

Coral Acclimatization to Disturbance

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Zusammenfassung

Die globale Verbreitung tropischer Flachwasserriffe wird durch Temperatur, Salzgehalt, Licht und Aragonitsättigung auf einen Gürtel entlang 30° Nord und Süd des Äquators beschränkt. Innerhalb dieser geographischen Grenzen spielen viele weitere Faktoren wie Strömung, Nährstoffgehalt oder das Vorkommen von Plankton und partikulärem oder gelöstem organischem Material eine wichtige Rolle für die Entstehung und das Fortbestehen von Riffen, sowie für deren Kondition.

Viele dieser Faktoren sind eng miteinander gekoppelt, verstärken sich gegenseitig oder schwächen sich ab und haben oft gleich mehrere direkte und indirekte Auswirkungen auf Organismus- oder Ökosystemlevel. Erhöhte Nährstoffeinträge (Kapitel I, IV, VI) verstärken nicht nur die Vermehrung der Symbionten in Korallen (Zooxanthellen) und deren Photopigmente, sondern fördern auch die Ausbreitung von benthischen Algen, welche als grösste Konkurrenten um Licht und Raum gelten. Übermässig angetriebenes Phytoplanktonwachstum kann ausserdem zu einer Trübung der Wassersäule und somit zu einer verminderten Lichtzufuhr für die Benthosgemeinschaft führen. Strömungen (Kapitel II) verringern die Grenzschicht zwischen Koralle und Umgebungswasser und erhöhen somit den Gas- und Nährstoffaustausch. Ausserdem gewährleisten sie den Nachschub von anorganischem und organischem Material für Photosynthese und aktive Nahrungsaufnahme, sowie den Abtransport ausgeschiedener Stoffe (Kapitel I, II, III). Zudem sind Strömungen für die Resuspension und Verbreitung von Sedimenten und assoziierten Teilchen verantwortlich, welche beim Verweilen in der Wassersäule Trübung verursachen und beim Absinken eine Erstickungsgefahr für benthische Organismen darstellen. Heftige Strömungen oder Wellen können ausserdem eine Bruchgefahr für Korallenskelette darstellen.

Viele dieser lokalen Einflüsse können sowohl natürlichen (Kapitel I bis V) als auch anthropogenen (Kapitel VI, VII) Ursprungs sein. Während der anthropogene Einfluss (abgesehen von globalen Veränderungen wie Temperaturanstieg oder Ozeanversauerung) mit Distanz zur Küste abnimmt, sind offshore-Riffe häufig stark von ihrer ozeanischen Umgebung bestimmt. Je nach Art, Intensität, Häufigkeit und Dauer der Störung wird die Funktionalität eines Riffes und seiner Bewohner mehr oder minder beeinflusst. Einige Faktoren wie Saisonalität oder Gezeiten können dabei sowohl für küstennahe (Kapitel I, VI), als auch für offshore-Riffe (Kapitel I bis VI) eine Rolle spielen.

Offshore-Riffe werden stark durch ihre ozeanische Umgebung beeinflusst (Kapitel I bis V), welche oftmals sehr variable sein kann. 60 km vor der Westküste Thailands werden die Riffe entlang der Westseite der Similaninseln von brechenden Internen Wellen Grosser Amplitude (Large Amplitude Internal Waves, LAIW) heimgesucht. Im Gegensatz dazu sind die Riffe auf der Ostseite der Inseln im geringeren Masse dem LAIW-Einfluss ausgesetzt. Die LAIW, welche impulsartig kaltes, sauerstoffarmes und CO₂- sowie nährstoffreiches Tiefenwasser in die Riffe eintragen, verändern den Metabolismus der dort siedelnden Korallen nachhaltig.

Abhängig von LAIW-Intensität und -Frequenz (Kapitel I), die sich innerhalb derselben Saison verschiedener Jahre drastisch unterscheiden kann, kommt es zu teilweise extrem hohen Nährstoffeinträgen. Diese fördern zwar Zooxanthellenwachstum und Pigmentbildung, die Photosyntheseleistung aber wird reduziert (Kapitel I, III, IV). Starke LAIW-verursachte Strömungen erhöhen den Fluss gelöster und partikulärer organischer Stoffe und unterstützen somit die aktive Nahrungsaufnahme der Korallen (Kapitel II). Gleichzeitig bewirkt die erhöhte Verfügbarkeit organischer und inorganischer Nährstoffe auch eine erhöhte Abgabe gelöster und partikulärer Substanzen (Schleim) durch die Korallen (Kapitel III). Die Kombination aus hohen Zooxanthellendichten und aktiver Nahrungsaufnahme auf der Westseite führen ausserdem zu höherer Biomasse und Energiespeicher in den Korallen (Kapitel I, II). Diese machen sie im Gegensatz zu den Korallen der Ostseiten belastbarer und überlebensfähiger in Extremsituationen (Kapitel II). Der Preis für die höheren Energiespeicher und Biomassen ist eine erhöhte Respiration und geringere, kostenintensivere Photosynthese (Kapitel III). Auch die Kalzifizierung unter LAIW-Einfluss ist aufgrund der geringeren Aragonitsättigung des aufgetriebenen Tiefenwassers dezimiert (Kapitel III). Zudem sind LAIW-eigene niedrige Temperatur und geringer Sauerstoffgehalt für langsames Korallenwachstum und niedrigere Photosyntheseraten verantwortlich. Zusätzlich zum SW-Monsun, der vor allem die Flachwasserbereiche der westlichen Inseln beeinflusst, führen die vielseitigen LAIW-Einflüsse zu einem stark reduzierten Riffwachstum (Kapitel V), mit geringeren Bedeckungsgraden, aber auch höherer Biodiversität. Die Anpassungen an den LAIW-Einfluss variieren zwischen den verschiedenen Korallenarten (Kapitel I). Inkubationen haben gezeigt, dass sich diese auch unter nicht LAIW-Konditionen entfalten (Kapitel III), bevor eine Anpassung an eine anderweitige Umgebung stattfindet (Transplantationsexperiment Kapitel II). Gleichwohl bleibt die Frage, ob es sich bei der hohen Flexibilität der Korallen unter LAIW-Einfluss um eine metabolische Anpassung oder gar eine genetische Adaptation handelt. Die Studien über die Anpassungsfähigkeit von Riffen an LAIW-Gegebenheiten dienen auch als Grundlage zum Verständnis, wie sich Riffe im

Hinblick auf den globalen Klimawandel (Temperaturanstieg und Ozeanversauerung) entwickeln könnten.

Einträge von Nährstoffen und Sedimenten an der Karbikküste Costa Ricas (Kapitel VI) sind stark von den Ausmassen der Trocken- und Regenzeit bestimmt. Mit ansteigendem Regen werden vermehrt Nährstoffe aus stark gedüngten Böden bewirtschafteter Felder in küstennahe Gewässer ausgespült und mit dem Fluss ins Meer eingetragen. Dort werden sie mit Hilfe der Strömungen bis in die Riffgebiete des Nationalparks von Cahuita verbreitet und nachweislich von den Korallen aufgenommen. Durch den exzessiven Anbau von Monokulturen im Küstenraum steigt auch die Bodenerosion, was durch hohe Silikateinträge deutlich wird. Als Konsequenz gelangen mit Flüssen und Strömungen hohe Mengen partikulären Materials in die Riffe, wo sie die Wassersäule trüben, Korallen bedecken und letztendlich ersticken. Verglichen mit Riffen ähnlicher geographischer Ausrichtung sind die im Nationalpark Cahuita starker Eutrophierung ausgesetzt.

Auch entlang der Nordostküste Hainans, China, fordern die Folgen der raschen Küstenentwicklung ihren Tribut (Kapitel VII). Starke Eutrophierung und Sedimentation durch unbehandelte Abwässer aus Aquakultur und rasant wachsenden Küstensiedlungen überdüngen die Küstengewässer und trüben die Wassersäule. Exzessive Aquakultur kann zusätzlich zur Einführung von Krankheiten, fremder Arten oder Pestizide führen. Ein weiteres grosses Problem ist die offensichtliche weite Verbreitung destruktiver Fischereimethoden, wie zum Beispiel Dynamitfischerei, welche bereits einen grossen Teil der Riffe zerstört hat. Die so entstandenen losen Böden sind unvorteilhaft für das Ansiedeln von Korallenlarven. Die Kombination aus Überfischung und hohen Nährstoffkonzentrationen stellt eine enorme Gefahr für Riffe dar, da eine Kontrolle des Algenwachstums durch herbivore Fische nicht mehr gewährleistet ist und die Algen sich auf dem losen Boden im nährstoffreichen Wasser besser durchsetzen können als Korallen. Überlebende Korallen haben eine geringere Photosyntheseleistung durch die Trübung der Wassersäule, vergleichbar mit Korallen aus tieferem Wasser. Die starke Sedimentierung erfordert zusätzlich einen hohen Energieaufwand der Korallen, welche sich durch Schleimproduktion von ablagerndem Sediment säubern müssen.

Eine Abnahme der Korallenlebensbedeckung und Diversität im Untersuchungsgebiet in Costa Rica und eine Verschiebung von einem Korallen dominierten zu einem Algen dominierten Riffsystem in Hainan sind deutliche Anzeichen, dass die Ökosysteme gefährdet sind und unter dem ständig wachsenden Druck über kurz oder lang drohen zu kollabieren. Da die Störungen

hier - im Gegensatz zu den impulsartigen Störungen der LAIW - chronisch sind und sich im Laufe der Zeit verstärken, ist ihre Bedrohung akut.

Summary

The global distribution of tropical shallow water coral reefs within the tropical belt of 30° North and South is determined by temperature, salinity, light and aragonite saturation state. Within these geographical limits various additional factors such as currents, nutrient conditions or abundance of plankton and particulate or dissolved organics are important for the development and persistence of reefs as well as for their condition.

Many of these factors are closely related, enhance or diminish each other and often have several direct or indirect impacts on organism or ecosystem level at once. Enhanced nutrient inputs (Chapter I, IV, VI) not only increase the density of the coral's symbiotic algae (zooxanthellae) and their photopigments, but also enhance the distribution of benthic algae which compete with corals for light and space. Excessive phytoplankton growth as a response to nutrification can further lead to a turbid water column resulting in decreased light availability for the benthic community. Currents (Chapter II) diminish the boundary layer between coral and surrounding water and increase gas and nutrient exchange. They also provide the supply of inorganic and organic material necessary for photosynthesis and active feeding, and disperse released metabolites (Chapter I, II, III). They are furthermore responsible for the resuspension and dispersal of sediments and associated compounds, which turbid the water column and can suffocate bottom dwellers when resettling. Additionally, fierce currents or waves hold the risk of breakage of coral skeletons.

Many of the local influences can be of natural (Chapter I to V) as well as anthropogenic (Chapter VI, VII) origin. Whereas the anthropogenic influence decreases with distance to shore (with the exception of global changes such as sea surface temperature rise or ocean acidification), offshore reefs are strongly influenced by oceanic conditions. According to type, intensity, frequency and duration of the disturbance, a reef and its inhabitants will be impacted to a stronger or lesser extent. Factors like seasonality or tides can herein play an important role in near-shore (Chapter I, VI) as well as in offshore reefs (Chapter I to V).

Offshore reefs are strongly influenced by open ocean conditions (Chapter I to V), which can be highly variable. 60 km off the Thailand west coast, the coral reefs along the west sides of the Similan Islands are affected by Large Amplitude Internal Waves (LAIW). Contrary, reefs on the east sides are only impacted to a lower extent. LAIW frequently introduce cold, oxygen depleted, CO₂- and nutrient-rich deep water into the reefs which strongly impacts the metabolism of corals.

LAIW impact can strongly vary between same seasons of different years, and dependent on the intensity and frequency, the nutrient input can become extremely high (Chapter 1). As a response, zooxanthellae densities and pigment concentrations increase, while conversely photosynthesis decreases (Chapter I, III, IV). Strong LAIW generated currents increase the flux of dissolved and particulate organic matter and support active feeding of corals (Chapter II). At the same time the high availability of organic and inorganic nutrients promotes an increase in release of dissolved and particulate substances by the coral (e.g. mucus) (Chapter III). The combination of high zooxanthellae densities and active feeding on the west side leads to an increase in biomass and energy reserves in corals (Chapter I, II). These features increase the corals' resilience and enhance survival in extreme conditions (Chapter II). The costs of elevated biomass and energy reserves are increased respiration and lower, more costly photosynthesis (Chapter III). Calcification as well is impacted by lowered aragonite saturation state due upwelled water low in pH (Chapter III). Furthermore, low temperature and oxygen concentrations associated with LAIW are responsible for slower coral growth and decreased photosynthesis. Additionally to the SW monsoon, which mainly influences the shallow water reefs on the west side of the islands, the diverse LAIW impacts lead to reduced reef formation (Chapter V) with lower coral cover but higher biodiversity. The adaptive mechanisms vary between different coral species (Chapter I). Incubations revealed, that acclimatization behavior persists under non-LAIW conditions (Chapter III), before adaptation to different conditions takes place (transplantation experiment, Chapter II). Nevertheless, the question remains, if the high acclimatization potential of corals from LAIW impacted reefs is a metabolic acclimatization or a genetic adaptation. These studies on acclimatization mechanisms serve as a basis for understanding, how reefs might develop in the face of global climate change (temperature rise and ocean acidification).

Input of nutrients and sediments at the Caribbean coast of Costa Rica (Chapter VI) are strongly dependent on dry and wet seasons. With rising rainfall nutrients are washed out of strongly fertilized soils from farmed land into near coastal waters. They are distributed by currents to the coral reefs of the National Park Cahuita, where they are verifiably taken up by corals. In addition, the extensive land clearing and cultivation of monocultures near the coast leads to erosion indicated by high silicate input. In consequence, high amounts of particulate matter are transported by the rivers and currents into the reefs leading to low light conditions and smothering of corals. The investigated reefs are highly impacted by eutrophication compared to reefs with similar geographic position.

Also along the northeast coast of Hainan, China, the consequences of coastal development are visible and devastating (Chapter VII). Strong eutrophication and sedimentation by untreated sewage from aquaculture and growing coastal populations fertilize and mist coastal waters. Excessive aquaculture holds the danger for input of diseases, alien species and pesticides. Another big problem is the obvious use of destructive fishing methods, i.e. dynamite fishing, which destroyed big parts of the reef already. The consequently loose substratum (coral rubble) is not suitable for coral larvae settlement. The combination of overfishing and increased nutrient input threatens the reefs as algal growth is no longer controlled by herbivorous fish. As algae are better competitors for nutrients and growth on instable substrate, there is the risk of imminent phase shift towards an algae dominated reef. Surviving corals have a low photosynthetic rate in the highly turbid environment comparable with that of corals from deeper water. Additionally, strong sedimentation leads to a high energy demand for coral mucus production crucial for sediment removal.

A decrease in live coral cover and biodiversity in the investigated reefs of Costa Rica, and an initiating phase shift from a coral to an algae dominated reefs in Hainan indicate the serious disturbance to these ecosystems and increasing anthropogenic pressure will inevitably lead to their collapse. In contrast to the natural occurring pulsed disturbances by LAIW, the chronic land based disturbances are permanently increasing and therefore an acute risk.

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Introduction

Coral symbiosis and metabolism

Scleractinian corals are entirely marine animals that comprise the largest order of the anthozoa class (phylum cnidaria). Even though some species are free-living and solitary, most of them are sessile and colonial with small polyps (Ruppert and Barnes 1994). They are hermatypic, contributing to construction of the reef framework by producing a calcium carbonate skeleton (Schuhmacher and Zibrowius 1985). In contrast to their cold-water counterparts (Roberts et al. 2006), tropical shallow water species mostly occur to be zooxanthellate, living in mutual symbiosis with unicellular dinoflagellate algae (Schuhmacher and Zibrowius 1985). While the zooxanthellae are provided with shelter and respiratory products of the animal (Muller-Parker and D'Elia 1997), up to 50 % of their photosynthates are allocated to the host (Muscatine and Cernichiarri 1969), supplying more than 100 % of its metabolic demands (Muscatine et al. 1981). Next to being phototrophic, these tropical shallow-water zooxanthellate stony corals (hereafter referred to as 'corals') are as well effective planktivores and suspension feeders (Glynn 1973; Sorokin 1973; Ferrier-Pagès et al. 1998; Anthony 2000) who can also derive more than 100 % of their metabolic demands (Palardy et al. 2008) by active feeding using their tentacles or stinging nematocysts (Lewis and Price 1975). The obedience on photo-versus autotrophy is species dependent (Wellington 1982; Palardy et al. 2005; Grottoli et al. 2006; Rodrigues and Grottoli 2006), but also regulated by the prevailing environmental conditions (Lewis 1976; Muscatine et al. 1989; Anthony and Fabricius 2000; Palardy et al. 2006). By virtue of their sessile nature, corals are strongly reliant on their immediate surroundings.

Benthic-pelagic coupling

Coral reefs have been described to be oases of extensive productivity in low-productive ocean surroundings (Odum and Odum 1955). The tight and efficient cycling of nutrients within these reef ecosystems (Smith 1984; Hatcher 1990,1997; Lesser 2004) has been used to explain the nutrient paradox (Darwin 1842) denouncing the antagonism of highly productive ecosystems in nutrient poor environments. On the organism level, the symbiosis between coral host and zooxanthellae guarantees the proficient utilization of

photosynthates by the coral animal, their break-down to inorganic nutrients and the recycling of the latter by the symbiotic algae (Muller-Parker and D'Elia 1997). In addition, inorganic nutrients (Szmant 1997) and organic material (Anthony 2000) are drawn from the water column and included into the holobiont metabolism. Portions of the metabolites can be released into the water column as dissolved or particulate organic matter (DOM or POM respectively) (Tanaka et al. 2008). The POM, or coral mucus, can trap further organic suspended material which settles and is then available to the microbial loop (Wild et al. 2004). The reef sediments hence act as a filter system where organic material is decomposed by high amounts of heterotrophic bacteria (Wild et al. 2004) and where the regenerated nutrients are released back into the water column via resuspension due to currents or waves (Grant and Madsen 1979). Also the reef framework functions as a sink for organic material (Richter and Wunsch 2001). Its enormous labyrinth of cracks and crevices is densely populated by filter feeding organisms such as cryptic sponges (Wunsch and Richter 1998) which intensely graze upon dissolved and particulate organic material (Van Duyl and Gast 2001) and subsequently fertilize the surrounding water by releasing inorganic nutrients (Richter and Wunsch 2001). On the further community level, many other reef-dwelling organisms such as algae (Larned 1998) and fish (Parrish 1989) contribute to the accumulation and cycling of metabolites and minerals. While for example algae are the corals' strongest competitors for space and light due to their high susceptibility of nutrient assimilation, their abundance is balanced by herbivorous fish (Lapointe 1997). The correlation and dependency between the various reef compartments can be high and the loss or diminishment of essential parts might weaken the ecosystem (Hughes 1994). As coral reefs are no closed systems but their surrounding environment constantly in exchange with adjacent environments, they are sensitive and vulnerable to disturbance from outside (Buddemeier and Smith 1999).

Environmental conditions

The major physico-chemical factors regulating the global distribution of tropical shallow water coral reefs are temperature, salinity, aragonite saturation state and light (Kleypas et al. 1999). The optimum average temperature for reef growth is determined to be around

28°C (Coles and Fadlallah 1991), salinity should range from 34 to 35 PSU (Coles and Jokiel 1992), the aragonite saturation state has its optimum at 3.8 (Takahashi et al. 1980; Archer 1996) and light at an average of 300 $\mu\text{E m}^{-2}\text{s}^{-1}$ (Chalker 1981; Achituv and Dubinsky 1990). The combination of these features is given within the tropical belt from approximately 30°N to 30°S (Barnes 1987), however not everywhere reefs are present as the ultimate constraint for reef formation is determined by the prevailing local factors (Kleypas et al. 1999). These can be of a wide variety including hydrodynamic factors such as river runoff and precipitation, or waves and storms (Macintyre and Adey 1990), biogeochemical conditions such as nutrient concentrations (Szmant 1997,2002) and particulate material suspension (Anthony 2000) or biological factors such as larval supply, geographic isolation, diversity or disease (Cortés 1997; Kleypas et al. 1999; Bruno et al. 2003; Nozawa and Harrison 2008). Many of these parameters like temperature and aragonite saturation state correlate as the dissolution potential of CO_2 is directly impacted by water temperature (Levitus 1994). Other feedbacks include the reduced light availability due to high particle loads (Anthony 2006) which in turn can be increased via waves or currents (Grant and Madsen 1979). The environmental impacts on corals are multifaceted and directly as well as indirectly affect the coral host and its algae (Brown 1997).

While high seawater temperatures (Lasker et al. 1984) and elevated irradiance (Falkowski and Dubinsky 1981) lead to a decrease in zooxanthellae densities within the coral tissue, nutrient availability increases symbiont propagation and pigment concentrations (Szmant 1997). Suspended organic material represents an important nutritional source for corals (Anthony 2000; Palardy et al. 2006), but can increase turbidity and reduce light availability for photosynthesis in higher amounts (Anthony and Fabricius 2000). Currents decrease the coral's boundary layer and enhance gas exchange as well as nutrient and organic matter uptake (Sebens et al. 1997; Hearn et al. 2001; Sebens et al. 2003). They stir up bottom material, freeing organics and nutrients into the water column, but also resuspending sediments which in turn increase turbidity (Grant and Madsen 1979).

Above the previous knowledge that coral reefs can most productively thrive in stable environments (Crossland et al. 1991; Hatcher 1997), there are many examples of reefs also to be found in variable environments (Cortés 1993; Dollar and Tribble 1993;

Macyntire et al. 1993; Kleypas et al. 1999; Hughes et al. 2003; Fabricius 2005; Anthony 2006). There are documentations of reefs (Kleypas et al. 1999) experiencing short-term temperatures of as low as 18 (northern Persian Gulf) and as high as 34°C (near Bahrain, Persian Gulf), or with salinities sometimes dropping below 25 (off Burma) or above 40 (Red Sea) PSU. Reefs in the vicinity of Galapagos, exposed to upwelling of water rich in CO₂ (Levitus 1994) persist in an environment with temporary aragonite saturation states of as low as 3.1 (Macyntire et al. 1993; Kleypas et al. 1999). In higher latitudes, e.g. in Japan or Florida, where the incident angle of sunlight is low during winter and light penetrates only to depths of less than ten meters with lowest intensities of 50 $\mu\text{E m}^{-2}\text{s}^{-1}$ reefs are still found (Harriott et al. 1995; Kan et al. 1995). Furthermore, reef growth has been documented in highly eutrophied (Szmant 2002) or turbid (Bak and Meesters 2000) waters.

Reefs in environments near or even beyond favorable limits are defined as ‘marginal reefs’ (Kleypas et al. 1999). The capability of corals to persist in such disturbed environments is dependent on the duration and the severity of the impact (Kleypas et al. 1999) and the welfare of the coral reef is set by the acclimatization potential of its inhabitants to the prevailing conditions (Gates and Edmunds 1999). The disturbances characterizing a marginal reef environment can be of natural as well as of anthropogenic origin (Grigg and Dollar 1990).

Natural disturbances on coral reefs – Large Amplitude Internal Waves

Internal waves (IW) travel along the interface of a two-layered fluid (Fig. 1), with their maximum amplitude at this interface and almost no displacement at the top or bottom of the water column (Jackson 2004). As IW can occur wherever strong tidal currents, stratification of the water column and irregular underwater topography co-occur, they are ubiquitous in the world’s oceans (Jackson 2004) and represent a significant mechanism of mass and energy transport (Osborne and Burch 1980). Not all mechanisms are yet understood, however, their creation has been documented when barotropic tidal currents of a stratified fluid overflow a barrier and so generate a downstream depression on the obstacle’s leeward side which is released upstream as IW after turning or abating of the tide (Maxworthy 1979). Another formation mechanism is their direct production by

shear-flow instabilities when strong currents overflow a sill creating upstream IW just after the sill crest (Farmer and Armi 1999). IW occur in wave packets, with the fastest wave of highest amplitude and wavelength travelling up front and can be detected as sharp drops in pycnocline depth (Jackson 2004). Their dissipation takes place via spreading, pycnocline instability, turbulence or bottom interactions (Jackson 2004). During the latter process (Fig. 1), IW disintegrate into secondary wave trains over shoaling bottom (Vlasenko and Stashchuk 2007) or internally brake (Vlasenko and Hutter 2002), causing mixing of the previously stratified water bodies and hence play an important role in the cross-shore transport of larvae, plankton, nutrients and particulate matter (Pineda 1991; Witman et al. 1993; Leichter et al. 1998).

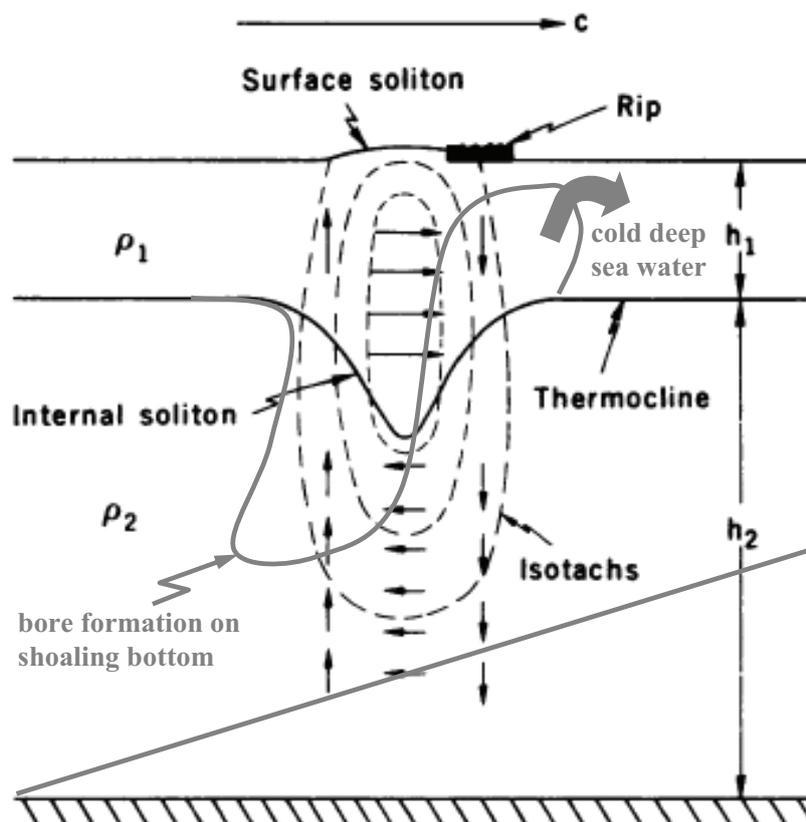


Figure 1: Schematic drawing of an internal wave (modified after Osborne and Burch 1980) visible as depression of the pycno/thermocline (black). Dissipation (gray) of an internal wave over shoaling bottom: bore formation and subsequent mixing with overlaying water body.

The Andaman Sea features internal waves of extraordinary amplitudes of up to 80 m (Osborne and Burch 1980). These Large Amplitude Internal Waves (LAIW) are generated by tidal flows over shallow ridges near Sumatra and the Andaman-Nicobar island arc (Fig. 2) from where they travel eastward (Osborne and Burch 1980) until dissipation as secondary waves or internal bores when they impinge the continental shelf (Vlasenko and Stashchuk 2007).

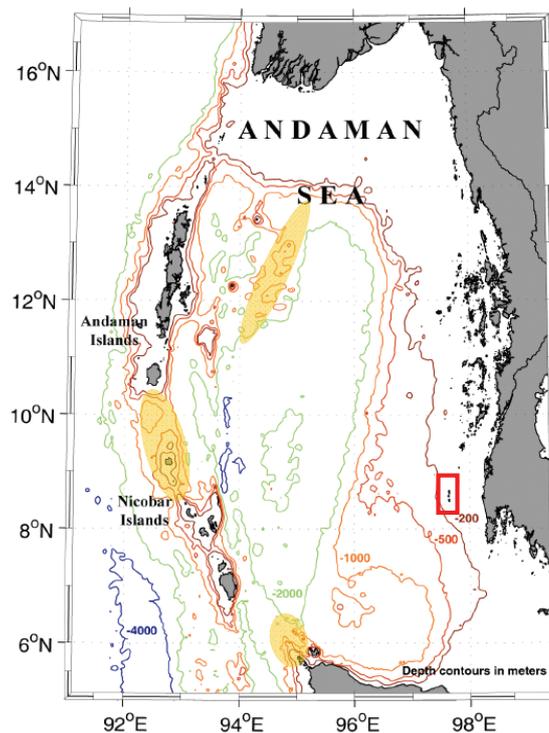


Figure 2: Map of the Andaman Sea (modified after Jackson 2002) indicating the shallow underwater topography areas of LAIW formation (yellow) and the location of the Similan Islands (red) close to the continental shelf (see depth contours).

