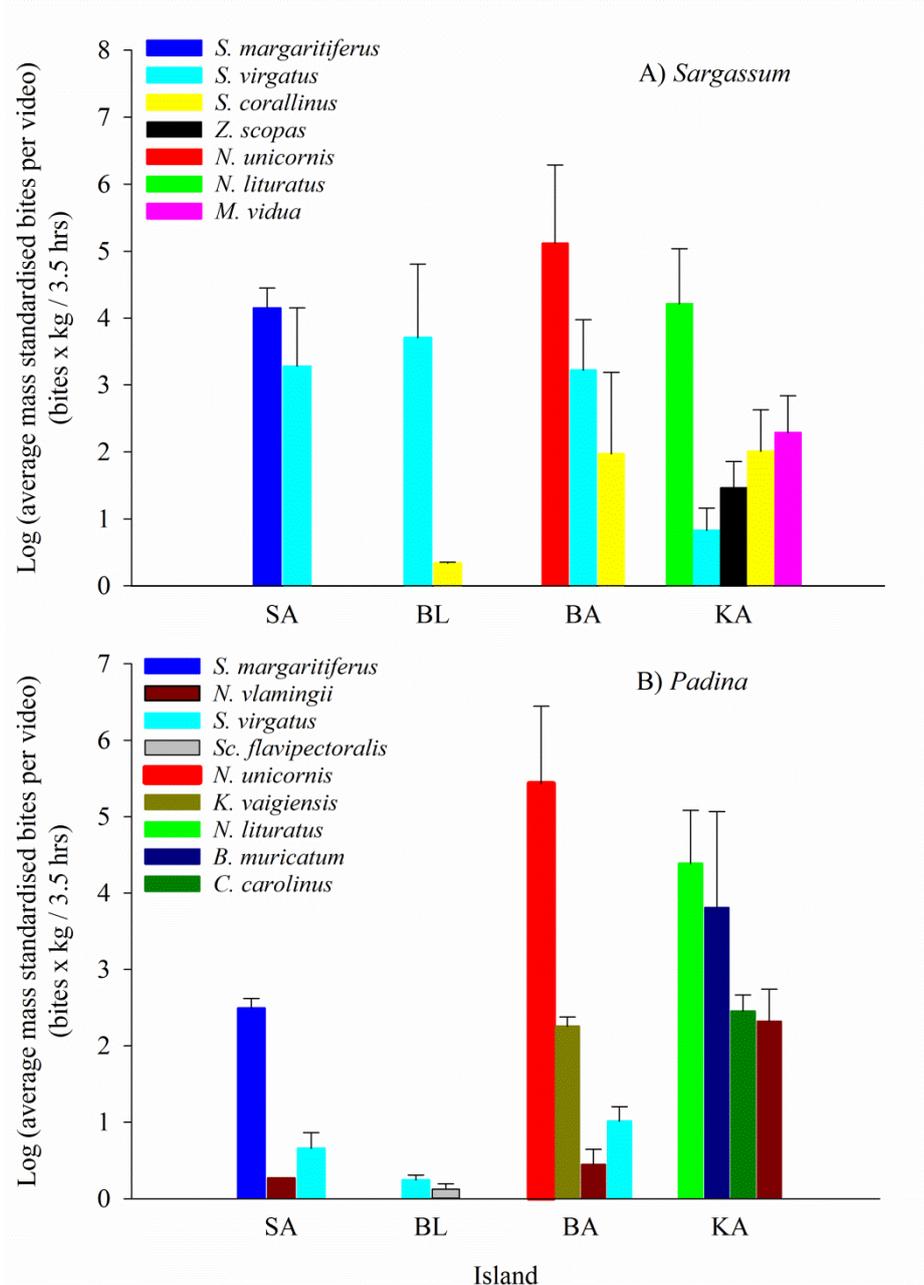


Figure 5.3. Average number of mass standardised bites (\pm SE) from A) *Sargassum* and B) *Padina* assays by fish species across all islands. No fish were observed for Lae Lae on the videos.

brown algae. Similarly, the siganids are an important group of fishes in the Spermonde Archipelago, as they were the only group observed feeding at all reefs with the exception of LL. However, their feeding diversity and impact was much more intense on *Sargassum*, a brown leathery alga. *S. virgatus* was the only species seen feeding at each site. On the GBR, the sister species of *S. virgatus*, *S. doliatatus* was also shown to be present at reefs across the continental shelf (Hoey et al. 2013). These observations suggest that only a few species may be robust in maintaining their function under changing environmental conditions, which lends importance to their conservation. However, the full ecological impact of the siganids is not completely clear as Fox and Bellwood (2008) note discrepancies between experimentally observed feeding and actual take-up of foods. Our observations cannot confirm the actual component ingested by the fishes, as we did not perform gut analysis as part of the study. However, siganids were directly observed removing and ingesting the algal assays. Previous studies on near-shore reefs of the GBR indicated that *N. unicornis* can be highly important in the removal of macroalgae (Hoey and Bellwood 2010; Lefèvre and Bellwood 2011), however we found this species, and the *Naso* group in general, to be nearly absent from the near-shore sites. These observations indicate regional plasticity in the diets of both the siganid and *Naso* species. We found a positive relationship for the removal of *Padina* and herbivore diversity, but not for *Sargassum*. In fact, the reef with the greatest diversity of consumers (KA) showed the second lowest biomass removal over 24 h for *Sargassum*, suggesting that diversity in herbivorous fishes may not directly relate to their capacity to remove algae and realised ecosystem services.

Increased input of nutrients and the removal of herbivores are continuously cited as the primary drivers of phase shifts on coral reefs (Burkpile and Hay 2006; Wilson et al. 2008; Hughes et al. 2010). In the Spermonde Archipelago, conditions have repeatedly been found to be eutrophic in the near-shore as far back as 1995 (Edinger et al. 1998), with suggestions of similar conditions well before these studies (Edinger et al. 1998, Sawall et al. 2011). The practice of destructive fishing techniques in the Spermonde Archipelago is well noted in the literature (e.g. Pet-Soede and Erdmann 1998; Sawall et al. 2013), however reporting of their effects is generally limited to changes in the benthic communities. In this study, however, we did not test direct links between nutrients and/or fishing practices with primary production or rates of herbivory. Rather, historical records of nutrient input and destructive fishing provide insight into the processes resulting in the current spatial patterns seen in the coral reef community composition of the archipelago. As such, the cross-shelf increase in herbivore diversity and biomass in the Spermonde Archipelago may be a product of anthropogenic processes, but the direct link is unclear. The increased observations of herbivorous species, for example of *Naso* and *Bolbometopon*, at off-shore sites may reflect either environmental impacts or fishing practices, as these fishes tend to be vulnerable to heavy fishing practices (Bellwood et al. 2012; Bejarano et al. 2013), spatial changes in preferred habitat, or a combination of both factors.

Table 5.4. Total number of herbivorous fish species counted during transect surveys. Also given are the species which occurred in both the video assays and transect survey.

Island	No. spp.	Species shared with video
Lae Lae	3	<i>Scarus flavipectoralis</i>
Samalona	15	<i>Siganus virgatus</i> <i>Scarus flavipectoralis</i>
Barrang Lompo	16	<i>Siganus virgatus</i> <i>Scarus flavipectoralis</i>
Badi	14	<i>Siganus corallinus</i> <i>Siganus virgatus</i> <i>Scarus flavipectoralis</i>
Kapoposang	17	<i>Acanthurus nigrofuscus</i> <i>Siganus virgatus</i> <i>Zebrasoma scopas</i> <i>Siganus corallines</i> <i>Naso vlamingii</i>

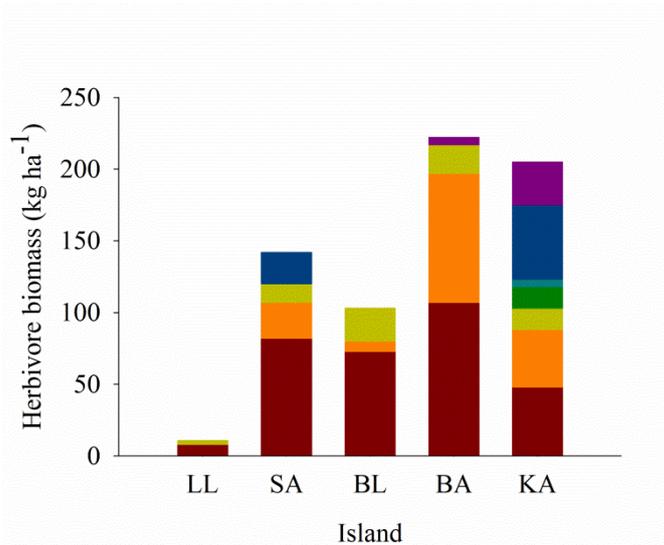


Figure 5.4. Biomass of roving herbivores from five islands based on visual transect surveys. Groups were broken into their genera (red is *Scarus*, orange is *Chlorurus*, yellow is *Siganus*, green is *Zebrasoma*, teal is *Naso*, blue is *Ctenochaetus*, purple is *Acanthurus*). Data represent means however error bars have been omitted for better visualisation. The largest standard error was for *Chlorurus* at BA ($\pm 37 \text{ kg ha}^{-1}$). Islands are ordered from closest (Lae Lae) to furthest from Makassar (Kapoposang).

within the herbivore function. The situation was much different at LL, the site closest to Makassar. The transplant experiment suggested that herbivory does not play a significant role in controlling macroalgae at this site. Alternatively, anecdotal evidence from the videos showed pieces of *Sargassum* breaking off from the bioassays. These observations suggest that, given the island's near-shore position, reduced light attenuation and sedimentation may play a larger role than herbivory in maintaining low macroalgae abundances via physiological and physical stress (Kleypas et al. 1999).

It should not be overlooked that this was an experimental situation where fully grown macroalgae were offered to consumers. Our observed differences between underwater transect and video methods probably directly reflect the experimental offering of foods. This likely attracted species to the area, which was previously devoid of these algae. Discrepancies between video and diver-based surveys are well noted in the literature (e.g. Mallet et al. 2014), nevertheless, observed patterns of the presence (transect survey and video) and impact (video) of herbivores both positively correlate with live coral and rugosity, suggesting that a healthier coral reef habitat supports a greater variety of herbivorous species. Similarly the experimental transplanting of macroalgae does not take into account all processes controlling macroalgal removal during the entire algal life cycle, which may involve different herbivore species or density-dependent processes that may affect herbivory. A further caveat of our experiment is that we were not able to assess possible urchin feeding at night. However, evidence from the videos, and in some cases the complete removal of full algal assays within the recorded 4.5 hours, strongly suggest that fish herbivory accounted for the majority of the algal loss.

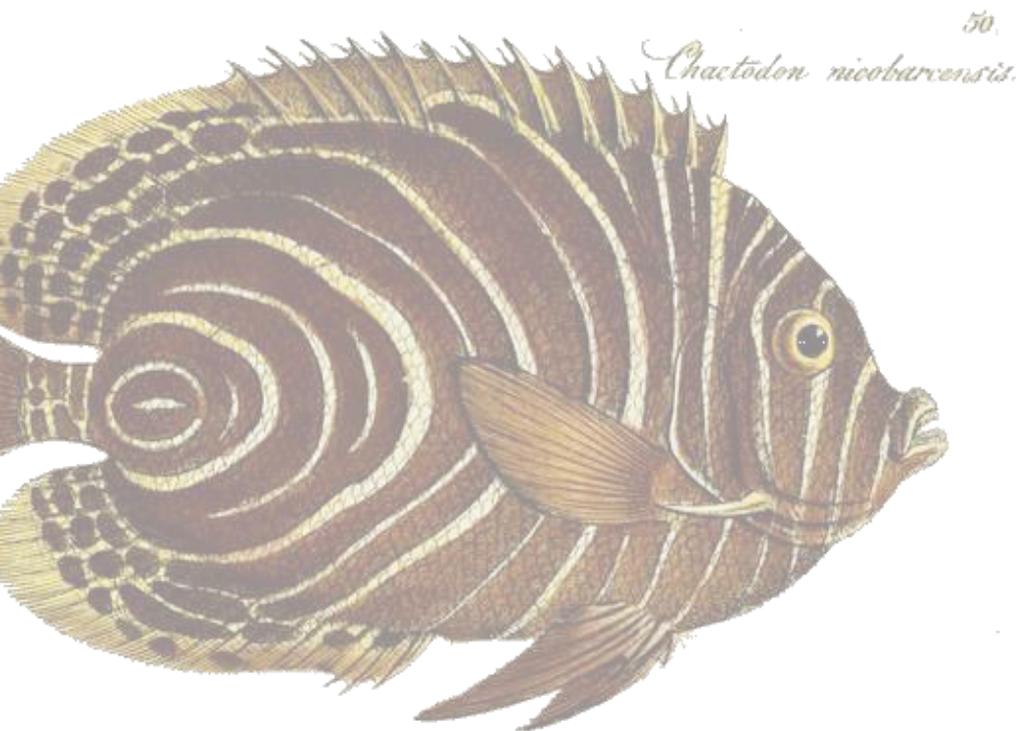
Nonetheless, our study shows that, in a system exposed to long-term anthropogenic disturbance, herbivores were able to remove the majority of both macroalgae over a 24 h period at all sites, failing to do so only when impacts became extremely strong. Capacity for herbivory and its resilience is perhaps facilitated by the high regional species diversity allowing for the functional replacement of species under varying levels of impacts. Even though the identity of herbivores contributing to algal

One of the primary concepts of ecological resilience is the capacity of systems to reorganise while undergoing change, yet retaining the same function (Walker et al. 2004). While the community composition of algal-feeding fishes, with the exception of one species with a low proportion of overall bites (*Siganus virgatus*), differed across sites, the herbivore communities were able to fulfil the function of macroalgal maintenance. The presence of *B. muricatum*, thought to be a bioeroder (Hoey and Bellwood 2009), at KA demonstrates that previously unknown species can also contribute to the important herbivory process (Bellwood et al. 2006b; Plass-Johnson et al. 2014), while variation in feeding by the siganids and *Naso* species exemplify the potential for resilience

removal in this study was highly variable along the cross-shelf gradient, herbivory was sustained throughout the system except for the site of the highest localised impacts, demonstrating remarkable resilience in herbivory on the scale of the shelf system.

Chapter VI

Recruitment and succession in the face of herbivory



This chapter is in revision as:

Plass-Johnson JG, Heiden JP, Abu N, Lukman M, Teichberg M. Experimental analysis of the effects of herbivory on recruitment and succession of a coral reef system along a water quality gradient: the Spermonde Archipelago, Indonesia. *Coral Reefs*

Abstract

The composition of coral reef benthic communities is strongly affected by changes in water quality and herbivore abundance and composition. This is particularly evident in highly productive coastal regions that depend on coral reef resources. We tested the effects of ambient water conditions along an established eutrophication gradient, and grazing pressure, on the recruitment and successional development of benthic communities of the Spermonde Archipelago, Indonesia, through caging experiments with settlement tiles. Benthic community composition of the closest reef to land, near the city of Makassar, was significantly different from other sites further off-shore within one month, driven primarily by the differences in recruitment of invertebrates as opposed to turf algae, respectively. In contrast to other caging experiments, herbivore exclusion had no effect after three months suggesting larger, mobile herbivores had little effect on the benthic communities of these reefs at all sites. Despite conditions that usually favour macroalgal development, this group was rarely observed on recruitment tiles even after four months of herbivore exclusion. Furthermore, tiles from both the caged and open treatments retained high proportions of open space indicating the possible role of smaller sized or non-fish herbivores that were not excluded from the experiment. These results indicate that, unlike many other studies, the role of herbivorous fishes in the Spermonde Archipelago has little effect on the recruitment and early succession of the reef habitat and that unexamined biota such as mesograzers may be significant in degraded systems.

Introduction

The increased introduction of terrestrial effluents into coastal marine systems and high fishing pressures due to increasing human populations along the coastal zone have strong impacts on coral reef benthic communities (Hughes et al. 2007). Generally coral reef communities have evolved under oligotrophic water conditions; however coastal development and/or alteration increases stress on coral reef systems due to increased inputs of dissolved inorganic nutrients and suspended particulate matter which reduce light attenuation and increase sedimentation (Fabricius 2005). Understanding the effects of changing water conditions is confounded because these same reef communities also experience high fishing pressures. For coral reefs the combined effects of increased inorganic nutrient input and particulate matter, and the removal of fish species can be far reaching because they impact competition among benthic biota, and thus potentially severely affect community composition (Bellwood et al. 2004).

In most experiments that have tested top-down and bottom-up controls on coral reefs, results have shown that increased nutrients and decreased grazing pressure facilitate growth of macroalgae leading to over-growth, reduction of light, and resultant competitive success over scleractinian corals (McCook et al. 2001). However, evidence of *in situ* phase shifts to macroalgal dominance has been ambiguous (Bruno et al. 2009) with examples being more predominant in Caribbean and Western Indian Ocean reefs rather than Indo-Pacific coral reefs. In fact Bruno et al. (2009) paralleled hard coral loss in the Indo-Pacific with higher levels of other non-algal taxa such as sponges and gorgonians.

The response of non-scleractinian coral reef species to changing water conditions can severely affect the health and abundance of scleractinian coral, the primary reef building organisms, thus affecting the greater community. Generally, non-coral organisms affect the reef by competing for space, inhibiting coral recruitment, and therefore, altering structural strength of the reef substratum by not contributing to reef accretion (Fabricius 2005). For instance, crustose coralline algae (CCA) are essential for coral settlement, yet their survival is compromised under conditions of fine sediment

accumulation or if it is organically enriched (Harrington et al. 2004). Filter feeders can thrive in degraded marine systems (Cooper et al. 2008) however, many of these species are also macrobioeroders which can physically bore into, or chemically erode (Lazar & Loya 1991) the carbonate reef substratum. Responses by algae to changing water conditions can be species- or group-specific, though increases in any type of algae create competition for space through chemical means or by the trapping of sediment and/or shading (Szmant 2002).

Generally it is accepted that the presence of a healthy herbivore population can mitigate algal populations when nutrient conditions are no longer limiting (Hughes et al. 2007). However, herbivore feeding can also physically alter the substratum by scraping or excavating algae from the benthic surface which erodes dead coral, generating sediments and also open space for recruitment of new benthic organisms. Behavioural and biological studies on parrotfish have found that, although algae are often the primary constituent of their diet, incidental consumption of other reef benthic biota does occur (Choat et al. 2002, Plass-Johnson et al. 2013). Likewise, other groups of fishes such as the wrasses (*Labridae*) and breams (*Nemipteridae*) are important feeders of non-algal benthic biota. These fishes can compose a significant proportion of fisheries among countries that rely on coral reefs for resources (Lokrantz et al. 2010), indicating that fishing can have indirect effects on benthic communities, even those experiencing increased nutrient input. In such situations, the removal of herbivorous and non-herbivorous fish species may be highly important if the reef systems are experiencing a high level of reduced functional redundancy.

Unfortunately, human impacted, highly disturbed coral reef systems are becoming commonplace (Burke et al. 2011). Thus, it is becoming essential to understand how these degraded systems will develop under varying and increasing disturbance. To obtain an accurate understanding of coral reef development, its examination should be conducted under representative conditions where coral reefs are exposed to conditions which are widely applicable. An area of particular concern is the Coral Triangle of Southeast Asia. This area is one of the most biodiverse areas on the planet with 75 % of known coral species and > 3000 fish species (Veron et al. 2009). These marine resources are used directly by more than 130 million people, even more with the resources that are directed overseas (Burke et al. 2011). Many of the reefs in the area have realised exposure to altered environments because of intense agriculture, aquaculture and destructive coral reef resource use combined with inefficient law enforcement. One of the largest reef fisheries in the region occurs among the Spermonde Archipelago of Southwest Sulawesi (Ferse et al. 2014). The reefs of the region are exemplary of heavily developed coastal regions where land run-off and destructive fishing practices have existed for decades (Edinger et al. 1998, Pet-Soede & Erdmann 1998, Pet-Soede et al. 2001). In the region, scleractinian coral biodiversity (Edinger et al. 1998, 2000), ecological dynamics (Sawall et al. 2011, 2013), and fish community composition (Pet-Soede et al. 2001) are subject to intense nutrient input and fishing pressure. All related studies have found strong links with localised eutrophication and fishing impacts (Cleary et al. 2005, Becking et al. 2006, Cleary & Renema 2007), the former being associated with patterns of live coral with distance to Makassar (Edinger et al. 1998, Renema & Troelstra 2001). Unselective, destructive fishing practices are common and intense in the area (Pet-Soede & Erdmann 1998), and near-shore water particulate matter and dissolved organic nutrient levels are high (Edinger et al. 1998, Sawall et al. 2011, 2012) for coral reefs. Despite a situation which would be expected to facilitate a change to macroalgal dominance, macroalgal populations on the reefs are relatively low, and live corals are still present even at the most impacted, near-shore sites (Sawall et al. 2013, Jompa unpub. data).

In this study we expand the knowledge about coral reef community development under pre-existing conditions of eutrophication and high levels of reef resource extraction. We observe the

recruitment and successional development of three reefs, varying in distance (1-19 km) from the main city Makassar, over a four month period, under conditions of natural consumer exposure and with large consumers excluded, to test the effects of further increased fishing pressures. Additionally, we observed temporal and spatial variation in benthic community recruitment to identify bottom-up insufficiencies in community maintenance. The main goals of our study were to 1) describe early succession of coral reef communities with varying water quality, 2) describe variation in monthly recruitment, 3) identify the impacts of consumers on the succession and recruitment of benthic communities and 4) discuss the implications of our results for future development of reefs among the Spermonde Archipelago.

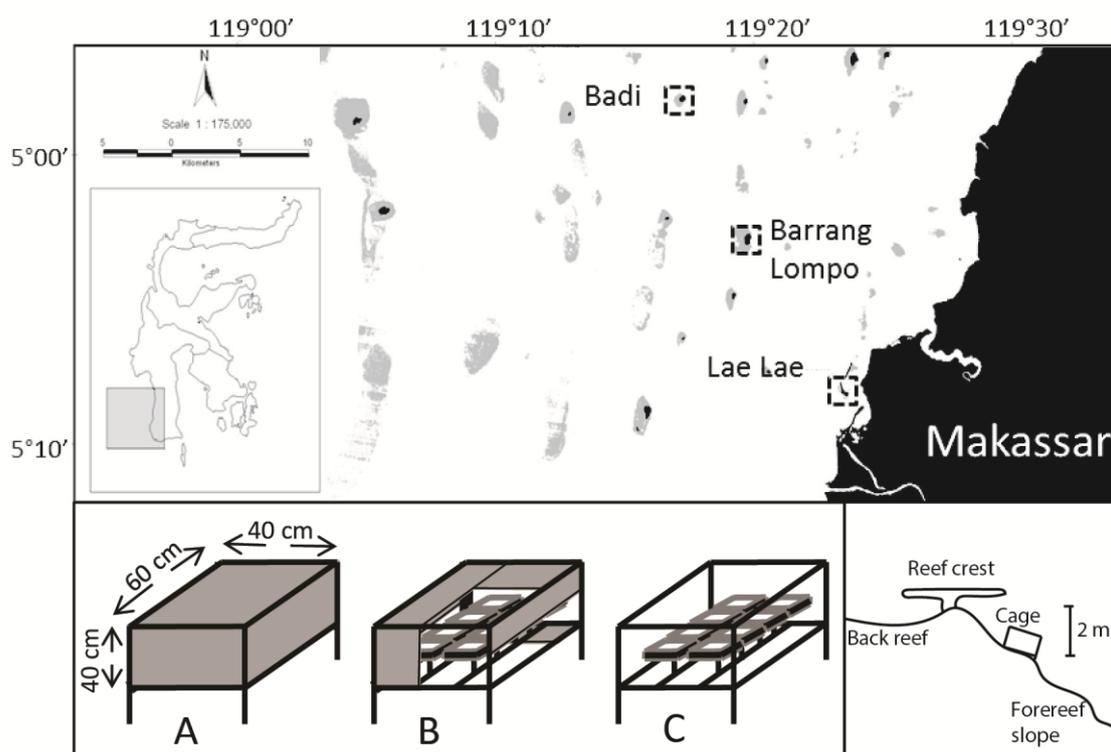


Figure 6.1. Map of the Spermonde Archipelago (top) with sampling sites indicated; Lae Lae (LL), Barrang Lompo (BL) and Badi (BA). Inset identifies the region of the Spermonde Archipelago on the island of Sulawesi. Lower left is the Treatments used for the experimental exclusion of benthic predators. (A) full cage for complete predator exclusion. (B) Procedural control to test caging artefacts. (C) Control, or fully open treatment. All treatments were replicated three times at each site. Tiles had a 10 mm diameter hole drilled through the middle for mounting on to the cage. The legs of the cages were hammered into the benthos and the grey area indicates area that was covered with netting. Caged area was 60×40×40 cm (L×W×H) and legs extended an extra 20 cm. Lower right panel displays the placement of the cages 2 m deep on the forereef.

Methods and Materials

Study Site

This study was conducted between the 16th of November 2012 and 20th of February, 2013, on three islands of the Spermonde Archipelago, Indonesia, along a transect of increasing distance from the city of Makassar (Fig. 6.1). The near-shore island, Lae Lae (LL; 05°08S, 119°23E) at 1 km from land, is highly affected by effluents from the city's harbour, sediments, aquaculture outflow and wastewater from the fluvial discharge of the nearby rivers (Renema & Troelstra 2001). Barrang Lompo (BL; 05°02S, 119°19E) is 11 km distance from the mainland and receives effluents from the

city regularly during the wet season. The farthest island, Badi (BA; 04°57S, 119°16E), is 19 km in distance and receives effluents only during the heaviest rains of the wet season (Renema & Troelstra 2001)(Fig. 6.1).

To standardise sampling among sites, we chose the northwest corner of the three islands which have similar bathymetric profiles. The western coast of the islands generally features a well-developed, carbonate fore-reef and a sandy back-reef and flat. The reef crest was shallow (~3 m) and the slope reaches down to 15 m.

Water parameters

All water quality parameters (particulate organic matter (POM), ammonium (NH₄⁺), nitrate + nitrite (NO_x), phosphorus (PO₄³⁻), chlorophyll-a (Chl-a), dissolved organic carbon (DOC), dissolved oxygen (HDO), salinity and light attenuation (K_d) were collected during two different samplings; during the first week of November (2012) and the first week of February (2013). Water samples were collected in six replicates from the same depth as the experimental cages. Salinity and Chl-a data were logged with a Eureka Manta logger (GEO Scientific Ltd.) recording at two minute intervals. K_d was calculated from underwater light profiles taken with a light meter (LiCor Li-192SA, Lincoln, USA), where:

$$K_d = \ln [Ed_{(z_2)}/Ed_{(z_1)}] * (z_1 - z_2)^{-1}.$$

Ed_(z₂) and Ed_(z₁) are measurements at 0.05 m (z₁) and 4.5 m (z₂) below the surface (Kirk 1994). Due to bad weather conditions, light data was not collected during the second sampling at all stations.

Habitat assessment

Benthic communities were quantified at each island in the first week of February 2013, with 25 benthic photographic quadrats per 50 m transect (see *Fish surveys*). Photographs were taken at 1 m above the substratum, every 2 m along the transect. Coral Point Count with Excel extensions (CPCE; Kohler and Gill 2006) was used to analyse twenty randomised points (based on results from power analysis) per photograph for the following functional groups: ascidians, sponges, soft corals, other invertebrates, blue-green algae, macroalgae, turf algae, live hard coral, sand, open space (non-overgrown hard substrate), and other (shadow, garbage, etc).

Fish surveys

Visual surveys of herbivore and invertivore fish species were conducted along 50 m long transects, within the area of the caging experiment. Surveys were completed twice in November (dry season) and twice in January (wet season), and for each day there were three replicates. The two days of sampling were grouped meaning that there were 6 replicates for each season. The surveys were conducted between 09:00 and 10:00 am, 2.5 m left and right of the 50 m transect line. All fish species >3 cm were counted and their size estimated to the nearest cm. Cryptic fishes were not recorded because accurate counts and identification could not be guaranteed. Species identification and diets followed Allen and Erdmann (2012) and FishBase.org (Froese & Pauly 2011). Biomass of fishes was calculated from individual size observations and length-weight relationships were obtained from Kulbicki et al. (2005).

Table 6.1. Table of all water quality parameters and abundances of herbivore and invertivore fishes measured in November (Season: N) 2012 and February (Season: F) 2013 at all three sampling sites (Lae Lae: LL, Barrang Lompo: BL, and Badi: BA). Statistical differences were tested with one-way ANOVA, and the inclusion of the Fisher's post hoc results indicates a significant ANOVA. ND indicates non-detectable and NA is not available.

	Season	LL	BL	BA	Post hoc
POM (mg L ⁻¹)	N	12.19 (0.97)	5.19 (0.25)	4.37 (0.33)	LL>BL=BA
	F	3.64 (0.70)	2.19 (0.63)	2.59 (0.30)	LL>BL=BA
NH ₄ ⁺ (μM)	N	0.22 (0.01)	0.05 (0.01)	ND	LL>BL
	F	0.07 (0.01)	0.07 (0.01)	0.06 (0.01)	
NO _x (μM)	N	0.60 (0.05)	0.18 (0.01)	ND	LL>BL
	F	0.46 (0.05)	0.48 (0.04)	0.25 (0.03)	LL=BL>BA
PO ₄ ³⁻ (μM)	N	ND	ND	ND	
	F	0.11 (0.01)	0.09 (0.01)	0.08 (0.01)	
Chl-a (μM L ⁻¹)	N	2.84 (0.05)	1.13 (0.04)	1.02 (0.01)	LL>BL=BA
	F	1.53 (0.02)	0.97 (0.02)	0.58 (0.02)	LL>BL=BA
DOC (μM)	N	122.09 (2.56)	104.67 (7.96)	109.37 (3.70)	LL=BL>BA
	F	78.46 (8.88)	84.90 (1.38)	87.36 (1.76)	LL<BL<BA
HDO (mg L ⁻¹)	N	5.71 (0.12)	6.543 (0.10)	6.478 (0.08)	LL<BL=BA
	F	5.69 (0.03)	6.31 (0.09)	6.19 (0.10)	LL<BL=BA
Salinity (ppt)	N	34.1	34.1	33.8	
	F	30.2	31.8	31.9	
Kd	N	0.36 (0.07)	0.46 (0.07)	0.19 (0.05)	LL=BL>BA
	F	NA	NA	NA	
Herb. Fish (g m ⁻²)	N	3.7 (0.8)	7.5 (2.3)	18.6 (5.6)	LL<BL<BA
	F	4.2 (1.5)	8.5 (1.3)	38.5 (9.1)	LL<BL<BA
Invert. Fish (g m ⁻²)	N	0.2 (0.1)	1.5 (0.5)	0.5 (0.1)	LL<BA<BL
	F	0.2 (0.1)	1.1 (0.8)	1.9 (0.5)	LL<BA

Experimental design and treatments

To separate the effects of grazing, recruitment, and succession within each site, tiles were exposed to a fully caged treatment, control (open) treatment, and procedural controls (Fig. 6.1). All were replicated three times at each site. To fully exclude large grazers, the caged treatments were 60 × 40 × 40 cm (L × W × H) and were fully covered with netting of 1.5 cm mesh. Procedural controls were used to account for any artefacts of the caged treatment and consisted of cages of the same size but only enclosed by 1/3 of the mesh on the top, sides and bottom (Fig. 6.1). The side for the mesh was randomly chosen for procedural controls. The open treatment consisted of a cage frame with no mesh. All cages were constructed from 12 mm steel rods. To make sure that cages did not move, all cages had 20 cm legs, which were hammered into the sediment, guaranteeing a secured attachment to the reef. Cages were cleaned of all epiphytic growth once per week. Within the cages, tiles were fastened to the steel rods via a welded stainless steel screw of 10 mm diameter. These rods placed the tiles 10 cm from the substratum allowing room for recruitment to the bottom of the tiles. Tiles were placed in two rows of four tiles with ~3 cm between tiles, and ~5 cm from the sides of the cage (Fig. 6.2).

