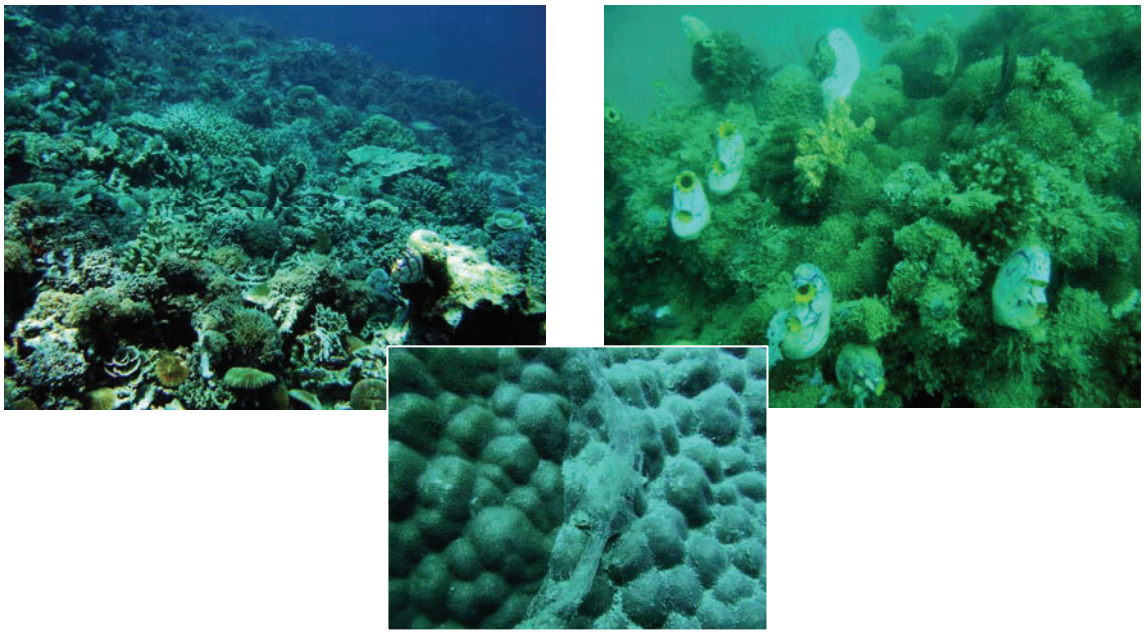
Coral Resistance to Natural and Anthropogenic Disturbances

Dissertation submitted by

Yvonne Sawall



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Universität Bremen

GLOMAR

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In partial fulfilment of the requirements for the degree of
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Thesis abstract

Coral reefs are among the most diverse ecosystems on earth with its peak in diversity lying in the center of the Indo-Pacific, also referred to as the Coral Triangle. Highly diverse systems are usually characterized by a higher resilience – "the ability of a system to absorb changes of state variables, driving variables, and parameters, and still persist" (Holling 1973). Coral reefs are also highly dynamic, meaning that there is no steady state but that the system is moving between different equilibriums. This also implies that the organisms within a system feature a large variability in metabolic performances and adaptations including reef-building corals.
The resistance of coral reefs has been highly challenged within the last few decades, largely due to overfishing and land-based pollution / eutrophication causing phase shifts from coral to algae dominated reefs. On top, sea surface temperature rise followed by coral bleaching and coral disease facilitates these phase shifts, as it has been largely documented in Caribbean coral reefs featuring a comparatively low diversity. However, not only Caribbean reefs, but also reefs in the Indo-Pacific including highly diverse reefs within the Coral Triangle suffer from localized damage due to eutrophication, overfishing and destructive fishing (cyanide and dynamite). The probably most severe bleaching event in the Indo-Pacific has recently been recorded (~ April – August 2010) indicating a loss of resilience also in highly diverse reefs. While there are numerous studies on reef dynamics in the Caribbean and the Great Barrier Reef, there is only little known about reef dynamics and resistance within the Coral Triangle, although these are heavily used and sustain the livelihood for millions of people in South East Asia.
The aim of this study was to increase the knowledge about reef functioning in these highly diverse but also heavily exploited coral reefs systems in particular in the Spermonde Archipelago located in SW-Sulawesi, Indonesia. Spermonde consists of numerous fringing and patch reefs and is situated on a 40 km wide carbonate shelf in front of the major city Makassar. Not only eutrophication caused by waste water and riverine discharge, but also overfishing and physical reef destruction by blast fishing are threatening these reefs. This already led to a strong decline in live coral cover and diversity and a shift towards an increase in heterotrophic filter-feeding organisms in near-shore reefs (**paper 1)**. Another area selected for comparative studies is located in the Andaman Sea of Thailand. Reefs within this area are of particular interest, firstly because they were hit by the 2004 Tsunami, providing a unique opportunity to study coral reef recovery after this major disturbance and secondly, because their off-shore reefs are strongly impacted by upwelling (large amplitude internal waves), providing an ideal setting to investigate the acclimatization potential of corals to rather coral unfriendly conditions.
The focus of the study was on the coral organism, firstly considered on an ecosystem level by assessing its recruitment patterns over space and time and its contribution to reef recovery (**paper 1 & 2**) and secondly, by looking at the metabolism of corals with a wide distribution pattern and assessing their mechanisms of acclimatization (**paper 3 & 4**). An additional study was performed on the temporal and spatial dynamics of bacterial communities in biofilms (**paper 5**), as they are essential for the conditioning of surfaces for (coral) larval settlement and contribute substantially to the nutrient turnover within the ecosystem, but are to date only poorly studied in coral reefs.

Coral recruitment is one of the key factors shaping coral reefs and supporting reef recovery after destructive events (**paper 1 & 2**). Coral spawning is synchronized and seasonally determined also in equatorial reefs which are characterized by a rather low seasonality. In Spermonde (**paper 1**) the spawning peak coincides with the period of lowest rain fall (July – October), calm weather conditions and lowest sea surface temperature as the spat densities on

settlement tiles revealed. A lot of factors are known to influence coral recruitment success, e.g. water quality in the context of fertilization success, surface structure and conditioning for larval settlement and space competition between sessile organisms. Those factors are strongly altered in disturbed reefs and can affect recruitment success. Highly nutrient enriched and sedimented water in near-shore reefs of Spermonde most like contributed to the strong dominance of the rather opportunistic Pocilloporidae on settlement tiles here, contrary to mid-shelf and off-shore reefs, where Acroporidae, Poritidae and others were found in rather high numbers (**paper 1**). This might be attributed to a decrease in light availability, which would force strongly light restricted species to settle on upper surfaces, which are densely occupied by filamentous algae in the near-shore reef (**paper 1**). It might also be due to changes in surface conditioning in terms of biofilms, which revealed altered bacterial composition near-shore (**paper 5**) and / or it might be the consequence of low fertilization success in other species due to degraded water quality. In terms of reef recovery after physical damage of natural (e.g. tsunami) or anthropogenic source (e.g. blast fishing), connectivity between reefs is particularly important (**paper 1 & 2**). Since the rather patchy pattern of destruction by blast fishing (**paper 1**) and by the tsunami (**paper 2**) ensured the existence of non-impacted reefs in the neighborhood (on a scale of m to few km), coral larvae could be provided to impacted reefs. Beside unconsolidated coral rubble, which hampers successful recruitment, solid substrate in form of dead coral boulders was abundant at all investigated reefs providing suitable substrate for larval settlement (**paper 1 & 2**). Additionally, a successful establishment of recruits was evident in tsunami impacted reefs (recruit census, **paper 2**), while this can also be assumed in blasted reefs due to still a significant abundance of live coral cover and low fleshy algae cover in all reefs, except near-shore (**paper 2**). Chronic impacts such as eutrophication are much more destructive on a longer run and compromise for a lower resilience, which makes the reefs unable to compensate for localized destruction of natural (e.g. storms, tsunamis and disease) and anthropogenic (e.g. global warming / bleaching) kind.

In eutrophied reefs, only robust and metabolic flexible coral species can survive. This led to a strong decimation in acroporid corals in near-shore reefs, while pocilloporid and poritid corals still significantly contributed to the live coral cover (**paper 1**). Although the contribution of Poritidae spat was rather low on the settlement tiles near-shore, the rather robust and competitive character of Poritidae might explain the abundance of adult colonies near-shore. To examine the different metabolic acclimatization mechanisms, the fast growing branching species *Stylophora subseriata* (Family: Pocilloporidae) (**paper 3**) and the slow growing massive species *Porites lutea* (Familiy: Poritidae) (**paper 4**), both featuring a large distribution in the Indo-Pacific in eutrophied and oligotrophic reefs, were studied in detail. Both were found to be well acclimatized to eutrophic conditions, where increased nutrient supply led to an increase in zooxanthellae densities and chlorophyll *a* concentrations, which further increased photosynthesis in near-shore reefs (**paper 3 & 4**). Both species did not show any obvious signs of stress, such as decreased calcification, increase in respiration and a decrease in photosynthetic efficiency (F_v/F_m) (**paper 3 & 4**), with one exception at the most polluted reef. There, *S. subseriata* revealed increased respiration rates, which might indicate that it reached its limit of stress resistance. However it could also be due to a strongly increased heterotrophy, since latter was also indicated by a higher biomass (**paper 3**). Most of the photosynthetically derived energy surplus in near-shore corals is most likely used for mucus production (not for calcification), which is essential for survival in turbid environments.
Investigations of *P. lutea* in the off-shore region impacted by large amplitude internal waves (Ko Racha, Andaman Sea) revealed a very different life strategy compared to the near- and

mid-shelf corals in Spermonde (**paper 4**). This was demonstrated by a 3-fold higher calcification rate in Ko Racha compared to all other reefs, although photosynthesis was comparatively low, e.g. only half to what was measured in the near-shore reef. Isotopic, protein and biomass values indicated elevated heterotrophy with intense recycling of resources within the holobiont including photosynthetic products. The latter lets assume that light respiration and consequently gross photosynthesis is dramatically underestimated. Thus derived energy in Ko Racha most likely supports the high calcification rate, which is needed to from highly dense skeletons to withstand strong hydraulic forces and corrosive upwelling water (**paper 4**).

The bacterial community in biofilms of different reefs within Spermonde were highly dynamic and revealed clear responses in community structure to eutrophication, seasonality and microhabitat (exposed/high light vs. sheltered/shaded) (**paper 5**). Diversity was generally higher on the exposed tile and was highest in near-shore eutrophied reefs, while seasonal fluctuations in diversity and community structure were most pronounced in the oligotrophic mid-shelf reef. The interaction between the bacterial and associated fouling community was evident, however rather low. This might be explained by the advanced succession of the two communities after 4 months, which possibly implies a development towards a higher independency. This indicates that nutrient availability most likely plays a larger role in structuring bacterial assemblages in established biofilms than the underlying surface (**paper 5**). This study provides a first overview on bacterial dynamics in coral reefs, which are lying within the most diverse ecosystems on earth. It might serve as a baseline for further studies in the context of larval settlement and environmental changes, while an approach including aspects of succession might reveal a higher interaction between the bacterial and fouling communities.

These case studies deliver important data about the functionality and dynamics in highly diverse coral reefs, subjected to eutrophication and physical destruction. In most reefs coral recruitment seemed to contribute significantly to the functionality of reef maintenance or recovery, while strong overfishing did not yet seem to favor phase-shifts towards algae dominated reefs. Some coral species can cope (*P. lutea*) and even take advantage (*S. subseriata*) of eutrophication and feature a highly flexible metabolism. However, these corals belong to the minority as indicated by the high loss of coral diversity in highly polluted reefs. Losses of species richness means a loss of functionality and further a lower resilience to additional stressors, such as sea surface temperature raise and entail risk of bleaching and disease.

Zusammenfassung

Korallenriffe gehören zu den artenreichsten Ökosystemen der Erde mit ihrem Höhepunkt der Artenvielfalt im Zentrum des Indo-Pazifik, auch „Korallendreieck“ genannt. Sehr artenreiche Ökosysteme sind normalerweise durch eine hohe Belastbarkeit (Resilienz) ausgezeichnet – die Fähigkeit eines Systems Veränderungen aufzunehmen verursacht durch verschiedene Faktoren und Parameter und trotzdem zu bestehen (Holling 1973). Korallenriffe sind sehr dynamische Systeme, was bedeutet, dass es keinen statischen Zustand gibt, sondern mehrere Zustände zwischen denen sich das System bewegt. Das beinhaltet auch, daß die Organismen innerhalb eines Ökosystems eine große Variabilität an Anpassungsmechanismen ihres Stoffwechsels mit sich bringen, inklusive der riff-bildenden Korallen.
Die Belastbarkeit von Korallenriffen wurde in den letzten Jahrzehnten stark herausgefordert, größtenteils durch Überfischung und landbasierte Verschmutzung / Eutrophierung, was zu sogenannten „phase-shifts“ führt, eine Verschiebung von korallen- zu algen-dominierten Riffen. Diese phase-shifts werden zusätzlich durch Erwärmung des Wassers und der daraus resultierenden Korallenbleiche und Korallenkrankheiten begünstigt, wie es größtenteils von karibischen Riffen mit vergleichsweise geringer Artenvielfalt dokumentiert wurde. Jedoch nicht nur karibische Riffe, sondern auch Riffe im Indo-Pazifik inklusive des artenreichen Korallendreiecks leiden unter lokaler Schädigung durch Eutrophierung, Überfischung und zerstörerische Fischereimethoden (Dynamit und Zyanid). Die wahrscheinlich verheerenste Korallenbleiche im Indo-Pazifik passierte erst letztlich (~ April – August 2010) was auf einen Verlust der Resilienz selbst in hoch diversen Korallenriffen hinweist.
Während es zahlreiche Studien über die Dynamik von Riffen in der Karibik oder im Großen Barriere Riff gibt, gibt es vergleichsweise wenig Information über die Riffdynamik und Resistenz im Korallendreieck, obwohl diese extrem genutzt werden und die Lebensgrundlage für Millionen von Menchen in Süd-Ost Asien bilden.
Das Ziel dieser Arbeit war es, das Wissen über die Rifffunktionen in hoch diversen aber gleichzeitig auch start genutzten Korallenriffökosysteme zu untersuchen, insbesondere im Spermonde Archipelago, welches in Süd-West Sulawesi, Indonesien liegt. Spermonde besteht aus zahlreichen Saum- und Plattformriffen und liegt auf einem 40 km breiten Karbonat-Schelf vor der Millionen Stadt Makassar. Nicht nur Eutrophierung, verursacht durch Abwasser und Flußeinträge, sondern auch Überfischung und physische Zerstörung durch Dynamitfischerei bedrohen diese Riffe. Das führte bereits zu einem starken Rückgang des Bedeckungsgrades von Korallen und deren Artenvielfalt und einen Zuwachs an heterotrophen Filtrierern in küstennahen Riffen (**Paper 1**). Ein anderes Gebiet wurde für vergleichende Studien in der Andamanen See von Thailand ausgesucht. Riffe in diesem Gebiet sind von besonderem Interesse, erstens weil sie vom 2004 Tsunami betroffen waren und somit eine einzigartige Möglichkeit zur Studie der Erholung der Riffe nach großräumigen Zerstörungen bietet und zweitens, weil dessen off-shore Riffe stark von Internen Wellen Grosser Amplitutde (Large Amplitude Internal Waves, LAIW) beeinflusst sind, welche somit ein ideales Umfeld zur Studie von Akklimatisationsprozessen von Korallen bietet.
Der Fokus dieser Studie lag auf dem Organismus Koralle, erstens untersucht auf dem Ökosystemlevel in Form von Rekrutierungsmuster über Zeit und Raum und deren Beitrag an der Erholung der Riffe (**Paper 1 & 2**), und zweitens in Form von Untersuchungen am Metabolismus von Korallen, welche eine weite Verbreitung aufweisen, um deren Akklimatisationsmechanismen zu erfassen (**Paper 3 & 4**). Eine zusätzliche Studie untersuchte die räumliche und zeitliche Dynamik von Bakteriengemeinschaften in Biofilmen (**Paper 5**), welche wichtig sind für die Konditionierung von Oberflächen für (Korallen) Larvenbesiedlung, und welche substantiell zur Nährstoffumwälzung und -bereitstellung in einem Ökosystem beitragen. Diese wurden bisher kaum in Korallenriffen untersucht.

Korallenrekrutierung ist eine Schlüsselfunktion in der Gestaltung von Korallenriffen und unterstützt die Erholung der Riffe nach zerstörerischen Ereignissen (**Paper 1 & 2**). Das Laichen der Korallen ist synchronisiert und saisonal bedingt, selbst in äquatorialen Riffen, welche durch eine geringe Saisonalität gekennzeichnet sind. In Spermonde (**Paper 1**) ist der Höhepunkt der Laichsaison in einem Zeitraum, in dem geringster Niederschlag (Juli – Oktober), ruhigste Wetterbedingungen und niedrigste Wassertemperaturen zusammen kommen, wie die Dichten der Korallensetzlinge auf den Besiedlungsplatten zeigten. Viele Faktoren beeinflussen den Erfolg von Korallenrekrutierung, z. B. Wasserqualität im Zusammenhang mir Befruchtungserfolg, Struktur der potentiellen Besiedlungsoberflächen und deren Konditionierung für das Anheften der Larven und der Wettstreit um Platz zwischen sessilen Organismen. Diese Faktoren können sich stark verändern in gestörten Riffen und können somit den Rekrutierungserfolg beeinflussen. Stark nährstoffhaltiges und sedimentbelastetes Wasser in küstennahen Riffen von Spermonde trugen höchstwahrscheinlich ihren Teil zu der großen Dominanz von eher opportunistischen Pocilloporidae auf Besiedlungsplatten bei, was in Kontrast ist zu den mid-shelf und off-shore Riffen, wo Acroporidae, Poritidae und andere Korallenarten in größeren Dichten gefunden wurden (**Paper 1**). Das könnte einer Reduzierung in Licht zugeschrieben werden, was stark lichtabhängige Arten dazu zwingt sich an der oberen Seite der Platte anzusiedeln, welche jedoch in küstennahen Gebieten von dicht gepackten filamentösen Algen besiedelt ist (**Paper 1**). Es könnte jedoch auch an der Konditionierung der Platten mit Hinblick auf die Struktur des Biofilms liegen, die im küstennahen Bereich eine veränderte bakterielle Zusammensetzung aufwiesen (**Paper 5**) und / oder an einem verringertem Fertilisationserfolg durch die verminderte Wasserqualität. In Bezug auf Erholung der Riffe nach natürlicher physischer Zerstörung (z. B. Tsunami) oder nach menschlicher Zerstörung (z. B. Dynamitfischen) ist die Verbundenheit der Riffe besonders wichtig (**Paper 1 & 2**). Da die eher fleckenartige Zerstörung durch Dynamitfischen (**Paper 1**) und durch den Tsunami (**Paper 2**) eine Existenz von nicht zerstörten Riffen in der Nachbarschaft sicherte (auf einer Skala von m zu wenigen km), konnten Korallenlarven zu den geschädigten Riffen transportiert werden. Neben losem Korallengeröll, welches erfolgreiche Rekrutierung verhindert, war auch solides Substrat in Form von toten Korallenblöcken in allen untersuchten Riffen vorhanden, was geeignetes Substrat für die Larvenbesiedlung bereitstellt (**Paper 1 & 2**). Zusätzlich konnte eine erfolgreiche Wiederbesiedlung in den durch den Tsunami gestörte Riffen festgestellt werden (Rekrutenzählungen, **Paper 2**), während das auch für die durch Dynamit zerstörten Riffe angenommen werden kann, da es immer noch eine recht hohe Bedeckung an lebend Korallen und eine geringe Bedeckung von fleischigen Algen in allen Riffen gab, außer im nächstgelegenem Riff zur Küste. Chronische Belastung durch Eutrophierung sind über einen längeren Zeitraum wesentlich schädlicher und erfordern Einbußen in der Resilienz, was dem Riff die Fähigkeit nimmt weiter Schäden natürlicher (z. B. Stürme, Tsunamis und Krankheiten) und anthropogener Ursache (z. B. globale Erwärmung / Korallenbleiche) aufzufangen.

In eutrophierten Riffen können nur sehr robuste und im Stoffwechsel flexible Korallenarten überleben. Das führte zu einem starken Rückgang in acroporiden Korallen in küstennahen Riffen, während pocilloporide und poritide Korallen immer noch einen signifikanten Teil zur Korallenbedeckung beitrugen (**Paper 1**). Obwohl der Anteil der poritiden Korallensetzlinge auf den Besiedlungsplatten eher gering war im küstennahen Riff, könnten die robusten und konkurrenzfähigen Eigenschaften der Poritidae wahrscheinlich dafür verantwortlich sein, das Vorkommen von adulten Kolonien im küstennahen Riff zu sichern. Um die verschiedenen metabolischen Mechanismen zur Akklimatisierung zu untersuchen, wurde die schnell

wachsende verzweigte Art *Stylophora subseriata* (Familiy: Pocilloporidae) (**Paper 3**) und die langsam wachsende massive Art *Porites lutea* (Family: Poritidae) (**Paper 4**) weitergehend untersucht. Beide Arten sind charakterisiert durch eine weite Verbreitung im Indo-Pazifik wie in eutrophierten als auch in oligotrophen Riffen. Beide zeigten sich gut angepasst an eutrophe Bedingungen, wo erhöhter Nährstoffeintrag zu erhöhten Zooxanthellendichten und Chlorophyll a Konzentrationen führte und dadurch die Photosynthese im küstennahen Riff steigerte (**Paper 3 & 4**). Beide Arten zeigten keine offensichtlichen Zeichen von Stress, wie z. B. reduzierte Kalzifizierungsraten, erhöhter Respirationsraten und eine Abnahme in der photosynthetischen Effizienz (F_v/F_m) (**Paper 3 & 4**), mit einer Ausnahme in dem am stärksten verschmutztem Riff. Dort zeigte *S. subseriata* eine erhöhte Respirationsrate, was ein Zeichen für das Erreichen der Stressresistenz sein könnte. Jedoch könnte dies auch mit einer erhöhten Heterotrophie zusammenhängen, da letzteres auch in einer erhöhten Biomasse zu sehen war (**Paper 3**). Das meiste der photosynthetisch hergestellten Energiezuschüsse in küstennahen Riffen wurde höchst wahrscheinlich zur Mucusproduktion (nicht zur Kalzifizierung) benutzt, da dies unabdingbar ist, um in einer trüben Umgebung zu überleben. Untersuchungen an *P. lutea* in der off-shore Region welches von LAIWs beinflußt ist (Ko Racha, Andamanen See) zeigten eine ganz andere Lebensstrategie verglichen zu küstennahen und mid-shelf Korallen in Spermonde (**Paper 4**). Das wurde durch eine 3-fach höherer Kalzifizierungsrate in Ko Racha verglichen mit den anderen Riffen sichtbar, obwohl die Photosyntheserate vergleichsweise niedrig war, z. B. nur halb so viel von dem was im küstennahem Riff gemessen wurde. Werte von Isotopen, Protein und Biomasse zeigten eine erhöhte Heterotrophie zusammen mit intensivem Recycling von Ressourcen innerhalb des Holobionten, einschließlich der photosynthetisch produzierten Produkte. Das letztere lässt daraus schließen, dass die Licht-Respirationsraten und schließlich auch die Brutto-Photosyntheseraten stark unterschätzt wurden in Ko Racha. Die so gewonnene Energie treibt höchst wahrscheinlich die Kalzifizierungsraten in die Höhe, was für die Herstellung von dichten Korallenskeletten essentiell ist, welche den starken hydraulischen Kräften und dem korrodierenden Wasser widerstehen (**Paper 4**).

Die Bakteriengemeinschaft in Biofilmen in verschiedenen Riffen in Spermonde zeigten eine hohe Dynamik und die Gesellschaftsstruktur zeigte eine klare Reaktion auf Eutrophierung, Saisonalität und Mikrohabitat (exponiert / viel Licht vs. geschützt / wenig Licht) (**Paper 5**). Die bakterielle Vielfalt war allgemein höher auf den exponierten (Besiedlungs-) Platten und war am höchsten in den eutrophierten küstennahen Riffen, während die saisonal bedingten Fluktuationen in bakterieller Vielfalt und Zusammensetzung im oligotrophen mid-shelf Riff am höchsten war. Es war eine Interaktion zwischen der Bakterien- und assoziierten Aufwuchsgesellschaft von Makroorganismen zu sehen, jedoch eher von geringem Ausmaß. Das könnte durch die schon fortgeschrittene Sukzession nach 4 Monaten erklärt werden, was eine Entwicklung in Richtung einer höheren Unabhängigkeit implizieren würde. Das zeigt auch, dass die Nährstoffverfügbarkeit eine größere Rolle spielt in der Strukturierung der Bakteriengesellschaft in den schon fortgeschrittenen Stadien des Biofilm, anstatt des zugrunde liegenden Substrates (**Paper 5**). Diese Studie liefert einen ersten Überblick über die bakteriellen Dynamiken in Korallenriffen, welche in dem artenreichsten Gebiet der Erde liegen. Diese Erkenntnisse können zur Grundlage für weitere Studien dienen, die im Zusammenhang mit Larvenbesiedlung und Umweltveränderungen stehen, während eine Vorgehensweise, die die Aspekte der Sukzession mit einbezieht sicherlich eine höhere Interaktion zwischen Bakterien und assoziierten Macroorganismen zeigen würde.

Diese Fallstudien liefern wichtige Daten über die Funktionalität und Dynamiken artenreicher Riffe des Korallendreiecks, welche Eutrophierung und physischen Störungen ausgeliefert

sind. In den meisten Riffen scheint die Korallenrekrutierung fundamental zur Funktionalität und Rifferhaltung oder -erholung beizutragen, während starke Überfischung im Augenblick noch nicht zu einem phase-shift Richtung Algendominanz führte. Manche Korallenarten scheinen sich gut an die gegebenen Bedingungen anpassen zu können (*P. lutea*), während andere sogar einen Vorteil aus eutrophierten Gewässern ziehen können (*S. subseriata*), was mit einer hohen Flexibilität des Stoffwechsels einhergeht. Jedoch bilden diese Korallen eine Minderheit was in dem Verlust der Artenvielfalt der Korallen in stark verschmutzten Riffen sichtbar ist. Der Rückgang der Artenvielfalt bedeutet einen Verlust in der Funktionalität und konsequenterweise eine geringere Resilienz gegenüber weiteren Stressoren, wie z. B. Erderwärmung welche die Risiken von Korallenbleiche und Krankheiten mit sich bringt.

Thesis Outline

	Approach		Factors investigated						
	Ecosystem level	Organism level	Eutrophication	Natural disturbance	Recovery	Seasonality	Diversity	Adaptation / Acclimatization
1. Spatio-temporal patterns of coral **recruitment** along a cross-shelf transect in Spermonde Archipelago, SW-Sulawesi, Indonesia.	■		■		■	■		
2. Coral **recruitment** and recovery after the 2004 Tsunami around the Phi Phi Islands (Krabi Province) and Phuket, Andaman Sea, Thailand.	■			■	■			
3. Nutritional status and metabolism of the coral ***Stylophora subseriata*** along a eutrophication gradient in Spermonde Archipelago (Indonesia).		■	■					■
4. Calcification, photosynthesis and nutritional status of the hermatypic coral ***Porites lutea:*** case studies from environmental extremes in Indonesia and Thailand.		■	■	■				■
5. Effects of eutrophication, seasonality and macrofouling on the diversity of **bacterial biofilms** associated with coral reefs of the Spermonde Archipelago, Indonesia.	■		■			■	■	

Paper outline

Paper 1

Yvonne Sawall, Jamaluddin Jompa, Andi Maddusila, Claudio Richter (in preparation)
Spatio-temporal patterns of coral recruitment along a cross-shelf transect in Spermonde Archipelago, SW-Sulawesi (Indonesia)

Contributions: The project on coral reef resilience (SPICE) was initiated by C Richter and J Jompa. The particular idea of this study was development by Y Sawall, C Richter and J Jompa. Data sampling was mainly conducted by Y Sawall and A Maddusila. Analyses of data and writing of manuscript were conducted by Y Sawall with improvements by C Richter.

Paper 2

Yvonne Sawall, Niphon Phongsuwan, Claudio Richter (2010)
Coral recruitment and recovery after the 2004 Tsunami around the Phi Phi Islands (Krabi Province) and Phuket, Andaman Sea, Thailand. Helgoland Marine Research 64:357-365

Contributions: The project on studying coral reef recovery after the tsunami was initiated by the German Technical Cooperation (GTZ) and the idea of this particular study was developed by Y Sawall, N Phonsuwan and C Richter. Data sampling and analyses were conducted by Y Sawall. The manuscript was written by Y Sawall with improvements by C Richter and N Phongsuwan.

Paper 3

Yvonne Sawall, Mirta Teichberg, Janina Seemann, Magdalena Litaay, Jamaluddin Jompa, Claudio Richter (in revision)
Nutritional status and metabolism of the coral *Stylophora subseriata* along a eutrophication gradient in Spermonde Archipelago (Indonesia). Coral Reefs

Contributions: The project on coral reef resilience (SPICE) was initiated by C Richter and J Jompa. The particular idea of this study was development by Y Sawall, M Teichberg and C Richter. Data sampling was conducted by Y Sawall, M Teichberg, J Seemann with logistical help by M Litaay. Data analyses and writing of the manuscript were conducted by Y Sawall with improvements by C Richter and M Teichberg.

Paper 4

Yvonne Sawall, Somkiat Khokiattiwong, Jamaluddin Jompa, Claudio Richter (submitted)
Calcification, photosynthesis and nutritional status of the hermatypic coral *Porites lutea:* case studies from environmental extremes in Indonesia and Thailand. Marine Ecology Progress Series

Contributions: The projects on coral reef resilience (SPICE) and impact of large amplitude internal waves (ORCAS) was initiated C Richter in collaboration with J Jompa (SPICE) and S Kkokiattiwong (ORCAS). The particular idea of this study was developed by Y Sawall and C Richter. Data sampling was conducted by Y Sawall and C Richter with support of S Khokiattiwong. Data analyses and writing of the manuscript were conducted by Y Sawall with improvements by C Richter.

Paper 5

Yvonne Sawall, Claudio Richter, Alban Ramette (in preparation)
Effects of eutrophication, seasonality and macrofouling on the diversity of bacterial biofilms associated with coral reefs of the Spermonde Archipelago, Indonesia

Contributions: The project on coral reef resilience (SPICE) was initiated by C Richter and J Jompa. The particular idea of this study was development by Y Sawall, A Ramette and C Richter. Data sampling was conducted by Y Sawall. Data analyses were performed by A Ramette and Y Sawall. The manuscript was written by Y Sawall with improvements by A Ramette.

Paper 1

Spatio-temporal patterns of coral recruitment along a cross-shelf transect in Spermonde Archipelago, SW-Sulawesi (Indonesia)

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In preparation

Abstract

Coral recruitment was assessed in Spermonde Archipelago, a barrier reef system subjected to land-based sources of siltation/pollution and destructive fishing at the heart of the Coral Triangle. Over a period of 2 years, settlement tiles were deployed in 7 reefs along a cross-shelf transect covering the range of siltation/eutrophication exposure from near- to offshore waters, with varying degrees of blast fishing impact. Tiles were exchanged every 4 months and the coral spat and fouling community assessed. Annual spat fall up to 705 spat m^{-2} yr^{-1} was dominated by Pocilloporidae (63 %), followed by Acroporidae (14.6 %), Poritidae (7.8 %) and others (14.6 %). Spat densities were highest on the lower face of the 45°-tilted tiles and displayed a strong seasonality with the highest values in the dry season (July – October), characterized by low rain fall (~40 mm $month^{-1}$), calm weather conditions and low SST (28°C). Spatial differences in spat composition and density were small but distinct, and differed mainly between the near-shore and the other areas mid-shelf and offshore, due to a shift in dominance between Pocilloporidae near-shore, and Acroporidae and Poritidae off-shore. Cross-shelf variations in spawning seasons were evident in Poritidae and Acroporidae with an earlier on-set of spawning off-shore. Poritidae attained highest spat densities in the period of transition from wet to dry season (March-June: > 65 spat m^{-2}, compared to < 29 spat m^{-2} in July-October). Blast-fishing affected reefs with lower live coral cover did not show significant reductions in recruitment, suggesting sufficient larval supply. Fouling showed an inverse pattern with low seasonal but high spatial variability, in response to the eutrophication gradient. While filamentous algae predominated the upper tile faces in near-shore reefs, they were replaced by crustose coralline red algae in off-shore waters. The lower tile faces, where most coral spat settled, harbored a diverse fouling community with less obvious differences along the eutrophication gradient suggesting an overall low effect of fouling organisms on coral recruitment, except for the closest near-shore reef, where the tiles were monopolized by Pocilloporids colonizing also the upper faces of the tiles.

Keywords: coral recruitment, seasonality, eutrophication, blast fishing, Spermonde Archipelago

Introduction

Spawning seasonality and synchronized multispecies spawning have been recorded, both in the tropics and subtropics (Baird et al. 2009). However spawning seasons vary tremendously between the regions not only concerning the time of the year, but also by the length of season or even in the number of seasons per year. Formerly it has been suggested that seasonality and synchrony of spawning decreases with proximity to the equator due to decreased variations in triggering environmental conditions, e.g. temperature (Oliver et al. 1988, Richmond & Hunter 1990), however a range of different activators have been suggested by now, which also occur in equatorial regions, although often less pronounced (Guest et al. 2005, Baird et al. 2009, van Woesik 2010). Temperature is one of the widely suggested generators, not only in the high latitude reefs (Harrison et al. 1984, Shlesinger & Loya 1985, Willis et al. 1985, Gleason 1996), but also in equatorial reefs, although annual temperature variations are sometimes less than 2°C (Baird et al. 2001, Guest et al. 2005, Romatzki 2008). However, temperature is often not enough to predict coral spawning, therefore several other variables or their combinations have been suggested for a better spawning prediction. For example, low rainfall and high temperature are reported to trigger gamete release in *Montastrea annularis* in the Caribbean (Mendes & Woodley 2002), supported by studies, where a decrease in salinity were found to affect young coral larvae floating near the surface (Harrison et al. 1984, Vermeij et al. 2006). Variations in solar radiation have been related to coral mass spawning in the Caribbean (van Woesik et al. 2006) and in Palau (Penland et al. 2004), where spawning occurred at near maximum solar insolation, and in a high latitude reef of Western Australia (Babcock et al. 1994), where spawning coincided with a certain day length. Occurrence of a neap tide during temperature increase was suggested as a spawning cue in the Great Barrier Reef and tropical western Australia (Babcock et al. 1986, Oliver et al. 1988) and a recent paper suggests that, in general, spawning coincides with the period of lowest wind independent of latitude (van Woesik 2010). Spawning during calm season ensures a higher fertilization success, a longer larval retention and higher local recruitment (van Woesik 2010). In regions with long calm seasons or biannual calm seasons, it was found that the season of spawning is either extended (e.g. in Kenya, where *Acropora* were found to spawn over a period of 7 months, (Mangubhai & Harrison 2008)) or split (e.g. in Palau, where 2 spawning peaks were found (Penland et al. 2004)).

Spawning patterns in equatorial reefs have been investigated more intensively in recent years (Guest et al. 2005, Mangubhai & Harrison 2008, Baird et al. 2009) including regions within the biodiversity hot spot, such as the Solomon Islands (Baird et al. 2001, Baird et al. 2002), Papua New Guinea (Oliver et al. 1988, Baird et al. 2009), the Philippines (Bermas et al. 1992, Vicentuan et al. 2008) and Indonesia (Fox et al. 2003, Fox 2004, Ferse 2008, Romatzki 2008, Baird et al. 2009). Baird et al. (2009) gave an overview on the multi-species spawning seasons in Indonesia, Fox et al. (2003) and Fox (2004) compared coral recruitment between blast-fishing impacted and non-impacted reefs in Komodo National Park, while Ferse (2008) and Romatzki (2008) investigated coral recruitment at different reefs in North Sulawesi. These studies revealed one to two multi-species spawning seasons throughout Indonesia, peaking in April/May and/or October/November (Fox 2004, Ferse 2008, Romatzki 2008, Baird et al. 2009). Spatial differences in spawning frequency can be pronounced, even within one coral family, as reported for North Sulawesi, where reefs separated by less than 40 km (Ferse 2008), suggesting potentially strong variability within one region.

In addition to the natural factors above, human-induced changes in water quality are known to interfere with coral recruitment. Eutrophication, pollution and sedimentation may severely

impact coral adults and recruits on several levels, from gamete production, over spawning timing and fertilization success, to larvae development, larvae settlement and recruit survival (Gilmour 1999, Hughes & Connell 1999, Abelson et al. 2005). Eutrophication is also known to foster the growth of potential space competitors of coral recruits (Tomascik 1991, Dunstan & Johnson 1998, Abelson et al. 2005) such as toxic cyanobacteria or macroalgae, which inhibit coral larvae settlement (Kuffner & Paul 2004).
Spermonde Archipelago (SW-Sulawesi, Indonesia) is a diverse coral reef system subjected to cross-shelf gradients of land run-off (eutrophication, pollution and sedimentation) and scattered impacts of destructive fishing (blast and cyanide fishing) and overfishing, which have collectively taken their toll on the reef communities (Edinger et al. 1998, Pet-Soede et al. 2001, pers. observ.). This is the first study of coral recruitment in Spermonde Archipelago, with the aim of assessing the seasonality of coral spawning, spat density and composition, along with potential space competitors in the fouling community, in relation to land run-off and blast fishing. The results are expected to provide insight into the dynamics, resilience and recovery potential of corals in one of the most diverse regions on the planet.

Material and Methods

Study sites
The study was conducted in the Spermonde Archipelago, SW-Sulawesi, Indonesia, featuring ~100 coral-fringed small islands scattered across a 40 km wide carbonate shelf. Most reefs flourish in the south, west and north faces of the island, with conspicuous reef gaps on the sandy steeper areas of the eastern sides (Moll 1983). The shelf depth ranges from 10 m (near-shore) to 40 m (off-shore). The near-shore reefs are subjected to the run-off of rivers north and south of the city of Makassar, carrying untreated waste water and industrial pollution from the 1.5 million inhabitants along with agricultural run-off, featuring only low coral cover and diversity (Edinger et al. 1998, Renema & Troelstra 2001). Mid- and outer shelf reefs are situated in a rather oligotrophic environment, while the near mid-shelf reefs are still effected by the land run-off during the wet season (November to February), but also local waste water discharge in some of the populated islands (Edinger et al. 1998, Renema &Troelstra 2001). The more remote mid-shelf and off-shore reefs at the shelf edge are exposed to oligotrophic waters, with oceanic conditions and intermittent upwelling from Makassar Strait at the margins (Moll 1983).
Seasonality is affected by the wet NW-monsoon from November to February (*wet*, in the following), the dry SE-monsoon from June to September (*dry*), and a transition period from wet to dry season between March and June (*trans*) (Table 1). A positive correlation between rainfall and sea surface temperature (SST) was recorded, with lowest rainfall corresponding with lowest SST (Aldrian & Susanto 2003), in spite of only small annual SST variations of about 2 °C (Table 1).
Destructive fishing practices are common in Spermonde. Blast fishing converts flourishing reefs to dead coral rubble, the scars of the bombs are visible as craters, and impacted sections are often dominated by macroalgae (Pet-Soede & Erdmann 1998, pers.observ.). Seven study sites were chosen along a cross-shelf transect and classified into four different shelf zones distinguished by distance to shore and associated degree of eutrophication (Fig. 1, Table 2): (1) Near-shore [LaeLae (LAE)], (2) near mid-shelf [Samalona South (SAM-S) and Samalona North (SAM-N)], (3) far mid-shelf [Bonebatang (BBA), Bonetambung (BTA)] and (4) off-

shore [Lanyukan West (LNK-W) and Lanyukan North (LNK-N). Each zone includes a low and highly bombed reef, except for near-shore with a low bombed reef only (Table 2).

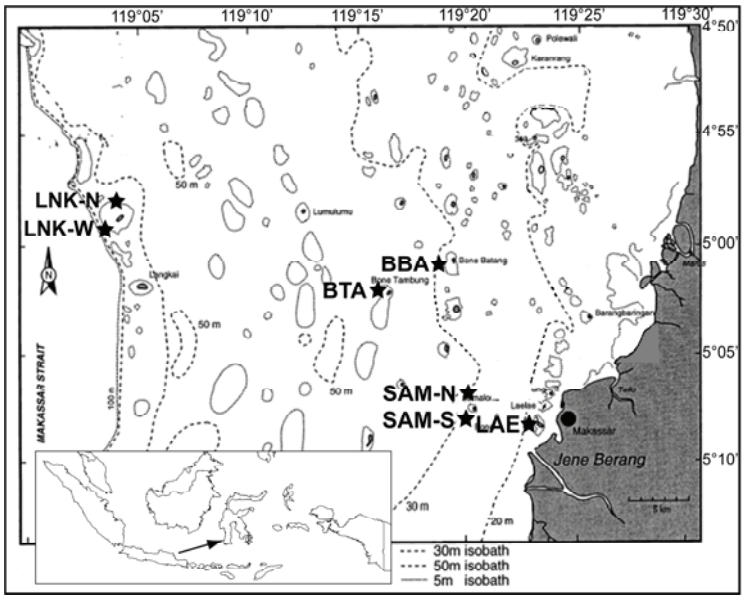

Fig. 1: Map of Spermonde Archipelago with the study sites: LaeLae (LAE), Samalona South (SAM-S), Samalona North (SAM-N), Bonebatang (BBA), Bonetambung (BTA), Lanyukan West (LNK-W), Lanyukan North (LNK-N).

Table 1: Seasonal rainfall and sea surface temperature (SST) during the wet season (wet), transition period from wet to dry season (trans) and dry season (dry). The rainfall extremes are bold.

Season	Months	Rainfall [mm month-1]*	SST [°C]
wet	Nov - Feb	273 (Nov) - **730 (Jan)**	29 - 30
trans	Mar - Jun	391 (Mar) - 66 (Jun)	28 - 29
dry	Jul - Oct	**15 (Aug)** - 83 (Oct)	28

*Source: World Meterological Organization (WMO) Geneva, Switzerland (averaged data for the 30-year period 1961-1990).

Table 2: Site description along a cross-shelf transect from near- to off-shore. Shelf zones are based on distances to shore and eutrophication impact, while the latter is characterized by the visibility and chlorophyll *a* concentration (Chl *a*) in the water. The blast fishing impact is founded on the occurrence of craters consisting of coral rubble and later quantified by the transect data.