In the vicinity of the LAIW swash zone close to the continental shelf break, lie the Similan Islands, an offshore island chain (Fig. 2) consisting of nine granite islands surrounded by coral reefs (Chansang et al. 1999). The arriving LAIW turbulences mix subthermocline cold, nutrient-rich, sub-oxic and low-pH waters into the shallow reef areas evident as frequent drops in temperature, salinity, oxygen or pH (Fig. 3). Such

disturbances have known effects on corals: low temperature decreases photosynthesis (Saxby et al. 2003) and undermines dense reef formation (Kleypas et al. 1999). Nutrients fuel zooxanthellae and pigment growth (Szmant 1997), however also growth of algae (Larned 1998), the main competitors for light and space (Lapointe 1997). Suboxic conditions are deleterious to aerobic organisms and low pH or aragonite saturation state decreases calcification (Fabry et al. 2008). So far the combined effects of LAIW impact on coral organism are unknown and the drivers for reduced and only scattered coral persistence along the LAIW exposed western Similan Island sides in contrast to dense reef formations in the sheltered east (Chansang et al. 1999) not identified.

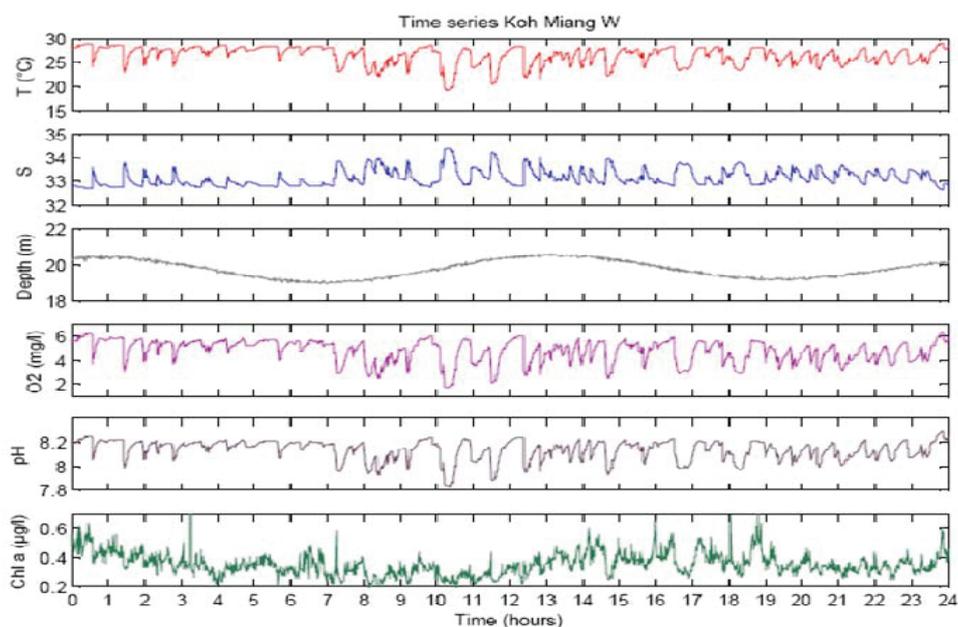


Figure 3: Example of a time series of LAIW impact recorded in the water of west Koh Miang (Similan Island #4). Temperature drops indicate passage of LAIW. Co-occurring are increases in salinity, as well as decreases in oxygen and pH (Richter unpubl.).

Anthropogenic disturbances on coral reefs

Next to the risks of global climate change, namely the rise of sea surface temperature as a response to extensive greenhouse gas emissions and the subsequent ocean acidification due to rising atmospheric CO₂ (Buddemeier and Smith 1999), local impacts are of great concern for coastal reef systems (Fabricius 2005) and have been identified to pose a far

more immediate threat to coral reefs (Brown and Ogden 1993). Due to high gradients and variability, the coastal zone is already a highly disturbed environment (Smith and Buddemeier 1992) and human alterations of the adjacent ecosystems or the reef itself often increase the frequency and severity of fluctuations or introduce additional disturbances. Extensive deforestation of coastal vegetation for cultivation of crop results in increased soil erosion and subsequent introduction of high sediment loads into the coastal areas via rivers or groundwater (West and van Woesik 2001; Fabricius 2005). The subsequent increased turbidity lowers photosynthesis and calcification (Brown 1997; Marubini et al. 2001), and sediment loads might cause coral suffocation (Weber et al. 2006) if removal becomes too costly (Schuhmacher 1977; Rogers 1990). Fertilization of acreage causes nutrient and heavy metal discharge into the surrounding water bodies (Guzmán and Jimenez 1992; Fabricius 2005). Increased nutrients cause phytoplankton growth (van Duyl et al. 2002) which increases turbidity or causes algal blooms resulting in anoxic condition for the underlying benthic community (Song et al. 2009). Also benthic algae growth is fuelled by nutrients (Larned 1998) and their better susceptibility to nutrients might outcompete corals (Lapointe 1997). Heavy metals can additionally i.e. impact the fecundity of corals or cause bleaching (Harland and Brown 1989; Esslemont 2000). Rising coastal development increases sewage disposal (ISRS 2004) and amplifies the effects of high particle and nutrient loads. Aquaculture farming in mangroves and along the shallow tropical coast has similar effects on coral reef ecosystems: enhanced nutrient inputs fertilize the coastal area causing eutrophication (Szmant 1997) and heavy metals are released into the surrounding (Chou et al. 2002). Additionally, aquaculture poses the risk of introducing disease (Sindermann 1984) or escaped species (Naylor et al. 2005). The use of anchors or destructive fishing gear has direct implications on the reef, as it rapidly destroys the calcium carbonate framework immediately killing the hit organisms and leaving unstable fields of coral rubble behind (McManus et al. 1997). The variety of human induced impacts makes it important to gain information on the steady-state of reefs to imply proper management regulations.

Scope of this thesis

This thesis aims to contribute to the understanding of coral acclimatization potential on the organism as well as the community level by identifying triggers of natural (Chapters 1 to 5) as well as anthropogenic (Chapters 6 to 7) disturbances and investigating the stress responses of individuals as well as the reef ecosystem. The key questions under investigation are:

- 1) How do Large Amplitude Internal Waves (LAIW) impact coral metabolism on the temporal, spatial and species level? Chapter I
- 2) How do LAIW alter the trophic state of corals and how do they contribute to their resilience? Chapter II
- 3) What is the actual difference in metabolism between LAIW exposed vs LAIW sheltered coral specimens under comparable conditions? Chapter III
- 4) How is the primary production affected by LAIW impact? Chapter IV
- 5) How does the combination of the above findings shape LAIW exposed reefs? Chapter V
- 6) How is the temporal and spatial impact of extensive altered land use on nearby coral reef ecosystems? Chapter VI
- 7) How do the combined impacts of destructive fishing, aquaculture and coastal development alter a coral reef ecosystem?

The correlations and feedbacks of investigated parameters are outlined in Figure 4.

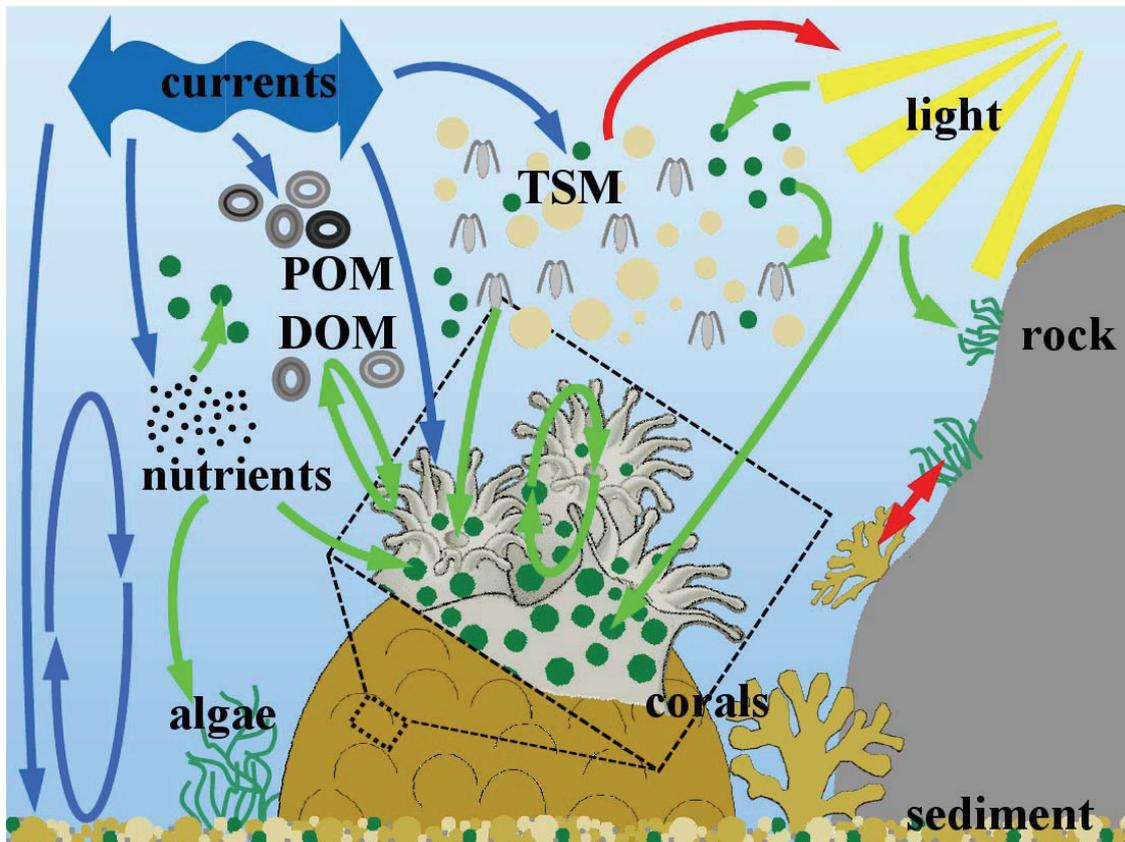


Figure 4: Schematic drawing of benthic-pelagic coupling. Green arrows: positive feedbacks / food web: the combination of light and nutrients is crucial for primary production. It increases plankton, algal and zooxanthellae growth. Primary producers are the base of the food web; phytoplankton is consumed by zooplankton which serves as heterotrophic food source for the coral animal. Within the coral holobiont, metabolic substances are exchanged between coral animal and symbiotic algae; while the photosynthetic products are passed on from the symbiont to the host, respiratory waste products are passed back to and recycled by the zooxanthellae. The coral holobiont is also able to release and take up dissolved and particulate organics (DOM and POM respectively). Red arrows: negative feedback / repression: increase in TSM, either by high rates of primary production, heavy resuspension or introduction of suspended material decrease light penetration and availability. Competition for food, light and space e.g. between coral and algae is energy costly. Blue arrows: influence of water motion (i.e. currents): with increasing currents there is an increase in fluxes, mixing and resuspension of nutrients, TSM (plankton as well as inorganics), DOC and POM. Currents also decrease the boundary layer over e.g. tissue surfaces of corals hence increasing the exchange rates of gases or the uptake rates of nutrients.

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Publication Outline

Chapter I

Roder C, Jantzen C, Schmidt GM, Phongsuwan N, Richter C (in revision) Metabolic plasticity of *Porites lutea* and *Diploastrea heliopora* exposed to Large Amplitude Internal Waves. Coral Reefs

The basic idea of a project on internal waves in the Andaman Sea was initiated by C Richter. The concept of this study was developed by C Roder and C Jantzen. Sampling and analyses were conducted by C Roder and C Jantzen. Elaboration of the manuscript was done by C Roder with input from C Richter.

Chapter II

Roder C, Fillinger L, Jantzen C, Schmidt GM, Khokiattiwong S, Richter C (accepted) Trophic response of corals to Large Amplitude Internal Waves. Marine Ecology Progress Series

The basic idea of a project on internal waves in the Andaman Sea was initiated by C Richter. The concept of this study was developed by C Roder, with input from C Richter. Data sampling and analyses was mainly conducted by C Roder with support from L Fillinger, C Jantzen and C Richter. The manuscript was written by C Roder with input from C Jantzen, G Schmidt and C Richter.

Chapter III

Roder C, Schmidt GM, Jantzen C, Khokiattiwong S, Richter C (in preparation) Comparative metabolic performance of *Porites lutea* from Large Amplitude Internal Wave (LAIW)-exposed and LAIW-protected habitats. Journal of Experimental Marine Biology and Ecology

The basic idea of a project on internal waves in the Andaman Sea was initiated by C Richter. The concept of this study was developed by C Roder, GM Schmidt and C Jantzen with input from C Richter. Sampling and analyses was conducted by C Roder, GM Schmidt and C Jantzen. Data evaluation and manuscript preparation was conducted by C Roder with improvements by GM Schmidt and C Richter.

Chapter IV

Jantzen C, Schmidt GM, **Roder C**, Wild C, Khokiattiwong S, Richter C (in preparation) Benthic primary production in response to Large Amplitude Internal Waves (LAIW) in coral reefs at the Similan Islands, Thailand.

The basic idea of a project on internal waves in the Andaman Sea was initiated by C Richter. The idea of this project was developed by C Jantzen with input from C Wild and C Richter. The manuscript was written by C Jantzen with improvements by C Wild, C Richter, GM Schmidt and C Roder.

Chapter V

Schmidt GM, Phongsuwan N, **Roder C**, Jantzen C, Khokiattiwong S, Richter C (submitted) Coral community and physico-chemical characteristics of the Similan Islands in response to Large Amplitude Internal Waves. Marine Ecology Progress Series

The basic idea of a project on internal waves in the Andaman Sea was initiated by C Richter. The particular idea of this manuscript was developed by GM Schmidt, N Phongsuwan and C Richter. Data sampling and analyses was conducted by N Phongsuwan, G Schmidt, C Roder, C Jantzen and C Richter. The manuscript was written by G Schmidt with support from N Phongsuwan, C Richter, C Roder and G Jantzen.

Chapter VI

Roder C, Cortés J, Jiménez C, Lara R (2009) Riverine input of particulate material and inorganic nutrients to a coastal reef ecosystem at the Caribbean coast of Costa Rica. Marine Pollution Bulletin 58: 1937-1943

The basic idea of the study was developed by C Roder, C Jiménez and R Lara. Data sampling and analyses were conducted by C Roder who also wrote the manuscript with improvements by J Cortés, C Jiménez and R Lara.

Chapter VII

Roder C, Wu Z, Richter C (in preparation) Field observations and preliminary notes on the metabolic status of NE-Hainan corals.

The basic idea of a project on Hainan, China, was developed by C Richter and ZMT colleagues. The concept of this study, fieldwork and sample analyses was carried out by C Roder with the help of Z Wu. The manuscript was written by C Roder with support from C Richter.

- Chapter I -

**Metabolic plasticity of *Porites lutea* and
Diploastrea heliopora exposed to Large Amplitude
Internal Waves**

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Abstract

The metabolic plasticity of the two mounding coral species *Porites lutea* (Milne-Edwards and Haime, 1860) and *Diploastrea heliopora* (Lamarck, 1816) was investigated under an impact gradient of Large Amplitude Internal Waves (LAIW) along the west and east side reefs of the Similan Islands, Andaman Sea, Thailand. Nutrient concentrations were highly regulated by LAIW intensity and resulted in marked effects on symbiont densities in both species, but the consequences were much stronger reflected in *D. heliopora* specimens. Zooxanthellae densities were increased more than threefold in *P. lutea*, but were more than ten times higher in *D. heliopora* under strong LAIW influence. Also pigment concentrations and protein content as well as host tissue and symbiont biomasses were generally elevated in *D. heliopora*. The data suggest a highly species-specific response to LAIW impact, where *D. heliopora* benefits stronger from increased nutrient and organic matter availability than *P. lutea* which might explain their contrary abundances in LAIW-exposed and sheltered reefs along the Similan Islands. As LAIW are ubiquitous in South-East Asia and beyond, the remarkable potential of acclimatization provides further understanding on how corals cope with disturbances on small and large temporal and spatial scales in a changing world.

Key words

Large Amplitude Internal Waves – coral metabolism – disturbance - acclimatization

Introduction

Scleractinian corals are presumed to populate tropical reef areas for more than 200 million years (Stanley 2003), reflecting their ability to adapt to changing environmental conditions (Veron 1995; Buddemeier and Smith 1999) on the temporal scale of minutes to decades (Sebens and DeRiemer 1977; Hoegh-Guldberg and Smith 1989a; Done 1992; Shashar et al. 1993; Brown 1997b; Gates and Edmunds 1999). Even though coral reefs

typically develop under fairly steady-state oligotrophic conditions (Lewis 1977; Muscatine and Porter 1977), large natural (Kinsey 1988; Woodley 1992; Cortés 1997) and anthropogenic (Kinsey 1988; Anthony and Fabricius 2000; Fabricius 2005) disturbances are known to occur, that require special acclimatization in corals which may be important in the context of climate change (Brown 1997a; Buddemeier and Smith 1999; Hoegh-Guldberg 1999; Hughes et al. 2003; Grottoli et al. 2006). Studies about the influences of recurring events or disturbances such as storms (Woodley 1992; Dollar and Tribble 1993), pollution (Heikoop et al. 2000b; Fabricius 2005; Anthony et al. 2009), warming (Szmant and Gassman 1990; Gleason 1993; Brown 1997a; Coles and Brown 2003), upwelling (Andrews and Gentien 1982; Cortés 1997; Leichter and Genovese 2006) or seasonality (Brown et al. 1999; Swart et al. 2005) on corals have greatly improved the understanding of coral plasticity under varying environmental conditions. However, often findings are species-specific (Brown et al. 1999; Stimson et al. 2002; Palardy et al. 2005) or seem to be not coherent as zooxanthellae densities, pigment concentrations or growth rates might not always uniformly correspond to the same kind of disturbance (Stimson 1997; Edinger et al. 2000; Sunagawa et al. 2008). Also most mechanisms of coral response to disturbance are not yet fully understood (Buddemeier and Smith 1999; Fitt et al. 2000b; Oku et al. 2003), which requires further intense studies on the metabolic functioning of scleractinian corals, their reaction to disturbances and potential of acclimatization (Buddemeier and Smith 1999; Gates and Edmunds 1999; Coles and Brown 2003).

The impact of seasonality on coral life history is obvious in coral calcification (Crossland 1984), displayed in skeleton banding patterns (Knutson et al. 1972), their reproductive cycles (Babcock et al. 1994) or their nutritional (Palardy et al. 2005) and proliferous (Kinsey 1977) characteristics. Annual or seasonal cycles have also been demonstrated to be reflected in coral tissue parameters, such as biomass (Fitt et al. 2000), protein (Crossland 1984) or lipid (Oku et al. 2003) content, zooxanthellae densities (Brown et al. 1999; Grimsditch et al. 2008) or pigment concentrations (Brown et al. 1999; Fitt et al. 2000b). Thereby, higher temperature (Lasker et al. 1984) and irradiance (Falkowski and Dubinsky 1981) tend to decrease zooxanthellae densities or chlorophyll concentrations (Fitt et al. 2000b), while nutrient inputs of ammonium (Muscatine and D'Elia 1978;

Muscatine et al. 1989b), nitrate (Franzisket 1974) or phosphate (D'Elia 1977) enhance symbiont and pigment propagation presumably due to nutrient (mainly nitrogen) limitation of the symbiotic algae (Muscatine et al. 1989b; Szmant et al. 1990; Muller-Parker et al. 1994; Fagoonee et al. 1999). Increases in zooxanthellae densities due to nutrient enrichment have been brought into relation with augmenting tissue biomass (Muller-Parker et al. 1994; Fitt et al. 2000b), lipid (Oku et al. 2003) or protein (Marubini and Davies 1996) production. On smaller scales such as depth gradients, variances of zooxanthellae densities (McCloskey and Muscatine 1984; Fitt et al. 2000b), chlorophyll concentrations (Dustan 1979; McCloskey and Muscatine 1984) or energetic status (Meesters et al. 2002) have also been described and were mainly attributed to light differences (Al-Moghrabi et al. 1995; Anthony 2006) and subsequent increases in feeding (Muscatine and Kaplan 1994; Palardy et al. 2005). However again, dependent on the species or region, the observed patterns were not consistent (McCloskey and Muscatine 1984; Fitt et al. 2000b), suggesting more complex relationships between coral host, its symbiont and the environment.

Internal waves might pose relevant impacts on coral reef ecosystems due to introduction of nutrients (Wolanski and Delesalle 1995; Leichter et al. 2003), plankton (Witman et al. 1993; Leichter et al. 1998), larvae (Pineda 1999) or suspended material (Bogucki et al. 1997) when running on shoaling bottom (Vlasenko and Stashchuk 2007) and subsequently forming bores that cause extensive mixing of the deeper with warm nutrient low surface waters (Jackson 2004). The Andaman Sea features internal waves of exceptional dimension. These large amplitude internal waves (LAIW) are generated by the waxing and waning of the tides over shallow topography near the Andaman-Nicobar island arc, from where they travel eastward in packets of 5-7 waves across the Andaman basin, depressing the thermocline by more than 80 meters (Osborne and Burch 1980). Over shoaling bottom near the shelf break the LAIW are modified (Vlasenko and Stashchuk 2007), disintegrate into secondary waves or break (Vlasenko and Hutter 2002). In the Indian Ocean, the mixing and upwelling associated with the dissipation of LAIW may generate sudden temperature drops of >5 °C (Sheppard 2009). The variations in temperature (Coles and Fadlallah 1991; Saxby et al. 2003), but also the injection of nutrients (Wolanski and Delesalle 1995; Leichter et al. 2003), plankton (Witman et al.

1993; Leichter et al. 1998), larvae (Pineda 1999) and suspended material (Bogucki et al. 1997) are likely to affect the sedentary biota exposed to these waves.

Information on coral reefs subjected to seasonal or year round upwelling and/or internal waves, focusing on nutrient (Leichter et al. 2003) or plankton (Leichter et al. 1998) regimes, biodiversity and coral cover (Cortés 1997), zooxanthellae and pigment concentrations (Sunagawa et al. 2008), growth rates (Leichter and Genovese 2006) or feeding (Palardy et al. 2005) is available. However, the LAIW induced variations investigated in this study by far exceed frequency and variation of earlier reported pulsed upwelling events (Leichter et al. 1996; Leichter et al. 2003; Leichter and Genovese 2006) and rank among the largest short-term fluctuations so far reported in tropical reef areas (Sheppard 2009). The plasticity of corals from reefs under such disturbances, and impacts of possible inter-annual variability are to date not examined. This study presents variations in biogeochemical water characteristics of reefs exposed to LAIW in greater or lesser extends and discusses their impact on coral metabolic plasticity.

Material and Methods

Study site

Sampling took place in the Andaman Sea along the Similan Islands, Thailand, a longitudinal oriented island chain 60 km off the western Thai coast (Fig 1). Being located close to the continental shelf edge, the islands are under influence of shoaling Large Amplitude Internal Waves (LAIW) created near Sumatra and the Andaman Nicobar Islands (Jackson 2004; Vlasenko and Alpers 2005). These bores force oceanic subpycnocline water masses upslope and introduce the nutrient rich, cold water into the reefs where they can be tracked as temperature plunges of strong intensities and frequencies on the windward, exposed island sides (W), while eastern island faces (E) are rather sheltered (Chansang et al. 1999). Compared to most other tropical islands, where coral reef growth is most intense on the windward side of islands and barriers (Veron and Stafford-Smith 2000; Spalding et al. 2001), coral cover on W Similan is rather disintegrated, while E side reefs are densely populated (Schmidt et al. *subm.*).

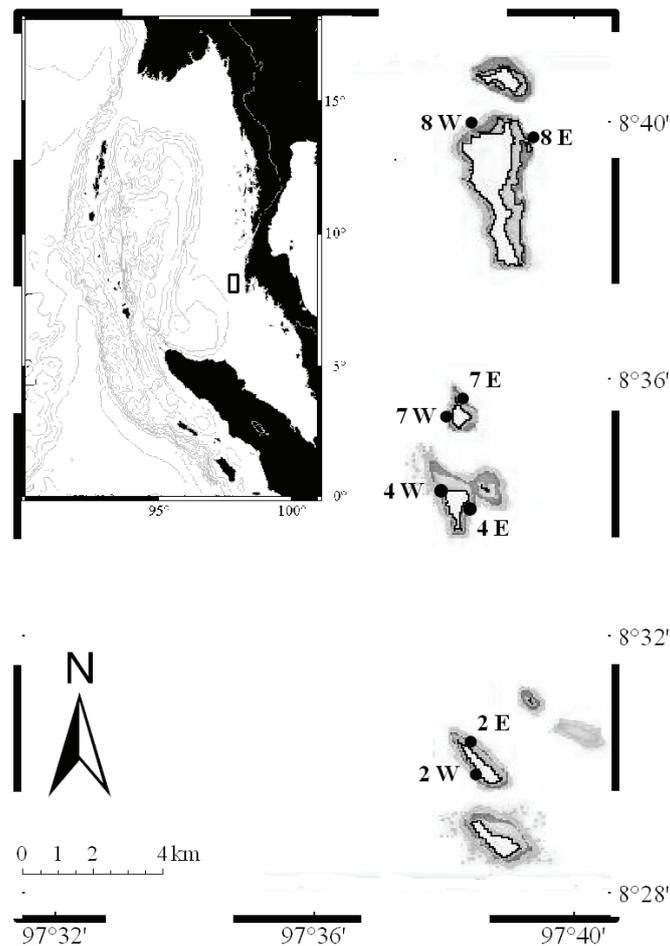


Figure 1: Map of the Andaman Sea with the location of the Similan Islands west of the coast of Thailand (small map) and the 9 Similan Islands with sampling sites on the W and E side reefs of Islands #2, 4, 7 and 8.

Coral sampling

In spring of 2007 (21 February to 16 March) and 2008 (23 February to 26 March), the seasonal period of strongest soliton intensity (Osborne and Burch 1980), fragments of the two scleractinian corals *Porites lutea* (Milne-Edwards and Haime, 1860) and *Diploastrea heliopora* (Lamarck, 1816) were collected in shallow (5 - 15 m) and deep (15 - 25 m) areas of various reefs along the W and E island faces of the Similan Islands (Fig 1) using SCUBA. Due to logistical restraints, in 2008 *D. heliopora* could (except for one fragment) only be collected on the W and E sides of Island #4. Apart from that, a balanced sampling along all islands was aspired. Both coral species have mounding

morphologies and can grow to large boulders in the Similan Island reefs (pers. obs.). While *P. lutea* has polyps of ~ 1 mm in size, the polyps of *D. heliopora* are > 5 mm and often up to 1.5 cm in diameter. Fragments of ~ 5 cm² (one per colony) were chiseled from the upper, non-shaded parts of the colonies, placed in ziplock bags (100 x 150 mm, max. 4 ml residual water) and transported to the lab for processing. In total 48 fragments of *P. lutea* and 35 fragments of *D. heliopora* were collected for analyses.