Tiles were cut in 10 × 10 cm (100 cm²) segments from flat, unglazed 1.5 cm granite rock slates. These had a naturally rough surface similar to that of terracotta tiles commonly used in recruitment experiments (Burt et al. 2009). A hole ~1 cm in diameter was drilled in the middle of the tiles for attachment to frames. Tiles were installed in double, one facing up (top) and one facing down (bottom), providing the same surface on both sides to allow discrimination between the differing settlement communities on light exposed (top) versus shaded (bottom) surfaces.

At each site, cages were haphazardly installed within a 100 m² area, at 2 m below the reef crest (~5 m deep) on the forereef (Fig. 6.1). The location of each cage was chosen because it allowed for the

legs to be hammered into the sediments. This introduced a level of bias because tiles were positioned directly above the lowest parts of the benthos, thus reducing recruitment which might prefer higher surfaces. However, this location was standardised among sites allowing for our comparisons to be relative to each other. Within the cages, the angle of the tiles was horizontal, but the angle of the cages *in situ*, was not constant and depended on the natural bathymetry of the attaching surface.

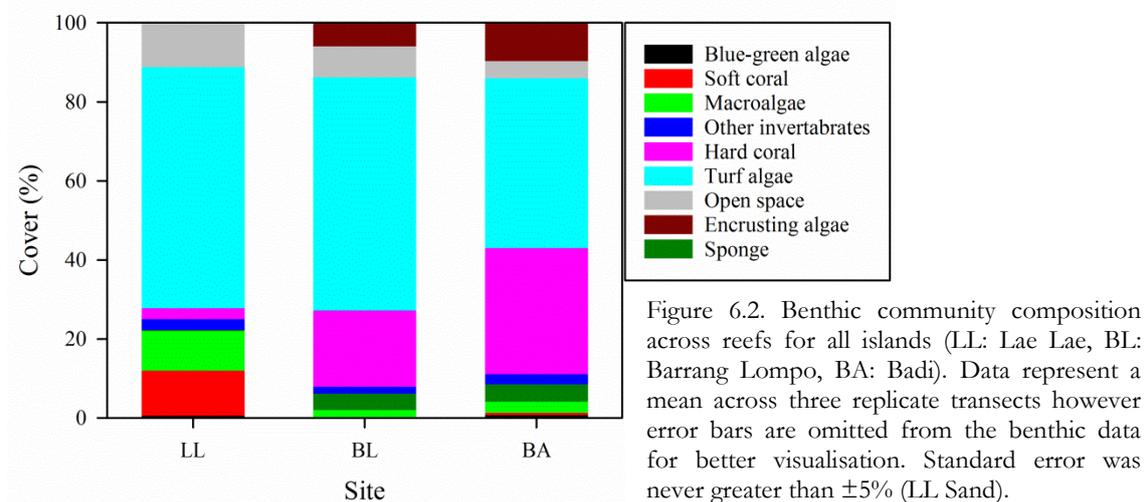
Allocation and sampling of tiles was formatted in two different temporal designs; either for recruitment or community succession. These time periods were applicable for both the top and bottom tiles. For recruitment, tiles were collected every month after one month of exposure to distinguish between differences in recruitment over the course of the experiment. Succession tiles were collected after accumulated times of one, two, three and four months of exposure to follow success of communities over the course of the experiment. For an individual cage at a specific sampling time, a total of eight tiles were collected. This included four recruitment tiles (two top and two bottom) and four succession tiles (two top and two bottom). Tiles were randomly collected, but they were always represented by a corner set and a side set of tiles, standardising edge effects. Tiles were collected *in situ* and allocated to pre labelled, ziplock bags. After collection, all tiles were cleaned of sediments, dried and photographed.

Data analysis

Tile photographs were analysed with the programme CPCE by overlaying 50 randomised points on each tile. This resulted in the percent cover of the benthic biota. Grouping of organisms was based on observed presence after collection. Organisms were categorised by functional groups: tube worms (polychaete worms), blue-green algae, moss animals (bryozoan), barnacles, hard coral, turf algae, macroalgae, encrusting algae, sponges, mussels, or open space.

For each sampling, data from the two sampled tiles (either the top or bottom) for each time period (recruitment or succession) per cage were collated to represent one replicate. Thus, an individual cage was the replicate represented by a surface area of 200 cm². Percent cover was square-root transformed to reduce the influence of the highly abundant organisms. The effect of site (3 levels) and treatment (3 levels) were tested among months for both recruitment and succession with a fully factorial permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001). PERMANOVA was chosen because it is robust to heteroscedasticity, an issue with our low replication ($n = 3$). A time-dependent sampling design can lend itself to a repeated measures analysis, however this was not applicable because new tiles were assessed at each time period. Pair-wise PERMANOVA comparisons were used to identify which treatment caused statistical differences. When the number of unique permutations were low (< 3 comparisons), the Monte Carlo test was employed. The effects of the procedural controls were tested against the open cages using a factorial PERMANOVA to check for artefacts of the cages. After pair-wise post hoc PERMANOVAs were applied on Month Four, similarity percentages (SIMPER) was used to identify groups of organism that contributed most to inter-site differences in communities. It should be noted that PERMANOVA and SIMPER analyses were conducted independently for both recruitment and succession, but also independently for the side (top or bottom) of the tiles. Open space was dropped from the analyses to identify changes specific to the benthic community. However a separate PERMANOVA was conducted on the open space alone because it can reflect the process of grazing and it also represents area for new recruitment. Open space was only analysed on the successional tiles and the statistical design was the same as for the community analysis. Weather conditions restricted the collection of recruitment tiles at LL for months Two and Three. These analyses did not

include LL as a level within factor site. All analyses were completed in Primer + (v.7) with the PERMANOVA add-on. Plots were created in the same programme but also with SigmaPlot (v.12.5). Differences among sites for water quality parameters and fish biomass were assessed with one-way ANOVAs. Differences among sites were established with Fisher's LSD test.



Results

Water parameters

Water quality conditions were generally less favourable at LL than the other two sites at the beginning and end of the experiment. Although water NH_4^+ , NO_x , and PO_4^{3-} were quite low in all sites, NH_4^+ and NO_x were significantly higher in LL in November (Table 6.1). POM and Chl-a were significantly higher at LL than at BL and BD in both sampling times, while DOC was more variable between sites and sampling dates. The HDO was significantly lower in LL than the other sites (Table 6.1). Differences between BL and BA were minimal although DOC varied between samplings (Table 6.1). In all three sites there was a noticeable decrease in salinity from November to February, influenced by increases in precipitation. Light attenuation was also higher in LL compared to BL and BD (Table 1).

Habitat assessment

Live coral cover was lowest at LL, the site closest to shore, and increased with distance from shore (Fig. 6.2). The benthic cover at LL was very distinct from the rest of the sites, with the highest proportion of sand, and relatively equal proportions of macroalgae, turf algae, soft coral and cyanobacteria. Surprisingly, macroalgae was not a dominant feature of the other sites and showed no clear relationship with distance from shore. Rather, turf algae were high at all sites, however the proportional contribution of turf algae decreased away from shore as coral cover and open space increased (Fig. 6.2).

Table 6.2. PERMANOVA results comparing difference among open and procedural control treatments for community structure.

Month	df	One			Two			Three			Four		
		ms	F	<i>p</i>									
Succession													
<i>Top Tiles</i>													
Tr	1	105.3	0.1	0.84	842.6	0.7	0.43	824.1	0.9	0.40	481.8	0.3	0.83
Res	12	821.5			1174.4			876.1			1892.5		
Total	17												
<i>Bottom Tiles</i>													
Tr	1	213.7	0.1	0.82	94.6	0.1	0.91	108.5	0.1	0.90	243.9	0.2	0.783
Res	12	1804.8			1266.8			732.4			976.1		
Total	17												
Recruitment													
<i>Top Tiles</i>													
Tr	1	649.1	1.2	0.51	617.1	2.6	0.09	1002.4	1.6	0.23	249.6	0.4	0.83
Res	12	546.1			239.4			616.0			614.0		
Total	17												
<i>Bottom Tiles</i>													
Tr	1	1997.2	0.9	0.42	3242.3	1.7	0.31	7446.1	1.6	0.24	2389.8	1.1	0.40
Res	12	2184.9			1853.0			4521.3			2247.8		
Total	17												

Fish biomass and composition

Fish biomass varied greatly among the sites with BA having the highest biomass of five times the mass as that of LL and twice that of BL (Table 6.1). Differences in biomass between samplings were minimal at LL and BL, however BA nearly doubled during the February sampling due to an increase in herbivores and invertivores. At all sites, herbivores were much more abundant than invertivores with roughly ten-times more biomass at BA (Table 6.1).

Caging artefacts

The main focus of the experiment was to test recruitment and succession in the absence of predation, in relation to the open treatment. For all times and sides of exposure, communities in the procedural controls never differed from that of the open treatments (Table 6.2). This indicates that there were no caging artefacts found throughout the experiment and, therefore, difference in community structure were due to the environment and to the exclusion of consumers.

Succession experiment

Individual groups of organisms responded differently depending on the site, treatment, or the side of the tile (Fig. 6.3). Bryozoans grew only on the bottom tiles at BA, specifically in the open cages. Mussels grew on the bottom, caged tiles at BL. Tube worms mostly grew at LL, but they were non-existent on the top tiles open to predation. Barnacles only grew at LL, but not on the shaded, caged tiles (Fig. 6.3). CCAs (encrusting algae) were low at all sites although it grew in small proportions at BL on both top and bottom tiles. Macroalgae were always absent except for one top, caged replicate

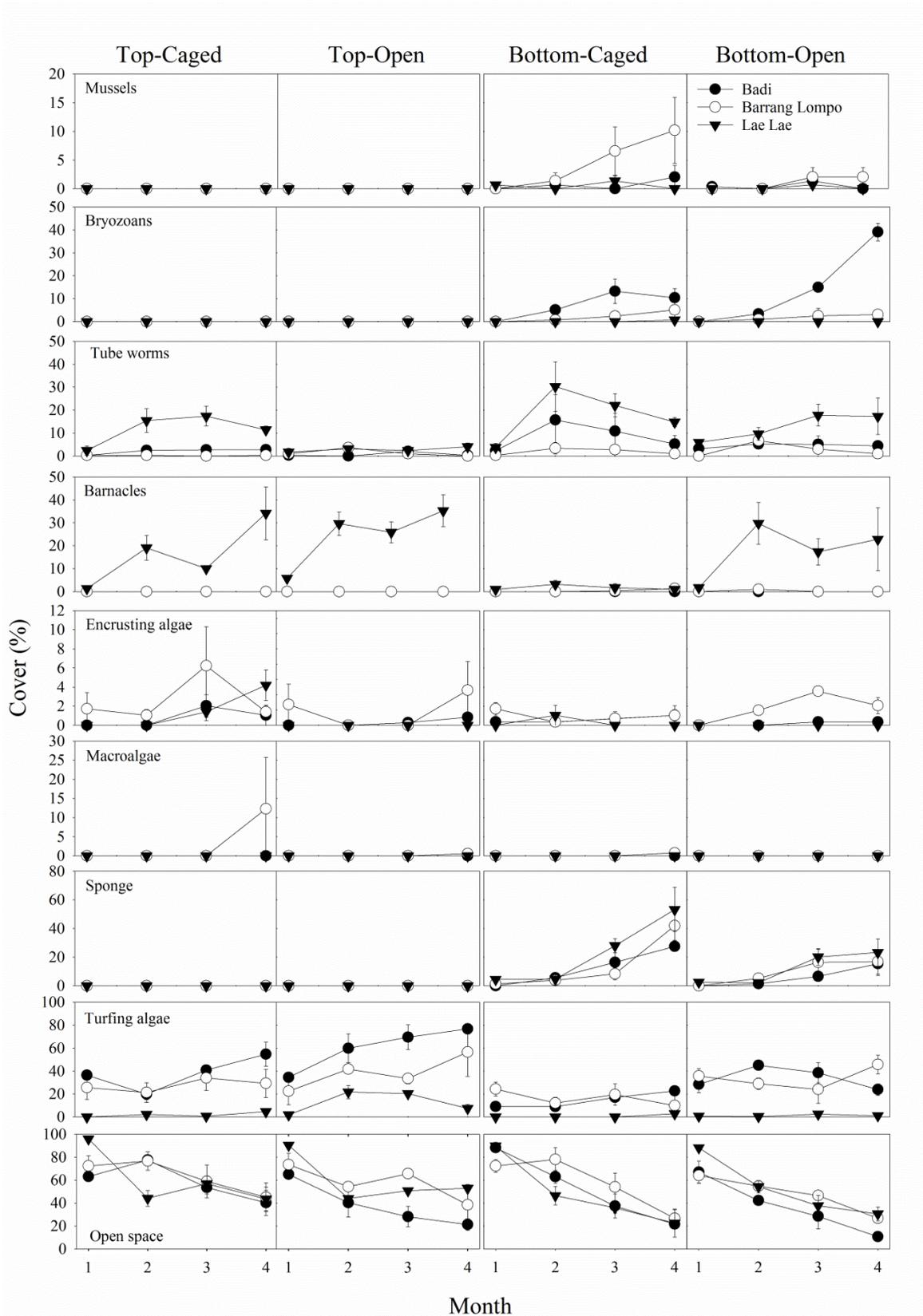
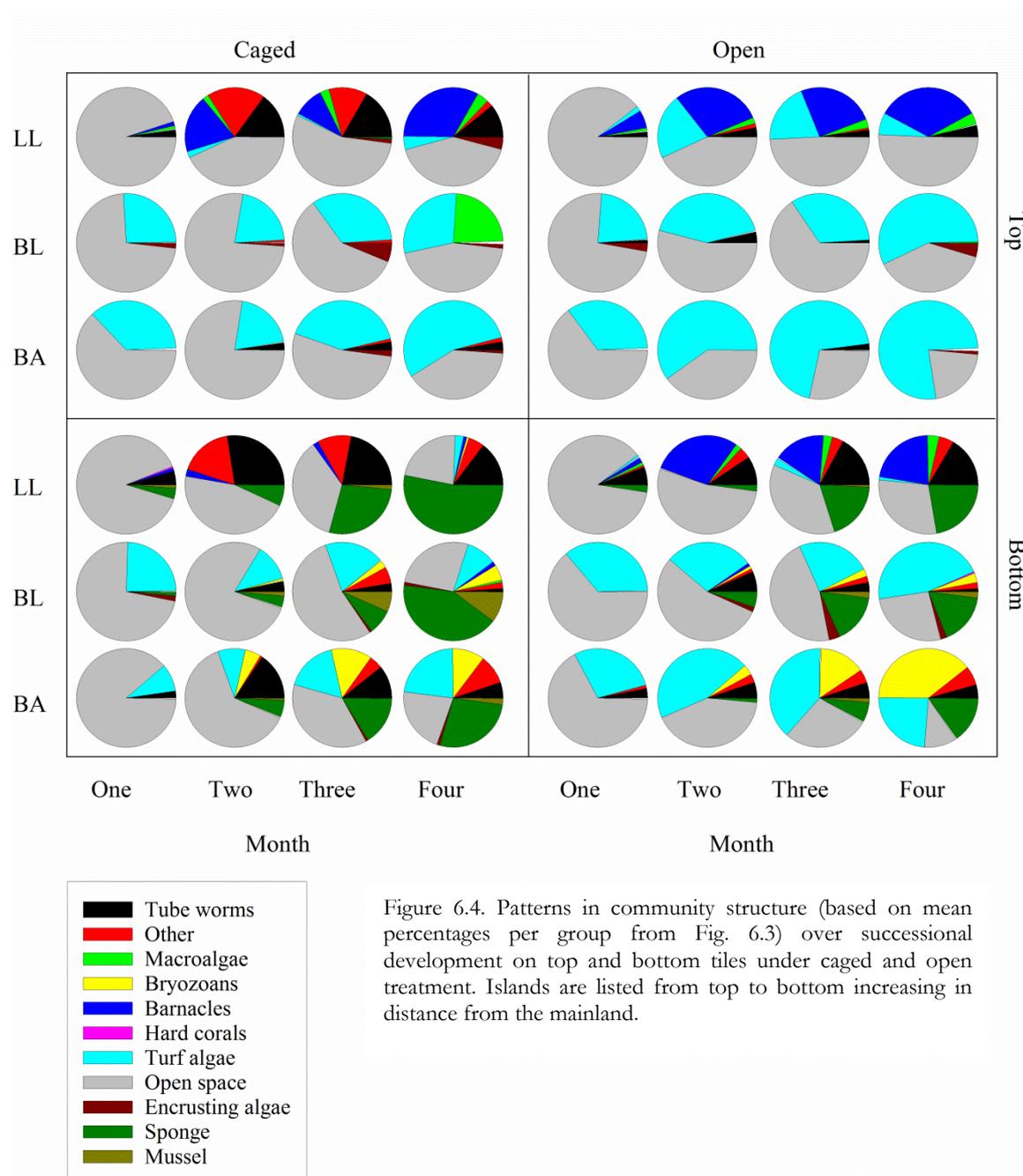


Figure 6.3. Percent cover (mean \pm SE) of functional groups over their successional development on top and bottom tiles under caged and open treatments over time (month one, two, three and four).



at BL at Month Four. Sponges grew on the bottom sides of the tiles only, and there was little effect of site. Turf algae grew at BA and BL, in both treatments for the top, but also in the bottom open treatment (Fig. 6.3). Turf algae were much lower at LL than either BL or BA (Fig. 6.3). Furthermore, differences in mussels, bryozoans, barnacles, encrusting algae and sponges suggest that caging had an effect on the bottom tiles, however this was not consistent among islands (Fig. 6.3).

Due to difference among individual groups, spatial differences in communities were apparent for both the top and bottom tiles by the end of the first month (Fig. 6.4 & Table 6.3). Differences between LL and the other two sites were persistent throughout the experiment. Predation (differences between caged and open treatments) affected both the top and bottom tiles, starting in Month Two and Month One respectively, but these effects were lost by Month Four (Fig. 6.4 &

Table 6.3). Predation affected the communities in both top and bottom tiles at LL and BA in Month Two (Monte Carlo: $p < 0.05$), but not at BL. The main differences in community composition between LL and the other site were due to high cover of tube worms and barnacles, while BL and BA were largely dominated by turf algae (Fig. 6.5 & Table 6.4)

For the top tiles at Month Four, all sites and treatments had ~45% open space with the exception of the open tiles at BA which were ~20% (Fig. 6.3 & 6.4). There was no statistical difference in the amount of open space among sites or between treatments with the exception of Month One and Two (Table 6.5). At Month One, there was a difference among sites on both the exposed and shaded tiles, while at Month Two there was a small effect of treatment for the exposed tiles (Table 6.5).

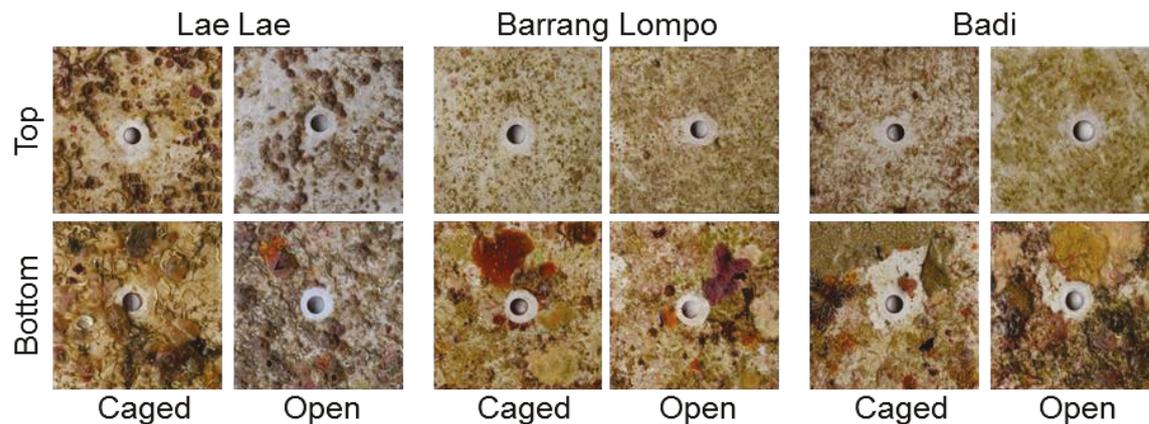


Figure 6.5. Photographs of representative benthic successional tiles after four months of exposure for caged and uncaged treatments at all islands.

Recruitment

There was much higher recruitment at both BL and BA than LL, based on Months One and Four (Fig. 6.6). In general there was much more recruitment on the bottom control tiles, and they also showed a higher diversity of recruits which was particularly evident in Month One and Two at BA (Fig. 6.6). Where LL was included in the analysis (Months One and Four), the effect of site was pronounced, alternatively, this was not apparent in months where LL was not included (Table 6.3). For BL and BA, recruitment on the top tiles was dominated by turf algae with small amounts of encrusting algae (Fig. 6.6). The bottom tiles were much more diverse, particularly at BA where the controls had higher proportions of barnacles and tube worms (Fig. 6.6). For the top tiles, LL was characterised by much less turf algae than the other sites. Overall, LL had little recruitment but the main group differences compared to the other sites were due to the occurrence of tube worms and encrusting algae (Fig. 6.6). Caging had an effect on bottom tiles at BL and BA (Monte Carlo: $p < 0.05$), and at BA (Monte Carlo: $p < 0.05$) for Month One and Four, respectively, resulting in a significant interaction (Table 6.3). There was no effect of caging during Months Two and Three for the top tiles (BL and BA only), but there was an effect for the bottom tiles. Interestingly, in the first two months BA had a large proportion of sponge recruits in the controls but not the caged treatments (Fig. 6.6).

Discussion

While several other studies have examined the effects of increased nutrients and the removal of fishes via caging experiments on coral reef benthic recruitment, most have done so through artificial nutrient enrichment (e.g. Miller et al. 1999, Smith and Smith 2001, Thacker et al. 2001, McClanahan et al. 2003, Burkepile and Hay 2009, Smith et al. 2010, Rasher et al. 2011, Jessen et al. 2013, 2014). Many of these studies show a stronger effect of herbivores and little effect of nutrients (summarised in Burkepile and Hay 2006). In our study, we did not manipulate nutrients experimentally, but instead observed changes in caged and uncaged communities over time in their natural environment at sites varying in their distance from shore. Although nutrients in the water column were generally low among our sites, all other water quality parameters, such as POM, Chl a, and DOC, were higher nearer to shore, which indicated a higher degree of nutrient and organic matter influence (Fabricius 2005). Therefore, our results provide an alternative approach to nutrient enrichment experiments that help capture the combined effects of degraded water quality due to nutrient pollution in structuring benthic communities. The influence of water quality at the sites can be seen by the difference in the communities that after four months of exposure between the site closest to the coast and the other two sites further from the coast. After four months, successional tiles showed that the exclusion of fishes had little effect on communities at any of the sites.

Table 6.3. PERMANOVA results for succession over time and recruitment (for each month). St is Site (Lae Lae, Barrang Lompo and Badi) and Tr is Treatment (caged and open). Recruitment tiles were not collected for Lae Lae at month two and three and PERMANOVA results represent a comparison of Badi and Barrang Lompo. Degrees of freedom (df) listed in () represent adjustments for the non-inclusion of Lae Lae in those months. All significant results are indicated in **bold**.

	df	One			Two			Three			Four		
		ms	F	<i>p</i>									
Succession													
<i>Top Tiles</i>													
St	2	1998.3	11.2	<0.01	2896.7	27.7	<0.01	2955.3	21.1	<0.01	4231.8	13.2	<0.01
Tr	1	16.0	0.1	0.84	1427.6	13.7	<0.01	1557.3	11.1	<0.01	551.2	1.7	0.18
St × Tr	2	155.5	0.9	0.54	493.1	4.7	<0.01	457.7	3.3	0.04	405.7	1.3	0.31
Res	12	179.9			104.6			140.0			321.5		
Total	17												
<i>Bottom Tiles</i>													
St	2	2394.6	24.5	<0.01	2684.4	10.9	<0.01	2798.7	10.1	<0.01	2758.5	8.6	<0.01
Tr	1	613.3	6.3	<0.01	908.4	3.7	0.02	359.3	1.3	0.29	879.5	2.7	0.07
St × Tr	2	142.6	1.5	0.28	608.0	3.5	0.03	274.1	1.0	0.47	617.2	1.9	0.09
Res	12	97.9			246.0			277.1			320.2		
Total	17												
Recruitment													
<i>Top Tiles</i>													
St	2(1)	7037.2	8.6	<0.01	379.8	0.9	0.50	209.0	0.5	0.60	1288.8	5.6	<0.01
Tr	1	105.3	0.1	0.84	721.4	1.6	0.20	448.0	1.1	0.38	537.6	2.3	0.12
St × Tr	2(1)	1080.6	1.3	0.29	250.7	0.6	0.68	1640.8	4.2	0.06	463.5	2.0	0.10
Res	12	821.5			443.4			393.7			231.5		
Total	17												
<i>Bottom Tiles</i>													
St	2(1)	7413.5	16.0	<0.01	1817.1	2.8	0.08	1735.4	1.7	0.20	2336.4	3.2	<0.01
Tr	1	2327.5	5.0	0.01	6547.8	9.9	<0.01	5529.2	5.3	<0.01	3726.8	5.1	<0.01
St × Tr	2(1)	3061.6	6.6	<0.01	961.7	1.5	0.28	898.8	0.9	0.50	2768.1	3.8	<0.01
Res	12	463.4			659.5			1051.6			731.1		
Total	17												

The differences in the LL communities compared to the other two sites were considerable with the former composing mostly of invertebrates on both the top and bottom tiles, and later composing mostly of turf algae. Differences in communities among sites were also reflected in the water quality suggesting that community composition at the near-shore site is a product of decreased water conditions. The non-significant effect of fish exclusion on community composition across the gradient after four months is particularly interesting because these results suggest that the effect of fish on the benthic community composition is minimal. Based on results from Month One and Four, spatial differences in recruitment were present and probably facilitated differences seen in the successional development of tiles. Interestingly, exposure to consumers increased recruitment and diversity on the bottom tiles at Months One and Four.

The differences in communities among sites, presumably driven in part by differences in ambient water quality, were immediate and long lasting. Throughout the year, regardless of the season, LL is exposed to continuous industrial wastes, untreated sewage outflow, sedimentation and commercial port activity (Edinger et al. 1998, Renema & Troelstra 2001), and this has impacted scleractinian and foraminifera diversity (Edinger et al. 2000, Renema & Troelstra 2001, Becking et al. 2006, Cleary & Renema 2007). Previous studies have shown that other sites close to Makassar differ in the community composition compared to sites further from shore (Plass-Johnson et al. in review, Sawall et al. 2013) and our data suggests that this exposure to effluents also affects benthic recruitment and early successional stages of reef development. Nutrients would increase phytoplankton biomass and particulate organic matter (POM) thus affecting light attenuation and increasing oxygen demand, possibly to the point where corals are impacted (Guzmán et al. 1990). Increases in phytoplankton,

Table 6.4. Results of the SIMPER conducted on Month Four of the successional tiles after PERMANOVA pair-wise post hoc indicated differences between LL and the other two sites, but not between BL and BA. % indicates how much difference a specific group contributed between the sites. Only the groups which contributed to greater than 5 % difference between sites was included. Percentage cover, and the change over time can be seen in Fig. 6.3 & 6.4.

Group	LL and BL	LL and BD
<i>Exposed</i>	%	%
Barnacles	33.18	35.47
Turfing algae	19.83	33.91
Tube worms	12.86	11.4
Macroalgae	12.59	
Encr. algae	9.78	5.83
<i>Shaded</i>	%	%
Turfing algae	23.78	22.37
Barnacles	20.94	19
Tube worms	16.43	11.23
Sponge	11.69	9.82
Bryozoans (moss animals)	6.78	22.85
Encr. algae	6.07	

POM and nutrients provide a competitive advantage for non-scleractinian coral organisms through sedimentation smothering existing colonies and also providing conditions for faster growth of algae. These effects are apparent in the greater reef community. LL retains much lower live coral cover compared to the other sites. Soft coral cover is higher, a group that has been shown to proliferate once hard corals have declined (Fox et al. 2003). After four months of succession, LL showed high abundances of barnacles but this is not reflected in the benthic community. This discrepancy could be a product of the benthic community sampling where identification of barnacles from photographs at 1-metre distance would not allow for identification of these small individuals or, that recruits are sourced from the nearby harbour but they do not grow to adults (Jones 1990).