Site	Distance	Shelf zone	Bombing impact	Visibility [m]*		Chl *a* [µg l^{-1}]**	
	to shore [km]		[low or high]	wet season	dry season	wet season	dry season
LAE	2	near-shore	low	0.5 - 2.5	2.5 - 5	1.6 ± 0.2	0.6
SAM-S	5	near mid-shelf	low	1 - 5	10 - 18	1.0 ± 0.1	0.5
SAM-N	5	near mid-shelf	high	1 - 5	10 - 18	1.0 ± 0.1	0.5
BBA	14	far mid-shelf	low	5 - 10	10 - 18	1.1 ± 0.1	0.3
BTA	17	far mid-shelf	high	8 - 20	10 - 30	1.1 ± 0.1	0.3
LNK-W	35	off-shore	low	8 - 20	10 - 30	1.2	0.6
LNK-N	35	off-shore	high	8 - 20	10 - 30	1.2	0.6

Source: * Renema & Toelstra 2001, **Sawall et al. 2010

Characterization of benthic community
Line intercept transects (English et al. 1997) were conducted in order to assess the benthic community structure at the different sites. A measuring tape was laid out over 60 m along the reef edge in 3 m depth and the underlying substrate was recorded to the nearest cm. The following substrate categories were applied: live coral (LC), dead coral (DC, >15 cm), coral rubble (RB, <15 cm), sand (SA), macroalgae (ALG) and others (OTH), while others were additionally divided into soft coral (SC), sponge (SPO), anemone (ANE), ascidians (ASC), hydrozoans (HYD) and bivalves (CLAM). The percentage contribution of each category was calculated. Additionally, the coral families Pocilloporidae, Acroporidae and Poritidae were identified and expressed as % cover of total LC cover.

Experimental design
The coral recruitment study was performed over 2 years from November 2007 until October 2009 and the sites were revisited every 4 months in order to detect seasonal changes, as defined in Table 1. Near-shore LAE was included into the second year of the study; therefore no data is available for the first year at this site. Settlement tiles were deployed in 3-4 m depth along the reef edge (n=16 for each site). Terracotta tiles (Harriott& Fisk 1987, Maida et al. 1995, Dunstan & Johnson 1998) (15 x 15 cm) were connected pairwise by a bolt, with the unglazed faces exposed. The non-corrosive 1 cm wide bolt holding the tiles was fixed at an angle of 45° to dead coral boulders, to prevent sediments accumulating on the tiles (English et al. 1997). An upper and a lower (sheltered) face of the tile pair were available for organism settlement (Supplementary [S] Fig. S1). The tiles were exchanged every 4 months, dried in the sun after recovery from the reefs and examined under the dissection microscope. There is one exception for the site BBA during the first season (I), where tiles were exchanged one month later (beginning of April instead of beginning of March).
Coral spat were identified after Babcock et al. (2003) to family level for Pocilloporidae, Acroporidae and Poritidae, while the remaining spat were categorized as “not identified” due to uncertainties in identification. Additionally, the spat diameter was recorded. The fouling community was described by estimating the coverage (%) of the taxa filamentous algae, crustose coralline red algae, bryozoans, sponges, ascidians and by counting (no. tile^{-1}) the taxa barnacles, spirorbid worms and bivalves.

Data analyses
Multivariate analyses were performed in order to assess patterns in the spat and fouling communities in response to blast fishing impact, eutrophication (shelf zones), seasonality, inter-annual differences and tile exposure (upper and lower face). Spat densities and abundances of fouling organisms, pooled for each pair of tiles, were used for all tests, except for analyses between the upper and lower face, where the data of the individual tiles were applied. One-way analyses of similarity (ANOSIM) were conducted to assess the effect of the above factors on the spat and fouling communities. Analyses of similarity percentage (SIMPER) were conducted in order to determine, which of the coral spat species or fouling taxa contribute most to the dissimilarities between seasons or shelf zones, respectively. Due to the fact, that spat-free tile pairs are common, which are discarded when a dissimilarity matrix is created, a “dummy” variable was added prior analyses (Clarke et al. 2006). The dummy variable represents an additional spat family with the value “1” for all samples. This zero-adjusted Bray-Curtis dissimilarity matrix secures the inclusion of empty tiles into the analyses with minimal distortion of the overall patterns described by the distances between the samples (Clarke et al. 2006). The fouling community data was standardized prior analyses to eliminate

the effect of different units (% and individual counts). Analyses were performed with the software Primer v6.

Results

Benthic community structure

Live coral cover ranged from 18.3 % in near-shore LAE to 52.5 % in near mid-shelf SAM-S, while the live coral cover was overall higher on sites with low bombing impact (37.8 ± 15.7 % [mean ± SD] including LAE; 44.3 ± 10.9 % without LAE) compared to highly bombed reefs (27.9 ± 2.4 %) (Fig. 2, Table S1). Although variation in the cover of coral rubble was high, an overall higher rubble cover was evident at highly bombed sites (31.1 ± 13.6) compared to low impacted sites (10.8 ± 12 %) (Fig. 2) and in the case where rubble cover was low, macroalgae contributed to a large fraction (LNK-N: 19.5 %). The highest abundance of various filter feeding organisms (others: clams, ascidians, sponges, hydrozoans, etc.) were found in eutrophied near-shore LAE (33.5 %) (Fig. 2).

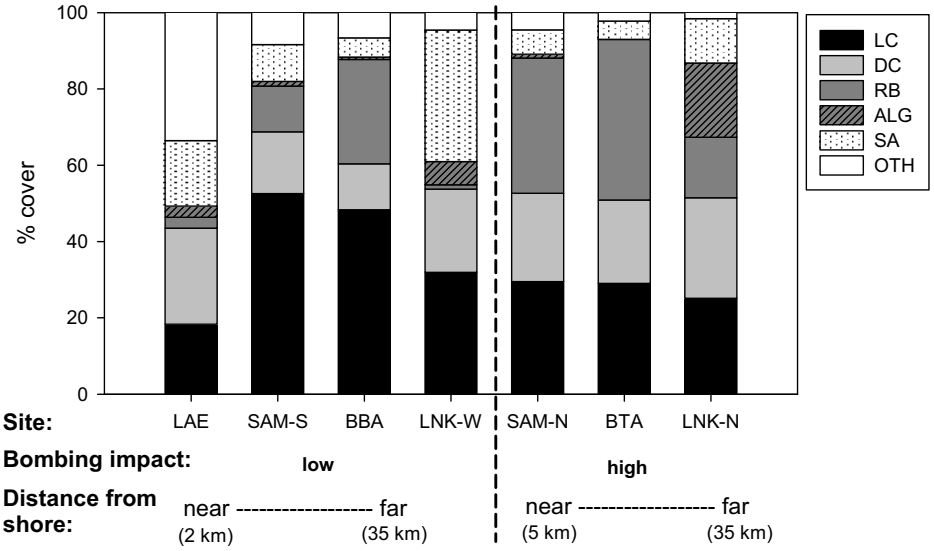

Fig. 2: Benthic composition along the cross-shelf transect, grouped by blast fishing impact. Live coral (LC), dead coral (DC), coral rubble (RB), sand (SA), macroalgae (ALG) and others (OTH).

Coral spat and fouling community

A total of 1058 tiles were investigated (some were lost), with a total of 2315 coral spat. The variation in spat densities was high, ranging between 0 and 38 spat tile^{-1} (each tile equivalent to 225 cm^2). 360 of the upper tiles and 187 of the lower tiles did not harbor any coral spat. Larvae were mostly found close to the edge of the lower tiles and usually directly on the edge of the upper tiles. Annual larvae spat fall was highest in LAE (705 spat m^{-2} yr^{-1}), followed by BBA (686), BTA (597), SAM-N (545), LNK-W (469), LNK-N (403) and SAM-S (286). The coral spat community was dominated by Pocilloporidae (63 % of all spat), followed by Acroporidae (14.6 %), Poritidae (7.8 %) and others (14.6 %) (Fig. 3).

There were pronounced differences in spat densities and fouling community composition between the upper and lower tile faces (Table 3). Spat densities were strongly elevated on the lower face, where the fouling community was most diverse and structurally complex. On the upper face, spat densities were low, except at near-shore LAE, and the fouling community

was comparatively homogenous consisting mainly of filamentous and crustose coralline red algae (Fig. 3 and 4).

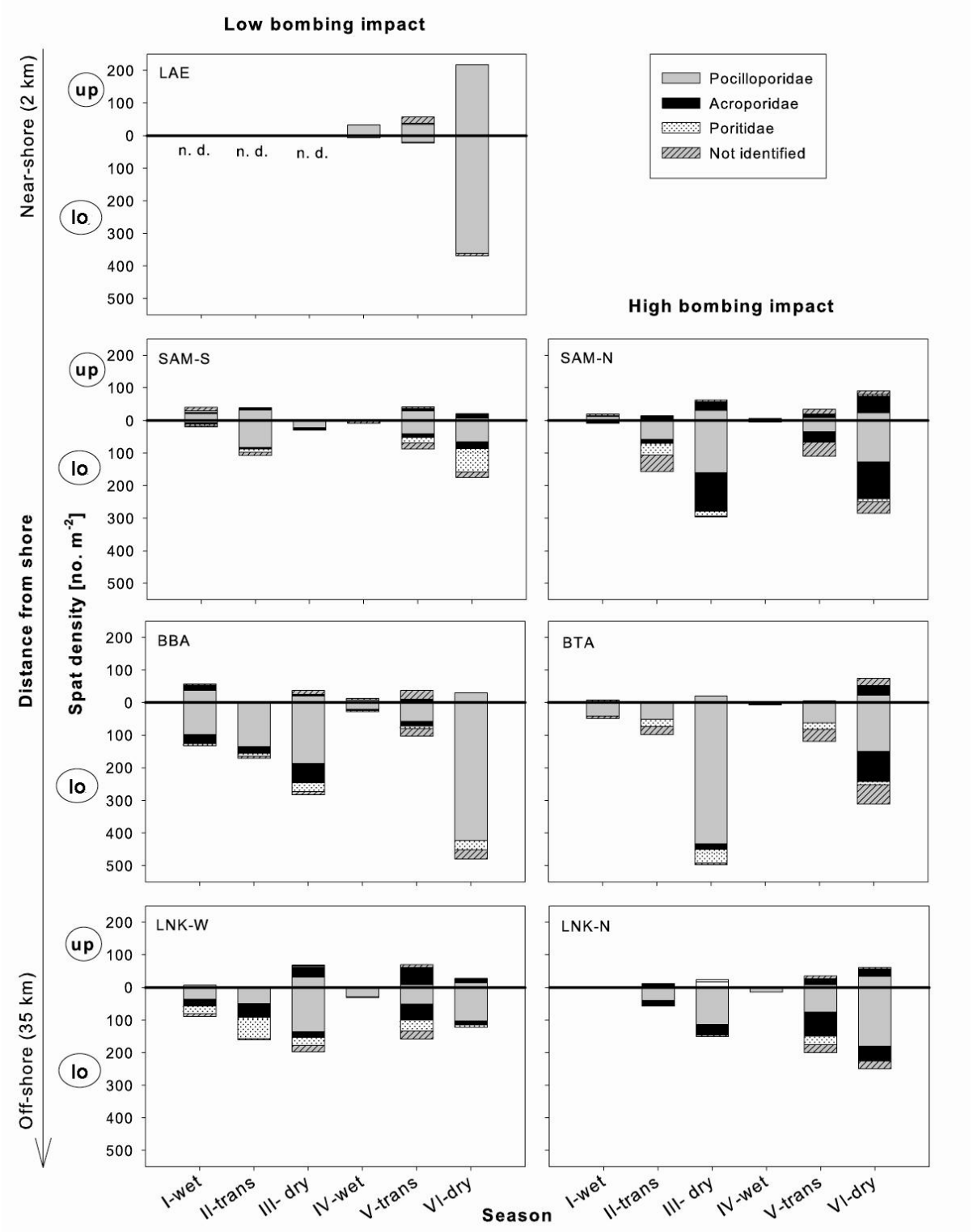

Fig. 3: Coral spat assemblages on settlement tiles on the upper (up) and lower (lo) face along the eutrophication gradient, grouped by seasons and blast-fishing impact. No data available (n. d.).

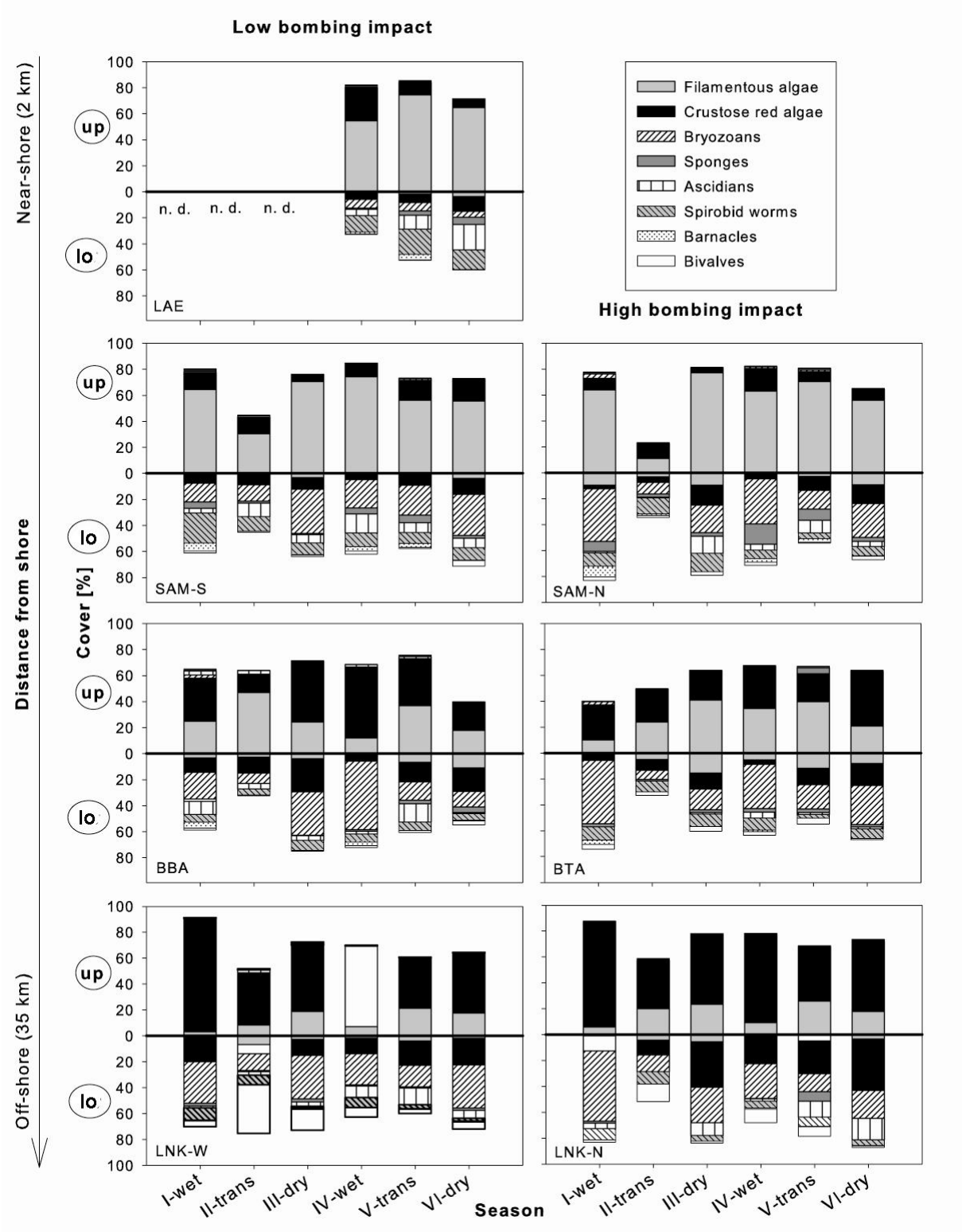

Fig. 4: Fouling community on settlement tiles on the upper (up) and lower (lo) face along the eutrophication gradient, grouped by seasons and blast-fishing impact. No data available (n. d.). Counted taxa were converted to % cover to simplify illustration (1 % cover = 5 barnacles, 10 spirobid worms or 1 bivalvae).

No impact of blast fishing on either coral spat community or fouling community could be detected (Table 3).
Seasonal differences were pronounced in the spat abundances, in particular between the wet season (I+IV) and the other two seasons (trans: II+V and dry: III+VI) (Table 3). Spat densities were lowest during the wet season (all sites combined: 45.5 ± 50.9 spat m^{-2} [mean ± SD]), intermediate in the transition period (146.2 ± 49.5) and highest in the dry season, between July and October (321.8 ± 160.0). The difference between the seasons was mostly explained by differences in Pocilloporidae, followed by Acroporidae (Table S2). Seasonality was overall low in the fouling community, however still significant in particular between the wet season and the other two seasons (Table 3), mostly due to changes in filamentous and crustose algae abundance (SIMPER, cumulative explanation of dissimilarity 29 % (wet-trans) and 31 % (wet-dry), Table S3).
Inter-annual differences in spat fall density and fouling community structure were not found (Table 3). Nevertheless, some inter-annual differences could be observed on individual sites (Fig. 3), e.g. at SAM-S, where strongly elevated Poritidae densities occurred in the second year (season IV to VI) compared to the first year (season I to III), while the opposite was found in SAM-N. Another example is given at BBA, where higher Acroporidae and lower Pocilloporidae densities occurred in the first year compared to the second year and the reverse pattern was evident in BTA.
Spatial differences in the spat community along the cross-shelf transect were small, however still significant and most pronounced between near-shore and near-mid-shelf and between near-shore and off-shore (Table 3). This was mostly due to a shift from Pocilloporidae in near-shore to Acroporidae spat further away from shore (Table S4), but also due to the absence of Poritidae in near-shore compared to the other shelf zones (Fig. 3). In contrast to the spat community, the fouling community revealed much stronger spatial differences, which was highest between the most distant reefs and lowest between near-shore LAE and close

Table 3: Results of Analyses of Similarity (ANOSIM) for the coral spat and fouling community. Differences were tested between the tile exposure (up/lo), blast fishing impact (high/low), seasons (wet/trans/dry), years (2008/2009) and land run-off impact (zones: near-shore, near mid-shelf, mid-shelf, off-shore). Global R is an indication for the dissimilarity lying between 0 (equal) and 1 (completely different). All highly significant differences are in bold (p=0.001).

Factor	Coral spat community	R	p	Fouling community	R	p
Tile exposure		**0.154**	0.001		**0.843**	0.001
Bombing impact*		0.001	0.320		0.005	0.021
Season		**0.180**	0.001		**0.032**	0.001
	Groups			Groups		
	Wet (I+IV) *vs.* Trans (II+V)	**0.150**	0.001	Wet (I+IV) *vs.* Trans (II+V)	**0.046**	0.001
	Wet *vs.* Dry (III+VI)	**0.296**	0.001	Wet *vs.* Dry (III+VI)	**0.041**	0.001
	Trans *vs*. Dry	**0.092**	0.001	Trans *vs.* Dry	0.014	0.002
Year**		0.005	0.072		0.008	0.002
Shelf zone (cross-shelf transect)		0.032	0.013		**0.093**	0.001
	Groups			Groups		
	Near-shore *vs.* Near mid-shelf	0.063	0.016	Near-shore *vs.* Near mid-shelf	0.006	0.339
	Near-shore *vs*. Far mid-shelf	0.008	0.268	Near-shore *vs* . Far mid-shelf	**0.140**	0.001
	Near-shore *vs*. Off-shore	0.062	0.019	Near-shore *vs* . Off-shore	**0.273**	0.001
	Near mid-shelf *vs*. Far mid-shelf	0.026	0.067	Near mid-shelf *vs*. Far mid-shelf	**0.058**	0.001
	Near mid-shelf *vs*. Off-shore	-0.013	0.859	Near mid-shelf *vs*. Off-shore	**0.156**	0.001
	Far mid-shelf *vs*. Off-shore	0.051	0.013	Far mid-shelf *vs* . Off-shore	**0.041**	0.001

* Without LAE data, since near-shore was only represented by a low bombing impacted reef
** Without LAE data, since LAE data was only available only for the second year

mid-shelf SAM-S / SAM-N (Table 3). These differences were mostly explained by a shift from filamentous algae to crustose coralline red algae in the near- to off-shore sites and a decrease in spirobid worms with distance from shore (SIMPER, cumulative explanation of dissimilarity 47.7 % Table S5, Fig. 4). Barnacles were higher close to shore, while bryozoans and bivalves were found further away form shore (Table S5, Fig. 4). All Poritidae spat were small, within the 1.0 ± 0.5 mm size class (Fig. 5). Pocilloporidae and Acroporitidae spat were generally larger (2.0 ± 0.5 mm) except at far mid-shelf BBA & BTA, where almost half of the Pocilloporidae spat was also found within the 1.0 ± 0.5 mm size class (Fig. 5).
A differentiation in the timing of spawning between the coral families was observed along the cross-shelf transect (Fig. 5). While Pocilloporidae revealed the same spawning time in all shelf zones (dry season), Poritidae revealed a shift from the dry season to the transition period in off-shore LNK-W/LNK-N. Acroporitidae followed the pattern of Poritidae in the off-shore reefs, although less pronounced (Fig. 5).

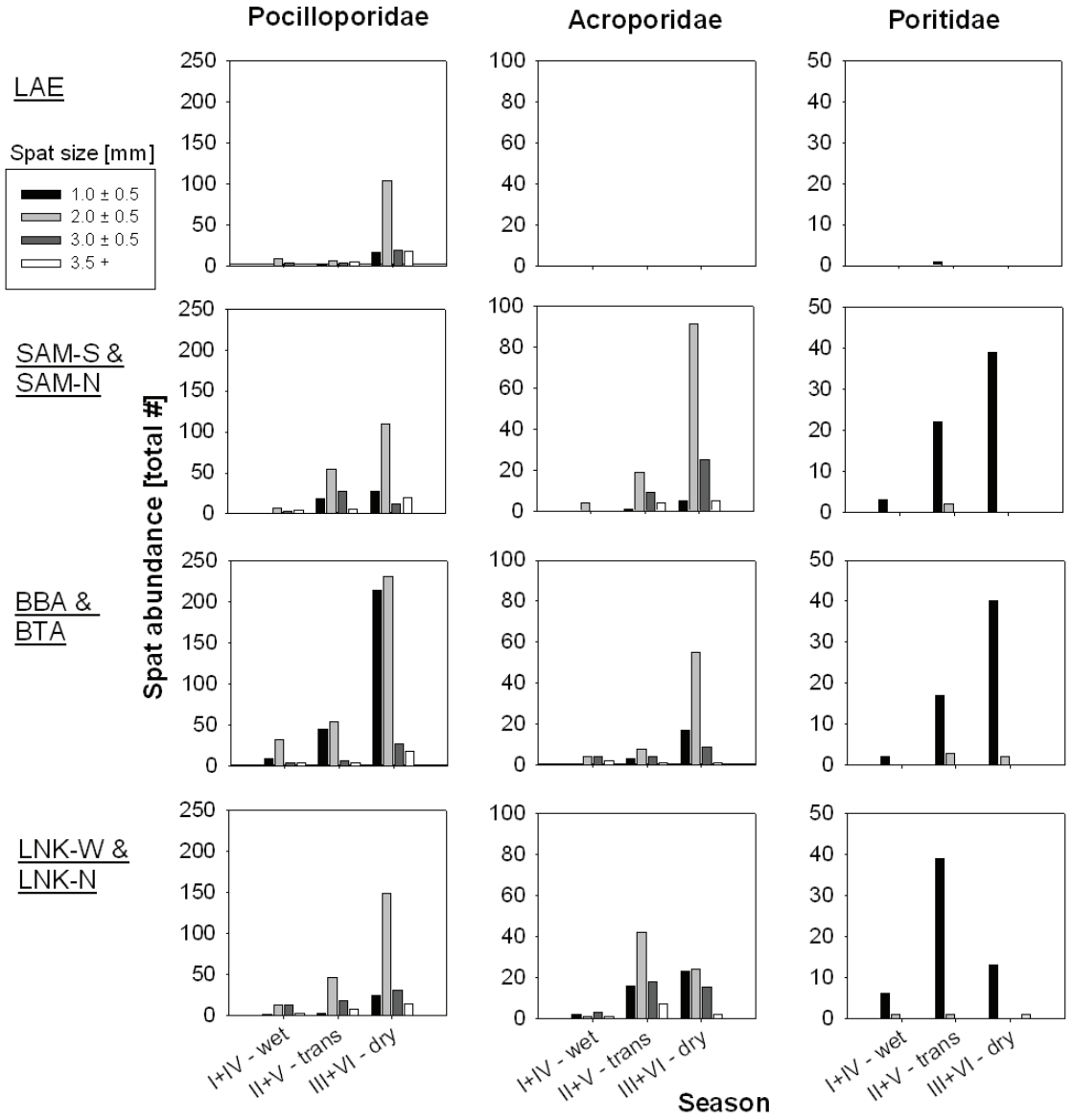

Fig. 5: Coral spat sizes of the different coral families. Spat data was summarized for the reefs within the same shelf zone, as well as for each season over the two years. Spat numbers are given in total numbers counted.

Coral spat versus adult community

The composition of coral spat is weakly reflected in the composition of adult corals, mostly due to the high discrepancy of Pocilloporidae contribution in the spat community (between 56 % in SAM-N and 89 % in LAE) compared to the adult community (between 4 % in LNK-W and 11 % in LAE) (Fig. 6). Nevertheless, significant correlation between adult and spat were found in the level of taxa. This was most pronounced in Poritidae (Fig. 7), where lowest spat (1%) and adult (16 %) contribution was found in near-shore LAE and highest contribution in off-shore LNK-W (16 % and 51 %, respectively) (Fig. 6). Acroporids revealed an overall low correlation, however this was strongly influenced by the high discrepancy between spat and adult at LNK-W (Fig. 6, Fig. 7). Excluding LNK-W, the correlation for Acroporidae was high (R^2=0.80, p<0.001).

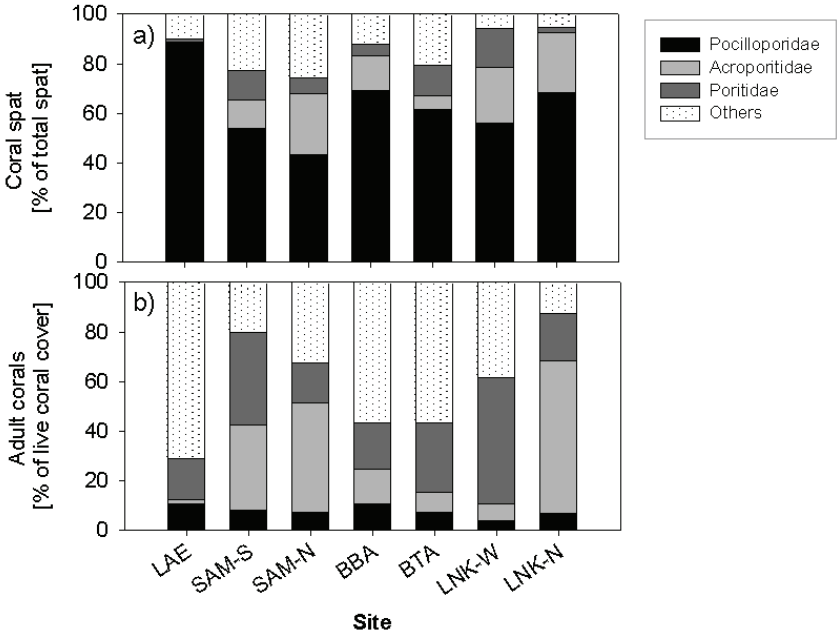

Fig. 6: Comparison of abundance in coral spat families and adult families for each site (pooled for all seasons).

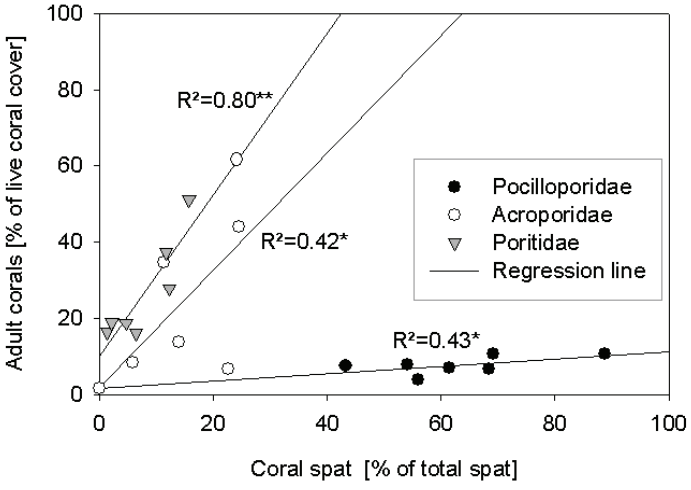

Fig. 7: Relationship between coral spat and adult coral families. Correlation coefficient (R^2) and significance (*p<0.05, **p<0.001) are presented.

Discussion

This study is the first study within the heart of the Coral Triangle, which investigated seasonal pattern of coral recruitment and the impact of eutrophication at the same time. While this provides insight into reef dynamics of highly diverse coral reefs and their ability to cope with pollution and to recover from physical destruction, this study also provides important data on the strongly debated seasonality of coral reproduction in equatorial reefs.

Seasonality

The seasons in Spermonde Archipelago are determined by the rate of precipitation and consequently land run-off, which is high during the NW monsoon (December – February) and extremely low during the SE monsoon (June – September). The highest spat densities were found in October after the driest period of the year, which coincides with previous suggested triggers for coral spawning, such as low rain fall (Mendes & Woodley 2002), calm weather conditions (van Woesik 2010) and high solar insolation (Penland et al. 2004, van Woesik et al. 2006, van Woesik 2010). Distinct elevated insolation levels were recorded for the period September / October and to a lesser extent in March / April at the latitude 5° S, the latitude of Spermonde (Penland et al. 2004). The transition period (March – June) is characterized by decreasing rain fall, calm weather conditions and slightly increased solar insolation, which allows some coral colonies to reproduce during this period, already. Temperature, in contrast, does not seem to play a role in the spawning behavior of Spermonde corals, since the lowest SST was found during highest spat fall, although a positive correlation between temperature and spawning has been found before even in equatorial reefs (Baird et al. 2001, Guest et al. 2005). In Spermonde, annual temperature variations of only 2°C might be overruled by more distinct environmental triggers.

In a study North of Sulawesi (Manado, 1.3° N) the main spawning season was found to be in April / May (Ferse 2008, Romatzki 2008), although the annual precipitation pattern is very similar to Spermonde. Here spawning was related to an increase in temperature of about 1.5 °C from April to June (Romatzki 2008). Nevertheless, conformity with this study was given in the lowest spat fall during the period with roughest weather conditions and highest precipitation from November to February (Ferse 2008, Romatzki 2008). A study on gonad development of different coral species over several regions in Indonesia revealed multi-species spawning peaks in March / April and October / November (Baird et al. 2009). While the first peak is supported by our Spermonde data, the second and more pronounced peak appears to be earlier in Spermonde, based on the similar size ranges of spat found on the tiles in June and in October. If the majority of spat had settled in October, as predicted by Baird et al. (2009), the coral spat on the October tiles (i.e. after less than one month) should be barely detectable, i.e. much smaller than the spat found on tiles in June (i.e. after three months).

With the exception at the reefs off-shore, all coral families showed a similar spawning behavior in the mid-shelf and near-shore reefs. At off-shore LNK the onset of spawning seems to be earlier in the year for Acroporidae and Poritidae, represented by equal (Acroporidae) or higher (Poritidae) spat densities in the transition period compared to the dry season. An overall earlier spawning peak was found in near-shore compared to off-shore reefs in the Great Barrier Reef, while here an earlier achievement of optimum temperature was found to be responsible for an earlier spawning near-shore (Willis et al. 1985, Babcock et al. 1986). This means, that cross-shelf variability in spawning seasonality is not exceptional, however it remains unclear, what causes this variability in the Spermonde Archipelago, since detailed water quality data are not available.

Inter-annual variability in spawning, as indicated in this study by differences in spat composition and abundances, is common (Gleason 1996, Dunstan & Johnson 1998, Glassom et al. 2004, Romatzki 2008) and might be attributed either to reproduction failures of some corals in some years, or to variations in larvae dispersal. The latter is inter alia dependent on small-scale current pattern formed by reef heterogeneity, which is further influenced by prevalent weather conditions and tides (Black et al. 1990). Small-scale current pattern also explain the patchiness of spat fall between the tiles (Bull 1986, Dunstan & Johnson 1998).

Effect of eutrophication and space competitors

The effect of eutrophication was clearly visible in the reefs close to shore (LAE, SAM-S, SAM-N), which is reflected in the algae composition on the upper tiles, shifting from a filamentous towards a crustose algae dominated community with distance from shore (Delgado & Lapointe 1994, Belliveau & Paul 2002). In contrast to the upper face, the lower face revealed only little changes along the cross–shelf transect. The lower face, however, harbored a high structural heterogeneity formed by various filter feeding organisms, which created a high 3-dimensionality. This spatial heterogeneity (Colgan 1981, Thongtham & Chansang 1999, Petersen et al. 2005) together with the calcareous tubes of spirobid worms (Glassom et al. 2004, Schmidt 2010) offer favored substrate for larval settlement at all sites. It provides shelter from predation by corallivore fishes and other coral feeding species (e.g. gastropods) (Harriott 1983), however it is a compromise for light, which also explains the preferential settlement towards the edge of the tile (Maida et al. 1994, Gleason 1996, Fox 2004). The situation is slightly different at near-shore LAE, where the almost monopolized pocilloporid spat community was found on upper and lower faces in about equal proportion. This can be explained firstly, by the opportunistic and robust character of some pocilloporids (Birkeland 1977, Tomascik 1991), which allows settlement on filamentous algae covered substrates (Harriot 1983) and secondly, by a decreased light availability (increased turbidity), which might cause preferred settlement on the upper face of some specimen (Sammarco 1991, Maida et al. 1994). This and other factors, such as a lower fertilization success in nutrient enriched (Harrison & Ward 2001) and sedimented water (Gilmour 1999), most likely explain the selectivity of spat towards an almost solely pocilloporid community in near-shore LAE.
The overall low spatial variation of the spat community, in particular concerning the near mid-shelf to off-shore reefs, goes together with the comparatively low variation of the fouling community on the below face, indicating a relatively homogenous pressure of space competitors at this stage. Nevertheless, this does not preclude a higher space competition, once the coral grows out of its “hiding place”, where filamentous algae, benthic heterotrophs and possibly toxic cyanobacteria (Kuffner & Paul 2004) might outcompete the coral recruits (Hughes & Jackson 1985, Sammarco 1991, Dunstan & Johnson 1998, Abelson et al. 2005). While reefs with high live coral and low macroalgae cover might offer a suitable environment for successful coral recruitment, near-shore LAE features extremely challenging conditions for coral recruitment at least for most coral species.

Coral larvae dispersal and reef recovery

The composition of the adult coral community was overall poorly reflected in the composition of the spat community, partly because of the strong dominance of Pocilloporidae on almost all tiles (63 ± 14 % [mean ± SD]), however, not in the adult community (8 ± 2 %). There was also a rather low variation in the contribution of pocilloporid adults to the live coral cover, which might not be enough to explain site specific variability in pocilloporid spat. Pocilloporids are brooders and have the ability to settle shortly after release, however some

species e.g. *Pocillopora damicornis* feature long competency periods, meaning that they have the potential to be drifted rather far, if no suitable substrate for settlement is available (Harrison & Wallace 1990, Tioho et al. 2001, Ferse 2008). In the other brooding family Poritidae, adult and spat abundances correlated, indicating a fast settlement after larvae release and therefore a rather low rate of dispersal (Tomascik 1991). Although Acroporidae are broadcast spawners, featuring usually a higher planktonic phase and therewith a higher potential of dispersion, they indicated a rather high larval retention visible in the correlation of spat and adult, except at LNK-W.

Although a certain self-seeding pattern was evident, there were no differences in spat densities found between low and highly bombed reefs. This can be ascribed to the patchy occurrence of bombing craters, where low dispersal is sufficient to reach coral cleared substrate and possibly to an adult community, which is not yet below a level of self-preservation. In the Komodo National Park, south-east of Sulawesi, blast fishing also caused tremendous loss of live coral cover and a strong increase in dead coral rubble and also here larvae supply was provided from neighboring reefs (Fox 2004). Nevertheless, recruitment success was low in Komodo, due to an inhibition of settlement on natural substrate, which was occupied by strongly expanding soft corals or due to abrasion of already settled coral larvae by moving coral rubble (Fox et al. 2003, Fox 2004). Although the presence of coral rubble is strongly elevated in bombed reefs of the Spermonde Archipelago, there are still solid dead coral boulders (22-26 %), which provide settlement space (Harrison & Wallace 1990, Thongtham & Chansang 1999).

Therefore it can be concluded, that the overall high spat densities together with solid settlement space and low algae cover in mid-shelf and off-shore reefs provide good conditions for the recovery of the coral community and that the overall functionality of the reefs is still given. Only near-shore reefs, such as LAE, seem to be seriously jeopardized by eutrophication and pollution, where low live coral cover, high abundance of heterotroph filter feeders and a low diversity in coral spat were evident, leading to a strongly lowered reef functionality and resilience.

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Supplementary Material

Table S1: Benthic community structure. Mean (± SD).

Site	Live coral	Dead coral	Coral rubble	Macroalgae	Sand	Others
Low bombing impact						
LL	18.3	25.2	2.8	2.9	17.2	33.5
SAM-S	52.5	16.2	12.0	1.3	9.7	8.4
BBA	48.4	12.0	27.3	0.6	5.0	6.6
LNK-W	31.9	21.8	1.1	6.1	34.5	4.6
Mean	**37.8 (15.7)**	**18.8 (5.9)**	**10.8 (12.0)**	**2.7 (2.5)**	**16.6 (12.9)**	**13.3 (13.6)**
Low bombing impact (without LAE)						
Mean	**44.3 (10.9)**	**16.7 (4.9)**	**13.5 (13.2)**	**2.7 (3.0)**	**16.4 (15.8)**	**6.5 (1.9)**
High bombing impact						
SAM-N	29.0	21.8	42.1	0.1	4.8	2.2
BTA	29.0	21.8	42.1	0.1	4.8	2.2
LNK-N	25.1	26.3	15.9	19.5	11.6	1.6
Mean	**27.7 (2.2)**	**23.3 (2.6)**	**33.3 (15.1)**	**6.6 (11.2)**	**7.1 (3.9)**	**2.0 (0.3)**

Table S2: SIMPER results. Comparison of spat composition between the different seasons with all species (variables) contributing > 90 % to the dissimilarity. Significant differences between seasons (tested with ANOSIM) are indicated by ** ($p<0.001$). Coral species: Pocilloporidae (POC), Acroporidae (ACR), Poritidae (POR), others (OTH).

Variable	Ø Abundance Group A	Ø Abundance Group B	Contribution to Ø dissimilarity	SD Ø dissimilarity	Cumulative % contribution
Ø Dissimilarity = 48.68 %**					
	Wet	**Trans**			
POC	0.63	1.72	23.46	1.14	48.20
OTH	0.13	0.72	9.63	0.69	67.98
ACR	0.12	0.76	9.46	0.66	87.42
POR	0.08	0.48	6.12	0.51	100.00
Ø Dissimilarity = 59.13 %**					
	Wet	**Dry**			
POC	0.63	5.40	38.24	1.41	64.67
ACR	0.12	1.46	12.11	0.73	85.16
OTH	0.13	0.54	5.07	0.54	93.74
Ø Dissimilarity = 57.17 %**					
	Trans	**Dry**			
POC	1.72	5.40	31.73	1.33	55.50
ACR	0.76	1.46	12.26	0.83	76.99
OTH	0.72	0.54	7.57	0.70	90.23

Table S3: SIMPER results. Comparison of fouling community composition between the different seasons with all taxa (variables) contributing > 90 % to the dissimilarity. Significant differences between seasons (tested with ANOSIM) are indicated by ** ($p<0.001$) and * ($p<0.05$).Taxa: filamentous algae (Filalg), crustose coralline red algae (CCA), barnacles (Barn), ascidians (Ascid), spirobid worms (Worms), bryozoans (Bryo), sponges and bivalves.

Variable	Ø Abundance Group A	Ø Abundance Group B	Contribution to Ø dissimilarity	SD Ø dissimilarity	Cumulative % contribution
Ø Dissimilarity = 74.62 %**					
	Wet	**Trans**			
Fil alg	0.09	0.09	11.65	0.82	15.61
CCA	0.10	0.08	10.15	0.79	29.21
Barn	0.21	0.07	10.01	0.61	42.62
Ascid	0.08	0.11	8.91	0.64	54.56
Worms	0.11	0.09	8.88	0.86	66.45
Bryo	0.13	0.06	8.87	0.79	78.34
Sponge	0.12	0.11	8.09	0.56	89.18
Bivalves	0.08	0.12	8.07	0.57	100.00
Ø Dissimilarity = 73.26 %**					
	Wet	**Dry**			
Fil alg	0.09	0.11	12.04	0.86	16.43
CCA	0.10	0.10	10.82	0.87	31.21
Bryo	0.13	0.10	10.77	0.84	45.92
Worms	0.11	0.08	8.79	0.82	57.91
Barn	0.21	0.02	8.58	0.57	69.62
Ascid	0.08	0.09	7.90	0.60	80.40
Sponge	0.12	0.06	7.24	0.56	90.29
Ø Dissimilarity = 71.36 %*					
	Trans	**Dry**			
Fil alg	0.09	0.11	12.73	0.89	17.84
Ascid	0.11	0.09	10.46	0.67	32.50
Worms	0.09	0.08	9.54	0.84	45.87
CCA	0.08	0.10	9.53	0.83	59.22
Bryo	0.06	0.10	8.70	0.77	71.41
Bivalves	0.12	0.08	8.69	0.57	83.59
Sponge	0.11	0.06	7.64	0.53	94.31

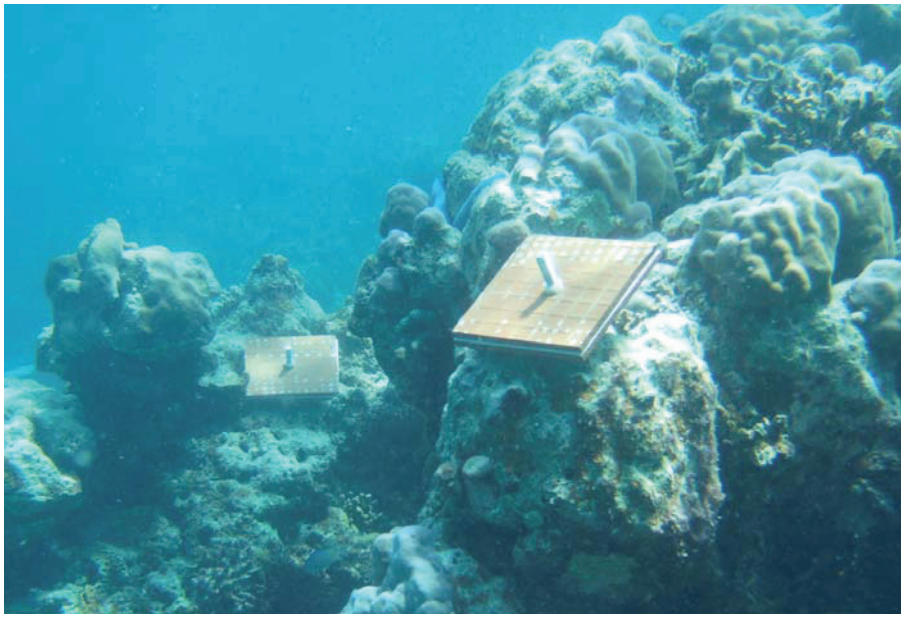
Table S4: SIMPER results. Comparison of spat composition between the different shelf zones with all species (variables) contributing > 90 % to the dissimilarity. Significant differences between shelf zones (tested with ANOSIM) are indicated by * (p>0.05). Shelf zones: Near-shore (LAE) near mid-shelf (SAM-S & -N), far mid-shelf (BBA & BTA), off-shore (LNK-W & -N). Coral species: Pocilloporidae (POC), Acroporidae (ACR), Poritidae (POR), others (OTH).