Coral processing

Coral tissue was removed from the skeleton using an artist's airbrush and filtered seawater. After homogenization (Ultra Turrax, 30 s) of the slurry, the solution was filled to a known volume of stock from which aliquots were taken for zooxanthellae density counts, chlorophyll and protein analysis. Zooxanthellae densities were determined by six replicate counts on a Fuchs-Rosenthal-haemocytometer using a microscope (Leitz, Portugal, 260 x magnifications). Three to six mL of stock solution were collected under vacuum on Whatman GF/F filters and frozen for chlorophyll analysis. Chlorophyll was extracted by 90% acetone at 4°C for 24 hours (Strickland and Parsons 1972) and absorbance read at 750 nm and 664 nm in a Shimadzu UV 1700 1nm Slit photometer and concentrations calculated after Lorenzen (1967). Total protein content was measured using the DC Protein Assay (Bio-Rad). A standard curve was established using bovine serum albumin and absorbance read spectrophotometrically (Shimadzu UV 1700 1nm Slit) at 750 nm (Lowry et al. 1951). The remaining stock solution of the homogenized tissue slurry was centrifuged to separate symbionts from coral host tissue (Muscatine et al. 1989a; Grottoli et al. 2004). Zooxanthellate pellets were washed several times before resuspension in distilled water. Known volumes of each fraction were loaded on pre-combusted and weighed filters (Whatman GF/F) under moderate suction (Millipore Vacuum Pump, max 200 mm Hg) and dried for 24 h at 40°C. Dry weight (DW) of the animal and symbiont fraction was determined on a microbalance (Mettler, AT21 Comparator, 1 µg accuracy) before elemental and isotopic analysis. Measurements of carbon and nitrogen concentrations as well as their isotopic signatures on coral tissue and symbionts were conducted with a NA2100 Protein Elemental Analyzer coupled with a Flash 1112 Isotope Ratio Mass Analyzer. Carbon and nitrogen measurements were

calibrated against an elemental CHNS standard (LECO). Isotopic ratios are given as conventional delta notations ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) relative to Pee Dee Belemnite ($\delta^{13}\text{C}$) standard and atmospheric nitrogen ($\delta^{15}\text{N}$). Fragment surface size was determined using Simple Geometry to the nearest 0.05 mm (Naumann et al. 2009) and each parameter calculated per cm^2 coral surface.

Water samples

In the same time period, water samples ($n = 86$) were collected in shallow (~ 7 m) and deep (~ 20 m) reef water of W and E Koh Miang using sterile 1 l PE bottles. Samples were transported to the laboratory and filtered (Millipore Vacuum Pump, 200 mm Hg) immediately on untreated (for chlorophyll-a determination) and pre-combusted and pre-weighed (for TSM determination) glass fiber filters (Whatman GF/F). TSM filters were kept frozen until desiccation (12 hours at 40°C), and dry weight of the total suspended matter (TSM) was determined gravimetrically (Mettler, AT21 Comparator, 1 μg accuracy). Chlorophyll-a was extracted from thawed filters by adding a certain volume of 90 % acetone (Strickland and Parsons 1972) and subsequent incubation at 4°C for 24 hours. Before reading absorption at 750 nm and 664 nm (Lorenzen 1967) in a Shimadzu UV 1700 1nm Slit photometer, samples were centrifuged at maximum speed to remove all particles in suspension.

Aliquots of the filtrate were poisoned with mercury chloride (Kattner 1999) and kept frozen in 25 ml PE bottles until analysis of inorganic nutrients (nitrite, nitrate, ammonium, phosphate and silicate) in a spectrometer (2007: GBC model UV/VIS981 with autosampler model FS3000; 2008: Evolution III autoanalyzer, Alliance Instruments, France) using established methods (Strickland and Parsons 1972; Grasshof 1983). More filtrate was transferred to glass ampoules, acidified with phosphoric acid to a pH of 2 before flame sealing and storage in the freezer until analysis of dissolved organic carbon (DOC) in a DOC/DIC analyzer (Rosemount DC-190) using a 10-point calibration with TOC standards (ULTRA Scientific).

Temperature records

During the sampling period, temperature was recorded in all sampled reefs (except for the shallow site at Island # 7 in 2007, where logger was lost due to storm activity) at two depths (7 and 20 m) and in temporal resolution of 1 to 8 minutes depending on exposure time using TidbiT v2 loggers (Onset, accuracy < 0.2 °C over 0 to 50 °C). To assess the LAIW impact during coral sampling, the temperature of a 14-day period (01.03.2007/2008 – 14.03.2007/2008) was utilized, as within this time frame data was available from all sampling sites (Fig. 1). Daily temperature ranges \pm SE were calculated for all sites to compare LAIW intensities.

Statistics

Temporal (2007 vs 2008) and spatial (W vs E, deep vs shallow, but also inter-island differences) variations of the daily temperature ranges were examined using the sign test for dependent non-parametric data (Dixon and Mood 1946).

Raw data of water and coral samples are given in the electronic supplementary material (Tables S1, S2 and S3). The overall composition of the water as well as the total tissue composition of either species investigated was compared for seasonal (2007 vs 2008), side (W vs E) and depth (shallow vs deep) differences using PRIMER v6 software (Clarke and Gorley 2006). Data were log-transformed before analysis to achieve normality, stabilize variance and offset discrepancies due to the different unit sizes.

To visualize constitutional similarities between the samples, multi-dimensional scaling (MDS) plots were generated which reduce the 8-dimensional (water samples: nitrite, nitrate, ammonium, phosphate, silicate, DOC, chlorophyll-a and TSM) or 13-dimensional (coral samples: zooxanthellae numbers, chlorophyll-a concentrations, protein content, host tissue and zooxanthellae dry weights, host tissue and zooxanthellae carbon and nitrogen, carbon and nitrogen isotopic composition of host tissue and zooxanthellae) sample coordinates into 2-D (axes arbitrary) space and where the (Euclidean) distance between the points denotes their similarity. The same plot was used to stepwise visualize each hierarchical level on its own (first years, then sides within years, then depths within sides) which allows for following a sample to its detailed depiction (Figs. 5, 7 and 8). In the cases of significant difference on lower hierarchical levels (btw sides and depths), the

same graph, displaying the multidimensional plot from a different view onto the plane by rotating to best illustrate the factorial differences, is additionally presented in the electronic supplementary material (Figs. S1 – S7).

Determination of significant temporal and spatial differences was accomplished conducting Analyses of Similarities (ANOSIM) with 9999 permutations (Gonzalez and Manly 1998) on each factor level (year, side, depth), always with the next hierarchically lower level nested within (side nested within year and depth nested within side). For the coral data, differences within the same factor (year or side) but between the samples' island of origin (# 2, 4, 7 or 8) were also tested with a nested approach (island nested within year or side).

To identify the parameters ('species') accounting for the observed temporal and spatial differences in water and coral data, a test on species contributions to similarity (SIMPER, similarity percentages) revealed the percental share of the parameters explaining $\geq 90\%$ of the dissimilarities (Clarke 1993). SIMPER analyses were only conducted to the factor level on which the ANOSIM tests revealed at least one significant ($p < 0.05$) difference (for water until depth level, for coral data until side level); for the sake of completeness, SIMPER results on these factorial level are all listed independent of significance, however only significant ANOSIM results are discussed in detail.

Results

Frequent, and often severe, temperature drops were observed, indicating the passage of large amplitude internal waves (LAIW). They were more frequent and severe in 2007 (Fig. 2) than in 2008 (Fig. 3), as evidenced by stronger daily temperature ranges in 2007 compared to 2008 (Fig. 4). The mean daily temperature ranges (\pm SE) and detailed statistical results of the various sign tests are listed in Table 1. The temperatures varied coherently within W- and E-exposed island faces (Table 1, Figs. 2, 3 and 4), but showed pronounced differences ($p < 0.001$) between the years (2007 > 2008) and between the four sites ($p < 0.001$; W deep > W shallow > E deep > E shallow) for the given year (Table 1).

Table 1: Daily temperature ranges (°C) from the investigated reef sites along the Similan Islands and sign test results. Diagonal (bold): mean daily temperature range (°C) and (SE). Upper right side: sign test results for spatio-temporal variations (2007/2008, W/E, deep/shallow); p levels and (below) Z-values. Below means (SE): results of sign test for inter-island differences (italics), significant different island numbers, Z value and significance level in brackets. Significance levels: * p < 0.05, ** p < 0.005, *** p < 0.001

	2007 W deep	2007 W shallow	2007 E deep	2007 E shallow	2008 W deep	2008 W shallow	2008 E deep	2008 E shallow
2007 W deep	6.30 (0.16) #4 vs #7 (2.94, **)	*** 6.33	*** 7.08	*** 7.35	*** 7.35	*** 7.35	*** 7.35	*** 7.35
2007 W shallow		4.36 (0.22)	0.090 1.70	*** 5.09	*** 3.86	6.02	6.33	6.33
2007 E deep			3.70 (0.09) #2 vs #7 (2.94, **) #4 vs #7 (3.47, ***) #4 vs #8 (2.94, **)	*** 7.08	0.894 -0.13	*** 6.55	*** 7.35	*** 7.35
2007 E shallow				2.27 (0.08) #4 vs #7 (3.47, ***) #4 vs #8 (2.41, **)	*** 6.01	0.894 0.13	*** 6.01	*** 7.08
2008 W deep					3.47 (0.11)	*** 6.82	*** 7.35	*** 7.35
2008 W shallow						2.28 (0.12)	*** 6.28	*** 6.82
2008 E deep							1.36 (0.08) #4 vs #7 (3.47, ***)	*** 3.88
2008 E shallow								0.95 (0.05) #2 vs #4 (2.41, *)

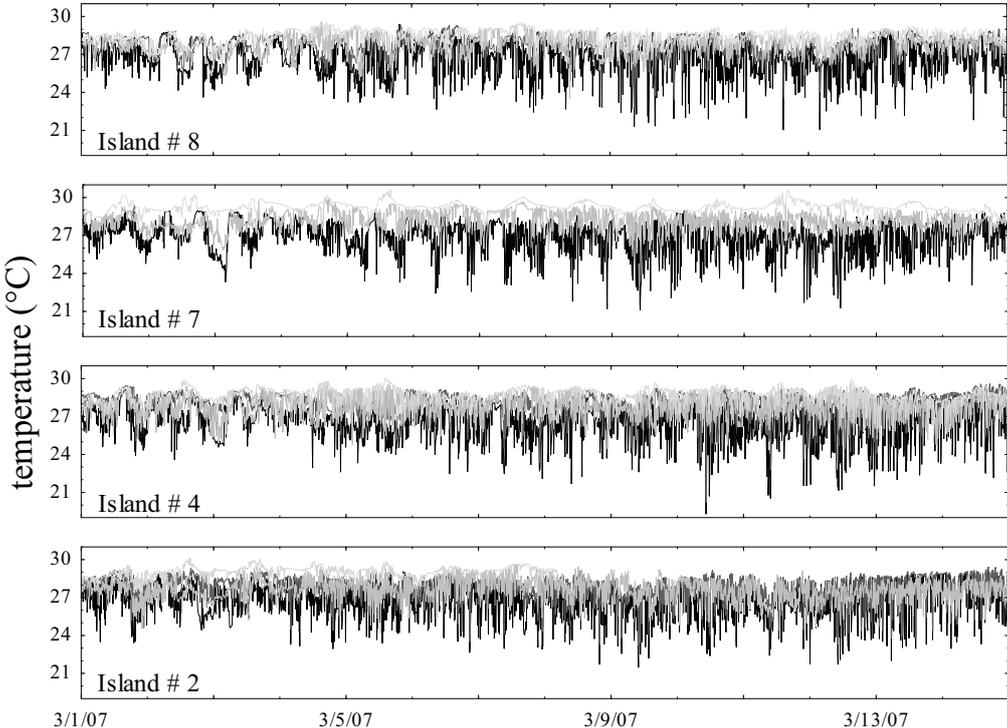


Figure 2: Temperature profile within W and E side reefs of all Island sites (#2, 4, 7 and 8) along the Similan Islands in 2007 (— W deep, — W shallow, — E deep, — E shallow)

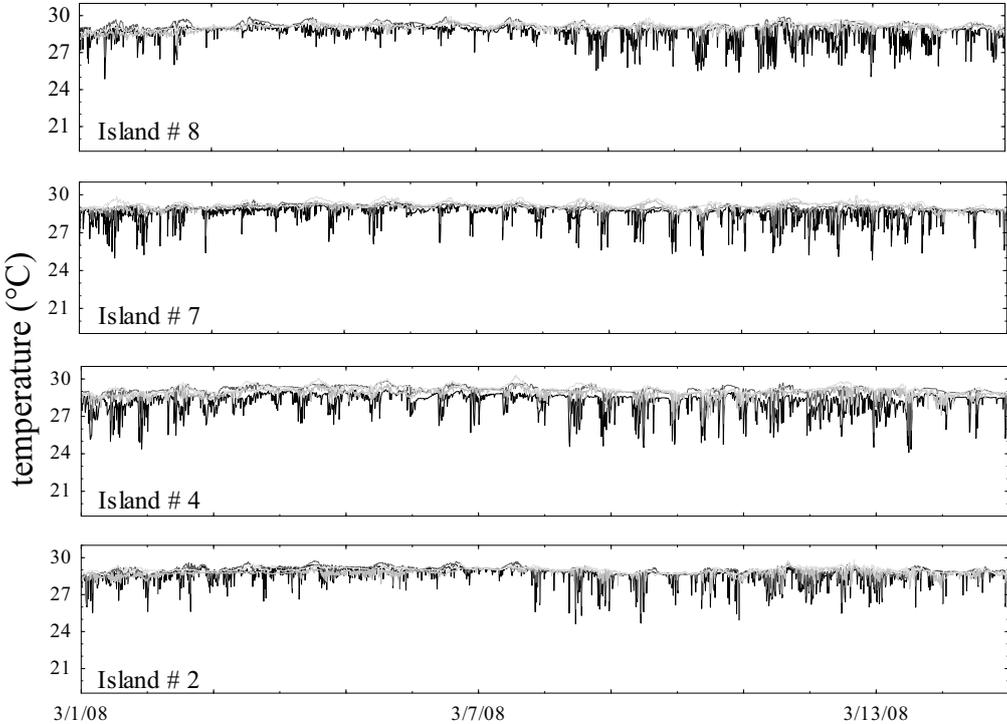


Figure 3: Temperature profile within W and E side reefs of all Island sites (#2, 4, 7 and 8) along the Similan Islands in 2008 (— W deep, — W shallow, — E deep, — E shallow)

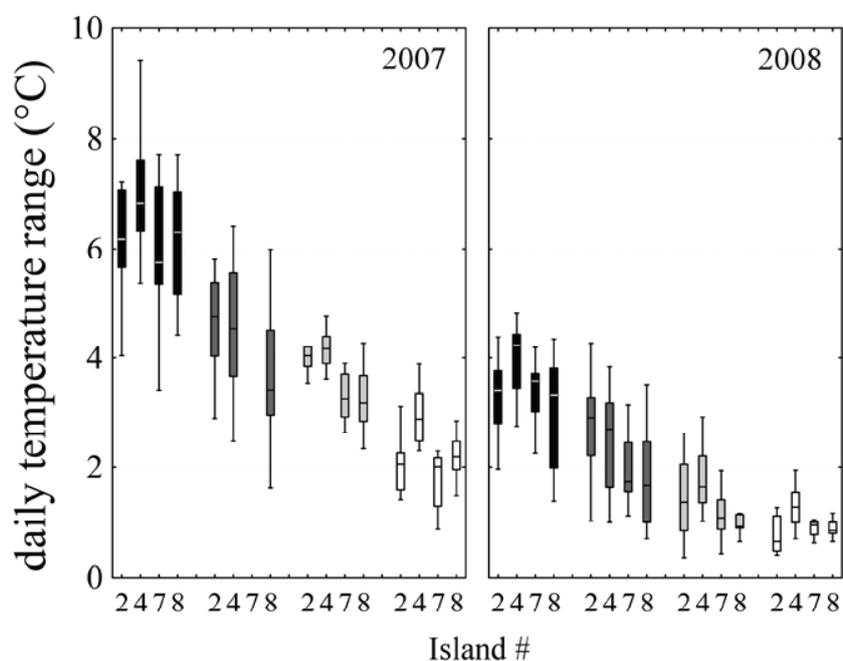


Figure 4: Daily temperature ranges (14 days) of all sampling sites along the Similan Islands during study period of 2007 and 2008

The nutrient characteristics of the reef waters (raw data Table S1) co-varied with LAIW intensity. The strongest differences ($p < 0.001$, Table 2) coincided with the largest temperature differences between 2007 and 2008 (Fig. 5). Nutrient stoichiometry varied between years: Interannual differences in nutrient concentrations exceeded an order of magnitude for nitrate, contrasting the conservative behavior of silicate which mirrored the two-fold temperature differences (Fig. 6). Nitrate and silicate contributed about 30 % and 25 % of the dissimilarities between the strong (2007: $1.34 \pm 0.26 \mu\text{M}$ nitrate Fig. 2; $6.12 \pm 0.67 \mu\text{M}$ silicate, Fig. 6) and weak (2008: $0.09 \pm 0.02 \mu\text{M}$ nitrate, Fig. 3; $2.59 \pm 0.12 \mu\text{M}$ silicate, Fig. 6) LAIW years (Table 3). DOC (2007: $0.86 \pm 0.05 \mu\text{M}$, 2008: $1.89 \pm 0.34 \mu\text{M}$), TSM (2007: $10.51 \pm 0.39 \text{ mg l}^{-1}$, 2008: $15.61 \pm 0.37 \text{ mg l}^{-1}$), nitrite (2007: $0.09 \pm 0.01 \mu\text{M}$, 2008: $0.60 \pm 0.09 \mu\text{M}$) and ammonium (2007: $0.55 \pm 0.06 \mu\text{M}$, 2008: $1.19 \pm 0.07 \mu\text{M}$) each add about further 10 % to the dissimilarity between the years (Table 3), all being more elevated during the year of less LAIW intensity (Table 3, Fig. 6).

Table 2: ANOSIM (Analysis of similarity) results after 9999 permutations of differences in water composition between the years of 2007 vs 2008 (all), between W vs E reef sides within each year, and between deep and shallow sites within each reef side. Each lower hierarchical factor is previously nested within the higher (W and E sides within respective years and deep and shallow sites within respective side).

source of variance		R	p
all	year	0.569	< 0.001*
	side(year)	0.085	0.007*
2007	side	0.097	0.024*
	depth(side)	0.207	0.005*
2008	side	0.077	0.055
	depth(side)	0.052	0.062
2007 W	depth	0.309	0.011*
2007 E	depth	0.142	0.035*
2008 W	depth	-0.014	0.518
2008 E	depth	0.083	0.056

W vs E concentration differences were significant in 2007 (Table 2, Fig. 5 and S2), but marginally not ($p = 0.055$) in 2008 (Table 2). In 2007, again nitrate (W: $1.83 \pm 0.49 \mu\text{M}$, E: $0.94 \pm 0.22 \mu\text{M}$) and silicate (W: $8.11 \pm 1.29 \mu\text{M}$, E: $4.50 \pm 0.38 \mu\text{M}$) concentrations together explain about three quarters of the differences in water quality (Table 4) with each in the mean being more than 50 % higher on W compared to E (Table 4, Fig. 6). Chlorophyll-a (W: $0.85 \pm 0.08 \mu\text{g l}^{-1}$, E: $1.24 \pm 0.09 \mu\text{g l}^{-1}$), ammonium (W: $0.63 \pm 0.12 \mu\text{M}$, E: $0.48 \pm 0.03 \mu\text{M}$) and TSM (W: $10.74 \pm 0.61 \text{ mg l}^{-1}$, E: $10.33 \pm 0.50 \text{ mg l}^{-1}$) concentrations substitute each about 5 % W-E dissimilarity (Table 4), with chlorophyll-a being higher concentrated on the E side and ammonium and TSM higher concentrated on the W (Table 4, Fig. 6). In 2008, the minor differences between W and E are due to DOC, nitrite, silicate, ammonium and TSM (Table 4, Fig. 6).

Table 3: Annual comparison of reef water composition with all species contributing > 90 % to the dissimilarities between 2007 and 2008

variable	$\bar{\text{O}}$ abundance 2007	$\bar{\text{O}}$ abundance 2008	contribution to $\bar{\text{O}}$ dissimilarity	SD $\bar{\text{O}}$ dissimilarity	cum. % contribution
$\mu\text{mol nitrate l}^{-1}$	0.68	0.08	0.66	0.99	28.38
$\mu\text{mol silicate l}^{-1}$	1.83	1.26	0.60	0.85	54.31
mg DOC l^{-1}	0.61	0.94	0.30	0.81	67.16
mg TSM l^{-1}	2.42	2.80	0.20	0.17	75.83
$\mu\text{mol nitrite l}^{-1}$	0.09	0.43	0.20	0.34	84.36
$\mu\text{mol ammonium l}^{-1}$	0.42	0.77	0.19	0.24	92.62
overall dissimilarity			2.32		

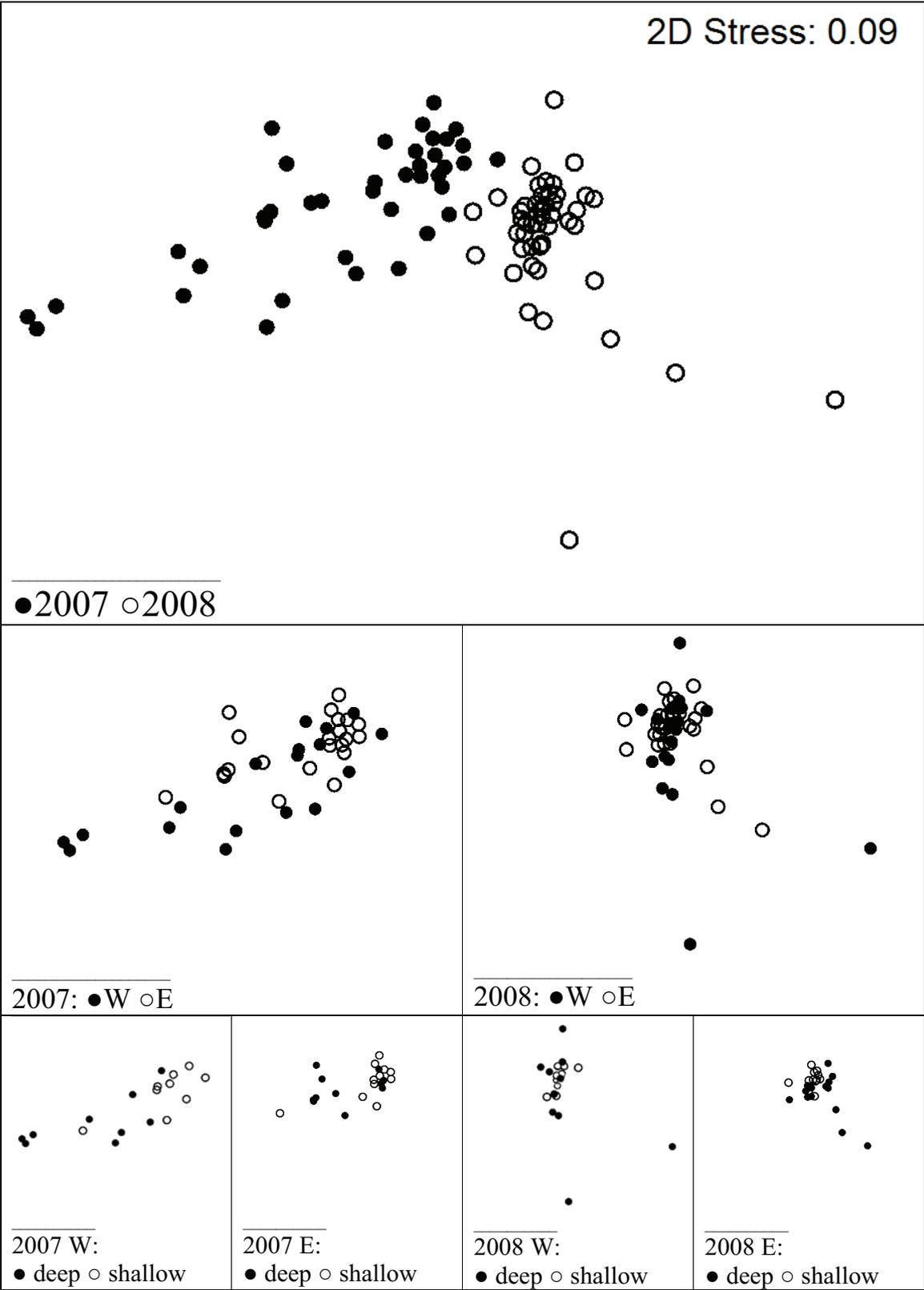


Figure 5: MDS ordination of all water samples collected during study periods 2007 and 2008 on W and E of Koh Miang Island, top: years, middle: sides of 2007 (left) and 2008 (right), down (from left to right): depths of 2007 W, 2007 E, 2008 W, 2008 E

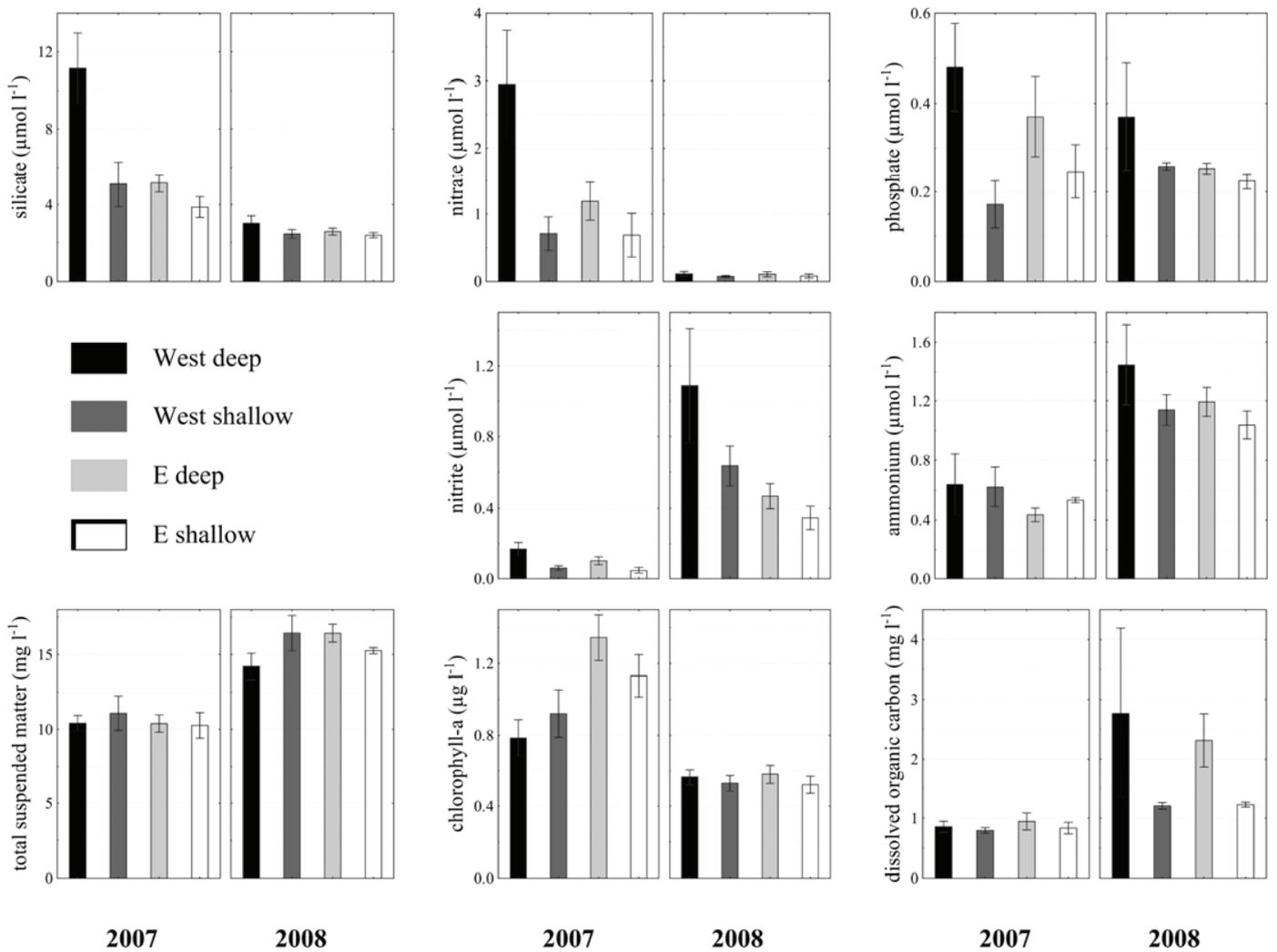


Figure 6: composition (means \pm SE) of shallow (~ 7 m) and deep (~ 20 m) water of the W and E Similan reefs.: upper row: main LAIW affected parameters (silicate, nitrate, phosphate), middle row: other N-derivates (nitrite, ammonium), lower row: TSM, chlorophyll-a and DOC

Table 4: Side (W vs E) comparison of reef water composition in 2007 and 2008 with all species contributing > 90 % to the dissimilarities between W and E

variable	Ø abundance W	Ø abundance E	contribution to Ø dissimilarity	SD Ø dissimilarity	cum. % contribution
2007					
µmol nitrate l ⁻¹	0.84	0.55	0.63	0.90	39.87
µmol silicate l ⁻¹	2.04	1.66	0.56	0.71	75.34
µg chlorophyll-a l ⁻¹	0.60	0.79	0.10	0.11	81.48
µmol ammonium l ⁻¹	0.45	0.32	0.08	0.15	86.38
mg TSM l ⁻¹	2.44	2.41	0.07	0.11	91.02
overall dissimilarity			1.59		
2008					
mg DOC l ⁻¹	0.92	0.96	0.33	0.87	40.07
µmol nitrite l ⁻¹	0.56	0.33	0.20	0.34	64.79
µmol silicate l ⁻¹	1.29	1.23	0.09	0.15	75.34
µmol ammonium l ⁻¹	0.80	0.74	0.09	0.17	85.39
mg TSM l ⁻¹	2.77	2.82	0.06	0.16	92.49
overall dissimilarity			0.81		

Depth differences in water quality within each side of each year (Fig. 5) were only significant for W (Fig. S2) and E (Fig. S3) of 2007, but again not in 2008 (Table 2). In 2007, once more nitrate (deep: 2.95 ± 0.80 µM, shallow: 0.71 ± 0.25 µM) and silicate (deep: 11.14 ± 1.83 µM, shallow: 5.07 ± 1.20 µM) concentrations on the W side are mainly responsible (each about 40 %) for the dissimilarities between the shallow and deep reef waters (Table 5), both being more than twice as high in deep water (Fig. 6). Higher ammonium (deep: 0.64 ± 0.20 µM, shallow: 0.62 ± 0.13 µM) and phosphate (deep: 0.48 ± 0.10 µM, shallow: 0.17 ± 0.05 µM) concentrations in the deeper water both contribute 5 % more to the dissimilarities between deep and shallow water on the W (Table 5). Also on the E side in 2007, nitrate (deep: 1.19 ± 0.28 µM, shallow: 0.68 ± 0.33 µM) and silicate (deep: 5.13 ± 0.48 µM, shallow: 3.86 ± 0.55 µM) cause more than 50 % of the discrepancies between deep and shallow water (Table 5), each being elevated in deep water (Fig. 6). Higher DOC (deep: 0.94 ± 0.14 mg l⁻¹, shallow: 0.83 ± 0.10 mg l⁻¹), chlorophyll-a (deep: 1.34 ± 0.13 µg l⁻¹, shallow: 1.13 ± 0.12 µg l⁻¹) and TSM (deep: 10.39 ± 0.58 mg l⁻¹, shallow: 10.26 ± 0.86 mg l⁻¹) concentrations in the deep water contribute another 9 to 7 % to the dissimilarities between shallow and deep water on the E side reef in 2007 (Fig. 6, Table 5). In 2008, main differences between the deep and

shallow waters of both, W and E, are posed by DOC concentrations, followed by nitrite, silicate and ammonium concentrations, which are all higher in deeper waters of W and E compared to shallow reef areas (Table 6, Fig. 6).