The results of Smith et al. (2010), in Hawai'i found that herbivore effects were immediately apparent, but the effects of nutrient enrichment were not realised until the third or fourth month. There were, however, particularly strong differences between Hawai'i and Spermonde where they saw relatively high herbivore biomass and high artificial nutrient levels (Hawai'i: herbivore biomass $\sim 40 \text{ g m}^{-2}$ and dissolved inorganic N $\sim 4.0 \mu\text{M}$) compared with Spermonde (herbivore biomass $\sim 6 \text{ g m}^{-2}$, $\text{NO}_x \sim 0.6 \mu\text{M}$). These differences were reflected in the algal communities where capacity for growth was limited by nutrients and herbivore communities were not adequate to maintain any growth. Our results from Spermonde are more similar to those from the Solomon Islands where differences between caged and control treatments were minimal at the most degraded sites showing comparable

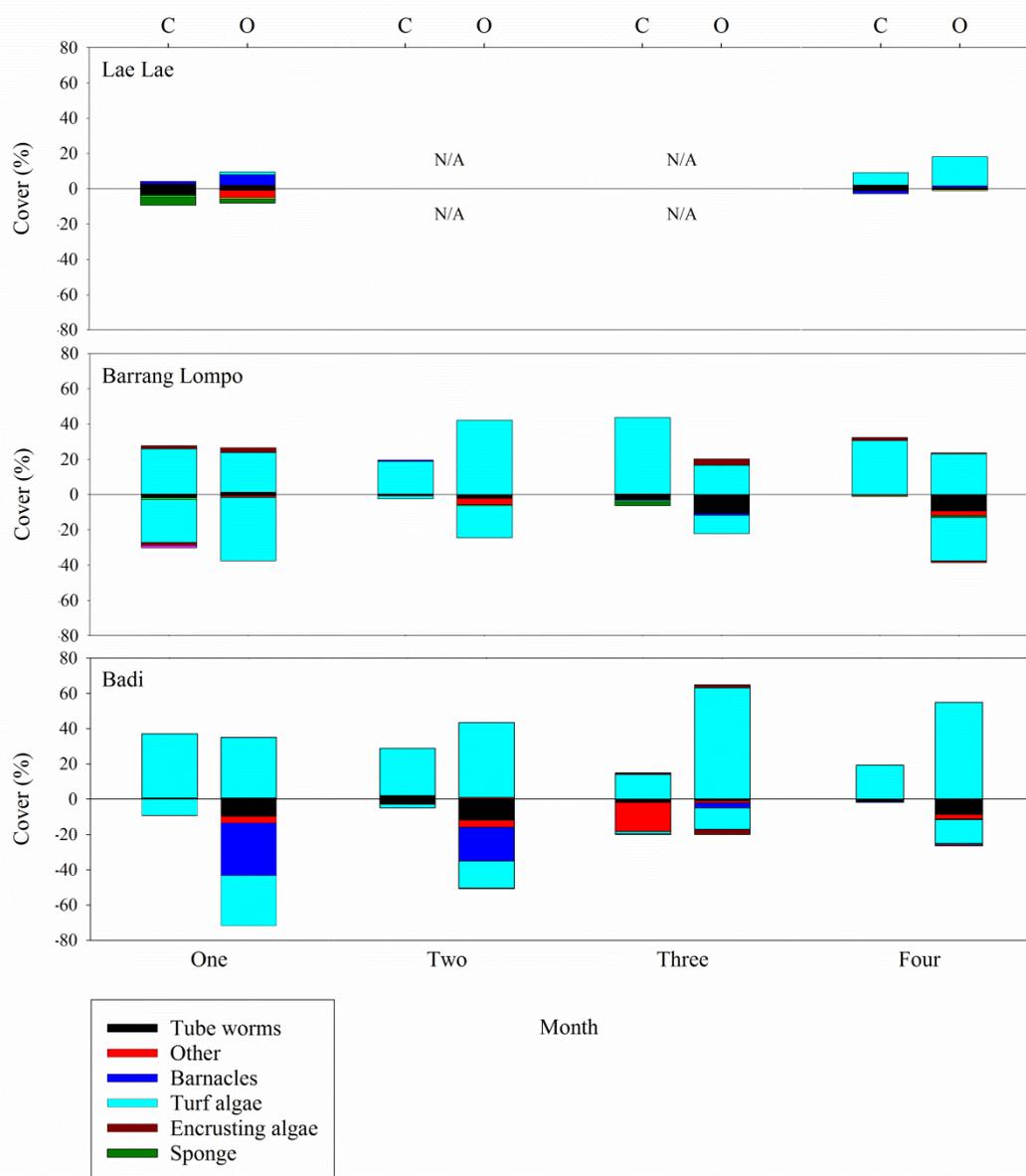


Figure 6.6. Recruitment each month by taxonomic groups for each site, month and treatment. The top section of each panel indicates the recruitment on top while the bottom indicates the recruitment on the bottom tiles for each site. Differences between total percentage displayed and 100 % is open space. Caged (C) and open (Co) treatments are indicated on the top x-axis.

nutrient and herbivore conditions (Solomon Islands: herbivore biomass $\sim 2.17 \text{ g m}^{-2}$ and $\text{NO}_x \sim 1.1 \mu\text{M}$) (Albert et al. 2008).

One of the most commonly cited phase changes in coral reef systems is that from a coral dominated to macroalgal dominated system. Despite this, the commonality of this has recently been questioned by Bruno et al. (2009), particularly in the Indo-Pacific. In the Spermonde Archipelago, macroalgae are not a common component of benthic communities of the reef crest and slope (Plass-Johnson et al., Sawall et al. 2013) and these observations seem uncharacteristic as diverse and abundant source macroalgal communities exist on the reef flat (JPJ and MT unpublished data). Alternatively, turf algae had the greatest successional development increasing cover at BL and BA to roughly 50 % after four months, however, turf algae were relatively low at LL. These results were consistent with the coral reef benthic composition, where turf algae make up a large proportion of the benthic cover. In Belize, McClanahan et al. (2003) found that experimental increase of POM inhibited turf- and macroalgal growth, even when inorganic nutrients were increased. This would help explain the low abundances of macroalgae and turf algae at LL, as POM may smother new recruits. However, in treatments exposed to increased POM and inorganic nutrients (McClanahan et al. 2003), they found an increase in the brown macroalgae, *Padina*. Our study indicates that macroalgal recruitment to the reef slope is low pointing at an inefficiency of bottom-up processes for the maintenance of macroalgal communities. However, the proliferation of turf algae should not be overlooked as this group can also have strong impacts on the benthic community. Turf algae can cause damage to other organisms through allelochemical mechanisms (Jompa & McCook 2003). Furthermore, filamentous algae can trap sediments (Stewart 1989) and shade other organisms (Nugeus & Roberts 2003) while also altering water flow (Eckman & Duggins 1991). Likewise, recent studies have found turf algae to have a significant effect on the coral composition of Belizean coral reefs (Wild et al. 2014) and also impede coral recruitment and development (Birrell et al. 2005, 2008, Vermeij & Sandin 2008, Barott et al. 2012). For our study, coral recruitment or development was never observed, possibly a result of direct competition for space with the faster growing turf algae. Furthermore, turf algae remain a dominant constituent of the greater coral reef community of Spermonde suggesting that our successional and recruitment tiles are representative of early community development.

Open space is generally rare on a coral reef, often only occurring after the feeding of herbivores. Thus, we expected open space to be more common on the treatments open to herbivores, an effect that is repeatedly shown in studies with similar methodology (Albert et al. 2008, Smith et al. 2010, Jessen et al. 2013). However, these studies also show that increasing nutrients and caging result in significantly less open space between 0-10 %. The presence of ~ 45 % open space in our caged treatments could indicate an artefact of the experiment, but also lends possible insight into other processes affecting the benthic community. Mesograzers, such as gastropods and amphipods were not quantified, yet their small size suggests they could have moved in and out of the caged treatments. This group can have a strong effect on algae, especially filamentous turf algae (Carpenter 1986). Overfishing of large-bodied fishes would reduce predation of this group increasing their effect on the coral reef. Furthermore, some species of mesograzers show little change under eutrophic conditions (Fox et al. 2009) while some are impacted by dissolved oxygen (Fox et al. 2008). It is possible that at LL, a subset of mesograzers would combine with sedimentation, twice as high POM as BL, to impact recruitment and succession. This indirect evidence of mesograzers may suggest a functional group that significantly affects the benthic community at the Spermonde Archipelago. If true, this may warrant further investigation into these mesograzers in the region and if they form sub communities that are able to withstand differing levels of water quality.

Caging experiments that utilize an artificial increase in nutrients to display potential changes in benthic coral reef communities to eutrophication and overfishing miss out on further abiotic processes happening within the greater environment such as the production of POM and DOC and decrease in dissolved oxygen. Thus, our results show that increased eutrophication and the exclusion of fishes along with changes in abiotic environmental conditions may not lead to the proliferation of macroalgae on all coral reefs; as seen in Spermonde, all three sites early successional communities were dominated by algal turf which responded with increasing abundance at sites away from shore despite herbivore presence. At the most impacted site, non-coral invertebrates were also continuously seen throughout the experiment. This was also associated with a continuation of open space, perhaps facilitated by unaccounted herbivores and POM. It is possible that the Spermonde Archipelago may be more representative of regional reefs because of the high levels of resource use, terrestrial effluents and seasonal changes. Therefore, coral reefs of the region might expect an increase in turf algae rather than macroalgae with an increase of nutrients and resource use. When these impacts become severe enough, change of the benthic community to one dominated by non-scleractinian invertebrates might be expected. In the face of ever increasing local stressors on coral reefs, we need to gain a better understanding of the dynamic relationships that occur between water quality, consumers and the greater community. Our study demonstrates the changes that can occur to benthic reef communities exposed to long term degradation of water quality and fishing pressure and also, this study highlights how the response of a benthic coral reef community to stressors can differ when compared to other tropical regions.

Section Four

Theoretical links in the coral reef system

Chapter VII

Coral bleaching

This chapter has been published as:

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Abstract

Bleaching of corals (reversible loss of endosymbiotic zooxanthellae) is an unspecific indicator for a range of environmental stressors including too high or too low water temperatures, sedimentation, high irradiance or turbidity, mechanical disturbance, or infection by microbial pathogens. Coral bleaching may result in the death of affected corals depending on the severity and duration of the environmental stressor that induced bleaching. We know that the frequency and extent of high temperature-induced coral bleaching increased over the last century with recent large-scale events and resulting mass coral mortality in the Indian Ocean (1998), the Pacific Ocean (2002), the Caribbean (2005), and even all the world oceans (1998 and 2010). This may lead to major changes in the benthic community composition (i.e., phase shifts) of coral reefs and pronounced modifications of biogeochemical cycles that support coral reef functioning.

Introduction

Coral bleaching is a dynamic process that includes multiple levels of systemic causes and effects. Interactions of the environment at multiple spatial and temporal scales affect coral reef systems. Coral bleaching can be effective as an indicator of large-scale, exogenous environmental processes, or alternatively, there can be indicators of bleaching at the level of the organism up to the ecosystem indicating endogenous processes. Likewise, there can be temporal processes at the scale of the organism or ecosystem that allow differing indications of bleaching cause and effect. Because of the multiple spatial and temporal scales that interact with the processes of bleaching, we try to identify

- (1) early warning indicators of bleaching and/or bleaching as an early warning indicator,
- (2) indicators of direct impacts on corals, and finally,
- (3) indicators of long-term changes under specific conditions within and among communities.

To clarify these ideas, below are examples of each group of indicators.

Early warning indicators of bleaching can be species or environmental parameters that can be highly susceptible to environmental changes, providing insight into developing issues before they affect the system as whole. For example, many corals are highly susceptible to changing water conditions, specifically changes in temperature. These changes in water conditions may be used as indicators of possible wide-scale, coral reef bleaching. Likewise, coral reefs are seen as indicators for global environmental change because they are found in environments at their physiological thresholds. Therefore, coral bleaching can be seen as an indicator of global processes.

Indicators of direct impacts are used to ascertain a process that is currently taking effect. For example, corals may release their symbiotic zooxanthellae prior to and during bleaching events. These changes in zooxanthellae numbers can work as indicators of direct effects.

Finally, indicators of long-term changes provide evidence of an event that has already taken place. There is a range of susceptibility to bleaching in coral reef organisms with some species being highly robust. Post-bleaching examination of coral reef species composition can provide insight into bleaching that has not been directly witnessed

We start this chapter by exploring the definition and historical knowledge of coral bleaching. The following three sections provide information about the causes of bleaching and the physiological processes. The final three sections cover the ecological consequences of bleaching, including some brief ideas on conservation and management strategies. The processes that induce bleaching in

corals and the response of these organisms are closely linked, and an indication of the bleaching processes at any level of organisation may help us to understand patterns and processes of local and global coral reef systems.

Definition and Occurrence of Coral Bleaching

The most conspicuous, rapid and destructive impact of global climate change on coral reef ecosystems is reflected by a physiological stress response of reef corals, a phenomenon called *coral bleaching*. The term coral bleaching is derived from the whitening of the tissue of reef corals that host endosymbiotic *Symbiodinium* microalgae (i.e., zooxanthellae) (Fig. 7.1a). This whitening results from the expulsion of the zooxanthellae and/or the loss of photosynthetic, algal pigments, allowing the white aragonite skeleton to become visible through the transparent coral tissue (Fig. 7.1b). Coral bleaching disrupts the mutualistic symbiosis between zooxanthellae and their cnidarian host, entailing the loss of an essential, internal photosynthetic energy transfer from the algal symbionts to the coral (Hoegh-Guldberg and Smith 1989). At times, bleaching may be reversible, but rapid mortality of weakened and/or diseased corals is common with repetitive or intense events. In extreme instances, consequences for the functioning of coral reefs can be severely negative, as bleaching can lead to systemic failures and serious ecosystem degradation caused by usually irreversible phase shifts of benthic reef communities (Douglas 2003; Wild et al. 2011).

The primary environmental factor triggering coral bleaching is elevated water temperatures, which cause physiological thermal stress (Hoegh-Guldberg 1999). Extreme levels of solar irradiance, including visible (Hoegh-Guldberg and Smith 1989; Banaszak and Lesser 2009) and ultraviolet radiation (Lesser et al. 1990; Shick et al. 1996), can create additional physiological stress to increase the deleterious impact of thermal bleaching. Furthermore, coral bleaching can result from a range of abiotic and biotic stressors as a product of their typical coastal, shallow water distribution. Often, many stressors act in concert to increase susceptibility of corals to thermal bleaching further by lowering their temperature threshold and, subsequently, exacerbating the degree of coral mortality (Lesser 2004, 2006).

Considering the main environmental factors that induce reef corals to bleach (temperature and light), the stability of the coral-zooxanthellae symbiosis can serve as a sensitive environmental indicator, in particular, for temperature anomalies, which are included in climate change projections (Hoegh-Guldberg et al. 2007). Because corals often live in environments where temperatures are close to their physiological thermal threshold, they are highly vulnerable to bleach at temperatures 1 °C above the historical mean summer maximum in many regions (e.g., Toscano et al. 2000). Satellite sea surface temperature data have shown that bleaching of variable severity can be expected if this warming persists for several weeks or increases, and this correlation is now used to forecast the global spatiotemporal distribution and intensity of coral bleaching events (Strong et al. 2006). Given the low thermal tolerance of many reef coral taxa, temperature anomalies can trigger widespread bleaching events posing serious threat to coral reefs world-wide (Hoegh-Guldberg 1999; Pandolfi et al. 2003, 2011).

The phenomenon of coral bleaching has been known for more than 100 years; however, the first comprehensive report on a temperature-induced bleaching event originates from 1929 when Yonge and Nichols (1931) recorded widespread coral bleaching and mortality on reef flats within the Great Barrier Reef. Thereafter, regular reports on bleaching observations can be found in the literature. The first Caribbean thermal “mass bleaching” event of the early 1980s had a widespread impact and led to increased awareness of other bleaching events induced by elevated water

temperatures and high solar irradiance (Glynn 1983, 1996; Lessios et al. 1983; Glynn and D'Croz 1990). Region-wide mass coral bleaching can affect thousands of square kilometres of reef-covered seafloor over relatively small time scales (i.e., within weeks) and thus, constitute a major cause for large-scale coral mortality and the simultaneous decline of coral reef ecosystems (Hoegh-Guldberg et al. 2007).

On a global scale, mass bleaching events can be associated with extended periods of elevated water temperatures generally associated with anomalies in the Southern Pacific Oscillation (i.e., El Niño or La Niña events), which can affect multiple oceanic regions (Hoegh-Guldberg 1999). In 1998, the first, and to date the most severe of four global bleaching events (Fig. 7.2a) affected reefs in all tropical and subtropical latitudes causing a loss of 16 % of corals world-wide (Wilkinson 2008). During this event, 80 % of all corals in the Western Indian Ocean bleached and nearly 50 % died, with up to 95 % mortality at some sites (Lindén and Sporrang 1999; Souter et al. 2000). Another global event occurred in 2002, where the Great Barrier Reef represented the major bleaching hotspot (Fig. 7.2b; e.g. Berkelmans et al. 2004). In 2005, the Caribbean was most severely affected resulting in more than 80 % of corals bleached and over 40 % mortality (Fig. 7.2c; Eakin et al. 2010). The most recent global bleaching event in 2010 (Fig. 7.2d) significantly impacted many regions throughout the Indo-Pacific (Burke et al. 2011; Krishnan et al. 2011; Guest et al. 2012; Furby et al. 2013), including Western Australia, which experienced up to 95 % bleaching and 84 % mortality in certain reef areas (Moore et al. 2012).

Intensity and frequency of world-wide coral bleaching events may be recognised as biological indicators for consequences of global climate change on coral reefs (Hughes 2000). If current rates of CO₂ emission and ocean warming persist, model predictions for the coming decades project the intensity and frequency of bleaching events may increase with possible annual occurrences (Hoegh-Guldberg 1999, 2011; Sheppard 2003; Donner et al. 2007; Hoegh-Guldberg et al. 2007; Lesser 2007; Eakin et al. 2009). One of the latest models predicts that preserving >10 % of coral reefs world-wide would require limiting warming to <1.5°C relative to pre-industrial levels, a figure considerably less than the globally agreed 2°C (Frierler et al. 2013). This prospect clearly constitutes a massive threat to the existence of present-day coral reef ecosystems. Due to the lack of human observers and limited reporting effort in remote locations, the analysis of global bleaching observation databases (e.g., ReefBase) is limited in spatial and temporal terms (Burke et al. 2011). As a consequence, many bleaching events remain unobserved and unreported, masking their actual global frequency and intensity.

These contrasting results have stimulated further research, which has suggested differing levels of thermal stress tolerance and acclimatisation of particular coral taxa, or possibly entire reef communities, acquired from past stress exposures and/or local mitigating environmental, abiotic factors (e.g., shading, current speed, upwelling zones or depth; Maynard et al. 2008; Brown and Cossins 2011). Nevertheless, the capacity for stress resistance and bleaching resilience appears highly variable and limited, as evidenced by recent mass bleaching events that affected much of the occurring coral taxa, and a subsequent, marginal recovery of these systems (Grimsditch and Salm 2006; Baird and Maynard 2008; Baker et al. 2008; Sheppard et al. 2008; Somerfield et al. 2008; Veron et al. 2009). Finally, the physiological capacity for stress acclimatisation may also be closely related to the actual type of active stressors, which will be addressed in more detail in the following sections.

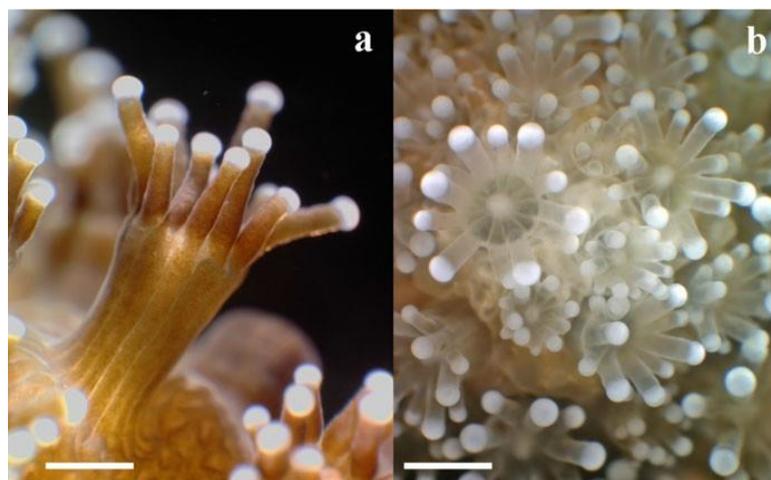


Figure 7.1. Macro photographs showing unbleached and bleached polyp tissue of the scleractinian coral *Stylophora pistillata*. Panel (a): lateral view of protruded unbleached polyps with visible zooxanthellae population, panel (b): overhead view of protruded bleached polyps with nearly transparent tissue; scale bars: 0.25 mm (a) and 0.5 mm (b) Photography: E. Tambutté (Centre Scientifique de Monaco).

Causes of Coral Bleaching

Although the mechanisms of coral bleaching are still not completely understood, various factors that may trigger this process have been the subject of intense research (Brown 1997a, b; Lesser 2011; Wooldridge 2013). Corals undergo bleaching if the environmental conditions that contribute to the stability of the relationship between *Symbiodinium* and the coral host fail (Sect. 9.2). Many field and laboratory studies found increased seawater temperature to be the major factor for the breakdown of the symbionts-host environment, leading to the subsequent occurrence of bleaching events (e.g. Hoegh-Guldberg and Smith 1989; Jokiel and Coles 1990; Lesser et al. 1990; Fitt et al. 1993; Glynn 1993). Temperature increases of 1–2 °C above the mean summer maximum, persisting for several consecutive weeks, can lead to coral bleaching (Jokiel and Coles 1990; Bruno et al. 2001) indicating that many coral species are living close to their upper thermal limits (Jokiel and Coles 1990). Therefore, thermal thresholds have been studied as early warning indicators of potential bleaching events. Rankings of susceptibility of different taxa to thermal stress have been published (Fitt et al. 2001; Loya et al. 2001; Marshall and Baird 2000; Okamoto et al. 2005) (Sect. 9.6). However, thermal thresholds vary among areas and it is not clear how these limits apply *in situ* where several processes (e.g., wind, wave action, and upwelling) can work synergistically to alter the effects of thermal stress (Abdo et al. 2012; Berkelmans and Willis 1999).

While thermal stress is viewed as the principal cause of coral bleaching, several other biotic and abiotic factors have been found to impact the stability of the symbiosis, including: reduced seawater temperatures (Muscatine et al. 1991; Gates et al. 1992; Kobluk and Lysenko 1994; Saxby et al. 2003); supra-optimal levels of visible or ultraviolet radiation (Gleason and Wellington 1993; Lesser and Farrell 2004; Brown and Dunne 2008); ocean acidification (Sect. 41.3) (Anthony et al. 2008); salinity fluctuations (Meehan and Ostrander 1997; Kerswell and Jones 2003); nutrient enrichment (Wiedenmann et al. 2013); bacterial infection (Rosenberg et al. 2009); and cyanide exposure (Jones and Hoegh-Guldberg 1999). Hoegh-Guldberg (1999) added copper ions and pesticides, while Glynn (1996) included sub-aerial exposure, sedimentation, and oil as contributory factors.

However, of critical importance is that mass coral bleaching events, such as those recorded in 1998, 2002, 2005, and 2010 (Goreau et al. 2000; Berkelmans et al. 2004; Guest et al. 2012) (Sect. 9.2), have been associated with the effects of anthropogenic global warming (Hughes et al. 2003; Donner et al. 2005), which has resulted in a steady rise of marine baseline temperatures. Consequently, forecasts of warming events on a global scale such as the occurrence of El Niño events serve as early warning indicators of potential bleaching of wide areas of coral reefs. Likewise, a sudden drop in seawater temperature induced by either atmospheric chilling or intense upwelling may also result in coral bleaching across wide areas (Hoegh-Guldberg et al. 2005) and should be monitored and used as an early warning indicator. Finally, ocean acidification and changes in solar radiation have the potential to cause mass bleaching across large spatial scales as climate change occurs (Anthony et al. 2008; Lesser 2011). These are indicators of long-term changes in coral reef communities and may be monitored with the use of time series data. All the large scale stressors mentioned above and their combined effects may have dramatic consequences on the geographic extent, increasing frequency, and regional severity of future mass bleaching events.

Local stressors such as pollutants, nutrient loading or sedimentation result in localised bleaching events (tens to hundreds of kilometres) because of the constrained nature of the stress source. However, these can act synergistically by effectively lowering the threshold temperature at which coral bleaching occurs, thereby reducing coral resistance and resilience to global climate change (Lesser 2004, 2006; Carilli et al. 2012; Wooldridge 2009; D'Angelo and Wiedenmann 2014). Consequently, these local stressors should also be monitored as they can act as indicators of subsequent bleaching events, especially if they occur simultaneously with high summer water temperatures.

While there is consensus in identifying the above described environmental drivers (e.g., temperature, light) as (direct or indirect) causes of coral bleaching, the scientific community is not in agreement on the role of bacteria as potential causative agents of bleaching. Most coral biologists contend that changes in the microbial community of bleached corals are a mere result of the process. Indeed, during a bleaching event, coral-associated microbial communities show major shifts in their composition and metabolism (Bourne et al. 2007), with an increase in microorganisms capable of pathogenesis (Littman et al. 2011). This has been confirmed by reports that found a positive link between coral bleaching events and subsequent coral disease epizootics (Miller et al. 2006; Muller et al. 2008; Brandt and McManus 2009; Cróquer and Weil 2009; McClanahan et al. 2009).

Consequently, the occurrence of coral diseases might be an indicator of an effect of coral bleaching on both the organism and the ecosystem level, or otherwise bleaching can be used as early warning indicator of subsequent susceptibility of the coral community to disease outbreaks. However, bleaching has also been found to occur as a direct result of bacterial infection in the coral tissue, particularly by gram-negative bacteria of the genus *Vibrio*. Kushmaro et al. (1996) found that bleaching of the Mediterranean coral *Oculina patagonica* was caused by *Vibrio shiloi*, which produces extracellular proline-rich peptides referred to as Toxin P, which blocks photosynthesis and bleaches and lyses zooxanthellae. However, the mere presence of the *Vibrio* bacterium is not sufficient to cause coral bleaching: virulence factors for adhesion and ingress into the coral and Toxin P are produced by the bacterium only at elevated seawater temperatures (Kushmaro et al. 1998; Toren et al. 1998; Banin et al. 2000). Similarly, *V. coralliilyticus* in combination with elevated temperature caused bleaching in the coral *Pocillopora damicornis* (Ben-Haim and Rosenberg 2002; Ben-Haim et al. 2003). These observations led to the Bacterial Bleaching Hypothesis (Rosenberg and Falkovitz 2004; Rosenberg et al. 2009), which proposes a microbial infection as the primary

trigger of coral bleaching. Conversely, Ainsworth et al. (2007) found no evidence to support this hypothesis and argued against its generalisation, suggesting that the bacterial infection is opportunistic rather than a primary pathogenic cause of bleaching and that non-microbial environmental stressors trigger coral bleaching in *O. patagonica*. Nevertheless, a recent experiment with the coral *Montipora digitata* demonstrated that corals exposed to thermal stress in synergy with external bacterial challenge (by different inoculated strains of *V. coralliilyticus*, *V. harveyi*, *Paracoccus carotinifaciens*, *Pseudoalteromonas sp.*, and *Sulfitobacter sp.*) undergo more severe bleaching than colonies exposed to thermal stress alone (Higuchi et al. 2013). Conversely, a ‘healthy’ microbial community (i.e., the microbial community found in healthy colonies) increases the thermal tolerance of the holobiont compared to that of coral colonies whose bacterial community was treated with antibiotics (Gilbert et al. 2012).

From these findings, it appears likely that environmental drivers act on the coral microorganisms as well as the coral host, causing a change in the microbial community that in some cases contributes directly or indirectly to bleaching (Rosenberg et al. 2009). Finally, these studies stress the importance of the inter-action between abiotic and biotic factors and of the stability of the coral microbiota for the resilience of the holobiont to bleaching, calling attention to a more careful consideration of bacteria as fundamental players in the bleaching process. Because of the present development of molecular techniques (e.g., qPCR, CARD-FISH), which are becoming accessible to more researchers every day, monitoring of the bacterial community or of a particular bacterial bioindicator (such as *Vibrio*) may serve as an early warning indicator of bleaching events or as an indicator of direct impact on corals once the bleaching process occurs.

As we come to understand the causes of bleaching and the interaction between different biotic and abiotic stressors across spatial and temporal scales, at both the organism and the ecosystem level, it is fundamental to develop environmental indicators that help in managing and protecting coral reef ecosystems from degradation. Finally, monitoring of these indicators, on both a global and local scale should be implemented and response protocols need to be developed if we are to save these ecosystems in the coming decades.

Mechanisms of Coral Bleaching

Coral bleaching is primarily induced by two factors: photoinhibition and oxidative stress. A clear indicator for coral bleaching is that the coral’s zooxanthellae are experiencing either one or both of these stressors. Photoinhibition is the process in which a constantly high absorption of excitation energy and a decrease in photo-synthetic electron transport combine to cause damage to the photosystem II reaction centre of photosynthetic organisms (Hoogenboom et al. 2012). Photoinhibition can be caused by exposure to thermal stress and increased ultraviolet radiation (UVR). It leads to a reduced yield from photosynthesis and energy expenditure on the repair of damaged tissues (Long et al. 1994). Oxidative stress occurs within an organism when the production and accumulation of Reactive Oxygen Species (ROS) exceed the organism’s capacity to control their levels (Fridovich 1998). ROS are a group of compounds (superoxide radicals, hydrogen peroxide, hydroxyl radicals, and ions) that, when they accumulate in the cells, can damage lipids, DNA, and proteins. They are normally controlled by anti-oxidants produced by the organism. ROS production can increase rapidly in photosynthetic organisms such as zooxanthellae when they are exposed to increased temperature and UVR (Suggett et al. 2008; Lesser and Farrell 2004). As these two factors increase, the production of ROS overwhelms the antioxidant defences and causes extensive damage (Martindale and Holbrook 2002). Besides being transferred to the host from

the zooxanthellae (Suggett et al. 2008), ROS are also produced by the cnidarian hosts as a response to thermal stress (Dykens et al. 1992). A build-up of ROS in coral tissues might be monitored as an indicator for a potential future bleaching event. As the host cells are exposed to, and damaged by, the built up ROS, there are several ways in which the symbiosis can be uncoupled. In apoptosis, a programmed cell death pathway is initiated due to exposure to ROS or extensive damage to the DNA or other cell components. In necrosis, the cell's functioning is disrupted to a degree where it disintegrates without a controlling pathway (Martindale and Holbrook 2002). Additionally, zooxanthellae can be expelled from the host tissue by exocytosis into the gastrovascular cavity, or the cell can be detached from the endoderm as a whole (Gates et al. 1992). For an extensive review of coral bleaching mechanisms, the authors refer the reader to Lesser (2011).

Photosynthesis by zooxanthellae can provide the coral host with a significant proportion of its energy demand (Tremblay et al. 2012). A loss of this contribution due to bleaching severely impacts coral fitness, reducing reproductive output and growth (Manzello 2010; Cantin et al. 2010; Brown 2012). Calcification can be “light enhanced” during the day (Gattuso et al. 1999; Schutter et al. 2012), and although the precise physiological mechanism behind this process is still under debate, a loss of zooxanthellae has a clear adverse effect on calcification (Moya et al. 2008). Coral bleaching can also increase the occurrence of growth anomalies, disturbing the normal development of coral colonies (McClanahan et al. 2009). The reproductive capability of the coral is influenced in the period following a bleaching event, with a reduced number of gametes being produced by bleached coral tissue (Armoza-Zvuloni et al. 2011). Coral reproduction is further impacted by increased water temperatures through reduced fertilisation success (Albright and Mason 2013), and reduced larvae survivorship and settlement (Randall and Szmant 2009a, b). There are, however, factors that seem to reduce the impact of thermal stress on coral reproduction. Cox (2007) found no change in reproductive parameters after a bleaching in *Montipora capitata* and hypothesized that this was due to the coral's capacity to increase its heterotrophic feeding. Along with carbon fixation by the zooxanthellae, heterotrophic feeding is an important source of energy for corals, and Grottoli et al. (2006) found that some corals are able to meet 100 % of their daily metabolic requirements through heterotrophic feeding. Corals of the species *M. capitata* were able to replenish their energy reserves within 6 weeks after a bleaching event when exposed to naturally available zooplankton. Plasticity in heterotrophic feeding has been found to help corals in both resistance to thermal stress (Borell et al. 2008) and recovery from a bleaching events (Connolly et al. 2012) (Sect. 9.7). The status of a reef's coral energy reserves in the time following a bleaching event would be a useful indicator of the chance of full recovery.

What Can We Learn from Bleaching of Other Symbiont-Bearing Organisms?