Variable	Ø Abundance Group A	Ø Abundance Group B	Contribution to Ø dissimilarity	SD Ø dissimilarity	Cumulative % contribution
Ø Dissimilarity = 52.51 %*					
	Near-shore	**Near mid-shelf**			
POC	5.41	1.68	36.07	1.31	68.69
ACR	0.00	0.99	7.06	0.53	82.13
OTH	0.26	0.54	6.16	0.49	93.86
Ø Dissimilarity = 53.20 %					
	Near-shore	**Far mid-shelf**			
POC	5.41	3.87	39.19	1.43	73.67
OTH	0.26	0.63	6.64	0.54	86.15
ACR	0.00	0.63	4.46	0.44	94.53
Ø Dissimilarity = 52.61 %*					
	Near-shore	**Off-shore**			
POC	5.41	2.09	36.55	1.35	69.47
ACR	0.00	1.02	8.38	0.63	85.39
OTH	0.26	0.30	3.92	0.39	92.84
Ø Dissimilarity = 53.57 %					
	Near mid-shelf	**Far mid-shelf**			
POC	1.68	3.87	29.80	1.22	55.64
ACR	0.99	0.63	10.19	0.69	74.67
OTH	0.54	0.63	8.71	0.70	90.92
Ø Dissimilarity = 50.90 %					
	Near mid-shelf	**Off-shore**			
POC	1.68	2.09	24.91	1.17	48.94
ACR	0.99	1.02	13.57	0.84	75.60
OTH	0.54	0.30	6.56	0.62	88.49
POR	0.38	0.40	5.86	0.49	100.00
Ø Dissimilarity = 54.00 %*					
	Far mid-shelf	**Off-shore**			
POC	3.87	2.09	30.89	1.26	57.21
ACR	0.63	1.02	10.91	0.77	77.42
OTH	0.63	0.30	6.91	0.65	90.22

Table S5: SIMPER results. Comparison of fouling community composition between the different shelf zones with all taxa (variables) contributing > 90 % to the dissimilarity. Significant differences between shelf zones (tested with ANOSIM) are indicated by ** ($p<0.001$). Shelf zones: Near-shore (LAE), near mid-shelf (SAM-S & -N), far mid-shelf (BBA & BTA), off-shore (LNK-W & -N).Taxa: filamentous algae (Filalg), crustose coralline red algae (CCA), barnacles (Barn), ascidians (Ascid), spirobid worms (Worms), bryozoans (Bryo), sponges and bivalves.

Variable	Ø Abundance Group A	Ø Abundance Group B	Contribution to Ø dissimilarity	SD Ø dissimilarity	Cumulative % contribution
Ø Dissimilarity = 71.29 %					
	Near-shore	**Near mid-shelf**			
Fil alg	0.15	0.14	14.48	0.98	20.31
Worms	0.18	0.12	12.86	0.89	38.36
Barn	0.18	0.17	12.18	0.79	55.45
Ascid	0.18	0.09	12.21	0.64	69.76
Sponge	0.10	0.16	9.51	0.67	83.10
Bryo	0.02	0.10	5.66	0.70	91.04
Ø Dissimilarity = 75.03 %**					
	Near-shore	**Far mid-shelf**			
Fil alg	0.15	0.08	15.13	0.99	20.16
Worms	0.18	0.08	12.94	0.89	37.41
Barn	0.18	0.07	10.74	0.74	51.72
Ascid	0.18	0.07	10.65	0.65	65.91
Sponge	0.10	0.07	7.70	0.59	76.17
CCA	0.05	0.10	7.39	0.80	86.01
Bryo	0.02	0.10	6.65	0.66	94.87
Ø Dissimilarity = 79.88 %**					
	Near-shore	**Off-shore**			
Fil alg	0.15	0.04	14.51	0.93	18.16
CCA	0.05	0.16	11.89	0.96	33.05
Worms	0.18	0.07	11.70	0.83	47.69
Ascid	0.18	0.11	11.50	0.70	62.08
Barn	0.18	0.02	9.10	0.71	73.47
Bivalve	0.01	0.21	8.51	0.53	84.13
Bryo	0.02	0.10	6.39	0.69	92.13
Ø Dissimilarity = 73.47 %**					
	Near mid-shelf	**Far mid-shelf**			
Fil alg	0.14	0.08	14.73	0.95	20.04
Worms	0.12	0.08	9.72	0.88	33.27
Bryo	0.10	0.10	9.68	0.81	46.45
Sponge	0.16	0.07	9.34	0.61	59.16
Barn	0.17	0.07	8.40	0.54	70.59
Ascid	0.09	0.07	8.19	0.60	81.74
CCA	0.04	0.10	8.07	0.76	92.72
Ø Dissimilarity = 78.24 %**					
	Near mid-shelf	**Off-shore**			
Fil alg	0.14	0.04	13.72	0.88	17.53
CCA	0.04	0.16	13.18	0.91	34.38
Bivalve	0.05	0.21	9.85	0.60	46.97
Ascid	0.09	0.11	9.30	0.65	58.85
Bryo	0.10	0.10	9.17	0.82	70.58
Worms	0.12	0.07	8.40	0.82	81.32
Sponge	0.16	0.05	7.88	0.56	91.38
Ø Dissimilarity = 69.78 %**					
	Far mid-shelf	**Off-shore**			
CCA	0.10	0.16	13.08	1.00	18.75
Bivalve	0.06	0.21	11.19	0.66	34.79
Bryo	0.10	0.10	10.51	0.82	49.85
Ascid	0.07	0.11	9.73	0.66	63.80
Fil alg	0.08	0.04	8.25	0.83	75.63
Worms	0.08	0.07	7.58	0.85	86.49
Sponge	0.07	0.05	5.42	0.45	94.26

Fig. S1: Settlement tile set-up. A non-corrosive 1 cm diameter, 15 cm long bolt was driven through the middle of the tile pair and hammered into dead coral material. The head of the bolt was equipped with a screw thread and a nut in order to allow tile exchange.



Paper 2

Coral recruitment and recovery after the 2004 Tsunami around the Phi Phi Islands (Krabi Province) and Phuket, Andaman Sea, Thailand

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Abstract

The 2004 tsunami left a discontinuous pattern of destruction in the reefs along Andaman Sea coast of Thailand. Here, a comparative assessment of coral recruitment was carried out to assess differences in recovery between damaged and undamaged sites in near-shore fringing reefs one year and three years after the tsunami. Settlement plates showed high frequencies of coral spat after 4 months (< 17 spat tile^{-1}) in both, damaged and undamaged locations. Field surveys carried out 3 years after the tsunami on natural substrate confirmed that tsunami damage did not suppress recruitment in damaged sites relative to no impacted controls. New and stable settlement space along with unabated larval supply supported post-tsunami recruit densities up to 7.2 m^{-2} year^{-1}. Mean recruit densities were found at the level of post-storm situations with rapid recovery success, suggesting that the duration of disturbance, degree of sorting and, hence, stability of coral rubble is a key determinant of recruitment success. Low regeneration success of some species e.g. branching acroporids and rebounding tourism industry at sites like Patong and partly around the Phi Phi Islands (dense carpets of filamentous algae) led to the assumption of selectivity and eventually to an alternation of the coral community even though live coral cover might be recovered soon.

Keywords: recovery, recruitment, corals, tsunami, destruction, tourism

Introduction

The 26 December 2004 hitting the west coast of Thailand had a much higher impact on land than in the sea (DMCR 2005). During a rapid assessment three weeks after the event, only about 13 % of the coral reefs in the Andaman Sea were found to be highly damaged (>50 % of corals destroyed), while almost 40 % showed no measurable impact by the tsunami (DMCR 2005). The degree of damage on coral reefs was found to be related to exposure to and amplification of the incident wave due to local differences in bathymetry and coastline leading to a localized pattern of destruction (Allen and Stone 2005; DMCR 2005). Generally, the highest impact was found between adjacent islands (funneling effect) and in areas with shallow embayments or shallow exposed reefs (Phongsuwan et al. 2006). Corals were overturned (the massive *Porites lutea* and table corals such as some *Acropora* and *Montipora* spp.), broken (branching species e. g., *Acropora* spp.) or buried by debris or sediment, while less consolidated colonies slid away with the substrate (DMCR 2005).

So far, there is no precedent in the scientific literature for a coral recovery study after tsunami. Time spans for recovery after other large-scale mechanical disturbances such as tropical storms are highly variable, e. g. from only few years in storm-beaten reefs in Florida (Shinn 1976) and Phuket Island (Phongsuwan 1991), from few year to several decades in Heron Island, Australia (Woodhead quoted by Pearson 1981, Connell et al. 1997) and Hawaii (Dollar and Tribble 1993), and up to a century in British Honduras (Stoddart 1974). Other reefs may fail to recover altogether under continued unfavorable combinations of natural and anthropogenic stressors (Woodley et al. 1981; Woodley 1989; Rogers and Miller 2006).

Reef recovery is driven by two processes: sexual propagation with re-colonization of freshly exposed substrate by new recruits and asexually, by regeneration of damaged coral colonies or fragments. The success of re-colonization is dependent on larval supply, suitability of substrate as well and competition and predation (Pearson 1981). It is not known at present to what extent the tsunami may have affected any of these factors governing coral recruitment.

On the one hand, the small-scale patchiness of destruction both between and within reefs (DMCR 2005) may allow for an uninterrupted supply of larvae from undamaged to adjacent damaged reefs. On the other hand, the loss of more than half of the colonies in heavily impacted reefs may have rendered reproductive success critically low (Allee effect; Stephens and Sutherland 1999), particularly for short range dispersing species. Although connectivity between reefs has been emphasized for many reef organisms at various scales (e.g., Williams et al. 1984; Roberts 1997), self-seeding with a significant fraction of propagules settling within the natal reef has been shown, as well, in studies of larval dispersal (Sammarco and Andrews 1989; Black et al. 1990; Jones et al. 1999).

The success of re-colonization is also governed by the substrate composition. Well-sorted rubble following tropical cyclones in response to a high number (>1,000) of huge waves, may provide a “killing field” for coral recruits (Thongtham and Chansang 1999, Tamelander 2002; Fox and Caldwell 2006). By contrast, unsorted rubble of various sizes, broken and overturned corals generated by large but few (<10) tsunami waves may provide an interlocking framework, thus enhancing substrate stability and, hence, coral recruitment. These different substrate characteristics need to be considered in the recruitment process, together with the abundance of potential space competitors such as algae, expanding adult coral colonies and bryozoans. In terms of predation, corallivore fishes were rare and herbivore fishes were abundant in ‘normal densities’ before, as well as after the tsunami (Allen & Stone 2005).

Generally, the asexual process of regeneration proceeds smoothly, if the lesion is not too large and the coral is healthy (Knowlton et al. 1981; Woodley et al. 1981). For some branching

species (e.g., *Acropora* spp.), mechanical fragmentation and subsequent regeneration is the dominant way of reproduction (Highsmith 1982), but also massive corals, such as *Porites lutea* dominating in the Andaman Sea of Thailand, are known for their rapid regeneration after damage (Highsmith 1980; Phongsuwan 1991; Brown et al. 2002).
The degree of damage determines the favorable mode of recovery, while heavy damage with high coral mortality results in a rather slow recovery process of re-colonization (Connell et al. 1997).
The aim of this study was to assess the recovery of tsunami impacted reefs relative to reefs less affected by destruction. Recruitment success was hypothesized to be high in areas with large areas of freshly exposed solid substrate in spite of a potentially patchy larval supply. Also regeneration was expected to be rapid compared to results of previous studies (Phongsuwan 1991; Brown et al. 2002). The following variables influencing coral recruitment and potential reef recovery were investigated: (1) Recruitment in damaged and undamaged sites, (2) abundance of suitable substrate for planula larvae to settle on, (3) abundance of potential space competitors of coral recruits and (4) survival of damaged corals. Two depths were chosen due to a much higher tsunami impact in the shallow reef (< 4m deep) compared to deeper areas.
The results of this study are discussed in the light of previous storm recovery studies in order to provide a baseline for conservation and management of the tsunami affected areas.

Materials and Methods

Study sites
The study was carried out in reefs fringing the island of Phuket as well as the Phi Phi Islands in Phang Nga Bay, which were affected to various degrees by the 2004 tsunami. Two depths were chosen in the context of higher tsunami impact in the shallow reef area (< 4m). The Thai region features a monsoonal climate, where the wet and stormy SW monsoon season is from May to November and the dry season with the calm NE monsoon is from December to April. In 2005 the SW monsoon was exceptionally dry in the beginning (except May) and above-average rainfall occurred during the end of the season (September – November) (Southern Meteorological Center, Thailand). The Andaman Sea is comparatively nutrient rich, due to upwelling and land run-off (Janekarn and Hylleberg 1989; Brown et al. 1999). In spite of growing anthropogenic pressures the coral reefs are still in a fairly good condition (Brown 2007).

Phi Phi Islands (Krabi Province):
The Phi Phi Islands consist of 6 limestone islands located 40 km southeast of Phuket and about 30 km west of Krabi in Phang Nga Bay, a large shallow bay not deeper than 30 m (Fig. 1). Well developed fringing coral reefs are found on the eastern sides of the islands or in areas protected from SW storms. At most sites, coral grow down to about 8 - 10 m depth, but to about 15 - 20 m at Ko Phi Phi Lae. The visibility ranges from 5 - 25 m. Massive *P. lutea*, branching *Acropora* spp., such as *A. formosa*, *A. grandis*, *A. subulata* and *A. austera* and the tabular *A. hyacinthus* and *A. subulata* are the dominant species.

Although the Phi Phi Islands were declared a marine national park in 1983, unrestricted access by the tourism industry has led to the degradation of the surrounding reefs (Chou et al. 2002). There is no sewage treatment plant, only some collecting ponds and it remains unclear, where the wastewater enters the sea. Some of the coral reefs were strongly hit by the tsunami

in December 2004 and suffered severe damage, while other areas remained untouched, providing an ideal setting for testing small scale differences (<10 km) in coral recruitment as a function of reef damage.
Seven study sites were chosen, three damaged (marked with a 'D' superscript in the following) and four undamaged sites (Fig. 1). Highest tsunami damage occurred at Ko Pai and at Lolana Bay (up to 50 % damage), and at the northern end of Ko Phi Phi Lae (30 – 50 % damage) (DMCR 2005).
The remaining study sites Ko Yoong, Leam Tong, Hin Phae and Ko Phi Phi Lae SE were only slightly damaged or completely untouched (DMCR 2005).

Phuket:

Coral reefs are well developed on the west coast in protected bays and on some areas along the southern coast. The study site South Patong in the Southwest of Phuket (Fig. 1) is a tourist hotspot with over 30,000 hotel bedrooms. Corals grow to about 7 m depth and the dominant species are *P. lutea*, *D. heliopora*, *Millepora* sp., *H. coerulea*, *Lobophyllia* sp., few branching corals such as *A. formosa*, few table corals and encrusting corals. About 30 % of waste waters of the city of Patong are untreated and being discharged into the bay only a few hundred meters away from the investigated reef smothering the corals. The visibility is 5 – 10 m.
South Patong is the only reef area on Phuket, which was severely impacted by the tsunami (DMCR 2005).

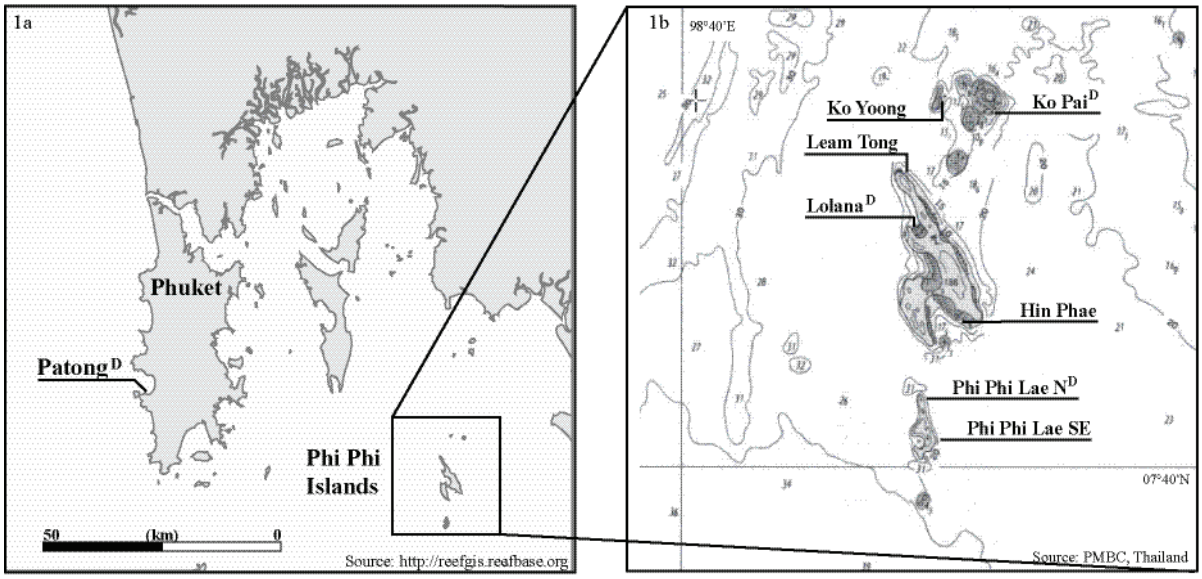

Fig. 1: Map of middle section of the Andaman coast of Thailand (7.57°N-8.60°N) (a) and the Phi Phi Islands (b), indicating the study sites.

Settlement plates
A settlement experiment was carried out one year after the tsunami to evaluate coral larvae distribution between damaged and undamaged sites and to quantify space-competing algae and fouling organisms. 12 x 12 cm plates were cut from acrylic board (2.5 mm thick), roughened with a metal brush and fixed in triplicates in a vertical position on 1 m iron rods. Six rods were fixed in an upright position for every location and depth (shallow: reef edge ~3 m and deep: lower reef slope ~7 - 10 m) resulting in 2 depths x 6 rods x 3 plates = 36 plates per study site. Although acrylic shares the disadvantages of all artificial settlement plate

material compared so far in being highly selective for certain taxa (Harriott & Fisk 1987; Dunstan & Johnson 1998; Heyward and Negri 1999; Petersen et al. 2005; Mangubhai et al. 2007), as opposed to natural reef substrate (e.g. Morse and Morse et al. 1996), they are nevertheless useful in detecting differences in coral recruitment in both, space and time.
All the settlement plates were deployed early November 2005. For a given site and depth the triplicate plates of rod number one were replaced after one month, the plates of rod number two after two months, etc., resulting in a time series of settlement of varying exposure period (up to four months, early November 2005 to early March 2006; Table1).
After removal, plates were allowed to dry in the sun for 2-3 days for examination with a magnifying glass and stereo microscope. Settlement plates were searched for coral spat and specimens identified to family level according to Babcock et al. (2003). The abundance of fouling organisms (filamentous algae, crustose coralline red algae and sessile fauna such as barnacles, bivalves, bryozoans and spirorbid worms) was recorded on an ordinal scale between 0 (absent) and 5 (replete). Category 5 applied to high densities of filamentous algae featuring long filaments; crustose coralline algae covering most of the plate in thick patches; bryozoans covering more than 40 % of the plate; spirorbid worms in excess of 40 individuals per plate; bivalves and barnacles with more than 25 individuals per plate, respectively.
Statistical analyses were conducted with the software SAS. The data collected on one rod (3 plates) were treated as one replicate. A Poisson regression was carried out since the coral spat densities followed a Poisson distribution. The data set of the four month period was used to assess the effects of three indicator variables (1) 'status' (damaged, undamaged), (2) reef 'sites' (Ko Yoong, Leam Tong, Hin Phae, Phi Phi Lae SE, Phi Phi Lae N, Ko Pai, Lolana, Patong) and (3) 'depth' (shallow, deep) on the response variable 'coral spat' density, whereas 'sites' were nested within 'status'. The effects of filamentous and crustose coralline red algae and of fouling organisms (additional indicator variables) on coral spat densities were analyzed in a separate run of Poisson Regression.
To test for differences in coral spat abundances between the two seasons (November – January end of rainy season, January – March dry season) data of the two month period were used and Poisson Regression was applied. The additional indicator variables was 'season', however the variable 'site' was eliminated, because each site was represented by only two data points (one deep rod, one shallow rod). The effect of seasonality on algae and fouling organisms was tested with univariate ANOVA using season and depth as fixed factors and the sites were treated as replicates. Levene´s test was applied to test homogeneity of residuals.
Succession over the four month period was analyzed graphically.

	exposure time			
	Nov - Dec	Dec - Jan	Jan - Feb	Feb - Mar
rod 1	1 month	3 months		
rod 2	2 months		2 months	
rod 3	3 months			1 month
rod 4	4 months			
rod 5	4 months			
rod 6	4 months			

Table 1: Experiment design for one study site und depth including the intervals of plate replacements. Exchanged plates (grey).

Visual census of coral recruits *in situ*
In this paper, we distinguish between newly settled corals ("coral spat") on settlement plates, and the young corals ("coral recruits") in the field.

Visual census of coral recruits was done one year (January / February 2006) as well as three years (November 2007) after the tsunami in proximity to the settlement plates at all sites, along the reef edge and the lower reef slope in order to quantify the success of coral recruitment. Recruits were counted on natural substrate using a 0.5 x 0.5 m square (0.25 m^{-2}) placed at random (n=10) in areas dominated by dead coral substrate and summed up (recruits 2.5 m^{-2}). Within the quadrates 0.5 - 2.0 cm coral recruits (diameter) were recorded. Visual census with unaided eye allowed undoubted recruit identification only for the genus *Pocillopora*; all other scleractinians were recorded as "other". Given linear extension rates of >1 cm $year^{-1}$ even for slow-growing taxa in the area (Phongsuwan 1991; Scoffin et al. 1992), it was assumed that the bulk of the recruits had settled after the tsunami.
For statistical analyses Levene´s test was applied to test homogeneity of residuals and univariate ANOVA was used to compare recruit abundances. Status and depth were fixed factors and the sites were treated as replicates.

Line intercept transects
Line intercept transects (English et al. 1994) were carried out in January / February 2006 (i.e. one year after the tsunami) to determine live coral cover and the availability of suitable substrate for coral larvae settlement. 20 m transects (n=3) were laid out with a measuring tape along the reef edge and the lower reef slope in proximity to the settlement plates at all sites. The substrate directly under the tape was assigned to the following categories - live coral (LC), dead coral (DC), other organisms (including soft coral, sponges and giant clams), coral rubble (RB), sand (SA), macroalgae and categories recorded to the nearest cm. RB included small pieces of coral skeleton (<10 cm long), while DC was composed of coral skeleton pieces larger than RB, dead patches on coral colonies and entire dead colonies up to few meters in diameter. The respective mean percentage cover of each component was calculated for each location and depth.

Results

Settlement plates
Coral spat
Pocilloporids dominated by far the coral spat on the settlement plates, in spite of the dominance of adult Acroporidae and Poritidae in the reefs. Spat were patchily distributed between the plates, ranging from 0 to 17 spat $plate^{-1}$ and a total of 394 spat for all plates. Coral spat densities were lower during the first two months of the experiment (November 2005 – January 2006), compared to the last two months (January – March 2006) (Table 3, Fig. 2). There was no detectable difference between damaged and undamaged sites after 4 months. More coral spat were found in the deeper areas; however the difference between the 2 depths varied between damaged and undamaged sites (Table 3) and the high number of coral spat at Ko Yoong deep (Table 2) strongly influenced this result. The high variations in spat abundances between the sites led to site effects at all sites in damaged as well as in undamaged reefs (Table 3, Supplementary [S] Fig. S1 shows graphical illustration of spat densities).
Coral recruitment showed a functional response to filamentous algae with highest coral spat densities on plates with intermediate algae cover (Fig. S2). A positive relationship between crustose coralline red algae and coral spat (Morse and Morse et al. 1996) was not detectable.

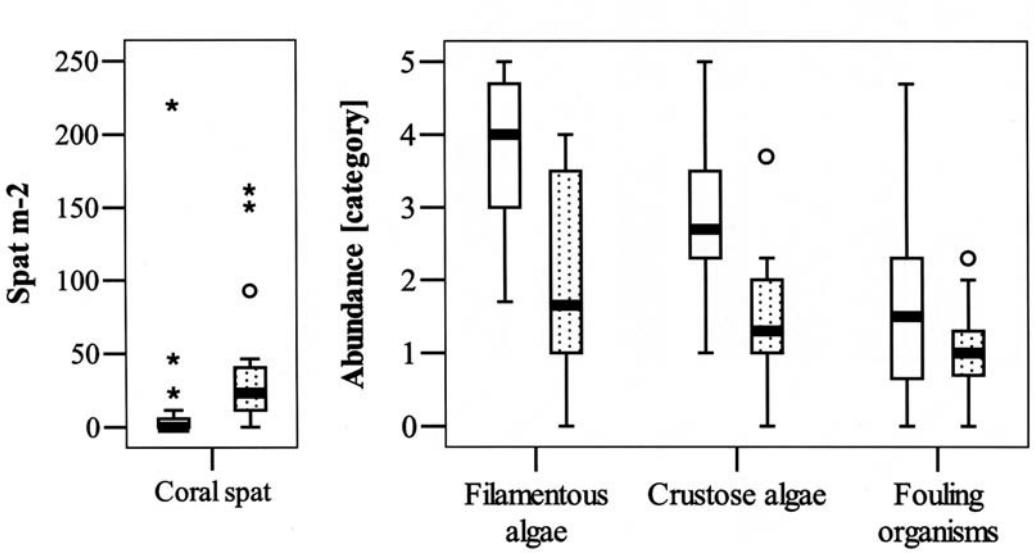

Fig. 2: Abundance of coral spat, filamentous algae, crustose algae and fouling organisms after 2 month: Nov 05 – Jan 06 (blank), Jan – Mar 06 (dotted), indicates seasonality. The y-axis represents the categories of abundance/density: 1= very low, 5= very dense / high abundance. Box: lower / upper quartile and median (bold black line); whisker (vertical line): extend of rest of the data; outliers: circle: measured value is higher/smaller than the upper/lower quartile + 1.5x quartile distance, star: measured value is higher/smaller than the upper/lower quartile + 3x quartile distance.

Table 2: Coral spat abundances on settlement tiles with an exposure time of 4 months. Average ± standard deviation.

	spat tile^{-1}		*Pocilloporidae* [%]		*Acroporidae* [%]		*Poritidae* [%]		others [%]	
	shallow	deep	shallow	deep	shallow	deep	shallow	deep	shallow	deep
Ko Yoong	0	8.9 ± 4.7	0	97	0	0	0	3	0	0
Leam Tong	2.8 ± 2.4	0.3 ± 1.0	96	100	0	0	0	0	4	0
Hin Phae	0.6 ± 0.9	2.6 ± 1.9	100	88	0	0	0	9	0	3
PP Lae SE	1.6 ± 2.3	0	100	0	0	0	0	0	0	0
PP Lae N^{D}	0.7 ± 1.4	0	77	0	8	0	0	0	15	0
Ko Pai^{D}	1.2 ± 1.9	0.6 ± 0.7	94	100	0	0	0	0	6	0
Lolana^{D}	0.7 ± 1.1	0.3 ± 0.5	81	67	0	17	13	17	6	0
Patong^{D}	3.3 ± 2.4	0.6 ± 1.1	95	33	0	33	4	17	2	17

Algae and fouling organisms

Filamentous and crustose coralline red algae showed a clear seasonality with a higher abundance within the first two months (Fig. 2, ANOVA $p<0.001$ for both). Depth had no effect on the distribution of filamentous algae (ANOVA $p>0.05$). However, crustose red algae were significantly more abundant in the shallow reefs (ANOVA $p=0.016$). There were pronounced differences in algal cover between sites: Lolana^{D} had the highest abundance of filamentous algae followed by Patong^{D}, while the lowest densities were found at Leam Tong and Phi Phi Lae SE (Fig. S3). Sediment was trapped between the algal filaments of densely covered plates especially in the deeper area of Ko Yoong and Lolana^{D}.

Highest abundances of crustose algae were found at Ko Pai^{D} and Lolana^{D} displaying thick algae crusts on the plates.

Table 3: Results of Poisson Regression: coral spat dependency on status (damaged / undamaged), depth and site (nested within status), using the 4 month data; effect of season, using 2 month data; effect of algae and fouling organisms on coral spat abundances, using 4 month data. ns (not significant). $p<0.05$ significant.

Source	df	SE	$\chi 2$	p
Coral spat (status & depth)				
Status	1	0.2443	0.20	ns
Depth	1	0.1782	19.00	<0.0001
Status x Depths	1	0.3571	37.33	<0.0001
site (status) Ko Yoong	0	0.0000	-	-
site (status) Leam Tong	1	0.2196	22.86	<0.0001
site (status) Hin Phae	1	0.2327	26.76	<0.0001
site (status) PPLae SE	1	0.2897	36.20	<0.0001
site (status) PPLae N^D	1	0.4419	15.93	<0.0001
site (status) Ko Pai^D	1	0.3018	6.73	0.0095
site (status) $Lolana^D$	1	0.3737	13.20	0.0003
site (status) $Patong^D$	0	0.0000	-	-
Coral spat (season)				
Season	1	0.2367	11.00	0.0009
Coral spat (algae and fouling organisms)				
Filamentous algae	1	0.1395	55.27	<0.0001
Crustose algae	1	0.1318	8.64	0.0038
Fouling organisms	1	0.1809	0.08	ns

Although the abundance of fouling organisms (bryozoans, spirorbid worms, bivalves, barnacles) was generally low, some plates had high abundances of certain groups (e.g., spirorbid worms) and variation was sometimes high on the level of a single rod. Peak abundances were visible in the deeper area of $Patong^D$, where bryozoans (>40 % coverage) and bivalves (9 – 15 ind. $plate^{-1}$) showed the highest abundances. Seasonality was not significant, but showed a similar pattern as filamentous and crustose algae (Fig. 2, ANOVA $p>0.05$). An overgrowth of spat by bryozoans was observed in some cases.
Succession took place following the expected pattern, in which filamentous algae and crustose coralline red algae are the first settlers being than gradually replaced by sessile animals, such as bryozoans and bivalves and finally by corals (Fig. S4).

Coral recruits on natural substrate

There was a significant increase in coral recruitment between one and three years after the tsunami (ANOVA $p=0.016$), but no differences between either damaged and undamaged or shallow and deep reefs (ANOVA $p>0.05$). One year after the tsunami the highest density of recruits was found at $Lolana\ Bay^D$ with more than 6 recruits m^{-2} in the shallow reef area followed by Leam Tong. Almost 2 yrs later Ko Yoong showed the highest recruit density and $Lolana\ Bay^D$ was situated around the average of all sites (Table 4). Generally, pocilloporids contributed the bulk of the recruits; but variation between sites was very large ranging from 0% pocilloporids in shallow Hin Phae after 1 yr to 100 % in shallow Leam Tong after 3 yrs (Table 4).
No relationship was visible between the number of spat and the number of recruits for either pocilloporid corals alone or the ensemble of corals. At Ko Yoong, which showed an

extremely high abundance of pocilloporids on the plates, the number of recruits was found within the range of other sites (Table 2 and 4). Also no connection between recruit densities and algae abundance (on plates) could be found (Fig. S5).
Additionally to the < 1 year old recruits some older recruits (1 - 3 yrs), in particular fast growing *Acropora* spp. (10 - 20 cm in diameter), were observed during the November 2007 survey on tsunami generated dead corals at Lolana Bay^{D} and Patong^{D}.

Table 4: Coral recruit abundances on natural substrate.

	Jan/Feb 2006						Nov 07					
	recruits m^{-2}		Pocilloporidae m^{-2}		others m^{-2}		recruits m^{-2}		Pocilloporidae m^{-2}		others m^{-2}	
	shallow	deep	shallow	deep	shallow	deep	shallow	deep	shallow	deep	shallow	deep
Ko Yoong	2.8	2.8	1.6	1.6	1.2	1.2	7.2	5.6	4.8	3.2	2.4	2.4
Leam Tong	4.8	3.2	3.6	1.6	1.2	3.2	2.8	4,0	2.8	0.8	0,0	3.2
Hin Phae	1.2	2.0	0,0	0,0	1.2	1.2	3.2	3.2	1.2	1.2	2,0	2,0
PPLae SE	2.4	1.6	1.6	0.8	0.8	1.2	6.4	2.4	4,0	0,0	2.4	2.4
PPLae N^{D}	3.2	3.2	0.4	0.4	2.8	2.8	2.8	4.4	0.8	0.4	2,0	4,0
Ko Pai^{D}	2.4	1.2	0.8	0.4	1.6	0.8	3.2	4.4	1.6	1.6	1.6	2.8
Lolana^{D}	6.4	3.2	2.4	0.8	4,0	2.4	4.8	4.8	2.4	0.4	2.4	4.4
Patong^{D}	4.0	2.0	1.2	0.8	2.8	1.2	6.4	2.4	2.8	0,0	3.6	2.4

Substrate composition and survival of damaged corals
Highest LC cover was found at Ko Yoong in the shallow reef (57 %). In five out of eight cases a higher LC cover was found in the shallow area; the opposite situation was observed at Lolana^{D} and Patong^{D} and Hin Phae. The cover by DC was highest in the shallow areas of damaged reefs in particular at Ko Pai^{D} and Lolana^{D} with 59 % largely due to overturned *Porites* heads. But also the deeper reef areas showed a higher abundance of DC compared to the undamaged sites. In contrast, we found no relation between RB cover and tsunami impact. The only site with high rubble cover was Phi Phi Lae SE deep with 49 %, while the other sites were lying generally between 10 and 20 % at other sites (Fig. 3, Table S1) presentation in numbers). No correlation was found between LC and coral recruit densities.
Many of the overturned or toppled *Porites* heads survived, showing partial re-growth around the edges. Branching coral species such as *Acropora* spp. were severely impacted in some areas; many fragments were dead in the shallow water, particularly on the reef flat. Some fragments on the reef slope survived and showed new outgrowth, unless covered by sand or debris. Dead *Acropora* table corals were found uprooted in the sand, and toppled over specimens in no direct contact with the sediment were found alive even in an upside down position. New little outgrowths directed to the light could be observed.

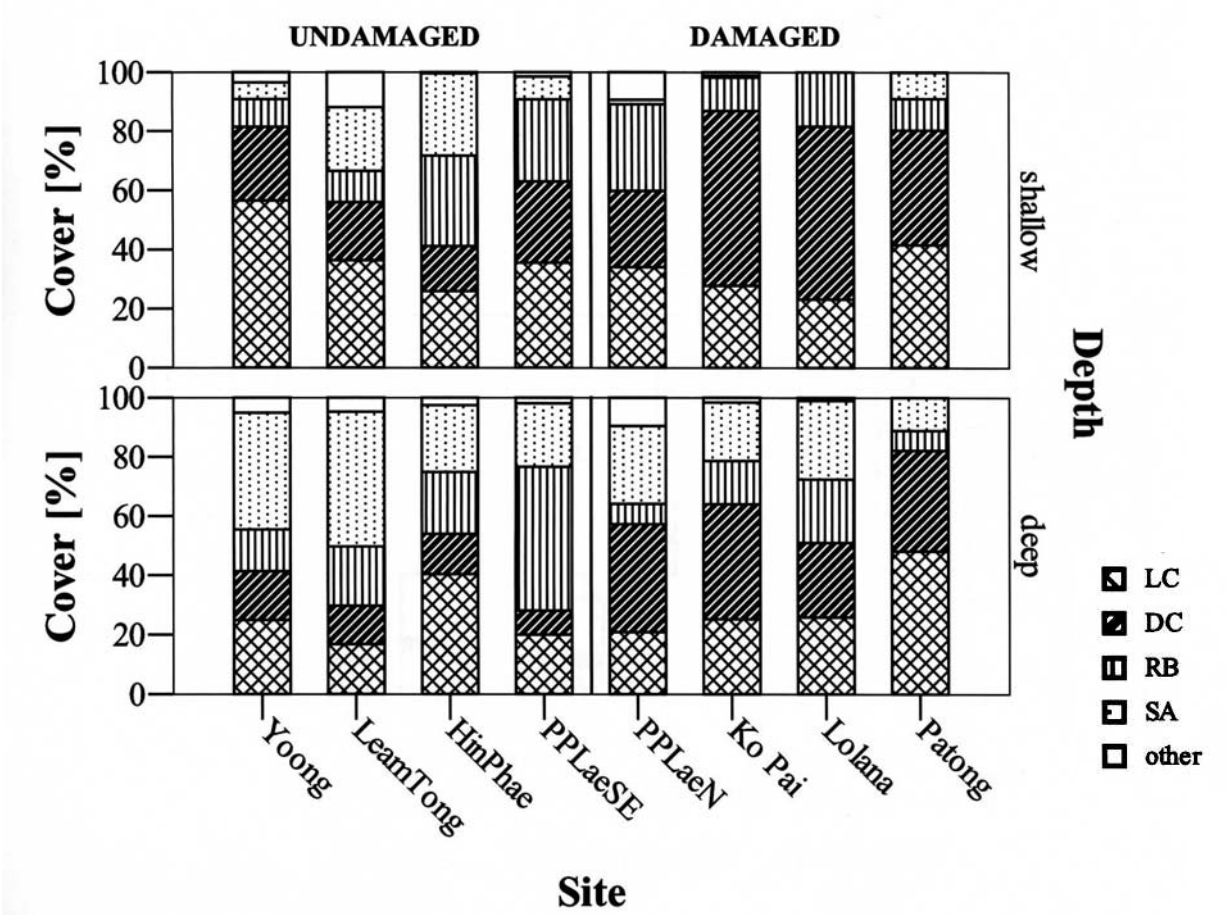

Fig. 3: Substrate composition at different sites and depths.

Discussion

The densities of coral spat recorded on the settlement tiles as well as the recruit abundances on the natural substrates indicate a successful supply of coral larvae and subsequent recruitment not only in the undamaged but also in the damaged reef areas. Although the predominance of pocilloporids on the settlement plates is likely biased, similar to the overrepresentations found in other settlement plate studies (Bak and Engel 1979; Harriott and Fisk 1987; Dunstan and Johnson 1998), the high densities show that these monthly reproducing brooders (Fadlallah 1983) are able to disperse to sites featuring only sparse adult brood stock over a range of several kilometers (cf. Table 5).

The high spat densities are reflected also in the densities of coral recruits on natural substrate which increased from an average 3.2 ± 1.6 m^{-2} in damaged areas and to 4.15 ± 1.3 m^{-2} after 3 years. While these findings suggest successful recovery, it must be kept in mind that the natural variability in recruitment between years can be pronounced (Dunstan and Johnson 1998). These results are lying within the recruit densities found during a 30-year study in the Great Barrier Reef (1.8 - 30.3 recruits yr^{-1}). The high fluctuation in the GBR was partly attributed to storm events and partly to natural temporal variability, while the recovery success after different storms was found to be strongly influenced by the severity of storm impact (Connell et al. 1997). At a storm- beaten reef in the Andaman Sea of Thailand high

recruitment success was found (17 – 19 recruits m^{-2}, size <5 cm Ø) due to the abundance of solid substrate (Phongsuwan 1991). Nevertheless our results are outstanding compared to another storm-shattered reef in the area, where low recruitment success was the consequence of long lasting unconsolidated rubble (2 – 4 recruits m^{-2}, size <5 cm Ø) (Thongtham and Chansang 1999). This leads to the suggestion that substrate stability plays a decisive role in recovery after large-scale disturbance. In the context of tsunami few but very energetic waves creates a heterogeneous and interlocking framework with coral debris of various forms and sizes, This was typical for reefs strongly hit by the tsunami such as Lolana^{D} and Ko Pai^{D}, where dead corals (59%) provide a solid foundation with a high variation of substrate orientation and surface complexity, which is known to be supportive for larval settlement and survival (Pearson 1981; Thongtham and Chansang 1999).

Table 5: Abundance of Pocilloporidae adults, spat and recruits. Damaged sites (^{D}). No data (n. d.).

	Adult [% of LC]	Spat [no. m^{-2}]	Recruits [no. m^{-2}]
Ko Yoong	10.96	137	1.5
Leam Tong	1.80	48	1.8
Hin Phae	0.51	42	0.4
PPLaeSE	n. d.	25	1.0
PPLaeN^{D}	n. d.	11	0.4
Ko Pai^{D}	0.00	23	0.6
Lolana^{D}	0.00	16	1.5
Patong^{D}	0.46	52	1.0

Space competing organisms such as algae and a range of small filter feeders did not seem to have a negative impact on coral spat- and recruit densities leading to the conclusion of a rather high resilience of corals in the Andaman Sea being able to successfully compete with other organisms. This idea is further supported by other studies in this area, in which high recruitment success and regeneration of damaged coral colonies after storms, sediment plumes from dredging, negative sea level anomalies and increased sea surface temperatures were found (Phongsuwan 1991; Brown et al. 2002; Brown and Phongsuwan 2004). Additional evidence for the corals ability to persist and / or recover quickly are: (1) high growth rates (Phongsuwan 1991; Scoffin et al. 1992), (2) high tolerance for sedimentation and elevated nutrient levels (Brown 2007) and (3) preferred spawning during the end of the dry season when algae growth is suppressed as shown in our results of the settlement plates and also found by Chanmethakul (2001) and Guest et al. (2005). Latter might also be a reason for the low contribution of many coral species on the settlement tiles, where plates were removed (March) just after the onset of the spawning period (February).