Table 5: Depth (deep vs shallow) comparison of reef water composition in W and E reefs in 2007 with all species contributing > 90 % to the dissimilarities between deep and shallow

variable	Ø abundance deep	Ø abundance shallow	contribution to Ø dissimilarity	SD Ø dissimilarity	cum. % contribution
West					
µmol nitrate l ⁻¹	1.21	0.48	0.97	1.05	42.32
µmol silicate l ⁻¹	2.40	1.69	0.90	0.89	81.53
µmol ammonium l ⁻¹	0.46	0.45	0.13	0.21	87.38
µmol phosphate l ⁻¹	0.37	0.15	0.10	0.10	91.88
overall dissimilarity			2.29		
East					
µmol nitrate l ⁻¹	0.69	0.41	0.44	0.49	45.37
µmol silicate l ⁻¹	1.78	1.53	0.21	0.23	66.72
mg DOC l ⁻¹	0.64	0.59	0.091	0.12	76.17
µg chlorophyll-a l ⁻¹	0.84	0.74	0.07	0.10	83.34
mg TSM l ⁻¹	2.42	2.40	0.07	0.10	90.47
overall dissimilarity			0.97		

Table 6: Depth (deep vs shallow) comparison of reef water composition in W and E reefs in 2008 with all species contributing > 90 % to the dissimilarities between deep and shallow

variable	Ø abundance deep	Ø abundance shallow	contribution to Ø dissimilarity	SD Ø dissimilarity	cum. % contribution
West					
mg DOC l ⁻¹	1.03	0.79	0.45	1.22	41.66
µmol nitrite l ⁻¹	0.64	0.47	0.24	0.35	63.69
µmol silicate l ⁻¹	1.35	1.23	0.11	0.17	74.21
µmol ammonium l ⁻¹	0.85	0.75	0.11	0.19	84.19
mg TSM l ⁻¹	2.70	2.84	0.10	0.24	93.59
overall dissimilarity			1.08		
East					
mg DOC l ⁻¹	1.11	0.80	0.25	0.45	50.93
µmol nitrite l ⁻¹	0.37	0.28	0.07	0.09	63.92
µmol silicate l ⁻¹	1.26	1.21	0.06	0.07	75.61
µmol ammonium l ⁻¹	0.77	0.70	0.05	0.07	86.11
µg chlorophyll-a l ⁻¹	0.45	0.41	0.03	0.04	91.47
overall dissimilarity			0.50		

Differences in host tissue and zooxanthellae composition between the two investigated coral species are noticeable on first view (Figs. 9 and 10), particularly during the strong LAIW season in 2007. Zooxanthellae densities, chlorophyll-a and protein content, host tissue and zooxanthellae dry weights, as well as host tissue and zooxanthellae nitrogen and carbon concentrations are generally higher in *D. heliopora* (Fig. 10) than in *P. lutea* (Fig. 9). Some of these differences prevail in 2008, but others (e.g. zooxanthellae densities) don't (Tables S2 and S3). For both species, the temporal (2007 vs 2008) and spatial (W vs E; shallow vs deep) differences were always much stronger (Table 7), than the differences among specimens sampled within the same sites from the various islands' reefs (Fig. 1) which totally lacked significant differences (Table 7).

Table 7: ANOSIM results, only main factor, each “beneath factor” separately nested ANOSIM (Analysis of similarity) results after 9999 permutations of differences in coral host tissue and zooxanthellae composition of *Porites lutea* and *Diploastrea heliopora* between the years of 2007 vs 2008 (all), between W vs E reef sides within each year, and between deep and shallow sites within each reef side. Each lower hierarchical factor is previously nested within the higher (W and E sides within respective years and deep and shallow sites within respective side). Also island of origin is nested as a factor within the hierarchical levels of year and reef side to test for significant differences among the same sides of the various islands.

source of variance		<i>Porites lutea</i>		<i>Diploastrea heliopora</i>	
		R	p	R	p
all	year	0.198	< 0.001*	0.769	< 0.001*
	side(year)	0.222	< 0.001*	0.302	0.001*
	island(year)	-0.06	0.803	0.176	0.144
2007	side	0.455	< 0.001*	0.889	0.029*
	depth(side)	-0.04	0.641	0.009	0.450
	island(side)	0.055	0.293	0.165	0.184
2008	side	0.028	0.217	0.454	0.001*
	depth(side)	-0.037	0.597	0.128	0.105
	island(side)	-0.020	0.529	0.260	0.231
2007 W	depth	-0.115	0.831	0.075	0.300
2007 E	depth	0.022	0.361	-0.259	0.800
2008 W	depth	-0.146	0.871	0.481	0.100
2008 E	depth	0.135	0.102	0.077	0.197

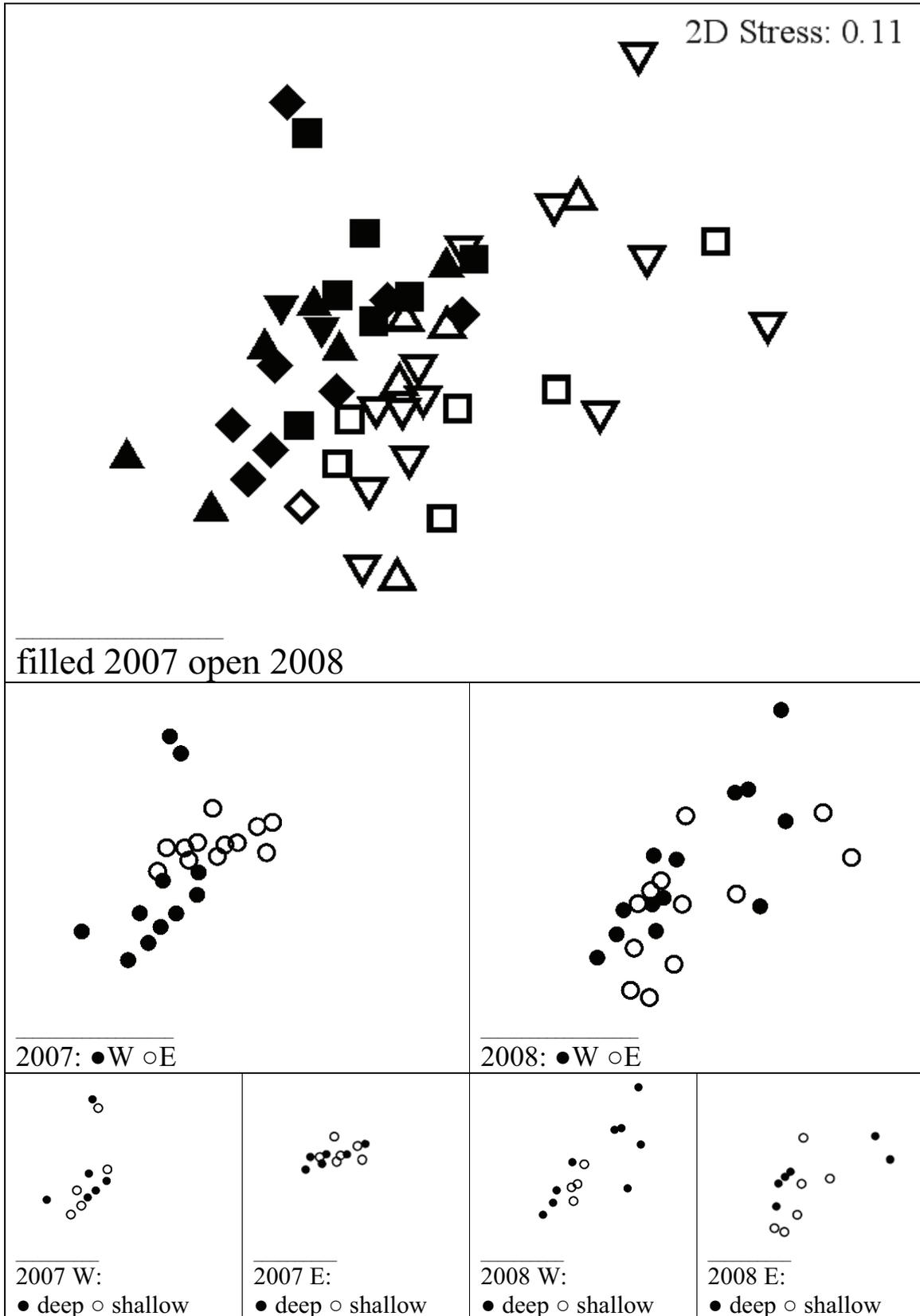


Figure 7: MDS ordination of all parameters measured in the tissue samples from *Porites lutea*; top: years (Island# 2 diamond, 4 downward triangle, 7 quadrate, 8 upward looking triangle), middle: sides of 2007 (left) and 2008 (right), down (from left to right): depths of 2007 W, 2007 E, 2008 W, 2008 E

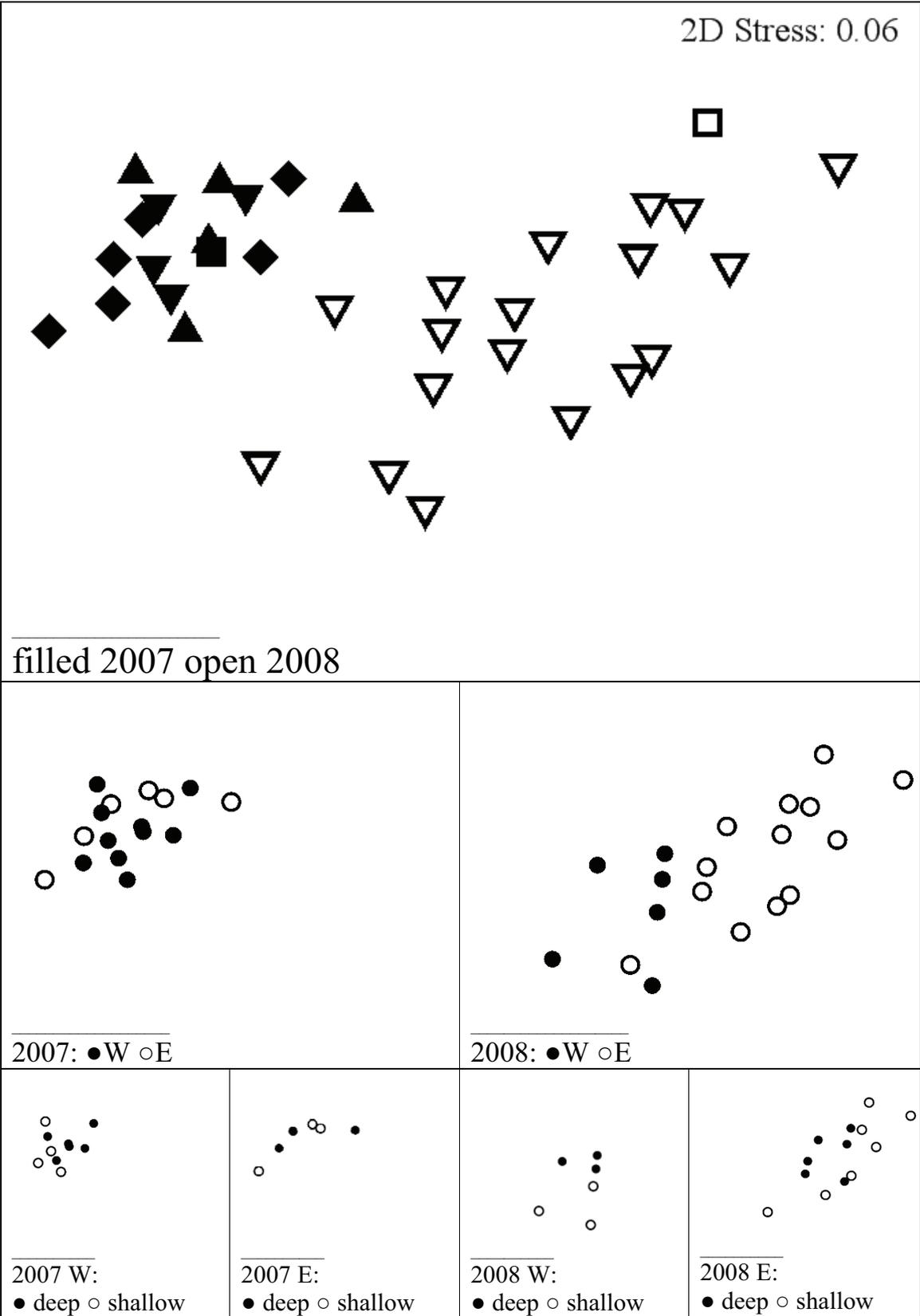


Figure 8: MDS ordination of all parameters measured in the tissue samples from *Diploastrea heliopora*; top: years (Island# 2 diamond, 4 downward triangle, 7 quadrate, 8 upward looking triangle), middle: sides of 2007 (left) and 2008 (right), down (from left to right): depths of 2007 W, 2007 E, 2008 W, 2008 E

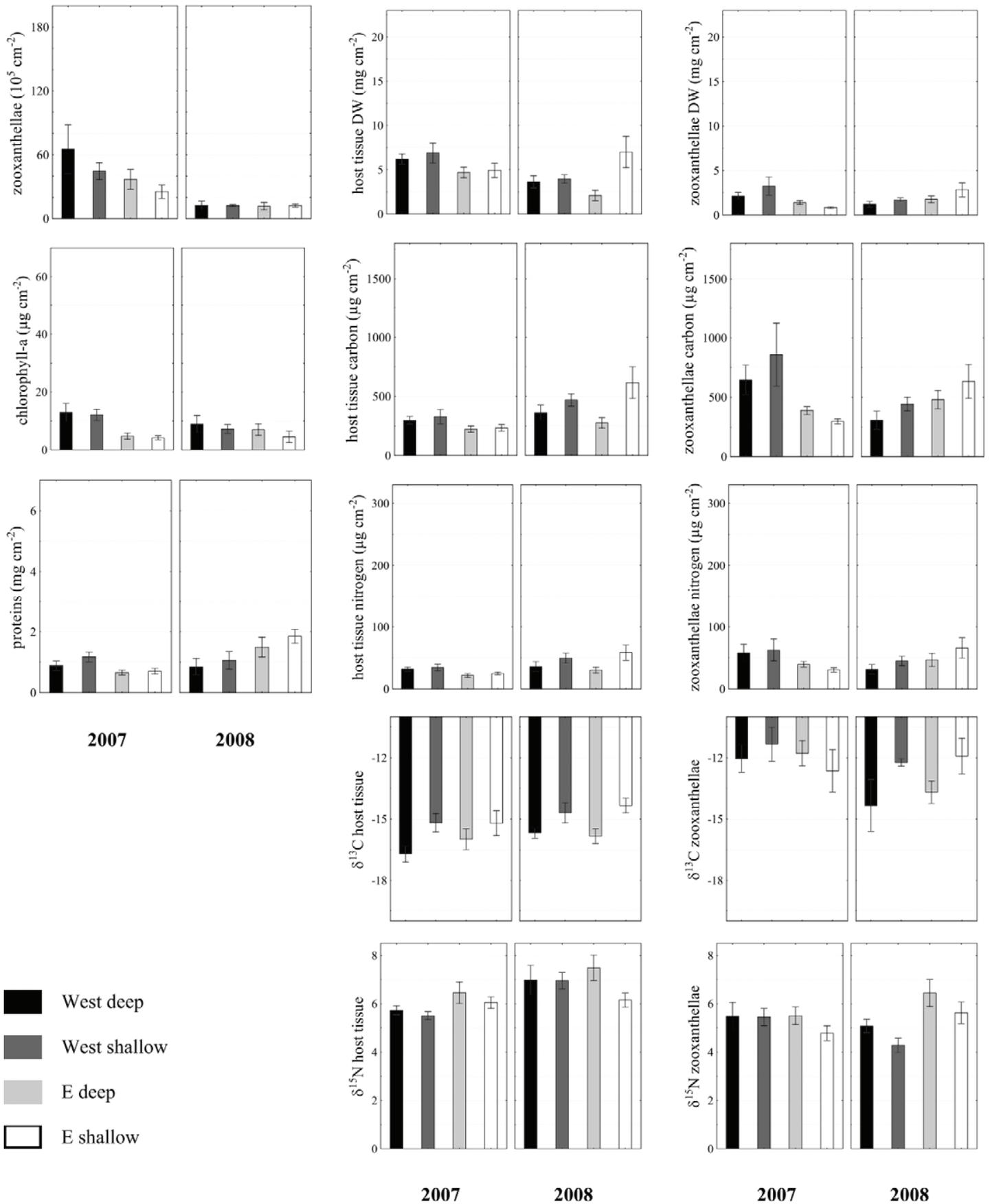


Figure 9: *Porites lutea* tissue composition (means \pm SE) in shallow (~7 m) and deep (~20 m) water along the W and E Similan reefs.: left column: holobiont parameters (zooxanthellae densities, chlorophyll-a concentrations and protein content); middle column: host tissue parameters (dry weight, carbon, nitrogen content, isotopic carbon and nitrogen ratios); right column: zooxanthellae parameters (dry weight, carbon, nitrogen content, isotopic carbon and nitrogen ratios)

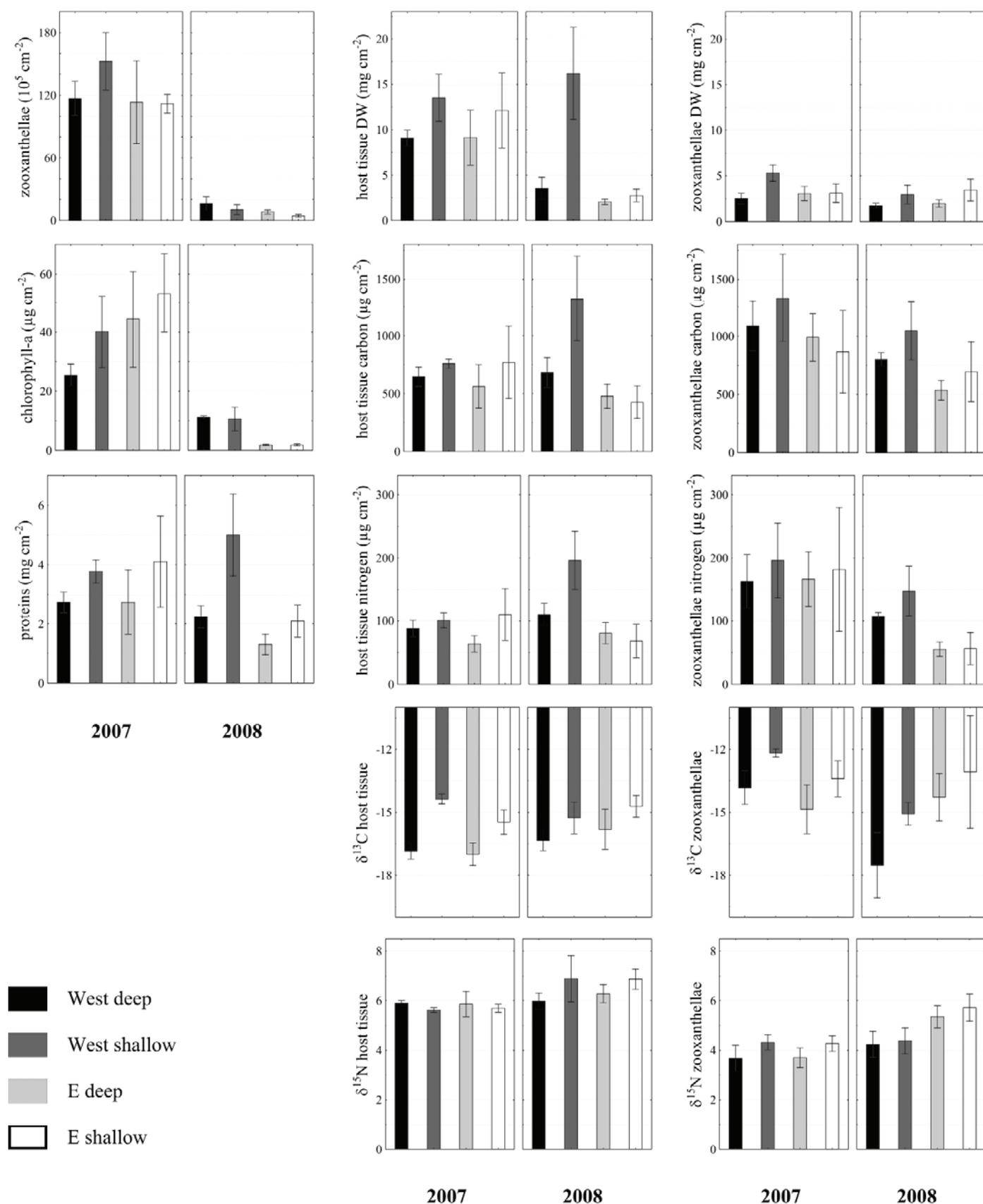


Figure 10: *Diploastrea heliopora* tissue composition (means \pm SE) in shallow (~7 m) and deep (~20 m) water along the W and E Similan reefs.: left column: holobiont parameters (zooxanthellae densities, chlorophyll-a concentrations and protein content); middle column: host tissue parameters (dry weight, carbon, nitrogen content, isotopic carbon and nitrogen ratios); right column: zooxanthellae parameters (dry weight, carbon, nitrogen content, isotopic carbon and nitrogen ratios)

Firstly, differences in host tissue and zooxanthellae composition of *P. lutea* (Fig. 7) and *D. heliopora* (Fig. 8) were significant between 2007 and 2008 (Table 7, Figs. 7 and 8). For both species, these yearly discrepancies are to 40 % due to higher zooxanthellae densities in 2007 compared to 2008 (Tables 8 and 9), with *P. lutea* stocking more than 3 times (2007: $4.30 \pm 0.71 \times 10^6 \text{ cm}^{-2}$, 2008: $1.23 \pm 0.16 \times 10^6 \text{ cm}^{-2}$) and *D. heliopora* even more than 10 times (2007: $12.42 \pm 1.14 \times 10^6 \text{ cm}^{-2}$, 2008: $0.84 \pm 0.16 \times 10^6 \text{ cm}^{-2}$) zooxanthellae in the year with strong LAIW intensity (Figs. 9 and 10). The yearly difference in the condition of *P. lutea* is further due to higher carbon (2007: $533.57 \pm 76.48 \text{ } \mu\text{g cm}^{-2}$, 2008: $448.66 \pm 51.80 \text{ } \mu\text{g cm}^{-2}$) and nitrogen (2007: $47.06 \pm 5.76 \text{ } \mu\text{g cm}^{-2}$, 2008: $45.57 \pm 5.90 \text{ } \mu\text{g cm}^{-2}$) contents of the zooxanthellae (each composing 10 % dissimilarity), and higher chlorophyll-a concentrations (2007: $8.31 \pm 1.26 \text{ } \mu\text{g cm}^{-2}$, 2008: $7.10 \pm 1.28 \text{ } \mu\text{g cm}^{-2}$) of the holobiont (also contributing 10 % dissimilarity) in 2007. To a minor extend (about 5 % each), dissimilarities in *P. lutea* are additionally due to a lower host carbon (2007: $268.50 \pm 19.57 \text{ } \mu\text{g cm}^{-2}$, 2008: $419.92 \pm 47.24 \text{ } \mu\text{g cm}^{-2}$) and nitrogen (2007: $28.01 \pm 1.98 \text{ } \mu\text{g cm}^{-2}$, 2008: $42.21 \pm 4.71 \text{ } \mu\text{g cm}^{-2}$) content, but a slightly higher total dry weight (2007: $5.63 \pm 0.41 \text{ mg cm}^{-2}$, 2008: $4.13 \pm 0.60 \text{ mg cm}^{-2}$) of the coral tissue in 2007 (Table 8, Fig. 9). In the holobiont composition of *D. heliopora*, yearly differences on the other hand are further determined by strongly increased amounts of chlorophyll in 2007 ($37.94 \pm 5.29 \text{ } \mu\text{g cm}^{-2}$) compared to 2008 ($4.71 \pm 1.13 \text{ } \mu\text{g cm}^{-2}$), composing another 20 % of the yearly dissimilarities, followed by elevated zooxanthellate nitrogen (about 8 % dissimilarity; 2007: $175.61 \pm 26.24 \text{ } \mu\text{g cm}^{-2}$, 2008: $78.56 \pm 13.70 \text{ } \mu\text{g cm}^{-2}$) and coral host dry weight (7 % dissimilarity; 2007: $10.76 \pm 1.16 \text{ mg cm}^{-2}$, 2008: $4.77 \pm 1.39 \text{ mg cm}^{-2}$) in 2007. Due to high coral host nitrogen concentrations in the shallow W side specimens collected in 2008 ($196.27 \pm 45.87 \text{ } \mu\text{g cm}^{-2}$; Fig. 10), yearly averaged coral host nitrogen concentrations were lower in 2007 (2007: $90.92 \pm 9.59 \text{ } \mu\text{g cm}^{-2}$, 2008: $98.96 \pm 16.18 \text{ } \mu\text{g cm}^{-2}$), while coral host carbon contents (2007: $681.89 \pm 68.26 \text{ } \mu\text{g cm}^{-2}$, 2008: $625.32 \pm 108.28 \text{ } \mu\text{g cm}^{-2}$) were higher in the year of strong LAIW intensity, both substituting further 4 % dissimilarity (Table 9, Fig. 10).