Research and literature addressing the symbiosis with *Symbiodinium* and bleaching has primarily focused on hard corals as indicators of bleaching, as these are the main builders of tropical coral reefs. However, symbioses between organisms other than corals and *Symbiodinium* remain poorly understood despite the fact that these relationships may help to provide clarification on processes within scleractinian corals and act as indicators for bleaching of various levels. Such symbioses are widespread within various ecologically relevant taxa of marine invertebrates and protists: Cnidaria (Hexa- and Octocorallia, some Scyphozoa such as *Cassiopea*), Mollusca (e.g., Bivalvia of the genera *Tridacna* and *Hippopus*: Hernawan 2008; Nudibranchia: Burghardt et al. 2008), Acoelomorpha (the genus *Waminoa*: Barneah et al. 2007), Porifera (Steindler et al. 2002), and Foraminifera (Lee et al. 1979). Similar to scleractinian corals, symbiosis with *Symbiodinium* in other organisms has evolved as a strategy to complement nutrition; these relationships can be either facultative or obligatory.

Despite many similarities (such as the cultivation of photosynthetically active and proliferating *Symbiodinium* in specific organs, specialised cell structures of host and symbiont, exchange of certain metabolites/chemicals), there are still important differences between corals and other symbiotic systems, particularly on the host side. In most symbioses, *Symbiodinium* lives intracellularly as endosymbionts; in Cnidaria, *Symbiodinium* are found within the cells of the endoderm, and in Nudibranchia, they reside within the digestive gland. In contrast, *Symbiodinium* in many bivalves (e.g., *Tridacna* spp.) are harboured extracellularly in specialised structures (Norton et al. 1992). Within the Acoelomorpha, they occur in parenchyma cells (intracellular) or in the lumen (extracellular; Barneah et al. 2007). In the unicellular Foraminifera, they reside in the endo- and ectoplasma (Köhler-Rink and Kühl 2000).

There is an abundance of literature on the impacts of a changing environment and the effects on scleractinian corals leading to their bleaching (e.g., Berkelmans and van Oppen 2006; Fitt et al. 2000). Throughout various non-coral taxa, investigations of other symbioses and bleaching susceptibility are, nevertheless, unfortunately scarce. Only a few studies have demonstrated that a large variety of *Symbiodinium* symbioses can suffer, and therefore indicate bleaching (octocorals: Goulet et al. 2008; Prada et al. 2010; Strychar et al. 2005; *Tridacna*: Buck et al. 2002; Norton et al. 1995; Porifera: Fromont and Garson 1999; Vicente 1990; Foraminifera: Talge and Hallock 2003). Bleaching mechanisms in these symbioses seem similar to coral systems and are mainly triggered by factors such as high water temperature and irradiance. Thus so far, non-coral symbiotic systems have rarely been used as indicators for bleaching, although they have an important ecological role and their examples in coral reef ecosystems are common. It would be crucial to include these symbioses in bleaching studies, since they reflect various host-symbiont-assemblages that might react differently from corals to bleaching conditions. Therefore, they represent an ideal array of indicators to monitor bleaching.

Many previous studies on corals highlight the importance of symbiont genotype in bleaching susceptibility, and the high diversity in *Symbiodinium* may be the key to the survival of coral reefs in times of coral bleaching. Diversity of *Symbiodinium* differs in various invertebrate hosts. Most scleractinian corals house clades A-D of *Symbiodinium*, but other symbiotic invertebrates and protozoans potentially house an even wider range of types. For example, in Foraminifera six different clades can be detected (A, C, F-I; Carlos et al. 1999; Pawlowski et al. 2001; Pochon and Gates 2010). Acoelomorph flatworms house clades A and C (Barneah et al. 2007), the jellyfish *Cassiopea* spp. houses clades A, B and D (LaJeunesse 2001; Lampert et al. 2011; Santos et al. 2002), sponges contain clades A, C and G (Hill et al. 2011), and various solar-powered nudibranchs cultivate clades A-D (Fitzpatrick et al. 2012; Loh et al. 2006; Wägele and Johnsen 2001). Symbiont acquisition is either vertical, which is the transfer of symbionts through oocytes or clonal cell division as seen in a few scleractinian corals, one species of *Waminoa* and foraminiferans, or more commonly, they are acquired horizontally where every generation needs to acquire new symbionts. Vertical transmission of symbionts offers a reliable pool of certain zooxanthellae suited for stable environmental conditions. Alternatively, this acquisition mode offers less flexibility. In contrast, horizontal transmission offers flexibility such that each new generation takes up suitable *Symbiodinium* types. Depending on the specificity of the symbiosis, this could be a disadvantage, since needed *Symbiodinium* types might not always be available in the environment. Since most symbioses practice horizontal symbiont transmission, they depend on pools of *Symbiodinium* available in the environment (free-living stages in the water column and sediment) and in other symbiotic organisms (connected by expulsion of living symbionts).

Both *Symbiodinium* diversity and symbiont acquisition seem to be important for bleaching susceptibility of the holobiont. Bleaching susceptibility has most often been attributed to the thermal tolerance of the algal symbiont (Ulstrup et al. 2006). *Symbiodinium* display significant differences in physiological performance both within and among clades (Baker 2003; Hennige et al. 2009; Robison and Warner 2006; Savage et al. 2002). These dissimilarities obviously affect host performance (Berkelmans and van Oppen 2006) and influence the holobiont's ability to handle environmental stresses such as increased temperature (D'Croz and Mate 2004; Goulet et al. 2005). It has been suggested that the high diversity in *Symbiodinium* might be the key to survival of coral reefs in times of coral bleaching. Most research has focused on whether or not corals are able to associate flexibly with diverse symbionts whose different physiologies impart greater resistance to environmental extremes (Baker 2003; Berkelmans and van Oppen 2006). This model has been called the 'Adaptive Bleaching Hypothesis' (ABH: Buddemeier and Fautin 1993). According to the ABH, zooxanthellae may enter the host from exogenous sources (symbiont 'switching') or, if multiple zooxanthellae already concurrently exist within the host, a shift in symbiont dominance may occur (symbiont 'shuffling'; Baker 2003). The ABH has been a point of contention with ambiguous results coming from studies largely based on reef-building corals. Nevertheless, the high diversity of *Symbiodinium* in various invertebrate taxa might be important in times of bleaching, since they offer pools of potentially resistant *Symbiodinium* genotypes to bleached corals. Additionally, many non-coral symbioses are mobile and could act as vectors for spreading genotypes that are better adapted to alternative environmental conditions. For instance, a study by Stat and Gates (2008) demonstrated that symbionts can be introduced to new geographic locations vectored by mobile symbiotic invertebrate hosts. They showed that new *Symbiodinium* genotypes were introduced into Hawaiian waters by *Cassiopea* sp.

In contrast to the many studies that focus on the responsibility of the symbiont in bleaching, divergences in host tolerance or, particular host-symbiont-assemblages, have been examined far less frequently as possible causes of bleaching (Brown et al. 2002; D'Croz and Mate 2004; Goulet et al. 2005). Studies have demonstrated that holobionts consisting of identical *Symbiodinium* types but differing in coral hosts react differently to environmental stressors and could, therefore, be used as indicators for bleaching with different sensibility (Baird et al. 2009; Barshis et al. 2010; Bellantuono et al. 2012; Bhagooli and Hidaka 2004). Another recent study by Oliver and Palumbi (2011) indicated that only the combination of heat-resistant symbionts with heat-acclimatised/adapted hosts resulted in thermal tolerant holobionts. Thus, the interplay of both partners seems to determine bleaching susceptibility (Fitt et al. 2009; Ralph et al. 2001).

Concerning bleaching tolerance, generally, the relative role of the host is better understood than the one of the symbiont (Abrego et al. 2008; Baird et al. 2009). Due to the diverse phylogenetic origins of different invertebrate hosts, micro-environments offered to symbionts can vary (Jimenez et al. 2011). Factors such as host tissue thickness appear crucial in holobiont susceptibility to bleaching (Ainsworth et al. 2008; Loya et al. 2001; Stimson et al. 2002), and furthermore, host-driven protective mechanisms that could contribute to the regulation of the holobiont's bleaching response include the production of anti-oxidant enzymes (Baird et al. 2009; Lesser et al. 1990), fluorescent pigments (Salih et al. 2000), and mycosporine-like amino acids (MAAs; Dunlap and Shick 1998).

In summary, there are four main reasons to focus more on non-coral symbioses with *Symbiodinium* as indicators for bleaching in the future. (1) The wide variety of *Symbiodinium* genotypes (with significant differences in physiological performance and thus thermal tolerance) in various invertebrate symbiotic systems might act as potential *Symbiodinium* pools by offering symbiont types

that are better suited for post-bleaching conditions. (2) Many non-coral symbiotic systems are (in contrast to corals) mobile. Mobile symbiotic systems are of particular interest since they can potentially adapt to changed environmental conditions by escaping to areas with more suitable environmental conditions (vertically and horizontally). They can potentially function as mobile *Symbiodinium* vectors by spreading symbiont types that are better suited for post-bleaching conditions by means of expulsion. (3) Since the relative contribution of the host in terms of bleaching tolerance is still unclear (Abrego et al. 2008; Baird et al. 2009), it is crucial to perform comparative studies investigating different symbiotic systems that share *Symbiodinium* as a symbiont. How do various host/symbiont-assemblages react to environmental stressors?

(4) Non-coral symbiotic systems can be used as indicators to trace bleaching conditions early. Some of these systems are already used as bio-indicators for other purpose, for instance foraminiferans (subfamily Soritinae) are important in mineral and calcium cycles (Fujita et al. 2000; Murray 1991) and are used as bio-indicators in reef monitoring programs (Hallock et al. 2003). Another example is the jellyfish genus *Cassiopea*. Niggel et al. (2010) demonstrated that organic matter derived from the jellyfish *Cassiopea* sp. may function as a newly discovered pathway for organic matter from the benthic environment to pelagic food chains in coral reefs. Thus, a combination of organism traits and ecosystem processes could be utilised as indicators for bleaching.

Ecological and Biogeochemical Consequences of Coral Bleaching

The impact of coral bleaching on fundamental physiological processes, such as coral growth, calcification, and reproduction, results in broad-scale consequences for the ecosystem functions and services provided by this ecosystem engineer (Wild et al. 2011). Reduced growth and reproduction may thereby result in reduced resilience of coral-dominated reef communities. Similarly, reduction in the abilities of corals to compete with other invertebrates or reef algae (Hughes 1994) can lead to fundamental changes in the community structure of tropical benthic assemblages. Branching, framework-building corals, including the genera *Acropora*, *Seriatopora*, *Pocillopora*, and *Stylopora*, are morphologies that are more sensitive to thermal stress and bleach more often than massive and encrusting growth forms (Loya et al. 2001; Marshall and Baird 2000; McClanahan et al. 2002). In addition, larger branching colonies are more susceptible to thermal stress than their smaller counterparts (Bena and van Woesik 2004; Mumby et al. 2001a; Nakamura and van Woesik 2001). Consequently, mass coral bleaching events will likely change the coral reef landscape from one supporting a diversity of coral colony morphologies and species to a landscape dominated by fewer species with robust, small, massive, and encrusting coral forms. Therefore, coral morphology and species composition across the benthic reef community are potential proxies for the ecological effects of bleaching events.

Coral-generated production of inorganic materials (i.e., framework structures and calcareous sands) will decrease substantially with increasing bleaching frequency and extent because of the bleaching-induced inhibition of calcification (Sect. 9.4). Parameters such as reef rugosity may therefore also act as potential indicators reflecting the reef ecosystem consequences of coral bleaching. The calcifying activities of reef-building corals ultimately result in a three-dimensional matrix that provides space, shelter, and food for many reef associated organisms (Sale et al. 2005). Coral reefs are therefore associated with high abundances of fishes (McClanahan and Shafir 1990) and other animals. Coral bleaching may reduce the framework building and habitat generation capacity of reef corals. The resulting reduction in structural complexity also reduces the availability of habitat space at a variety of scales and leads to a considerable reduction in coral

reef fish diversity (McClanahan and Shafir 1990). This highlights fish abundance and diversity as good indicators for coral bleaching consequences on the associated organisms.

Scleractinian corals continuously release particulate and dissolved organic matter (POM and DOM) (e.g., Wild et al. 2004). During thermal-induced bleaching, two different kinds of organic matter are increasingly released: (1) POM as zooxanthellae, and (2) POM derived from the coral host (Niggel et al. 2009). Degradation of these two POM sources by reef microbes is much lower for the released zooxanthellae ($<1\% \text{ h}^{-1}$) than for the coral-derived POM ($>5\% \text{ h}^{-1}$) (Wild et al. 2005). The very low microbial degradation rates for the cellulose-containing zooxanthellae indicates that most of the suspended zooxanthellae released during coral bleaching are not degraded and recycled by the reef microbes fast enough to allow recycling to take place in the reef. Alternatively, zooxanthellae are exported from the reef via the prevailing water currents. Thus, from a biogeochemical point of view, coral bleaching most likely involves a considerable loss of energy and essential nutrients from the reef ecosystem. In contrast, coral-derived POM may function as an energy carrier and particle trap (Huettel et al. 2006; Wild et al. 2004). This material, because of its fast microbial degradation rates, potentially stays within the reef system and is recycled, particularly by the benthic community (Wild et al. 2004). Histological analyses (Fitt et al. 2009) indicate that internal mucus production in the coral tissue is depleted during bleaching so that mucus-POM release by corals is most likely stimulated only during the early phase of bleaching, but drops to lower levels the longer the bleaching event lasts. This dynamic flux of POM was confirmed by the study of Piggot et al. (2009), who demonstrated that the number of mucus-producing cells (i.e., mucocytes) in coral tissue is potentially a good indicator for bleaching because they decline after an initial bleaching response. Coral bleaching thereby largely reduces the metabolic exchange between corals and all reef organisms that feed on coral-derived organic matter (e.g., microbes, filter feeders, fish) while also reducing the capacity of corals to trap organic matter. This may lead to further loss of POM from the reef system with subsequent important biogeochemical consequences.

Corals can recover from bleaching (Sect. 9.4), which also allows the reoccurrence of organic matter release by this key ecosystem engineer. The respective recovery time scales range from weeks to months (Gates 1990; Jokiel and Coles 1990), so that short- to mid-term effects on organic matter cycles driven by the corals can be expected from a brief impediment of the coral engineer during reversible bleaching. However, this may include long-term changes in the reefs nutrient recycling capacity. The initiation of carbon and nutrient cycles by coral-derived organic matter will, therefore, likely be reduced by coral bleaching.

Bleaching-induced mortality of the coral polyp also results in the exposure of bare skeletons. These structures are particularly sensitive to physical, chemical, and biological erosion processes (Stoddart 2008). In addition, colonisation of these stable surfaces by microbial biofilms, algae, or other invertebrates may not only reduce coral recruitment success (e.g. Webster et al. 2004), but also change important biogeochemical processes in the reef, such as nitrogen fixation (Davey et al. 2008).

Coral Susceptibility and Resilience to Bleaching and Subsequent Reef Degradation

Susceptibility and resilience

In corals, photosynthesis of endosymbiotic zooxanthellae is significantly affected by light availability and water temperature. These environmental factors can affect coral susceptibility and resilience to bleaching, and because of this, considerable work has gone into understanding the parameters that influence light and temperature conditions in coral reef ecosystems (reviewed in:

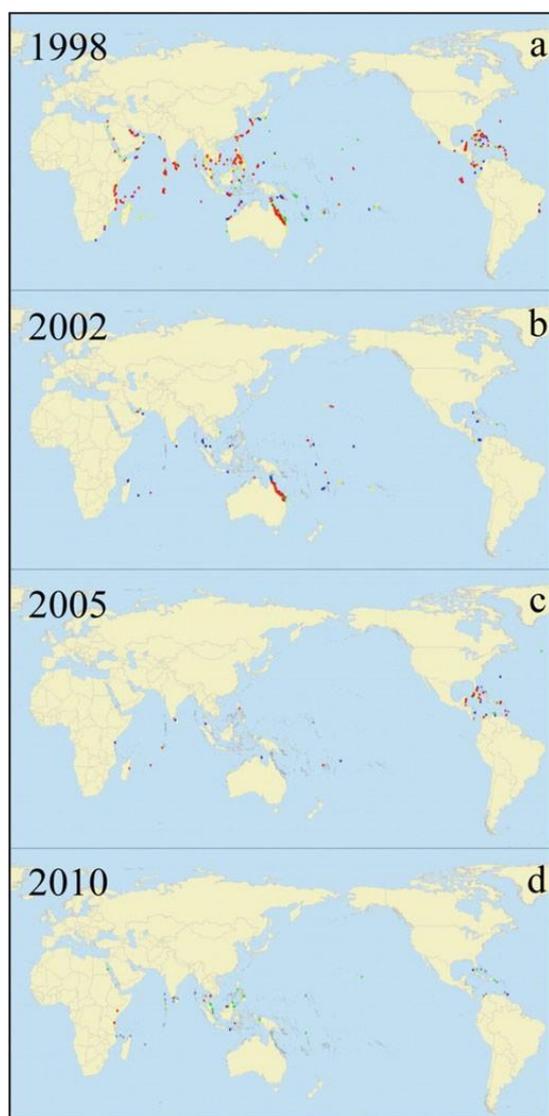


Figure 7.2. Overview of bleaching reports covering the four global mass bleaching events since 1998. Panels (a–d): 1998, 2002, 2005 and 2010, respectively. Bleaching severity indicated by colour coding: *red* ¼ high, *yellow* ¼ medium, *blue* ¼ low, *grey* ¼ severity unknown, *green* ¼ no bleaching (Maps adopted and modified from ReefGIS online services (<http://www.reefgis.reefbase.org>) based on the comprehensive ReefBase database (2013) compiled by contributions of UNEP-WCMC, The WorldFish Center, National Oceanographic and Atmospheric Administration (NOAA), Great Barrier Reef Marine Park Authority, Australian Institute of Marine Science and coral-list (<http://coral.aoml.noaa.gov/mailman/listinfo/coral-list/>) maintained by NOAA).

Brown 1997a, b; Hoegh-Guldberg 1999; Loya et al. 2001; Baker et al. 2008; Van Woesik and Jordán-Garza 2011). Given the spatial and temporal heterogeneity in marine environments and in climatic processes, and their dynamic interactions that are potentially confounding, it has not been easy to unequivocally discern all environmental processes affecting coral reef systems.

Ecological resilience is the potential of an ecosystem to absorb repeating disturbances and adapt to change while keeping its function and structure (Holling 1973; Nyström et al. 2000, 2008; Scheffer et al. 2001). Resilience of corals against coral bleaching encompasses the processes of resistance and recovery (Pimm 1984; West and Salm 2003), which represent two important environmental indicators of how corals cope with climate change and direct anthropogenic and natural disturbances. Resistance describes the capability of corals to withstand or to survive bleaching and bears an extrinsic (function of environmental factors) and an intrinsic, species-specific component (West and Salm 2003). Recovery is the process of regeneration after a severe bleaching event that resulted in significant mortality, and is directly associated with the growth and the replenishment of communities via coral recruitment (Marshall and Schuttenberg 2006; Diaz-Pulido et al. 2009).

At the ecosystem level, there is a degree of overlap in resilience and susceptibility, because those factors that make a coral reef susceptible can also increase systemic resilience depending on temporal and spatial occurrence of impacting factors. Research addressing the environmental factors that can mitigate coral bleaching and enhance recovery potential and resilience has identified several environmental indicators. Factors that mitigate thermally induced coral bleaching (Brown 1997a, b; Hoegh-Guldberg 1999; Hughes et al. 2003; van Oppen and Lough 2009) include decreased temperature stress during warm periods through either local seasonal upwelling (Glynn 1996; Riegl and Piller 2003; Chollett et al. 2010) or long amplitude internal wave pulses (Wall et al. 2012). Currently, upwelling-induced mitigation of coral bleaching, and consequently resilient reefs were observed in the western coast of Mexico (Glynn and Leyte-Morales 1997; Reyes-Bonilla 2001; Reyes-Bonilla et al. 2002), the Gulf of Panama (Glynn et al. 2001; Podestá and Glynn 1997), the Gulf of Papagayo/Costa Rica (Jiménez et al. 2001), the Bahamas (Riegl and Piller 2003), South Africa (Riegl 2003), Northern Madagascar (McClanahan et al. 2007a, b), and the Colombian Caribbean (Rodríguez-Ramírez et al. 2008; Bayraktarov et al. 2012, 2013). In addition, Wall et al. (2012) observed that corals of the Andaman Sea/Thailand exposed to deep-water intrusions by long amplitude internal waves were less susceptible to coral bleaching than corals at sheltered sites. Less coral bleaching and faster recovery was also observed in regions with exposure to a naturally high water flow (Bayraktarov et al. 2013; Nakamura and van Woesik 2001; Nakamura et al. 2003; West and Salm 2003). Hydrodynamics enhance water flow-induced mass exchange (e.g., respiration or uptake of nutrients) and molecular transport processes (Huettel et al. 2003), and have considerable consequences for coral physiology (Atkinson et al. 1994; Mass et al. 2010; Wild et al. 2012). They play a role in the removal of toxic Reactive Oxygen Species (ROS) and its derivatives, which are produced during bleaching (Nakamura and van Woesik 2001; Lesser 2006) (Sect. 9.4).

Bleaching can also be influenced by the amount and type of irradiance that arrives at the corals through the atmosphere and water. An increase in particle concentrations within either environment results in the scattering of light and the lessening of its intensity. This has been demonstrated in the Tuamotu Islands, where the absence of bleaching was attributed to high cloud cover (Mumby et al. 2001b). Likewise, coastal reefs with high levels of suspended terrigenous material display less bleaching than reefs further from shore (West and Salm 2003). Similarly, coral bleaching was less in areas that received shading, such as reefs near tall cliffs in the Pacific (Salm et al. 2001). However, it is not just the quantity of light that reaches the corals, but also the quality of light can have strong impacts. Increases in ultraviolet radiation can cause photoinhibition (Sect. 9.4) and this can be a concern for corals in shallow water or in geographical areas with a damaged atmospheric layer (Shick et al. 1996). Bleaching has also been attributed to other factors including reduced salinity (Kerswell and Jones 2003) and exposure to toxins (Jones et al. 1999) (Sect. 9.3), and although these can present localised confounding factors, most managers assessing bleaching susceptibility consider the mediation of high water temperatures of most importance due to its widespread implications (Sect. 9.8). Faster recovery from bleaching and thereby higher resilience in the long term was attributed to corals that increased their heterotrophically acquired carbon budget (Grottoli et al. 2006) (Sect. 9.4).

Understanding the effect of varying environmental conditions on corals is becoming increasingly important, because climate change is likely to increase the spatial and temporal variability of these factors, some of which are directly related to coral bleaching. When high temperature anomalies are severe and prolonged, as can be experienced during El Niño years, regional-scale bleaching can be pronounced (Glynn 1993) (Sect. 9.3). In some regions, the frequency

and intensity of tropical storms may also increase (Hughes et al. 2003), although, there are indications that storms may provide a net benefit to coral reefs because they mix warming surface layers with deeper waters (Riegl 2007). Changes in global weather patterns will lead to more extreme rainfall in some areas (Hoegh-Guldberg et al. 2007). This, combined with increasing coastal populations, may increase pollution and eutrophication on near-shore reefs (Glynn 1996), reducing overall coral fitness and making them more susceptible to bleaching. Moreover, thermal expansion of the oceans indicates that sea levels will continue to rise, and further redistribution of heat in the oceans may lead to changes in the dominant currents known as the “global conveyor belt” (Hoegh-Guldberg and Bruno 2010). Although not a direct factor of coral bleaching, ocean acidification may lead to a reduction in carbonate accretion and density, resulting in a decrease in overall coral fitness (Hoegh-Guldberg et al. 2007). The synergistic effects of these factors, and the changes on spatial and temporal scales, indicate that reefs will experience increasingly variable environmental conditions, and thus, increasing stress that promotes the likelihood of coral bleaching events. This is particularly true for reefs with pre-existing environmental factors, such as land-based pollution of areas with limited cold water exchange, which may increase their susceptibility and make them less resilient to bleaching events.

Reef degradation

In worst case scenarios, combined stressors will interact before, during and after bleaching events leading to increased degradation of reefs. Within coral reef communities, there is taxonomic variation in susceptibility to bleaching (van Woesik et al. 2011) (Sect. 9.6). Coral reefs are generally resilient to localised disturbances because depleted populations can be repopulated by unaffected populations (Sale 1991). However, the extent of coral bleaching can vary depending on population composition and susceptibility (Sect. 9.6), and community effects can vary based on the extent of bleaching events. Immediate ecological responses to bleaching events are less studied than longer-term responses, but studies have shown that other (non-coral) species are affected by their degree of specialisation to corals and their ability to shift resources during alternative ecological states (Pratchett et al. 2009). Specifically, species that rely on corals for food or habitat, such as fish, show the quickest changes in populations, while reduction in coral populations may have sub-lethal effects on coral-specific organisms because later generations are not able to find habitat for recruitment. For example, butterfly fish and certain damselfish populations that experienced losses after extreme bleaching events were able to shift to bleached coral for habitat, but declined because the impacted reef was not suited for larval recruitment (Wilson et al. 2006). Therefore, it may be possible to use species that react strongly to changes in coral communities as pre-bleaching indicators of potential, post-bleaching, coral reef health.

Bleaching-induced changes in habitat can lead to the long-term loss of species and function and overall degradation of reefs. On the community level, continuing function depends on the pre- and post-condition of the reef. In the Caribbean, reefs that existed in equilibrium state between corals and algae became algae-dominated after a relatively minor bleaching event due to an already reduced herbivore community (Ostrander et al. 2000), indicating that the pre-bleaching status of the ecosystem leads to higher levels of susceptibility. Sub-lethal effects on coral reef species, or inter-generational effects, depend on the recovery of the current system.

Although the susceptibility of coral reefs to degradation in relation to coral bleaching events is not easy to understand fully, many indications of possible effects can depend on the environment (changes in light attenuation and water temperature) and the community composition

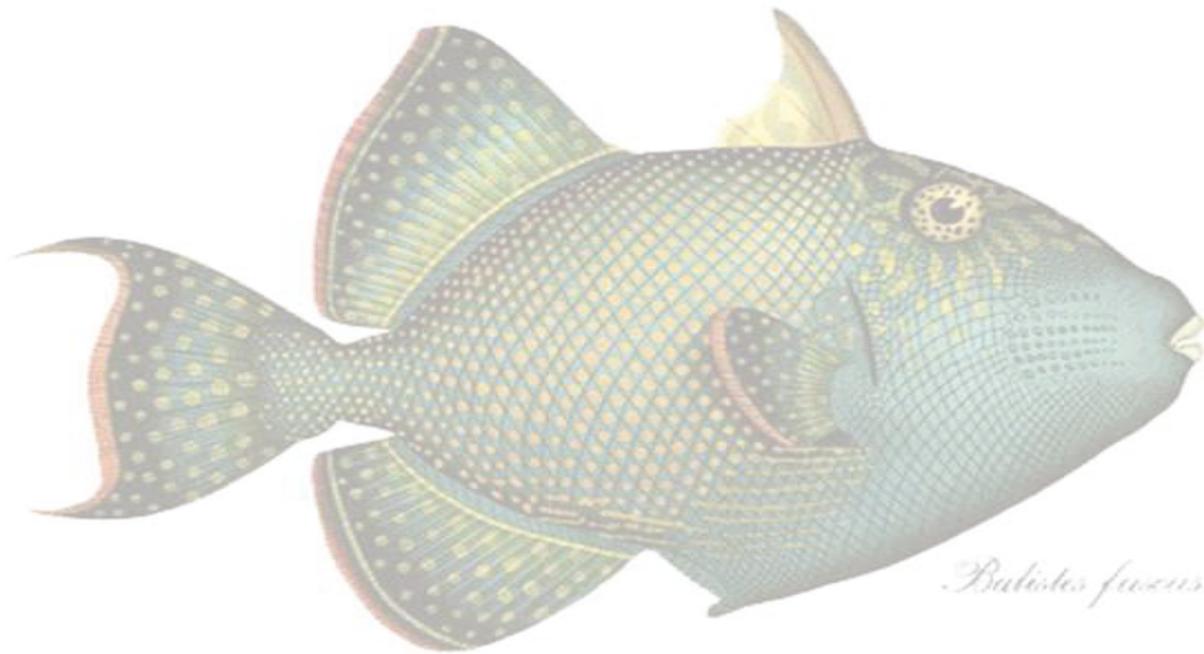
(present groups of organisms). It may be possible to use these conditions as an indication of susceptibility and the possible effects on these vulnerable ecosystems.

Management strategies against coral bleaching

Coral survival and recovery prospects can be promoted through appropriate marine protected area (MPA) design (Salm et al. 2001). Conservation priority is often focused on areas of high-biodiversity (hotspots) that are currently exposed to local anthropogenic stressors (Myers et al. 2000). The disadvantage of this conservation strategy is that the influence of climate change is hardly manageable because local processes such as overfishing or pollution reduce reef resilience prior to climate change driven impacts. Therefore, West and Salm (2003) suggested identifying areas with low exposure to climate threats and reducing human impact on these particular regions (Sect. 9.7). This would assure the potential for corals to persist in “refugia” and resist bleaching in times of changing climate (Glynn 2000; Riegl and Piller 2003). Current conservation strategies should take into account reef resilience assessments during climate change in order to define management priorities (Maynard et al. 2010; Obura and Grimsditch 2009). McClanahan et al. (2012) recently proposed an evidence-based framework for the identification of climate change resilience of coral reefs to define conservation priorities. This novel framework includes the measurement of 11 key factors selected by perceived importance, empirical evidence, and feasibility of measurement (McClanahan et al. 2012). Rau et al. (2012) go one step further and encourage marine science and management communities to actively evaluate all marine management strategies, including unconventional ones such as shading of local reefs from solar radiation during increased thermal stress (Jones et al. 1998; Jones 2008; Hoegh-Guldberg 1999), low-voltage direct current, which has been proposed to stimulate coral growth (Sabater and Yap 2002, 2004; Goreau et al. 2004), and wave- or tidal powered artificial upwelling (Kirke 2003; Hollier et al. 2011). In times of dramatic climate change, our hope lies in the most resilient reefs and the increase of reef resilience through management actions, which should, therefore, be considered as essential conservation priorities.

Chapter VIII

Niche utilisation



Balistes fuscus

This chapter is in preparation as:

Plass-Johnson JG, Bednarz VN, Ferse SCA, Teichberg M. Cross-shelf variation in the trophic niche of two coral reef fishes, *Chlorurus bleekeri* and *Dischistodus prosopotaenia*. *Coral Reefs*

Abstract

Habitat modification of coral reefs is becoming increasingly common due to increases in coastal urban populations. Coral reef fish are highly dependent on the benthic habitat, however the capacity for acclimation to resource and habitat change will determine the persistence of a fish species. This study identifies variation in niche utilisation, based on $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values, of two coral reef fishes with contrasting resource preferences. Furthermore, this study utilised coral reefs along a spatial gradient of changing habitats to identify possible fine-scale variation in resource use of the two species. The parrotfish, *Chlorurus bleekeri*, increased feeding of nutritional sources enriched in ^{15}N closer to shore while increasing sources (greater change across $\delta^{13}\text{C}$ value) of the same trophic level at sites off shore. In contrast, the damselfish *Dischistodus prosopotaenia*, was able to maintain its trophic niche displaying little change in isotopic indices among sites. These results help to resolve the potential of coral reef fishes to change niche utilisation under habitat change. Thus, it seems that parrotfish are able to spread feeding across new nutritional sources while the damselfish is able to self-maintain its own habitat.