After demonstrating all the positive features of corals in this region, some weakness in the recovery of branching acroporids was found. In contrast to massive (e.g. *Porites lutea,* faviids) and table like corals (e.g. *Acropora hyacinthus, A. clathrata*, *Montipora* spp.), regeneration by tissue re-sheeting was hardly visible in branching *Acropora* spp. resulting in high mortality rates. Only few coral fragments were still alive after three years - in spite of its alleged fast fixation (Phongsuwan 2006) and their naturally high recovery potential (Highsmith 1982; Veron 1993). This goes in line with the findings at a reef off Phuket, where

recovery of branching acroporids after stress from low sea levels and increased temperature was unsuccessful in contrast to other species (Brown and Phongsuwan 2004).
After all, this might lead to selection of coral species not only concerning the regeneration process but consequently also the recruitment diversity. Unfortunately, the recruitment diversity has not been assessed; however the relatively high contribution of pocilloporids and the intermediate numbers of coral recruits support the idea of selectivity. Even though the percentages of live coral cover might be restored, lower diversity in areas with strongly degrading water quality such as Patong and partly around the Phi Phi Islands (Chou et al. 2002; Yeemin 2004) might be the consequence.
Therefore, higher sensitivity of the coral community can not be ruled out, which leads to a higher vulnerability of a reef ecosystem to natural disturbances e.g. heavy storms. This emphasizes the need of further monitoring activities and the need of effective coastal management to maintain viable conditions for Andaman Sea coral reefs, especially where tourism is growing in great numbers.

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Supplementary material

Table S1: Substrate composition [%] 1 yr (January / February 2006) after the tsunami at different sites. Damaged sites (^{D}).

shallow	Live coral	Dead coral	Sand	Coral rubble	Other
Ko Yoong	56,5	24,9	5,6	9,4	3,5
Leam Tong	36,3	19,7	21,7	10,4	11,9
Hin Phae	34,2	14,7	27,9	30,0	0,4
PPLae SE	35,5	27,5	7,7	27,9	1,4
PPLae N^{D}	34,0	25,8	1,5	29,4	9,3
Ko Pai^{D}	27,7	59,2	0,5	11,4	1,2
Lolana^{D}	23,1	58,5	0,0	18,4	0,0
Patong^{D}	41,5	38,7	8,9	10,8	0,1
deep					
Ko Yoong	24,9	16,4	39,5	14,1	5,1
Leam Tong	16,8	12,8	45,4	20,1	4,8
Hin Phae	40,4	13,8	22,7	20,9	2,9
PPLae SE	19,9	8,1	21,4	48,6	1,9
PPLae N^{D}	20,8	36,4	26,3	7,0	9,6
Ko Pai^{D}	25,2	38,8	19,7	14,7	1,6
Lolana^{D}	25,9	25,1	26,6	21,5	1,1
Patong^{D}	48,1	34,0	11,1	6,8	0,0

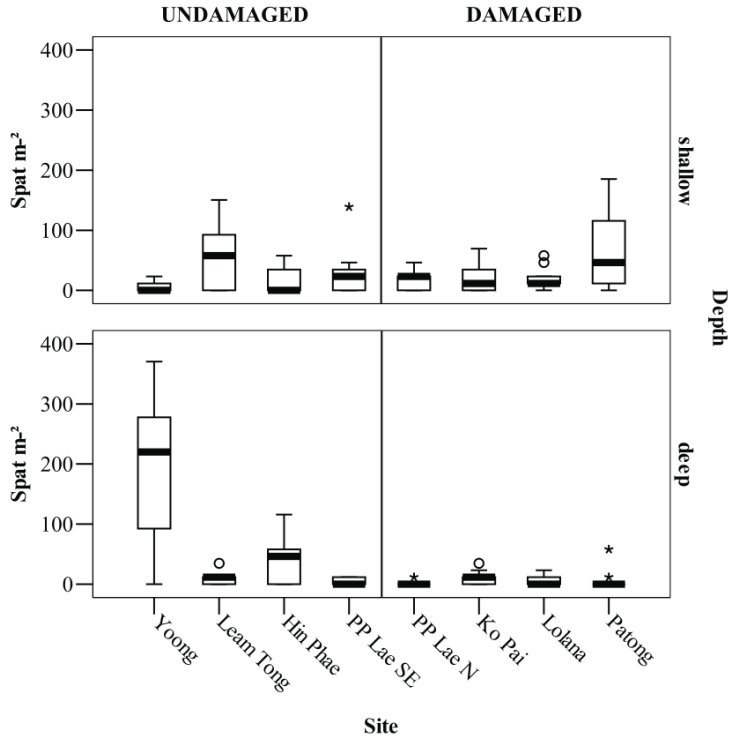

Fig. S1: Abundance of coral spat in undamaged and damaged sites after 4 months. Box: lower / upper quartile and median (bold black line); whisker (vertical line): extend of rest of the data; outliers: circle: measured value is higher/smaller than the upper/lower quartile + 1.5x quartile distance, star: measured value is higher/smaller than the upper/lower quartile + 3x quartile distance.

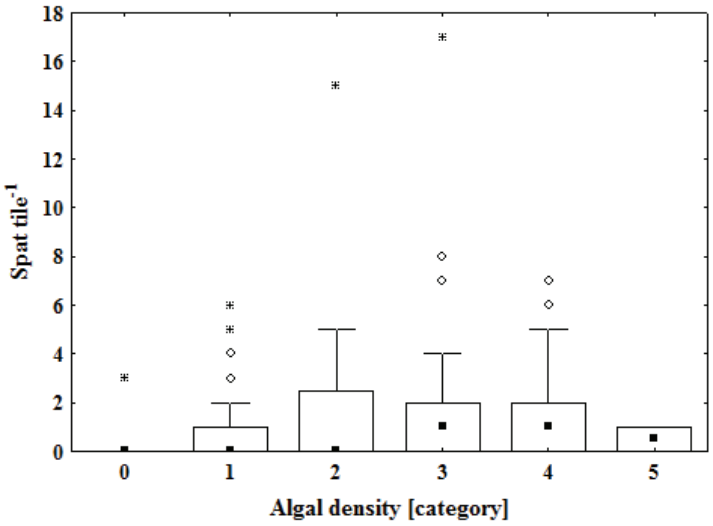

Fig. S2: Coral spat density vs. filamentous algal density after 4 months. The x-axis represents the categories of density: 1= very low density, 5= dense carpet of algae. Box: lower / upper quartile and median (bold black line); whisker (vertical line): extend of rest of the data; outliers: circle: measured value is higher/smaller than the upper/lower quartile + 1.5x quartile distance, star: measured value is higher/smaller than the upper/lower quartile + 3x quartile distance.

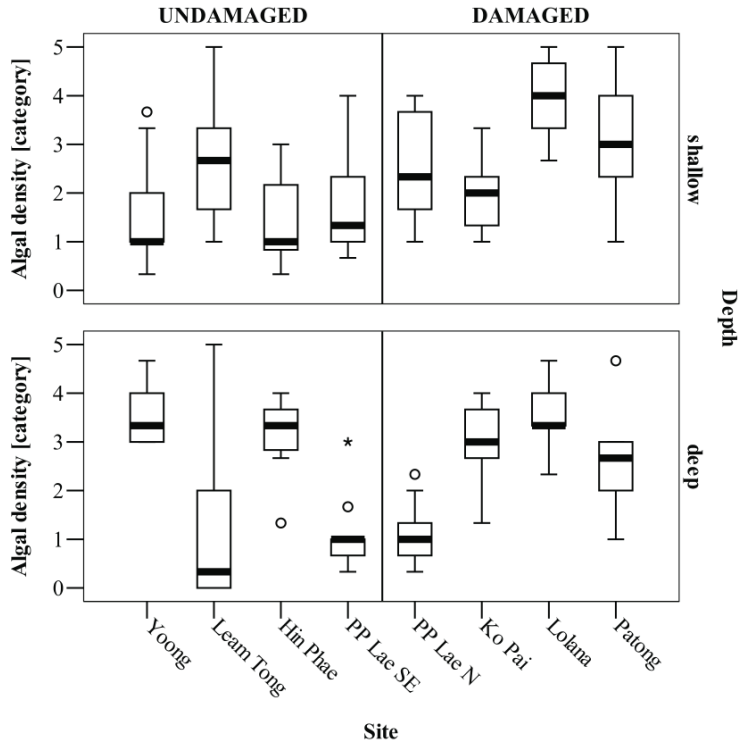

Fig. S3: Abundance of filamentous algae at undamaged and damaged sites after 4 months. The y-axis represents the categories of density: 1= very low density, 5= dense carpet of algae. Box: lower / upper quartile and median (bold black line); whisker (vertical line): extend of rest of the data; outliers: circle: measured value is higher/smaller than the upper/lower quartile + 1.5x quartile distance, star: measured value is higher/smaller than the upper/lower quartile + 3x quartile distance.

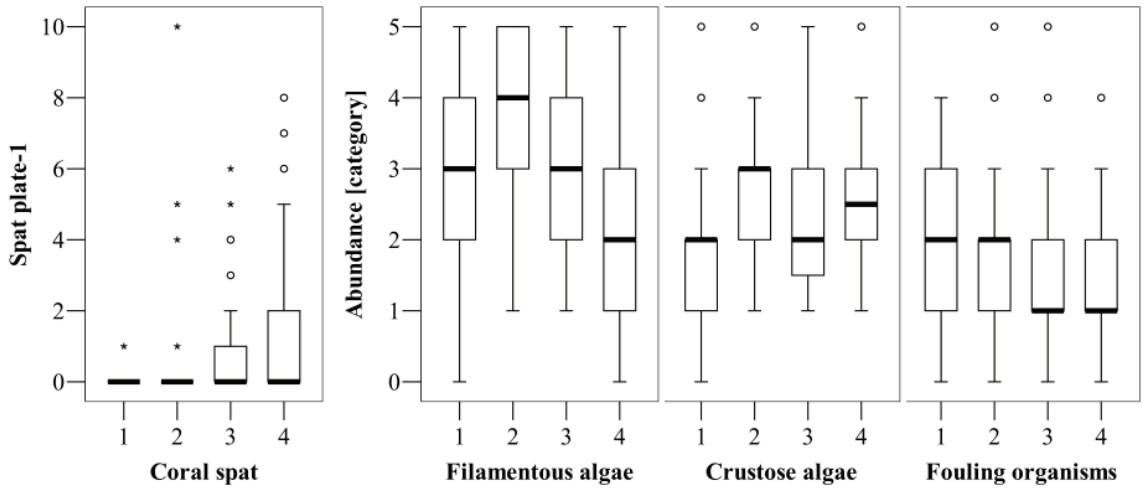

Fig. S4: Abundance of coral spat, filamentous algae, crustose algae and fouling organisms after 1, 2, 3 and 4 months to visualize succession. The y-axis represents the categories of abundance/density: 1= very low, 5= very dense / high abundance. Box: lower / upper quartile and median (bold black line); whisker (vertical line): extend of rest of the data; outliers: circle: measured value is higher/smaller than the upper/lower quartile + 1.5x quartile distance, star: measured value is higher/smaller than the upper/lower quartile + 3x quartile distance.

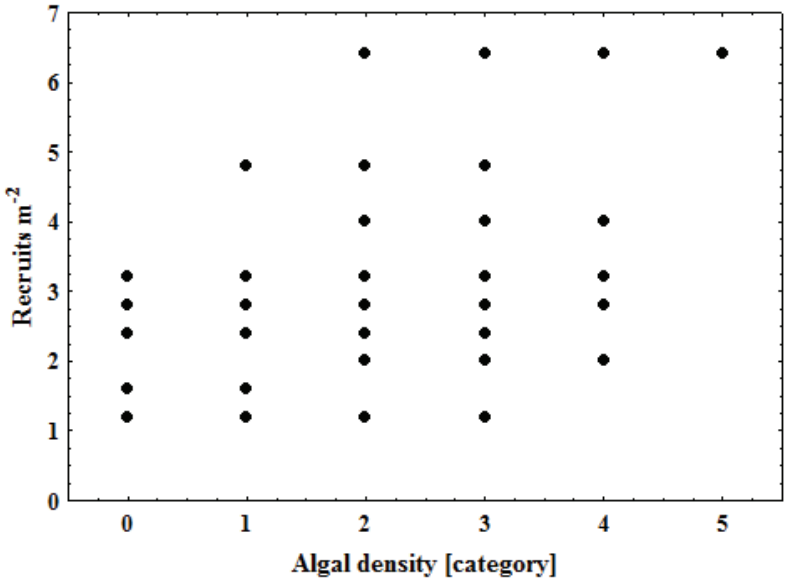

Fig. S5: Coral recruit density vs. abundance of filamentous algae. The x-axis represents the categories of density: 1= very low density, 5= dense carpet of algae.

Paper 3

Nutritional status and metabolism of the coral *Stylophora subseriata* along a eutrophication gradient in Spermonde Archipelago (Indonesia)

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In review (Coral Reefs)

Abstract

Coral responses to degrading water quality are highly variable between species and depend on their trophic plasticity, acclimatization potential and stress resistance. To assess the nutritional status and metabolism of the common scleractinian coral, *Stylophora subseriata, in situ* experiments were carried along a eutrophication gradient in Spermonde Archipelago, Indonesia. Coral fragments were incubated in light and dark chambers to measure photosynthesis, respiration and calcification in a number of shallow reefs along the gradient. Chlorophyll *a* (chl *a*), protein content, maximum quantum yield (F_v/F_m) and effective quantum yield (Φ PS II) were measured on the zooxanthellae, in addition to host tissue protein content and biomass. Photosynthetic rates were 2.5-fold higher near-shore than mid-shelf due to higher areal zooxanthellae and chl *a* concentrations and a higher photosynthetic efficiency (Φ PS II). A 2- and 3-fold increase in areal host tissue protein and biomass was found, indicating a higher nutritional supply in coastal waters. Dark respiration, however, showed no corresponding changes. There was a weak correlation between calcification and photosynthesis (Pearson r=0.386) and a the lack of metabolic stress, as indicated by constant respiration and F_v/F_m and the "clean" and healthy appearance of the colonies in spite of high turbidity in near-shore waters, suggesting that part of the energetic gains through increased auto- and heterotrophy were spent on metabolic expenditures, e.g. mucus production. While coastal pollution is always deleterious to the reef ecosystem as a whole, our results show that the effect on corals may not always be negative. Thus, *S. subseriata* may be one of the few examples of corals actually profiting from land-based sources of pollution.

Keywords: metabolism, acclimatization, photosynthesis, nutritional status, eutrophication, *Stylophora subseriata*

Introduction

Eutrophication is one of the major threats to coral reefs (Jackson et al. 2001) affecting coral health and community composition (McCook 1999; Nyström et al. 2000; Fabricius 2005; Costa Jr et al. 2008; Reopanichkul et al. 2009) and the ecological balance between corals and space-competing macroalgae (McCook 1999; Costa Jr et al. 2008; Reopanichkul et al. 2009). The ability of coastal corals to adapt to changing nutrient and sediment loads can be highly variable between species (Fabricius 2005). The coral holobiont consists of the coral animal and endosymbiotic unicellular algae (zooxanthellae of the genus *Symbiodinium*), and, therefore, is potentially mixotrophic, subsisting to varying degrees on hetero- and autotrophy. Heterotrophy contributes most to the material needs (nitrogen compounds), while photoautotrophy contributes to the energy and carbon demand of the coral (Anthony and Fabricius 2000; Piniak et al. 2003; Piniak and Lipschultz 2004; Houlbrèque and Ferrier-Pagès 2008). The intense recycling and exchange of nutrients between the coral animal and the zooxanthellae make corals particularly adapted to life in nutrient-limited waters (Muscatine and Porter 1977; Ferrier-Pagès et al. 1998a; Furla et al. 2005; Yellowlees et al. 2008).
Nutrient and sediment run-off change the water quality and light environment in coastal waters. The increased organic and inorganic nutrient and particle loads, turbidity and sedimentation rates may affect coral metabolism (Tomascik and Sander 1985; Lough and Barnes 1992; Telesnicki and Goldberg 1995; Anthony and Fabricius 2000). While higher concentrations of organic matter may be beneficial for some corals by enhancing heterotrophy in certain areas (Anthony and Fabricius 2000; Ferrier-Pagès et al. 2003), increased sediment loads have mostly been shown to smother, damage or stress corals (Brown et al. 1990; Rogers 1990; Stafford-Smith 1993; Wesseling et al. 2001). This is often reflected in increased respiration rates (Abdel-Salam et al. 1988), decreased P/R ratios (Riegl and Branch 1995; Anthony and Fabricius 2000), decreased photophysiological performance (Philipp and Fabricius 2003) and/or decreased calcification rates (Cortes and Risk 1985; Rogers 1990). Increased particle loads may also enhance coral mucus production in response to particles settling on the coral surface (Stafford-Smith 1993; Riegl and Branch 1995; Brown and Bythell 2005). In spite of significant inputs of riverine nutrients, the associated changes in inorganic nutrient concentrations are often insignificant due to their rapid incorporation by nutrient-starved plankton in near-shore reefs (Furnas et al. 2005).
Increased heterotrophy in response to enhanced availability of organic matter, including dissolved and particulate organic matter and nano- to mesoplankton, may also foster photosynthesis in corals (Ferrier-Pagès et al. 2003; Borell et al. 2008) through the transfer of nitrogen from the host to the zooxanthellae and by enhanced zooxanthellae division rates (Piniak and Lipschultz 2004; Houlbrèque and Ferrier-Pagès 2008). In *Stylophora*, the growth response of the zooxanthellae may be faster than the build-up of the light harvesting chlorophyll-protein complex within the zooxanthellae. This may result in a lag in chlorophyll *a* (chl *a*) build-up relative to an increase in zooxanthellae numbers resulting in a decrease in chl *a* zooxanthella^{-1} (Dubinsky et al. 1990). Areal chl *a* concentration may, however, increase with zooxanthellae density, in response to increased feeding in *Stylophora* (Ferrier-Pagès et al. 2003; Houlbrèque et al. 2003) and *Turbinaria* (Treignier et al. 2008), thus, helping to maintain constant cell-specific chl *a* concentrations. Increased feeding is often associated with increased respiration (Houlbrèque et al. 2003; Houlbrèque and Ferrier-Pagès 2008) leading to an increase in biomass, lipids (Anthony 2006) and proteins (Houlbrèque and Ferrier-Pagès 2008). A shift from protein to lipids, however, may occur under low light conditions (Treignier et al. 2008).

In low light and nutrient-replete conditions, photoacclimation increases the photosynthetic efficiency in corals (Dustan 1982; Mass et al. 2007; Hoogenboom et al. 2009) by increasing the areal pigment (e.g. chl *a*) and light harvesting protein concentrations (Dubinsky et al. 1990; Titlyanov et al. 2001). The efficiency of the photosystem is proportional to the light absorbed by the photosystem II in the chloroplasts. It may be expressed as the maximum quantum yield (F_v/F_m) after dark adaptation or as the effective quantum yield (Φ PS II) at a given ambient light intensity, when neglecting interfering effects, e.g. photorespiration (Maxwell and Johnson 2000; Ralph et al. 2005; Warner 2005).
Calcification is increased by elevated heterotrophy (Houlbrèque and Ferrier-Pagès 2008) due to one or more of the following processes: (1) increased biomass, epithelial transport molecules and energy availability to transport inorganic carbon to the calcification site (Houlbrèque and Ferrier-Pagès 2008), (2) increased respiration rates providing internal inorganic carbon (Furla et al. 2000; Houlbrèque et al. 2003), (3) increased availability of limiting amino acids necessary for the organic matrix involved in the calcification process (Allemand et al. 1998) and (4) increased photosynthesis. The influence of photosynthesis on calcification was recognized early (Goreau and Goreau 1959), and the theory of light enhanced calcification is widely accepted; the underlying mechanism, however, is still strongly debated (Gattuso et al. 1999; Furla et al. 2000; Allemand et al. 2004; Colombo-Pallotta et al. 2010). Calcification is not only dependent on the metabolic behavior of the holobiont, but also directly affected by environmental factors. In particular, inorganic nutrients were found to have a negative effect on calcium carbonate precipitation (Marubini and Davies 1996; Ferrier-Pagès et al. 2000; Fabricius 2005).
The effects of land run-off on corals have been extensively studied in laboratory experiments (reviewed in Fabricius 2005) to determine the roles of individual stressors on the metabolism of shallow water corals. Very few studies have been done on the interacting effects of stressors, and field data are available mainly from well-studied U.S. and Australian reefs. The most biodiverse coral reefs in South-East Asia which are subject to the highest risks of land-based sources of pollution have so far been neglected. Many populated regions along the coastline of South-East Asia are polluted by land run-off of fertilizers and untreated waste-waters (Edinger et al. 1998). Although the ecosystem level responses – losses in diversity, structural complexity, shifts in trophic structure – have been documented (Edinger et al. 2000), the nutritional status, trophic plasticity and acclimatization potential of the frame-building corals are still largely unknown. While most species appear to be sensitive, some corals occupying a wider physiological niche are considered to be more resistant to eutrophicaton and sedimentation. This resistance usually coincides with a higher trophic plasticity, which for example, can be found in *Galaxea retiformis* and *Turbinaria mesenterina* in contrast to *Porites cylindrica* and *Acropora valida* (Anthony and Fabricius 2000; Anthony and Connolly 2004; Houlbrèque and Ferrier-Pagès 2008).
In situ measurements are needed to identify the main stressors, quantify their effects on the metabolic response of corals, and assess their plasticity and tolerance to anthropogenic changes in their coastal environment. In the present study, the metabolic response of the common scleractinian coral *Stylophora subseriata* to an eutrophication gradient was investigated *in situ* in Spermonde Archipelago, Indonesia, with regard to changes in (1) zooxanthellae characteristics, including their photosystem, (2) the coral tissue, and (3) the metabolic rates, including photosynthesis, respiration and calcification.

Material and Methods

Study site

Our study was performed in Spermonde Archipelago, an island group in Makassar Strait in southwest Sulawesi, Indonesia. The archipelago consists of >100 small islands situated on a 40 km wide carbonate shelf platform in front of the city Makassar, populated with 1.5 M people. The islands feature well developed highly diverse fringing coral reefs on their western sides and sandy eastern sides. The reefs usually consist of an extended reef flat and a reef slope reaching down 10-15 m near-shore, and up to 40 m off-shore (Moll 1983). The near-shore areas are affected by effluents from the Makassar harbor and the fluvial discharge by the river Jene Berang to the south and several small rivers to the north of Makassar. These rivers introduce terrigenious sediments, waste water and aquaculture outflows to the nearshore reefs (Renema and Troelstra 2001). A clear demise in coral diversity and cover from low impacted mid-shelf reefs to highly polluted near-shore reefs was demonstrated by Edinger et al. (1998). A decrease in live coral cover and *Acropora* cover from 54 to 18 % and 24 to 3.5 %, respectively, and an increase in algae and other sessile benthic invertebrates from 1.3 to 13 % and 7 to 9 %, respectively, was reported (Edinger et al. 1998).

Six islands, ranging between 1.2 and 17 km distance from shore and varying in intensity of eutrophication and turbidity, were selected as study sites (Fig. 1): Kayangan (KAY), Lae Lae (LL), Samalona (SAM), Lankadea (LAN), Bonebatang (BBA) and Bonetambung (BTA). An eutrophication gradient decreasing from near-shore to outer-shelf reefs was previously described by Edinger et al (1998) and Renema and Toelstra (2001). The study sites can be characterized as (1) near-shore reefs (KAY, LL) impacted by sewage, sedimentation and harbor activities, and with silt-like high nutrient sediment, a visibility between 0.5 and 5 m, chl *a* concentrations between 1.5 and 2.9 µg l^{-1} and suspended particulate matter (SPM) of about 20 mg l^{-1}; (2) mid-shelf reefs (SAM, BBA), impacted slightly by pollution from the city in the wet season (impacts only in SAM) with a visibility between 10-18 m (< 10 m in wet season), chl *a* concentration between 0.5 – 0.8 µg l^{-1} and SPM at around 8.2 mg l^{-1}; (3) outer shelf reef (BTA) with no impacts from the city, visibility ranges from 10-30 m (7.5-20 m in wet season) and chl *a* concentration is about 1.0 mg l^{-1}. Although LAN has a similar distance

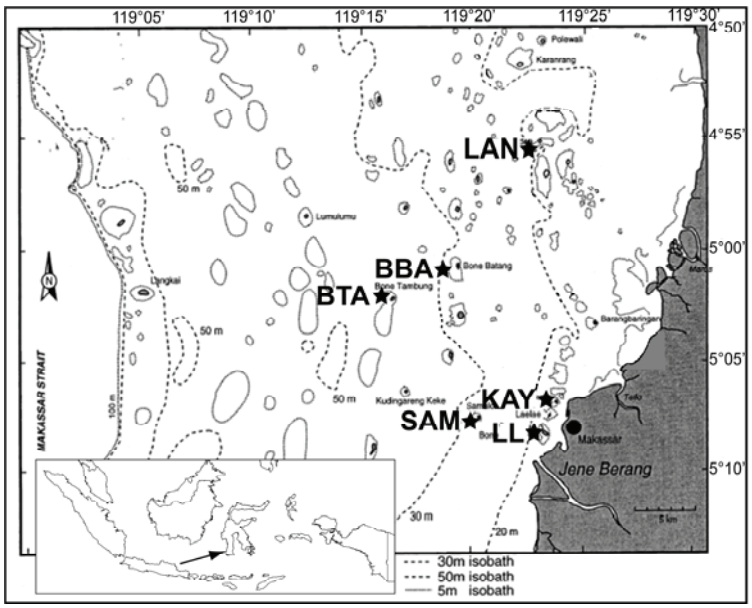

Fig. 1: Map of the Spermonde Archipelago, SW Sulawesi. Study sites: Kayangan (KAY), Lae Lae (LL), Samalona (SAM), Lankadea (LAN), Bonebatang (BBA), Bonetambung (BTA). Map adapted from Renema & Troelstra (2001).

to shore as BBA, it has been categorized as northern near-shore due to a low shelf depth. However, it features a visibility and chl *a* concentrations similar to mid-shelf reefs. Sea surface temperature varies little around 28.5 °C in all sites throughout the year, and salinity is about 33 ‰, however it can be lower in the near-shore reefs during the wet season.

Environmental parameters

Environmental parameters were measured during the experiment, representing the conditions at the end of the dry season at the study sites. Water samples were taken with a 5 l Niskin bottle at 3 m depth. Triplicate samples for chl *a* were filtered on GF/F filters. Pre-combusted and pre-weighed GF/F filters were used for total particulate carbon (C_{tot}) and nitrogen (N_{tot}) and for particulate organic carbon (POC) samples (each n=3). C_{tot}, N_{tot} and POC concentrations were measured with an Elemental Analyzer (NA2100 Protein, calibrated with CHNS standard [LECO]) and expressed in µg l^{-1}. Chl *a* was used as a more reliable measure of eutrophication in oligotrophic waters (Bell 1992, Jameson and Kelty 2004; Fabricius et al. 2005) than inorganic nutrients which are incorporated immediately by a nutrient-starved phytoplankton community (Furnas et al. 2005). Chl *a* was extracted from the filter with 90% acetone following the procedure described below for the tissue chl *a*.

Light intensity (PAR) was measured during the incubation period with an underwater light meter (LiCor Li-192SA, Lincoln, USA) above the ocean surface (PAR_{air}), just below the surface and every 1 m down to 6 m. The light attenuation coefficient (K_d) was calculated from the light profile as a measure of turbidity according to the equation $K_d = (\ln PAR_1 - \ln PAR_2) / (depth_2 - depth_1)$, with PAR_1 as the light intensity in 1 m depth, PAR_2 in 6 m depth, and $depths_{1,2}$ (Dennison et al. 1993). Note that K_d reflects the ratio in light intensities between surface and depth, and is hence independent of insolation, which varied considerably between days, and hence, sites, due to differences in cloudiness.

Coral collection and preparation

For the incubation experiments, 15 fragments from different *S. subseriata* colonies were collected from each site along the reef slope from a depth of 3 m. The 5 to 8 cm high fragments were carefully removed from the middle part of the colonies with a hammer and chisel and taken on board in a box filled with seawater. They were fixed to a plastic screw with underwater epoxy, exposing the fragments to air less than 3 min. The screws with the fragments were fixed to a basket, which was returned to 3 m depth. Fragments were allowed to recover for 2 to 3 weeks prior to the experiments. All of the fragments survived, showing re-sheeting of tissue across the exposed skeleton within 2 weeks.

Experimental design

In situ incubations were conducted at all sites within 3 weeks at the end of the dry season (September-October 2008). Sixteen (8 light and 8 dark) cylindrical acrylic chambers (1.8 l) were randomly distributed onto 4 plastic frames suspended at 3 m depth, 1 m above the bottom (Fig. 2). Chambers were filled with the surrounding sea water. Five of the light and dark chambers, respectively, were fitted with one coral fragment (screw cleaned from fouling organisms). The remaining 3 light and dark chambers served as coral-free controls. Glass marbles introduced into the chambers ensured mixing of the incubation water as ascertained by dye experiments carried out prior to the experiments, due to inertial motion of the marbles on the chamber bottom in the swaying motion of the suspended racks. Corals were fixed out of reach of chamber walls or marbles. The incubations started at 1300 hrs local time and

lasted between 1 and 1.5 h. One experiment was carried out per site and day resulting in 5 repeated measurements per site, with 5 (3) replicates for light/dark (control) each.
Initial water samples were taken with sealable beakers and syringes (both 50 ml) at the time of chamber sealing from the surrounding water. Final water samples were taken with syringes directly from the chamber after opening on board. Dissolved oxygen (precision 3 µmol O_2 l^{-1}) was measured with an oxygen sensor (IntelliCal LDO™ Sensor HACH Lange GmbH, Germany) in the beakers (n=3) and post incubation in each chamber immediately after opening. The samples in the syringes (initial: n=5, final: n=2 per chamber) were filtered through Whatman GF/F glass fiber filters, pore size 0.7 µm, and stored in airtight tubes in a cooler until measurement of Total Alkalinity (TA) after returning from the field.

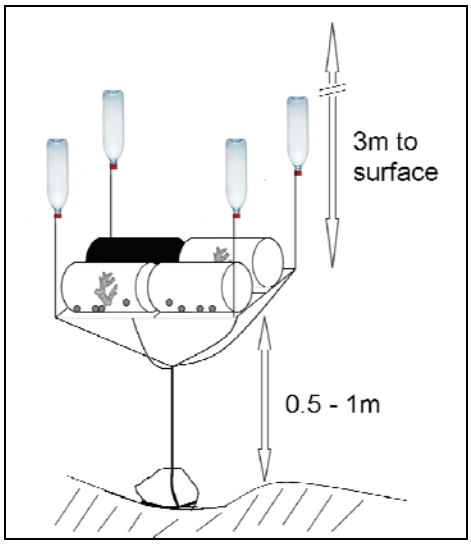

Fig. 2: Schematic drawing of the *in situ* incubation setup for 1 out of 4 racks with 4 chambers randomly distributed on the rack. Respiration chamber in black, photosynthesis chambers transparent, while the empty chamber is a control chamber. The rack is floating and can move with the waves and/or current. Grey marbles inside the chambers for mixing.

Coral metabolism
Net photosynthesis (P_n) and dark respiration (R) was calculated from the difference in dissolved oxygen values before and after the incubation in light and dark chambers, respectively. Gross photosynthesis (P_g) was calculated from P_n and R, assuming that light and dark R are equal. The calcification rate was determined in the light (G_L) and in the dark (G_D) using the alkalinity anomaly method as described by Schneider and Erez (2006). Total alkalinity (TA) of the initial and final water samples was analyzed via potentiometric titration with an automated titrator (Titrino, Metrohm AG, Switzerland) using 50 ml of sample and 0.01 M HCl (0.1 M Titrisol, Merck, Germany) with a precision of ± 4%. TA was calculated using the Gran approximation by determining the second endpoint of the titration curve (Grasshoff et al. 1983) and the difference in TA of the initial and final sample was used to calculate G after the following equation:

$$G\ [\mu mol\ CaCO_3\ cm^{-2}\ h^{-1}] = \frac{\Delta\ TA/2 \times (V_{chamber} - V_{coral}\ [l]) \times water\ density\ [kg\ l^{-1}]}{time\ of\ incubation\ [h] \times surface\ area_{coral}\ [cm^{-2}]}$$

TA is given in µeqv kg^{-1}, which corresponds to 1 µmol and is divided by two, since Ca^{2+} is divalent meaning that a change in TA of 2 µeqv corresponds to 1 µmol $CaCO_3$.
Photophysiological measurements were conducted on the coral fragments with a pulse amplitude modulation (PAM) fluorometer to assess the efficiency of the photosystem II

(Diving-PAM, Walz, Germany) (Maxwell and Johnson 2000; Ralph et al. 2005; Borell and Bischof 2008). Maximum quantum yield (F_v/F_m) was measured after incubation from all fragments of the dark chamber (dark adapted) onboard the boat. Fragments were transported to the laboratory and placed in an aquarium with fresh seawater from their site of origin for >3 h to recover from transportation. Each coral was dark adapted for 15 min followed by a gradual light adaptation over 3 min until 985 µmol photons m^{-2} s^{-1} PAR, which roughly corresponds to the measured light intensity in 3m depth on a bright sunny day. The effective quantum yield (Φ PS II = $[F'_m - F_t]/F'_m$) was measured at this light intensity (Maxwell and Johnson 2000; Ralph et al. 2005).

Coral nutritional status

Coral tissue was removed from the skeleton with an air gun and ~30 ml filtered seawater. The volume of the tissue slurry was measured and sub-samples stored at -20°C until further analyses. Zooxanthellae were counted with a haemocytometer (Fuchs-Rosenthal haemacytometer) under the light microscope and the zooxanthellae density determined. Chl *a* was measured fluorometrically (Boto and Bunt 1978) by adding 4.5 ml 100% acetone to 0.5 ml of the slurry (final concentration 90%), extracting over night at 4°C, centrifuging the slurry for 5 min at 4000 rpm and measuring the dissolved chl *a* with a fluorometer (10-AU Fluorometer, Turner Design, CA) in a glass cuvette. The fluorometer was calibrated with chl *a* standard (Fluka, Sigma-Aldrich, Switzerland). For the gravimetric determination of tissue biomass (dry weight [DW]), 3 ml of tissue slurry was filtered on a pre-weighted GF/F filter, the salt removed by shortly rinsing with distilled water and the filter dried at 40°C for at least 24 h. The protein content was determined photometrically (Coomassie Blue, λ 595 nm) after Bradford with bovine serum albumin as a standard (BioRad Protein Assay kit II, Munich, Germany). Protein was measured separately in the tissue ($prot_T$) and in zooxanthellae ($prot_Z$) after the cells were "opened" by ultrasonic maceration to release intracellular protein.

The surface area of the coral was determined gravimetrically using the wax coating technique (Glynn and D'Croz 1990; Naumann et al. 2009). Candle wax was melted in a beaker and kept at a constant temperature of 65°C in a water bath. Air-dried fragments were dipped into the hot wax for 3 s, left to dry for 3 min and weighed. The procedure was repeated, yielding a weight difference proportional to the area of the coral fragment. Absolute values were obtained by calibration with objects of known areas (wooden cubes of various sizes) subjected to the same coating procedure ($r^2 = 0.973$).

Oxygen evolution (P_n, P_g) and consumption (R), calcium carbonate precipitation (G), as well as the tissue parameters (zooxanthellae, chl *a*, DW, $prot_T$) were standardized to the coral surface area. Consequently P_n, P_g, R and G were expressed in µmol O_2 cm^{-2} h^{-1} and µmol $CaCO_3$ cm^{-2} h^{-1} respectively, calculated after Schneider and Erez (2006).

Data analyses

Forward stepwise multiple regression analyses were conducted in order to determine the most explaining parameters (independent) for the metabolic variables P_g, R, G_L and G_D (dependent). Analysis of residuals of the explaining variables was performed in order to validate linearity. For the sake of clarity, all variables defined by negative values (oxygen decrease: respiration (R) and light extinction coefficient ($-K_d$)) were (-1)-transformed to absolute values to allow for comparisons between overall positive variables. The software STATISTICA 9 was used for the analyses. All values are represented as mean ± standard error.

Results

Environmental data

A strong spatial gradient was evident in the environmental data, with notable increases in chl *a*, POC and turbidity towards the coast and a concomitant decrease in the C/N ratio of particulate organic matter (POM) (Fig. 3). All parameters were significantly correlated to each other with r>0.8 (Pearson). Chl *a* increased almost 3-fold between mid-shelf (BTA: 0.28 ± 0.01) and near-shore (0.75 ± 0.03 µg l^{-1}) and was chosen as a parameter for eutrophication in the remainder of the manuscript.

A spatial gradient in light intensities was masked by up to 5-fold temporal variations in PAR between days due to variations in cloudiness during the study (cf. Table 1).

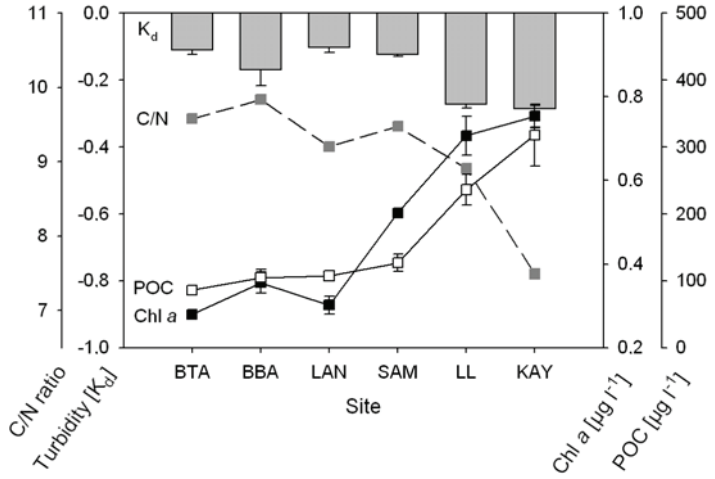

Fig. 3: Environmental parameters: C/N ratio of total particulate matter (POM), chl *a* and POC concentration (n=3); turbidity (Kd) (n=2-8). The sites follow the distance from shore from furthest (BTA) to closest (KAY) distance. Mean ± SE.

Table 1: Weather condition, light availability [µmol photons m^{-2} s^{-1}] in the air (PAR_{air}) and in 3 m depth (PAR_{-3m}) and turbidity (K_d) during the time of incubation. Sunny* indicates a very clear day. Mean ± SE.

	Site					
	BTA	LAN	BBA	SAM	LL	KAY
Weather	sunny	cloudy	sunny	slightly cloudy	sunny	sunny*
PAR_{air}	1650 ± 47	438 ± 76	1611 ± 21	967 ± 51	1684 ± 36	2158 ± 12
PAR_{-3m}	979 ± 22	208 ± 5	546 ± 31	394 ± 10	622 ± 19	935 ± 6
K_d	-0.110 ± 0.013	-0.102 ± 0.015	-0.170 ± 0.047	-0.124 ± 0.006	-0.272 ± 0.021	-0.285 ± 0.058

Photosynthesis and zooxanthellae characteristics

A 2.5- to 3-fold increase of photosynthesis (P_g and P_n) with increasing eutrophication was evident, as indicated by the oxygen production vs. water chl *a* (Fig. 4). The areal zooxanthellae densities and tissue chl *a* concentrations followed this pattern (Fig. 5a), however, for the oligotrophic waters (lowest water chl *a* concentration; BTA, LAN and BBA) the initial increase in tissue chl *a* was less dramatic than the increase in zooxanthellae. In the mesotrophic part of water chl *a* gradient (SAM and LL) the zooxanthellae densities remained conspicuously constant while tissue chl *a* increased compared to oligotrophic BBA. Finally, in the most near-shore reef (KAY), both zooxanthellae density and tissue chl *a* concentration were highest (Fig. 5a). As a consequence, the cell-specific chl *a* content decreased in the mid-shelf reefs, while it stayed on a rather high level in the near-shore reefs (Fig. 5b). Based on the

different response to eutrophication in corals further away and close to the shore, the reefs were henceforth classified as mid-shelf (BTA, LAN, BBA) and near-shore reefs (SAM, LL, KAY) for the rest of the manuscript. The cell-specific protein content followed the pattern of chl *a* in the mid-shelf reefs, but remained low in the near-shore reefs (Fig. 5b). Due to this non-linear response, the overall correlation between cell-specific protein and chl *a* was comparatively low (Pearson r=0.431, $p<0.05$).
The photophysiological measurements included the maximum quantum yield F_v/F_m (dark adapted) and the effective quantum yield Φ PS II at 985 µmol photons m^{-2} s^{-1}. While F_v/F_m did not show any relationship to the environmental gradient, Φ PS II showed a weak positive relationship (Fig. 5c). Consequently, Φ PS II is correlated to areal chl a (Pearson, r=0.416, $p<0.05$), however, it is not related to zooxanthellar chl *a* (Pearson, r=0.029, $p>0.05$) and slightly negatively correlated to zooxanthellar protein (Pearson, r=-0. 278, $p<0.05$).

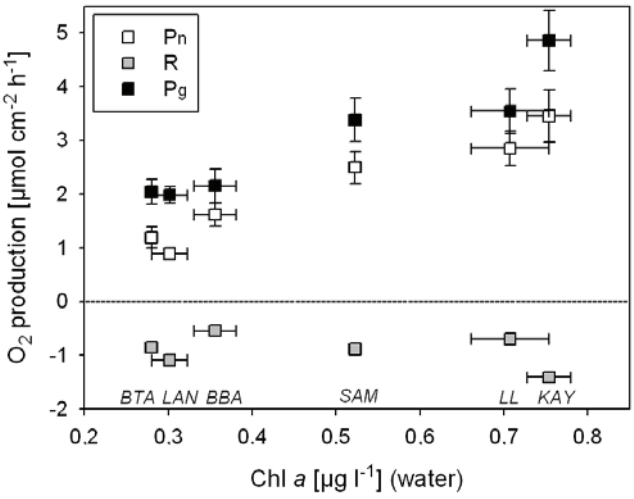

Fig. 4: Net photosynthesis (P_n), respiration (R) and gross photosynthesis (P_g) along the eutrophication gradient (chl *a* (water)). N=5, mean ± SE.