Table 8: Annual comparison of coral host tissue and zooxanthellae composition of *Porites lutea* with all species contributing > 90 % to the dissimilarities between 2007 and 2008

variable	Ø abundance 2007	Ø abundance 2008	contribution to Ø dissimilarity	SD Ø dissimilarity	cum. % contribution
zooxanthellae cm ⁻²	15.00	13.7	3.3	4.52	39.59
µg zooxanthellae carbon cm ⁻²	6.04	5.91	1.04	1.60	51.99
µg zooxanthellae nitrogen cm ⁻²	3.69	3.64	0.09	0.13	62.73
µg chlorophyll-a cm ⁻²	2.04	1.87	0.85	1.15	72.85
µg coral host carbon cm ⁻²	5.54	5.89	0.54	0.65	79.33
µg coral host nitrogen cm ⁻²	3.32	3.62	0.51	0.62	85.38
mg DW coral host cm ⁻²	1.85	1.49	0.51	0.66	91.38
overall dissimilarity			8.40		

Table 9: Annual comparison of coral host tissue and zooxanthellae composition of *Diploastrea heliopora* with all species contributing > 90 % to the dissimilarities between 2007 and 2008

variable	Ø abundance 2007	Ø abundance 2008	contribution to Ø dissimilarity	SD Ø dissimilarity	cum. % contribution
zooxanthellae cm ⁻²	16.3	13.30	9.40	5.31	43.71
µg chlorophyll-a cm ⁻²	3.51	1.45	5.07	3.55	67.30
µg zooxanthellae nitrogen cm ⁻²	5.01	4.11	1.71	2.09	75.26
mg DW coral host cm ⁻²	2.40	1.44	1.56	1.50	82.52
µg coral host nitrogen cm ⁻²	4.40	4.53	0.93	1.33	86.85
µg coral host carbon cm ⁻²	6.46	6.17	0.83	1.17	90.71
overall dissimilarity			21.51		

W and E side differences of the holobiont condition in 2007 (Fig. 2) were also significant (Table 7) for *P. lutea* (Fig. S4) and *D. heliopora* (Fig. S5). In 2007, chlorophyll-a concentrations in both coral species accounted for 20 % of the dissimilarities between W and E side corals (Tables 10 and 11 respectively), being more than twice as high on the W side in *P. lutea* specimens (Fig. 9; W: $12.54 \pm 1.84 \mu\text{g cm}^{-2}$, E: $4.44 \pm 0.61 \mu\text{g cm}^{-2}$), while concentrations in *D. heliopora* were about 50 % higher on the E side (Fig. 10; W: $31.33 \pm 5.51 \mu\text{g cm}^{-2}$, E: $48.95 \pm 9.68 \mu\text{g cm}^{-2}$). Zooxanthellae densities (*P. lutea*: W: $5.59 \text{ cm}^{-2} \pm 0.13 \times 10^6 \text{ cm}^{-2}$, E: $3.11 \pm 0.06 \times 10^6 \text{ cm}^{-2}$; *D. heliopora*: W: $13.12 \pm 0.15 \times 10^6 \text{ cm}^{-2}$, E: $11.25 \pm 0.18 \times 10^6 \text{ cm}^{-2}$), zooxanthellate carbon (*P. lutea*: W: $742.12 \pm 133.86 \mu\text{g cm}^{-2}$, E: $342.39 \pm 23.42 \mu\text{g cm}^{-2}$; *D. heliopora*: W: $1188.15 \pm 189.98 \mu\text{g cm}^{-2}$, E: $928.18 \pm 185.54 \mu\text{g cm}^{-2}$) and zooxanthellate nitrogen (*P. lutea*: W: $60.07 \pm 10.45 \mu\text{g cm}^{-2}$, E: $35.14 \pm 2.99 \mu\text{g cm}^{-2}$; *D. heliopora*: W: $176.43 \pm 33.06 \mu\text{g cm}^{-2}$, E: $174.26 \pm 48.02 \mu\text{g cm}^{-2}$).

cm⁻²) further contributed 15 – 20 % (*P. lutea*) and 10 – 15 % (*D. heliopora*) to the dissimilarities between the W and E side reefs (Tables 10 and 11 respectively), all being higher concentrated on the W island sides (Figs. 9 and 10). Being also elevated in W side corals, the dry weight of the zooxanthellae (dissimilarity contribution just under 10 %; W: 2.65± 0.51 mg cm⁻², E: 1.14 ± 0.14 mg cm⁻²), as well as the coral host's nitrogen (W: 33.08 ± 2.91 µg cm⁻², E: 23.36 ± 1.95 µg cm⁻²) and carbon (W: 311.71 ± 31.26 µg cm⁻², E: 228.89 ± 18.87 µg cm⁻²) contents (each about 4 % dissimilarity contribution) further had a minor share on the W vs E dissimilarities of *P. lutea* (Table 10, Fig. 9). In *D. heliopora*, coral host carbon (W: 691.35 ± 52.95 µg cm⁻², E: 666.11 ± 169.65 µg cm⁻²) and nitrogen (W: 93.24 ± 9.02 µg cm⁻², E: 87.04 ± 22.05 µg cm⁻²), and the dry weight of zooxanthellae (W: 3.64 ± 0.65 mg cm⁻², E: 3.09 ± 0.58 mg cm⁻²) as well as coral host (W: 10.84 ± 1.30 mg cm⁻², E: 10.62 ± 2.39 mg cm⁻²) administered for seven to eight more percent of the spatial W-E dissimilarities (Table 11), all again elevated within W side coral samples (Fig. 10).

Table 10: Side (W vs E) comparison of coral host tissue and zooxanthellae composition of *Porites lutea* in 2007 and 2008 with all species contributing > 90 % to the dissimilarities between W and E

variable	Ø abundance W	Ø abundance E	contribution to Ø dissimilarity	SD Ø dissimilarity	cum. % contribution
2007					
µg chlorophyll-a cm ⁻²	2.51	1.6	1.23	1.40	21.01
µg zooxanthellae carbon cm ⁻²	6.30	5.81	1.22	0.87	41.79
zooxanthellae cm ⁻²	15.40	14.80	1.07	1.55	60.05
µg zooxanthellae nitrogen cm ⁻²	3.83	3.55	0.96	0.88	76.33
mg DW zooxanthellae cm ⁻²	1.19	0.74	0.48	0.51	84.47
µg coral host nitrogen cm ⁻²	3.49	3.16	0.26	0.35	88.97
µg coral host carbon cm ⁻²	5.70	5.40	0.25	0.32	93.17
overall dissimilarity			5.86		
2008					
µg chlorophyll-a cm ⁻²	2.06	1.45	0.91	0.96	24.32
µg zooxanthellae nitrogen cm ⁻²	3.78	4.02	0.55	0.60	38.85
µg zooxanthellae carbon cm ⁻²	6.06	6.31	0.46	0.53	51.14
mg DW coral host cm ⁻²	1.59	1.95	0.41	0.47	62.12
µg coral host carbon cm ⁻²	6.14	6.30	0.34	0.33	71.23
µg coral host nitrogen cm ⁻²	3.88	3.97	0.33	0.38	80.02
mg DW zooxanthellae cm ⁻²	0.99	1.24	0.30	0.38	87.88
mg protein content cm ⁻²	0.694	1.03	0.21	0.22	93.44
overall dissimilarity			3.75		

Table 11: Side (W vs E) comparison of coral host tissue and zooxanthellae composition of *Diploastrea heliopora* in 2007 and 2008 with all species contributing > 90 % to the dissimilarities between W and E

variable	Ø abundance W	Ø abundance E	contribution to Ø dissimilarity	SD Ø dissimilarity	cum. % contribution
2007					
µg chlorophyll-a cm ⁻²	3.34	3.79	0.78	0.98	19.68
µg zooxanthellae nitrogen cm ⁻²	5.02	4.99	0.69	0.81	37.16
µg zooxanthellae carbon cm ⁻²	6.98	6.73	0.46	0.60	48.77
zooxanthellae cm ⁻²	16.3	16.20	0.38	0.57	58.53
µg coral host carbon cm ⁻²	6.51	6.36	0.34	0.32	67.18
µg coral host nitrogen cm ⁻²	4.50	4.36	0.32	0.37	75.30
mg DW zooxanthellae cm ⁻²	1.44	1.36	0.30	0.34	82.86
mg DW coral host cm ⁻²	2.42	2.35	0.29	0.35	90.24
overall dissimilarity			3.94		
2008					
µg chlorophyll-a cm ⁻²	2.40	1.02	2.16	1.23	17.00
µg coral host nitrogen cm ⁻²	4.96	3.99	1.84	2.11	31.54
mg DW coral host cm ⁻²	2.10	1.14	1.71	2.04	44.99
zooxanthellae cm ⁻²	13.90	13.1	1.63	2.04	57.82
µg coral host carbon cm ⁻²	6.81	5.87	1.60	1.95	70.39
µg zooxanthellae nitrogen cm ⁻²	4.81	3.78	1.59	1.51	82.95
µg zooxanthellae carbon cm ⁻²	6.79	6.23	0.74	0.80	88.76
mg protein content cm ⁻²	1.44	0.91	0.64	0.78	93.78
overall dissimilarity			12.69		

In 2008, when LAIW were weaker (Fig. 3), the condition of only *D. heliopora* (Fig. S6), but not that of *P. lutea* specimens differed significantly between W and E side reefs (Table 7). Again chlorophyll-a concentrations (W: $10.89 \pm 1.79 \mu\text{g cm}^{-2}$, E: $1.86 \pm 0.22 \mu\text{g cm}^{-2}$), this time more than four times as high on the W side reefs, were the strongest contributor to spatial dissimilarity (more than 15 %) in *D. heliopora* (Table 11), followed, with 15 to 5 % dissimilarity contribution, by coral host nitrogen content (W: $153.34 \pm 29.24 \mu\text{g cm}^{-2}$, E: $73.87 \pm 15.60 \mu\text{g cm}^{-2}$), zooxanthellae densities (W: $1.33 \pm 0.39 \times 10^6 \text{ cm}^{-2}$, E: $0.61 \pm 0.13 \times 10^6 \text{ cm}^{-2}$), coral host carbon (W: $1005.95 \pm 227.03 \mu\text{g cm}^{-2}$, E: $449.64 \pm 87.46 \mu\text{g cm}^{-2}$), zooxanthellate nitrogen (W: $127.79 \pm 20.04 \mu\text{g cm}^{-2}$, E: $55.84 \pm 14.07 \mu\text{g cm}^{-2}$) and carbon contents (W: $924.15 \pm 127.11 \mu\text{g cm}^{-2}$, E: $621.33 \pm 140.56 \mu\text{g cm}^{-2}$) as well as total protein concentrations (W: $3.62 \pm 0.89 \text{ mg cm}^{-2}$, E: $1.73 \pm 0.35 \text{ mg cm}^{-2}$), all of which being increased at about 50 % in W side corals compared to their E side counterparts (Table 11, Fig. 10). Non-significant side differences in *P. lutea* samples from 2008 were made of similar contributions of these parameters (Fig. 9).

Discussion

This study shows a marked effect of LAIW on the metabolic state of corals reflected in their tissue. The fluctuations in nutrient loads alter the symbiont density and chlorophyll-a concentrations stronger than previously reported for seasonal variations elsewhere (Stimson 1997; Brown et al. 1999; Fagoonee et al. 1999; Fitt et al. 2000a; Stimson et al. 2002; Grimsditch et al. 2008) and are in *Diploastrea heliopora* more than an order of magnitude higher when the LAIW intensity is doubled. The combined effect of enhanced nutrient availability (Kinsey and Davies 1979; Hoegh-Guldberg and Smith 1989b; Muscatine et al. 1989b; Fagoonee et al. 1999) and their increased uptake with strong currents (Hearn et al. 2001) increases zooxanthellae density and enhances pigment production and the consequences are stronger reflected in *D. heliopora* compared to *Porites lutea*. This might be the result of genotypic differences; nevertheless, phenotypic reasons can not be excluded. Due to its skeletal structure, where the calices are shaped like parabolic mirrors, *D. heliopora* might be a better collector of available light (Enríquez et al. 2005) especially in shallow water, plus a more efficient feeder as indicated by lower $\delta^{13}\text{C}$ values of the coral host tissue (Rodrigues and Grottoli 2006), especially in deeper water pointing to increased allochthonous contribution to nutrition (Muscatine et al. 1989a) and higher protein concentrations indicative of heterotrophic input (Bachar et al. 2007), as has been proposed for large-polyped corals (Porter 1976). Overall, our data suggest a strong fertilizing effect of LAIW, enhancing zooxanthellae densities (Muscatine et al. 1989b) and pigment concentrations (Brown et al. 1999). Along with an increased uptake of organic material (Roder et al. accepted), this flux of allochthonous material may explain the observed increased in biomass and protein content in both species, similar to the findings of (Fitt et al. 2000b) and (Bachar et al. 2007), respectively.

The $\delta^{13}\text{C}$ ratios of the zooxanthellae suggest decreased fractionation due to high turnover rates of the internal dissolved inorganic carbon (DIC) pool in response to LAIW: strong LAIW intensity periods correspond with higher $\delta^{13}\text{C}$ ratios of the zooxanthellae which is in line with decreased fractionation when the dissolved inorganic carbon pool (DIC) becomes exhausted (Muscatine et al. 1989a; Swart et al. 2005) as a result of high DIC

demand due to high zooxanthellae densities and pigment concentrations. While the increased currents during LAIW may diminish the boundary layer surrounding the corals (Dennison and Barnes 1988) and increasing gas exchange, the DIC demand increases in the course of dark adaptation and nutrient assimilation (i.e. increased zooxanthellae and pigment densities) (Muscatine et al. 1989a). The $\delta^{15}\text{N}$ isotope data support the fractionation scenario for *D. heliopora* zooxanthellae (Muscatine and Kaplan 1994; McCutchan et al. 2003) in response to an ample supply of nitrogen (Heikoop et al. 1998; Heikoop et al. 2000a) during LAIW impact. The host tissue $\delta^{15}\text{N}$ ratios are as a result also lower in the strong LAIW season and reflect the upward fractionation and subsequent ratio shift of 1.4 to 3.3 ‰ determined for nitrogen from one trophic level to the next (McCutchan et al. 2003).

The data suggest species-specific responses to LAIW, where some species (e.g. *D. heliopora*) benefit stronger from the replenishment of nutrients and organic matter by LAIW than others (e.g. *P. lutea*). This is reflected by the occurrence of *D. heliopora* in exposed areas (Veron and Stafford-Smith 2000) and its higher abundance in LAIW-exposed compared to sheltered E reefs along the Similan Islands. *P. lutea* on the other hand is more abundant in LAIW-sheltered E reefs compared to W (Schmidt et al. *subm.*). The reefs along the Similan Islands experience seasonal exposure to LAIW impacts (Osborne and Burch 1980), however not always of the same intensity. Internal waves occur where tidal currents advect stratified water across abrupt topography (Jackson 2004). In the absence of interannual differences in tides and topography, the two-fold differences in LAIW impact observed between the two sampling years must be interpreted as a consequence of differences in water column stratification. Impact was strongest in the deep W side reef waters. Mixing extended to the shallower parts of the W side reefs, followed by the sheltered E deep and shallow reef sites. The temperature variations coincided with the upwelling of nutrients: silicate, nitrate and phosphate concentrations in the LAIW affected areas were up to an order of magnitude higher than in other reef areas (Brown et al. 1999). The pattern of increased nutrient introduction with increasing LAIW impact remain the same when focusing on differences between W and E side reefs within the same season (2007 and 2008 respectively), however the differences are more striking when the LAIW impact is higher as happened in 2007. On

the scale of within-year W-E side comparisons, the pattern was further observed for nitrite, ammonium, dissolved organic carbon or suspended material indicating upwelling of these compounds. It was however overlapped on larger temporal scale, when comparing strong (2007) and moderate (2008) influence of LAIW due to both faster turnover and rapid uptake or because of lesser upwelled amounts which were subsequently faster discharged from the system by stronger currents (Roder et al. accepted.). Also, for these substances, upwelling may not be the only source: e.g. an important fraction of the dissolved organic carbon (van Duyl and Gast 2001; Wild et al. 2004) and ammonium (Muscatine and D'Elia 1978; Dickson and Wheeler 1995) is known to be released by reef communities. Depth differences within the same reef are due to the rapid uptake of phosphate and nitrogenous compounds by primary producers under high-light conditions (Wiebe et al. 1975; Muscatine and D'Elia 1978; Capone and Carpenter 1982; Kokkinakis and Wheeler 1987; Larned 1998).

The combined effects on coral metabolism are strong and seem to be beneficial to some extent, which appears at odds with the fact that reef growth and framework are less pronounced on the W Similan Island sides (Chansang et al. 1999). Upwelled, corrosive waters (Feely et al. 2008) might limit coral growth (Fine and Tchernov 2007) while introduced nutrients might fuel algae (Larned 1998) increasing the competition for space in corals (Lapointe 1997). Also storms often created during the SW-monsoon present in the area between May and October (Wu and Zhang 1998) might pose mechanical disturbance to corals (Dunne and Brown 1996) growing in the shallower waters especially on the W side reefs. Furthermore, there are few studies that demonstrated the harmful effects of phosphorus (Kinsey and Davies 1979) or nitrogenous (Marubini and Davies 1996) compounds on corals, however in concentrations exceeding those reported in our study. Nevertheless, coral growing along the W reef sides of the Similan Island show strong acclimatization potential to the natural disturbances of LAIW. For example, *P. lutea* has often been mentioned to be a coral with high bleaching resilience (Harriott 1985; Glynn 1990; Gleason 1993) often dominating highly impacted reefs (Cortés-Núñez and Risk 1985; Cortés 1993). So far, no data are available, to the best of our knowledge, on the metabolism of *D. heliopora* in spite of its potential in sclerochronology (Watanabe

et al. 2003; Bagnato et al. 2004; Corrège et al. 2004) and its widespread distribution in the Red Sea, Pacific and Indian Ocean (Veron and Stafford-Smith 2000).

In the light of the large number of coral species (> 600, Veron and Stafford-Smith 2000) and wide-spread occurrence of LAIW in the coral triangle of South-East Asia (Jackson 2004) this study suggests an extraordinary potential of acclimatization to a range of LAIW-modified environmental régimes (temperatures, nutrients, currents, organic matter etc.) which may provide important insights into how corals cope with disturbances on small and large temporal and spatial scales in a changing world.

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Supplemental data Chapter I

Table S1: means and (SE) of all parameters measured in water samples collected at the W and E side in deep and shallow reef waters of Island Koh Miang Island in 2007 and 2008

	2007				2008			
	W		E		W		E	
	deep	shallow	deep	shallow	deep	shallow	deep	shallow
μmol nitrite l-1	0.17 (0.04)	0.06 (0.01)	0.10 (0.02)	0.05 (0.02)	1.09 (0.32)	0.64 (0.11)	0.47 (0.07)	0.35 (0.07)
μmol nitrate l-1	2.95 (0.8)	0.71 (0.25)	1.19 (0.28)	0.68 (0.33)	0.11 (0.03)	0.07 (0.01)	0.10 (0.04)	0.07 (0.03)
μmol ammonium l-1	0.64 (0.2)	0.62 (0.13)	0.44 (0.05)	0.53 (0.02)	1.45 (0.27)	1.14 (0.1)	1.19 (0.1)	1.04 (0.09)
μmol phosphate l-1	0.48 (0.1)	0.17 (0.05)	0.37 (0.09)	0.25 (0.06)	0.37 (0.12)	0.26 (0.01)	0.25 (0.01)	0.22 (0.02)
μmol silicate l-1	11.14 (1.83)	5.07 (1.2)	5.13 (0.48)	3.86 (0.55)	3.01 (0.39)	2.46 (0.22)	2.58 (0.18)	2.39 (0.14)
mg DOC l-1	0.86 (0.09)	0.79 (0.05)	0.94 (0.14)	0.83 (0.1)	2.77 (1.42)	1.20 (0.05)	2.31 (0.45)	1.22 (0.04)
μg chlorophyll-a l-1	0.78 (0.1)	0.92 (0.13)	1.34 (0.13)	1.13 (0.12)	0.56 (0.04)	0.53 (0.04)	0.58 (0.05)	0.52 (0.05)
mg TSM l-1	10.41 (0.52)	11.08 (1.14)	10.39 (0.58)	10.26 (0.86)	14.20 (0.88)	16.43 (1.18)	16.42 (0.6)	15.25 (0.21)

Table S2: means and (SE) of all parameters measured in tissue samples of *Porites lutea* collected at the W and E sides in deep and shallow reef waters along the Similan Islands in 2007 and 2008

	2007				2008			
	west		east		west		east	
	deep	shallow	deep	shallow	deep	shallow	deep	shallow
$\mu\text{g chl-a cm}^{-2}$	12.90 (3.16)	12.12 (1.9)	4.72 (1.07)	4.17 (0.68)	8.88 (2.98)	7.24 (1.53)	6.99 (2.01)	4.46 (1.97)
10^6 zooxanthellae cm^{-2}	6.53 (2.28)	4.47 (0.8)	3.70 (0.93)	2.53 (0.64)	1.30 (0.4)	1.24 (0.09)	1.18 (0.35)	1.23 (0.14)
mg protein cm^{-2}	0.88 (0.15)	1.17 (0.16)	0.66 (0.08)	0.70 (0.1)	0.85 (0.27)	1.06 (0.29)	1.49 (0.33)	1.85 (0.23)
mg DW cm^{-2}	6.22 (0.58)	6.90 (1.13)	4.69 (0.59)	4.94 (0.81)	3.65 (0.67)	3.98 (0.46)	2.09 (0.58)	7.00 (1.77)
$\mu\text{g C cm}^{-2}$	297.20 (33.56)	329.12 (59.54)	223.64 (26.78)	234.15 (28.95)	361.49 (66.62)	470.51 (51.31)	276.56 (44.31)	617.22 (133.01)
$\mu\text{g N cm}^{-2}$	31.87 (3.42)	34.54 (5.29)	21.73 (3.27)	24.98 (2.24)	36.13 (7.74)	49.40 (8.05)	30.35 (4.64)	58.39 (12.37)
$\delta^{13}\text{C}$	-16.70 (0.4)	-15.18 (0.45)	-15.99 (0.51)	-15.20 (0.61)	-15.68 (0.26)	-14.69 (0.49)	-15.84 (0.36)	-14.34 (0.36)
$\delta^{15}\text{N}$	5.73 (0.19)	5.51 (0.17)	6.46 (0.44)	6.05 (0.24)	6.98 (0.62)	6.95 (0.33)	7.49 (0.52)	6.16 (0.29)
mg DW cm^{-2}	2.15 (0.4)	3.26 (1.02)	1.42 (0.21)	0.85 (0.1)	1.23 (0.32)	1.72 (0.21)	1.77 (0.38)	2.84 (0.8)
$\mu\text{g C cm}^{-2}$	645.29 (123.6)	858.33 (263.52)	387.91 (34.48)	296.87 (19.87)	307.47 (74.64)	441.83 (58.32)	479.89 (75.32)	633.77 (142.22)
$\mu\text{g N cm}^{-2}$	57.91 (13.82)	62.66 (17.65)	39.61 (4.42)	30.66 (3.43)	31.48 (7.8)	44.96 (7.53)	46.72 (10.51)	65.94 (16.55)
$\delta^{13}\text{C}$	-12.05 (0.67)	-11.35 (0.83)	-11.79 (0.62)	-12.65 (1.04)	-14.34 (1.26)	-12.24 (0.18)	-13.69 (0.55)	-11.92 (0.87)
$\delta^{15}\text{N}$	5.48 (0.58)	5.45 (0.36)	5.51 (0.37)	4.78 (0.3)	5.08 (0.28)	4.29 (0.3)	6.44 (0.56)	5.63 (0.45)

Table S3: means and (SE) of all parameters measured in tissue samples of *Diploastrea heliopora* collected at the W and E sides in deep and shallow reef waters along the Similan Islands in 2007 and 2008

	2007				2008			
	west		east		west		east	
	deep	shallow	deep	shallow	deep	shallow	deep	shallow
$\mu\text{g chl-a cm}^{-2}$	25.42 (3.69)	40.20 (12.24)	44.46 (16.39)	53.43 (13.41)	11.18 (0.55)	10.60 (3.94)	1.85 (0.23)	1.86 (0.37)
10^6 zooxanthellae cm^{-2}	11.70 (1.64)	15.25 (2.76)	11.32 (4)	11.18 (0.89)	1.63 (0.66)	1.03 (0.49)	0.81 (0.2)	0.44 (0.13)
mg protein cm^{-2}	2.74 (0.35)	3.77 (0.39)	2.74 (1.09)	4.11 (1.53)	2.24 (0.39)	5.00 (1.38)	1.30 (0.35)	2.09 (0.55)
mg DW cm^{-2}	9.05 (0.89)	13.51 (2.59)	9.13 (3.02)	12.12 (4.14)	3.54 (1.22)	16.22 (5.09)	2.05 (0.29)	2.74 (0.71)
$\mu\text{g C cm}^{-2}$	646.26 (82.17)	758.99 (40.12)	562.10 (188)	770.13 (312.64)	682.83 (128.29)	1329.07 (369.93)	477.43 (105.81)	425.82 (142.17)
$\mu\text{g N cm}^{-2}$	88.05 (12.99)	101.03 (12.43)	63.70 (13.21)	110.38 (41.37)	110.42 (18.12)	196.27 (45.87)	80.59 (16.73)	68.10 (26.3)
$\delta^{13}\text{C}$	-16.86 (0.38)	-14.37 (0.23)	-17.00 (0.53)	-15.47 (0.58)	-16.35 (0.49)	-15.27 (0.76)	-15.81 (0.96)	-14.72 (0.52)
$\delta^{15}\text{N}$	5.89 (0.11)	5.63 (0.09)	5.86 (0.52)	5.70 (0.16)	5.98 (0.33)	6.89 (0.94)	6.28 (0.37)	6.87 (0.41)
mg DW cm^{-2}	2.52 (0.57)	5.32 (0.9)	3.07 (0.78)	3.11 (1.03)	1.73 (0.28)	2.95 (1.02)	1.97 (0.4)	3.45 (1.21)
$\mu\text{g C cm}^{-2}$	1088.74 (214.11)	1337.28 (379.13)	990.35 (204.32)	866.01 (355.7)	801.27 (56.91)	1047.03 (249.9)	535.19 (84.97)	695.15 (257.4)
$\mu\text{g N cm}^{-2}$	163.23 (42.5)	196.22 (58.85)	166.91 (43.18)	181.60 (98.03)	107.77 (6.12)	147.80 (39.61)	55.28 (11.43)	56.33 (25.34)
$\delta^{13}\text{C}$	-13.82 (0.8)	-12.17 (0.19)	-14.86 (1.17)	-13.40 (0.86)	-17.52 (1.55)	-15.07 (0.54)	-14.28 (1.13)	-13.07 (2.69)
$\delta^{15}\text{N}$	3.67 (0.54)	4.32 (0.31)	3.70 (0.4)	4.27 (0.31)	4.24 (0.54)	4.38 (0.52)	5.35 (0.45)	5.72 (0.55)

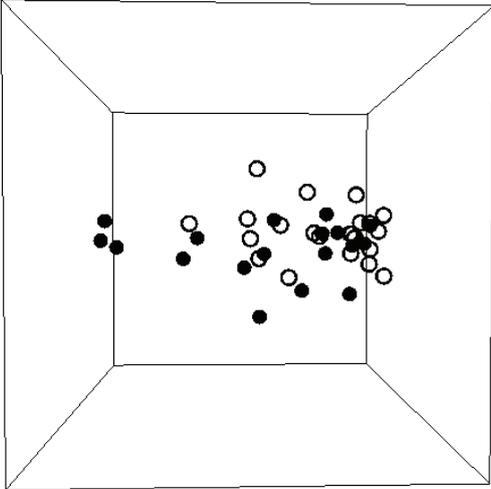


Figure S1: 3D-MDS (stress: 0.07) plot of all parameters measured in reef water from 2007 W (filled) vs E (open)