Introduction

Unsustainable natural resource use and coastal terrestrial effluents combine to cause regional and local changes in coral reef communities. Increasing evidence is unveiling that the magnitude of change in coral reef communities can depend on the relative exposure to increased nutrients and the degree of resource extraction (Burke et al. 2011). For example, extensive removal of herbivores and increasing nutrient levels has a cascading effect on the ecosystem whereby macroalgae are able to overgrow the reef-framework building scleractinian corals (Hughes 1994, Burkepile and Hay 2006). Any degree of impact can alter the resource availability and predator-prey relationships on a coral reef and thus will affect habitat use and niche utilisation by the biotic constituents (Jones and Syms 1998, Syms and Jones 2000).

The effects of terrestrial derived gradients in marine water across coral reefs have been noted from many parts of the world (Edinger et al. 1998, Fabricius et al. 2005, Lirman and Fong 2007). Coral reefs closer to shore are generally characterised by less hard coral abundance, an increase in fleshy algae, and by a decrease in coral and fish species diversity or even complete shifts in the sets of species (Fabricius et al. 2005, Plass-Johnson et al. 2015b). Thus, changes in coral reef communities along water quality gradients would be associated with a change in their trophic structure (Chapter I) and composition (Chapter V & IX). However, the trophic structure of coral reef communities is highly complex and discerning the specific change of habitat use of any individual species can be ambiguous due to the high biological diversity (Fenner 2012). Nevertheless, understanding change in the trophodynamics of a coral reef community may offer better interpretation of the potential community change under varying environmental stress (Done 1992).

The trophic niche of an organism has been described as the bionomic portion of a species' ecological niche, divisible to n -dimensions based on the sum of all nutritional resource use (Hutchinson 1978). Given the complexity of coral reef communities, there may be limited practicality in observing all resource use and how this changes among environments. The ambiguity associated with the identification of all the resources of a consumer has led to the use of composite markers of a diet, generally through the use of stable isotopes ratios (DeNiro and Epstein 1978). Stable isotope ratios of a consumer are closely linked to their diet (Post 2002) and thus, is similar to the bionomic niche axis. Stable nitrogen (^{15}N) and stable carbon (^{13}C) isotopes accrue in consumers with an increase in trophic level, and the isotopic structure of a system can depend on the availability and

resource use of dissolved inorganic nitrogen (DIN) and carbon (DIC) by the system's primary producer (Post 2002). Given a distinct isotopic signature among the different DIN and DIC sources and differences in the DIN and DIC source among systems, it has been shown that this difference can be reflected at higher trophic levels (Harvey and Kitchell 2000, Post 2002, Letourneur et al. 2013).

Because increased degradation of coral reefs is related with an increase in primary production in the form of fleshy algae, particular concern is given to primary consumers given their impact on systemic control (Bellwood et al. 2006, Hughes et al. 2007, Bonaldo et al. 2014). This group can remove excess growth that might compete with corals for spatial and light resources and thus represent a group of interest with respect to variation in trophodynamics. However, this group is diverse in their feeding with preferences differing between erect macroalgae and turf algae (Choat et al. 2002, 2004). Turf algae is becoming increasingly recognised as a potential impediment to coral reef development (McCook 2002, Vermeij et al. 2010a, 2010b) and thus, this study explores variation in the trophic niche space of two consumers of turf algae. Individuals of the parrotfish, *Chlorurus bleekeri*, and the farming damselfish, *Dischistodus prosopotaenia*, were collected at islands of the Spermonde Archipelago, Indonesia, representing a spatial gradient away from the urban centre of Makassar. These reefs have shown variation in their habitat composition with relation to water quality (Edinger et al. 1998, Cleary and Renema 2007) with turf algae increasing in recruitment and abundance (Chapter I & VI) at reefs closer to shore. *C. bleekeri* and *D. prosopotaenia* were both observed to persist among the reefs exposed to differing levels of perturbations and thus they were believed to reflect habitat changes in the greater reef community. However, these fishes may show differences in habitat use due to their feeding behaviour. The parrotfish, *C. bleekeri*, is highly mobile with ability to forage up to one km for resources (Welsh and Bellwood 2012). *D. prosopotaenia* is a farming damselfish that continuously maintains a patch of turf algae approximately one square metre in size (Hoey and Bellwood 2010). This study examines the variation of the trophic niches of the two fish species assuming that variation in habitat degradation has altered their trophic niche space through habitat modification; however, it is assumed that this will have a greater effect on *C. bleekeri* than *D. prosopotaenia* due to the latter's ability to self-maintain its nutritional resources and subsequently, its trophic niche space.

Materials and Methods

Benthic community assessment

Benthic communities were quantified with 50 photographic quadrats per 50 m transect. Photographs were taken at 1 m (standardised with a measuring pole) above the substratum, every 2 m along the transect. At every second metre, a photograph was taken on both sides of the transect tape, with a section of the tape within the picture, to identify total area of the picture. Analysis of the pictures was conducted with Coral Point Count with Excel extensions (CPCE; Kohler and Gill, 2006) analysed with fifty randomised points (based on results from power analysis) per photograph for the following biotic groups: ascidians, sponges, soft corals, crustose coralline algae (CCA), other invertebrates, cyanobacteria, macroalgae, turf algae, live hard coral. Biotic groups including any epiphytic growth despite the surface structure type. To compliment this, surface structures was also quantified despite the biotic growth. These groups included sand, rubble and pavement with pavement with the latter defined as any flat, low-relief or sloping solid benthic space. Rugosity was the last measurement of the benthic habitat, and this was assessed with the linear distance-fitted chain method (Risk 1972). The chain length used was 20 m, and measurement was conducted once per

transect, starting at the first 10 m point. Lastly, morphology of the live coral was also recorded. The selection of benthic groups and coral morphologies was based on English et al. (1997).

Fish and algae collection

Muscle tissue from 74 *Chlorurus bleekeri* and 44 *Dischistodus prosopotaenia* were collected during November 2014, at six islands of the Spermonde Archipelago, Indonesia varying in distance from the city of Makassar (Fig. 1). Samalona (SA; 05°07'S, 119°20'E, 7 km distance) was the closest to the mainland, followed by Barrang Lompo (BL; 05°02'S, 119°19'E, 11 km distance), Bonetambung (BO; 05°01'S, 119°16'E, 14 km distance), Badi (BA; 04°57'S, 119°16'E, 19 km distance), Karang Kassi (KA; 04°53'S, 119°09'E, 27 km distance) and Kapoposang (KP; 04°41'S, 118°57'E, 55 km distance). November represents the end of a four month dry season minimising seasonal effects of nutrient inputs into primary producers of the habitats.

Fish were collected between 3 and 15 m depth within a 200 m long strip of the northwest corner of each island, except for KP, to standardise the sampling sites among reefs. The western side of the islands generally features a well-developed, carbonate fore-reef and a sandy back-reef and flat. The reef crest is shallow (~3 m) and the slope reaches down to 15 m. The last study site, KP, is located on the outer shelf wall of the archipelago and is exposed to deep oceanic waters, contributing to well-developed coral reefs and high biodiversity. Work at KP was conducted at the northeast side of the island at the edge of the carbonate shelf, which was more consistent with the environmental conditions at the other sites.

Fish were collected with a speargun using SCUBA. After returning to the field lab (greatest travel time 2 hr), dorsal white muscle was sampled and dried at 60 °C for 48 hours. To identify variation in the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ at the level of primary producers, or the basal level, the brown algae *Padina* sp. and turf algae were collected within the 200 m strip of reef coinciding with fish collection, however the collection depth was standardised at 5 m below low tide. Algal samples were collected in replicates of five. Algae were cleaned of detritus and rinsed with distilled water once back at the field lab, and then dried in a similar fashion to fish muscle tissue.

Fish and algae samples for stable isotope analysis were ground to powder with mortar and pestle. Subsamples of *Padina* were treated with hydrochloric acid and rinsed with deionised water for analysis of organic $\delta^{13}\text{C}$, and the remaining untreated sample was used for $\delta^{15}\text{N}$. Samples were analysed for stable isotope ratios of carbon ($^{13}\text{C}/^{12}\text{C}$) and nitrogen ($^{15}\text{N}/^{14}\text{N}$) using Delta Plus mass spectrometer (EA3000 Elemental Analyser) connected to the Carlo Erba Flash EA elemental analyser via a Finnigan ConFloII interface. Results are expressed in standard d unit notation as:

$$\delta X(\text{‰}) = [(R_{\text{sample}}/R_{\text{reference}})-1] \times 1000$$

where X is ^{13}C or ^{15}N , and R is the ratio of $^{13}\text{C}/^{12}\text{C}$ for carbon and $^{15}\text{N}/^{14}\text{N}$ for nitrogen. The analytical precision of the measurement was <0.06‰ for both carbon and nitrogen. The standard material for carbon was Pee Dee Belemnite limestone and atmospheric nitrogen for nitrogen.

Data analysis

To determine the within-site trophic niches of *C. bleekeri* and *D. prosopotaenia*, and differences of trophic niches among sites, we used SIBER (Stable Isotope Bayesian Ellipses in R)(Jackson et al. 2011) from the SIAR (Stable Isotope Analysis in R)(Parnell and Jackson 2013) package. SIBER was supported with further quantitative population metrics (Layman et al. 2007) for each species investigating trophic structure among sites. Metrics included nitrogen (dNR_b) and carbon (dCR_b)

ranges detailing the total range of nitrogen and carbon values of exploited sources; mean distance to the centroid (CD_b), providing a description of trophic diversity; standard deviation of nearest neighbour distance ($SDNND_b$), which provides a measure of trophic evenness; and standard ellipse area (SEA_c), which provides a bivariate measure of the mean isotopic niche (Layman et al. 2007, Jackson et al. 2011). The calculation of SEA_c allows for subsequent analysis of the degree of niche overlap (%) which can then be used as a quantitative measure of dietary similarity among sites (Jackson et al. 2012, Jackson and Britton 2013). A small sample size correction for improving accuracy to SEA values was applied as suggested in Jackson et al. (2011). All metrics were bootstrapped ($n = 100,000$) to allow for comparisons among sites (Jackson et al. 2011).

Results

Benthic community

Many of the benthic groups showed spatial gradients according to distance from shore (Table 8.1). The benthic community at many of the islands was largely dominated by turf algae with SA, BL and BO composing of ~50 %. At many of the islands, the second most abundant group was live coral. This group was lower in the first three islands and increased in the outermost three islands besides for KS. Also, BO was particularly low. Of the other benthic groups, macroalgae, CCA, sponge and cyanobacteria were generally low (<10 %), however general spatial trends could be seen with decreasing macroalgae, and in increase in all the other groups with increasing distance from shore (Table 8.1). Spatial changes in the structural components of the sites, rugosity, sand, pavement and rubble, were also clear. Rugosity and pavement increased while sand and rubble decreased with increasing distance from shore (Table 8.1).

Table 8.1. Mean (\pm SE below) percent cover of primary benthic and structural groups and relative rugosity score. Sites (SA = Samalona, BL = Barrang Lompo, BO = Bonetambung, BA = Badi, KS = Karang Kassi, KP = Kapoposang) are ordered by increasing distance from the mainland.

Site	SA	BL	BO	BA	KS	KP
Distance (km)	7	11	14	19	27	55
<i>Biotic benthic groups</i>						
Macroalgae	1.41	0.53	4.17	1.35	0.58	1.88
	0.54	0.41	0.67	0.51	0.41	0.21
CCA	2.79	2.95	2.53	9.24	5.05	20.15
	0.66	0.16	0.45	0.68	0.54	3.41
Sponge	1.65	4.13	6.26	4.50	16.83	4.77
	0.27	0.60	1.66	0.40	9.10	0.01
Cyanobacteria	0.28	0.90	5.27	1.01	19.37	0.70
	0.11	0.22	0.66	0.30	6.28	0.19
Live coral	13.44	21.94	7.92	35.73	16.19	31.30
	3.34	7.32	1.18	1.37	1.37	1.94
Turf algae	60.29	44.82	57.15	34.42	29.32	20.40
	2.69	3.59	1.43	2.76	4.13	2.28
<i>Structural groups</i>						
Rugosity score	1.57	1.91	1.65	1.98	2.19	1.70
	0.09	0.15	0.11	0.12	0.04	0.15
Sand	7.13	13.31	10.39	3.84	4.34	9.44
	1.96	1.49	2.10	1.54	4.02	0.45
Pavement	22.24	27.19	30.44	19.98	18.83	39.07
	6.58	2.45	4.03	1.07	1.92	0.87
Rubble	46.59	27.84	32.89	29.85	18.65	10.87
	4.33	2.86	5.76	2.26	3.55	0.86

Trophic niches between species

Stable isotope values for *D. prosopotaenia* and *C. bleekeri* were largely differentiated based on their $\delta^{13}C$ values. *C. bleekeri* ranged in $\delta^{13}C$ from -12‰ to -8.2‰ while *D. prosopotaenia* ranged from -16.5‰

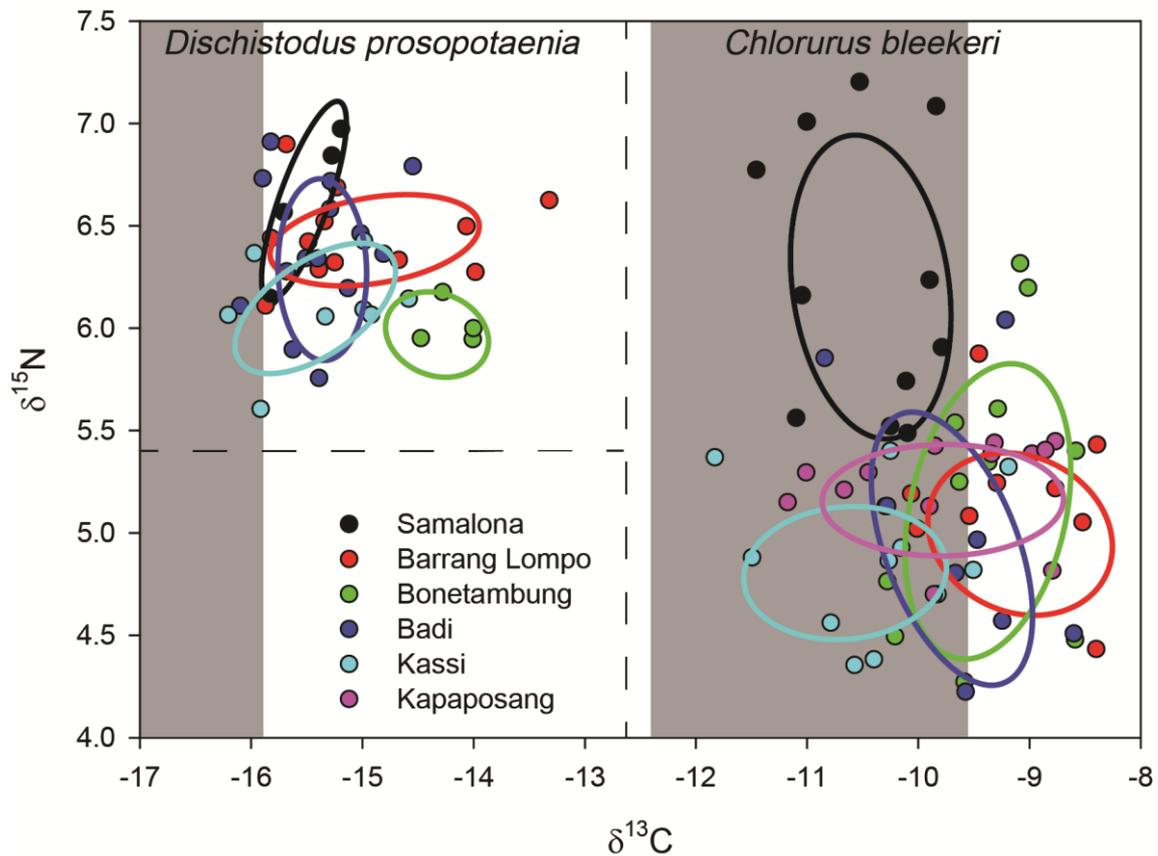


Figure 8.1. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ bi-plot displaying the corrected standard ellipse areas (SEA_c), representing the primary niche space of *C. bleekeri* and *D. prosopotaenia* by site. Dashed lines are a visual aid to identify differing niche areas of the two fish species. Grey shading denotes the $\delta^{13}\text{C}$ value range of turf algae (left) and *Padina* sp. (right).

to -13‰ (Fig. 8.1). $\delta^{15}\text{N}$ values of *D. prosopotaenia* were within the range of the most enriched *C. bleekeri* values with the former ranging from 5.6‰ to 7.0‰ and the latter from 4.2‰ to 7.3‰ (Fig. 8.1). The stable isotope metrics of *D. prosopotaenia* and *C. bleekeri* showed that the damselfish trophic niches (SEA_c) were approximately half the size of that of the parrotfish (Table 8.2). This was reflected in both the range of foods (dCR_b) and trophic levels (dNR_b) indicating the damselfish had a much more restricted diet than the parrotfish (Table 8.2). Concurrently, the lower CD_b and SDNND_b values for the damselfish indicate lower trophic diversity and trophic evenness, respectively, than the parrotfish (Table 8.2). At no point did the trophic niches of the two fishes overlap (Fig. 8.1) with the parrotfish enriched in C by $\sim 5\text{‰}$ and the damselfish $\sim 1.5\text{‰}$ higher in N (Fig. 8.1).

Differences in spatial variation among sites per fish were mostly reflected in the SEA_c values. For the damselfish, only BO was significantly smaller than the other sites (Table 8.2 & 8.3) and this was also reflected in the most limited dietary ranges (dCR_b and dNR_b ; Table 8.2). There were no differences in SEA_c between the other sites and there was limited overlap in ellipses besides between BA and BL.

The parrotfish displayed greater differences among sites than did the damselfish with fishes at SA and BO having larger ellipse areas than the other sites (Table 8.2 & 8.3). There was a clear increase in the range of foods fed on (dCR_b) by the parrotfish. This was not reflected in the trophic level (dNR_b) however SA was clearly enriched in ^{15}N compared to the other sites (Fig. 8.1). Also, the

furthest site, KP, had the greatest range of feeding across trophic levels (Table 8.2). There was more overlap of niches between sites in the parrotfish than the damselfish.

Some of the differences in ellipse overlap can be accounted for in differences at the basal level of the food web. *Padina* $\delta^{15}\text{N}$ values were 2-5‰ less than *C. bleekeri* and 4-7‰ less than *D. prosopotaenia* and $\delta^{13}\text{C}$ values were within the range of *C. bleekeri* (Fig. 1 & 2). Nitrogen ($\delta^{15}\text{N}$) isotopic values were highest at the closest sites to the mainland, lowest at BO, and then increased again until KP (Fig. 8.2). *Padina* carbon ($\delta^{13}\text{C}$) isotopic values ranged from -12.5 ‰ to -9.6 ‰ (Fig. 8.2) overlapping with *C. bleekeri*. The turf algae carbon ($\delta^{13}\text{C}$) was most enriched at -15.9 ‰, slightly depleted from that of *D. prosopotaenia*.

Table 8.2. Species, sample size (n), average fish length and length range, and mean stable isotope metrics: dNR_b $\delta^{15}\text{N}$ range; dCR_b = $\delta^{13}\text{C}$ range; CD_b = mean distance to centroid; SDNND_b = SD mean nearest neighbour distance; SEA_c = standard ellipse area.

Site	n	Mean	Length	dNR _b	dCR _b	CD _b	SDNND _b	SEA _c
		length	range					
<i>D. prosopotaenia</i>								
Samalona	4	8.8	6.8-11.4	0.820	0.640	0.393	0.164	0.182
Barrang Lompo	14	13.8	11.4-15.4	0.790	2.55	0.736	0.097	0.582
Bonetambung	4	11.5	10.5-12.5	0.230	0.470	0.214	0.143	0.116
Badi	14	15.5	13.9-17.0	1.150	1.550	0.463	0.118	0.481
Karang Kassi	8	15.3	13.4-16.8	0.820	1.630	0.550	0.161	0.519
<i>C. bleekeri</i>								
Samalona	11(4:7)	24.9	19.8-28.4	1.443	1.670	0.662	0.125	1.340
Barrang Lompo	9(6:3)	21.9	14.2-27.5	2.006	1.670	0.803	0.376	0.878
Bonetambung	12(6:6)	23.1	15.8-28.0	1.640	1.710	0.671	0.156	1.262
Badi	8(5:3)	24.1	20.8-30.5	0.885	2.240	0.638	0.171	1.439
Karang Kassi	11(10:1)	19.9	16.4-24.0	1.452	2.64	0.695	0.241	1.012
Kapoposang	13(0:13)	22.8	17.1-27.8	2.198	2.40	0.932	0.168	0.668

Discussion

Localised disturbances to coral reef ecosystems can involve important alterations of habitat, and consequently the ecological niches of the associated fish communities. Nonetheless, few studies have identified changes in the niche utilisation of primary consumers associated with spatial change in their habitat. In the Spermonde Archipelago there exists a spatial gradient in benthic condition associated with a water quality gradient originating from the mainland (Plass-Johnson et al. 2015c). Near-shore sites are associated with higher abundances of turf algae and rubble while sites located further offshore have higher live coral cover and higher structural complexity (rugosity). Both *C. bleekeri* and *D. prosopotaenia* displayed changes in the total area (SEA_c) of their trophic niche only at the most degraded sites. The trophic niche of the parrotfish, *C. bleekeri*, was greatest at SA and BO while the niche of the damselfish, *D. prosopotaenia*, was smallest at BO. These two sites had the lowest coral cover and structural complexity, and highest turf algae and rubble abundance.

The high turf algae cover and overall loss of structural complexity at the islands closest to the mainland are likely due to the increased nutrient load from urban derived wastes. Anthropogenic effluents are generally enriched in ^{15}N and this is reflected in the overall ^{15}N enrichment found in the

Table 8.3. Percentage (%) of niche area (SEA_c) overlapping between sites for *C. bleekeri* (grey) and *D. prosopotaenia* (white). *D. prosopotaenia* was not collected from Kapoposang (KP). An asterisk (*) indicates a significant difference in the standard ellipse area (SAE_c) and the direction of difference can be obtained from Table 8.2 and Fig. 8.1.

	SA	BL	BO	BA	KS	KP
SA	█	5	0*	11	<1	NA
BL	<1*	█	<1*	25	6	NA
BO	<1	60	█	0*	0*	NA
BA	2*	50	87*	█	19	NA
KS	<1*	2	24*	34	█	NA
KP	<1*	37	48*	54	19	█

Parrotfishes are functionally seen as herbivores feeding on both turf and macro-algae, but their feeding can indirectly include detritus and invertebrates (Choat et al. 2002, Dromard et al. 2014). Furthermore, scleractinian corals are also proposed as an important nutritional constituent for parrotfishes (Cole et al. 2008, Bonaldo and Bellwood 2011, Plass-Johnson et al. 2013, Dromard et al. 2014) and greater reliance on corals would result in higher $\delta^{15}\text{N}$ values (Carassou et al. 2008, Plass-Johnson et al. 2015d). Thus, it is possible that parrotfish at sites further from shore accessed more algal resources and few coral resources, while individuals at sites closer to shore fed proportionally more on coral and less algae, but the number of different sources in both cases was reduced. This change in feeding could have been facilitated by a proportional change in the benthic hard structure. Species within the *Chlorurus* genus show differences in preferred feeding surface (Bellwood 1995, Bonaldo and Bellwood 2009) but at these two sites (SA and BO), rubble was proportionally high compared to other hard substrates possibly resulting in a shift in feeding behaviour and/or preference of *C. bleekeri*. The close relationship between the $\delta^{13}\text{C}$ value of *C. bleekeri* and *Padina* suggest that parrotfish may use this as a food source. However, a previous, extensive experiment with *Padina* as an algal transplant assay never revealed *C. bleekeri* feeding on this alga. Alternative food sources within a similar $\delta^{13}\text{C}$ value range include crustose coralline algae and halimeda (Cocheret de la

Moriniere et al. 2003); algae commonly fed upon by parrotfish (Choat et al 2002, 2004)

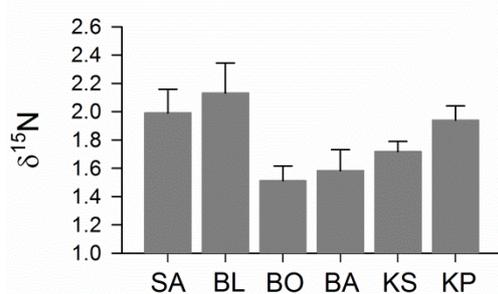


Figure 8.2. $\delta^{15}\text{N}$ values of *Padina* sp. representing basal isotopic values at each site. Sites are listed from left to right increasing in distance from the mainland.

primary producer, *Padina* spp. For the consumers, this is also reflected as a net enrichment of ^{15}N but not increased variability, because the $\delta^{15}\text{N}$ value of the muscle tissue of a consumer is a product of months of dietary assimilation (Plass-Johnson et al. 2015c). For the parrotfish, there was a clear increase in resources utilised ($d\text{CR}_b$) with distance from shore, but at most sites this was not accompanied by a change in trophic level from which they fed. Increase in the ellipse areas at the two most degraded sites, SA and BO, was largely a product of increased $d\text{NR}_b$ and lowest $d\text{CR}_b$ values at the same time. Wider and uneven (SDNND_b) variation across N ($d\text{NR}_b$) suggests some individuals relied on fewer resources spread across trophic levels when compared to the other sites. For instance, BA had a high $d\text{CR}_b$ range but low $d\text{NR}_b$ suggesting more foods at the same trophic level.

In the case of the damselfish, *D. prosopotaenia*, there was little structural change in the trophic niche, although there was a clear enrichment of $\delta^{13}\text{C}$ from SA, BL to BO (Fig. 8.1). This did not, however, correlate with an increase in $d\text{CR}_b$. Farming damselfishes are highly territorial, cultivating the algal mats which they use as a food source (Ceccarelli 2007). The damselfish feed from the cultivated algae but also from the invertebrate communities that become established in the algal mat (Wilson and Bellwood 1997, Dromard et al. 2013). The close relationship between the the ^{13}C

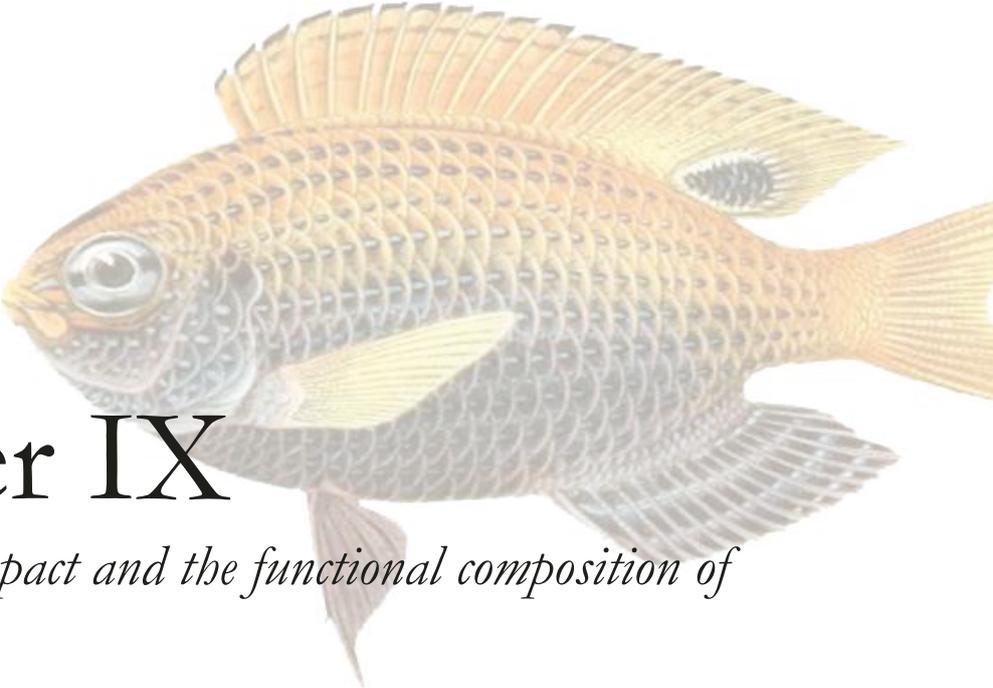
signature of the turf algae and the damselfish confirm this suggesting an micro-food web originating in turf algae. In the Spermonde Archipelago, previous recruitment experiments have shown different invertebrate recruits at the near-shore sites (Chapter VI, Sawall et al. 2013), suggesting possible variation in availability of invertebrate resources recruiting to the damselfish territories. A compositional change in the availability of invertebrates might result in a changing $\delta^{13}\text{C}$ value of *D. prosopotaenia* without a substantial change in $\delta^{15}\text{N}$ values as observed. Nevertheless, there was little change in the niche area of the damselfish despite changes in the greater habitat, suggesting successful maintenance of its required habitat.

Interestingly, there was never overlap in the niche space at any one site between the two species. Farming damselfishes aggressively defend their territory from other herbivores (Ceccarelli et al. 2005) including parrotfish (Ceccarelli et al. 2011), and our results suggest a high level of success in *D. prosopotaenia* over *C. bleekeri*. Furthermore, these results may provide insight into the development of Spermonde reefs. The trajectory of coral reef benthic algae development are expected to progress from bare space to a microalgal film, and then to turf algae and crustose coralline algae, and finally to erect macroalgae (McClanahan 2000, Diaz-Pulido and McCook 2002, Diaz-Pulido et al. 2007). Foraging by herbivores, such as parrotfish, results in ‘mature’ algal communities dominated by calcified and encrusting algae (Zanini et al. 2006) which allow for recruitment and development of corals (Ritson-Williams et al. 2009). Benthic communities dominated successfully by farming damselfishes tend to host monospecific assemblages of algal turfs (Hata and Kato 2002, 2003, Ceccarelli 2007) inhibiting further development of the reefs. If this holds true in the Spermonde Archipelago, it is possible that farming damselfish may be responsible in part for the high turf algae abundances seen at the near shore sites. However, this would need further clarification through assessing the effects of these farmer fish on the benthos through experiments and quantification of their relative abundances in benthic communities.

The occurrence of local and global disturbances to coral reefs is increasing because of climate change and resource use (Burke et al. 2011). These disturbances result in modification of the coral reef habitat, and this will have detrimental effects on the associated fish species. In the worst case scenario, habitat modification may result in localised extinction in some fish species. This mechanism depends on resource specificity and flexibility, but in most cases, reliance on resources by a specific species is poorly understood (Graham et al. 2011). The maintenance of the trophic niche by *D. prosopotaenia* across the spatial gradient suggests that resource utilisation by this fish remained stable, and local disturbances had little effect on their habitat. In contrast, the habitat and resource availability changed for *C. bleekeri* across sites, and the shift of its trophic niche indicates successful adaptation of the fish to habitat changes. Overall, a high flexibility in feeding behaviour and resource exploitation may support the success of reef fish to survive in altered habitats, while very specialized and inflexible fish species are more susceptible to local extinction from local disturbances. For instance, a high level of resource specificity in the filefish, *Oxymonacanthus longirostris*, resulted in localised extinction from reefs after coral bleaching removed its key prey coral, *Acropora millepora* (Brooker et al. 2014). Thus, the continuation of a species during habitat modification seems dependent on the flexibility of habitat utilisation, or as exemplified in the damselfish, the ability to maintain its habitat.