To determine the effect of different light intensities on P_g, which occurred on the different sites and days, P_g was plotted against PAR prevalent in 3 m depth (PAR_{-3m}) (Fig. 6). This revealed that the light intensity was hardly reflected in the oxygen production, since P_g changes only little over the different light intensities within the categories mid-shelf and near-shore. This is evident for P_g cm^{-2} as well as for P_g (µg chl *a*)$^{-1}$ (Fig. 6). In order to determine the effect of chl *a* concentration on photosynthesis, P_g was standardized to chl *a* (Fig. 6b). Here, it becomes evident, that the chl *a* concentration has a large impact on P_g visible in an inversion of the oxygen production rate of mid-shelf and near-shore corals, if standardized to chl *a* (Fig. 6). This was further supported by multiple regression analyses, where areal chl *a* explained 66 % of the variation of P_g, followed by Φ PS II with 8 %, while light intensity explained only 2 % of the variation (Table 2). The zooxanthellae density was not included into regression analyses of P_g due to a high correlation with areal chl *a*.
To constrain the range of zooxanthellae characteristics and their relation to P_g, the two most dissimilar reefs in terms of environmental conditions are directly compared in Table 3.

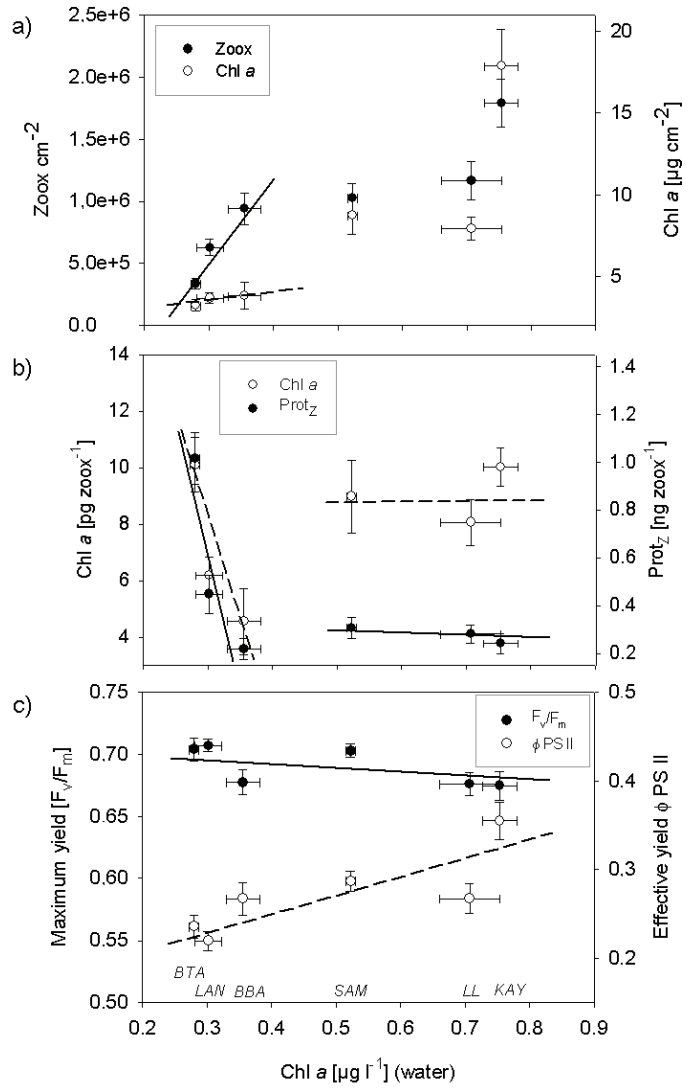

Fig. 5: Zooxanthellae characteristics along the eutrophication gradient (chl *a* (water)). **a**) Zooxanthellae (zoox) density and tissue chl *a* concentration, black (zoox) and dashed (chl *a*) line indicate the differential pattern of increase in the mid-shelf reefs. **b**) Cell-specific chl *a* and protein ($Prot_Z$) content, black (chl *a*) and dashed ($Prot_Z$) line indicate the differential pattern in mid-shelf and near-shore reefs. **c**) Maximum quantum yield [F_v/F_m] and effective quantum yield Φ PS II at 985 µmol photons m^{-2} s^{-1}, black (Fv/Fm) and dashed (Φ PS II) line indicate trends along the gradient. Each point is represented by n=10, except Fv/Fm with n=5. Mean ± SE.

Table 2: Results of multiple regression analysis with the dependent variable gross photosynthesis (P_g) and the independent (ind.) variables of areal and cell-specific chl *a*, effective quantum yield at 985 µmol photons m^{-2} s^{-1} (Φ PS II), light intensity [µmol photons m^{-2} s^{-1}] in 3 m depth (PAR_{-3m}), maximum quantum yield (F_v/F_m) and cell-specific protein concentration ($Prot_Z$). $p < 0.05$ (bold).

Ind. variable	Multiple R	Multiple R^2	R^2 change	F - value	p - value	Variables incl.
Chl *a* [µg cm^{-2}]	0.813	0.662	**0.662**	115.407	**0.000**	1
Φ PS II	0.862	0.743	**0.081**	18.307	**0.000**	2
PAR_{-3m}	0.873	0.762	**0.019**	4.498	**0.038**	3
F_v/F_m	0.882	0.778	**0.017**	4.238	**0.044**	4
$Prot_Z$ [ng $zoox^{-1}$]	0.887	0.786	0.008	2.069	0.156	5
Chl *a* [pg $zoox^{-1}$]	0.899	0.808	**0.021**	5.951	**0.018**	6

Table 3: Comparing the oligotrophic and eutrophic conditions (chl *a* water), zooxanthellae (zoox) characteristics including areal zoox densitiy and chl *a*, as well as the effective quantum yield at 985 PAR µmol photons m^{-2} s^{-1} (Φ PS II) and metabolic output (bold) in terms of areal gross photosynthesis (P_g) and P_g per unit tissue chl *a* at the two most dissimilar study sites Bonetambung (BTA) and Kayangan (KAY). Mean ± SE.

	BTA	KAY	~ ratio of increase
Chl *a* [µg l^{-1}] (water)	0.28 ± 0.01	0.75 ± 0.03	x 3
Chl *a* [µg cm^{-2}]	3.23 ± 0.36	17.87 ± 2.27	x 5.5
Zoox cm^{-2}	3.38 ± 0.40 x 10^5	17.92 ± 1.93 x 10^5	x 5.5
Φ PS II	0.236 ± 0.012	0.355 ± 0.021	x 1.5
P_g [µmol O_2 cm^{-2} h^{-1}]	2.05 ± 0.23	4.86 ± 0.56	**x 2.5**
P_g / Chl *a* [µmol O_2 μg^{-1} h^{-1}]	0.73 ± 0.16	0.27 ± 0.05	**x 1/3**

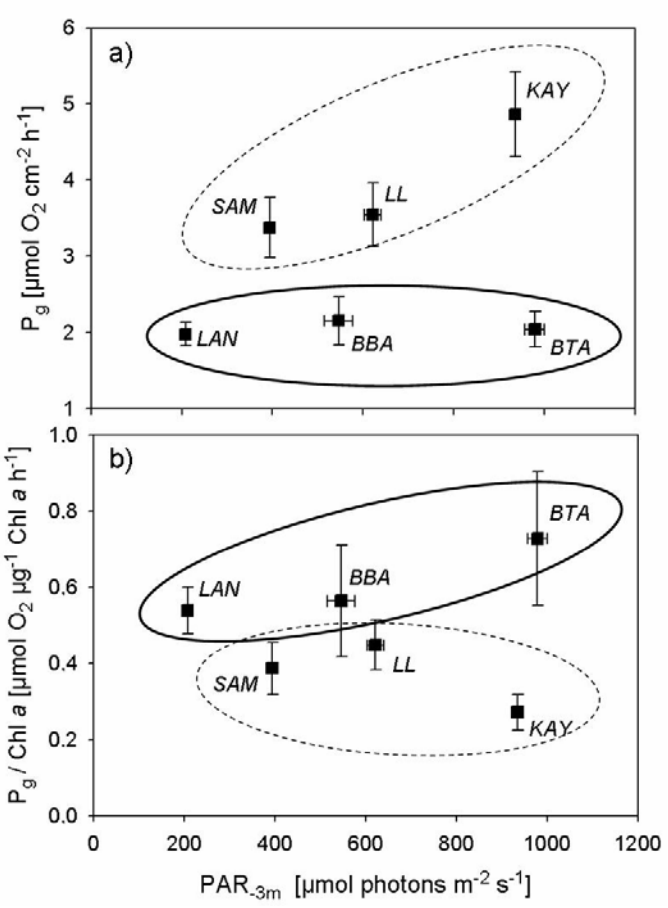

Fig. 6: a) Gross photosynthesis (P_g) and b) P_g per unit chl *a* vs. light intensity in 3m depth during the time of incubation (PAR_{-3m}). Mid-shelf reefs (black circle) and near-shore reefs (dashed circle). N=5, mean ± SE.

Respiration and tissue nutritional status

In contrast to photosynthesis, R did not show a clear trend along the eutrophication gradient, although highest R occurred at the most eutrophied reef KAY (Fig. 4). Nevertheless, a 3-fold increase in tissue protein (LAN: 0.16 ± 0.02 to KAY: 0.48 ± 0.04 mg cm^{-2}) and almost a doubling in biomass (LAN: 4.85 ± 0.31 to KAY: 8.80 ± 0.80 mg DW cm^{-2}) (Fig. 7) was found along the gradient. In consequence, only a weak relationship was found between R and tissue protein, and no relationship was found between R and tissue biomass and POC, the latter

serving as a potential food source (Table 4). Zooxanthellae which contribute to respiration did not show an effect on R either (Table 4).

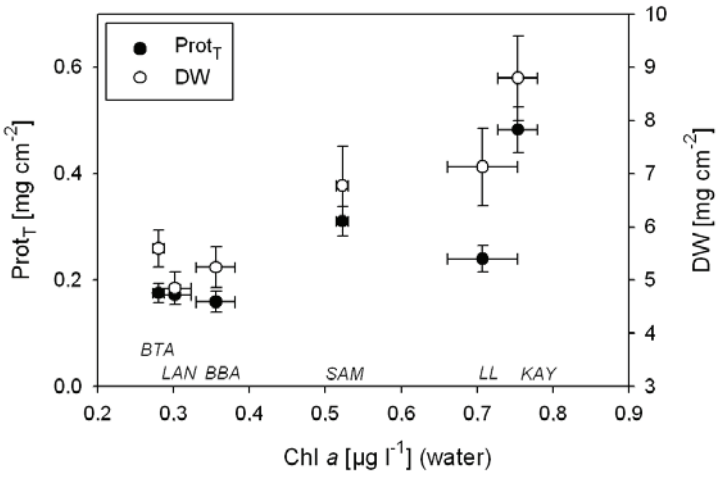

Fig. 7: Coral tissue parameter along the eutrophication gradient (chl *a* (water)). Tissue protein ($Prot_T$) and dry weight of biomass (DW). N=10, mean ± SE.

Table 4: Results of multiple regression analysis with the dependent variable respiration (R) and the independent variables: protein concentration ($Prot_T$) and biomass dry weight (DW) of the host tissue, zooxanthellae density (zoox) and particulate organic matter concentration in the water (POC). $p < 0.05$ (bold).

Ind. variable	Multiple R	Multiple R^2	R^2 change	F - value	p - value	Variables incl.
$Prot_T$ [mg cm^{-2}]	0.370	0.137	**0.137**	9.363	**0.003**	1
Zoox cm^{-2}	0.426	0.182	0.045	3.174	0.080	2
POC [µg l^{-1}]	0.435	0.190	0.008	0.556	0.460	3
DW [mg cm^{-2}]	0.440	0.194	0.004	0.290	0.592	4

Calcification

G_L showed a low but discontinuous increase towards the coast between 1.05 ± 0.10 (BTA) and 1.73 ± 0.13 (KAY) µmol $CaCO_3$ cm^{-2} h^{-1}, resulting in a weak correlation between G_L and P_g (Pearson r=0.386, p<0.05) (Fig. 8).

Multiple regression analyses showed that P_g explained only 18 % of the variation in G_L, with light intensity explaining an additional 6 % (Table 5). Tissue biomass and protein content, as well as the protein content of the zooxanthellae did not show an influence on G_L (Table 5). G_D ranging from 0.60 ± 0.14 to 1.41 ± 0.22 µmol $CaCO_3$ cm^{-2} h^{-1} did not reveal any relationship to R, nor could it be explained by the tissue biomass, protein content or POC concentration (Table 6). G_L and G_D correlated weakly with each other (Pearson r=0.509, p<0.05).

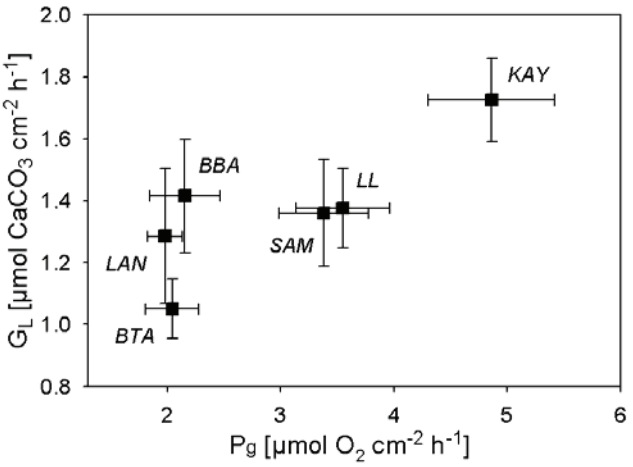

Fig. 8: Light calcification (G_L) vs. gross photosynthesis (P_g). N=5, mean ± SE.

Table 5: Results of multiple regression analysis with the dependent variable light calcification (G_L) and the independent variables: gross photosynthesis (P_g), light intensity in 3 m depth [PAR µmol photons m^{-2} s^{-1}] (PAR_{-3m}), protein concentration ($Prot_T$) and biomass dry weight (DW) of the host tissue and protein concentration of the zooxanthellae ($Prot_Z$). $p < 0.05$ (bold).

Ind. variable	Multiple R	Multiple R^2	R^2 change	F - value	p - value	Variables incl.
P_g [µmol O_2 cm^{-2} h^{-1}]	0.418	0.175	**0.175**	12.492	**0.001**	1
PAR_{-3m}	0.482	0.233	**0.058**	4.370	**0.041**	2
DW [mg cm^{-2}]	0.494	0.244	0.011	0.863	0.357	3
$Prot_Z$ [mg cm^{-2}]	0.500	0.250	0.006	0.416	0.522	4
$Prot_T$ [mg cm^{-2}]	0.507	0.258	0.008	0.587	0.447	5

Table 6: Results of multiple regression analysis with the dependent variable dark calcification (G_D) and the independent variables: protein concentration ($Prot_T$) and biomass dry weight (DW) of the host tissue, respiration rate (R) and particulate organic matter concentration in the water (POC). $p < 0.05$ (bold).

Ind. variable	Multiple R	Multiple R^2	R^2 change	F - value	p - value	Variables incl.
$Prot_T$ [mg cm^{-2}]	0.184	0.340	0.034	1.937	0.170	1
DW [mg cm^{-2}]	0.226	0.051	0.017	0.969	0.329	2
R [µmol O_2 cm^{-2} h^{-1}]	0.237	0.056	0.005	0.290	0.592	3
POC [µg l^{-1}]	0.238	0.057	0.000	0.021	0.885	4

Discussion

To the best of our knowledge this is the first study of coral metabolism along a pollution gradient in the central Indo-Pacific region, the global center of marine biodiversity (Renema and Hoeksema 2007).

Over the last years, there has been intense debate about the negative or putatively also positive effects of nutrification on corals (Szmant 2002; Loya and Kramarsky-Winter 2003; Rinkevich et al. 2003). While most authors agree that coastal nutrification and sedimentation

are deleterious on the ecosystem level (reviewed in Fabricius 2005) because they shift the ecological balance between corals and space-competing macroalgae (Fabricius et al. 2005; Costa Jr et al. 2008) when herbivores are rare or absent (McCook 1999; Smith et al. 2001; Jompa and McCook 2002), there are examples in the literature suggesting that increased nutrient levels may, paradoxically, have positive effects on the metabolic performance of some corals (Bongiorni et al. 2003). Here, near-shore individuals of the common *S. subseriata* were found to outperform mid-shelf specimens in terms of nutritional status, P_g and G, and withstand adverse conditions of increased suspended sediment loads with no signs of respiratory and photophysiological stress. The results of this study support the view that the most wide-spread corals in a coastal environment spanning a wide nutrient gradient, are of the opportunistic "weedy" type, while the vast majority of the >580 species known to occur in the coral triangle (Veron 2000) may be less able to adapt to anthropogenic changes in the quality of coastal waters.

Environmental gradient

Although the observed increases in chl *a*, POC, nitrogen and turbidity in near-shore waters are a clear hallmark of eutrophication, the gradient is less pronounced than in previous studies, where chl *a* concentrations varied six-fold between mid-shelf and coastal waters (Edinger et al. 1998). The difference in our findings might reflect seasonal differences between the end of the dry season when land run-off is low and nutrients are largely depleted, and the transition period from wet to dry (Edinger et al. 1998). It is not known to what extent larger- (interannual) or shorter-scale (day-to-day) variations may have contributed to the observed differences in gradient strength. In spite of these uncertainties, the recurrent appearance of significant cross-shore gradients in all these studies suggests that pollution is chronic in the area (Edinger et al. 1998, Renema andToelstra 2001).

Photosynthesis and photoacclimation

The increase in P_g between the mid-shelf and near-shore reefs was almost linear with increasing eutrophication (water-chl *a*) (Fig. 4), contrasting the non-linear changes in the areal tissue chl *a* and zooxanthellae concentrations (Fig. 5a). These findings suggest the following mechanistic model linking coral nutritional status to P_g: (1) riverine nutrients were incorporated by the planktonic food web (hence the cross-shore water-chl *a* gradient), (2) incorporation of this plankton by corals fuelled growth of nutrient-limited zooxanthellae (linear increase between BTA and BBA, Fig. 5a), and (3) excess nutrients fuelled zoox-chl *a* synthesis (zoox-chl *a* increase between BBA and SAM, Fig. 5a) (Dubinsky et al. 1990). (4) Further increase of external nutrients near-shore (organic and inorganic) stimulated the concomitant increase of both zooxanthellae and chl *a* (LL and KAY, Fig. 5a) (Dubinsky et al. 1990; Ferrier-Pagès et al. 2003; Houlbrèque et al. 2003). Initially, zooxanthellar protein, as an important component of the photosynthetic apparatus (Dubinsky et al. 1990; Zonneveld 1997), followed the pattern of zooxanthellar chl *a* due to nutrient limitation (between BTA and BBA, Fig. 5b). However, in the near-shore reefs the nutrient and energy investment into cell-specific protein was comparatively low compared to chl *a* in near-shore reefs (SAM to KAY, Fig. 5b). One explanation could be that the energy costs for chl *a* is less than for proteins and a further build-up of proteins to optimize the photosystem was not necessary.
The scenario above would imply a decrease in the effective quantum yield with eutrophication due to the decrease in zooxanthellar chl *a* in the mid-shelf reefs and low zooxanthellar protein content in the near-shore reefs. However, the opposite was found (Fig. 5c). This suggests that

the optimum conditions for *S. subseriata* corresponded to moderate levels of nutrients and turbidity, such as in BBA - not in the most oligotrophic mid-shelf reefs (e.g. in BTA). In BTA very high radiation intensities might cause extremely low zooxanthellae densities and low photosynthetic efficiencies in stress response to high UV (cf. Gleason and Wellington 1993). In the near-shore reefs, particularly at KAY, *S. subseriata* revealed its high acclimatization potential to nutrient enrichment, which seemed to be even advantageous for the corals metabolic performance, including photosynthetic efficiency. Overall, these mechanisms led to an increase in P_g with eutrophication, although P_g increased on a much lower rate than the increase in areal chl *a* concentration and/or zooxanthellae density, which can be explained by self-shading effects of densely packed zooxanthellae near-shore.
The main driver of photoacclimation, expressed in an increase of zooxanthellae density and areal tissue chl *a,* was increased eutrophication rather than decreased light levels. Even though turbidity increased significantly closer to shore, there seems to be sufficient light in the rather shallow reef area of 3 m depth, reaching up to 1000 µmol quanta m^{-2} s^{-1} PAR on sunny days in the closest reef to shore (KAY). The highly variable light intensities prevalent at the different days of incubation in our study had a low impact on the P_g. This was supported by photosynthesis-irradiance curves (P-I curves) in previous studies with the congener *S. pistillata* featuring a similar distribution pattern as *S. subseriata*: Field experiment as well as laboratory experiments found values of saturation irradiance (I_k) at 80-270 µmol quanta m^{-2} s^{-1} PAR in light adapted corals (Porter et al. 1984, Ferrier-Pagès et al. 1998b), indicating that the light intensities measured in our study (PAR_{-3m}) were in the plateau region of maximum photosynthesis P_{max}. This is further supported by previous findings where *Stylophora* is found in a wide range of light intensities, and, therefore, seems to be less responsive to changes in light availability (Falkowski and Dubinsky 1981).
There was no evidence of a stress response of *S. subseriata,* in terms of decreased maximum quantum yield of zooxanthellae, to increased sedimentation or pollutants towards the coast (Philipp and Fabricius 2003).

Respiration, nutritional status and stress
Although it is known that R increases with feeding (Houlbrèque et al. 2003) and stress (Telesnicki and Goldberg 1995), R was not influenced by the increased food availability and higher sedimentation that increased in the eutrophication gradient. R varied between the sites, and only the corals in the most near-shore reef KAY showed a distinct increase in R. This suggests that heterotrophy and/or stress may have exceeded a threshold in the most enriched coastal waters, enhancing R to approximately 50% above background levels. However, an overall increase in heterotrophy at KAY and the other near-shore sites was supported by the nutritional status of the coral host, revealing an increase in biomass and protein levels towards the coast. This shows that the use of R as an indicator for feeding is limited, as previously demonstrated by Anthony and Fabricius (2000), where increased food supply under unchanged light conditions led to significant tissue growth without increasing R in the two investigated coral species *Goniastrea retiformis* and *Porites cylindrica*. A possible explanation could lie in the time of feeding, which is mostly during the night (Coles 1969; Muscatine and Porter 1977). Zooplankton availability is often elevated during the night (Yahel et al. 2005), and its accessibility was found to be related to the food ingestion in various coral species (Anthony 2006; Palardy et al. 2006). This would mean that increased R is only measurable in the night and not during the day, when this study took place. In terms of stress, it can be assumed that *S. subseriata* is well adapted to turbid conditions because its

respiratory response and the maximum quantum yield of zooxanthellae seem to be rather stable.

Calcification

Despite the common occurrence of a decrease of G with an increase in eutrophication and sedimentation (Fabricius 2005), G_L still slightly increased towards the coast and even peaked in the most near-shore reef KAY. This led to a weak correlation between G_L and P_g, indicating that some additional energy acquisition by increased photosynthesis is used for calcification. At the same time elevated nutrient input (including inorganic nutrients) in near-shore reefs which increase P_g most likely hamper G_L, explaining the overall low increase in G_L with respect to P_g. Reasons for decreased G_L under high nutrient levels are found in a decoupling of symbiont and host (Dubinsky et al. 1990; Ferrier-Pagès et al. 2000; Allemand et al. 2004; Fabricius 2005) or a direct inhibition of carbonate crystallization by inorganic nutrients (Simkiss 1964, Gattuso et al. 1999). A support of G (light and dark) by either R or elevated nutritional status of the coral host (Lough and Barnes 1992; Houlbrèque et al. 2003; Houlbrèque and Ferrier-Pagès 2008) was not evident in this study, except possibly at KAY, where highest R and highest G occurred together. This is in line with the findings of Anthony and Fabricius (2000) who found no changes in the G rate even though tissue biomass doubled in consequence of increased feeding.

Interaction between photosynthesis, respiration and calcification

In general, healthy corals under high light conditions provide more than 70 % of the corals' energy demand by photosynthesis (Muscatine et al. 1981; Edmunds and Davies 1989), and translocation of photosynthates to the host is even further increased with elevated photosynthesis (Muscatine 1990). The host respires a large portion of photosynthates and the acquired ATP is used i.a. for G (Al-Horani et al. 2003; Allemand et al. 2004) and mucus production (Brown and Bythell 2005), while the other portion provides compounds for the synthesis of cellular proteins and lipids (Muscatine and Cernichiari 1969; Dubinsky and Jokiel 1994), amino acids for the extracellular organic matrix involved in skeleton formation (Cuif et al. 1999; Puverel et al. 2005) and mucus (Crossland 1987). The latter can account for 20 – 45 % of the net photosynthate production (Brown and Bythell 2005).

The "clean" appearance of *S. subseriata* colonies in near-shore reefs suggests that the surplus of energy derived from P_g not used for G went into mucus production, a costly inversion necessary for survival in sediment-loaded coastal waters (Edmunds and Davies 1989; Riegl and Branch 1995; Telesnicki and Goldberg 1995). Although we did not measure mucus production in our study, we know that the congener *S. pistillata,* releases up to 6-fold more mucus than other common reef corals (Naumann et al. 2010). Although it has been found that an increase in inorganic nutrients (e.g. DIN derived from land run-off) reduces the mucus release in some corals due to a shift in energy allocation towards zooxanthellae propagation (Naumann et al. 2010, Tanaka et al. 2010), it is assumed that increased mucus release in response to increased sedimentation is paramount.

In addition to the energy and photosynthates supply, P_g also provides O_2, which allows an increased light R (Allemand et al. 2004). Light respiration (R_L) is difficult to measure in the field, but laboratory studies have shown a 6- to 11-fold higher R_L than R due to the internal recycling of O_2/CO_2 within the holobiont (Kühl et al. 1995; Al-Horani et al. 2003). In these studies, microsensors were used to measure the oxygen consumption within the first few seconds after turning off the light, corresponding to the brief period where photosynthesis was shut down but light respiration still in full swing. Undetected high levels of R_L could be an additional explanation for the low increase of P_g towards the coast compared to the much

stronger increase in zooxanthellae density and areal chl *a* concentration, as well as the optimization of the photophysiological performance.
In conclusion, this study demonstrates that there are corals that are able to tolerate, if not take advantage of eutrophication. Increased inorganic and organic nutrition enhanced autotrophy and, most likely, heterotrophy of *S. subseriata*. This is partly used for the calcium carbonate precipitation where it overcompensates the negative effect of inorganic nutrients on G. Another large portion of the surplus in energy and photosynthates is most likely used for mucus production involved in sediment removal. Symptoms of stress usually reflected in increased R and decreased photosynthetic efficiency were not evident.
Due to its high trophic plasticity and photoacclimative potential *S. subseriata* is a highly flexible species compared to other coral species in the area. For the vast majority of less tolerant coral species, however, human-induced pollution and degradation of coastal water quality has caused a dramatic loss in coral reef biodiversity and complexity in Spermonde Archipelago, the wider South-East Asia, and beyond (Edinger et al. 1998, Wilkinson 2008).

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Paper 4

Calcification, photosynthesis and nutritional status of the hermatypic coral *Porites lutea:* case studies from environmental extremes in Indonesia and Thailand

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Abstract

The acclimatization potential and metabolic performance of *Porites lutea* was investigated in case studies from Indonesia and Thailand in order to explore the energy acquisition and allocation strategies of this wide-ranging species in contrasting environmental conditions. Calcification, photosynthesis and respiration was determined along with the zooxanthellae density, chl *a* content, protein content and isotopic composition ($\delta^{13}C$ and $\delta^{15}N$) of the host and zooxanthellae tissues. A series of *in situ* incubation experiments was conducted in Spermonde Archipelago (Indonesia) subjected to a coastal pollution gradient, another one in the Andaman Sea (Thailand) subjected to oceanic internal waves. Two reefs were investigated in each region: in Spermonde Archipelago, an oligotrophic midshelf reef BBA vs. a eutrophic coastal reef LL (both 3 m); in the Andaman Sea, a shallow KR-S (7 m) vs. a deep KR-D (20 m) reef on the west face of Ko Racha. The most striking result was a 3-fold higher calcification in KR-S compared to all other sites, while photosynthesis was 2- to 3-fold higher in LL compared to all other sites. Isotopic, protein and biomass values indicate increased heterotrophy in Ko Racha corals, with intense internal cycling between zooxanthellae and host during photosynthesis. Light respiration may have significantly underestimated photosynthesis in KR-S. Thus produced high energy may explain the high calcification rates in Ko Racha. Spermonde corals, by contrast, are mainly photoautotrophic, where the energy surplus in LL is diverted from calcification to zooxanthellae propagation and mucus production in response to eutrophic, turbid and polluted near-shore environments. No signs of photoinhibition stress were found in the study. Although the findings suggest that *P. lutea* is adapted to a wide range of natural and anthropogenic variations in the environment, its resilience to global warming and ocean acidification remains an open issue.

Keywords: *Porites lutea*, resilience, eutrophication, large amplitude internal waves, energy acquisition, energy allocation

Introduction

In contrast to many other reef taxa, most shallow-water hermatypic corals are far-ranging species extending across vast biogeographic provinces (Veron 2000), with only few range-restricted or endemic species (Roberts et al. 2002). As a result, the same species may occur in strikingly different environments. Hughes et al. (2003) pointed out that 35 % of the coral species occurring in the Arabian Gulf also exist in Lord Howe Island off E Australia, where the mean summer maximum temperatures are 12 °C lower – suggesting a large intraspecific plasticity to a range of associated environmental factors. One of the zonally most wide-ranging species is *Porites lutea*, which is found from the Red Sea across the Indian and Pacific Ocean to the western shores of Mexico (Veron 2000). Beside its prevalence in typical oligotrophic coral environments, it is also abundant in highly sedimented, eutrophied and polluted near-shore reefs as well as in exposed, upwelling- impacted off-shore reefs. This dome-shaped coral can grow for centuries up to several meters in size and contribute significantly to the coral reef framework, particularly in shallow back-reef environments (Done 1982, Potts et al. 1985, Veron 2000). *P. lutea* is exceptionally abundant in the Andaman Sea off Thailand, where it outranks all other species in terms of areal cover (Phongsuwan et al. 2008, Schmidt 2010). It also appears to grow much faster here than elsewhere (Phongsuwan 1991, Scoffin et al. 1992, Crabbe & Smith 2005, Carricart-Ganivet et al. 2007, Cooper et al. 2008, Tanzil et al. 2009), where linear extension rates range between 1.7 and 2.4 cm y^{-1} (Tanzil et al. 2009) and up to 3.5 cm y^{-1} (Scoffin et al. 1992), compared to only 0.4-1.7 cm y^{-1} in Indonesia and in the Great Barrier Reef (Lough & Barnes 2000, Crabbe & Smith 2005). The mechanisms underlying the large spatio-temporal differences in *P. lutea* growth are so far unknown, and may be due to both, intrinsic and extrinsic factors.

Of the former, the corals' symbiotic microalgae (zooxanthellae) providing most of the energy for coral calcification (Muscatine et al. 1984, Dubinsky & Jokiel 1994) may hold the answer to this question, since corals were found to harbor a variety of *Symbiodinium* genotypes featuring different physiological characteristics adapted to the prevalent conditions (Buddemeier & Fautin 1993, Mass et al. 2007, Frade et al. 2008, LaJeunesse et al. 2010). However, a recent study of region-wide and mesoscale variation in zooxanthellae genotypes from different coral species revealed a particularly low genotypic diversity in *P. lutea* zooxanthellae, compared to other coral species (LaJeunesse et al. 2010). Ruling out genetic differences in the zooxanthellae, the causes for the observed spatio-temporal differences in *P. lutea* growth may speculatively be related to genetic differences in the coral host, or to a high physiological plasticity of the zooxanthellae and/or coral host in response to extrinsic factors.

Physiological plasticity in zooxanthellae is reflected, for example, in their capacity for photoacclimation, which allows the algae to maintain constant levels of photoautotrophy in spite of vertical (depth) and/or horizontal (turbidity) variations in light. Photoacclimation usually results in an optimization of the photosynthetic efficiency through an increase in chlorophyll *a* (chl *a*) and/or photosynthetically active proteins enabling the zooxanthellae to compensate reduced light availability (Dubinsky et al. 1990, Zonneveld 1997, Titlyanov et al. 2001, Mass et al. 2007, Hoogenboom et al. 2009). Since increased turbidity mostly goes in line with increased nutrient supply, this may foster zooxanthellae propagation and thereby increase photosynthesis (Dubinsky et al. 1990, Fabricius 2005).

Physiological plasticity may involve also the capacity of the coral host to vary energy acquisition through heterotrophy (Anthony & Connolly 2004, Grottoli et al. 2006). Although heterotrophy is considered to contribute only little to the corals energy needs, it may play a larger role in the corals' nutrient supply (Dubinsky & Jokiel 1994, Piniak et al. 2003,

Houlbrèque & Ferrier-Pagès 2008). However, when autotrophic input is low due to severe light limitation, or stress related zooxanthellae dysfunction or loss (i.e. bleaching), heterotrophy may become the prime source of energy for the holobiont. The ability to switch between auto- and heterotrophy is called trophic plasticity. It has been found to be a highly species-specific and important factor relating to coral resilience (Anthony & Fabricius 2000, Anthony & Connolly 2004, Grottoli et al. 2006, Houlbrèque & Ferrier-Pagès 2008). While heterotrophy was shown to vary inversely with autotrophy, other studies showed a positive relation with food supply, particularly in plankton-rich near-shore reefs (Anthony 2006, Palardy et al. 2006) or reefs subjected to currents (Roder et al. 2010). Increased heterotrophy fosters coral tissue, zooxanthellae functioning and skeleton growth (Houlbrèque et al. 2003, Houlbrèque & Ferrier-Pagès 2008).

Stressed corals may have to re-allocate energy from reproduction and growth to stress mitigation. For example, corals subjected to high sedimentation and pollutants, may divert significant parts of their metabolic energy into mucus production in order to avoid smothering or poisoning (Edmunds & Davies 1989, Riegl & Branch 1995). Likewise, corals subjected to thermal stress invest part of their energy into the transcription of heat shock proteins (Gates & Edmunds 1999).

In this study the nutritional status and metabolic performance of *P. lutea* was assessed in two contrasting tropical settings – Spermonde Archipelago in SW Sulawesi (Indonesia) subjected to a horizontal (i.e. cross-shelf) gradient of nutrients and sediment from land, and Koh Racha in the Andaman Sea (Thailand) subjected to a vertical gradient (i.e. depth) influenced by large amplitude internal waves introducing nutrients, low temperature, pH and oxygen in a pulsed fashion (Roder et al. 2010). The nutritional status was assessed by determining the host tissue protein and biomass; the pigment (chl *a*) and protein concentration of the zooxanthellae; as well as the isotopic composition ($\delta^{13}C$, $\delta^{15}N$) of tissue, zooxanthellae and potential food (i.e. particulate organic matter). The metabolic performance was assessed by measuring oxygen fluxes (net photosynthesis and respiration) and calcification *in situ* through chamber incubations. The photophysiological response of the coral was measured by pulse amplitude modulated (PAM) chl *a* fluorescence.

The overall objective was to assess the trophic plasticity of *P. lutea* to contrasting environmental conditions of high land-runoff and ocean impact, respectively, and to reveal the mechanisms supporting the previously reported high *Porites* growth rates in the Andaman Sea. The understanding of adaptive and/or acclimatization potential in corals is extremely important in the light of global climate change.

Material and Methods

Study sites

Field experiments were carried at four reef sites; two sites in the Spermonde Archipelago, Sulawesi, Indonesia and two sites at Ko Racha, Andaman Sea, Thailand.

The Spermonde Archipelago, situated in the Makassar Strait southwest of Sulawesi, consists of >100 small islands placed on a 40 km wide carbonate shelf platform in front of the major harbor city Makassar. Untreated effluents of the city, as well as land-run off from aqua- and agriculture create a strong cross-shelf gradient in water quality with very turbid and polluted waters near-shore (Edinger et al. 1998, Renema & Troelstra 2001). Coral species diversity and coral cover increases with increasing distance from shore (Edinger et al. 1998). The near-shore reef Lae Lae (LL, 2 km distance to shore) and the mid-shelf reef Bonebatang (BBA, 12

km distance to shore) were selected as representative sites from opposite ends of the eutrophication and sedimentation gradient (Fig. 1). P. lutea contributes with 13 % to the live coral cover in LL (19 %) and with 17 % at BBA (39 % live coral cover) (unpublished transect data).

Ko Racha is an exposed granite island 11 km south of Phuket in the Andaman Sea close to the shelf edge featuring oceanic conditions (Scoffin et al. 1992). Large amplitude internal waves (LAIW) occurring in the Andaman Sea (Osborne & Burch 1980) were found to generate secondary waves or break along the shelf slope (Vlasenko & Hutter 2002), introducing cold and low-pH water into shallow waters (Roder et al. 2010). The slope is steep (>45°) giving way to a flat sandy bottom around 20 m depth. Corals are scarce in shallow water, likely in response to monsoon surface waves (Schmidt 2010). One shallow (7 m) and one deep (20 m) site on the western side of Ko Racha (KR-S and KR-D) were chosen (Fig. 1), while coral collection and experiments were performed in the corresponding depth. No data of coral cover is available for Ko Racha, however it features a very similar reef structure as the Similan Islands north of Ko Racha, where Porites (mainly *P. lutea*) contributed with 16 % to a live coral cover of 36 % in 7m depth and with a similar contribution to a live coral cover of 12 % in 20 m depth (Schmidt 2010, pers. comm. N. Phongsuwan). The time of experiments was during the end of the dry season in Spermonde (October / November 2008) as well as at Ko Racha (March 2009).

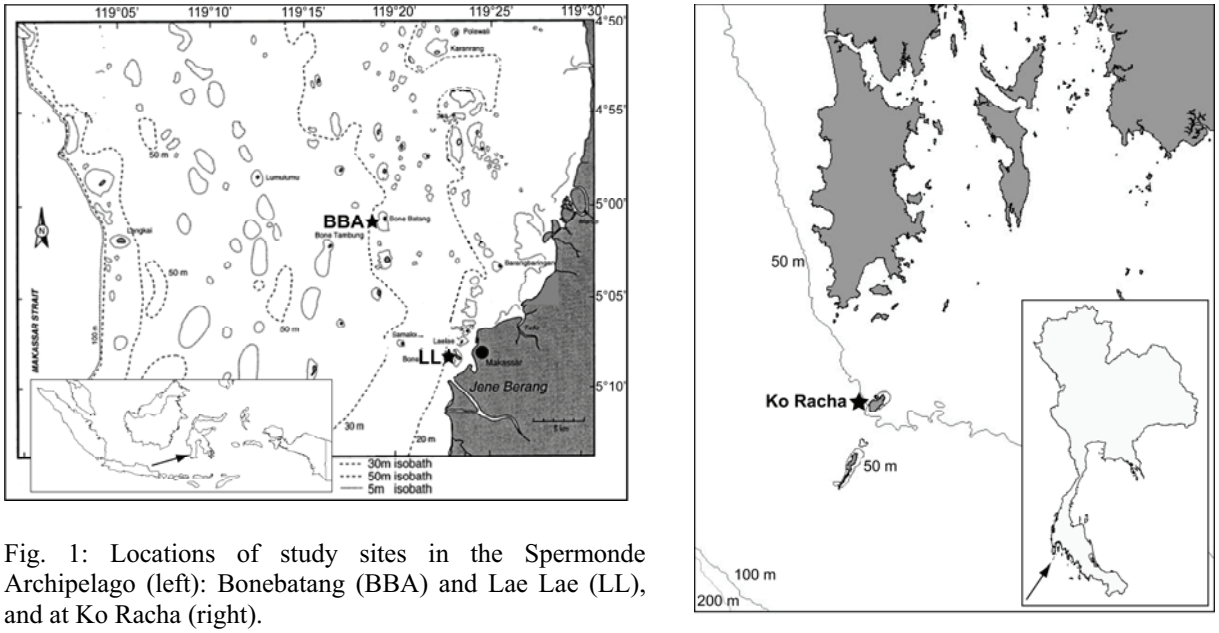

Fig. 1: Locations of study sites in the Spermonde Archipelago (left): Bonebatang (BBA) and Lae Lae (LL), and at Ko Racha (right).

Environmental data collection

Light intensity profiles were taken during each incubation with an underwater light meter (LiCor Li-192SA, Lincoln, USA), measuring the photosynthetic active radiation (PAR, µmol photons m^{-2} s^{-1}) just above and below the surface and every 0.5 m down to 6 m depth. The light attenuation coefficient (K_d) was calculated as a measure of turbidity (Dennison et al. 1993) for each site and the PAR intensities in z = 7 (KR-S) and 20 m (KR-D) depth were calculated from the equation $I(z) = I_o \times e^{-K_d \times z}$, using I_o = average PAR µmol photons m^{-2} s^{-1} just below the surface during the incubation periods ($PAR_{in\ situ}$). Additionally, the theoretical light intensity for an average sunny day was calculated for each sites in the corresponding

depth (PAR_{sun}) by using I_o=1700 µmol photons m^{-2} s^{-1} as a mid-day light intensity and the site-specific K_d and z value.
Water samples were taken at all sites in the corresponding depth with a 5-l Niskin bottle during the incubations (n=3). From each water sample one 1-l sub sample was filtered on a GF/F filter to determine the chlorophyll *a* (chl *a*) concentration, three 1-l subsamples were filtered on three pre-combusted and pre-weighed GF/F filter, for analyses of total carbon (C_{tot}) and nitrogen (N_{tot}), organic carbon (POC) and stable isotope ratios ($\delta^{13}C$, $\delta^{15}N$) of the particulate matter. Filters were stored at -20°C. A 10-ml sample from the filtrate was filled into a glass ampoule, acidified with H_3PO_4 (pH < 2.0) and flame sealed for dissolved organic carbon (DOC) analyses. Chl *a* was extracted from the filter with 90 % acetone over 24 h at 4 °C, the sample was centrifuged (4000 rcf, 5 min) and measured fluorometrically (10-AU Fluorometer, Turner Design, CA) in a glass cuvette at an emission wavelength of 668 nm and an extinction wave length of 430 nm (Boto & Bunt 1978). Calibration was carried out with a chl *a* standard (Fluka, Sigma-Aldrich, Switzerland). C_{tot}, N_{tot} and POC concentrations were measured with an elemental analyzer (NA2100 Protein, calibrated with CHNS standard [LECO]), while the filters for POC were acidified with 1 N HCl and dried prior analyses to remove the inorganic carbon. $\delta^{13}C$ and $\delta^{15}N$ were analyzed with a elemental analyzer (Flash EA 1112, ThermoFinnigan) connected to an interface (Conflo III, ThermoFinnigan) and further to the an isotope ratio mass spectrometer (Delta plus, ThermoFinnigan). $\delta^{13}C$ was related to the Pee Dee Belemnite standard and $\delta^{15}N$ to atmospheric nitrogen.
DOC was measured via the combustion method with a total organic carbon analyzer (TOC-V_{CPH}, Shimadzu) using low carbon and deep sea water standards (Hansell, RSMAS, Univ. of Miami).
Current velocity was measured with an Acoustic Doppler Current Profiler (1200 kHz Workhorse Sentinel ADCP, Teledyne RD Instruments) 1 m above the seafloor in the depths of experiments except KR-S, where no data are available, however which is most likely similar to KR-D due to their spatial proximity. Temperature data were obtained in 10 and 20 m depth of Ko Racha by temperature loggers (Tidbit v2 Temp, Bourne, MA, USA, precision ± 0.2°C at 25°C) deployed after the experiment (27.01. to 18.03.2010) in order to confirm the occurrence of from LAIWs.