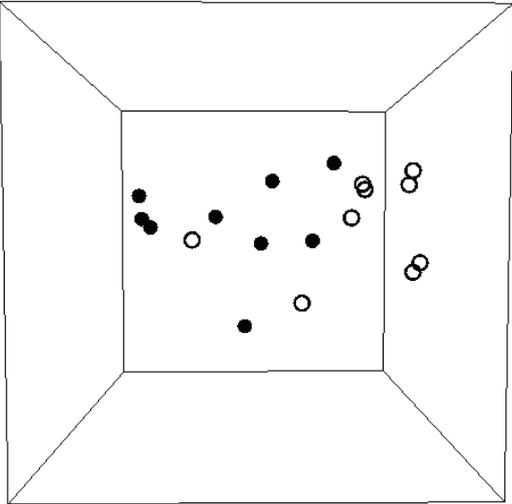


Figure S3: 3D-MDS plot (stress: 0.06) of all parameters measured in reef water from 2007 W deep (filled) vs shallow (open)

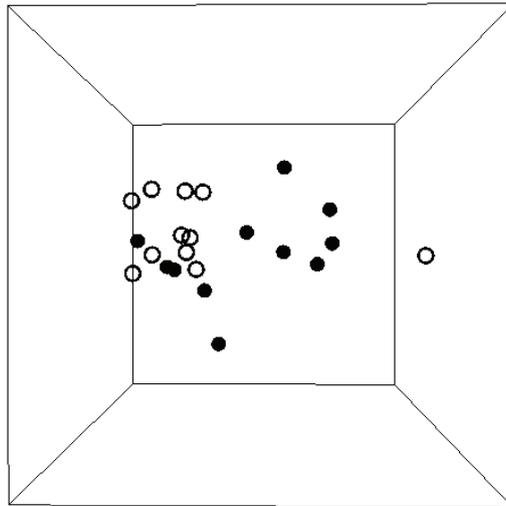


Figure S3: 3D-MDS plot (stress: 0.06) of all parameters measured in reef water from 2007 E deep (filled) vs shallow (open)

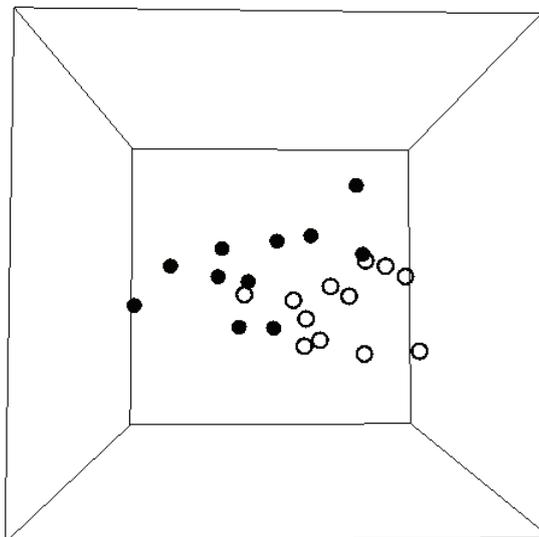


Figure S4: 3D-MDS plot (stress: 0.03) all parameters measured in the tissue samples of *Porites lutea* from 2007 W (filled) vs E (open)

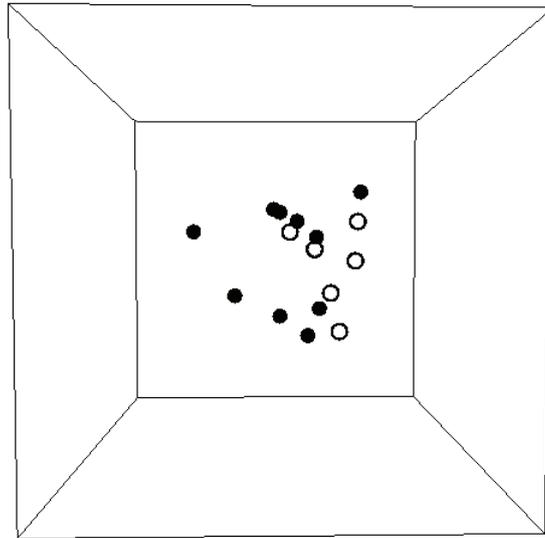


Figure S5: 3D-MDS plot (stress: 0.06) of all parameters measured in the tissue samples of *Diploastrea heliopora* from 2007 W (filled) vs E (open)

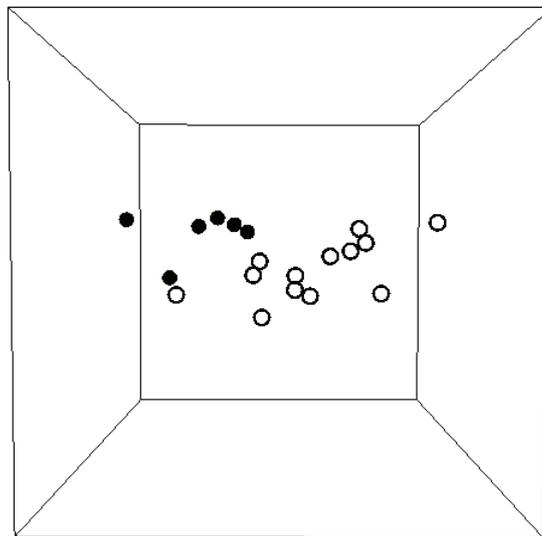


Figure S6: 3D-MDS (stress: 0.03) plot of all parameters measured in the tissue samples of *Diploastrea heliopora* 2008 W (filled) vs E (open)

- Chapter II -

Trophic response of corals to Large Amplitude Internal Waves

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Abstract

The trophic response of the scleractinian coral *Pocillopora meandrina* (Dana 1846) to Large Amplitude Internal Waves (LAIW) was investigated in the Andaman Sea. Corals living on the west sides of the Similan Islands (Thailand) exposed to LAIW showed significantly higher biomass and protein content than sheltered corals on the east sides. LAIW-exposed corals were also more heterotrophic, displaying lower $\delta^{13}\text{C}$ ratios in their tissues and higher rates of survival in artificial darkness compared to sheltered counterparts. Heterotrophic nutrition in concert with photosynthesis leads to higher energy reserves in corals from LAIW-exposed reefs making them more resilient to disturbance. As these differences in trophic status are due to LAIW-enhanced fluxes of organic matter, LAIW may play an important role in supporting coral metabolism and survival in these monsoon beaten reefs.

Key words

Large Amplitude Internal Waves – corals - heterotrophic plasticity – current regime – *Pocillopora meandrina* – Andaman Sea

Running head: Trophic response of corals to LAIW

Introduction

The trophic response of corals to natural and anthropogenic stressors has been addressed in several studies (Anthony 2000, Anthony & Fabricius 2000, Palardy et al. 2005, Anthony 2006, Palardy et al. 2006, Rodrigues & Grottoli 2006, Borell et al. 2008, Palardy et al. 2008). Although most reef corals are functionally mainly photoautotrophic, deriving the bulk of their energy from photosynthesis (Franzisket 1969, Muscatine & Cernichiaro 1969, Muscatine & Porter 1977), heterotrophy can supply 11 - 46 % of the coral's daily carbon requirements (Houlbrèque & Ferrier-Pagès 2009), and more than 100 % in bleached corals (Palardy et al. 2008). While corals have been traditionally viewed as planktivores by virtue of their armature of tentacles and stinging nematocysts (Yonge 1930, Abe 1938, Lewis & Price 1975), their

diet comprises a much wider range of food including microphytoplankton (Glynn 1973), nano- and picoplankton (Ferrier-Pagès et al. 1998, Houlbrèque et al. 2004b), bacteria (Sorokin 1973, Bak et al. 1998), dissolved organic matter (Sorokin 1973, Grover et al. 2008), detritus and organic matter laden sediments (Anthony 2000).

To detect and quantify the importance of photoauto- vs. heterotrophy in coral metabolism, stable isotopes have been established as a useful indicator (Muscatine et al. 1989, Grottoli 2002, Swart et al. 2005). The $\delta^{13}\text{C}$ ratio of the coral host tissue is the combined result of photosynthetically derived products and nutritional inputs from allochthonous sources (Muscatine et al. 1989). The ratio depends on the fractionation potential of the zooxanthellae, the consequential isotopic signature of their translocates, and the signature of heterotrophic carbon. The $\delta^{13}\text{C}$ ratio in corals is higher when photosynthetic rates are high and the internal carbon pool depleted (Muscatine et al. 1989). It decreases with light at increasing depths in response to a decrease in photosynthesis and the increased proportionate heterotrophic uptake of isotopically lighter zooplankton and other oceanic particulate and dissolved organic materials (Muscatine et al. 1989, Grottoli 1999, Grottoli & Wellington 1999, Grottoli 2002).

Along with photosynthesis, heterotrophy enhances skeletal (Grottoli & Wellington 1999, Houlbrèque et al. 2003, Houlbrèque et al. 2004a) and tissue growth (Ferrier-Pagès et al. 2003) by building up energy stores including lipids (Anthony 2006, Rodrigues et al. 2008, Treignier et al. 2008) and proteins (Ferrier-Pagès et al. 2003, Houlbrèque et al. 2003, Houlbrèque et al. 2004a). Heterotrophy has been shown to support coral photosynthesis (Grottoli 2002, Ferrier-Pagès et al. 2003, Houlbrèque et al. 2004a, Borell et al. 2008) and resilience to stress such as turbidity (Anthony 2006), warming (Borell et al. 2008) and bleaching (Grottoli et al. 2006, Palardy et al. 2008). Although active feeding does not generally constitute the dominant carbon source for zooxanthellate corals, it may reduce temporary energy deficits (Anthony 2000, Anthony et al. 2009, Fitt et al. 2009) so that corals with high capability to heterotrophically assimilate carbon may be more effective in surviving multiple bleaching events and become dominant in future reefs (Grottoli et al. 2006).

The relative proportion of heterotrophy to coral metabolism may vary markedly between species (Grottoli et al. 2006) and this heterotrophic plasticity has been documented in several studies. For example Wellington (1982) observed that the branching coral *Pocillopora damicornis* grew independent of zooplankton supply and was more markedly affected by shading than the massive coral *Pavona clavus*. Sebens & Johnson (1991) documented higher capture rates with increasing current strength by *Madracis decactis*, but not by *Meandrina meandrites*. Rodrigues and Grottoli (2006) showed that *Montipora capitata* host tissue $\delta^{13}\text{C}$

ratios decreased when bleached because of increase in heterotrophic feeding, while *Porites compressa* did not alter its nutrition. And also Palardy et al. (2008) observed that the feeding response to one disturbance may vary significantly between different coral species.

The importance of heterotrophic feeding in coral metabolism may further vary between environments (Lewis 1976, Palardy et al. 2005). Decreasing light and photosynthesis (Muscatine et al. 1989, Palardy et al. 2008) have shown to increase coral feeding in deep (Ferrier-Pagès et al. 1998, Palardy et al. 2005) and turbid environments (Anthony 2000, Anthony 2006). Coral feeding was also shown to be stimulated by high concentrations of dissolved organic matter (Houlbrèque et al. 2004b) and zooplankton prey (Ferrier-Pagès et al. 1998, Ferrier-Pagès et al. 2003, Palardy et al. 2006), and to be influenced by prey behavior (Palardy et al. 2005), coral feeding effort (Sebens et al. 1996, Palardy et al. 2005, Palardy et al. 2008) and water currents (Lewis 1976, Sebens et al. 1996, Sebens et al. 1998).

Until now, internal waves as source of ambient variability in coastal currents, turbidity and plankton (Pineda 1991, Leichter et al. 1996) are poorly investigated. These subsurface waves are ubiquitous in the ocean (Jackson 2004) and propagate along the density interface (pycnocline) between warm surface and cold and nutrient-rich deep waters, but their potential effect on the trophic state of corals is virtually unexplored. The Andaman Sea features non-linear internal waves of extraordinary amplitude, displacing the depth of the pycnocline by more than 80 m (Perry & Schimke 1965, Osborne & Burch 1980). Because these Large Amplitude Internal Waves (LAIW) are tidally generated, travel over long distances, and disintegrate into wave trains over shoaling bottom (Vlasenko & Stashchuk 2007), reefs located in the swash area of LAIW are potentially subjected to frequent disturbances of the physico-chemical environment. So far, it is not known if and to what extent turbulent boluses generated by shoaling LAIW (Vlasenko & Stashchuk 2007) advecting cold, nutrient rich waters upslope affect the trophic state of corals in LAIW-environments.

Here, we combine observational data on the biomass, protein and stable isotope content of LAIW-exposed and -sheltered corals with in situ light-exclusion and transplantation experiments, to explore the role of LAIW on the trophic state of corals in response to the combined effect of increased currents (Sebens et al. 1998, Nakamura et al. 2003), fluxes of particulate matter (Anthony 2000) and plankton (Wellington 1982, Al-Moghrabi et al. 1995, Ferrier-Pagès et al. 1998, Ferrier-Pagès et al. 2003), along with lack of photosynthesis (Rodrigues & Grottoli 2006).

Materials and methods

Study site

The Similan Islands located 60 km off the west coast of Thailand consist of 9 granite islands (Fig 1). The west sides (W) of the islands feature barren rock and scattered corals, the east sides (E) dense coral reefs (Chansang et al. 1999). The asymmetry in coral distribution corresponds to the western exposure of the islands in the swash zone of breaking LAIW generated near Sumatra and the Andaman-Nicobar islands (Jackson 2004, Vlasenko & Alpers 2005). Upslope propagating density intrusions emanate from the near shelf break (Vlasenko & Hutter 2002, Vlasenko & Stashchuk 2007) and are evident as frequent temperature drops and overall lower mean temperatures on the LAIW-exposed W sides (LAIW+) of the islands compared to the sheltered E sides (LAIW-) (Schmidt et al. *subm.*).

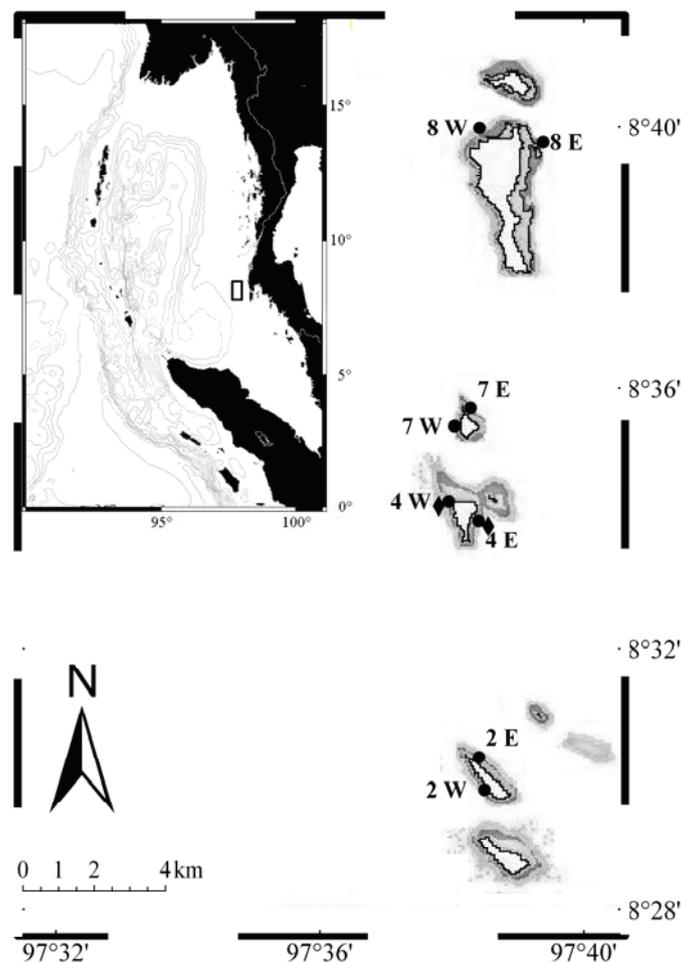


Figure 1: Map of the Similan Islands in the Andaman Sea off the coast of Thailand. Experimental sites (circles) on W (LAIW+) and E (LAIW-) of Island # 4 (Koh Miang Island) are also locations of water and near-reef plankton sampling. Off-reef plankton sampling sites (on Island # 4) are indicated with diamonds. Samples used for the multi-dimensional analysis were collected at all indicated reefs (2W, 2E, 4W, 4E, 7W, 7E, 8W, 8E).

Coral sampling and experimental design

The scleractinian coral *Pocillopora meandrina* (Dana, 1846), a common species on both LAIW+ and LAIW- reefs of the Similan Islands (Schmidt et al. subm.), was chosen as model organism for the study.

Reef fragments - To detect differences between sides (LAIW+ vs LAIW-) and within sides of the different islands (# 2, 4, 7 and 8), fragments of *P. meandrina* (one per colony) were collected randomly (1 to 12 fragments per site) between 5 and 25 m depth from various LAIW+ (18 fragments) and LAIW- (21 fragments) reefs of the Similan Islands (Fig. 1) between 20.02.2008 and 24.03.2008. Fragments were placed in Ziploc bags (100 x 150 mm, max. 4 ml residual water) and transported to the laboratory for immediate processing.

Light-exclusion experiment - The light-exclusion experiment (Fig 2A) was conducted from 20.02.2008 to 24.03.2008. On each side of Koh Miang (Similan Island # 4), three donor colonies of *P. meandrina* were collected at a depth of 20 m. From each colony, 21 fragments were clipped off and attached to two rails (control and experimental rail) made out of plastic wire by clamping the base of the fragment into cut out holes of the rail. Because branch spacing has an impact on flow patterns within the coral colony and, hence, feeding capacity (Sebens et al. 1997), only single undivided branches were used in the experiment. Fragment-bearing rails were moored to a PVC-frame and left in the reef to recover for one month. At the onset of the experiment, triplicate start fragments (one from each donor colony) were collected and the rails (each now bearing 10 fragments) placed in perspex flow pipes. A 3x2 stack of these flow pipes (Fig 2A) was mounted on a rack equipped with a current vane which allowed the set-up to rotate freely around an iron rod anchored into the sediment (20 m depth), so that the upstream openings of the tubes (50 cm length, 10 cm diameter) were always facing into the current, ~ 1 m above the bottom. Drag of the chamber set-up itself, as measured in repeat runs (n = 6) with fluorescent dye, was not found to have a significant effect on water velocity, reducing the ambient water flow by < 5 %. The upper row of translucent tubes held the control fragments (photosynthesis +), the lower row of tubes were shaded off with opaque foil (photosynthesis -), so that light levels near the fragments, measured with the light meter of a Diving-PAM, were below the compensation light intensity for photosynthesis (< 5 $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$). Sampling always took place before noon. Triplicate samples from controls and light-deprived fragments (one fragment per tube) were collected 6, 8, 10, 12, 14, 16, 20, 24, 28 and 32(LAIW-)/33(LAIW+) days after the onset of the experiments. Live fragments were placed into 100*150 mm Ziploc bags (max. 4 ml

supernatant), transported to the laboratory and immediately processed. Dead fragments were recorded.

Transplantation experiment - Within the same timeframe (20.02.2008 to 24.03.2008), a cross-transplantation experiment (Fig 2B) was conducted to detect changes in coral tissue composition due to transplantation. On each, W (LAIW+) and E (LAIW-) Koh Miang, three additional donor colonies of *P. meandrina* were sampled. Sampling and fragment cultivation was identical to the light-exclusion experiment (but one fragment less on each rail). At experimental onset, triplicate start fragments (one from each donor colony) were collected and the experimental rails (now each bearing 9 fragments) cross-transplanted between W (LAIW+) and E (LAIW-). Rails transplanted from LAIW- to LAIW+ were subsequently exposed to higher flows of plankton, while rails transplanted in the opposite direction experienced lower food supplies compared to origin conditions. Control fragments and cross-transplanted fragments were left anchored next to each other in the reef (20 m depth) and triplicate samples of controls (feeding +) and feed-altered (transplanted from LAIW- to LAIW+: feeding ++; transplanted from LAIW+ to LAIW-: feeding +/-) fragments collected 2, 4, 8, 12, 16, 20, 24, 28, 32 (LAIW+) and 3, 5, 9, 13, 17, 21, 25, 29, 33 (LAIW-) days after the onset of the experiments. Collected fragments were placed into 100*150 mm Ziploc bags (max. 4 ml supernatant), transported to the laboratory and immediately processed.

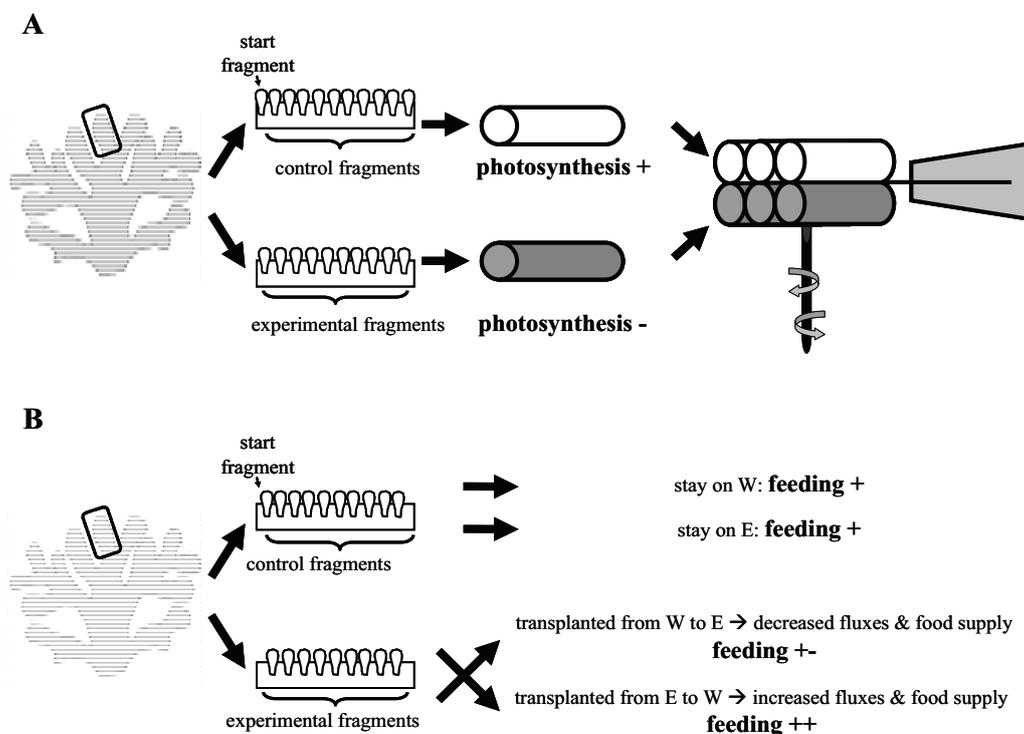


Figure 2: Schematic representation of the experimental designs: A) Light-exclusion experiment: 3 donor colonies per island side, each colony providing 21 fragments (1 start, 10 control and 10 light-deprived fragments). One chamber set-up on each island side (W/LAIW+ and E/LAIW-). B) Transplantation experiment: 3 donor colonies per island side, each colony providing 20 fragments (1 start, 9 control and 9 transplanted fragments).

Coral processing

For each fragment, the full set of parameters described below was analyzed. Coral tissue was removed from the skeleton using an airbrush and filtered seawater. After homogenization of the slurry, 6 ml aliquots were retained for zooxanthellae density counts and protein analysis, and 5 ml aliquots were filtered under 200 mm Hg vacuum (Millipore Vacuum Pump) on glass fiber filters (Whatman GF/F) and frozen for chlorophyll analysis.

Zooxanthellae densities - The total symbiont cell numbers were determined under a microscope (Leitz, Portugal, 260x magnification) using a Fuchs-Rosenthal haemocytometer. Concentrations were calculated on an areal basis as the mean of six replicate counts after correction for the homogenate volume and surface area of the coral fragment.

Chlorophyll-a analysis – Chlorophyll was extracted by adding few 90 % acetone to the thawed chlorophyll samples (Strickland & Parsons 1972); after cautious shaking, samples were incubated for 24 hours at 4°C for chlorophyll extraction and centrifuged at high speed (10000g, 30 sec) to remove all particles in suspension before measurement (Szmant & Gassman 1990, Gardella & Edmunds 1999, Fitt et al. 2000). Chlorophyll-a concentrations were determined spectrophotometrically in a Shimadzu UV 1700 1nm Slit photometer at 750 nm and 664 nm (Lorenzen 1967).

Protein content - Total protein content was determined after Lowry et al. (1951) using a protein assay (*DC* Protein Assay Kit, Bio-Rad) and bovine serum albumin standards. Protein concentrations were measured spectrophotometrically (Shimadzu UV 1700 1nm Slit) at 750 nm.

In the remaining slurry, zooxanthellae and host tissue were separated by centrifugation and the host tissue was loaded (Millipore Vacuum Pump, ~100 mm Hg) on pre-combusted and pre-weighed filters (Whatman GF/F) and dried before further elemental and isotopic analyses (see below) (Muscatine et al. 1989, Grottoli et al. 2004, Swart et al. 2005). Fragment surface area was calculated using Simple Geometry (determining the geometric form that best resembles the shape of the fragment and calculating its surface with respective the geometric formula) to the nearest 0.05 mm and an Approximation Factor for *Pocillopora* as proposed by Naumann et al. (2009).

Total suspended matter, particulate and dissolved organic carbon

In the course of the experiment, during fragment collection and when possible once again in the afternoon, water samples (LAIW+: n = 19; LAIW-: n = 24) were taken by divers close to the experimental setup for subsequent analyses of total suspended matter (TSM), total

particulate organic carbon (TPOC), and dissolved organic carbon (DOC). In several occasions, sampling occurred during LAIW-passage, shortly before or after. Therefore, temperature at time of sampling was recorded (TidbiT v2, Onset, 1 minute resolution and an accuracy of $<0.2^{\circ}\text{C}$). Water samples were taken with 1 l PE bottles, transported to the lab, filtered (Millipore Vacuum Pump, 200 mm Hg) on pre-combusted and pre-weighed Whatman GF/F filters, dried for following elemental analyses (see below) and weighed on a microbalance (Mettler, AT21 Comparator, 1 μg accuracy). Aliquots of the filtrates were transferred into pre-combusted glass vials and acidified with phosphoric acid (20 %) to a pH of 2 before sealing and storage on ice. DOC concentrations were determined with a DOC/DIC analyzer (Rosemount DC-190) using a 10-point calibration with TOC standards (ULTRA Scientific).

Plankton

Plankton sampling occurred only during the day. Concomitant with each fragment sampling, near-reef zooplankton was collected by SCUBA push net tows (0.25 m diameter steel frame with a 55 μm mesh and 1 m sleeve), swimming along a 40 m swath along the 20 m isobath, 0.5 – 1 m above bottom. Mean temperature during sampling was recorded (TidbiT v2, Onset, 1 minute resolution and an accuracy of $<0.2^{\circ}\text{C}$) to determine LAIW impact at time of sampling. Samples were transferred to the laboratory where they were separated into different size classes (55, 100, 150, 200 and 300 μm) over a fractionation tower. The different size classes were collected (Millipore Vacuum Pump, 200 mm Hg) on pre-combusted and pre-weighted filters (Whatman GF/F) and dried for 12 h at 40°C . The dry mass of the plankton was determined gravimetrically using a microbalance (Mettler, AT21 Comparator, 1 μg accuracy). Clogging was not a problem at the low volumes (8 m^3) fished. Filtered volume was calculated from swimming distance and cross-sectional area of the net opening, assuming 100% filtration efficiency (Smith et al. 1968).

Pump-sampled off-reef zooplankton was collected from a boat anchored at 35 m depth in front of the LAIW+ and LAIW- face of Koh Miang (Fig. 1), with the hose intake located in mid-water 15 meters above bottom and equipped with a temperature logger (TidbiT v2, Onset, 1 minute resolution and an accuracy of $<0.2^{\circ}\text{C}$). Sampling took place in 15 minute intervals for 4 hours simultaneously on both island sides by boat the afternoon of the 11th, 17th, 21st and 25th of March 2008. Water was pumped through a plastic tube (6 cm diameter, 245 l min^{-1}) and filtered for 5 min through a 50 μm plankton net. Samples were divided in half using a Folsom-splitter, one sub-sample was preserved in formalin (5 %) for taxonomic

identification (data presented elsewhere), the other was filtered (Millipore Vacuum Pump, 200 mm Hg) on pre-combusted and pre-weighted filters (Whatman GF/F) and dried (12 h at 40°C) for mass determination (microbalance Mettler, AT21 Comparator, 1 µg accuracy) prior to elemental analysis. Pumped volume was determined by assessing the number of seconds it took to fill an 8 l container (3 trials each) in order to be able to relate plankton values to volume.