The analysis of stable isotopes in coral reef food webs offers a powerful tool in elucidating trophic variation among consumers (Cocheret de la Moriniere et al. 2003, Carassou et al. 2008, Kolasinski et al. 2009, Greenwood et al. 2010, Dromard et al. 2013, 2014, Plass-Johnson et al. 2013, 2015c). This tool, however, seems further applicable in demonstrating intra-specific trophic variation in relation to habitat alteration. In our study, where turf algae became abundant at the degraded sites and the

habitat was less favourable, the parrotfish *C. bleekeri* increased its trophic niche to include resources of higher trophic levels. These results run contrary to many studies suggesting an algal preference (Choat and Robertson 2002, Choat et al. 2004). Additionally, the trophodynamics of many parrotfish are still being uncovered (Plass-Johnson et al. 2014). At the same sites, the farming damselfish *D. prosopotaenia*, was able to maintain its trophic niche suggesting successful defence of its algal resources and associated organisms. These findings help understand both the intra- and inter- specific capacity of coral reef fishes to change or maintain their trophic relationship within the context of a changing environment. Lastly, the role of habitat degradation and specialisation in explaining local extinction of coral reef fishes is poorly understood, and this study sheds light on the potential capacity of parrotfish and farming damselfish to persist along gradients of habitat loss.



Chapter IX

Environmental impact and the functional composition of fish communities

This chapter is in review as:

Plass-Johnson JG, Taylor M, Husain AAA, Teichberg M, Ferse SCA. Non-random variability in the functional composition of reef fish communities along an environmental gradient. *Ecology*

Abstract

Changes in the coral reef complex can affect predator-prey relationships, resource availability and niche utilisation in the associated fish community, which may be reflected in changes and decreased stability of the functional traits present in a community. This is because particular traits may be favoured by a changing environment, or by habitat degradation, while others are selected against, and because degradation can relax the association between fishes and benthic habitat. We characterised six important ecological traits for fish species occurring at seven sites across a disturbed coral reef archipelago in Indonesia, where reefs have been exposed to eutrophication and destructive fishing practices for decades. Functional diversity was assessed using two complementary indices (FRic and RaoQ), correlated to important environmental factors (live coral cover, rugosity and distance from shore), and examined for both a change in their mean, and temporal and spatial variability. Furthermore, variability in individual traits was examined to identify which traits are most affected by habitat change. Increases in the general reef health indicators, live coral cover and rugosity (correlated with distance from the mainland), were associated with decreases in the variability of functional diversity and with community-level changes in the abundance of several traits (notably home range size, maximum length, microalgae, detritus and small invertebrate feeding and reproductive turnover). A decrease in coral cover increased variability of RaoQ while rugosity and distance both inversely affected variability of FRic, however averages for these indices did not reveal particular patterns associated with the environment. These results suggest that increased degradation of coral reefs is associated with increased variability in fish community functional composition resulting from selective impacts on specific traits, thereby affecting the functional response of these communities to increasing perturbations.

Introduction

Coral reefs are among the most diverse ecological systems in the world due to their complex biogenic composition (Connell 1978). Physical (e.g. structural complexity) and biological (e.g. live coral cover and/or benthic diversity) characteristics interact to create high structural heterogeneity, providing habitat for many life forms. Most coral reef fishes are dependent on coral reef habitat for shelter and food resources, implying that the structural and biological components of the habitat exert an influence on the composition of the associated fish community. Accordingly, most studies find positive correlations between structural complexity and fish abundance (Graham and Nash 2013), number of species (Gratwicke and Speight 2005, Wilson et al. 2008), biomass (Friedlander and Demartini 2002) and species diversity (Öhman et al. 1997, Ferse 2008).

Coral reefs can experience ecological restructuring in response to anthropogenic disturbances such as changing water chemistry and resource extraction (Graham et al. 2014). Resource use and habitat modification can be intense, and spatially and temporally dynamic, resulting in differing feedback mechanisms of community structure and function. Localised disturbances can change the relative role of niche utilisation by affecting such processes as movement patterns, competition, predation and recruitment (Warwick and Clarke 1993). Trait-specific responses to habitat modification are apparent in most cases because species with traits that are favoured by the changed environment are able to benefit, becoming more abundant than prior to the impact. As such, disturbances act as filters on communities, whereby certain species or functions are lost due to environmental constraints (niche filtering; (Zobel 1997)) but species with traits that allow access to new habitat provisions are able to persist or establish themselves. Coral reef fishes are highly diverse, both taxonomically, but also with a broad range of morphological, biological and behavioural

traits (Sale 2002). This diversity of traits allows for resource partitioning within this highly speciose group (Ross 1986). Conversely, the removal of resources through disturbances can result in communities becoming depauperate in traits, functions and/or diversity (Mouillot et al. 2007). Traits have been linked to ecosystem processes (Mouillot et al. 2007, Mason et al. 2008, Villéger et al. 2010, 2012) and because of this, trait-based approaches to understanding ecosystem processes have been developed in recent years to help identify mechanisms of community assembly (Violle et al. 2007, Mouillot et al. 2013b, Mason et al. 2013a) and to understand observed patterns of species coexistence (Petchey and Gaston 2006, Mason et al. 2013b). Trait-based approaches have proven essential in understanding how in plant communities, processes respond to environmental change (Violle et al. 2007, Flynn et al. 2009, Jung et al. 2010). For coral reef fish assemblages, trait-based functional analyses have revealed the importance of rare species (Mouillot et al. 2013a), functional hot-spots (Stuart-Smith et al. 2013) and areas of functional loss (D'agata et al. 2014). These studies have helped describe global assemblage rules; however, local disturbances are increasingly recognised as drivers of coral reef communities (Burke et al. 2011), with the emergence of large-scale patterns as a result of local processes (Mora 2008).

Localised disturbances, such as point sources of nutrient input, result in spatial gradients that affect coral reefs at different levels. Coral reefs around point sources of pollution may display locally reduced coral biodiversity, low coral recruitment, low skeletal density, high rates of bioerosion and a transition from coral-dominated communities to those dominated by non-reef building organisms (Dudgeon et al. 2010, Fung et al. 2011), and an overall loss of habitat complexity. Furthermore, the scale of habitat degradation usually depends on the type and magnitude of impact. For point sources of pollution, long-term exposure may, at a local scale, result in a loss of habitat diversity, reducing niche availability for the associated fish assemblages (Fabricius 2005). Conversely, less impacted sites may have higher biological diversity, offering greater resources for niche diversification (Bythell et al. 2000). Loss in available niches may increase competition for the remaining resources leading to negative density-dependence (McCormick 2012), while loss in resources and habitat fragmentation can also result in reduced stability of the community due e.g. to increased vagility (Ault and Johnson 1998). The loss of habitat structure affects the associated fish community unevenly, with stronger effects observed on small-bodied species and those with direct dependence on corals for food and shelter, and larger individuals with wider home ranges becoming more prominent in areas of the reef that have lost structural complexity (Pratchett et al. 2008, Alvarez-Filip et al. 2011, Nash et al. 2013). Many authors note that habitat degradation increases taxonomic and/or abundance variability in the associated fish fauna among repeated samples (Dawson Shepherd et al. 1992, Öhman et al. 1997, Lindahl et al. 2001). Local disturbance reduces available benthic resources, such as live coral and structural complexity, leading to trait-specific responses of the associated fish community, with reduction or loss of particular traits (Syms and Jones 2000, Graham et al. 2007). This leads to the question, does a healthy environment host a higher number of functions, thus contributing to higher stability in the functional composition; or conversely, does a degraded habitat result in a community with a reduced and less stable trait composition? While responses of fish communities to localised habitat degradation have been assessed in terms of abundance, biomass, size structure and species richness, our understanding of the extent to which the functional composition of fish communities varies in response to localised reef degradation remains limited. Environmental gradients across a number of distinct reefs allow for the identification of how and which traits are most suited to utilise the immediate environment. Furthermore, a change in the variability in fish traits or community functioning along environmental gradients may act as potential indicators of environmental stress.

While few studies have linked functional loss and functional change of reef fishes to habitat degradation, no study has attempted to identify the specific mechanisms of trait-based functional variability and loss in these assemblages. Results from previous studies on the effects of loss of structural complexity and live coral cover on fish community composition suggest a shift towards larger, less site-attached individuals, potentially leading to more variability in the species and functions present at a particular point in time; however, this has yet to be tested empirically. Because a changing environment may not equate to net loss of species and/or traits, measuring variability in the composition of traits that are indicative of environmental impact may better reflect the effect of a changing environment on the fish assemblage. This study, therefore, goes beyond traditional taxonomic-based evaluation of habitat degradation, and uses a coral reef archipelago in Indonesia exposed to varying environmental conditions to investigate localised spatial changes in the functioning of coral reef fish assemblages. The Spermonde Archipelago of Southwest Sulawesi has been identified as a coral reef system which has experienced long-term degradation and eutrophication due to high levels of coastal population, industrialisation and marine resource use in the area (Edinger et al. 1998, Cleary et al. 2005). On-shore to off-shore patterns of live coral cover have been associated with distance from the coastal city of Makassar (Edinger et al. 1998, Renema and Troelstra 2001), which is reflected in a nutrient gradient (Edinger et al. 1998, Sawall et al. 2011).

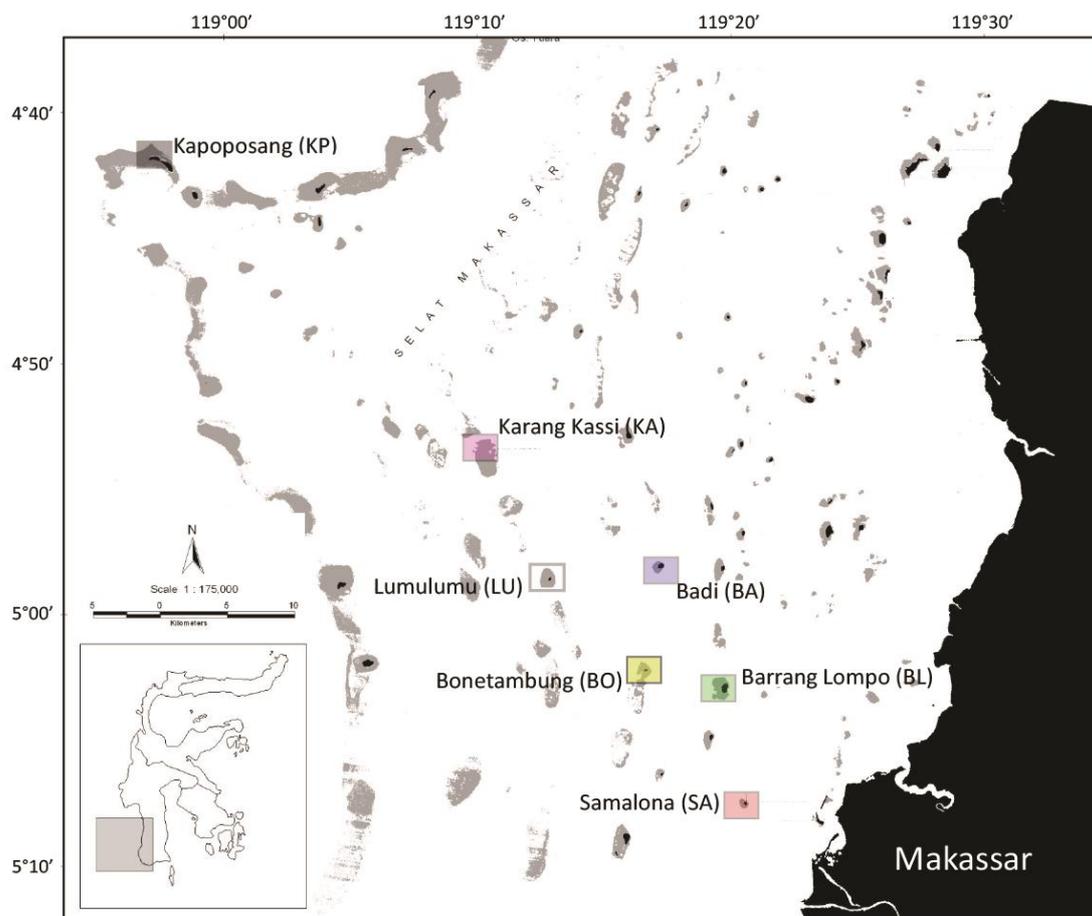


Figure 9.1. Map of the Spermonde Archipelago. Dashed squares indicate the sampling sites and the in-text acronym is given in parentheses. Colours correlate with subsequent figures.

We investigated the importance of two key parameters of coral reef health, live coral cover and benthic rugosity, in relation to the functional assembly of the associated fish communities along the spatial gradient. Through a null model approach, we use both the mean of functional indices and the variability of functional composition, along with specific responses of traits, to detect non-random processes affecting coral reef fish community assembly. We hypothesized that reductions in reef health would be reflected in higher variability of the functional composition of the fish community. Furthermore, we predicted that variability in community composition would be driven by traits associated with fish size and trophic dependence on live corals. Lastly, given the importance of identifying habitat loss in coral reef systems, changes in trait-based indices are discussed for the detection of anthropogenic effects.

Methods and Materials

Study sites and sampling protocol

Sampling occurred between the 26th of September and the 2nd of October, 2013, on seven islands of the Spermonde Archipelago, Indonesia, representing a transect of increasing distance from the city of Makassar (Fig. 9.1). Makassar is populated by 1.4 million people, and the near-shore islands are affected by effluents from the city's harbour, sediments, aquaculture outflow and wastewater from the fluvial discharge of the nearby rivers (Renema and Troelstra 2001). Samalona (SA; 05°07'S, 119°20'E, 7 km distance) was the closest to the mainland, followed by Barrang Lompo (BL; 05°02'S, 119°19'E, 11 km distance), Bonetambung (BO; 05°01'S, 119°16'E, 14 km distance), Badi (BA; 04°57'S, 119°16'E, 19 km distance), Lumulumu (LU; 04°58'S, 119°12'E, 22 km distance), Karang Kassi (KA; 04°53'S, 119°09'E, 27 km distance) and Kapoposang (KP; 04°41'S, 118°57'E, 55 km distance; Fig. 9.1).

The northwest corner of each island, except for KP, was used to standardise the sampling sites among reefs. The western side of the islands generally features a well-developed, carbonate fore-reef and a sandy back-reef and flat. The reef crest is shallow (~3 m) and the slope reaches down to 15 m. The last study site, KP, is located on the outer shelf wall of the archipelago and is exposed to deep oceanic waters, contributing to well-developed coral reefs and high biodiversity. Work at KP was conducted at the northeast side of the island at the edge of the carbonate shelf, which was more consistent with the environmental conditions at the other sites.

Fish and benthic surveys were conducted along three 50 m transects at each site. Transects were standardised at 2 m below the reef crest, which for each site fell between 4 and 5 m depth at low tide. Transects were separated by 5 m, and the beginning and end were marked with steel rebar to provide attachment points for the transect tapes. Sampling was timed to occur during the neap tide cycle and during the dry season to ensure consistent conditions for all sampling days.

At each site, the three transects were surveyed three times throughout the day to account for instantaneous variability in fish community composition (McClanahan et al. 2007). The first set was started at the same time of day (8:30 am \pm 15 min) at each site, and each transect required approximately 45 min. Surveys were started 30 min after the transect tapes were laid to allow fishes to become acclimated to the presence of the tape, and 30 min were allocated between sets of transects. The number and species of all fishes >3 cm were recorded within a 5 m wide belt along each 50 m transect. Individuals of the cryptic families, Gobiidae and those in the Blennioidei were not recorded.

Table 9.1. Life history traits used to characterise a species' function including weight (in parentheses), definition and values.

Trait	Definition and functional significance	Values
Dietary group (3)	Fish species were described by their most important dietary constituents. Diet acts as a broad descriptor of ecological interaction, and also, it is a proxy for susceptibility to predation (Kulbicki et al. 2005, O'Gorman et al. 2011).	DG _{CO} : Sessile invertebrates (corals and sponges) DG _{C1} : Small benthic invertebrates DG _{C2} : Large benthic invertebrates DG _D : Detritus DG _{H1} : Macro-algae and seagrass DG _{H2} : Micro-algae and cyanobacteria DG _P : Fish or nekton DG _Z : Zooplankton
Home range (2)	Species were grouped into three categories based on their normal movements. Sedentary would explain damsel fishes which are specific to a coral colony; Mobile indicates movement in the 100s m; Wide indicates movement across reefs. Home range indicates the foraging method along with predation risk and prey defence (O'Gorman et al. 2011, D'agata et al. 2014)	HR _S : Sedentary HR _M : Mobile HR _W : Wide ranging
Schooling behaviour (2)	Schooling is defined on the normal behaviour of adults of the species. Schooling behaviour is an indication of susceptibility to predation (O'Gorman <i>et al.</i> 2011).	SB _A : Solitary SB _B : Paired SB _C : Small, loosely aggregated schools SB _D : Medium size schools SB _E : Large schools
Reproductive turnover (2)	High: Less than 15 months; Medium: Between 1.4 and 4.4 years; Low: 4.5 to 14 years. Reproductive turnover indicates the capacity for adaptation to quickly changing environments (Doherty and Fowler 1994).	T _H : High T _M : Medium T _L : Low
Depth range (1)	The range of depths which an individual species can transverse, and is an indication of fishing pressures (Roberts and Hawkins 1999).	DR: Depth in metres
Max length (3)	Maximum length that a species can potentially reach. Max length indicates the metabolic rate and secondary production (O'Gorman et al. 2011, D'agata et al. 2014).	L _m : Length in cm

Environmental variables

Live coral cover was quantified at each island with 25 benthic photographic quadrats per 50 m transect. At every second metre, photographs were taken at a standardised height (1 m) above the substratum. On each photograph, ten randomised points were analysed for live hard coral (not displaying necrosis) with Coral Point Count with Excel extensions (CPCE; (Kohler and Gill 2006)). Rugosity was assessed with the linear distance-fitted chain method (Risk 1972). The chain length used was 20 m, and measurement was conducted once per transect, starting at the first 10 m point.

Life history traits of fishes

Our choice of traits was similar to those used in recent studies exploring change in functional diversity (FD) of coral reef fishes across large spatial scales (Mouillot et al. 2013a, 2014, Stuart-Smith et al. 2013, D'agata et al. 2014) and for which data are widely available (FishBase, <http://www.fishbase.org>) (Table 9.1 & S5). They are a combination of morphological, trophic, reproductive and behavioural traits which can be affected by environmental disturbances, leading to changes in species and functional composition (reviewed in Mouillot et al. 2013b). Moreover, the use of combined life-history traits has the potential to better elucidate the effect of disturbance processes on communities (Violle et al. 2007, Mouillot et al. 2013b) because disturbances can act on differing sets of traits. Ontogenetic changes of trait values in species were not considered because information on adults is more widely available. Although a direct comparison of fish traits and their ecological importance is not available in the literature, traits were given a weighting, from 1 to 3, based on their ecological importance as interpreted from the literature (Table 9.1). Trophic and size traits were given the highest weight because they provide a direct biological indication of how species interact with each other and the habitat. Behavioural traits were weighted intermediately because they can change depending on social structure, and depth distribution was given the least weighting because it is limited at all reefs (Table 9.1).

Measuring observed and expected functional diversity

We constructed a species \times species functional distance matrix from a species \times trait matrix of all species observed using Gower's distance (Pavoine et al. 2009). Rao's quadratic entropy (RaoQ) (Botta-Dukat 2005) and functional richness (FRic) were calculated by relating the species \times species distance matrix to the species abundances. RaoQ reflects changes in the abundance-weighted sum of pairwise functional distance between species and allows for the evaluation of functional diversity among species (Mouchet et al. 2010). Alternatively, FRic measures the volume of multidimensional functional space occupied by the community (Mouillot et al. 2013b). In practical terms, FRic will become greater with increased, trait-specific, functional composition while RaoQ measures the differences among species based on their functional composition. For FRic, we followed the convex hull method proposed by Villéger et al. (2008). For further descriptions of the calculation of FRic and RaoQ, see Botta-Dukat (2005), Villéger et al. (2008), Laliberté and Legendre (2010). These two indices were chosen because they display adequate power to test ecological constraints across environmental gradients (Mouillot et al. 2013b, Mason et al. 2013a).

The standardized effect size (SES) of observed RaoQ and FRic were calculated based on the distribution of null model indices as suggested by (Gotelli and McCabe 2002):

$$SES = (I_{obs} - I_{sim}) / \sigma_{sim},$$

where I_{obs} is the observed index, and I_{sim} and σ_{sim} are the mean and the standard deviation of the simulated null model indices, respectively, giving a SES for both RaoQ (SES_{RaoQ}) and FRic (SES_{FRic}). In order to calculate functional diversity indices for the null model, the community matrix of observed occurrence frequencies, sample (rows) \times species (columns), was permuted 999 times, while the trait matrix was maintained in its original configuration. Null models were generated using the "independent swap" algorithm of (Gotelli 2000), which randomizes species' occurrence frequencies by sample (i.e. values within each column), but is constrained to only accept permutations that maintain species richness across samples. Although the independent swap null model is designed to maintain patterns of sample richness, sample diversity and abundance are also correlated to some

degree. An example of the null model procedure is available as an R script in the Supplementary materials. The null model effectively removes any link between environmental variables and species and their associated traits.

Relationship between functional diversity and the environment

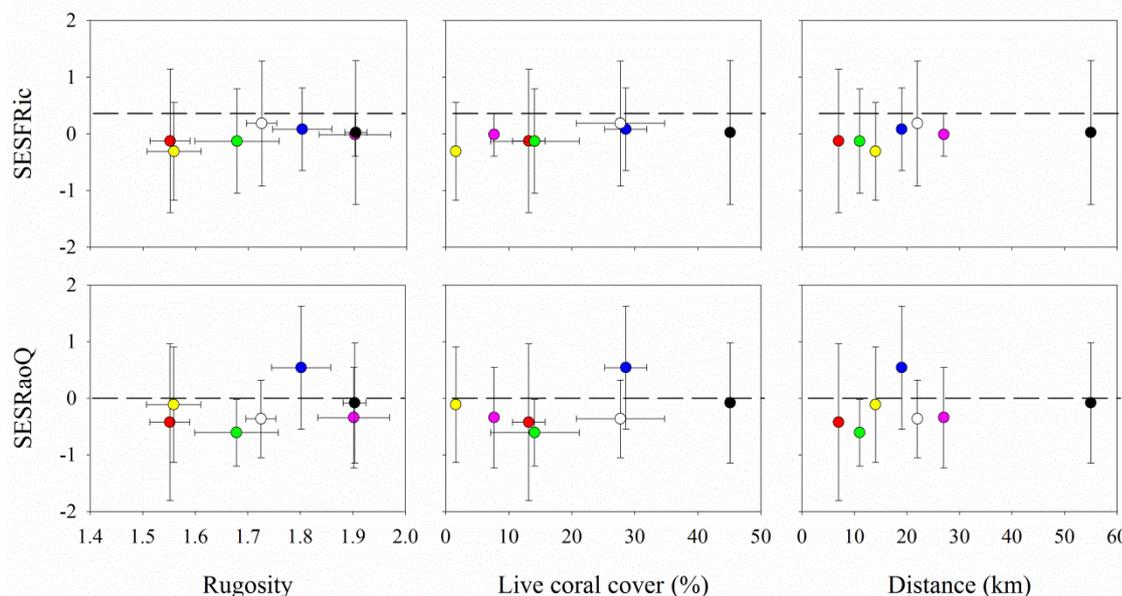
As species richness between replicate counts on individual transects differed due to instantaneous variability in abundance (McClanahan et al. 2007), representing the range of possible numbers of species at a transect, the mean functional diversity indices per transect were derived by calculating the SES values for each of the three replicate counts against all iterations for that transect pooled together (3 x 1000). The average of all nine values per island was used as the average index for that island, thus accounting for both temporal and spatial variability at the island level. Variance was calculated by deriving transect-specific SES values for each of the replicate samples (based on 999 permutations), then obtaining a standard deviation (SD) associated with one transect across the three samplings. This created three SDs per site. Mean and variance of both indices were plotted against environmental conditions to check for associations.

Relationships between the SD of the SES indices and the environmental covariates were explored with multiple linear and non-linear models. Collinearity in the covariates was checked with a correlation coefficient, using a threshold of 0.8, and the variance inflation factor (VIF) with a threshold of 3. Coral cover and rugosity were both positively correlated with distance from the mainland (Fig. S1). However, the correlation coefficient was never greater than 0.8 (Fig. S2) nor were the VIFs greater than three (coral cover = 1.4, rugosity = 1.6, and distance from shore = 1.8). These results meant that all covariates were considered for calculating relationships with SESFRic and SESRaoQ. Generalised linear models (GLM) and generalised additive models (GAM) with a gamma distribution were fitted to the full set of covariates, and selection of best sub-models was based on a minimisation of the Akaike Information Criterion (AIC). Model validation was completed via residual plots.

For all transects, community-level weighted mean values (CWM) were calculated for each trait as the mean trait value weighted by the relative abundance of the species. Mean CWM values per transect were analysed for their responses in relation to the environmental variable. In addition, variability for individual trait CWM was calculated as SD across the three samples of one transect. Linear regression was then applied to see which trait means and variability were most closely linked to the environmental variables. KP was removed from the trait-distance relationship because it generally was an outlier, altering the linear relationship seen with the six other sites. To identify trait-based associations among species, the first three axes of the principal coordinate analysis (PCoA; applied to the species × species functional distance matrix for calculation of SESFRic) were plotted against each other along with vectors indicating the influence of independent traits. The 15 most abundant species were identified to show how they were related in trait space.

Gower's distance, Rao's quadratic entropy, and CWM were calculated with the 'FD' package (Laliberté and Legendre 2010), the independent swap null model was introduced with the 'picante' package (Kembel et al. 2010), non-linear models were created with 'mgcv' package (Wood 2012) in R statistical software (R Core Team 2013).

Figure 9.2. Mean index-environment relationship. The dashed line at 0 of the index represents the expected value while mean values (\pm SE) above or below indicate change in from the expected as calculated by the standard effect size (SES). Colours represent sampling sites and correlate with Fig.1: red = SA, green = BL, yellow = BO, blue = BA, white = LU, pink = KA, and black = KP.

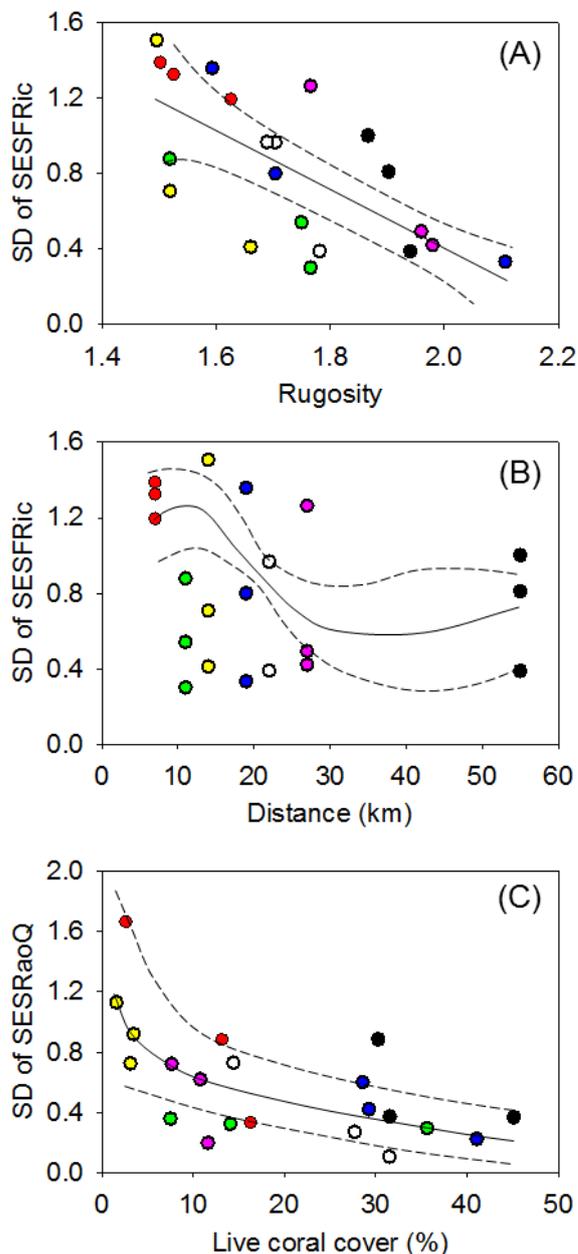


Results

Based on analysis of the mean index values (Fig. 9.2), we found little evidence that live coral cover, rugosity or distance from the mainland affected functional diversity and richness at a constant rate. For SESFRic, no sites differed from the values expected in randomly-assembled communities, while SESRaoQ at BL was below the expected values (Fig. 9.2).

Model validation with consideration of AICs indicated that a GAM model including the covariates rugosity and distance from shore was most suited for evaluating the SD of SESFRic (Table S2). For SESRaoQ, a GLM with the covariate coral cover was selected (Table S3). Although the mean values of the two indices did not directly relate to the environmental variables, within-transsect variability displayed strong correlations (Fig. 9.3). SD of SESFRic showed a highly significant relationship with rugosity (GAM, $df = 1$, $F = 23.8$, $p < 0.001$; Fig. 4A) and a moderately significant relationship with distance from shore (GAM, $df = 4$, $F = 3.6$, $p = 0.027$; Fig. 9.3B). For SD of SESFRic, the inclusion of both rugosity and distance from shore explained 76.3% of the deviance in the GAM. Variability in SESFRic decreased linearly with an increase in rugosity. Variability in SESFRic decreased sharply within the first 25 km from shore but remained similar beyond that distance. However, a lack of sampling sites between 27 km and 55 km distance reduced the accuracy of the GAM within this range. SD of SESRaoQ showed a strong, significant relationship with coral cover (GLM, $F_{19,20}$, $p = 0.002$; Fig. 9.3C), with coral cover explaining approximately 40.2% of the deviance. Variability in SESRaoQ decreased considerably with an increase in coral cover. For instance, a coral cover in the range of 0 – 10 % had twice higher SD of SESRaoQ than when coral cover was in the range of 30 – 40 % (Fig. 3C).