Coral sampling and experimental set up
Fragments of *P. lutea* were chiseled off from the upper portion of different colonies with an inter-colony distance of at least 10 m in order to reduce the chances of sampling clone colonies. Species identification was ascertained by the author (J.J. for Spermonde) and a coral expert at the partner institute in Thailand (Niphon Phonsuwan for Ko Racha) equipped with the taxonomic expertise to differentiate *P. lutea* from other congeners (Veron 2000). Each fragment was fixed to a plastic screw with under water epoxy and fixed to a plastic rack equipped with nuts. The fragment rack was fixed to the reef bottom in the corresponding depth and coral fragments were allowed to recover and heal for 2 weeks. *In situ* incubation experiments were carried out at all sites, while 8 light and 8 dark cylindrical acrylic chambers (1.8 l) were randomly fixed on 4 floating incubation racks. Each incubation rack was attached to the reef bottom by a rope attached to a dead coral and air floats were attached on each corner of the rack to keep it floating and swaying with the wave and current movement (Fig. S1). Five marbles inside each chamber moved with the wave and current motion and thereby assured mixing of the water in the chambers. The coral fragment was fixed inside the chamber in a way that it is not touching the chamber walls or touched by the marbles, but only scoured by the water. At the Ko Racha sites, 5 light and 5 dark chambers were supplied with one coral

fragment each, the remaining 3 light and 3 dark chambers were kept empty serving as controls to account for the possibility of changes introduced by the microbiota in the incubation water. The incubations were repeated on 3 different days with different coral fragments resulting in 15 replicates per site. At the Spermonde sites 2 light and 2 dark chambers were equipped with one coral fragment each per day, while 2 light and 2 dark chambers served as controls. The experiment was repeated on 3 days resulting in 6 replicates per site. Prior each incubation experiment the chambers were flushed and filled with the surrounding seawater. All incubations started at 1300 hrs (chamber sealing) and lasted for 1 to 1.5 h.

Measurements of photosynthesis, dark respiration, light and dark calcification

Initial water samples (n=3) were taken with sealable beakers and syringes (both 50 ml) at the time of chamber sealing from the surrounding water. Final water samples were taken with syringes directly from the chamber after opening on board. Dissolved oxygen (precision 3 µmol O_2 l^{-1}) was measured with an oxygen sensor (IntelliCal LDO^{TM} Sensor, HACH Lange GmbH, Germany) in the beakers and post incubation in the each light (photosynthesis) and dark (respiration) chamber. The samples in the syringes (initial: n=5, final: n=2 per chamber) were filtered (Whatman GF/F, pore size 0.7 µm), stored in airtight tubes and kept in a cooler before warming again to ambient temperature for Total Alkalinity (TA) measurements.

The difference between the initial and final oxygen concentration was calculated for the light chambers as a measure of net photosynthesis (P_n) and for the dark chambers as a measure of respiration (R). Gross photosynthesis (P_g) was the sum of P_n and R values, assuming, that dark and light R are equal (Schneider & Erez 2006, Borell et al. 2008). The calcification rate was determined in the light (G_L) and in the dark (G_D) using the alkalinity anomaly method as described by (Schneider & Erez 2006). Total alkalinity (TA) was analyzed via potentiometric titration with an automated titrator (Titrino, Metrohm AG, Switzerland) using 50 ml sample and 0.01 M HCl (0.1 M Titrisol, Merck, Germany) with a precision of ± 4%. TA was calculated using the Gran approximation of determining the second endpoint of the titration curve (Grasshoff et al. 1983). The metabolic parameters P_g, R, G_L and G_D were standardized to the surface area and expressed in µmol O_2 cm^{-2} h^{-1} and µmol $CaCO_3$ cm^{-2} h^{-1}, respectively.

Photophysiological measurements were taken based on the chl *a* fluorescence properties with a pulse amplitude modulation (PAM) fluorometer (Diving-PAM, Walz, Germany) (Maxwell & Johnson 2000, Borell & Bischof 2008). Maximum quantum yield (F_v/F_m) was measured on dark-adapted coral fragments on board right after the incubation. After transportation to the laboratory, corals recovered in an aquarium for few hours filled with water from their origin, before they were dark adapted (15 min) and rapid light curves (RLC) were performed. The PAR intensities for the RLCs ranged from 252 to 3231 µmol photons m^{-2} s^{-1}, while intensities increased over 8 steps (each step involving 1 min. light exposure). From each RLC the following parameters were calculated after the equation of (Eilers & Peeters 1988): the steepness of the slope (α) as a measure of efficiency of light capture, the maximum relative electron transport rate ($rETR_{max}$) as a measure of photosynthetic capacity and the saturation irradiance (E_k), the point of minimum irradiance to reach maximum electron transport (Ralph & Gademann 2005). RLC derived data are used to provide hints on the photophysiological performance, while an absolute comparison is not possible due to the lack of the absorption coefficient (Enriquez et al. 2005).

Tissue extraction and measurements of tissue parameters

Tissue was removed from the skeleton with an airgun by placing the fragment in a zip-lock plastic bag with ~15 ml of filtered seawater. A template with a square hole of 3×3 cm was

placed over the coral to ensure a tissue removal of 9 cm². The volume of the tissue slurry was measured, homogenized with an Ultra Turrax and sub-samples were stored at -20°C. Zooxanthellae were counted with a haemocytometer (Fuchs-Rosenthal chamber) under the light microscope and the zooxanthellae density determined. Chl *a* was measured fluorometrically by adding 4.5 ml 100% acetone to 0.5 ml of the slurry (final concentration 90%) and following the same procedure as for chl *a* in the water, explained above. The biomass of the tissue was measured by filtering 2 ml of tissue slurry on a pre-weighted GF/F filter, briefly rinsing with distilled water to remove the salt, drying for 24 h at 40°C and weighing the biomass filters to obtain the dry weight. For protein and stabile isotope measurements the tissue slurry was separated in zooxanthellae and host tissue by centrifugation (3500 rcf, 5 min). For protein analyses the 2 compartments zooxanthellae and host tissue were treated with an ultra sonic to further break down the cell structure to release intracellular protein. Protein concentrations were determined photometrically (Coomassie Blue, λ 595 nm, photometer UV-1700 PharmaSpec, Shimadzu) after Bradford with bovine serum albumin as a standard (BioRad Protein Assay kit II, Munich, Germany). All tissue and zooxanthellae parameters were standardized to surface area and/or zooxanthella.
For $\delta^{13}C$ and $\delta^{15}N$ measurements zooxanthellae and host tissue were filtered on a pre-combusted GF/F filter, dried (40 °C, 24 h) and analyzed as described above for the particulate matter of the water.
The surface area of the coral fragments was determined gravimetrically using the wax coating technique (Glynn & D'Croz 1990, Naumann et al. 2009).

Statistical analyses
Prior to the statistical tests, the data were tested for normal distribution and transformed, if needed, to approximate normal distribution, either by √x or log x, if right skewed or by 1/(c+x) or log(c-x) with c as a constant, if left skewed. One-way ANOVA and post-hoc Tukey were applied to assess differences between the sites for each parameter, except for the isotopes. Those have been tested by a nested ANOVA and post-hoc Tukey with tissue and zooxanthellae nested within site. For all tests the software Statistica 9 was used. All data is represented in mean ± SE.

Results

Environmental conditions
Clear differences in the environmental conditions between the regions and between the sites within each region were evident (Table 1). In Ko Racha, the current velocity is 2-3-fold higher and fluctuating compared to Spermonde (see also Fig. S2) and temperature drops up to 5°C indicate the abundance of LAIWs (Fig. 2). Further differences between the regions were visible in the DOC concentration, which was 4-5-fold increased in Ko Racha, in the light intensity due to different depths and in the $\delta^{13}C$ signature of POM, being ~ 3 ‰ lighter in Ko Racha (Table 1). Differences between the sites BBA and LL in Spermonde clearly followed the effects of eutrophication, by a 3.5-fold increase in TSS, an increase of $\delta^{15}N$ by ~ 4 ‰ and a doubling in turbidity, water chl *a* and POC concentration in near-shore LL (Table 1). The site specific differences in Ko Racha was most pronounced in the light intensity dropping to 1/5 in KR-D, while TSS and DOC were ~ 1.5-fold increased in KR-D (Table 1).

Table 1: Water parameter at the sites Bonabatang (BBA) and Lea Lae (LL) in the Spermonde Archipelago and at the sites Ko Racha shallow (KR-S) and Ko-Racha deep (KR-D) at the off-shore island Ko Racha. Calculated light intensity on a sunny day (PAR_{sun}) and measured light intensity at the days of incubation ($PAR_{in\ situ}$), total suspended solids (TSS), chlorophyll *a* (chl *a*), particulate organic carbon (POC), particulate organic matter (POM), dissolved organic carbon (DOC). Values in mean (standard error). No data (n.d.).

	Spermonde		Ko Racha	
	BBA	LL	KR-S	KR-D
Depth [m]	3	3	7	20
PAR_{sun} [µmol photons m^{-2} s^{-1}]	1023	691	389	57
$PAR_{in\ situ}$ [µmol photons m^{-2} s^{-1}]	596 (93)	611 (103)	326 (11)	61 (2)
Turbidity [K_d]	-0.17 (0.00)	-0.30 (0.00)	-0.21 (0.00)	-0.17 (0.00)
TSS [mg l^{-1}]	1.98 (0.61)	6.93 (1.53)	5.05 (0.31)	7.17 (0.41)
Chl a [µg l^{-1}]	0.36 (0.03)	0.71 (0.05)	0.51 (0.10)	0.39 (0.03)
POC [µg l^{-1}]	104.7 (11.8)	236.2 (22.8)	133.3 (13.9)	143.3 (9.5)
C/N ratio POM	9.57 (1.65)	7.83 (1.02)	7.98 (0.94)	9.18 (1.00)
$\delta^{13}C$ POM [‰]	-21.85 (0.32)	-20.52 (0.43)	-24.07 (0.26)	-24.41 (0.27)
$\delta^{15}N$ POM [‰]	2.65 (0.60)	6.5 (0.51)	3.72 (0.40)	3.32 (0.19)
DOC [µM]	52.19 (7.10)	61.66 (0.76)	209.39 (30.66)	306.33 (88.10)
Temperature [°C]	29.41 (0.01)	29.95 (0.01)	n.d.	28.77 (0.01)
pH	8.40 (0.00)	8.38 (0.00)	n.d.	8.14 (0.00)
Oxygen [µM]	182.47 (1.04)	175.66 (0.55)	n.d.	170.44 (0.35)
Salinity [PSU]	34.45 (0.00)	34.58 (0.00)	n.d.	32.34 (0.01)
Current velocity [m s^{-1}]	0.045 (0.001)	0.035 (0.001)	n.d.	0.104 (0.002)

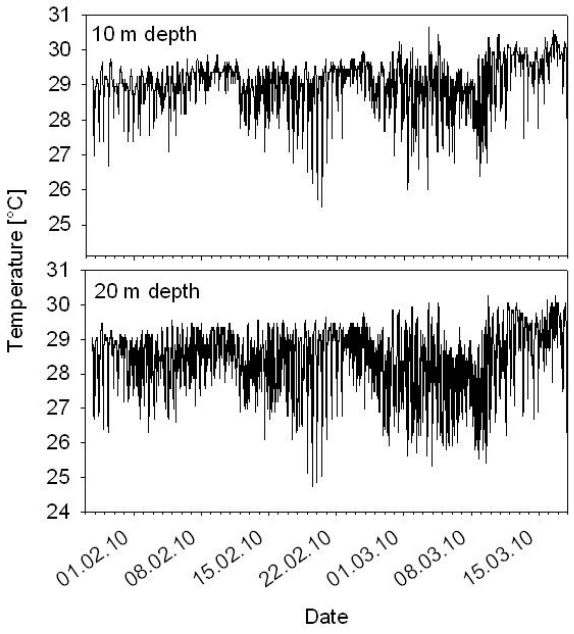

Fig. 2: Temperature profiles at Ko Racha in 10 and 20 m depth. The variations indicate the occurrence of Large Amplitude Internal Waves (LAIWs).

Metabolic performance

G_L of *P. lutea* did not vary significantly between BBA (1.55 ± 0.13 µmol $CaCO_3$ h^{-1} cm^{-2}) and LL (1.85 ± 0.16 µmol $CaCO_3$ h^{-1} cm^{-2}), however it was almost 3 times higher in KR-S (4.31 ± 0.31 µmol $CaCO_3$ h^{-1} cm^{-2}) compared to KR-D (1.51 ± 0.21 µmol $CaCO_3$ h^{-1} cm^{-2})

and also compared to BBA and LL (Fig. 3a). In contrast, P_g was more than 65 % higher in near-shore LL (4.22 ± 0.22 µmol O_2 h^{-1} cm^{-2}) compared to mid-shelf BBA (2.52 ± 0.14 µmol O_2 h^{-1} cm^{-2}) (Fig. 3b), while being exposed to similar average PAR intensities of around 600 µmol m^{-2} s^{-1} during the measurements (Table 1). At Ko Racha, P_g was almost equal in shallow (1.63 ± 0.01 µmol O_2 h^{-1} cm^{-2}) and deep (1.56 ± 0.06 µmol O_2 h^{-1} cm^{-2}) (Fig. 3b), while the light intensity was more than 5 times higher in 7 m compared to 20 m depth (Table 1). Since P_g was measured on different days and consequently different light intensities (cloudiness) within each site, P_g was also plotted against PAR for each day and site, revealing a lack of correlation between photosynthesis and light intensity, although the light intensity varied up to 4-fold within one site (Fig. 4).
G_D was similar at all sites except KR-D, which was significantly lower than KR-S (Fig. 3a) and R was very similar at all sites (Fig. 3b).
Rapid light curves (RLC) revealed significant differences between the sites (Fig. S5), most pronounced in the light capture efficiency (α) (Fig. 5). Furthermore, saturation irradiance (E_k) and maximum electron transport rate ($rETR_{max}$) were both reduced in turbid LL compared to clear BBA although not significantly, while in Ko Racha E_k and $rETR_{max}$ were both significantly lower in low light KR-D compared to higher light exposed KR-S (Fig. 5). Maximum quantum yield (F_v/F_m) varied only within a small range between the sites (0.63 to 0.69) (Fig. 5).

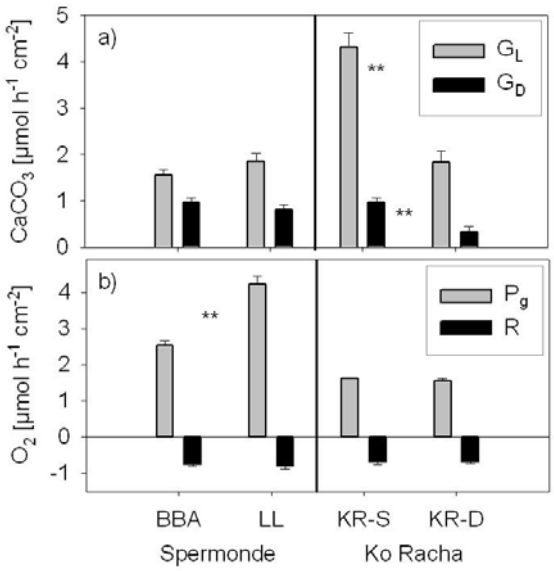

Fig. 3: Metabolism of the coral holobiont. **a**) Light calcification (G_L) and dark calcification (G_D). **b**) gross photosynthesis (P_g) and respiration (R). Mean ± SE. Significant differences between sites are indicated by an asterisk ($p < 0.05$ *; $p < 0.001$ **).

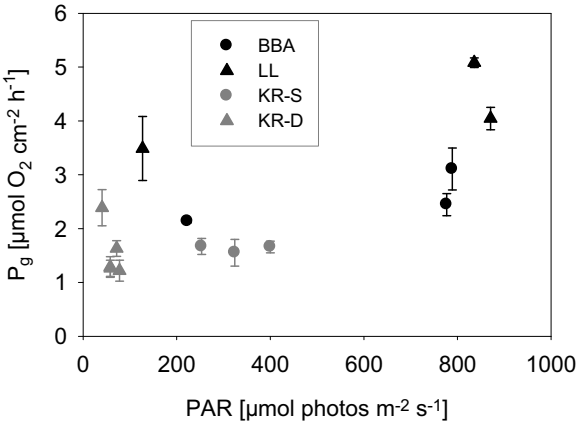

Fig. 4: Gross photosynthesis (P_g) versus light intensity (PAR). Each point represents the measurement if one day and different light intensities occurred at the different days. Mean ± SE.

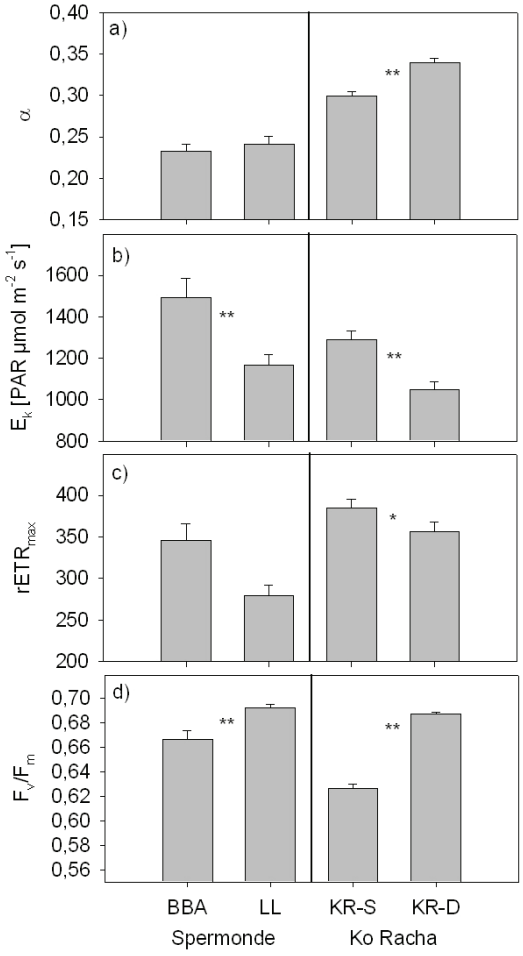

Fig. 5: Photophysiological performance of zooxanthellae. 4a-c) Results of the rapid light curves: initial slope (α), saturation irradiance (E_k) and maximum relative electron transport rate ($rETR_{max}$). 4d) Maximum quantum yield (F_v/F_m). Mean ± SE. Significant differences between sites are indicated by an asterisk ($p < 0.05$ *; $p < 0.001$ **).

Zooxanthellae and tissue parameter

Zooxanthellae density was almost 75 % higher in LL (9.16 ± 0.91 x 10^5 zooxanthellae cm^{-2}) compared to BBA (5.25 ± 0.57 x 10^5 zooxanthellae cm^{-2}) and the chl *a* concentration was even more than double in LL (7.47 ± 0.81 µg cm^{-2}) compared to BBA (3.56 ± 0.21 µg cm^{-2}) (Fig. 6) leading to a slightly higher zooxanthellar chl *a* in near-shore LL (Fig. 7). In Ko Racha, zooxanthellae densities were not significantly different in shallow (6.58 ± 0.56 x 10^5 zooxanthellae cm^{-2}) and deep (7.13 ± 0.36 x 10^5 zooxanthellae cm^{-2}), however the chl *a* concentration was significantly higher in KR-D (17.87 ± 0.86 µg cm^{-2}) than in KR-S (12.09 ± 0.96 µg cm^{-2}) (Table 2, Fig. 6), leading to higher chl *a* per zooxanthella values in low light KR-D (Table 2, Fig. 7). The cell-specific protein content in LL (0.34 ± 0.04 ng zooxanthellae^{-1}) was only about half the BBA value (0.67 ± 0.12 ng zooxanthellae^{-1}). Also in KR-D (0.40 ± 0.04 ng zooxanthellae^{-1}) values were much lower than in KR-S (0.73 ± 0.06 ng zooxanthellae^{-1}) (Fig. 7).

Investigations of the animal tissue revealed similar protein contents in BBA (0.29 ± 0.03 mg cm^{-2}) and LL (0.35 ± 0.05 mg cm^{-2}) corals and elevated protein concentrations in KR-S (0.85 ± 0.11 mg cm^{-2}) compared to KR-D (0.62 ± 0.04 mg cm^{-2}) (Fig. 8a). Also the protein percentage of biomass was higher in KR-S (average ~10 %) compared to all other sites (Fig. 8c). The C/N ratio of coral tissue and zooxanthellae were not significantly different at any site, however it was most dissimilar at KR-D (tissue: 8.96 ± 0.44; zooxanthellae: 7.87 ± 0.21)

(Fig. 8d). Concerning differences between sites slightly lower C/N ratios were found in LL compared to BBA and significantly higher C/N ratios occurred in KR-D compared to KR-S (Fig. 8d).

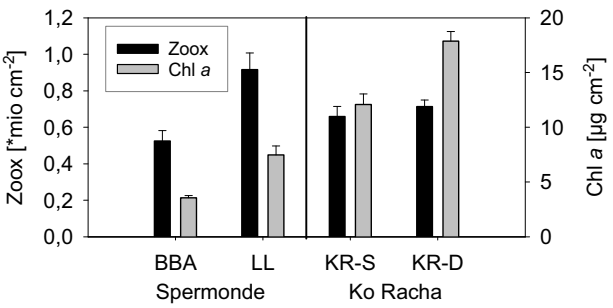

Fig. 6: Zooxanthellae density and chl *a* concentration at the different sites and regions. Mean ± SE.

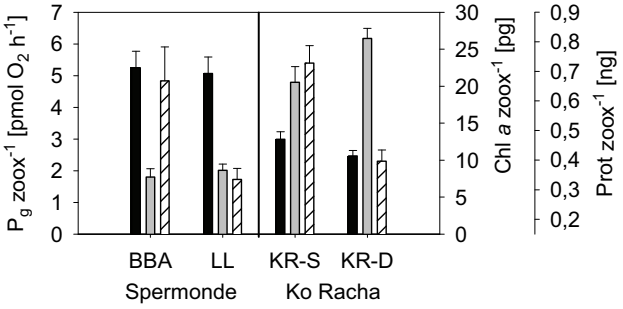

Fig. 7: Zooxantheallar gross photosynthesis (P_g zoox^{-1}) [black], chl *a* concentration (chl a zoox^{-1}) [grey] and protein content (Prot zoox^{-1}) [dashed]. Mean ± SE.

Isotopic composition: $\delta^{13}C$ and $\delta^{15}N$

In Spermonde, tissue and zooxanthellae $\delta^{13}C$ showed almost equal values, which were also similar at the two sites varying around -15 ‰ (Fig. 9a). At Ko Racha, KR-S showed a significantly ligher $\delta^{13}C$ signature in zooxanthellae (-15.49 ± 0.33 ‰) than in the tissue (-14.00 ± 0.11 ‰) (Fig. 9a), while tissue and zooxanthellae did not differ significantly at KR-D. However corals of KR-D were overall more depleted of ^{13}C (tissue and zooxanthellae around -18.3 ± 0.40 ‰) compared to KR-S (Fig. 8a). The strongest difference in $\delta^{13}C$ between the particulate organic matter in the water (POM) and the coral tissue was found in KR-S with about 10 ‰ (Fig. 9a).

The isotopic signature of $\delta^{15}N$ revealed a similar pattern as $\delta^{13}C$ concerning the difference between tissue and zooxanthellae. Only corals of KR-S showed a significant difference between tissue (7.19 ± 0.42 ‰) and zooxanthellae $\delta^{15}N$ (5.71 ± 0.12 ‰), at all other sites the difference was not significant (Fig. 9b). Looking at the between site differences a ^{15}N enrichment was evident at LL compared to BBA and an overall ^{15}N depletion in KR-D compared to KR-S (Fig. 9b). Concerning the difference between POM and coral tissue, LL was the only site where ^{15}N depletion was higher in the tissue compared to POM (Fig. 9b).

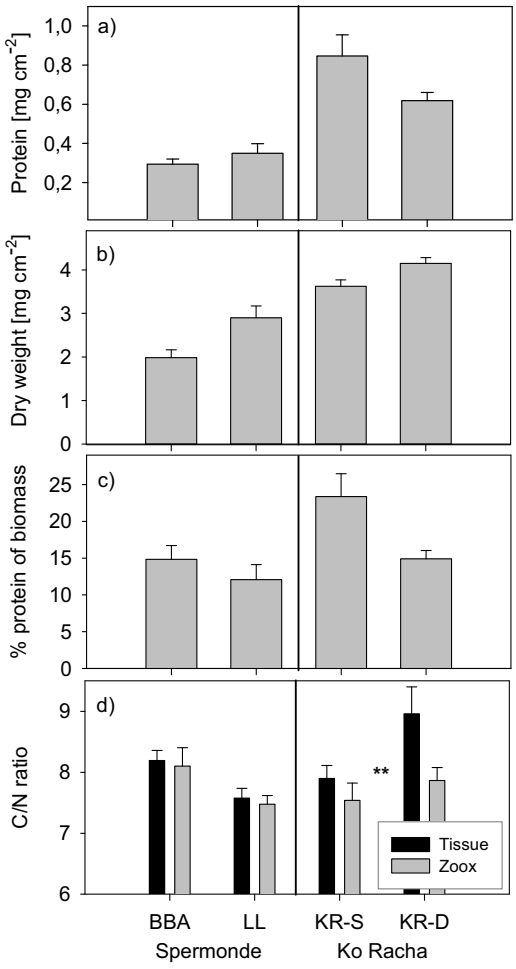

Fig. 8: Nutritional status of the coral host tissue: protein content (a), biomass (dry weight, b) and percentage protein of biomass (c). C/N ration of the host tissue and zooxanthellae (d). Mean ± SE. Significant differences between sites are indicated by an asterisk ($p < 0.05$ *; $p < 0.001$ **).

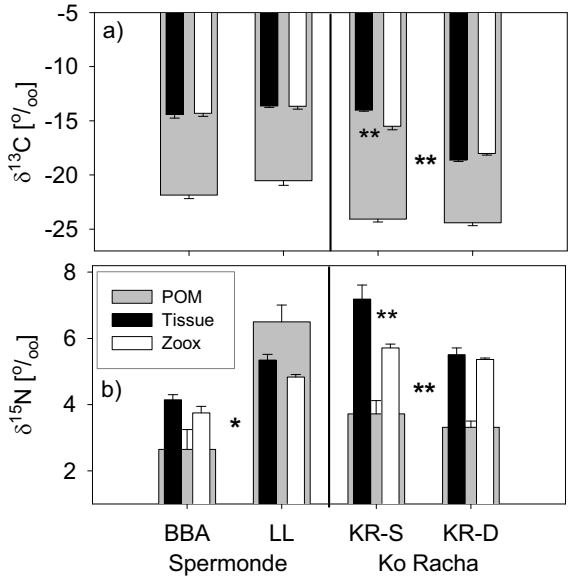

Fig. 9: Isotopic composition of $\delta^{13}C$ (a) and $\delta^{15}N$ (b) in the particulate organic matter in the water (POM), the coral host tissue and the zooxanthellae. Mean ± SE. Significant differences between tissue and zooxanthellae of one site are indicated by a normal asterisk, while overall differences between the sites are indicated by a bold asterisk ($p < 0.05$ *; $p < 0.001$ **).

Discussion

The two regions Spermonde and Ko Racha feature very contrasting environmental conditions: Spermonde represents a large barrier reef shelf lagoon system subjected to a strong anthropogenic eutrophication gradient (Edinger et al. 1998, Renema & Troelstra 2001), while Ko Racha is an offshore island near the shelf break subjected to oceanic swell (NW monsoon only) and large amplitude internal waves (LAIWs). LAIWs particularly occur during the end of the dry season (January to March, Roder et al. 2010), which was confirmed by our results. In the former case, land run-off and waste water input inject inorganic and organic nutrients, sediment as well as pollutants into the reef. This happens laterally in a more or less

continuous way, which increases primary (water chl *a*) and secondary production (zooplankton as part of TSS and POC) and further the turbidity (Tomascik & Sander 1985, Bell 1992, McCook et al. 2001). In the latter, LAIWs introduce deep sea water vertically in a pulsed fashion featuring high nutrients and low temperature, pH and oxygen (Andrews & Gentien 1982, Schmidt 2010). Additionally, currents can be strong and wave action high especially during the monsoon season (May through November). Therefore it is not surprising that these high environmental variations are reflected in the metabolic performance of *P. lutea,* which showed remarkable differences between the two regions. The most outstanding result is the 3-fold higher G_L in KR-S compared to all other sites, which underpins the previous findings of higher growth rates of *P. lutea* in the Andaman Sea compared to other regions (Phongsuwan 1991, Scoffin et al. 1992, Crabbe & Smith 2005, Carricart-Ganivet et al. 2007, Cooper et al. 2008, Tanzil et al. 2009). There is no easy explanation for the large G, given the lack of correlation with P_g as the main energy source (Muscatine et al. 1984, Dubinsky & Jokiel 1994). This suggests high variations in feeding behavior (hetero- vs. autotrophy), in internal exchange processes between animal and zooxanthellae, as well as in energy allocations, which will be discussed in the following.

Spermonde

The susceptibility of corals to increased particle loads, as it is present in LL, is highly species-specific, while few species including *P. lutea* were found to be able to cope with high sediment loads (Tomascik & Sander 1987, Scoffin et al. 1992, Nugues & Roberts 2003, Philipp & Fabricius 2003). Indeed, our findings revealed no signs of stress to near-shore pollution in *P. lutea,* such as decreased G_L (Dodge & Brass 1984, Tomascik & Sander 1985), decreased tissue biomass (Anthony et al. 2002), increased R (Abdel-Salam et al. 1988, Telesnicki & Goldberg 1995) or decreased F_v/F_m (Saxby et al. 2003, Borell & Bischof 2008).
In contrast to Ko Racha, the Spermonde sites revealed rather low G_L, however high P_g, in particular in near-shore LL. Light availability was high in both sides, BBA and LL, during the experiment, therefore high P_g in LL can mainly be explained by strongly increased zooxanthellae density and a concomitant increase in chl *a* in consequence of increased nutrient input (Ferrier-Pagès et al. 2001, Fabricius 2005). However, G_L does not follow P_g, which is in line with previous studies along eutrophication gradients, where elevated nutrient supply and not increased light intensity increased P_g (review, (Fabricius 2005). There are some explanations, which have been suggested for this phenomenon: If the coral is exposed to both, high light and high nutrients at the same time, most of the surplus energy goes into the zooxanthellae propagation (Muscatine et al. 1989a) instead of translocation to the host (Edmunds & Davies 1989), leading to a decoupling of zooxanthellae and host (Dubinsky et al. 1990, Allemand et al. 2004). If nutrients are scarce and light remains high, photosynthetically derived energy (carbon rich photosynthates) is preferably given to the host, where it can be used e.g. for G_L (Dubinsky & Jokiel 1994) and mucus production (Crossland 1987, Naumann et al. 2010). Both scenarios are applicable for this study: in eutrophic LL, the surplus energy may support both, high zooxanthellae densities and translocation of surplus energy to the host. In the host G_L is maintained on a comparable level to oligotrophic BBA, while the surplus may be needed to enhance mucus production necessary to prevent smothering in sediment-loaded waters (Edmunds & Davies 1989, Riegl & Branch 1995, Telesnicki & Goldberg 1995). An intense exchange of products instead of a decoupling of host and zooxanthellae is further supported by the C/N ratio and isotopic signature of $\delta^{13}C$ and $\delta^{15}N$, each being very similar in tissue and zooxanthellae, indicating a vivid recycling of products

under high light conditions (low fractionation - (Muscatine et al. 1989b, Muscatine & Kaplan 1994).
The isotopic composition also provides inside into the feeding mode, where the similarity of $\delta^{13}C$ in tissue and zooxanthellae indicates a predominance of autotrophy as the source of energy (Muscatine et al. 1989b) at both sites. A minor importance of heterotrophy (and hence, dominance of autotrophy) is also supported by the $\delta^{15}N$ results, which showed only minor enrichments (factor 1.2 between BBA and LL) in the host tissue, in spite of much larger enrichments in potential food (i.e. an almost 4-fold increase in POM from BBA to LL). However, the interpretation of $\delta^{15}N$ in coastal waters is fraught with the difficulty that there are several sources of nitrogen (inorganic and organic) with contrasting $\delta^{15}N$ values. Inorganic nitrogen from waste water is heavy ($\delta^{15}N > 10$ ‰), compared to agricultural run-off (fertilizer $\delta^{15}N$ 0 ‰) (Heaton 1986). Particulate matter in the water is a mixture of particles and plankton which vary in their $\delta^{15}N$ signature (soil ~ 5 ‰, every trophic step in animals results in an increase of 3.4 ± 1.1 ‰) (Minagawa & Wada 1984, Heaton 1986). The maintenance of autotrophy as the main energy source in the eutrophied and turbid reef is further supported by the constant host protein content, while an increase in heterotrophy is usually reflected in an increase in host protein content under high light conditions (Ferrier-Pagès et al. 2003, Houlbrèque & Ferrier-Pagès 2008, Treignier et al. 2008). Heterotrophic input was also found to be insignificant for the congener *Porites porites* in turbid environments (Edmunds & Davies 1989), which demonstrates a certain steadiness within this genus.

Ko Racha
Only few coral species have been shown to grow and develop well in upwelling regions, including *Porites compressa* and *P. lutea* (Burns 1985, Coles & Fadlallah 1991, Lirman et al. 2003, Schmidt 2010). This is in line with our findings where *P. lutea* seems to grow surprisingly well and even faster under the harsh conditions of Ko Racha compared to more typical coral environments, such as BBA. The 3-fold higher G_L in KR-S compared to all other sites and equal G_L in low-light KR-D compared to high-light Spermonde sites requires a high energy input, which cannot be explained solely with autotrophy, but requires an additional energy input through heterotrophy (Allemand et al. 1998, Houlbrèque et al. 2003, Houlbrèque & Ferrier-Pagès 2008). An increased heterotrophic input is supported in our results, firstly by a high protein content and high biomass of the animal tissue (Ferrier-Pagès et al. 2003, Bachar et al. 2007) and secondly, by a significant enrichment in the $\delta^{15}N$ of the coral tissue relative to the potential food (POM). Latter even follows the general rule of ^{15}N enrichment in the food web, which proceeds at steps of ~3.4 ‰ for each trophic level (Minagawa & Wada 1984). An increased heterotrophy is supported also by another studies in the area (Similan Islands north of Ko Racha), where significant differences in nutritional status of the coral *Pocillopora meandrina* found and attributed to enhanced food supply in response to LAIW upwelling (Roder et al. 2010). The strongly elevated DOC level in Ko Racha is an additional potential food source for corals (Sorokin 1973, Wang & Douglas 1998, Houlbrèque et al. 2004).
However, the relative importance of heterotrophy and autotrophy is not always evident. At KR-S, the strong $\delta^{15}N$ enrichment in the tissue indicates strong heterotrophic input, strong $^{14}NH_4$ excretion and, hence, limited internal $^{14}NH_4$ cycling, as $^{14}NH_4$ cycling would lower the $\delta^{15}N$ signature in the holobiont (Reynaud et al. 2009). This high throughput scenario is difficult to reconcile with the $\delta^{13}C$ values, which showed a very large difference between host tissue and potential food (POM) ^{13}C concentrations (~ 10 ‰) and, hence, a large dependence on autotrophy (Muscatine et al. 1989b, Heikoop et al. 2000). As high autotrophy decreases

fractionation, which has the consequence that zooxanthellae also use and recycle heavy ^{13}C excreted by the host (e.g. $^{13}CO_2$) (Muscatine et al. 1989b). Therefore, the enrichment of both, ^{15}N and ^{13}C, is an indication for a temporal decoupling in the holobiont's metabolic processes, namely the animal host heterotrophy and zooxanthellaes' photosynthesis: while feeding takes place mainly at night (Coles 1969, Muscatine & Porter 1977) and digestion is very rapid (within hours Yonge & Nicholls 1930, Porter 1974), the release of light metabolic waste products such as $^{12}CO_2$ and $^{14}NH_4$ into the water should keep the levels of heavy isotope high. Diel photosynthesis relying on heavy metabolites accumulated during the night ($^{13}CO_2$ and $^{15}NH_4$) may help reconcile the heavy isotope signatures with autotrophy and internal cycling, (Muscatine et al. 1984, Bachar et al. 2007).

Although the proposed scenario of high, but temporally decoupled, levels of auto- and heterotrophy accounts for both, the isotopic signatures and the energy necessary to sustain the enigmatically high G_L rates in KR-S highlighted earlier, the overall low levels of R and the strongly light-enhanced calcification (factor 4.5 between G_D and G_L), suggest that the direct heterotrophic contribution to G is only marginal. Therefore, a rather indirect support is likely, where heterotrophy supports zooxanthellae functioning, e.g. by increasing photosynthesis related proteins, which is reflected in the high zooxanthellar protein content. Increased photosynthetic performance in consequence of higher nutrient supply through heterotrophy has been reported before (Houlbrèque et al. 2003, Borell et al. 2008) as well as a higher stress resistance e.g. against temperature raise (Borell & Bischof 2008, Ferrier-Pagès et al. 2010). However, if the very high levels of G depend on P_g, the mismatch between P_g and G_L levels at KR-S might either be explained by an overestimation of G_L or an underestimate of oxygen production. Overestimates in G_L may arise from DOM release in the incubations, i.e. changes in the acid/base proportion of DOM substances confounding the alkalinity measurements (Koeve et al., unpubl.); however this has not been measured in this study. This seems to be unlikely to produce such major error anyway, if compared to Spermonde, where an increase in DOM release seems to be much more likely in LL compared to BBA, however which did not show an increase in G_L as a consequence. Therefore an underestimation of P_g is much more likely. This becomes eminent, if the assumption of a time-invariant respiration is violated and light respiration (R_L) exceeds the measured R in the dark. Higher R_L in response to higher O_2 and energy supply by the zooxanthellae has been suggested before (Edmunds & Davies 1988, Allemand et al. 2004) and some elaborate laboratory studies revealed tremendously increased R rates during light compared to dark (6- to 11-fold, Kühl et al. 1995, Al-Horani et al. 2003). Strong evidence for an underestimation of P_g, particularly at KR-S was found, firstly by the high photophysiological performance of Ko Racha corals, secondly by the comparison of P_g and G_L between KR-S and KR-D and thirdly, by the already demonstrated isotopic signature of tissue and zooxanthellae. Ko Racha corals have higher chl *a* and zooxanthellar protein concentrations compared to the Spermonde corals, which is known to compensate for decreased light intensities (Falkowski & Dubinsky 1981, McCloskey & Muscatine 1984, Masuda et al. 1993, Mass et al. 2007, Hoogenboom et al. 2009). This is even more pronounced in KR-D compared to KR-S in order to maximize photosynthesis in very low light conditions in deep. However, it seems to be unlikely that photoacclimation can fully compensate a decrease in light intensity to 1/5, as indicated by an equal P_g in KR-S and KR-D. And it can even be ruled out, if the 3-fold increased G_L in KR-S compared to KR-D is considered, which can only be explained by an underestimation of R_L and consequently an underestimation of P_g.

An overall decrease in calcification (G_L and G_D) in KR-D compared to KR-S is most likely due to an overall lower metabolism and to high environmental fluctuations, which is in line

with the findings at LAIW exposed corals on Similan West (Schmidt 2010). In contrast, growth rates of different massive *Porites spp.* did not vary either over a depth gradient similar to ours in an off-shore reef of the Great Barrier Reef (5-20 m) (Carricart-Ganivet et al. 2007) or between LAIW sheltered sites of the off-shore Similan Islands (7 and 20 m) (Schmidt 2010), which further highlights the exceptional response of *P. lutea* calcification to LAIW (and monsoon, not measured here) exposed reefs.

Spermonde vs. Ko Racha - different life strategies

Pronounced differences in energy acquisition as well as in energy allocation of *P. lutea* were evident in the two regions. Spermonde corals covered most of their energy needs by autotrophy and conducted a vivid recycling of products making additional food uptake by heterotrophy indispensible. Ko Racha corals gained a substantial amount of energy by heterotrophy, beside an effective energy acquisition through P_g in particular in KR-S. A decoupling of the two feeding modes - feeding in the night and photosynthesis during the day – shows that corals growing in harsh conditions are adapted in a way, which allows them to take the maximum of energy and nutrition offered by light and prey. Even though conclusive evidence is lacking, it is likely that P_g was underestimated due to high R_L in KR-S, masking the expected linear relation between P_g and G_L.

In terms of energy allocation the photosynthetically derived energy in Spermonde was used for zooxanthellae propagation and most likely for mucus production, in particular in the eutrophied and turbid near-shore reef. In contrast, heterotrophically derived energy and nutrition in Ko Racha increased the nutritional status of coral host and zooxanthellae and the photosynthetically derived energy supported mainly G_L. These findings are in line with comparative studies in LAIW exposed and sheltered reefs north of Ko Racha along the Similan Islands, where a higher biomass and heterotrophy occurred on exposed sites (Roder et al. 2010) and higher growth rates in exposed shallow (7 m) compared to deep (20 m) (Schmidt 2010). Therefore it can be concluded, that corals in extreme oceanic conditions with high hydraulic forces (currents, storms, low pH upwelling water) are well adapted to the prevailing conditions. Their increased G_L rates are used to form highly dense and stable skeletons (Scoffin et al. 1992) and their increased nutritional status (biomass, protein) makes them more resistant to unfavorable conditions (Edmunds & Davies 1986, Hoeksema & Moka 1989, Marshall & Clode 2004).

In conclusion, it can be said, that *P. lutea* is a highly flexible coral species, found in various environmental settings including extreme conditions, such as high land-based pollution and oceanic upwelling. There metabolism is well adapted to the provided energy sources as well as to the particular need of energy usage to withstand potential stressors. The high metabolic flexibility might further enable *P. lutea* to be a less susceptible species to stressors connected to global change, such as ocean acidification, sea surface temperature and increased eutrophication pressure, however it remains an open question.