Visual inspection of the samples showed no detectable damage of the plankton by either of the sampling procedures.

Elemental and isotopic analyses of coral tissue, total suspended matter and plankton

Total carbon and nitrogen content of the coral tissue, as well as the particulate organic carbon content of the TSM (TPOC) and plankton (POC) was determined using an Elemental Analyzer (NA2100 Protein) calibrated against an elemental CHNS standard (LECO). Carbon stable isotope ratios ($\delta^{13}\text{C}$) were measured in a gas isotope ratio mass spectrometer (Flash 1112 Analyzer) relative to Pee Dee Belemnite standard. For organic content of TSM (TPOC) and plankton (POC), the samples were acidified with 0.1 M HCl prior to analyses until all inorganic carbon was removed. Coral samples did not require acidification as tissue was obtained without contamination from skeletal material.

Currents and fluxes

Autonomous upward-looking Acoustic Doppler Current Profilers (ADCP) were deployed for the time of experiment in the vicinity of the flow chamber setups (RDI Teledyne Workhorse Sentinel, 600 kHz and 300 kHz on W and E of Koh Miang, respectively) to measure the 3-D current field at 1 m vertical and 1 min temporal resolution with an accuracy of 0.3 to 0.5 % of the water velocity ± 0.3 to 0.5 cm s^{-1} . Data stored in the flash memory of the instruments were downloaded after the experiment, imported into Matlab (rdradcp.m by Rich Pawlowicz, U. of British Columbia, <http://www2.ocgy.ubc.ca/~rich/>) and analyzed. Mean daily fluxes of near-reef and off-reef plankton (total and POC), TSM, TPOC and DOC were calculated by multiplying their concentrations with the average daily current speeds during samplings (averaged across 12 hours prior to 12 hours post sampling time).

Temperature

To record LAIW incidences during experimental time, temperature loggers (TidbiT v2, Onset) were deployed in close vicinity of the experimental setup. Temperature was logged in

1 min temporal resolution (with an accuracy of $<0.2^{\circ}\text{C}$ over 0 to 50°C) and data downloaded using HOBOWare 2.2.

Statistical analyses

Datasets were tested for normal distribution and homogeneity of variances using Kolmogorov-Smirnov and Levene's tests, respectively, transformed if necessary and subjected to parametric or non-parametric statistical analyses (below), as appropriate.

To detect spatial differences between island sides and among sides of the different islands on the basis of coral tissue composition (zooxanthellae numbers, chlorophyll content, tissue carbon and nitrogen, protein concentrations and isotopic composition) we performed a two-factorial permutational MANOVA (PERMANOVA, Anderson et al. 2008) using PRIMER v6 multivariate statistical software (Clarke & Gorley 2006). The PERMANOVA allowed us to test for significant differences based on similarity (using Euclidean distance) between island side and island number (nested in island side). Data were log-transformed prior to analysis to account for differences in unit sizes. As sampling constraints led to an imbalanced data set over depth and sites, depth differences were 'regressed out' by treating depth as a covariate and removing possible depth effects prior to testing for site differences (Anderson et al. 2008, Mirto et al. 2009), and the low and unevenly distributed number of data were compensated for by running a large number ($n = 9999$) of permutations of the residuals (Gonzalez & Manly 1998, Anderson 2001, Anderson & Ter Braak 2003, Anderson et al. 2008). The randomly collected reef fragments and the start fragments of both time series experiments were included in this analysis.

For the time series data gained from fragments subjected to the shading (d06 – d32/33) and transplant (d02 – d32/33) experiments, we developed general linear models to test for the factors 'treatment' (i.e. control, light-deprivation or transplantation; nested within the respective side, fixed), 'colony' (nested within treatment, random) and 'day' (over treatment time, fixed) (Satterthwaite 1946). Prior to model application, the residuals of all time series (i.e. for each parameter and colony) were tested for autocorrelation (Ljung & Box 1978) on as many lags (2 to maximum 33 days) as possible to ensure the effectual independence of data, despite repeated samplings of the same colony or rack. Significant differences between treatments and sides were determined using the Fisher LSD post-hoc test.

Differences in mortality during the light-exclusion experiment were tested with a survival analysis. The survivorship functions (Kaplan Meier curves) of the W and E side were compared using Cox's F-test.

Water and plankton samples as well as fluxes were statistically tested for LAIW-exposure using Student's t-tests. Size differences in near-reef plankton weight, organic content and isotopic signatures were tested using one-way ANOVA. Pearson's correlation analyses with temperature were conducted to reveal possible relation between LAIW passage and TSM, TPOC, DOC or plankton concentrations.

LAIW-related W (LAIW+) and E (LAIW-) current differences were analyzed using Student's t-test after Box-Cox transformation of the data. Pearson's correlation analyses between temperature and current velocities followed by Student's t-tests were conducted to examine correlations and their statistical significance.

Results

Temperature, currents, plankton, TSM, TPOC and DOC fluxes

The temperature time series showed strong differences between the LAIW+ and LAIW- side of Koh Miang (Fig 3A). Although the modal values were similar ($\Delta T < 0.2^\circ\text{C}$), the LAIW+ face showed a violent spiking with temperature drops of up to more than 4°C occurring at subtidal frequencies indicative of the passage of internal waves. The temperature drops were associated with surges in current velocities (Fig 3A and B, $p < 0.001$ for LAIW+ and LAIW-), so that the overall mean current velocity was 30 % stronger on the LAIW+ than on LAIW-side of the island (0.1008 ± 0.0004 vs 0.0772 ± 0.0003 m s^{-1} , $p < 0.001$).

The stronger currents resulted in significantly higher ($p < 0.001$ for all) TSM, TPOC, DOC and plankton fluxes (Fig 4) on the LAIW+ side of the island. Composition of the near-reef plankton was not different between LAIW+ and LAIW- (Fig. S1) and the concentrations alone (means \pm SE in Table S1), of both near- or off-reef plankton and POC (Figs. S1 and S2), TSM, TPOC or DOC (Fig. S3), showed no detectable differences between island sides ($p > 0.05$). Correlations with temperature were not significant for any of the parameters ($p > 0.05$) except for the offshore abundance of plankton individuals (not off-reef POC), where the correlation was negative ($r^2 = 0.33$; $p < 0.05$) due to two sampling events exactly within LAIW incidents.

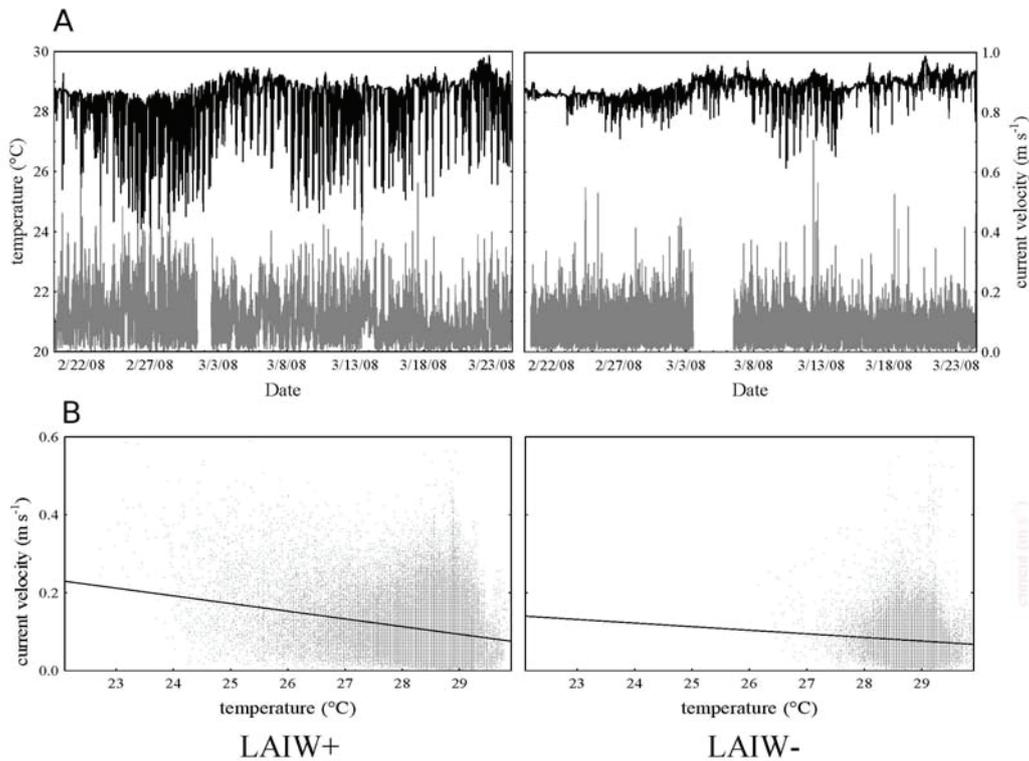


Figure 3: Temperature and currents on the W LAIW-exposed (left panels) and E LAIW-sheltered face of Koh Miang. A) Time series of temperature (black) and current velocity (gray) over the study period. Blank periods in the current data are due to recovery, cleaning and redeployment of the current meters. B) Correlation between temperature and current velocities. Correlations are significant for either side (both $p < 0.001$), but stronger for the W than for the E face ($r^2 = 0.06$ and 0.005 respectively).

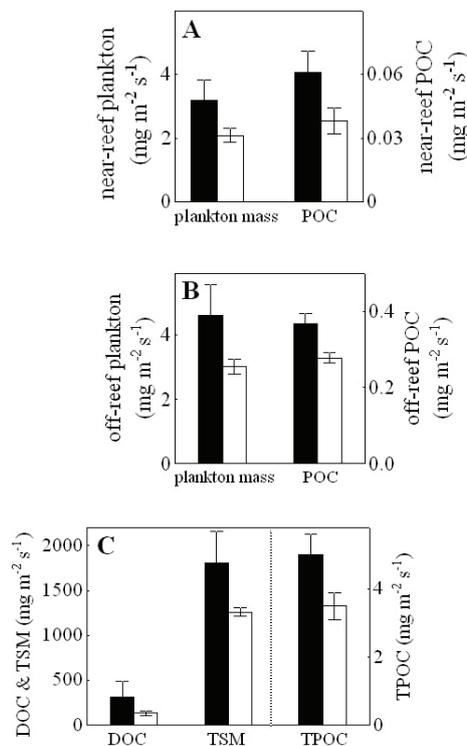


Figure 4: Daily mean fluxes (\pm SE) of A) near-reef plankton and its organic carbon fraction B) off-reef plankton and its organic carbon fraction and C) reef water DOC, TSM and TPOC from LAIW+ (black) and LAIW- (white) Koh Miang. All LAIW+ and LAIW- side samples are statistically significant different.

Coral tissue

Corals showed significant differences in their tissue composition between LAIW-exposed and LAIW-sheltered sides of the Similan Islands, but none among the LAIW+ and LAIW- faces of the different islands (Table 1), as illustrated also in the multidimensional scaling (MDS) plot, showing overlap among but only little overlap between LAIW+ and LAIW- samples, respectively (Fig 5).

Table 1: Results of the 2-factorial (W vs E and between Islands # 2, 4, 7 and 8) PERMANOVA routine on tissue composition of *Pocillopora meandrina* collected along W and E sides of different islands (nested within respective side) after removal of the covariate effect of depth. Tissue compositions of fragments from different islands do not show significant differences, while differences between W and E are significant (asterisk). SS = sum of squares; MS = means square; F = F-value; p = probability level.

source of variance		SS	MS	F	p
covariate:depth	1	0.802	0.8015	1.057	0.351
side	1	7.878	7.878	3.129	0.032*
island(side)	6	5.355	0.893	1.254	0.245
residuals	42	29.9	0.712		
total	50	43.935			

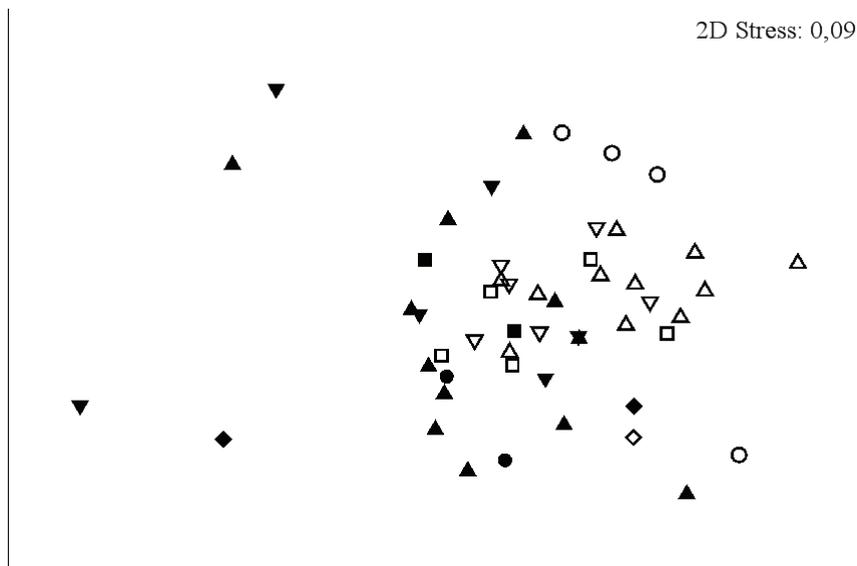


Figure 5: MDS ordination of fragments from LAIW+ (n = 18 plus 6 start fragments from both experiments) and LAIW- (n = 21 plus 6 start fragments from both experiments) sides of all islands to illustrate the multidimensional similarities in coral tissue composition (in terms of zooxanthellae densities, chlorophyll-a, tissue carbon and nitrogen content, protein concentrations and isotopic carbon ratios) in a two-dimensional space. The Euclidean distance between two points represents their similarity. Quadrate: Island # 8; circle: Island # 7; upward-pointed triangle: Island # 4; diamond: Island # 2; downward looking triangles: start fragments from the experimental set-ups. Filled symbols: LAIW+ side fragments; clear symbols: LAIW- side fragments.

In both experiments (Figs. 6 and 7), we were unable to detect bias due to repeated samplings from a limited number of donor colonies: we found no significant differences between the donor colonies and no trend over time (treat×day), neither in control or in experimental colonies (Tables 3 and 5).

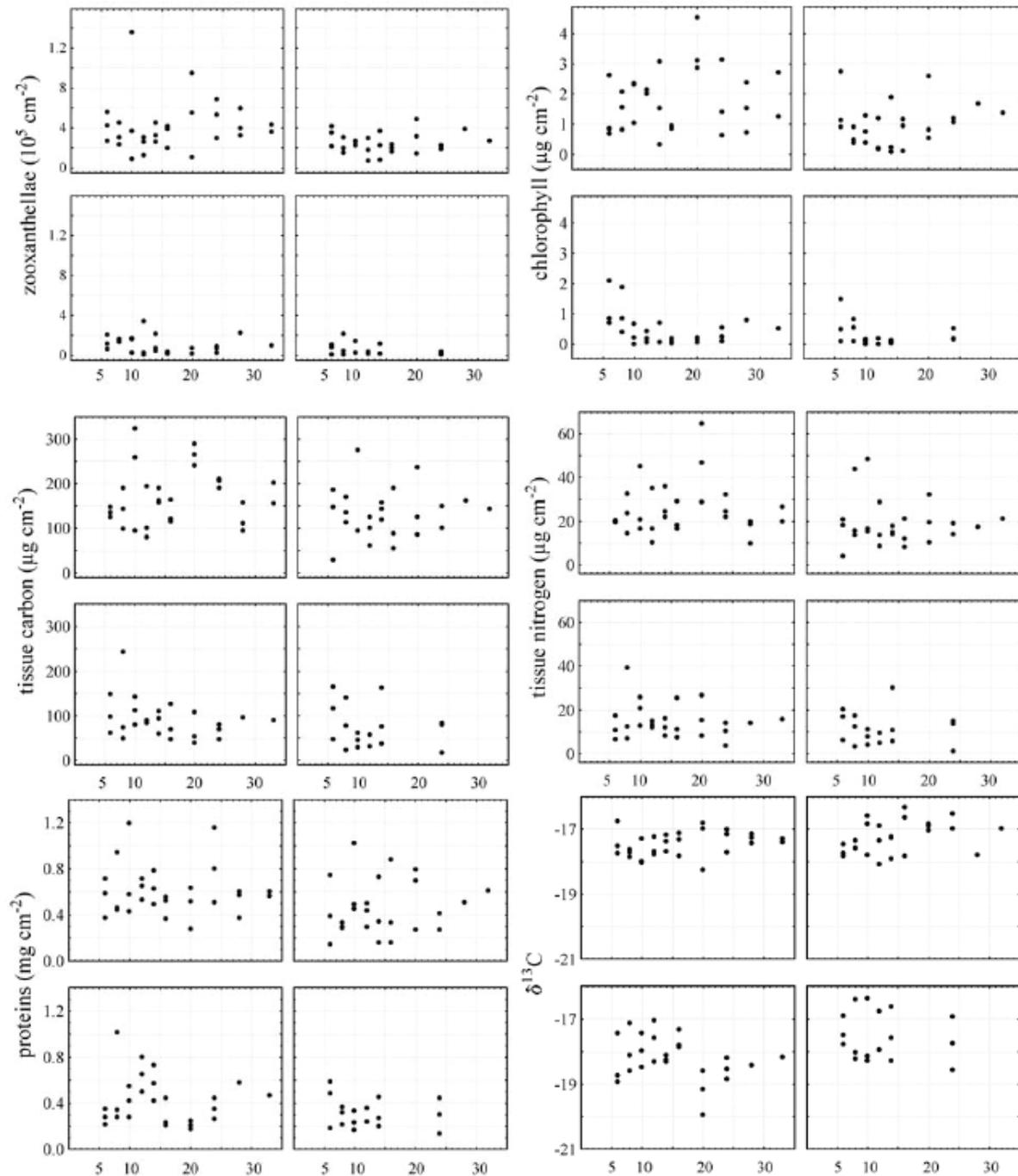


Figure 6: Time-series of all tissue parameters (from top to bottom: 1) zooxanthellae densities, chlorophyll content, 2) carbon tissue content, nitrogen tissue content, 3) protein concentrations and isotopic carbon ratios) measured in controls and light-deprived fragments from W (LAIW+) and E (LAIW-) over experimental time (x-axis as days of experiment). Upper left sides: photosynthesis + (LAIW+). Upper right sides: photosynthesis + (LAIW-). Lower left sides: photosynthesis - (LAIW+). Lower right sides: photosynthesis - (LAIW-).

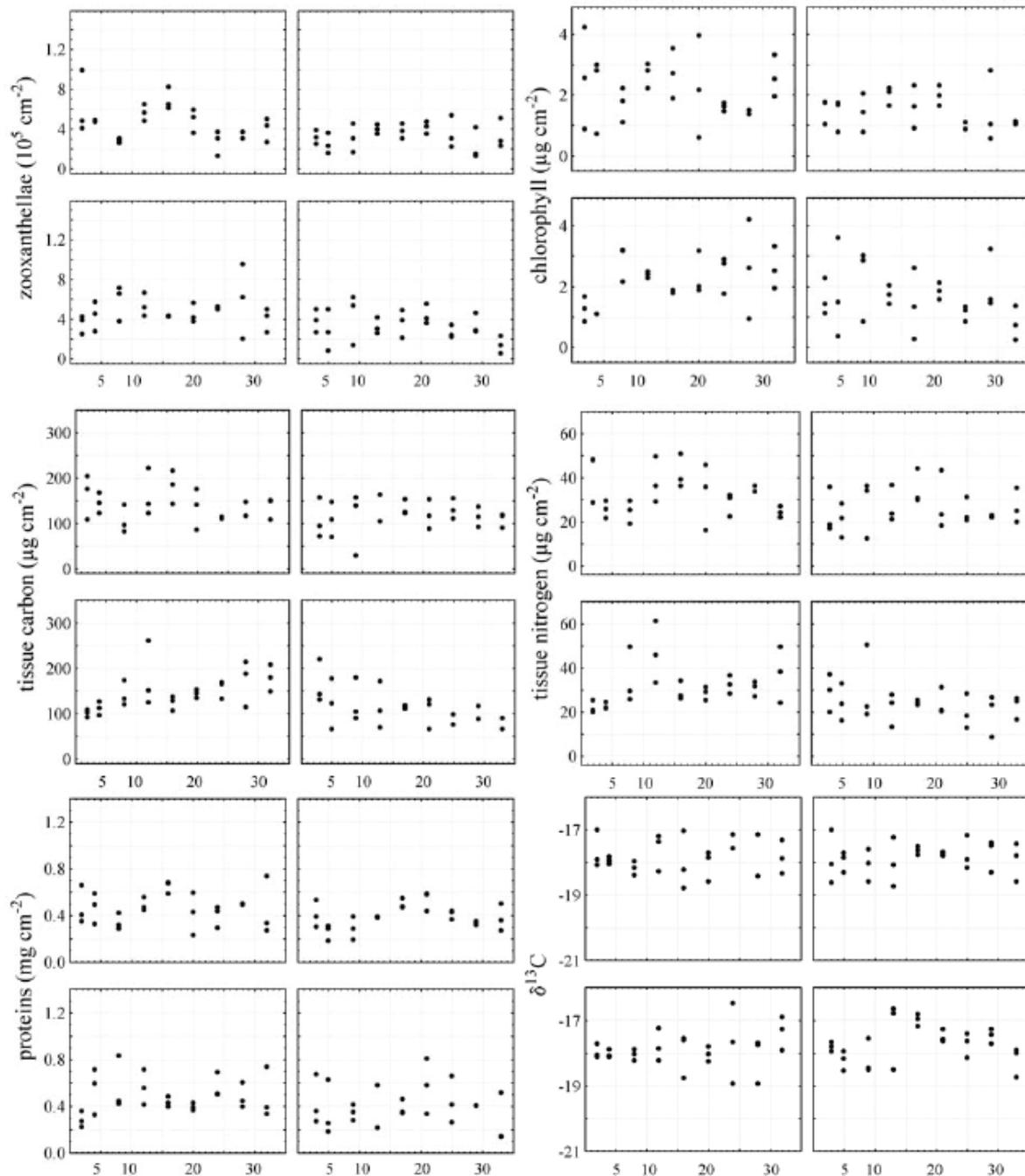


Figure 7: Time-series of all tissue parameters (from top to bottom: 1) zooxanthellae densities, chlorophyll content, 2) carbon tissue content, nitrogen tissue content, 3) protein concentrations and isotopic carbon ratios) measured in controls and feed-altered fragments from W (LAIW+) and E (LAIW-) over experimental time (x-axis as days of experiment). Upper left sides: feeding + (LAIW+). Upper right sides: feeding + (LAIW-). Lower left sides: feeding ++ (transplanted from LAIW- to LAIW+). Lower right sides: feeding +- (transplanted from LAIW+ to LAIW-).

Table 2: Tissue composition of *Pocillopora meandrina*. Tissue parameters measured in control (photosynthesis +) and light-deprived (photosynthesis -) fragments from W (LAIW+) and E (LAIW-) during the light-exclusion experiment, and in control (feeding +) and transplanted (from LAIW- to LAIW+: feeding ++; from LAIW+ to LAIW-: feeding +/-) fragments from W (LAIW+) and E (LAIW-) during the transplantation experiment are given as means and standard errors (brackets). Missing data are due to mortality (light-exclusion experiment) or sample loss during analysis (transplantation experiment); one control fragment (LAIW+) from the transplantation experiment (colony 2, d28) was lost.

	LAIW+				LAIW-			
light-exclusion experiment	photosynthesis +		photosynthesis -		photosynthesis +		photosynthesis -	
	n	mean (se)						
zooxanthellae cm ⁻²	29	412205(47578)	26	95454(16679)	25	247178(20270)	17	49383(14237)
µg chlorophyll a cm ⁻²	29	1.80(0.19)	26	0.45(0.10)	25	0.96(0.14)	17	0.29(0.09)
µg tissue carbon cm ⁻²	29	169.08(11.60)	26	90.44(8.24)	25	130.88(10.97)	17	73.38(11.43)
µg tissue nitrogen cm ⁻²	29	25.22(2.17)	26	14.54(1.51)	25	18.64(2.03)	17	11.10(1.79)
mg protein cm ⁻²	29	0.60(0.04)	26	0.42(0.04)	25	0.46(0.05)	17	0.31(0.03)
δ13C	29	-17.46(0.07)	26	-18.21(0.13)	25	-17.26(0.10)	17	-17.54(0.18)
transplantation experiment	feeding +		feeding ++		feeding +		feeding +/-	
	n	mean (se)						
zooxanthellae cm ⁻²	26	463338(36475)	27	475997(30455)	27	330515(22089)	27	328249(28513)
µg chlorophyll a cm ⁻²	26	2.21(0.19)	25	2.24(0.16)	26	1.51(0.11)	27	1.62(0.17)
µg tissue carbon cm ⁻²	26	141.52(7.41)	27	145.26(7.69)	27	116.89(6.18)	27	111.94(7.64)
µg tissue nitrogen cm ⁻²	26	32.36(1.93)	27	31.58(1.92)	27	26.19(1.64)	27	23.89(1.59)
mg protein cm ⁻²	26	0.46(0.03)	27	0.48(0.03)	27	0.39(0.02)	25	0.39(0.04)
δ13C	26	-17.85(0.10)	27	-17.89(0.10)	27	-17.87(0.09)	27	-17.71(0.11)

In the light-exclusion experiment (Fig. 6), most tissue parameters were significantly higher for control corals from the LAIW+ side of the island, compared to the LAIW- controls (Table 4). Zooxanthellae densities and chlorophyll concentrations were more than 40 % higher, tissue carbon, nitrogen and protein concentrations were more than 20 % higher in LAIW-exposed corals (Fig. 6, Table 2). Only differences in the carbon isotopic ratio of the control host tissue were not significantly different between LAIW+ and LAIW- reefs (Tables 2 and 4). Under artificial darkness, about 80 % of all zooxanthellae were lost on LAIW+ as well as on LAIW- and chlorophyll-a decreased to a third of the original concentration on both sides (Fig. 6, Table 2). Also in LAIW+ as well as LAIW- reefs, losses in tissue carbon and nitrogen were over 40 % while protein content was about 30 % lower than in the control fragments (Fig. 6, Table 2). All depletions were significant comparing controls and light-deprived fragments from either side (Table 4). Even though, the protein content decreased on both sides, the decrease was less marked on the LAIW-exposed side, where protein levels of light-deprived fragments remained about 25 % higher than their LAIW- counterparts and in the range of the LAIW- control fragments (Tables 2 and 4). During light-exclusion, the LAIW- fragments did change their isotopic ratios only little (-0.28 ‰) (Fig. 6, Table 2), while the LAIW+ fragment ratios decreased significantly by -0.75 ‰. Subsequently, light-deprived

LAIW+ fragments differed significantly from LAIW- light-deprived fragments as well as from control fragments of both sides (Fig. 6, Table 4).

Table 3: Analysis of spatio-temporal variation of tissue parameters in *Pocillopora meandrina* fragments collected in a time series during a light-exclusion experiment. Compared are time series of control and light-deprived fragments exposed (LAIW+) or sheltered (LAIW-) from LAIW. df = degrees of freedom; MS = means square; F = F-value; p = probability level. Significant p-values are marked with an asterisk. n.s.: not significant.

source of variance		df	MS	F	p
zooxanthellae cm⁻²					
intercept	fixed	1	7.443×10 ¹¹	31.616	*
treat (side)	fixed	2	1.702×10 ¹¹	6.618	*
colony(treat)	random	4	1.419×10 ¹⁰	0.552	n.s.
treat×day	fixed	2	1.654×10 ¹⁰	0.643	n.s.
error		87	2.572×10 ¹⁰		
µg chlorophyll a cm⁻²					
intercept	fixed	1	14.865	29.184	*
treat (side)	fixed	2	4.695	8.911	*
colony(treat)	random	4	0.434	0.824	n.s.
treat×day	fixed	2	0.914	1.735	n.s.
error		87	0.527		
µg tissue carbon cm⁻²					
intercept	fixed	1	261382.101	100.716	*
treat (side)	fixed	2	11151.604	3.911	*
colony(treat)	random	4	1497.650	0.525	n.s.
treat×day	fixed	2	2853.269	1.001	n.s.
error		87	2850.995		
µg tissue nitrogen cm⁻²					
intercept	fixed	1	5964.492	64.522	*
treat (side)	fixed	2	384.813	4.036	*
colony(treat)	random	4	80.013	0.839	n.s.
treat×day	fixed	2	7.389	0.078	n.s.
error		87	95.337		
mg protein cm⁻²					
intercept	fixed	1	3.857	95.532	*
treat (side)	fixed	2	0.201	4.605	*
colony(treat)	random	4	0.026	0.602	n.s.
treat×day	fixed	2	0.008	0.190	n.s.
error		87	0.044		
δ13C					
intercept	fixed	1	5596.603	18468.703	*
treat (side)	fixed	2	2.189	7.359	*
colony(treat)	random	4	0.327	1.100	n.s.
treat×day	fixed	2	1.064	3.577	n.s.
error		87	0.297		

Table 4: Significance levels of Fisher LSD tests for fragments of *Pocillopora meandrina* of the light-exclusion experiment. Circles represent LAIW- side, quadrates LAIW+ island side colonies. Light-deprived data sets are shown by filled, control sets by clear symbols. Significant differences are marked with an asterisk.