Among traits, only consumption of small invertebrates (DG_{C1}) showed a significant response to increase in rugosity, coral cover and distance (Table 9.2). Maximum length (L_m) and small and large home range size (HR_S and HR_L) were negatively correlated with rugosity and coral cover. None of the traits were associated with rugosity or distance from mainland alone. In addition, two dietary groups (microalgae / cyanobacteria feeding, DG_{H2} , and detritus feeding, DG_D) as well as medium home range size (HR_M), swimming in large schools (SB_E), and reproductive turnover were all negatively correlated with coral cover. The correlation between coral cover and home range decreased with home range size, and the correlation with reproductive turnover similarly was strongest for high turnover. High and medium reproductive turnover (T_H and T_M) were furthermore negatively correlated with increased distance (Table 9.2). Variability in traits, measured as SD, was negatively correlated with complexity and coral cover for all cases where significant relationships were detected (Table S4). The first two PCoA axes were able to explain a substantial amount of the variation (axis 1 ~33 %, axis 2 ~16 %)



of traits among species (Figure 9.4a), while the inclusion of axis 3 and 4 resulted in ~68 % explanation of the variation (axis 3 ~10 %, axis 4 ~9 %). T_H and HR_S contributed to the separation of ten out of fifteen of the most abundant species in the PCoA (Figure 9.4b). Of the most abundant species, nine belonged to the Pomacentridae family, four to Labridae, one to Scaridae and one to Balistidae (Figure 9.4a). A total of 31,725 individual fishes were counted, belonging to 144 different species. The species richness was lowest at BL (17.6 ± 1.4) and BO (15.4 ± 2.1), and highest at BA (31.3 ± 1.2), KA (29.6 ± 1.4) and KP (29 ± 1.7). Average species abundance was twice as high at BA as at the next site (KA), and the lowest abundances were observed at BL. Despite being the farthest from Makassar, KP had relatively low species abundances (Table S1).

Figure 9.3. Variability (standard deviation, SD) in the standard effect size of FRic (SESFRic) and RaoQ (SESRaoQ) as a function of significant environmental covariates. The GAM for SESFRic indicated significant relationship with A) rugosity and B) distance from shore and a GLM indicated that C) coral cover was significantly related with SESRaoQ. Plots include the expected (solid line) and $\pm 95\%$ confidence intervals (dashed lines). Colours represent sampling sites and correlate with Fig. 9.1: red = SA, green = BL, yellow = BO, blue = BA, white = LU, pink = KA, and black = KP.

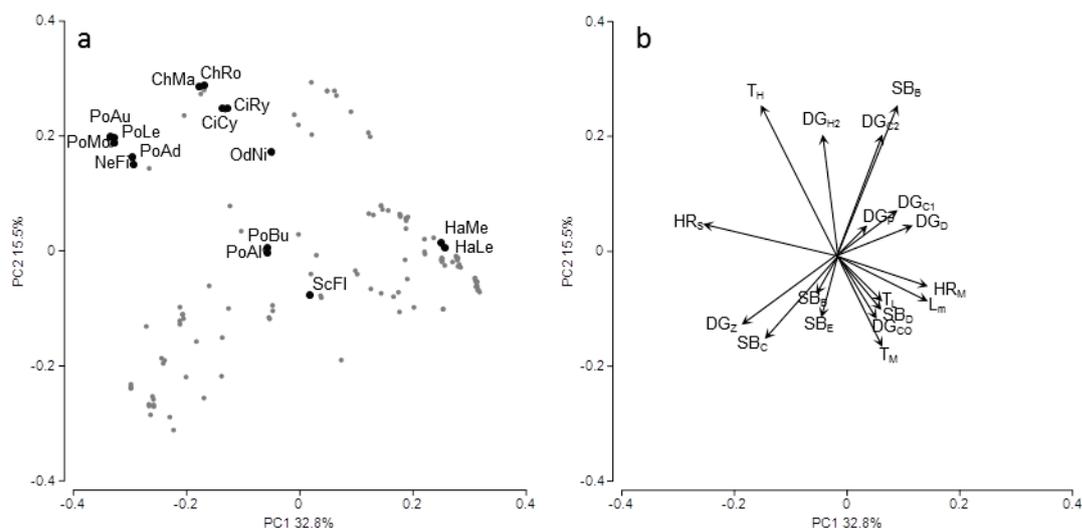


Figure 9.4. Biplot of a) first and second PCs of principal coordinate analysis conducted on fish species and traits. These axes were then used to calculate SESFRic. The fifteen most abundant species have been labelled and are: *Chromis margaritifer* (ChMa), *Chrysiptera rollandi* (ChRo), *Cirrhilabrus cyanopleura* (CiCy), *C. ryukyuensis* (CiRy), *Halichoeres leucurus* (HaLe), *H. melanurus* (HaMe), *Neopomacentrus filamentosus* (NeFi), *Odonus niger* (OdNi), *Pomacentrus adelus* (PoAd), *P. alexanderiae* (PoAl), *P. aurifrons* (PoAu), *P. burroughi* (PoBu), *P. lepidogenys* (PoLe), *P. moluccensis* (PoMo), *Scarus flavipectoralis* (ScFl). b) Vectors identifying traits (see Table 1 for trait labels) that discriminate species along PCoA axes in plot a.

Discussion

Coral reefs around the world are facing multiple disturbances, both local and global, which are increasingly understood as having impacts not only on biodiversity, but also on the functional composition of the communities (Nyström 2006, Bellwood et al. 2012, Eggers et al. 2014, Micheli et al. 2014). We used a trait-based approach to investigate the functional assembly of coral reef fish communities along an environmental gradient. Most previous studies considering functional composition have focused on the change in mean values of functional indices and/or mean species trait diversity values (Mouillot et al. 2013a, Stuart-Smith et al. 2013, D'agata et al. 2014), however we have also considered variability around repeated samples to account for short-term variation within fish communities that occur under increasing habitat heterogeneity (Warwick and Clarke 1993, Chapman et al. 1995).

Mean functional indicators of the fish communities did not display a strong, correlative relationship with any of the investigated environmental parameters. Conversely, the variability of fish communities, across samples repeated on a small temporal scale (a few hours), decreased with increases in coral cover, rugosity and distance from the mainland, thus indicating that the state of the coral reef habitat is important in functional constancy of the fish assemblage. There was a stronger relationship between fish community variability and the environment with regards to functional richness (SESFRic) than diversity (SES RaoQ), suggesting that the functional richness of fish assemblages may become more variable with habitat degradation, while overall functional diversity is not as strongly impacted.

The present study is the first to directly investigate variability in the functional composition of coral reef assemblages. Increased community and population variability, i.e. a reduction in the similarity of spatially or temporally repeated samples from a specific community or population, has been suggested as an early warning signal of impending ecological phase shifts (Carpenter and Brock

2006). Warwick et al. (1990) observed increased variability in the species composition of a coral community in response to thermal stress. In temperate environments, increased variability in the composition and relative species abundance of benthic communities has been observed in response to environmental impacts, and this measure has been suggested as an indicator of environmental stress (Warwick and Clarke 1993, Chapman et al. 1995). Using a modelled fisheries food web, Biggs et al. (2009) observed increased variance in the planktivore population prior to an impending phase shift. Fishing impacts have been shown to lead to an increased variability in the abundance of exploited fish populations (Hsieh et al. 2006). Dawson Shepherd et al. (1992) demonstrated increased variability in parameters of biodiversity of reef fish communities exposed to habitat loss through coral mining. In this instance, non-mined sites displayed much higher abundances of small planktivores (pomacentrids), suggesting an impact on trophic functioning within mined sites. Similarly, Pratchett et al. (2008) and Alvarez-Filip et al. (2011) observed that the loss of structural complexity and live coral cover led to a disproportional impact on smaller-bodied species at lower trophic levels and species depending on live corals for food and shelter. When considering specific traits, our results are partially in line with these findings. Maximum length (L_M) showed the steepest decline in response to loss of both structural complexity and coral cover. Furthermore, communities at sites with reduced coral cover comprised relatively more individuals with large and medium home range sizes, contributing to higher variability among temporally repeated samples. However, the trends in other traits reflect additional, nuanced responses in community composition. The only trait responding negatively to all three independent environmental variables was consumption of small invertebrates (DG_{C1}), which was characteristic of several larger labrid species that displayed high relative abundances when live coral-associated damselfishes became scarce. Their larger home range would result in high turnover between repeated samples, thus contributing to the observed variability at degraded sites. The higher values of detritivory and microalgae/cyanobacteria feeding at sites with lower coral cover reflect shifts in benthic resources, with detritus, microalgae and cyanobacteria being inversely related to live coral (Plass-Johnson et al. unpublished manuscript). In Spermonde, these trophic roles were to a large extent fulfilled by several pomacentrid species that were highly abundant at the degraded sites, occur in dense aggregations (SB_E), have small home ranges (HR_s), feed on micro-algae (DG_{H2}), and/or have high reproductive turnover (Γ_H). The high abundance of these species at degraded sites with low coral cover and structural complexity again likely contributed to high fluctuations among repeated samples. Furthermore, it may explain why, in contrast to the initial prediction based on Pratchett et al. (2008) and Alvarez-Filip et al. (2011), small home range size was negatively correlated with coral cover and structural complexity. The observed trait responses suggest that degraded sites maintained minimal habitat for most species but allowed a few species to become proportionally more abundant, leading to fewer species and high turnover on short temporal scales. The higher coral cover and rugosity of off-shore sites were more adequate for a broader range of species, allowing individuals of more species to co-exist and contribute to a more stable community composition. With respect to individual traits, it is important to note that variability increased with decreasing habitat quality, similarly to the composite indicators FRic and RaoQ. This indicates that individual traits are affected by the environment as is functional composition of a community.

Multiple studies have applied trait-based functional indices to identify community assembly rules (Mouillot et al. 2007, Villéger et al. 2008, Mouchet et al. 2010, Villéger et al. 2010, Mouillot et al. 2013b, Mason et al. 2013a). Unlike these other studies the Spermonde Archipelago did not display clear patterns based on mean index values indicating changes in the environment did not completely remove traits from the communities. However, mechanisms structuring coral reef fish assemblages may be more apparent in the variability of functional diversity indices. Responses in the CWM of

Table 9.2. CWM trait-environment relationships. The table lists significant results of linear regression of individual transect-level CWM of the examined traits against three environmental parameters (rugosity, coral cover and distance from mainland). Coefficients (Coef.), the y-intercept (Inter.) and the relationship (R^2) are provided.

Trait	Rugosity			Live Coral			Distance		
	Coef.	Inter.	R^2	Coef.	Inter.	R^2	Coef.	Inter.	R^2
DR	-0.066	0.904	0.00	-0.006	0.900	0.05	-0.006	0.920	0.06
L_m	-1.168	2.625	0.29	-0.014	0.903	0.27	-0.008	0.793	0.11
DG _P	-0.001	0.006	0.00	-0.001	0.006	0.09	-0.001	0.006	0.12
DG _{C1}	-0.017	0.041	0.31	-0.001	0.016	0.38	-0.001	0.016	0.32
DG _{C2}	-0.009	0.037	0.01	-0.001	0.027	0.06	-0.001	0.027	0.06
DG _Z	-0.004	0.033	0.00	-0.001	0.037	0.12	-0.001	0.033	0.05
DG _{H1}	-0.006	0.019	0.06	-0.001	0.010	0.08	-0.001	0.009	0.02
DG _{H2}	0.011	0.008	0.01	-0.001	0.042	0.22	-0.001	0.030	0.01
DG _{Co}	0.001	0.007	0.00	-0.001	0.009	0.07	-0.001	0.008	0.01
DG _D	-0.010	0.030	0.07	-0.001	0.018	0.28	-0.001	0.016	0.07
HR _S	-0.046	0.104	0.40	-0.001	0.036	0.39	-0.001	0.031	0.16
HR _M	-0.017	0.043	0.18	-0.0003	0.020	0.28	-0.001	0.018	0.17
HR _L	-0.024	0.057	0.19	-0.001	0.022	0.21	-0.001	0.020	0.11
SB _A	0.001	0.025	0.00	-0.001	0.032	0.08	-0.001	0.029	0.02
SB _B	-0.005	0.013	0.07	-0.001	0.006	0.01	-0.001	0.005	0.00
SB _C	0.003	0.019	0.00	0.001	0.024	0.00	-0.001	0.028	0.02
SB _D	0.004	0.001	0.01	-0.001	0.011	0.07	-0.001	0.010	0.05
SB _E	0.001	0.008	0.00	-0.001	0.013	0.21	-0.001	0.010	0.00
T _H	-0.005	0.026	0.01	-0.001	0.031	0.49	-0.001	0.027	0.26
T _L	-0.005	0.014	0.07	-0.001	0.008	0.22	-0.001	0.007	0.05
T _M	-0.004	0.023	0.01	-0.001	0.028	0.43	-0.001	0.025	0.24

particular traits suggest a close relationship between these traits and increasing stochasticity in fish community functioning in relation to increased disturbance. For coral reef fishes, habitat filtering initially would act upon traits without removing them completely from the communities, thus contributing to an increased stochasticity evident in repeated samples. For example, localised disturbances may lead to loss of corals and structural complexity, resulting in homogenisation of habitat on the within-transect scale, and thus leading to more weight on medium-range, less site-attached species (Alvarez-Filip et al. 2011). Importantly, some traits showed responses that were in contrast with previous observations (i.e. small home range size), but were generally in line with habitat filtering allowing particular traits to become abundant. Processes that lead to more heterogeneity in the occurrence of traits without completely removing them from a site would not become apparent in the means of the indices, as variability becomes masked when averaging across repeated transects. Increased variability without simultaneous changes in mean indices may thus constitute a useful early warning sign of habitat degradation.

Niche differentiation, on the other hand, is expected to lead to different responses in the indicators. Less variability in trait CWM and SESRaoQ only indicates constancy across samples, not differentiation in habitat use. The combination of a lack of responses in mean functional richness, higher variability and reduction of particular traits thus lends support to niche filtering in degraded habitats, but shows no indication of limiting similarity with increasing habitat quality. Conversely, habitat degradation and the associated loss of benthic resources led to higher stochasticity and thus variability in fish community composition.

For many of the traits reported here, or at least the species that display these traits, there is considerable evidence linking them to ecosystem functioning. For instance, small invertebrate feeding

by semi-mobile wrasses reduces prey abundances, modifying assemblage structure (Jones 1999). Species that feed on micro-algae are important for clearing benthic space for new coral recruitment (Bellwood and Choat 1990). In addition to a change in the mean values of particular traits, increased variability in traits means that they are not present consistently in communities, impairing the fulfilment of certain ecological functions. The present results underline that there are clear linkages between the functional assembly of coral reef fishes, their traits, and an environmental gradient of increased habitat degradation. Increased variability of the taxonomic composition of marine communities has been related to stress (Warwick and Clarke 1993). Importantly, our results indicate that community functioning is equally impacted. In light of increasing localised stressors on reefs around the world, this is of high concern because feedback loops between reef fishes and the environment (Hatcher 1984, Knowlton 1992) are key in the maintenance of coral reef ecosystem functioning (Bellwood et al. 2004).

In light of rapidly decreasing biodiversity across the planet, the link between biological diversity and ecosystem functioning has received increasing attention in recent years, including examples from coral reefs (Mora et al. 2011, Cardinale et al. 2012). Concepts around ecosystem stability suggest that weakly interacting species stabilise communities by reducing the effects of disturbances which destabilise consumer-resource interactions (McCann 2000), and this is reflected in coral reefs through evaluation of functional redundancy (Nyström 2006). If this holds true, then a decrease in biological or trait diversity, particularly when resulting from a loss of resources and thus ecological niches, would be accompanied by an increase in the strength of interactions among the organisms in the community, thus destabilising the system. In the Spermonde Archipelago, increases in the variability of functional diversity and richness were associated with a more impacted habitat suggesting that increased variability in the functional composition is a symptom of a change in species' interactions. Furthermore, an increase in disturbance may have greater impact on the most variable reefs because they may lack the capacity to respond consistently to stressors, and thus may comprise less response diversity (Chapin et al. 2000, Plass-Johnson et al. In Press) compared to reefs of lower variability. These findings of increased functional variability broaden the understanding of competitive interactions along disturbance gradients, thus contributing to improving our predictions of how coral reefs will react in a changing environment (Graham et al. 2014). Based on these findings, we suggest that further assessments of variability of functional indices in response to stress are a promising avenue for future work on community assembly and functioning under conditions of environmental change.

Section Five

General Discussion

Live coral cover and abundance of coral reefs have been in decline for several decades (Gardner et al. 2003, Bruno and Selig 2007). The causes are numerous and can be attributed to both natural and anthropogenic factors such as climate change, disease, predator outbreaks, changing land use practices and unsustainable resource use (Glynn 1993, McManus et al. 1997, Hughes et al. 2003, Sato et al. 2009, Plass-Johnson et al. 2015, Chapter VII). Ideally, hard corals are the dominant biotic constituent of tropical reef habitats, but in extreme cases, changes in the communities have resulted in reefs becoming dominated by non-coral groups (Done 1992, Knowlton 1992, Norström et al. 2009). Similarly, recent literature has suggested that coral communities switch between coral dominance and non-coral dominated states (Knowlton 1992, Bellwood et al. 2004). However, given that these states relate to polar extremes on the spectrum of coral reef ecological condition, and their states depend on the stabilisation of ecological feedbacks (Nyström et al. 2012), more recent work has shown that the majority of the world's reefs fall between these two extremes with varying ratios in benthic composition among differing biota (Bruno et al. 2009). If reef management is based on increasing “resilience”, understanding coral reefs at various stages of ecological change should be prioritised, in order to acknowledge the true state(s) of contemporary reefs (Done 1999, Hughes et al. 2010, Nyström et al. 2012). Likewise, the status of a coral reef is generally described as a factor of its benthic composition overlooking the physical structure and associated communities. In that sense, managers of ecological communities seeking to find general rules within ecological systems that allow for the comparison of those systems across space and time need to consider the totality of functional relationships. By comparing ecological states and processes of coral reef communities along a disturbance gradient, this thesis explored varying stages of coral reef communities and provides a mechanistic understanding of ecosystem functioning within them.

Processes affecting benthic composition

The description of coral reef benthic community composition has been a central theme in coral reef ecology for decades (Vaughan 1915). These habitats are generally composed of biotic organisms such as corals, algae and sponges, however, their proportional contributions can change in space and time. These communities arise from environmental influences such as water depth, wave exposure, light availability, storms and riverine export (Sheppard 1982, Kleypas et al. 1999, Fabricius et al. 2005) interacting with biological influences such as larval dispersal, competition and the spread of disease (Benayahu 1981, Fisk and Harriott 1990, Zvuloni et al. 2009), all dependent on historical geological configuration (Hubbard 1997). These factors interact synergistically, implying that understanding the status of the benthic composition provides minimal explanatory power of larger deterministic processes (Quinn and Dunham 1983). Surveys of benthic communities of the Spermonde Archipelago found that near shore sites had higher abundances of turf algae and off shore sites increased in hard coral cover (Chapter I) and diversity (Edinger et al. 2000a). At the site closest to shore (Lae Lae), the benthic community was dominated by sand (Chapter I). Indeed, these patterns related to changes in the water quality associated with terrestrial and riverine export, with near-shore sites displaying higher particulate organic matter (POM) and light attenuation (Chapter I). This agreed with a comprehensive review on the topic by Fabricius (2005) where an increase in nutrients is usually associated with a change from symbiotic corals to increasing proportions of algae and heterotrophic filter feeders. However, it is with the experiments on recruitment, succession and herbivory, in association with the water quality gradient, that a greater understanding of the causative processes that maintain these differing states could be obtained.

Water quality and recruitment

Along the gradient, turf algae were the dominant biotic recruits to experimental tiles and this dominance continued after four months of development (Chapter VI), being further reflected at the reef scale (Chapter I). Likewise, there was no difference between caged and uncaged successional tiles (Chapter VI), and experimental transplant of two common macroalgae suggested healthy browsing herbivore communities at most of these sites (Chapter V). Thus it would seem that fish herbivores are important in structuring benthic communities at early stages of reef development. However the persistence of large proportions of “open space” on caged successional tiles (Chapter VI) runs contrary to studies conducted with similar methods and time periods (Stuhldreier 2012, Jessen et al. 2014, Roth et al. 2015). The exclusion of fish herbivores with cages retains experimental artefacts and in this instance, caging may not have excluded benthic herbivores such as mesograzers (Carpenter 1986). These results show that the functional role of herbivory may be shared between fishes and smaller invertebrates, a situation commonly observed in Caribbean reef systems (Hay 1984). However, the exact division of this function remains unclear. The role of herbivory is questioned at the site nearest to shore. Here, herbivore biomass is very low (Chapter I) and no browsing was observed (Chapter V). Despite the seemingly low potential from herbivores, successional tiles also retained high proportions of open space (Chapter VI). However this is better explained in light of the greater environment. High concentrations of particulate matter and chlorophyll-a in the water column would restrict light availability and smother benthic primary producers (Fabricius 2005) resulting in slow benthic development.

One of the more promising results concerning coral reef health in the Spermonde Archipelago concerns coral recruitment. Scleractinian coral recruitment in the Spermonde Archipelago shows little variation along the spatial gradient despite habitat condition (Sawall et al. 2013) suggesting adequate source populations. Again, only at Lae Lae does coral recruitment become limited and recruitment is largely dominated by one family (Pocilloporidae). In the experiment by Sawall et al. (2013), coral recruits were offered clear benthic space via recruitment tiles over four months. Given the statistical differences in the recruitment of non-coral biota seen between Lae Lae and the other sites in my study (Chapter VI), these finding would support previous work suggesting that sedimentation plays an important role in coral recruitment (Birrell et al. 2005). Unfortunately coral recruitment and the recruitment of other benthic biota were not able to be quantified simultaneously due to methodology (Chapter VI). However results from Chapter VI show that coral recruits will primarily compete with turf algae for benthic space, an effect which is increased at near-shore sites but further discussed in the “*Phase shift*” section of this thesis.

In Spermonde, the successful recruitment of benthic organisms does not guarantee development to adult stages. Here, coral species diversity becomes extremely reduced at near-shore sites (Edinger et al. 1998) and coral growth rates are retarded compared to off-shore, clear water sites (Edinger et al. 2000b). This disconnect between recruitment (Sawall et al. 2013) and adult composition suggests that there are processes affecting coral development. One important constriction on development is physiological adaptability to strong variation in abiotic conditions. Sawall et al. (2011) showed that *Stylophora subseriata*, a scleractinian coral, increased heterotrophic feeding at near-shore sites resulting in varying metabolic usage. Furthermore, environmental adaptability may be the driving characteristic of benthic composition given the little variation seen in recruitment at sites past Lae Lae. However, unlike recruitment tiles, open space is rare on the substratum, generally occurring in limited amounts after parrotfish excavate benthic material during feeding (Bellwood 1994). Thus, new recruits increase the probability of interacting with turf algae with every site closer to shore necessitating a competitive dominance over this group.

Near-shore sites of the Spermonde Archipelago are composed of higher proportions of rubble (Chapter I). Previous work has shown that reefs with high proportions of live, branching coral subjected to disturbance can result in the accumulation of rubble (Chong-Seng et al. 2014). The onset of acute disturbances are not rare in the Spermonde Archipelago (Chapter II & III, Baird et al. 2013) and may contribute to the accumulation of rubble, however the strong relationship between rubble and water conditions (Chapter I) suggest a water related cause. This relationship was not directly tested, but it might be expected that increasing exposure to poor water quality at sites closer to shore would result in increased live coral mortality resulting in increased rubble. However, because live coral would be the source of rubble, higher levels of live coral would have been needed at earlier time periods. Unfortunately, this cannot be determined within this study. This should, however, not be overlooked, that the effects of rubble in determining benthic composition. The physical instability of rubble interferes with successful macro-benthic and coral recruitment (Fox et al. 2003, Francini-Filho et al. 2013, Chong-Seng et al. 2014) thus maintaining low structural complexity and low benthic diversity (Fox et al. 2003, Wilson et al. 2006). Furthermore, our results show a strong positive relationship between rubble and turf algae (Chapter I). Rubble covered in turf algae would impede the recruitment of calcifying algae (Vermeij et al. 2011), a prerequisite for benthic consolidation and the development of important benthic macrofauna (Smith et al. 2010).

Localised disturbances

Continuous recruitment of corals and adequate herbivory by fishes suggests that the benthic composition of the Spermonde Archipelago is largely driven by variation in the capacity of benthic organisms to vary metabolic needs to environmental conditions. Given the range of water conditions across the archipelago, this will have a strong limiting effect on benthic organisms as most organisms require a narrow range of environmental conditions (Pandolfi et al. 2003b, Hughes et al. 2003). These water conditions may lead to the death of many hard coral, contributing to a rubble dominated state, which turf algae are able to overgrow due to their fast growth rates and capacity for poor water conditions (Fabricius et al. 2005). Thus, the driving factor of decreasing benthic conditions in the Spermonde Archipelago is most likely to be exposure to poor water conditions. In the worst situation, high sedimentation, such as that found at the closest site, controls benthic assemblages by reducing light attenuation and smothering organisms. However, the effects of water quality on benthic organisms can be overshadowed by intense, acute disturbances.

Benthic communities of the Spermonde Archipelago are also impacted by the biological disturbance of the coral-predating starfish, *Acanthaster planci* (Chapter II, Baird et al. 2013). High densities of this organism in 2012 resulted in loss of >50% of live coral at two sites (Chapter II) while observations also placed high densities at the two sites nearest shore in 2007 (Baird et al. 2013). Further mechanical disturbances to benthic communities include destructive resource use such as bomb fishing (Pet-Soede and Erdmann 1998a, 1998b, Pet-Soede et al. 1999, 2001), cyanide fishing (Erdman and Pet-Soede 1997) and coral mining (reviewed in Chapter I). Both biological and mechanical disturbances reduce cover of live coral, increasing rubble and allowing settlement and development of faster growing algae (Chapter VI), thereby increasing or sustaining low benthic diversity. The exact effects of constant exposure to local disturbances are unknown but the most likely result is highly reduced live coral cover (Pet-Soede et al. 1999). However, observations at Karang Kassi, an uninhabited reef complex, may provide insight on consequences. This site is subject to continuous bomb fishing due to the lack of management (J Jompa pers. comm.) and this has resulted in very high cover of the sponge *Ircinia* sp. (Chapter I & III). At some sites, this sponge is the

dominant benthic constituent (Chapter I). The exact mechanisms leading to this overtake of parts of the reef are unknown, but observations indicated that it was competitively dominant over other benthic organisms, overgrowing corals and turf algae. Perhaps bombing has little negative effect on the health of the sponge, yet the blast may allow for its proliferation and redistribution into other areas of the reef. Likewise, this site is also associated with high levels of cyanobacteria, suggesting an ecological association with *Ircinia* sp., however this requires further investigation.

These observations show that the effects of localised impacts can be far reaching and, that these can be confounding when trying to resolve disturbance effects. Nonetheless, localised disturbances such as *A. planici* outbreaks and destructive fishing techniques can substantially inhibit reef recovery. Furthermore, in the most disturbed scenarios, it is possible that continuous exposure may result in unexpected outcomes, as seen with the *Ircinia* sp. sponge outbreak (Chapter III).

The effect of changing benthic condition on fish assemblages and ecological feedbacks

Most coral reef fishes are dependent on coral reef habitat for shelter and food resources, implying that the structural and biological components of the habitat exert an influence on the composition of the associated fish community. Accordingly, most studies find positive correlations between structural complexity and fish abundance (Graham and Nash 2013), number of species (Gratwicke and Speight 2005, Wilson et al. 2008), biomass (Friedlander and Demartini 2002) and species diversity (Öhman et al. 1997, Ferse 2008). Likewise, in the Spermonde Archipelago, fish species diversity and biomass increased with distance from the shore in accordance with greater coral cover and structural complexity (Chapter I). However, the mechanism for this relationship between fish community composition and the habitat is reflected in the fish's ability to adapt to the changing environment. Similar to the loss of benthic groups at sites closer to shore and capacity to adapt to changing water quality (see above), fish must have traits or mechanisms that allow them to utilise the remaining available resources or they become vulnerable to localised extinction (Syms and Jones 2000). For instance, the parrotfish *Chlorurus bleekeri* and the farming damselfish *Dischistodus prosopotaenia* are able to either expand or maintain their nutritional resources in response to a changing habitat (Chapter VII). Alternatively, Chaetodontidae, or the butterflyfishes are highly susceptible to changes in live coral cover (Pratchett et al. 2013). Some show minimal capacity to change their coral prey (Cole et al. 2008), but undergoing such adaptation also affects their physiological capacity by reducing reproductive output (Pratchett et al. 2004), resulting in long term declines in the populations.

Although a key trait, the adaptability of fish species goes beyond simply nutritional preferences, because other traits such as mobility, schooling behaviour and size determine the species capacity to find new food sources and secure competitive dominance (Sale 2002). In the Spermonde Archipelago, the loss of live coral cover and structural complexity firstly resulted in fish communities being composed of fewer species, and they were mainly composed of small-bodied planktivores (Chapter I & IX). At very high levels of coral loss, the small-bodied fishes were lost and the community became dominated by medium-sized fishes with medium to wide home ranges feeding on cyanobacteria and turf algae (Chapter I & IX). Thus, there was a gradual compositional change in fish communities, determined by trait composition, and therefore supporting the concept of niche filtering (Mouillot et al. 2013). This, however, has implications for the functional capacity of the fish assemblages. A positive relationship between fish abundances and coral cover, along with changes in trait composition, resulted in the fish communities becoming more stochastic (Chapter IX). Indeed, in Bonetambung, a site highly disturbed by an *A. planici* outbreak (Chapter II), exhibits the highest variability in functional composition (Chapter IX). Here, it seems that increased stochasticity in the

functional composition of the fish community is a product of habitat degradation, providing an indicator of possible change in the greater reef community. Yet this indicates serious limitations within fish ability to acclimatise to changing conditions.

Limitations in habitat adaptability are further observed in the important browsing herbivore group. Results from the Spermonde Archipelago show that this functional group may benefit in functional compensation from the high species diversity within the region. There was high species turnover among sites, but the herbivory was continuously maintained by new species compositions (Chapter V). Unfortunately the sampling method of Chapter IX limited observations of the browsing herbivore group, primarily because of its high mobility (Green and Bellwood 2009, Welsh and Bellwood 2012), but species diversity of the herbivores was positively related to coral cover, again suggesting niche filtering processes.

Herbivory by fishes is considered a key function in maintaining coral dominance on coral reefs (Hughes et al. 2007). However the same corals provide food and shelter for most coral reef fishes (Alvarez-Filip et al. 2015). Disturbances that disrupt this balance, such as reduced water quality, favour algae and reduce habitat quality for fishes thereby resulting in less herbivory. In the Spermonde Archipelago, browsing herbivores seem to benefit from the regionally high diversity, resulting in continued function. (Chapter V). However this does not seem to be the same for the scraping herbivores or the group of herbivores that remove turf algae via mechanical scraping of the substratum, thereby creating free space for recruitment. The parrotfish *Chlorurus bleekeri*, was chosen for a trophic study (Chapter VIII) because it was observed across all sampling sites. Stable isotope analysis suggested that although this species seems to be able to adapt to changing resources, it might not fulfil the same function across all sites. At sites closer to shore, its food choice changed to that of higher trophic levels (Chapter VIII). Generally, this genus feeds on turf algae (Choat et al. 2002) but an increase in trophic level suggests a dietary change to live coral (Plass-Johnson et al. 2013, Dromard et al. 2014). A shift from herbivory to corallivory with increasing disturbance runs contradictory to the functional role of this species, particularly at sites that are most susceptible to further disturbance. Further positive and negative feedbacks can be seen at extremes of the Spermonde environmental gradient. The mobile herbivores avoided Lae Lae (Chapter VI), most likely a predator avoidance mechanism in low visibility (Collin and Hart 2015), resulting in low capacity for algal removal. On the opposing end of the environmental gradient, the most important excavating herbivore, *Bolbometopon muricatum* (Bellwood et al. 2003) was observed functioning as a browsing herbivore in the reef furthest from shore (Chapter IV). This observation supports the concept of species conservation: the functions carried out by each species may go beyond current observations and research.