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Supplementary Data

Table S1: Summary of all metabolic, zooxanthellae and host tissue parameter of *Porites lutea* in the mid-shelf site Bonebatang (BBA) and near-shore site Lae Lae (LL) in the Spermonde Archipelago and at Ko Racha shallow (KR-S) and Ko Racha deep (KR-D) at the western site of the off-shore island Ko Racha. Light intensity at the days of incubation ($PAR_{in\ situ}$), net photosynthesis (P_n), gross photosynthesis (P_g), respiration (R), light calcification (G_L), dark calcification (G_D), photosynthetic efficiency (α), saturation irradiance (I_k), maximum relative electron transport rate ($rETR_{max}$), maximum quantum yield (F_v/F_m), zooxanthellea (zoox), chlorophyll *a* (chl *a*), protein of zooxanthellae ($Prot_Z$) and host tissue ($Prot_T$), dry weight (DW) and isotopic rations of $\delta^{13}C$ and $\delta^{15}N$ of zooxanthellae and tissue.

	Spermonde		Ko Racha	
	BBA	LL	KR-S	KR-D
Depth [m]	3	3	7	20
$PAR_{in\ situ}$ [µmol photons m^{-2} s^{-1}]	596 (93)	611 (103)	326 (11)	61 (2)
Metabolic parameter				
P_n [µmol O_2 cm^{-2} h^{-1}]	1.81 (0.15)	3.46 (0.30)	0.93 (0.08)	0.91 (0.06)
P_g [µmol O_2 cm^{-2} h^{-1}]	2.52 (0.14)	4.22 (0.22)	1.63 (0.01)	1.56 (0.06)
P_g [pmol $zoox^{-1}$ O_2 h^{-1}]	5.25 (0.52)	5.07 (0.52)	2.99 (0.24)	2.47 (0.17)
R [µmol O_2 cm^{-2} h^{-1}]	-0.75 (0.05)	-0.79 (0.11)	-0.70 (0.05)	-0.69 (0.06)
G_L [µmol $CaCO_3$ cm^{-2} h^{-1}]	1.55 (0.13)	1.85 (0.16)	4.31 (0.31)	1.51 (0.21)
G_D [µmol $CaCO_3$ cm^{-2} h^{-1}]	0.96 (0.10)	0.81 (0.10)	0.96 (0.11)	0.14 (0.12)
α	0.233 (0.008)	0.241 (0.009)	0.300 (0.005)	0.339 (0.005)
I_k [µmol photons m^{-2} s^{-1}]	1492 (94)	1165 (53)	1290 (42)	1050 (35)
$rETR_{max}$	346 (21)	280 (13)	385 (10)	356 (12)
F_v/F_m	0.666 (0.007)	0.692 (0.003)	0.626 (0.003)	0.687 (0.001)
Zooxanthellae and host tissue parameter				
Zoox density [no. cm^{-2}] x 10^5	5.25 (0.57)	9.16 (0.91)	6.58 (0.56)	7.13 (0.36)
Chl *a* [µg cm^{-2}]	3.56 (0.21)	7.47 (0.81)	12.09 (0.96)	17.87 (0.89)
Chl *a* [pg $zoox^{-1}$]	7.72 (1.13)	8.63 (0.84)	20.53 (2.11)	26.45 (1.36)
$Prot_Z$ [mg cm^{-2}]	0.30 (0.02)	0.29 (0.03)	0.42 (0.03)	0.25 (0.02)
$Prot_Z$ [pg $zoox^{-1}$]	0.67 (0.12)	0.34 (0.04)	0.73 (0.06)	0.40 (0.04)
Biomass (DW) [mg cm^{-2}]	1.98 (0.18)	2.90 (0.27)	3.62 (0.15)	4.15 (0.13)
ProtT [mg cm^{-2}]	0.29 (0.03)	0.35 (0.05)	0.85 (0.11)	0.62 (0.04)
C/N ratio zoox	8.10 (0.30)	7.48 (0.14)	7.54 (0.28)	7.87 (0.21)
C/N ratio tissue	8.19 (0.17)	7.58 (0.16)	7.90 (0.21)	8.96 (0.44)
$\delta^{13}C$ zoox [‰]	-14.31 (0.28)	-13.66 (0.25)	-15.49 (0.33)	-18.01 (0.15)
$\delta^{13}C$ tissue [‰]	-14.41 (0.34)	-13.62 (0.13)	-14.00 (0.11)	-18.62 (0.14)
$\delta^{15}N$ zoox [‰]	3.75 (0.20)	4.84 (0.08)	5.71 (0.12)	5.36 (0.05)
$\delta^{15}N$ tissue [‰]	4.14 (0.16)	5.34 (0.17)	7.19 (0.42)	5.51 (0.20)

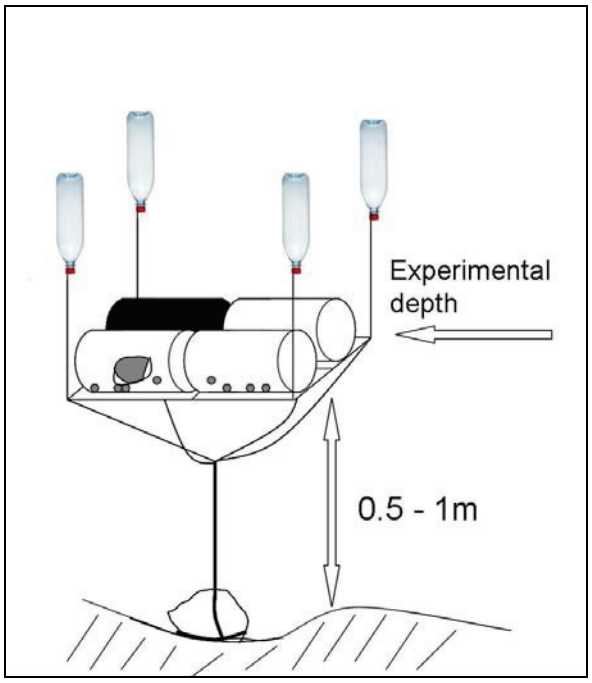

Fig. S1: Schematic drawing on the in situ incubation set up for one out of 4 chambers randomly distributed on the rack. Respiration chamber in black, photosynthesis chambers transparent, with the empty chamber is a control chamber. The rack is floating and able to move with the waves and/or current. Grey marbles inside the chambers provide mixing.

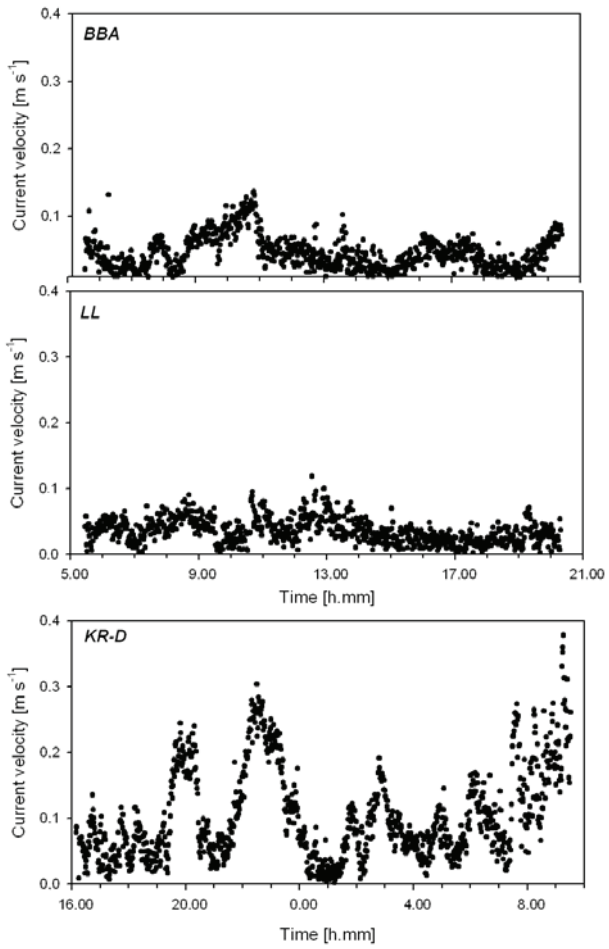

Fig. S2: Current velocity I m above the bottom in Bonebatang (BBA), Lae Lae (LL) and Ko Racha deep (KR-D).

Paper 5

Effects of eutrophication, seasonality and macrofouling on the diversity of bacterial biofilms associated with coral reefs of the Spermonde Archipelago, Indonesia

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Abstract

It is well known that biofilms play an important role as a settlement cue for invertebrate larvae and that they significantly contribute to the nutrient turnover in aquatic ecosystems. However, only little is known about their response to environmental changes and about possible interactions with the associated macrofauna. This study aimed to identify patterns of bacterial dynamics in coral reef biofilms in response to microhabitat (exposed vs. sheltered), eutrophication and seasonality, and by considering the interactions between the bacterial and associated macrofouling communities. Settlement tiles were deployed at four reef sites along a cross-shelf eutrophication gradient and were exchanged every 4 months during 20 months. The fouling community composition on the tiles was recorded and the bacterial community structure was assessed with the community fingerprinting technique "automated 16S rRNA intergenic spacer analysis" (ARISA). Changes in bacterial community structure were analysed with non-metric multidimensional scaling (MDS) and analysis of similarity (ANOSIM), while the impact of the different factors was assessed with variation partitioning and path analysis. Bacterial diversity was generally higher on the exposed tiles, where fouling community was rather homogenous and dominated by algae in contrast to the sheltered habitat, where the fouling community consisted of a variety of heterotrophic filter feeders. Further, bacterial diversity was highest in eutrophied, near-shore reefs concomitant with the highest filamentous algal cover. Seasonality was most pronounced in the most oligotrophic mid-shelf reef with dramatic changes in the number of bacterial types (95-316 OTUs), while the fouling community overall changed only little between seasons. These results suggest a large dependency of the bacterial community on nutrient availability and a lower response to fouling community, although significant, yet weak associations between the communities were evidenced. This low association might be explained by the advanced succession of the two communities after 4 months. Overall, the complex interplay of multiple environmental and biological factors structures the bacterial community of reef biofilms, which may explain its high temporal and spatial dynamics.

Keywords: biofilm, diversity, macrofouling, coral reef, seasonality, eutrophication

Introduction

Microbial biofilms play an important role in aquatic systems by providing a conditioned surface for larval settlement and metamorphosis of sessile organisms (Wieczorek & Todd 1998) and by contributing to the nutrient turnover and productivity (Costerton et al. 1995, Poltak & Cooper 2010). Biofilms generally have a high microbial diversity, which is maintained by exogenous as well as endogenous mechanisms. Exogenous drivers may first consist of a top-down control by predation or viral lysis of bacteria, which limits the dominance of certain species in the community and would allow for the co-existence of different species within the same niche. Second, a bottom-up control may consist of the wide variety of energy sources and substrates available in an ecosystem, which offer a large variety of niches for bacteria (Torsvik et al. 2002). Endogenous mechanisms include interactions between microbial species, with dynamic exchanges of metabolites, which thereby further contribute to the formation of various ecological niches (Poltak & Cooper 2010).

Although diversity is generally high, biofilm community structure can vary greatly with changes in environmental conditions (Hall-Stoodley et al. 2004, Qian & Dahms 2009), such as nutrient availability, temperature, salinity and light, which can moreover fluctuate over space and time (Costerton et al. 1995, Lau et al. 2005, Moss et al. 2006, Webster & Negri 2006). Nutrient availability was found to be one of the major factors affecting biofilm diversity and composition (reviewed by Costerton et al. 1995), and this factor can vary with seasons (Claret et al. 1998, Lau et al. 2005) or due to human induced eutrophication (Meyer-Reil & Köster 2000, Nocker et al. 2004, Webster & Negri 2006). Higher nutrients generally cause a shift from autotrophic to heterotrophic and to sulphur reducing bacteria as a response to decreased light availability and increased load in organic material (Meyer-Reil & Köster 2000, Webster & Negri 2006, Uthicke & McGuire 2007), while the overall biofilm diversity has been found to either remain on the same level (Moss et al. 2006, Pringault et al. 2008) or increase (Ford 2000, Nocker et al. 2004).

Biofilm studies are extremely rare in the oligotrophic coral reefs so far, although hard substrates (coated by a biofilm) are essential for the settlement of most benthic reef organisms including framework building corals. The response of coral larvae metamorphosis to biofilm composition at different levels of succession and at different water depths has been examined (Webster et al. 2004), as well as the effects of underlying substrate (crustose algae) on overlying bacteria and on the further settlement of coral larvae (Negri et al. 2001). The latter study demonstrated that interactions between biofilm composition and macrofouling may exist, in which initial biofilm formation influences the settlement of macroorganisms and the macroorganisms may thereafter affect subsequent biofilm formation (see also (Walls et al. 1993, Gillan et al. 1998). The dynamics of the microbial and macrofouling communities and their interactions in response to environmental variations (spatial or temporal) have not been investigated so far to the best of our knowledge. However, this becomes increasingly important in the context of anthropogenic changes in water quality, which might have a strong effect on the interactions of those two key components and consequently on the stability of the coral reef ecosystem.

In this study, the diversity and dynamics of colonizing bacterial communities were investigated on tiles, which were deployed so as to create sheltered and exposed microhabitats in several coral reefs of the Spermonde Archipelago, Indonesia, over 20 months. Spermonde

is characterized by a land-based eutrophication gradient and by seasonal effects mainly due to variation in rain fall. In addition to the microbial community, the macrofouling community was examined to understand its relationships with biofilm diversity and dynamics. The following main questions were addressed: (1) What effects have tile-associated microhabitats on the bacterial diversity structure? (2) How much do eutrophication and seasonality affect bacterial diversity and community structure? (3) How important is the presence and composition of the fouling community for microbial dynamics in the context of microhabitats, eutrophication and seasonality?

Material and Methods

Study sites and sampling design

Four reefs were sampled along a cross-shelf transect in the Spermonde Archipelago, Sulawesi (Indonesia), situated within the biodiversity hotspot of the Coral Triangle (Renema & Hoeksema 2007). The archipelago consists of more than 100 small islands situated on a 40 km wide carbonate shelf surrounded by coral reef which are best developed on the Southern and Western sides of the island (Moll 1983). Due to environmental and ecological variability across the shelf, the archipelago has been divided into different ecological zones running parallel to the coast line (Moll 1983, Renema & Troelstra 2001). The near-shore zone, which includes the study sites Lae Lae (LAE, 2 km distance from shore), is most strongly impacted by land run-off discharging waste water, fertilizers and erosion products from the 1.5 million people harbor city Makassar and surroundings (Edinger et al. 1998, Renema & Troelstra 2001). Consequently this zone is highly eutrophied, sediment loaded and polluted, and features the lowest diversity in various benthic reef taxa (Cleary et al. 2005). The mid-shelf zone includes our study sites Samalona (SAM, 5 km) and Bonebatang (BBA, 14 km); while SAM can still be influenced by land run-off during the rainy season (Renema & Troelstra 2001), and can therefore be classified as near mid-shelf. BBA is situated in an oligotrophic environment characterized by the highest diversity in corals (Moll 1983) and other benthic reef taxa (Cleary et al. 2005). The 4th study site Lanyukan (LNK, 35 km) is situated off-shore within the outer shelf zone, which is purely influenced by oceanic waters from the Makassar Strait. Upwelling of low magnitude has been proposed along the shelf edge (Hoeksema & Moka 1989, Kinkade et al. 1997), which increases the nutrient supply. Biodiversity is a little lower compared to mid-shelf reefs (Moll 1983). A clear shift in community composition from near- to mid-shelf / off-shore has been described for corals, sea urchins, sponges and foraminifera (Moll 1983, Cleary et al. 2005, Becking et al. 2006, de Voogd et al. 2006).

The seasons are characterized by the monsoons with the wet NW monsoon prevailing from November to February (peak of rainfall: January, 730 mm month^{-1}) and the dry SE monsoon from June to September (lowest rainfall: August, 15 mm month^{-1}) (World Meteorological Organization). In this study, 3 seasons were considered: The wet season (wet: November to February; IV: 2008/09), the transition period from wet to dry season (trans: March to June; II: 2008 and V: 2009) and the dry season (dry: July to October; III: 2008, VI: 2009).

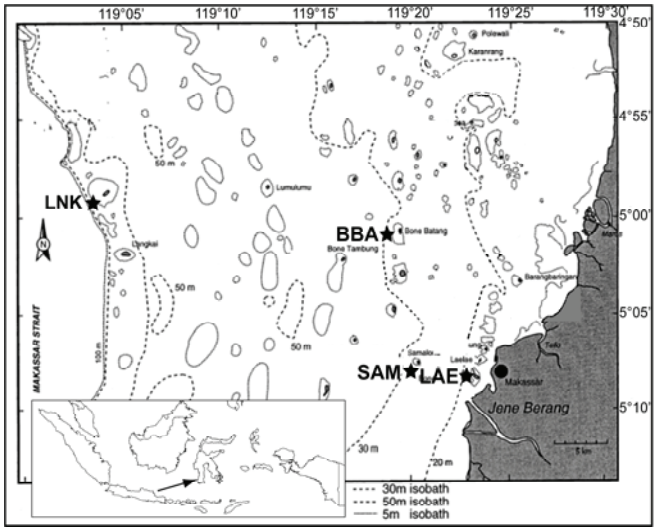

Fig. 1: Map of the Spermonde Archipelago, SW Sulawesi (Indonesia) with the study sites indicated by stars: Near-shore Lae Lae (LAE), near mid-shelf Samalona (SAM), mid-shelf Bonebatang (BBA) and off-shore Lanyukan (LNK).

The experiment was set up along the reef edge, which lies in about 3 m depth and harbors the highest live coral cover and reef diversity (Moll 1983). Up to 16 units of settlement tiles per site were deployed along the reef edge, with each settlement tile unit consisting of 2 bathroom tiles with a size of 15 x 15 cm, which were laid on top of each other by facing the unglazed rough sides to the outside, resulting in one upper (exposed) and one lower (sheltered) face. The tile pairs were fixed on dead coral boulders in an angle of about 45° with a steel-less screw through the middle of the tiles. The tile pairs were exchanged every 4 months between the seasons as described above in order to capture the effects of seasonality. Sampling was performed under water by randomly choosing 3 pairs of tile, from which a small piece of each upper and lower tile was carefully broken and individually placed in small zip-lock bags. They were kept cool (max. 2 h) and subsequently frozen (-20°C) until microbial investigations were performed. The rest of the tile and the remaining tiles were dried in the sun for the examination of the fouling community.

Description of fouling community

Upper and lower faces of all tile pairs were inspected under a dissecting microscope and the following taxa of fouling community were distinguished and recorded in % cover: Filamentous algae, crustose coralline red algae, bryozoans, sponges, ascidians, barnacles, spirorbid worms and bivalves.

Description of benthic community composition

A 60 m line-intercept transect was conducted at each site along the reef edge at the end of the experiment in order to assess the benthic community composition of the reef (English et al. 1997). The following categories were applied, recorded on cm-scale and calculated in percentage contribution: live coral (LC), dead coral (DC; >15 cm), coral rubble (RB; <15 cm), sand (SA), macroalgae (ALG) and others (OT), which include soft coral, sponge, anemone, ascidians and hydrozoans.

Water parameters

Water samples (n=3) were taken with a 5-l Niskin bottle at the time of tile exchange at all sites. From each water sample, a 1-l subsample was filtered through a GF/F filter for chlorophyll *a* (Chl *a*) measurement and two 1-l subsamples were filtered through a pre-combusted and pre-weighed GF/F filter for analyses of total nitrogen and organic carbon of

the particulate matter (particulate organic carbon: POC), respectively. Filters were stored at -20°C. A 10-ml sample of each filtrate was filled into a glass ampoule, acidified with H_3PO_4 (pH<2.0) and flame sealed for dissolved organic carbon (DOC) analyses. Chl *a* was extracted from the filter with 90% acetone over 24 h at 4°C, the sample was centrifuged (4000 rcf, 5 min) and measured fluorometrically (10-AU Fluorometer, Turner Design, CA) in a glass cuvette at an emission wavelength of 668 nm and an extinction wave length of 430 nm (Boto & Bunt 1978). Calibration was carried out with a Chl *a* standard (Fluka, Sigma-Aldrich, Switzerland). Nitrogen and POC concentrations were measured with an elemental analyzer (NA2100 Protein, calibrated with CHNS standard [LECO]), while the filters for POC were acidified with 1 N HCl and dried prior analyses to remove the inorganic carbon. The C/N ratio was calculated by dividing the POC with nitrogen value. DOC was measured via the combustion method with a total organic carbon analyzer (TOC-V_{CPH}, Shimadzu) using low carbon and deep sea water standards (Hansell, RSMAS, Univ. of Miami).

DNA extraction and automated rRNA intergenic spacer analysis (ARISA)

To investigate changes in microbial diversity and community structure automated ribosomal intergenic spacer analysis (ARISA) was used as a method which allows fine-scale differentiation of microbial community structures discriminating between sub-species and clades occupying different ecological micro-niches (Fisher & Triplett 1999, Brown et al. 2005, Fuhrman et al. 2008, Ramette 2009).

An area of 2.25 cm² (1.5 x 1.5 cm) of each tile piece was carefully scraped with a scalpel. The removed matter was diluted in 0.5 ml sodium phosphate buffer (120 mM, pH 8.0) in an 1.5-ml Eppendorf tube and placed on a shaker (300 rpm, 10 min) to detach microorganisms from the macrobenthos and particles. The mixture was filtered through a 1.0 µm glass fiber filter (Type APFC, Millipore) to remove macrobenthos and particles, the filter was rinsed with additional 0.3 ml sodium phosphate buffer and the filtrate was further processed according to the manual of the UltraClean soid DNA isolation kit (MoBio Laboratories, Inc., Carlsbad, CA, USA). After the extraction the DNA concentration was determined (ND-1000 Nanodrop, Peqlab, Biotechnology, Erlangen, Germany) and a rather low DNA concentration was found in most samples. Therefore, DNA was concentrated by isopropanol precipitation, and after a short period of air-drying, the DNA pellet was re-dissolved in 20 µl PCR water and later adjusted to 10 ng μl^{-1}.

ARISA-PCR were conducted in triplicates after the standard protocol described by Ramette (2009) using a 50 µl reaction, the universal primer ITSF and eubacterial ITSReub, the latter being labeled with the phosphoramidite dye HEX, 0.05 U ml^{-1} Taq polymerase (Peqlab) and 20 ng of sample DNA. PCR products were purified with Sephadex G-50 Superfine (Sigma-Aldrich, Germany) and the DNA concentrations were determined photometrically (Infinite 200 NanoQuant, Tecan). Prior fragment analyses via capillary electrophoresis on a 80-cm – capillary ABI Prism 3130xl genetic analyzer (Applied Biosystems) 100 ng of sample DNA was added to a separation cocktail containing 0.5 µl of internal size standard Map Marker 1000 Rox (50-1000 bp) (BioVentures, Inc., Washington D.C., USA) and 14.5 µl of deionized Hi-Di formamide (Applied Biosystems, Foster City, CA, USA) (Ramette 2009).

Phylogenetic analyses of microorganisms

ARISA profiles were analyzed using the GeneMapper Software v3.7 (Applied Biosystems) and the operational taxonomic units (OTUs) were identified for peaks with a minimum of 50 fluorescence units (Ramette 2009). The GeneMapper output tables were further analyzed with custom R scripts. A “fixed window” binning strategy with a bin size of 2 bp was applied and

OTU sizes between 100 and 1,000 bp were considered (Hewson & Fuhrman 2006a, Ramette 2009).

Statistical analyses

General patterns in bacterial and fouling communities between the sites, seasons and tile position were explored by using non-metric multidimensional scaling (MDS) ordination based on the Bray-Curtis dissimilarity matrix between samples. Analyses of Similarity (ANOSIM) were conducted to assess the significance (p) and community overlap (Global R) for the overall data set and for specific groupings of samples according to sites, seasons and tile position. The p-values of ANOSIM were Bonferroni corrected, which allows a rather conservative significance level after multiple pairwise comparisons (see (Clarke 1993, Ramette 2007) for methods of multivariate analyses).

In a following step, the specific effects of the main factors (site distance from shore, season, tile position, water parameters, fouling community, benthic cover) and their covariations on bacterial community structure were assessed using "variation partitioning" and "path analysis", both based on simple and partial regression analyses between the available parameters (Legendre & Legendre 1998). Prior to performing those tests, a consensus community profile was determined for each sample by merging the triplicate PCR and by considering an OTU present if it appeared at least twice among the triplicates (Ramette 2009). The merged table was Hellinger transformed to minimize the effects of the strongly left skewed distribution curve (Legendre & Gallagher 2001). Variation partitioning was performed to determine the relative contribution of individual or combined (co-varying) factors on the total variation in bacterial community structure. The effects of the overall model as well as those of each specific factor were determined by simple and partial redundancy analyses (i.e. multivariate regression approaches) and by testing their significance using 1000 Monte Carlo permutation tests. Path analysis allows simultaneous modeling of several related regression relationships in a causal modeling framework (Legendre & Legendre 1998), creating a network of dependencies between factors and/or variables. The path analysis approach enables testing the likelihood of different scenarios (i.e. path models), while the causal order among variables must be determined before, based on a priori hypotheses. The factors are linked with pre-determined (hypothesized) paths always pointing into one direction (explanatory to response variable) and the path coefficients are estimated using multiple linear regression models. The fit of the model is based on the amount of explained variation and the number of explanatory variables, while the first one increases and the latter on decrease the model fit (Legendre & Legendre 1998, Johnson & Omland 2004).

MDS and ANOSIM were performed with the multivariate statistic software PRIMER v6, variation partitioning and path analyses were conducted with the statistical platform R (http://cran.r-project.org/) using the *vegan* and *sem* packages, respectively, as well as custom R scripts.

Results

Spatial variation in benthic community structure

The benthic community in near-shore LAE featured the lowest live coral cover (18.3 %) and the highest abundance of dead coral (25.2 %) and other organisms (33.5 %) (Fig. 2a), while latter included mainly soft corals (14.4 %) and hydrozoans (9.1%) (Table S1). The highest live coral cover was found in the mid-shelf reefs (SAM: 52.5 % and BBA: 48.4 %), while off-

shore LNK featured a live coral of 31.9 %, however a high cover by sand (34.5 %) compared to the other sites (Fig. 2a).

Seasonal and spatial variations in water parameters

Seasonal fluctuations and spatial differences were reflected in the water parameter (Fig. 2b), with highest Chl *a* concentrations towards the end of the wet season (IV) at all sites, while it was most pronounced in near-shore LAE (1.59 ± 0.16 µg l^{-1}) (mean ± SE) compared to mid-shelf and off-shore reefs (1.0 ± 0.08 to 1.17 µg l^{-1}) (in LNK season IV, only one water sample was available). The POC concentration was also highest in near-shore LAE during in the end of the wet season (IV) (236 ± 23 µg l^{-1}) and peaked in the same season in off-shore LNK (137 µg l^{-1}). The mid-shelf reefs SAM (127 ± 13 µg l^{-1}) and BBA (105 ±12 µg l^{-1}) had a weaker peak, which occurred towards the end of the dry season (III) (Fig. 2b). C/N ratios and DOC concentrations showed less pronounced seasonal and spatial patterns with C/N ratios between 5.7 and 9.8 and DOC concentrations between 52.2 ± 7.1 and 147.1 µM (Table S2).

Seasonal and spatial variations in the fouling community

A total of 246 tile pairs were examined for the fouling community composition and revealed pronounced differences between the upper and lower face (ANOSIM R=0.819, p=0.001); Table S3) with a strong dominance of algae on the upper and heterotrophs on the lower face throughout the sites and seasons (Fig. 2c, Table S4). Spatial differences overall were relatively low (R=0.097, p=0.001; Table S1), due to a low spatial variation on the lower face (R=0.138, p=0.001), while they were high on the upper face (R=0.696, p=0.001), due to a shift from filamentous algae towards crustose algae form near- to off-shore (Fig. 2c). Seasonal variation overall was low and only significant at near-shore LAE (R=0.142, p=0.001) and mid-shelf BBA (R=0.102, p=0.001, Table S3). See also Supplementary Information for MDS plots of the fouling community (Fig. S1).

Seasonal and spatial variations in bacterial OTU number

On the 97 examined tiles, a total of 445 OTUs were detected, with 400 OTUs occurring on more than 3 tiles. Overall, more OTUs were found on the upper side (356 OTUs on >3 tiles) compared to the lower side of the tiles (307 OTUs), with 289 OTUs being shared. Differences between the upper and lower side of the tiles were most pronounced in near-shore LAE and the overall OTU number was higher in the reefs close to shore (LAE and SAM) compared to mid-shelf BBA and off-shore LNK (Fig. 2d): The highest OTU number was found in near mid-shelf SAM (dry season VI: 330 OTUs), followed by near-shore LAE (wet season IV: 324 OTUs) (Fig. 2d). The lowest OTU number was found in mid-shelf BBA (transition period V: 95 OTUs) ranging from 95 to 316 OTUs in the transition period V and dry season VI, respectively (Fig. 2d). The lowest OTU number was found in BBA during the transition period II with 119 OTUs and in the dry period III with 151 OTUs (Fig. 2d).

Factors influencing bacterial community structure

In order to assess the individual and combined effects of contextual parameters on bacterial community structure, variation partitioning was applied. Only complete data sets were used, meaning that the data of season VI in LAE, SAM and BBA were excluded from the analysis (also for path analysis), due to a lack of water parameters. Each parameter (season, site, tile position: p<0.001 and water parameter: p=0.007) revealed a significant effect on the bacterial community structure, although the explained variance was rather small. Highest variation was

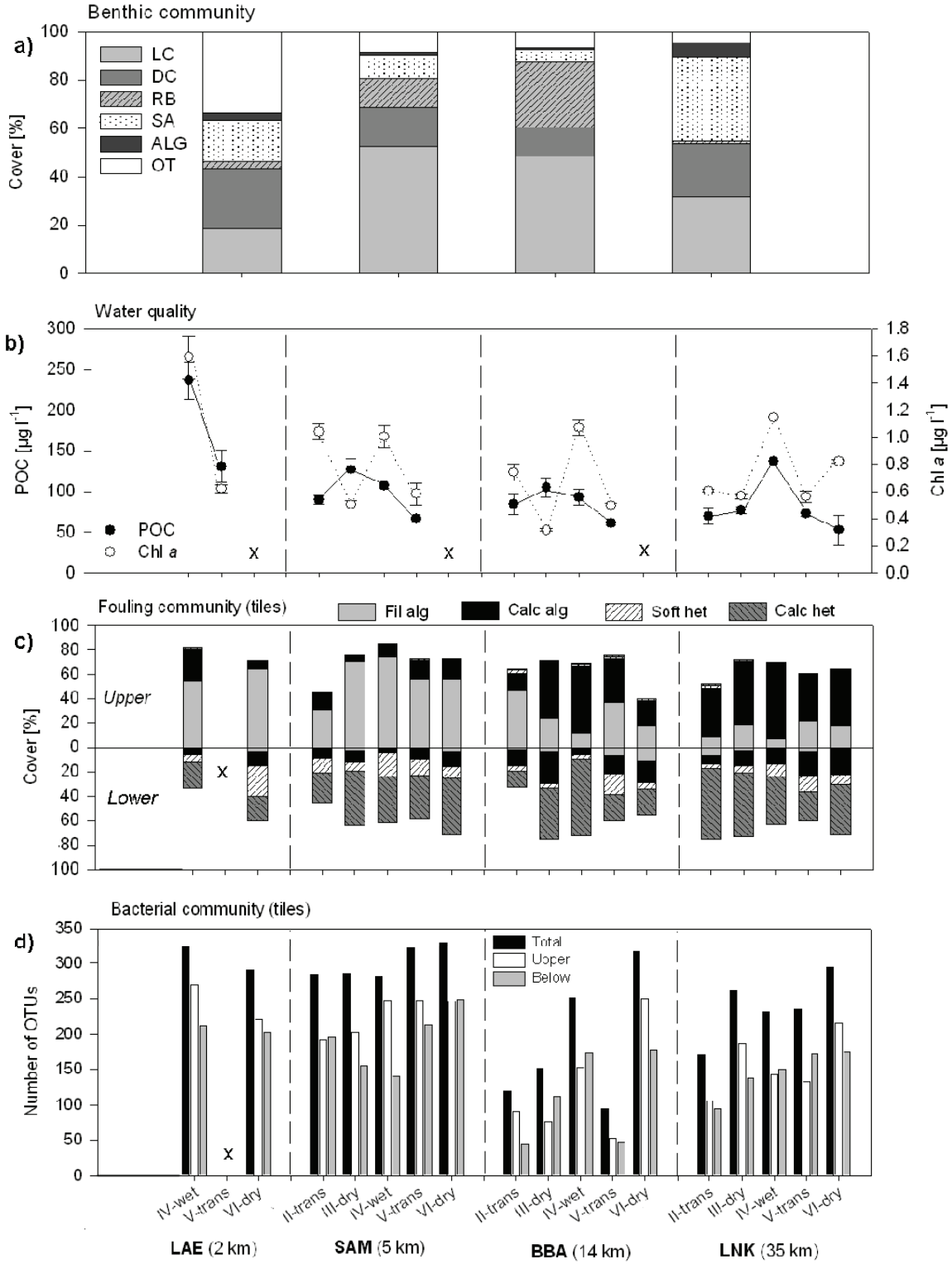

Fig. 2: Spatial pattern of (**a**) the benthic community structure including live coral (LC), dead coral (DC), coral rubble (RB), sand (SA), macroalgae (ALG) and others (OT). Spatial and seasonal patterns of (**b**) the major water parameter (mean ± SE): particulate organic carbon (POC) and chlorophyll *a* (chl *a*), (**c**) the fouling community on the upper and lower face of the tile pairs: filamentous algae (Fil alg), crustose coralline red algae (CCA), soft heterotrophs (Soft het: sponges and ascidians) and calcareous heterotrophs (Calc het: barnacles, spirorbid worms and bivalves), (**d**) the bacterial community (OTU number) on the tile pairs and on the upper and lower face separately. No data available (**x**).

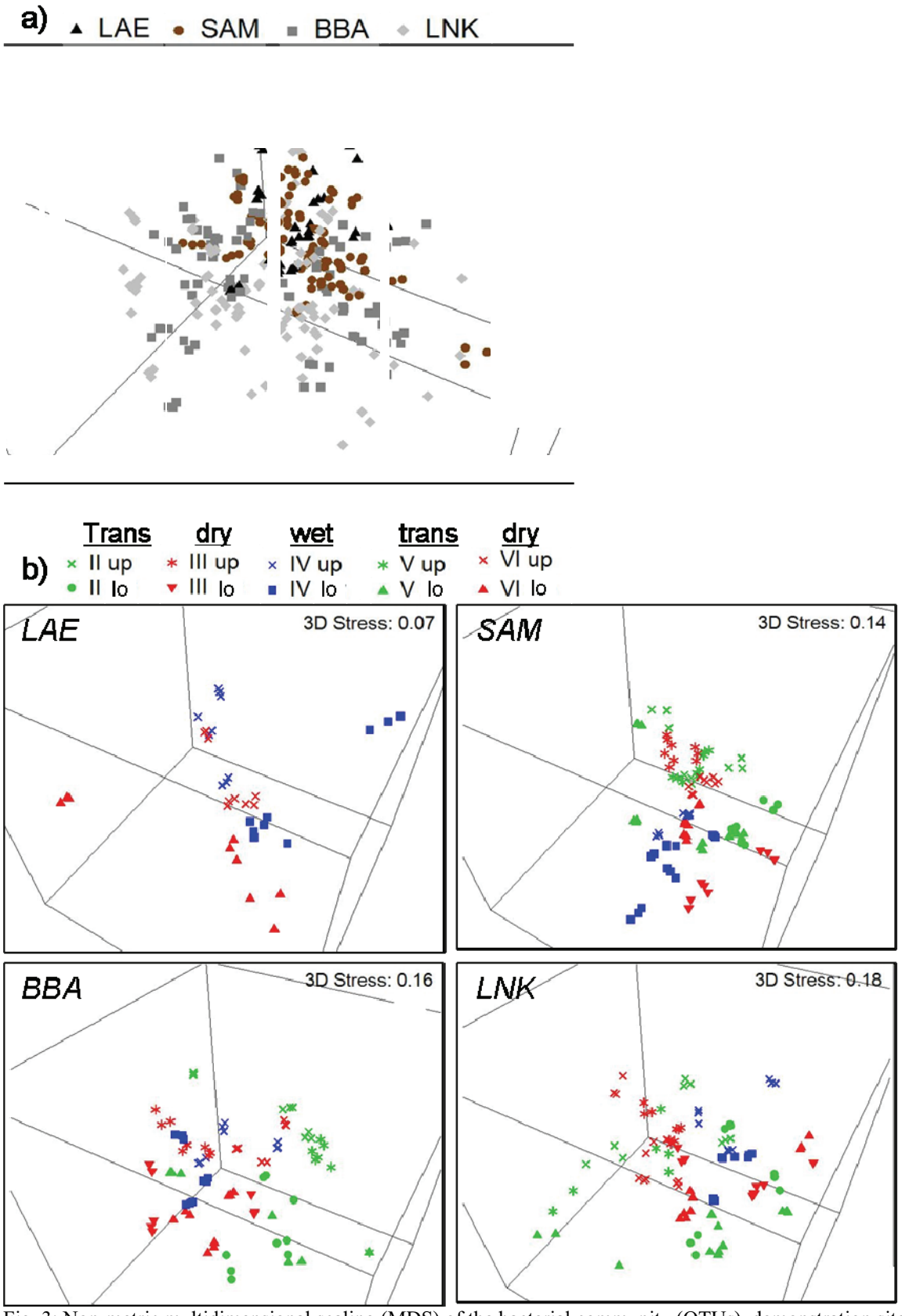

Fig. 3: Non-metric multidimensional scaling (MDS) of the bacterial community (OTUs), demonstration site difference (**a**) and seasonal and tile position (upper vs. lower) differences at the individual sites (**b**). Seasons: transition period (trans: II & V), dry season (dry: III & VI), wet season (wet: IV).

When the fouling community composition was included as a factor in the variation partitioning approach, the contribution of each single factor became insignificant, despite an overall significance of the multivariate model (data not shown), suggesting that more factor confounding was introduced in the model. Complementary, between group differences in community structure were detected in seasonality, which was higher on the upper tiles (ANOSIM, R=0.191, p=0.001) compared to the lower tiles (R=0.164, p=0.001, Table S3) and was overall strongest in mid-shelf BBA (R=0.312, p=0.001) and weakest in off-shore LNK (R=0.127, p=0.001, Table S3). Site differences were strongest between near mid-shelf SAM and off-shore LNK (R=0.156, p=0.001) and generally strongest during the wet season (IV: R=0.363, p=0.001) Table S3).

While variation partitioning is a powerful tool to assess the effects of several explanatory factors on the variation in one response data set (i.e. bacterial community structure), path analysis can go one step further by testing multivariate relationships in a causal modelling framework (Legendre & Legendre 1998). The likelihood of models involving directed dependencies (as represented by arrows) between the response variables and additional factors can be statistically determined and compared between models presenting different ecological scenarios. Because the factor "tile position" was nested into the site factor and a large number of samples is generally required for path analysis, the distinction of "tile position" was not further considered in path models (its significant effect was clearly demonstrated by variation partitioning though). Beginning with the most plausible relationships, the adequacy between the overall causal model and the original correlation matrix (as determined by simple and partial Mantel correlations) was assessed by Chi-square tests (here the P value should not be significant, because the proposed model should be in good agreement with the data at hand and not reject it) and the Bayesian Information Criterion (BIC, (Johnson & Omland 2004) that measures model fit and complexity (i.e. a lower BIC value indicates a better fit of the model). The initial model (Fig. 4a) resulted in a model (BIC = -18.85), in which bacterial community structure was directly influenced by environmental parameters (i.e. combined variation in POM, CN, DOC, and Chl *a*) with a path coefficient of 0.19, the fouling community (coefficient of 0.20), location (0.19), and to a lesser extent by benthic cover (0.14). Environmental parameters were mostly changing as a function of seasons (0.53) and geographic location (0.16). When other modifications of the initial configuration were tested, two best fitting models were found (BIC= -30.48 and -30.86), which can be described as followed: Model 1 (Fig. 4b), in which seasonality has a large effect (0.54) and distance from shore (site / distance) has a rather low effect (0.16) on the water parameters, which further influences the bacterial community (0.21). The bacterial community was also influenced by the fouling community (0.21) and directly by distance from shore (0.21). Together with the water parameters, they contribute to almost equal parts. Model 2 (Fig. 4c), in which the difference to Model 1 lies in the reversion of the arrow from bacterial community to fouling community, which resulted in an even better model fit with an increased site effect (0.23) and a higher influence of the bacterial community on the fouling community (0.25) than in Model 1 (0.21). The benthic cover was not included into the best fitting models, since it was shown to lower the model fit (e.g. in Model 2: adding an arrow from the benthic cover to bacterial community results in BIC of -28.14 or to the fouling community in BIC of -27.53).

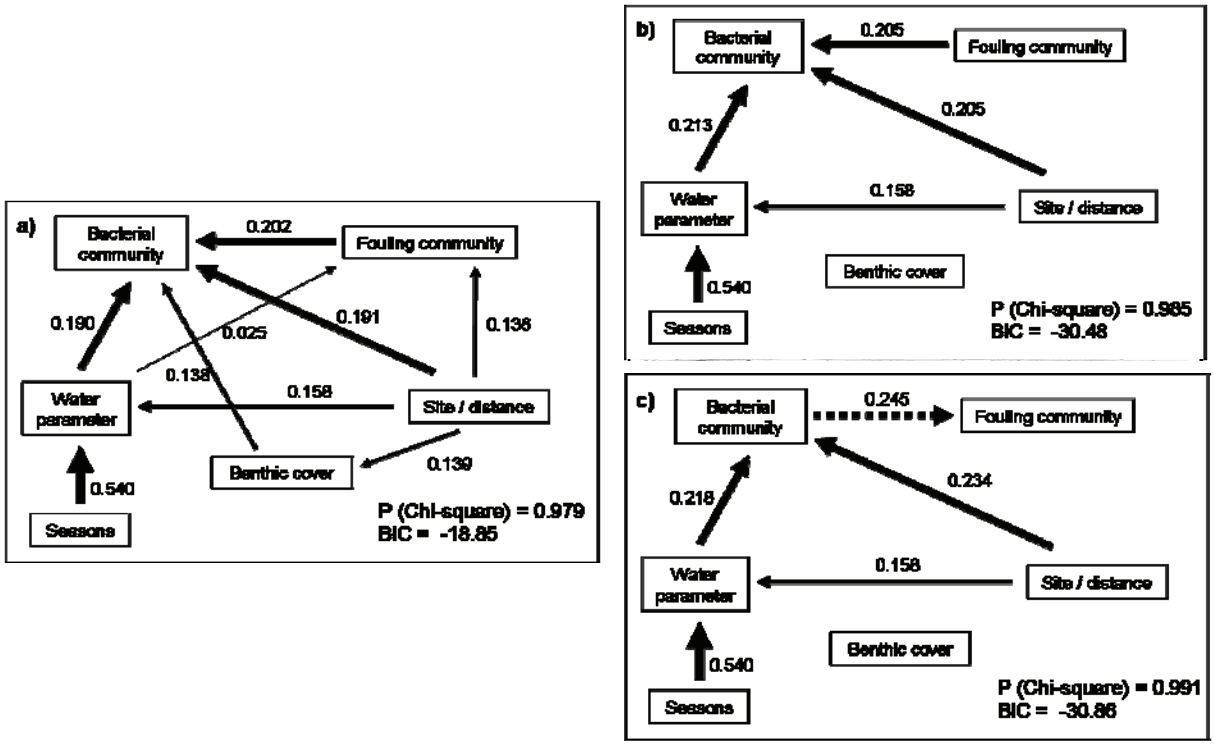

Fig. 4: Results of path analysis including the initial (**a**) and final models (**b, c**). In the initial model the path is directed from the fouling to the bacterial community (**b**) and in the second from the bacterial to the fouling community (**c**). The significance value for the Chi-square test is given, assessing whether the model is significantly different from the corresponding correlation matrix. The Bayesian Information Criterion (BIC) is a measure of the goodness-of-fit and needs to be minimized. The number on the arrow indicates the partial correlation coefficient associated with each causal relationship is indicated along the corresponding arrow, and arrow thickness is also proportional to the partial correlation value.