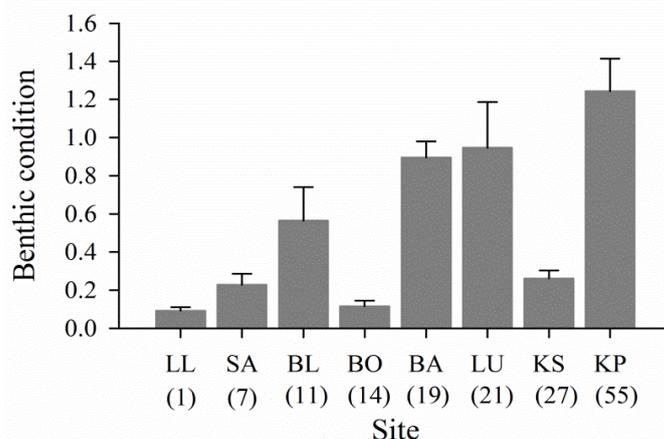


Figure D.1. Benthic condition of the reefs of the sampling sites of the Spermonde Archipelago. Sites (LL = Lae Lae, SA = Samalona, BL = Barrang Lompo, BO = Bonetambung, BA = Badi, LU = Lumu Lumu, KS = Karang Kassi, KP = Kapoposang) are listed from left to right increasing in distance (in brackets) from the mainland. Benthic condition is calculated as live coral cover divided by the sum of the percent cover of other important benthic groups (macroalgae, turf algae, sponge and cyanobacteria)

Phase shifts in the Spermonde Archipelago

In 2009, Bruno and colleagues (Bruno et al. 2009) noted that the current paradigm of healthy coral reefs shifting to macroalgal dominance was over-extrapolated from a limited set of observations (Coté et al. 2013) and that coral cover exists on a continuum in ratio with other benthic groups. Similarly, they recommended that other benthic groups be taken into consideration when debating the state of a reef. At the studied sites in Spermonde, macroalgae was rare, always contributing to less than 10% of total cover (Chapter I) while at most reefs, turf algae was generally high, but this could be overshadowed by cyanobacteria and sponge (Chapter I). The dominance of these groups is largely driven by terrestrial effluents and the capacity of macro-benthic organisms to live within the abiotic environment. However other disturbances such as blast fishing can further change the benthic assemblages. Thus, as Bruno and colleagues suggested, the reefs of the Spermonde Archipelago exist at differing levels of health. Figure D.1 shows the state of the reefs with increasing distance from Makassar, where benthic condition is percent live coral cover divided by the sum of the percent cover of other important benthic groups (macroalgae, turf algae, sponge and cyanobacteria). The evident trend is related to distance from the mainland, however Bonetambung (BO) and Karang Kassi (KS) provide evidence of how localised disturbances can overshadow coral importance. Evidence for the classically termed “phase shift” in the Spermonde Archipelago was only present at Karang Kassi, where persistent, extreme, physical alterations to the benthic community allow for alternative states. Even at the site closest to the mainland, live coral remains present in low proportions and no single other group can be considered as dominant (>50% cover) (Chapter I). Nevertheless, the establishment of phase shifts are dependent on an organism’s capacity to maintain dominance. Although the ecological feedbacks of the sponge driven state are not known, its condition seems associated with human interference. Thus, a decrease in human interference may return the reef to a state maintained by water quality; a situation with extensive research potential.

Although previous studies have shown that macroalgae can dominate when nutrients are increased and herbivory is decreased (Burkepile and Hay 2009), this situation is not currently found in Spermonde, because browsing herbivore communities are still mostly intact (Chapter V). However, the dominance of turf algae is an increasing global trend (McClanahan et al. 2002, Vermeij et al. 2012, Roth et al. 2015). Turf algae can cause damage to other organisms through allelochemical mechanisms (Jompa and McCook 2003). Furthermore, filamentous algae can trap sediments (Stewart 1989) and shade other organisms (Roberts 2003) while also altering water flow (Duggins et al. 1990). Likewise, recent studies have found turf algae to have a significant effect on the coral composition of Belizean coral reefs (Wild et al. 2014) and can also impede coral recruitment and development (Birrell et al. 2005, 2008, Vermeij and Sandin 2008, Barott and Rohwer 2012). In Spermonde, turf algae recruited constantly to free space with little interference by fish herbivores (Chapter V), while turf recruitment on rubble would inhibit reef consolidation by encrusting carbonate organisms (Rasser and Riegl 2002). However, turf algae cannot be seen as a stable state because it is not competitively dominant over established coral (McCook 2001) and is susceptible to increased sedimentation (McClanahan et al. 2005). This suggests that a change in water quality, either increasing and allowing for greater coral recruitment and development or decreasing and resulting in more sedimentation, could reduce turf abundance, a situation demonstrated along the Spermonde Archipelago (Chapters I, V).

Management and future direction

Recent work has noted that the coral reefs of Southeast Asia are more threatened by localised human impacts, such as terrestrial effluents and resource use, than by global stressors such as warming water temperatures and acidification (Burke et al. 2011). These reefs are, of course, not immune to global processes. Yet the cause for concern arises from the region's increasing human population and growing reliance on coral reef resources. (Burke et al. 2012). Similarly, it is recognised that deteriorated coral reef conditions due to these localised impacts increases susceptibility to global stressors (Hughes et al. 2003, Pandolfi et al. 2003, Bellwood et al. 2004; Chapter VII). This dissertation shows that coral reef conditions within the Spermonde Archipelago are largely determined by the water quality of the region and to a lesser extent, resource use. Within this concept and admitting oversimplification, it is easy to make management suggestions. Increasing water quality and reducing destructive fishing practices would create an ecological balance that favours coral recruitment and growth and should therefore form a strategic part of coral reef management. Subsequently, this would create habitat for fishes, possibly resulting in better yields for fishermen. These concepts are not new. Control of water quality is a priority for the managers of the Great Barrier Reef (Authority 2014), acknowledging the economic benefits from the reef (Emslie et al. 2015). Furthermore, marine protected areas are a well-documented strategy that has been practiced for decades and their dynamics on coral reef communities and contingent outcomes have been discussed in detail (Roberts and Polunin 1991, Halpern and Warner 2002, Abesamis et al. 2014). Outlining the requirements for creating an environment within Indonesian communities that acknowledges and manages for better ecological conditions is beyond the scope of this thesis. There are, however, commonalities that are shared around the globe where human communities interact with the natural environment.

Indonesia's development as a country, also reflected in the greater Southeast Asian region, coincides with an exponential increase in development and access to technology. Advancing technologies and an increasing human population reliant on natural resources means that people are interacting with the environment at a significant scale (Jackson 2010), with differing priorities (Hicks et al. 2009). However, population increases are largely focused in urban areas (Jones 2014, McDonald 2014), increasing the social disconnect from nature and creating environmental disregard in management and planning (Ismail 2014). Thus, one of the key priorities for better ecological management is education and acknowledgment of the human components within the broader social-ecological system. Understanding that human and ecological components interact and create feedbacks, where economic wellbeing are contingent on healthy ecosystem services is crucial to formulating effective and achievable management strategies (Hicks et al. 2009, Nyström et al. 2012).

At a smaller scale, the examination of coral reef ecological states along a water quality gradient provides simple, but tractable clues to the possible outcomes of better water management. In Spermonde, water quality is the strongest determinant of reef status. Lowering the exposure to eutrophic conditions at any one site over time could result in an ecological state represented by sites further from shore. Alternatively, if water quality decreases, a single site might become more similar to those closer to shore. This situation is further justified because coral recruitment seems unimpeded (Sawall et al. 2013). However current high levels of rubble may act as a bottleneck (Chong-Seng et al. 2014) and furthermore, it depends on healthy parental sources of recruits (Connell et al. 2004). This concept becomes uncertain when multiple stressors interact (Chapter II, III & VII), suggesting that further focus should be placed on fishing practices. Reducing destructive fishing techniques slows live coral loss and provides more sources for coral reproduction. However, as stated above, personal

observations suggest that a lack of ecological understanding among fishers drives practices beyond sustainability suggesting that focus on education should be priority.

Primary finding and concluding remarks

In summary, discrete coral reef ecological states exist at the extremes of the continuum in habitat quality, however most reefs exist within the ecological continuum somewhere between coral and algal dominance. This thesis has shown that the benthic and pelagic communities of the coral reefs of the Spermonde Archipelago are comprised of various combinations of biota (Chapter I) and structured through processes occurring at varying strengths (Chapter V & VI). Sites exposed to low water quality exhibited a loss of biodiversity (Chapter I & V) driven in part by the adaptability of the organism, with physiological and ecological characteristics interacting with habitat change (Chapter VIII). In coral reef fishes, ecological adaptability is reflected in trait composition of a species (Chapter VIII & IX). Nonetheless, unfavourable trait combinations and the loss of species reduce functional overlap, resulting in the instability of fish assemblages (Chapter IX). The loss of biodiversity and functional instability suggest high susceptibility of the community to further disturbances, because response diversity of the fish assemblage has been eroded. However, functional redundancy in the browsing herbivores maintains coral-competing macroalgae at low levels despite changes in water quality (Chapter V). Alternatively, continuous exposure to low water quality, and/or acute disturbances (Chapter II & III) increases coral mortality, contributing to high coral rubble abundances (Chapter I). The instability of rubble favours the recruitment of turf algae (Chapter VI), negatively affecting the recruitment of live corals; the primary reef ecosystem engineers. Nevertheless, ecosystem resilience in Spermonde appears to be high, as coral recruitment continues despite impact exposure. Thus, reducing the chronic exposure to low water quality and maintaining healthy fish communities may result in positive responses from corals in the form of coral accretion, contributing to habitat construction and mitigating ecological vulnerability to global environmental changes (Chapter VII).

The results from this thesis expand on previous knowledge about the functioning of coral reefs at differing ecological states by disseminating state and process driven characteristics of benthic and pelagic communities along an environmental gradient. The primary outcomes of this work are:

- 1) In the Spermonde Archipelago, chronic environmental impacts have not resulted in coral reefs changing to a traditionally defined, macroalgal state. Rather, increased exposure to reduced water quality reduces live coral cover and structural complexity, but other biotic groups such as turf algae, crustose coralline algae, sponges and cyanobacteria can combine to account for benthic space dominance. The latter two become increasingly prevalent when communities are exposed to further mechanical disturbances.
- 2) Despite the level of impact on the coral reef habitat, fish communities in highly speciose regions retain capacity for functional compensation of the herbivorous functional group. Functional compensation can occur through complete replacement of species within communities. Only at the highest level of impact does the functioning of the fish herbivore group break down. However, at this stage macroalgae can be further maintained by abiotic conditions.

3) The functional composition of fish communities becomes more variable with increasing environmental impacts. This occurs because the loss of habitat incrementally reduces fish trait diversity, resulting in those species with traits allowing access to far-ranging resources. Increasing variability in trait composition of fish communities may be an indication of stress on coral reef communities.

4) The functional role of a fish species may be context dependent where its impact in the community depends on resource availability, competitors and individual trait composition.

5) Although it is beyond the scope of this thesis to explain all functional processes of the coral reefs of the Spermonde Archipelago, these findings combined with previous studies show that recruitment, organismal physiology and ecology, and herbivory exist along a dynamic continuum in relationships determining site specific diversity.

Likewise, this thesis highlights topics that need further investigation to discern possible trajectories of coral reefs under changing conditions:

- 1) How does the functional role of individual species change along gradients?
- 2) Are there individual species that should be favoured by conservationists and managers because of their physiological capacity to persist under stressful abiotic conditions?
- 3) Why has the sponge at Karang Kassi become so dominant? Is this a threat to other reefs?
- 4) Would localised conservation practices, such as marine protected areas, outweigh regional, water quality driven disturbance?
- 5) What is the best means of implementing environmental education schemes in Makassar to increase perceived values of local coral reefs?

Although it takes much more than one thesis to define all functional processes of a reef, these findings allow for greater understanding of differences among coral reef states and allow for a more detailed mechanistic view when prioritising management of reef systems. It is the hope of all managers and enthusiasts of the natural world that coral reefs will survive the next turbulent decades. However, understanding that we live in a changing world, embracing new ecological systems, or understanding how current systems change and managing for current threats may be the best practice rather than straining towards unreasonable outcomes. Of course I hope that coral reefs of the Coral Triangle will continue for centuries as a wonder of the natural world, providing resources, intrigue and beauty to all the people that rely on or visit them. Thus, I hope this thesis provides some clarity to the decision-makers and practitioners involved in securing their longevity.

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Appendix A: Supplemental material

Table S1. Average number of functional groups, average species richness, and average abundance of individual fishes (\pm SE) for each of the surveyed Spermonde islands. Sites are listed from left to right in order of increasing distance from Makassar.

	SA	BL	BO	BA	LU	KA	KP
Distance (km)	7	11	14	19	22	27	55
Species richness	22.3	17.6	15.4	31.3	25.8	29.6	29.0
(SE)	(1.92)	(1.39)	(2.10)	(1.22)	(1.38)	(1.44)	(1.71)
Abundance	267.4	147.2	335.7	1243.3	426.7	666.4	438.2
(SE)	(20.3)	(19.1)	(25.5)	(327.2)	(45.2)	(115.5)	(60.7)

Table S2. AIC scores of competing GAMs assessing their relationship with FRic

Factor	Ref. df	df	F	Dev. Exp.	AIC	Int.	F1	F2	F3
Dist +Rug	3	3	5.75	71.9	2.878	<0.001	0.007	<0.001	
LC+Rug+Dist	3	3	1.141	77.6	4.131	<0.001	0.369	<0.001	0.241
LC+Rug	3	3	1.569	54.1	13.367	0.022	0.236	0.003	
Rug	2	2	6.253	42.7	14.107	<0.001	0.009		
LC	3	3	1.142	16.5	24.247	<0.001	0.36		
Dist	2	2	0.908	7.93	24.372	<0.001	0.421		
LC+Dist	3	3	0.833	23.1	28.461	<0.001	0.714	0.498	

Table S3. AIC scores of competing GLMs assessing their relationship with RaoQ. Models are presented based on increasing AIC score. R^2 was calculated by subtracting the residual deviance from the null deviance and then dividing by the null deviance. F1, F2, F3 correspond to the model's factors (Factor).

Factor	Null dev.	df	Resid. Dev.	df	R^2	AIC	Int.	F1	F2	F3
LC	8.249	20	5.096	19	0.38	5.44	0.002	0.002		
LC+Dist	8.249	20	4.851	18	0.41	6.36	0.003	0.005	0.325	
LC+Rug	8.249	20	5.069	18	0.39	7.32	0.431	0.008	0.752	
LC+Rug+Dist	8.249	20	4.825	17	0.42	8.24	0.833	0.007	0.755	0.338
Rug	8.249	20	7.723	19	0.06	14.60	0.654	0.252		
Dist	8.249	20	7.951	19	0.04	15.25	0.004	0.418		
Rug+Dist	8.249	20	7.713	18	0.07	16.57	0.786	0.457	0.877	

Table S4. CWM trait-environment relationships. The table lists significant results of linear regression of transect-level standard deviations around the mean for individual CWM traits against three environmental parameters (rugosity, coral cover and distance from mainland).

Trait	Slope	y-int	R ²	P-value
<i>Rugosity</i>				
L _M	-1.1675	2.6251	0.29	0.014
DG _{C1}	-0.0172	0.0409	0.31	0.011
HR _S	-0.0461	0.1035	0.40	0.002
HR _M	-0.0165	0.0423	0.21	0.049
T _H	-0.0409	0.0885	0.52	0.001
<i>Coral Cover</i>				
L _M	-0.0173	1.0068	0.29	0.012
DG _{C1}	-0.0002	0.0158	0.38	0.004
DG _Z	-0.0004	0.0274	0.27	0.026
DG _{H2}	-0.0009	0.0469	0.35	0.006
DG _D	-0.0003	0.0181	0.28	0.014
HR _S	-0.0008	0.0382	0.58	<0.001
HR _M	-0.0003	0.0197	0.28	0.016
HR _L	-0.0004	0.0232	0.24	0.025
T _H	-0.0005	0.0309	0.49	<0.001
<i>Distance</i>				
L _M	-0.0281	1.1485	0.25	0.049
DG _{C1}	-0.0004	0.0187	0.25	0.049
HR _S	-0.0010	0.0409	0.26	0.035
HR _M	-0.0006	0.0240	0.27	0.034
SB _D	-0.0004	0.0138	0.29	0.024
T _L	-0.0002	0.0093	0.48	0.003

Figure S1. Correlation coefficients among all environmental covariates used as predictors for the SD of SESFRic and SESRaoQ. A correlation coefficient of 0.8 was considered a strong relationship at which a covariate would be removed from the subsequent models. Colours represent sampling sites and correspond to Fig.1: red = SA, green = BL, yellow = BO, blue = BA, white = LU, pink = KA, and black = KP.

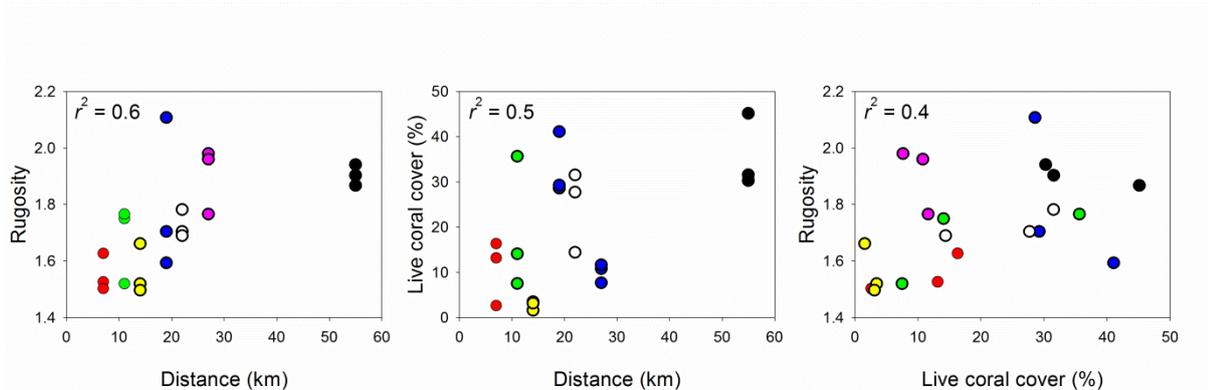


Table S5. List of species and their traits as determined provided by fishbase.org. Trait definitions can be found in Table 9.1.

Species	Ra	Lm	DG1	DG2	HR	SC	Turn
<i>Abudedefduf vaigiensis</i>	14	20	C2	Z	W	D	H
<i>Acanthochromis polyacanthus</i>	64	14	Z	H1	S	D	H
<i>Acanthurus leucocheilus</i>	27	45	C2	H2	W	D	M
<i>Acanthurus lineatus</i>	15	38	C2	H2	W	D	M
<i>Acanthurus nigricaudus</i>	13	40	C2	H2	W	A	H
<i>Acanthurus nigrofuscus</i>	24	21	H2		W	D	M
<i>Acanthurus pyroferus</i>	56	29	H2		W	C	M
<i>Acanthurus thompsoni</i>	115	27	C2	Z	W	D	H
<i>Amblyglyphidodon aureus</i>	42	13	C2	Z	S	A	H
<i>Amblyglyphidodon curacao</i>	39	11	Z	H2	M	C	H
<i>Amblyglyphidodon leucogaster</i>	43	13	Z	H2	S	A	H
<i>Amphiprion clarkii</i>	59	15	Z	H2	S	B	M
<i>Amphiprion perideraion</i>	37	10	Z	H2	S	B	M
<i>Amphiprion sandaracinos</i>	17	14	Z	H2	S	B	H
<i>Amphiprion ocellaris</i>	14	11	Z	H2	S	B	H
<i>Arothron nigropunctatus</i>	22	33	C1	Co	M	B	M
<i>Aulostomus chinensis</i>	119	80	P	C2	M	A	M
<i>Balistapus undulatus</i>	47	30	C2	Co	M	A	M
<i>Bodianus axillaris</i>	98	20	C1	C2	M	A	M
<i>Bodianus bimaculatus</i>	30	10	C1	C2	M	C	H
<i>Bodianus mesothorax</i>	35	25	C2	Z	M	A	M
<i>Canthberbines dumerilii</i>	60	38	C1	Co	M	A	M
<i>Canthigaster bennetti</i>	11	10	H1	H2	M	B	H
<i>Canthigaster papua</i>	44	10	H1	H2	W	B	H
<i>Centropyge bicolor</i>	24	15	C2	H2	M	A	L
<i>Centropyge tibicen</i>	51	19	H2		M	C	H
<i>Cephalopholis boenak</i>	63	30	P	C2	M	A	M
<i>Cephalopholis leopardus</i>	39	24	C1		M	A	H
<i>Cephalopholis miniata</i>	148	50	P	C1	M	C	L
<i>Cephalopholis urodeta</i>	59	28	P	C1	M	A	H
<i>Chaetodon kleinii</i>	57	15	C2	Co	M	B	H
<i>Chaetodon lunulatus</i>	17	14	Co		M	B	M
<i>Chaetodon octofasciatus</i>	17	12	H2	Co	M	B	H
<i>Chaetodon punctatofasciatus</i>	44	12	H2	Co	M	B	H
<i>Chaetodontoplus mesoleucus</i>	19	18	C1	H2	W	C	H
<i>Cheilinus chlorourus</i>	29	45	C1	C2	M	A	M
<i>Cheilinus fasciatus</i>	54	40	C1	C2	M	A	L
<i>Chilomycterus reticulatus</i>	80	70	C1	C2	M	A	L
<i>Chlorurus bleekeri</i>	20	49	H1	H2	W	C	M
<i>Chlorurus sordidus</i>	50	40	H1	H2	W	D	M
<i>Chrysiptera bemicyanea</i>	37	7	Z	H2	S	C	H
<i>Chromis margaritifer</i>	18	9	Z		S	C	H
<i>Chrysiptera oxycephala</i>	15	9	Z		S	B	H
<i>Chrysiptera rollandi</i>	33	8	Z		S	C	H
<i>Cirrhilabrus cyanopleura</i>	27	15	Z		S	E	M
<i>Cirrhilabrus lubbocki</i>	41	8	Z		S	D	H
<i>Cirrhilabrus ryukyuensis</i>	28	15	Z		S	E	M
<i>Ctenochaetus binotatus</i>	45	22	H2		W	A	H
<i>Ctenochaetus cyanocheilus</i>	45	16	H2		W	A	H
<i>Ctenochaetus striatus</i>	27	26	C2	H2	W	A	H
<i>Dascyllus reticulatus</i>	49	9	Z	H2	S	D	H
<i>Diproctacanthus xanthurus</i>	18	10	C2	Co	M	C	H
<i>Dischistodus melanotus</i>	11	16	H2		M	A	H
<i>Dischistodus perspicillatus</i>	9	18	H2		M	A	M
<i>Dischistodus prosopotaenia</i>	11	17	C2	Z	M	A	M
<i>Epibulus brevis</i>	15	19	P	C1	M	A	M

<i>Epibulus insidiator</i>	41	54	P	C2	M	A	L
<i>Epinephelus merra</i>	49	32	P	C2	M	A	H
<i>Fistularia commersonii</i>	131	160	P	C1	S	C	L
<i>Gomphosus varius</i>	34	30	P	C2	M	A	M
<i>Halichoeres chloropterus</i>	9	19	C1	C2	M	A	M
<i>Halichoeres hortulanus</i>	29	27	C1	C2	M	A	H
<i>Halichoeres leucocanthus</i>	53	12	C1	C2	M	A	H
<i>Halichoeres leucurus</i>	13	13	C1	C2	M	A	H
<i>Halichoeres melanurus</i>	15	12	C1	C2	M	A	H
<i>Halichoeres prosopion</i>	38	13	C1	C2	M	A	H
<i>Halichoeres richmondi</i>	20	19	C1	C2	M	C	M
<i>Hemiglyphidodon plagiometopon</i>	19	18	H2		W	A	M
<i>Hemigymnus melapterus</i>	29	90	C1	C2	W	A	L
<i>Heniochus varius</i>	29	19	C2	Co	M	A	H
<i>Hoplolatilus starcki</i>	85	16	C1	C2	M	B	L
<i>Labracinus cyclophthalmus</i>	18	24	P	C2	M	C	H
<i>Labrichthys unilineatus</i>	20	18	C2	Co	M	C	H
<i>Labroides bicolor</i>	38	15	C1	C2	M	A	H
<i>Labroides dimidiatus</i>	39	14	C1	C2	M	A	M
<i>Labropsis manobei</i>	25	10	C2	Co	M	C	H
<i>Lutjanus decussatus</i>	28	35	P	C2	W	A	M
<i>Macropharyngodon meleagris</i>	30	15	C1	C2	M	A	M
<i>Macropharyngodon negrosensis</i>	24	12	C1	C2	W	B	H
<i>Naso unicornis</i>	79	70	H1		W	C	L
<i>Naso vlamingii</i>	49	60	Z	H1	W	A	L
<i>Neoglyphidodon melas</i>	11	18	C1	Co	S	A	M
<i>Neoglyphidodon nigroris</i>	21	13	C1	H1	S	A	H
<i>Neopomacentrus cyanomos</i>	25	10	Z	H2	S	D	H
<i>Neopomacentrus filamentosus</i>	8	11	Z	H2	S	A	H
<i>Novaculichthys taeniourus</i>	22	30	C1	C2	M	B	L
<i>Odonus niger</i>	35	50	Z	Co	M	D	M
<i>Ostracion cubicus</i>	279	45	C2	H2	M	A	H
<i>Ostracion meleagris</i>	29	25	H2	Co	M	A	H
<i>Oxycheilinus celebicus</i>	27	24	C1	C2	M	A	M
<i>Oxycheilinus digrammus</i>	43	40	C1	C2	M	A	L
<i>Oxycheilinus orientalis</i>	65	20	C1	C2	M	B	H
<i>Parupeneus barberinus</i>	99	60	C1	C2	M	A	M
<i>Pempheris vanicolensis</i>	20	20	C2	Z	M	E	H
<i>Pentapodus trivittatus</i>	14	25	P	C2	M	E	H
<i>Plectorhinchus chaetodonoides</i>	29	72	P	C2	M	A	L
<i>Plectorhinchus lessonii</i>	34	40	P	C2	M	A	M
<i>Plectroglyphidodon lacrymatus</i>	39	10	C2	H2	M	A	L
<i>Pomacentrus sexstriatus</i>	57	46	C2	Co	S	B	M
<i>Pomacentrus adelus</i>	6	9	Z	H2	S	A	H
<i>Pomacentrus alexanderae</i>	55	9	C2	H2	S	A	H
<i>Pomacentrus amboinensis</i>	38	9	Z	H2	S	C	H
<i>Pomacentrus aurifrons</i>	12	6	Z	H2	S	C	H
<i>Pomacentrus bankanensis</i>	11	9	C2	H2	S	C	H
<i>Pomacentrus burroughi</i>	14	9	C2	H2	S	A	H
<i>Pomacentrus lepidogenys</i>	11	9	Z	H2	S	C	H
<i>Pomacentrus moluccensis</i>	13	9	Z	H2	S	C	H
<i>Pomacentrus philippinus</i>	11	10	Z	H2	S	C	H
<i>Pomacentrus sp</i>	20	10	Z	H2	S	A	H
<i>Pomacentrus vaiuli</i>	44	10	C2	H2	S	A	H
<i>Premnas biaculeatus</i>	15	17	Z	H2	S	B	M
<i>Pseudanthias dispar</i>	17	10	C2	Z	M	E	H
<i>Pseudocheilinus hexataenia</i>	33	10	C2	Z	M	C	H
<i>Pseudojuloides kaleidos</i>	30	10	C2	Z	M	C	H
<i>Pteragogus guttatus</i>	10	9	C1	C2	M	A	H
<i>Pygoplites diacanthus</i>	47	25	C2	Co	M	A	M
<i>Rhinecanthus verrucosus</i>	19	23	C2		M	C	H

<i>Sargocentron rubrum</i>	83	32	C1	C2	M	A	H
<i>Scarus dimidiatus</i>	11	40	H2	D	W	C	H
<i>Scarus flavipectoralis</i>	18	40	H2	D	W	C	H
<i>Scarus frenatus</i>	17	47	H2	D	W	D	M
<i>Scarus ghobban</i>	33	90	H2	D	W	A	M
<i>Scarus niger</i>	14	40	H2	D	W	A	H
<i>Scarus oviceps</i>	14	35	H2	D	W	A	H
<i>Scarus psittacus</i>	23	30	H2	D	W	C	H
<i>Scarus quoyi</i>	16	40	H2	D	W	C	H
<i>Scarus scaber</i>	19	37	H2	D	W	C	H
<i>Scolopsis bilineatus</i>	24	23	P	C2	M	B	H
<i>Scolopsis ciliatus</i>	20	19	P	C2	M	C	H
<i>Scolopsis margaritifera</i>	20	28	P	C2	M	B	H
<i>Scolopsis temporalis</i>	34	35	P	C2	M	A	M
<i>Scolopsis xenochrous</i>	45	21	P	C2	M	C	H
<i>Siganus canaliculatus</i>	47	30	H1	H2	M	D	H
<i>Siganus corallinus</i>	27	35	H1	H2	M	B	H
<i>Siganus doliatus</i>	4	25	H1	H2	M	B	H
<i>Siganus punctatus</i>	39	40	H1	H2	M	D	H
<i>Siganus vulpinus</i>	29	25	H1	H2	M	B	H
<i>Stethojulis bandanensis</i>	27	15	C2	Z	M	A	H
<i>Sufflamen bursa</i>	87	25	C1		M	A	H
<i>Sufflamen chrysopterus</i>	29	30	C1	C2	M	A	M
<i>Thalassoma hardwicke</i>	14	20	C2	Z	W	C	H
<i>Thalassoma jansseni</i>	14	20	C2	Z	W	C	M
<i>Thalassoma lunare</i>	19	45	C1	C2	W	A	M
<i>Zanclus cornutus</i>	179	23	C1	C2	M	B	H
<i>Zebrasoma scopas</i>	59	40	H1	H2	M	D	L

*In loving memory of my Mom,
Jannis Kaye Johnson*

Erklärung

Gemäß §6 der Promotionsordnung der Universität Bremen für die mathematischen, natur- und ingenieurwissenschaftlichen Fachbereiche vom 14. März 2007 versichere ich, dass die vorliegende Arbeit mit dem Titel,

„The Functioning of Coral Reef Communities Along Environmental Gradients“

1. ohne unerlaubte fremde Hilfe selbstständig verfasst und geschrieben wurde
2. keine anderen als die angegebenen Quellen und Hilfsmittel benutzt wurden
3. die den benutzten Werken wörtlich oder inhaltlich entnommenen Stellen als solche kenntlich gemacht wurden
4. es sich bei den von mir abgegebenen Arbeiten um 3 identische Exemplare handelt.



Bremen, 02. Juni 2015

Jeremiah Graham Plass-Johnson