Discussion

The aim of the study was to assess the bacterial diversity of biofilms in coral reefs, their dynamics in relation to the associated macrofouling community and their response to seasonal and spatial variation in environmental conditions. Bacterial community structure associated with hard or sediment surfaces in coral reefs revealed spatial differences in response to eutrophication (Uthicke & McGuire 2007), possibly wave energy (Hewson & Fuhrman 2006b) and light availability (depth gradient) (Webster et al. 2004), while the effect of seasonality has not been addressed so far. This is the first study which explored eutrophication and seasonality at the same time and which further took into account the dynamics of the associated macrofouling community. Additionally, this study provides first data on bacterial dynamics in biofilms of coral reefs, which are situated within the global biodiversity hotspot, close to the equator, where seasonal fluctuations are not determined by temperature or light availability but rather by the amount of rain fall.

Concerning bacterial OTU number, the fact that Spermonde lies in the equatorial region with high an rather constant water temperatures, does not seem to enhance microbial richness, as it has been suggested for bacterioplankton over large geographic scales (Fuhrman et al. 2008). Indeed bacterial OTU number was highly variable (95 to 330 OTUs per sampling time and site) and was found to be within the range of previous studies, regardless of latitude or habitat,

although no robust comparisons are difficult to make, due to either differences in the applied fingerprinting technique (e.g. 60 OTUs identified by T-RFLP in the biofilm of an estuary [Nocker et al. 2004]), or due to the investigation of a different substrate (e.g. 51-148 OTUs in coral reef surface sediment in the Great Barrier Reef [Hewson & Fuhrman 2006b], 178-246 OTUs in temperate coastal sediment [Böer et al. 2009], 150 OTUs with high variability in deep water sediment off the coast of Norway [Schöttner et al. 2009]). A low latitudinal impact on biofilm microbial diversity was previously found in a study on coral reefs (Webster et al. 2004) and in the Antarctica (Webster & Negri 2006), although Antarctic biofilms may take longer to develop to reach comparable diversity. This together with our findings demonstrates that latitude and related temperature variability *per se* might not determine variation in bacterial OTU number in biofilms, but the fluctuations would much more depend on regional and habitat related variations in nutrient and light availability, which can vary greatly over space and time.

Although biofilms are known to consist of specific habitats that internally recycle nutrients and are protected by an extracellular matrix from possible hostile environments (Costerton et al. 1995, Hall-Stoodley et al. 2004), their dynamics strongly depend on the surrounding environment (Qian & Dahms 2009). This environmental effect was reflected in our study by remarkable differences in the bacterial diversity and composition within our investigated region. Bacterial diversity and composition could be significantly related to microhabitat, distance from shore (eutrophication) and seasons, although the overall explained variation was rather small (8 %), indicating that other factors not yet identified in this study may also be at play. Future studies would need to determine the nature and contribution of such factors to biofilm diversity.

Effect of microhabitat (sheltered vs. exposed)

The microhabitats created by the tiles, which provided a sheltered/shaded and exposed/high light environment, were associated with the greatest differences in colonizing bacterial communities as compared to regional or seasonal influences. While the sheltered habitat was characterized by low light and a heterogeneous fouling community structure that may provide a variety of surfaces for bacterial colonization, the exposed habitat was characterized by high light and a rather homogeneous algal cover. Interestingly bacterial OTU richness was higher on the exposed tiles, suggesting that the bacterial community may depend more on the energy resources than on the offered substrate diversity. Organic material permanently settles on the upper tiles and is produced by the algae themselves, and this provides a large variety and quantity of nutrients for bacterial growth (Cole 1982) and diversification (Costerton et al. 1995, Ford 2000). In contrast, on the lower side of the tiles the supply of organic material is lower, due to the low abundance of algae and light and obviously to the lesser amount of settling particles. Additional reasons for a higher diversity on the exposed tiles may first come from the possibly higher disturbance on the upper tiles (e.g. grazing by fishes), which continuously creates space for new species (Qian & Dahms 2009) and second, from the higher antibacterial spectrum and activity of the bioactive substances generally produced by macrofouling organisms (e.g. Al-Ogily & Knight-Jones 1977, Slattery et al. 1995, Armstrong et al. 2001) on the lower tile.

Effect of eutrophication

The eutrophication gradient was clearly evidenced in the fouling community structure by a shift from filamentous to crustose algae, which has previous been described as an indicator for eutrophication (Delgado & Lapointe 1994, Belliveau & Paul 2002). The benthic community

structure revealed strong signs of eutrophication and pollution in the most near-shore reef by a shift from hard corals to soft heterotrophic filter-feeding organisms (Edinger et al. 1998). However, eutrophication was hardly reflected in the measured water parameters, which is most likely due to the punctual, discontinuous nature of our water sampling campaign. Consequently, water parameters were weak indicators of eutrophication effects on bacterial community structure. Nevertheless, bacterial communities significantly changed with distance from shore, resulting in a higher diversity on near-shore reefs. This might be explained by the abundance of dense filamentous algae carpets in near-shore reefs, which provide an effective trap for sediment, particulate organic matter and associated pollutants, additionally to the above mentioned processes of sedimentation and of organic matter production by the algae themselves. Further, waste water discharge and riverine input provide a highly heterogeneous energy sources for bacterial decomposition, which supports diversity (Ford 2000) and usually entails a shift from auto- to heterotrophic bacteria (Meyer-Reil & Köster 2000, Uthicke & McGuire 2007). Considering the described scenario, it is also not surprising that the response of the bacterial community to eutrophication was stronger on the upper side compared to the lower side of the tiles.

Effect of seasonality

Seasonality was strongly reflected in the water parameters and only weakly in the fouling community. However, changes in bacterial community structure revealed a pronounced seasonality, which further suggests a high dependency on nutrition and the comparatively low response to substrate availability. The seasonal response of the bacterial community was most dramatic in the mid-shelf reefs (SAM & BBA): While near mid-shelf SAM kept high OTU numbers and the bacterial community structure varied to great extent, oligotrophic mid-shelf BBA experienced large differences in OTU richness, which consequently altered the community structure. Lowest OTU numbers were found on tiles from the transition period, most likely representing the most nutrient-depleted period occurring at the end of the transition period from wet to dry season. The low seasonality at off-shore LNK was most likely due to other oceanic factors (e.g. currents, upwelling) weakening seasonal patterns that normally dominate on the shelf, while low seasonality in near-shore LAE might be masked by chronically high nutrient supply.

Relationships between bacterial and fouling communities

Numerous studies have demonstrated the effects of biofilms on larval settlement by revealing large variations in species-specific responses and sensitivities (reviewed by Wieczorek & Todd 1998). Some newer studies have included the effect of environmental parameters on biofilms e.g. small changes in the type of organic nutrient supply or UV intensity, which caused significant changes in the microbial physiology or community structure and further affected larval settlement behavior (Hung et al. 2005, Jin & Qian 2005, Huang et al. 2007). Noticeably, settling macroorganisms also react to environmental changes, and thereby modify the chemical composition of their surface and consequently directly affect the bacterial community living on top (Armstrong et al. 2001). These strong dependencies were found in coral reef environments at the organism level as well (i.e. coral larvae, Webster et al. 2004) and in our study on a community level between the bacterial and fouling communities as clearly evidenced, although it was of rather low magnitude. Indeed, general trends over the region revealed different responses of the two communities: While the effect of eutrophication was evident on both communities and even more pronounced in the fouling community, seasonal fluctuations were clearly accompanied by changes in bacterial

community structure, but were almost not followed by the fouling community. Although we can not rule out, that the characterization of the two communities at different levels of taxonomic resolution might have masked some relationships between the two communities, the following reasons most likely explain part of this decoupling: First, after 4 months of tile deployment the bacterial community has established their own microenvironments (Costerton et al. 1995, Hall-Stoodley et al. 2004), which might have led to some independency from the fouling community. The same might be valid for the fouling community, which is also in an advanced state of succession after 4 months (Fairfull & Harriott 1999) allowing a certain independency from the biofilm. Second, the different generation times of micro- and macroorganisms might explain that microorganisms develop and adapt to environmental changes at different time scales as compared to the fouling community.

In conclusion, this study identified bacterial patterns in biofilms of coral reefs and the likely factors that significantly affect them, be there microhabitat, eutrophication level, seasonality or co-occurring fouling community. The emerging hypothesis is that nutrient availability may be a key parameter to investigate further if we are to better understand changes in diversity, community structure, and ultimately in functions. Because all factors had significant, yet modest contribution, other yet unknown factors may be at play in the study area and would need to be identified in the future. By incorporating additional deterministic and stochastic parameters in the models, the large amount of unexplained biological variation usually found in the ecological modelling of microbial communities (Ramette & Tiedje 2007, Fuhrman et al. 2008, Böer et al. 2009) can be reduced.

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Supplementary Material

Table S1: Composition of the benthic community at the different sites.

	Benthic cover [%]					
Site	Live coral	Dead coral	Coral rubble	Sand	Macroalgae	Others
LAE	18.3	25.2	2.8	17.2	2.9	33.5
SAM	52.5	16.2	12.0	9.7	1.3	8.4
BBA	48.4	12.0	27.3	5.0	0.6	6.6
LNK	31.9	21.8	1.1	34.5	6.1	4.6

	Composition of category "Others", benthic cover [%]				
Site	Soft coral	Sponge	Anemone	Ascidian	Hydrozoan
LAE	14.4	5.5	0.0	4.6	9.1
SAM	5.7	0.8	0.2	0.2	1.5
BBA	5.2	0.3	0.0	1.2	0.0
LNK	2.6	1.2	0.0	0.4	0.3

Table S2: Water parameter at the different sites and during the different seasons. Particulate organic carbon (POC), organic carbon / nitrogen ratio of particulate organic matter (C_{org}/N), dissolved organic carbon (DOC) and chlorophyll a (chl *a*). Sites from near- to off-shore: Lae Lae (LAE), Samalona (SAM), Bonebatang (BBA) and Lanyukan (LNK). N=3, mean (SE), no data available (n. d.).

Site	Season	POC [µg l^{-1}]	C_{org}/N ratio	DOC [µM]	Chl *a* [µg l^{-1}]
LAE	IV-wet	236.3 (22.8)	7.84 (1.02)	61.7 (0.8)	1.59 (0.16)
LAE	V-trans	130.8 (19.9)	6.72 (2.23)	95.4 (12.1)	0.62 (0.07)
LAE	VI-dry	n. d.	n. d.	n. d.	n. d.
SAM	II-trans	89.9 (5.6)	8.05 (0.58)	71.9 (6.6)	1.04 (0.06)
SAM	III-dry	126.9 (13.3)	7.24 (1.73)	55.7 (5.4)	0.50 (0.03)
SAM	IV-wet	106.9 (2.6)	6.69 (0.51)	74.7 (1.4)	1.00 (0.08)
SAM	V-trans	66.6 (1.7)	8.39 (0.49)	95.8 (1.8)	0.58 (0.08)
SAM	VI-dry	n. d.	n. d.	n. d.	n. d.
BBA	II-trans	84.3 (12.8)	7.84 (1.60)	98.9 (7.4)	0.74 (0.06)
BBA	III-dry	104.8 (11.8)	9.57 (1.66)	52.2 (7.1)	0.32 (0.01)
BBA	IV-wet	92.9 (9.8)	8.38 (1.40)	147.1	1.07 (0.06)
BBA	V-trans	60.7 (1.9)	8.32 (0.78)	76.8 (2.6)	0.50 (0.02)
BBA	VI-dry	n. d.	n. d.	n. d.	n. d.
LNK	II-trans	69.8 (10.1)	8.32 (1.42)	133.1 (35.4)	0.61 (0.01)
LNK	III-dry	77.0 (4.0)	7.69 (0.80)	68.0 (2.9)	0.57 (0.02)
LNK	IV-wet	137.0	9.76	124.3	1.17
LNK	V-trans	72.7 (2.6)	8.74 (0.05)	133.8 (24.5)	0.56 (0.04)
LNK	VI-dry	52.8 (18.1)	5.65 (2.00)	84.5 (1.6)	0.82 (0.01)

Table S3: Results of Analysis of Similarity (ANOSIM) representing the spatial and seasonal pattern of the bacterial and fouling community. (Global) R is a measure of community overlap with 0=completely overlapping and 1=completely dissimilar. Significant results are indicated by an asterisk: * $p<0.05$ and ** $p<0.001$ and $R>0.2$ in bold.

Factor	Bacterial community (OTUs)	Global R	Fouling community	Global R
Tile position (upper/below)		**0.202****		**0.819****
	strongest at LAE	**0.401****	strongest at SAM	**0.976****
	lowest at BBA	**0.272****	lowest at BBA	**0.725****
Season		0.149**		0.035*
	strongest btw II & IV and V & IV	**0.259**, 0.252****	strongest btw II & V	0.094*
	lowest btw II & V	0.058*	lowest btw IV & VI	0.005
	strongest at BBA	**0.312****	strongest a LAE & BBA	0.142**, 0.102**
	lowest at LNK	0.127**	lowest at SAM & LNK	0.031, 0.035
upper face		0.191**		0.046
	strongest btw. IV & V	**0.359****	strongest btw. II & III	0.058*
	lowest btw. II & III	0.044	lowest btw. IIII & IV	0.007
	strongest at SAM & BBA	**0.506**, 0.468****	strongest at BBA	**0.296****
	lowest at LNK	**0.309****	lowest at SAM	0.131**
lower face		0.164**		0.105**
	strongest btw IV & V	**0.228****	strongest btw II & III	0.115**
	lowest btw III & IV	0.084*	lowest btw V & VI	0.060
	strongest at BBA & SAM	**0.402**, 0.379****	strongest at BBA	**0.373****
	lowest at LNK	**0.220****	lowest at SAM	0.141**
Site (distance from shore)		0.085**		0.097**
	strongest btw SAM & LNK	0.156**	strongest btw LAE & LNK	**0.272****
	lowest btw BBA & LNK	0.058**	lowest btw LAE & SAM	0.006
	strongest in IV	**0.363****	strongest in III & IV	0.173**, 0.145**
	lowest in III & II	0.171**, 0.172**	lowest in III & II	0.097*
upper face		0.196**	lowest in II	0.330**
	strongest btw SAM & BBA	**0.215****	strongest btw LAE & LNK	**0.696****
	lowest btw LAE & SAM	0.136	lowest btw LAE & SAM	0.011
	strongest in season V	**0.617****	strongest in season IV	**0.586****
	lowest in season II	**0.285****	lowest in season V	**0.320****
lower face		0.148**		0.138**
	strongest btw LAE & LNK	**0.203****	strongest btw LAE & LNK	0.397**
	lowest btw LAE & SAM	0.101	lowest btw SAM & BBA	0.055
	strongest in season II & IV	**0.558**, 0.524****	strongest in season II & IV	**0.391**, 0.375****
	lowest in season V	0.151*	lowest in season V	0.195**

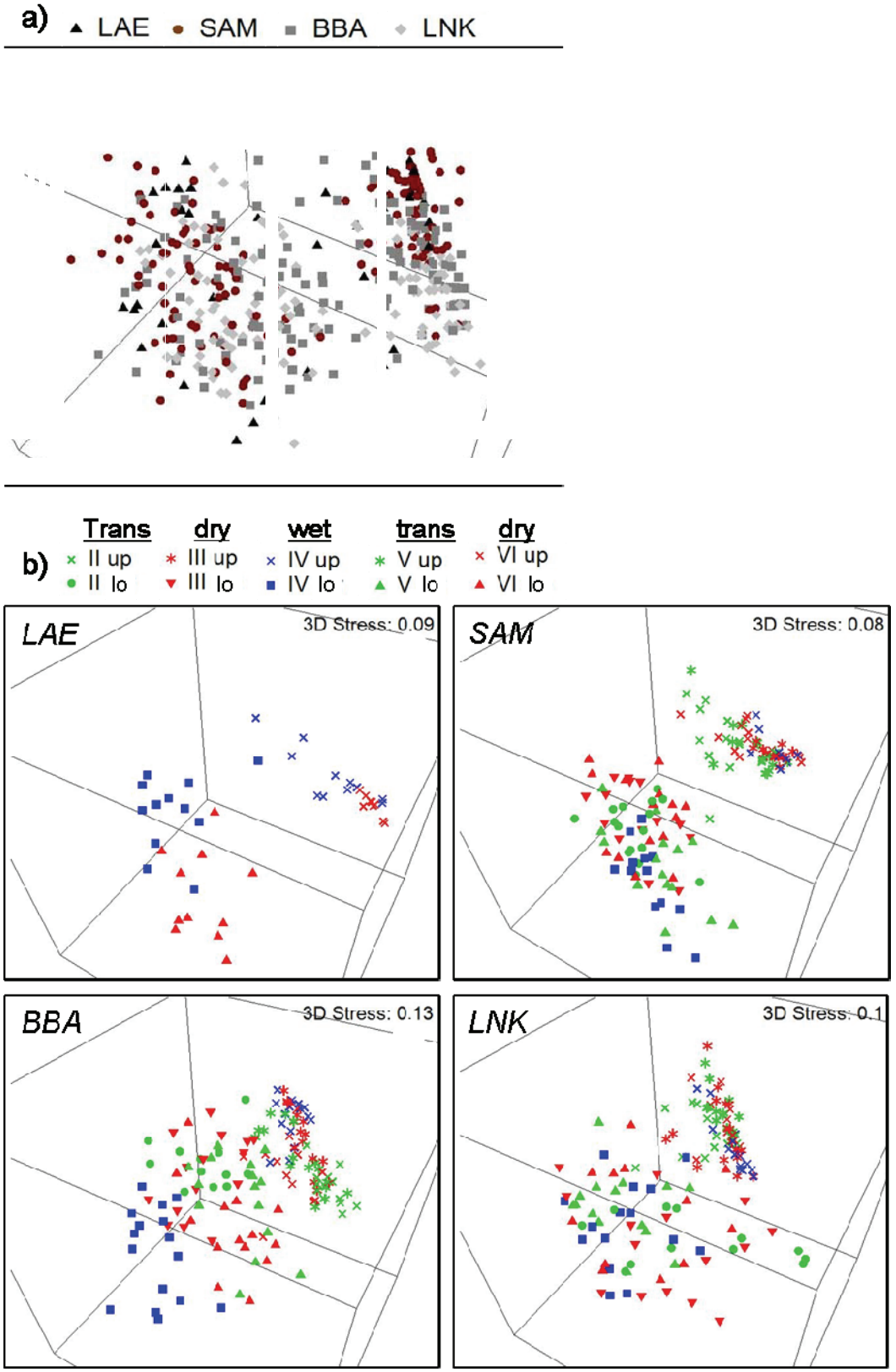


Fig. S1: Non-metric multidimensional scaling (MDS) of the fouling community, demonstration site difference (a) and seasonal and tile position (upper vs. lower) differences at the individual sites (b). Seasons: transition period (trans: II & V), dry season (dry: III & VI) and wet season (wet: IV).

Table S4a: Composition of fouling community on the tiles. Replicate number refers to tile pairs. Data is given in %, mean (SE).

			Filamentous algae		Crustose coralline red algae		Soft heterotrophs		Calcareous heterotrophs	
Site	Season	Replicate #	upper	lower	upper	lower	upper	lower	upper	lower
LAE	II-trans	0								
LAE	III-dry	0								
LAE	IV-wet	11	54.5 (10.2)	1.25 (0.7)	25.5 (5.5)	4.6 (1.3)	0.0	5.8 (2.6)	2.0 (1.1)	21.2 (6.0)
LAE	V-trans	0								
LAE	VI-dry	11	64.5 (4.1)	3.6 (1.5)	6.8 (0.8)	11.4 (2.0)	0.0	25.0 (10.0)	0.1 (0.1)	19.9 (5.9)
SAM	II-trans	15	30.3 (5.1)	1.25 (0.6)	13.0 (1.9)	7.5 (1.0)	1.0 (1.0)	11.9 (4.5)	0.5 (0.2)	24.4 (3.6)
SAM	III-dry	16	70.7 (3.4)	3.2 (0.8)	5.3 (1.1)	8.9 (1.8)	0.0	7.5 (3.8)	0.1 (0.0)	44.3 (9.4)
SAM	IV-wet	13	74.2 (4.7)	0.0	10.4 (3.9)	4.6 (0.9)	0.0	19.2 (5.7)	0.1 (0.1)	38.1 (9.8)
SAM	V-trans	15	56.1 (7.0)	1.3 (0.8)	15.4 (4.6)	7.7 (1.0)	0.0	13.7 (4.5)	1.8 (1.0)	35.1 (7.9)
SAM	VI-dry	16	55.7 (6.4)	4.0 (1.0)	16.9 (3.9)	12.0 (2.4)	0.0	9.3 (3.1)	0.4 (0.2)	46.0 (9.4)
BBA	II-trans	13	47.1 (4.7)	2.5 (0.8)	13.9 (2.4)	12.5 (5.3)	2.9 (1.5)	4.2 (1.9)	0.2 (0.1)	13.2 (2.5)
BBA	III-dry	16	24.4 (3.7)	4.0 (0.9)	46.3 (5.1)	25.3 (4.4)	0.6 (0.4)	3.9 (1.8)	0.2 (0.1)	41.8 (9.2)
BBA	IV-wet	16	12.2 (1.5)	1.25 (0.8)	54.1 (4.7)	4.4 (0.5)	1.9 (1.0)	3.5 (1.8)	0.5 (0.5)	63.2 (10.8)
BBA	V-trans	16	36.9 (5.5)	6.6 (2.4)	36.3 (4.8)	1.50 (2.3)	1.3 (0.7)	16.9 (4.2)	1.3 (0.5)	22.1 (5.7)
BBA	VI-dry	14	17.9 (2.4)	11.1 (2.7)	20.7 (5.2)	17.9 (3.0)	1.1 (1.1)	5.1 (2.0)	0.2 (0.2)	20.8 (5.0)
LNK	II-trans	15	8.3 (1.1)	6.7 (1.5)	40.4 (4.4)	7.1 (1.1)	2.1 (1.7)	3.8 (1.7)	1.1 (0.5)	57.9 (15.3)
LNK	III-dry	16	18.8 (3.8)	2.7 (1.1)	51.3 (6.4)	12.3 (5.3)	0.9 (0.5)	5.7 (2.7)	1.4 (0.8)	52.1 (11.4)
LNK	IV-wet	16	7.2 (1.6)	1.7 (0.8)	62.2 (5.3)	12.0 (1.8)	0.0	10.0 (2.7)	0.6 (0.2)	29.3 (8.8)
LNK	V-trans	15	21.3 (2.0)	4.0 (1.4)	39.0 (3.4)	18.7 (3.2)	0.0	14.0 (3.2)	0.0	23.4 (5.0)
LNK	VI-dry	12	17.5 (2.2)	1.7 (1.1)	46.3 (4.9)	20.8 (3.3)	0.4 (0.4)	7.9 (3.5)	0.3 (0.2)	41.5 (8.7)

Table S4b: Composition of soft heterotrophs and calcerous heterotrophs on tiles. Data is given in %, mean (SE)

		Soft heterotrophs				Calcareous heterotrophs							
		Sponges		Ascidians		Bryozoans		Barnacles		Spirobid worms		Bivalves	
Site	Season	upper	lower	upper	lower	upper	lower	upper	lower	upper	lower	upper	lower
LAE	II-trans												
LAE	III-dry												
LAE	IV-wet	0.0	0.8 (0.6)	0.0	5.0 (2.0)	0.5 (0.5)	6.7 (2.7)	0.3 (0.1)	1.6 (0.2)	1.0 (0.3)	12.4 (2.7)	0.3 (0.2)	0.5 (0.3)
LAE	V-trans												
LAE	VI-dry	0.0	5.5 (2.0)	0.0	19.5 (8.1)	0.0	4.5 (1.8)	0.0	0.2 (0.1)	0.1 (0.1)	15.1 (3.9)	0.0	0.0
SAM	II-trans	0.0	1.6 (0.8)	1.0 (1.0)	10.3 (3.7)	0.0	12.5 (0.6)	0.0	0.1 (0.1)	0.4 (0.1)	11.1 (1.7)	0.1 (0.1)	0.6 (0.3)
SAM	III-dry	0.0	1.1 (0.6)	0.0	6.4 (3.2)	0.0	34.0 (7.1)	0.0	0.3 (0.1)	0.1 (0.0)	8.9 (1.7)	0.0	1.1 (0.6)
SAM	IV-wet	0.0	4.6 (1.6)	0.0	14.6 (4.1)	0.0	21.9 (5.1)	0.0	3.6 (1.3)	0.1 (0.1)	10.3 (2.7)	0.0	2.2 (0.7)
SAM	V-trans	0.0	6.0 (2.1)	0.0	7.7 (2.3)	1.4 (0.8)	23.0 (4.5)	0.0	3.0 (1.1)	0.4 (0.1)	8.3 (2.0)	0.0	1.0 (0.4)
SAM	VI-dry	0.0	2.3 (0.7)	0.0	7.0 (2.5)	0.0	31.7 (5.5)	0.0	0.2 (0.1)	0.2 (0.1)	9.7 (1.7)	0.1 (0.1)	4.4 (2.0)
BBA	II-trans	0.0	0.0	2.9 (1.5)	4.2 (1.9)	0.0	7.9 (1.6)	0.0	0.0	0.2 (0.1)	4.6 (0.6)	0.1 (0.1)	0.7 (0.3)
BBA	III-dry	0.0	0.3 (0.3)	0.6 (0.4)	3.6 (1.4)	0.0	33.3 (7.5)	0.0	0.0	0.1 (0.0)	7.8 (1.4)	0.1 (0.1)	0.6 (0.3)
BBA	IV-wet	0.0	1.3 (0.8)	1.9 (1.0)	2.2 (1.1)	0.3 (0.3)	52.8 (7.4)	0.0	3.0 (1.3)	0.1 (0.1)	5.9 (1.3)	0.1 (0.1)	1.4 (0.7)
BBA	V-trans	0.0	2.8 (1.4)	1.3 (0.7)	14.1 (2.8)	0.0	14.1 (3.9)	0.0	0.0	1.2 (0.4)	6.5 (1.0)	0.1 (0.1)	1.5 (0.8)
BBA	VI-dry	0.0	4.3 (1.5)	0.7 (0.7)	0.8 (0.5)	0.0	12.1 (2.3)	0.0	0.5 (0.2)	0.1 (0.0)	5.0 (1.5)	0.1 (0.1)	3.2 (1.0)
LNK	II-trans	0.0	0.8 (0.6)	2.1 (1.7)	2.9 (1.1)	0.0	12.9 (2.9)	0.0	0.0	0.9 (0.3)	7.5 (0.8)	0.3 (0.2)	37.4 (11.6)
LNK	III-dry	0.0	2.3 (1.0)	0.9 (0.5)	3.3 (1.7)	0.6 (0.4)	33.7 (7.0)	0.0	0.8 (0.2)	0.1 (0.0)	1.5 (0.3)	0.6 (0.3)	16.1 (3.8)
LNK	IV-wet	0.0	1.0 (0.5)	0.0	9.0 (2.2)	0.0	24.0 (5.0)	0.0	0.1 (0.0)	0.1 (0.0)	7.8 (1.3)	0.5 (0.2)	7.4 (2.4)
LNK	V-trans	0.0	1.0 (0.5)	0.0	13.0 (2.7)	0.0	16.7 (2.9)	0.0	0.2 (0.1)	0.2 (0.1)	3.1 (0.3)	0.1 (0.1)	3.4 (1.6)
LNK	VI-dry	0.0	1.7 (0.7)	0.4 (0.4)	6.3 (2.8)	0.0	33.3 (5.3)	0.0	0.4 (0.2)	0.1 (0.0)	2.3 (0.5)	0.2 (0.2)	5.6 (2.7)

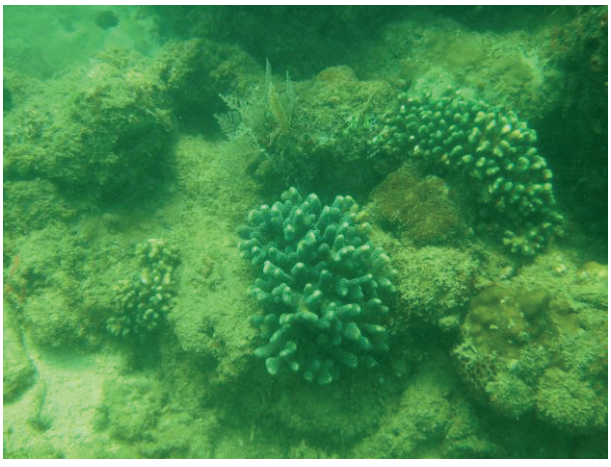
Impressions

Near-shore Lae Lae

Harbor of Makassar

Island Lae Lae in front of Makassar (distance ~2 km)

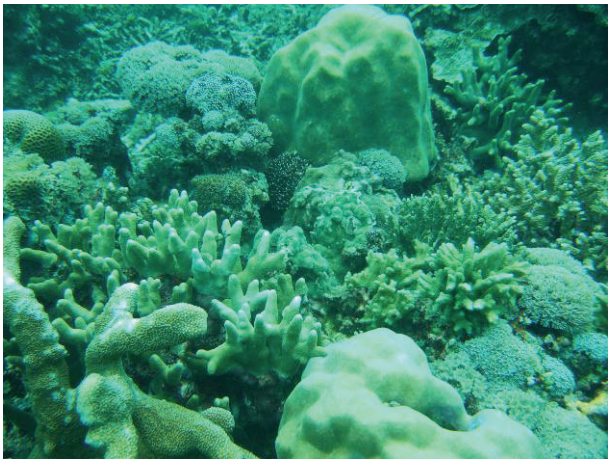
Benthic community structure



Stylophora in Lae Lae

Mid-shelf Bonebatang

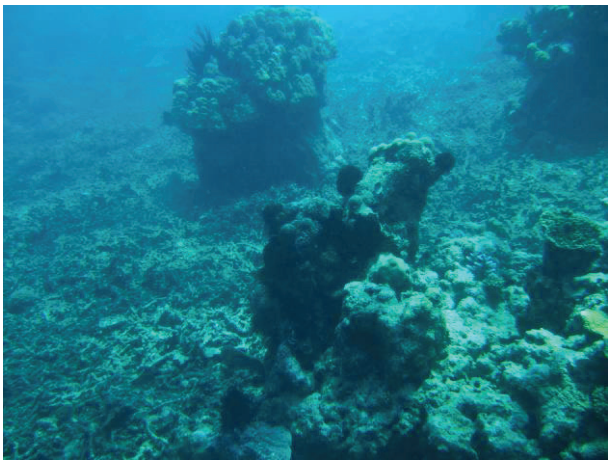
Island Bonebatang (distance from Makassar ~14 km)

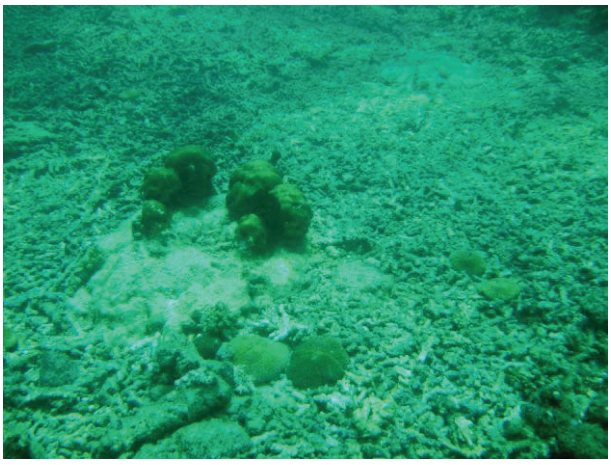


Benthic community structure

Benthic community structure

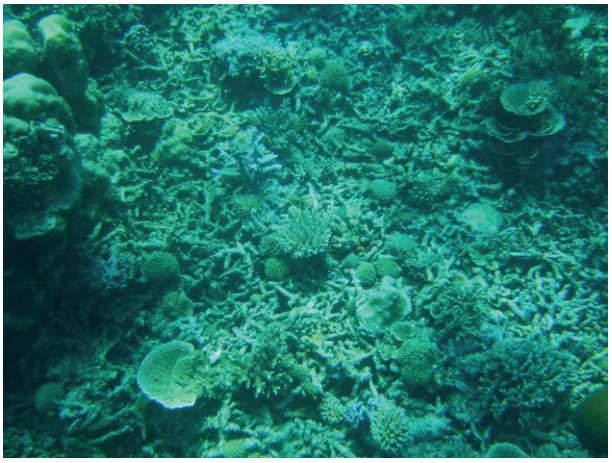
Bombing impact ...





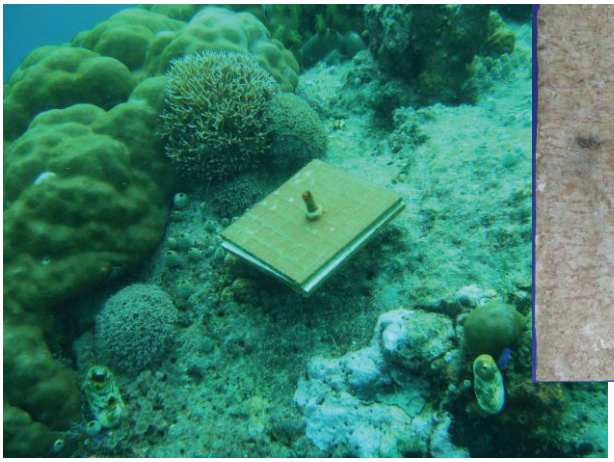
Rubble fields and bombing crater

and recovery



Young coral colonies on rubble

Settlement-tiles and coral spat

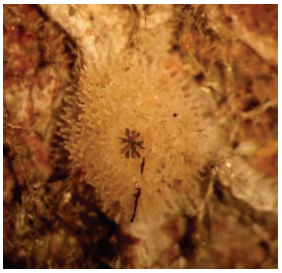


Fixation of tile pair (15 x 15 cm)

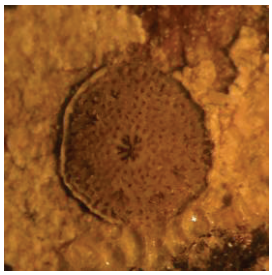
Upper tile from Samalona with filamentous algae

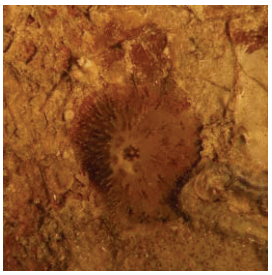
Upper tile from Lanyukan with crusose algae

Coral larvae settlement on tile edge

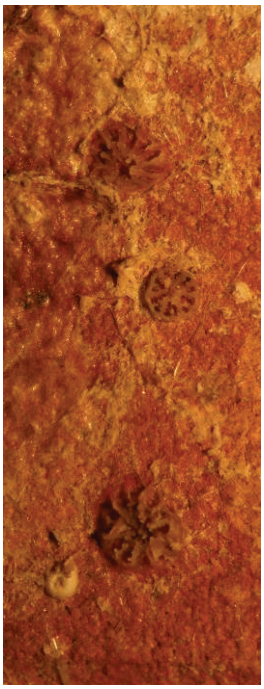


Acroporidae (Ø 2.5 mm)





Acroporidae (Ø 3.5 mm) and Pocilloporidae (4 mm)

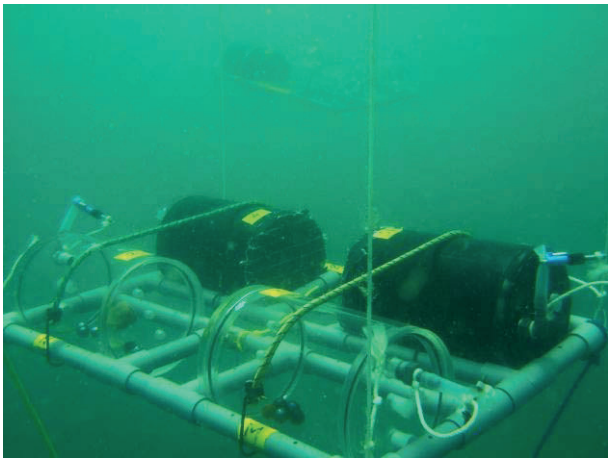


Poritidae (middle, Ø 0.8 mm) and others

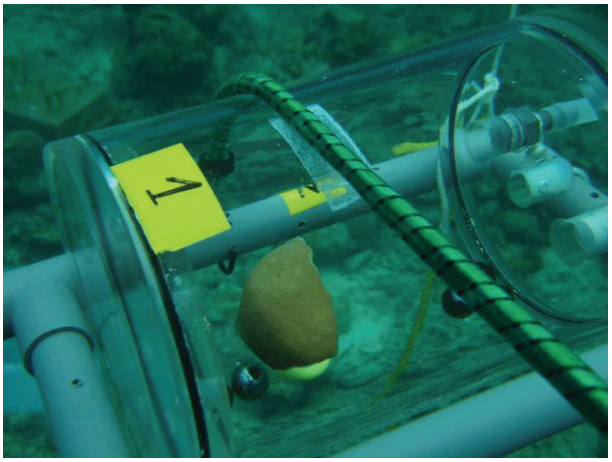
Coral spat (Ø 2.5 mm) between spirobid worms and bryozoans

Diverse coral spat (Ø 2.5 – 3 mm)

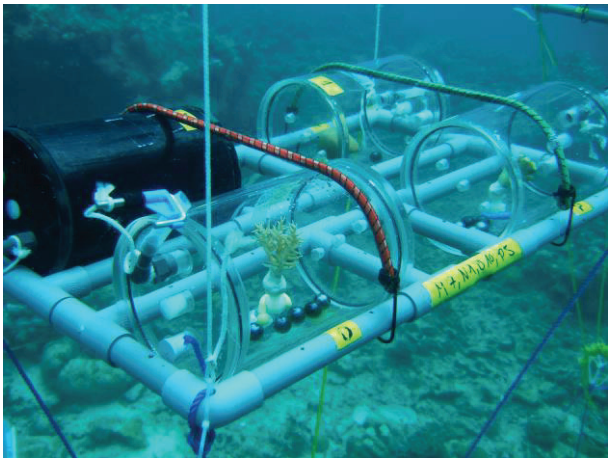
In situ *incubations*



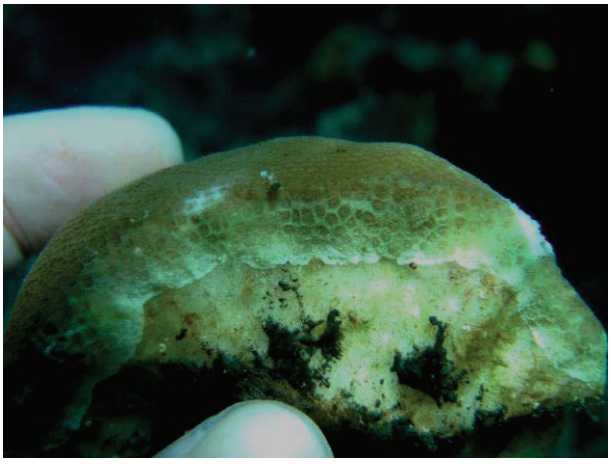
Incubations at near-shore Lae Lae



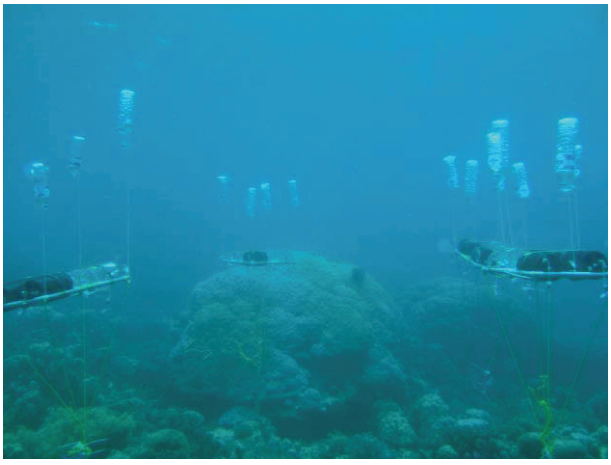
Incubation of a *Porites lutea* fragment



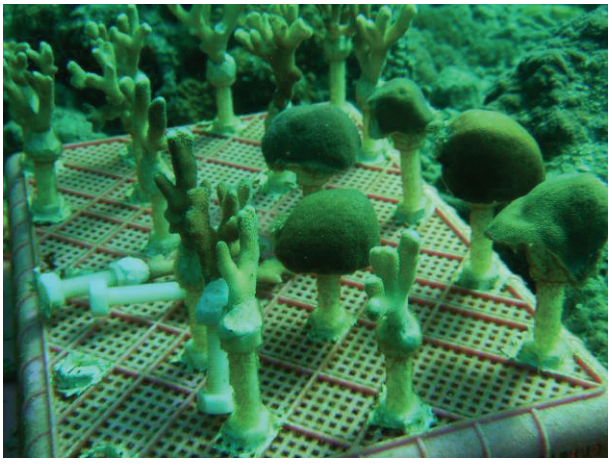
Incubations at far mid-shelf Bonebatang



Re-sheeting tissue of a *Porites lutea* fragment



Incubations at far mid-shelf Bonetambung



Preparation of coral fragments (*Porites lutea* & *Stylophora subseriata*)