	○	●	□	■
	photosynthesis +	photosynthesis -	photosynthesis +	photosynthesis -
zooxanthellae cm⁻²				
○	photosynthesis +			
●	photosynthesis -	0.000*		
□	photosynthesis +	0.000*	0.000*	
■	photosynthesis -	0.001*	0.360	0.000*
µg chlorophyll a cm⁻²				
○	photosynthesis +			
●	photosynthesis -	0.004*		
□	photosynthesis +	0.000	0.000*	
■	photosynthesis -	0.015*	0.461	0.000*
µg tissue carbon cm⁻²				
○	photosynthesis +			
●	photosynthesis -	0.001		
□	photosynthesis +	0.010*	0.000*	
■	photosynthesis -	0.008*	0.309	0.000*
µg tissue nitrogen cm⁻²				
○	photosynthesis +			
●	photosynthesis -	0.016*		
□	photosynthesis +	0.016*	0.000*	
■	photosynthesis -	0.137	0.262	0.000*
mg protein cm⁻²				
○	photosynthesis +			
●	photosynthesis -	0.026*		
□	photosynthesis +	0.013*	0.000*	
■	photosynthesis -	0.530	0.088	0.002*
δ13C				
○	photosynthesis +			
●	photosynthesis -	0.113		
□	photosynthesis +	0.183	0.657	
■	photosynthesis -	0.000*	0.000*	0.000*

LAIW-exposed corals showed also a much higher dark survival than LAIW-sheltered specimens (Fig 8): all fragments survived well into the third week of the experiment, scarcely exceeding 10 % total mortality at the end of the experiment. The LAIW- corals, by contrast, suffered heavy losses of about 40 % of all light-deprived fragments. The first fatalities were detected already after one week of the experiment and continued until total elimination of the

fragments after four weeks. Testing the cumulative proportion of LAIW+ and LAIW- cases surviving up to the time of fragment collection (Fig 8) showed that probabilities of survival were significantly higher for LAIW+ corals ($p < 0.001$).

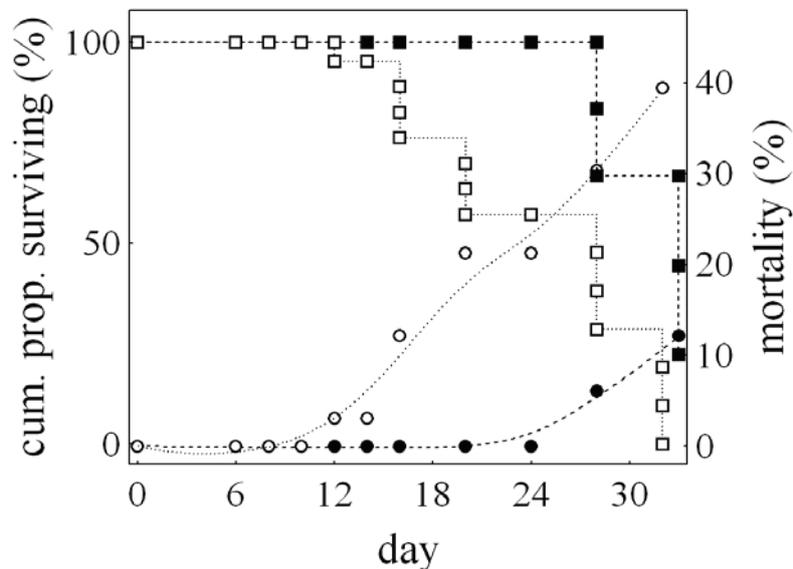


Figure 8: Survival analysis of *Pocillopora meandrina* in the light-exclusion experiment. Kaplan Meier cumulative proportion survival curves (left y-axis, squares) of corals from LAIW+ (closed symbols) and LAIW- (open symbols) reefs of Koh Miang over experiment time (x-axis), showing the cumulative proportion of living light-deprived corals per sampling. The right y-axis displays the percent mortality (circles) of all light-deprived corals from LAIW+ (closed) and LAIW- (open) reefs of Koh Miang over experiment time. Control corals are not shown.

In the transplantation experiment (Fig. 7), acclimatization to the new environment was rapid and occurred within the first days after transplantation. All transplanted corals did not differ in tissue composition from control corals of their new environment (Fig. 7, Table 6). However, differences between the transplanted corals and their corresponding control colonies from the same donor colony (control corals from the other island side) and between controls from LAIW+ and LAIW- were obvious. Zooxanthellae densities and chlorophyll-a concentrations were both about 30 %, tissue carbon and nitrogen contents about 20 % elevated in LAIW+ corals compared to significantly lower concentrations in LAIW- corals (Fig. 7, Tables 2 and 6). The feeding ++ corals transplanted from LAIW- to the feed-enriched LAIW+ side ended up significantly enriched in protein content (Fig. 7, Table 6) compared to the LAIW- controls or fragments transplanted to the LAIW- side (feeding +-). Even though differences between LAIW+ control corals and LAIW- control or feed-deprived (feeding +-) corals were marginally not significant (Table 6), protein content was about 20 % higher in the LAIW+ controls (Fig. 7, Table 2).

Table 5: Analysis of spatio-temporal variation of tissue parameters in *Pocillopora meandrina* fragments collected in a time series during a transplantation experiment. Compared are time series of control fragments exposed (LAIW+) or sheltered (LAIW-) from LAIW and of fragments transplanted into higher (from LAIW- to LAIW+) or decreased water fluxes (from LAIW+ to LAIW-), respectively. df = degrees of freedom; MS = means square; F = F-value; p = probability level. Significant p-values are marked with an asterisk. n.s.: not significant.

source of variance		df	MS	F	p
zooxanthellae cm⁻²					
intercept	fixed	1	5.315×10 ¹²	236.297	*
treat (side)	fixed	2	2.540×10 ¹¹	10.676	*
colony(treat)	random	4	1.980×10 ¹⁰	0.795	n.s.
treat×day	fixed	2	2.300×10 ¹⁰	0.965	n.s.
error		97	2.379×10 ¹⁰		
µg chlorophyll a cm⁻²					
intercept	fixed	1	100.587	156.618	*
treat (side)	fixed	2	5.619	8.131	*
colony(treat)	random	4	0.503	0.728	n.s.
treat×day	fixed	2	0.224	0.324	n.s.
error		94	0.691		
µg tissue carbon cm⁻²					
intercept	fixed	1	483775.133	366.965	*
treat (side)	fixed	2	11456.002	7.881	*
colony(treat)	random	4	943.407	0.649	n.s.
treat×day	fixed	2	78.897	0.054	n.s.
error		97	1453.670		
µg tissue nitrogen cm⁻²					
intercept	fixed	1	23834.669	219.450	*
treat (side)	fixed	2	643.984	7.905	*
colony(treat)	random	4	183.810	2.256	n.s.
treat×day	fixed	2	9.424	0.116	n.s.
error		97	81.461		
mg protein cm⁻²					
intercept	fixed	1	4.878	240.621	*
treat (side)	fixed	2	0.090	4.067	*
colony(treat)	random	4	0.015	0.674	n.s.
treat×day	fixed	2	0.004	0.195	n.s.
error		97	0.022		
δ13C					
intercept	fixed	1	9132.298	37651.938	*
treat (side)	fixed	2	0.199	0.722	n.s.
colony(treat)	random	4	0.149	0.541	n.s.
treat×day	fixed	2	0.259	0.938	n.s.
error		95	0.276		

Table 6: Significance levels of Fisher LSD tests for fragments of *Pocillopora meandrina* of the transplantation experiment. Circles represent donor colonies from LAIW- side, quadrates donor colonies from LAIW+ side colonies. Filled symbols represent fragments exposed to LAIW (LAIW+), clear symbols are fragments cultivated on sheltered LAIW- side. Significant differences are marked with an asterisk.

	○	□	■	●
	feeding +	feeding +/-	feeding +	feeding ++
zooxanthellae cm⁻²				
○	feeding +			
□	feeding +/-	0.958		
■	feeding +	0.002*	0.002*	
●	feeding ++	0.001*	0.001*	0.766
µg chlorophyll a cm⁻²				
○	feeding +			
□	feeding +/-	0.619		
■	feeding +	0.003*	0.011*	
●	feeding ++	0.002*	0.009*	0.908
µg tissue carbon cm⁻²				
○	feeding +			
□	feeding +/-	0.634		
■	feeding +	0.021*	0.006*	
●	feeding ++	0.007*	0.002*	0.722
µg tissue nitrogen cm⁻²				
○	feeding +			
□	feeding +/-	0.352		
■	feeding +	0.015*	0.001*	
●	feeding ++	0.031*	0.002*	0.754
mg protein cm⁻²				
○	feeding +			
□	feeding +/-	0.898		
■	feeding +	0.068	0.096	
●	feeding ++	0.025*	0.038*	0.685
δ13C				
○	feeding +			
□	feeding +/-	0.283		
■	feeding +	0.887	0.356	
●	feeding ++	0.868	0.216	0.760

Discussion

Introduction of upwelled subthermocline water into reef communities and the possible effects on water quality (Andrews & Gentien 1982, Leichter et al. 1996, Leichter et al. 2007), biodiversity (Cortés 1997), coral growth (Leichter & Genovese 2006) or feeding (Palardy et al. 2005) have been addressed in previous studies. Here, we compare reefs growing in close vicinity around an island chain unilaterally exposed to temperature oscillations more severe and frequent than previously reported in other areas (Leichter et al. 1996, Leichter & Genovese 2006) and among the highest so far observed (Sheppard 2009). Given the close proximity of the W (LAIW+) and E (LAIW-) sides of the islands (<200 m), the differences in the physical oceanographic parameters between the two island sides are striking. Variability in temperature and currents (this study), but also oxygen, pH and nutrient concentrations (Schmidt et al. *subm.*) are much more pronounced on LAIW-exposed reefs compared to their sheltered counterparts, resulting in lower mean temperatures, stronger mean current velocities (Fig. 3) and increased input of corrosive, nutrient-rich deep water.

We demonstrated that in spite of the disparities in tissue composition of *P. meandrina* between LAIW+ and LAIW-, the average amount or stable isotope composition of the plankton and the TSM are similar (supplemental material). TSM, TPOC (near- and off-reef), DOC or near-reef plankton concentrations are not dependent on LAIW impact; however, upwelled water seems to be depleted in planktonic individuals. The lack of difference in the biological and chemical oceanographic parameters appears at odds with the pronounced differences in the physical oceanographic variables, suggesting that processes other than mixing are involved.

Previous studies showed that internal waves can act as a 'plankton pump' supplying phyto- and zooplankton to benthic communities (Witman et al. 1993, Leichter et al. 1998), thus fuelling growth rates of corals (Leichter & Genovese 2006). In the Andaman Sea featuring a pronounced oxygen minimum zone (OMZ) below the surface mixed layer, the concentration of plankton depends on the depth of the upwelled water: Below the surface mixed layer and thermocline, the concentrations of phyto- and zooplankton decrease dramatically along with oxygen concentrations (Madhu et al. 2003, Nielsen et al. 2004) leading to lower zooplankton concentrations in cold (<3 °C relative to modal temperature) upwelled water. During periods of weak or intermittent upwelling, enrichment and depletion of nutrients from upwelling/mixing and primary production, respectively, may even out (Kinsey 1988, Cushing 1989). Increased current strength increases nutrient uptake by corals (Hearn et al. 2001) and

fuels zooxanthellate primary production (Szmant 2002), which has further been shown to be highest in cooler water with temperatures of 23 to 26°C (Al-Horani 2005). Strong currents enhance photosynthesis and calcification by altering the thickness of the boundary layer over the coral tissue and increasing gas exchange (Dennison & Barnes 1988). Current-induced turbulence may also mitigate the negative effects of oxygen-low water on coral metabolism (Shashar et al. 1993), where turbulence may be further enhanced by coral tentacle expansion (Patterson 1992) during feeding (Sebens & DeRiemer 1977). At the same time currents are indispensable for corals (Sebens et al. 1998), which are passive suspension-feeders whose prey capture potential raises with increasing current strength (Sebens & Johnson 1991). Survival probability of corals exposed to high temperatures (Nakamura & van Woesik 2001), as well as rates and time of recovery after bleaching are positively influenced by increased water flow (Nakamura et al. 2003).

Low temperature may further affect coral metabolism in various ways. Saxby et al. (2003) observed a decrease in photosynthetic performance in waters <20°C and other studies showed that slowed polyp contraction decreased the feeding activity of corals on zooplankton during upwelling time periods (Palardy et al. 2005) and in cold water (Johannes & Tepley 1974).

Also 'corrosive' low-pH water (Feely et al. 2008), another LAIW-distinctive factor (Schmidt et al. *subm.*), is known to alter trophic pathways by diverting energy from energy consuming calcification into somatic growth (Fine & Tchernov 2007).

Because the LAIW-induced unfavorable conditions in terms of temperature, oxygen and pH persist for only minutes (Fig. 3), it is difficult to assess their potential impact on coral status over days and weeks. It is also difficult to discern antagonistic effects, e.g. negative temperature effects from possibly positive nutrient effects on coral photosynthesis. Antagonistic effects may also affect coral feeding, where positive effects of enhanced plankton supply may be offset by possible negative effects of polyp retraction (Johannes & Tepley 1974).

As sampling was limited, for logistic reasons, to day-time hours, both, the nocturnal feeding habit of the corals (Lewis & Price 1975, Muscatine & Porter 1977, Sebens & DeRiemer 1977) and the nocturnal emergence of demersal zooplankton (Porter & Porter 1977, Heidelberg et al. 2004, Genin et al. 2005, Yahel et al. 2005) may have introduced a bias in our analysis with respect to coral feeding. The potential feeding bias is likely to have been mitigated in our experiment where light-deprived fragments were subjected to constant darkness and feeding was presumed to take place at any time. The plankton bias, on the other hand, may have affected only the sheltered E Similan reef, given the lack of a coral framework on the LAIW-

exposed W side of the island and the observation that the concentration of demersal zooplankton increases with the complexity of the reef substrate (Porter & Porter 1977).

In artificial darkness, LAIW-exposed *P. meandrina* was able to subsist exclusively on heterotrophy and energy reserves (Fig. 6). The sharp drop in zooxanthellae numbers and chlorophyll-a concentrations illustrates the capacity of the light-deprived corals to rapidly adapt metabolically to the lack of phototrophy, in contrast to the LAIW sheltered corals from E Koh Miang that eventually all died (Fig. 8). The concomitant decrease in the surviving corals' tissue carbon, nitrogen and total protein concentrations (Fig. 6) is reminiscent of the declines in tissue carbon (Szmant & Gassman 1990) and lipid concentrations (Grottoli et al. 2004) which have been reported for bleached corals and attributed to the consumption of energy reserves when photosynthetic contribution to coral metabolism was reduced. Also the higher protein concentrations, in spite of eroding differences in tissue biomass between the light-deprived LAIW+ and LAIW- corals, indicates a sustained supply of protein-rich plankton food in the LAIW-exposed reef, as heterotrophic carbon has been found to be incorporated into cnidarians mainly as protein (Bachar et al. 2007). This is further corroborated by the stable isotope data showing $\delta^{13}\text{C}$ depletion for light-deprived LAIW-exposed corals only (Fig. 6), similar in magnitude to the depletion reported for vigorously feeding *Montipora capitata* during and after bleaching (Rodrigues & Grottoli 2006). Strong water flows do not only enhance food supply (Sebens et al. 1998), but also prevent a steady-state boundary layer over the coral surface hence increasing suspension feeding of particulate and adsorption of dissolved organic material (Helmuth & Sebens 1993), eventually resulting in longer and higher survival in periods of deprived phototrophy compared to LAIW-unaffected corals.

Acclimatization to LAIW-exposure and –shelter as well as to the accompanied altered food provision was rapid and resulted in increased zooxanthellae numbers, chlorophyll-a content, tissue carbon, nitrogen, and proteins when exposed to LAIW and in their decrease when transplanted out of LAIW-impact (Fig. 7). While upward changes in zooxanthellae numbers and chlorophyll-a content might be the combined result of increased nutrient availability (Szmant 2002), currents (Dennison & Barnes 1988, Hearn et al. 2001) and overall lower mean temperatures (Al-Horani 2005), our results suggest, that the higher energy reserves are the consequence of heterotrophic nutrition acting in combination with photosynthesis (Borell et al. 2008). Similar to previous reports of feeding experiments, where fed corals exhibited higher levels of protein than starved ones (Ferrier-Pagès et al. 2003, Borell et al. 2008) and lipid levels were increased when corals were kept under low light conditions and fed with

zooplankton (Treignier et al. 2008), the higher tissue carbon, nitrogen and protein concentrations indicate higher heterotrophic input and larger energy stores in LAIW exposed corals.

Our results show that heterotrophic plasticity and trophic status of a coral may vary intraspecifically, depending on its environment, particularly water flow (Skirving & Guinotte 2001) and food supply. LAIW-enhanced supplies of food may be crucial for coral resilience to stress and survival during periods of reduced or inactivated photosynthesis, as are known to occur after coral bleaching events (Brown 1997, Hoegh-Guldberg 1999). *P. meandrina* adapts rapidly to changing environmental conditions, but might only have limited heterotrophic plasticity, as indicated by the lack of change in isotopic carbon composition in the sheltered LAIW- corals. The potential of plasticity, however, is enhanced when food supply is increased by increasing current strength as shown for the LAIW+ coral fragments. Because other coral genera may be more efficient feeders than *Pocillopra* (Palardy et al. 2005, Palardy et al. 2008), it is likely that different species acclimatize variously to LAIW influences. In the absence of genetic data, however, we can only speculate whether such profound differences may reflect adaptation or acclimatization to LAIW.

As LAIW are ubiquitous in the ocean, particularly in tectonically active areas such as South East Asia featuring a rich underwater topography, strong density stratification and tidal currents, LAIW may play an important yet unexplored role in the capacity of corals to adapt to a changing marine environment.

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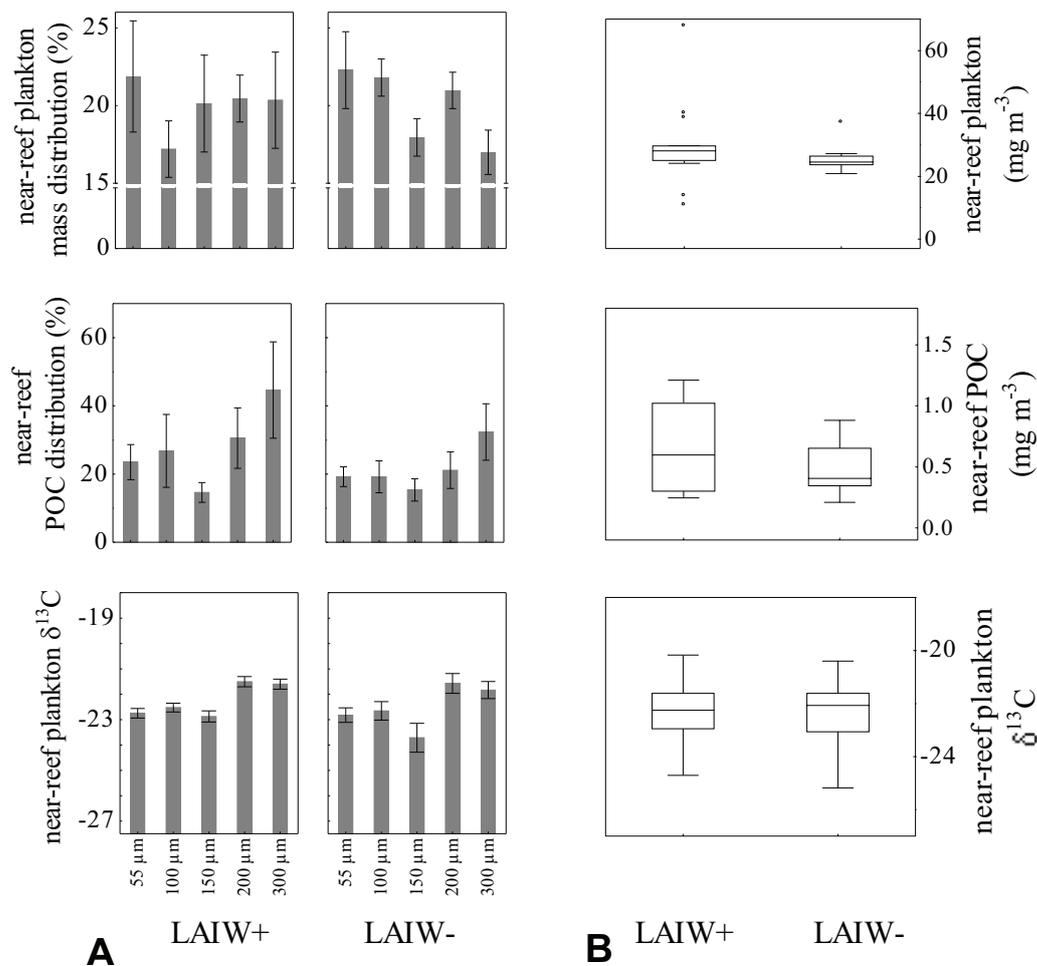
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Supplemental data Chapter II

Table S1: Composition of near-reef (total mass, POC content and $\delta^{13}\text{C}$ ratio) and off-reef (zooplankton numbers, total mass and POC content) plankton and DOC, TSM and TPOC compositions in reef waters.

	LAIW+	LAIW-
near-reef plankton mass (mg m^{-3})	33.9 ± 5.5	26.9 ± 2.6
near-reef POC (mg m^{-3})	0.63 ± 0.09	0.49 ± 0.07
near-reef $\delta^{13}\text{C}$ (‰)	-22.3 ± 0.11	-22.52 ± 0.21
off-reef zooplankton numbers ($\text{individuals m}^{-3}$)	$4.0 \times 10^3 \pm 0.4 \times 10^3$	$4.5 \times 10^3 \pm 0.4 \times 10^3$
off-reef plankton mass (mg m^{-3})	53 ± 6.9	43 ± 2.4
off-reef POC (mg m^{-3})	4.5 ± 0.3	4 ± 0.2
DOC (mg m^{-3})	$1.86 \times 10^3 \pm 0.7 \times 10^3$	$1.66 \times 10^3 \pm 0.3 \times 10^3$
TSM (mg m^{-3})	$12.40 \times 10^3 \pm 0.7 \times 10^3$	$13.39 \times 10^3 \pm 0.2 \times 10^3$
TPOC (mg m^{-3})	75.06 ± 2.6	99.36 ± 3.4

**Figure S1:** Near-reef plankton composition on LAIW+ (left panels) and LAIW- reef sides (right panels) of Koh Miang. A) Mean mass, particulate organic carbon proportion and isotopic carbon ratios (\pm SE) of each size class.

No significant difference between size classes or sides. B) Central tendency box plots (line: median, box: variability (25th and 75th percentile), whiskers: non-outlier range) with extremes (circles) of near-reef plankton mass, particulate organic carbon and isotopic carbon ratios. All size classes within each side were pooled. No significant differences between sides. See Table S1 for values.

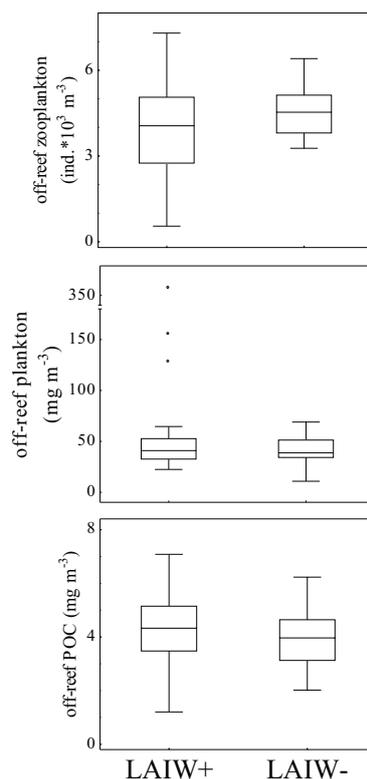


Figure S2: Off-reef plankton composition in LAIW+ (left panels) and LAIW- reefs (right panels) of Koh Miang. Central tendency box plots (line: median, box: variability (25th and 75th percentile), whiskers: non-outlier range) with extremes (circles) of off-reef zooplankton concentrations from LAIW+ and LAIW-, off-reef plankton mass from LAIW+ and LAIW- and particulate organic carbon from LAIW+ and LAIW-. No significant difference between sides. See Table S1 for values.

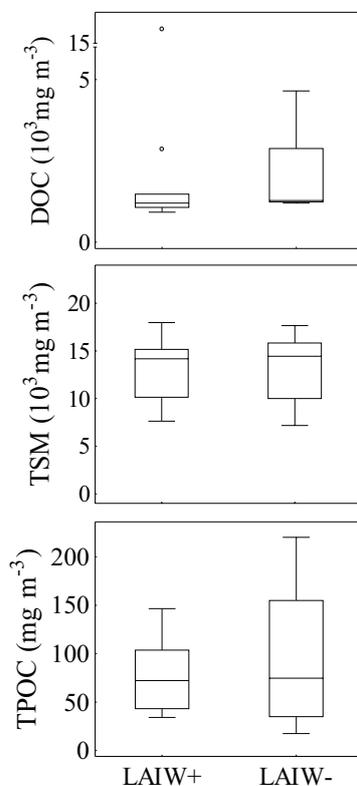


Figure S3: Biogeochemical composition of near-reef waters in LAIW+ (left panels) and LAIW- reefs (right panels) of Koh Miang. Central tendency box plots (line: median, box: variability (25th and 75th percentile), whiskers: non-outlier range) with extremes (circles) of dissolved organic carbon, TSM and TPOC concentrations. No significant differences between sides. See Table S1 for values.

- Chapter III -

Comparative metabolic performance of *Porites lutea* from Large Amplitude Internal Wave (LAIW)-exposed and LAIW-protected habitats

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In preparation

Abstract

Coral fragments of *Porites lutea* (Milne-Edwards and Haime, 1860) were collected in the Similan Islands (Thailand), Andaman Sea, from areas subjected to Large Amplitude Internal Waves (LAIW), and LAIW-sheltered controls less than 1 km away. In a field laboratory, the fragments from two depths (7 and 20 m) were all incubated in the same temperature bath under screened natural sunlight to assess their metabolic potential under simulated LAIW-free conditions at shallow depth. Corals from the LAIW-impacted sites were richer in biomass and displayed lower photosynthesis and calcification but higher release rates of dissolved and particulate organic material compared to LAIW-sheltered controls. The differences suggest metabolic acclimatization (or perhaps even genetic adaptation) of LAIW-exposed coral to lowered pH and temperature, and increased fluxes of inorganic and organic materials.

Introduction

Internal waves are ubiquitous in the ocean (Jackson 2004). Large amplitude internal waves (LAIW) may form when stratified waters are advected across abrupt changes in underwater topography, such as seamounts and sills (Farmer and Armi 1999; Jackson 2004). Over the deep ocean, LAIW may travel for hundreds or thousands of kilometers away from their generation sites until approaching shallow bottom, e.g. near the continental shelf, where the waves dissipate, disintegrate into secondary waves (Vlasenko and Alpers 2005), or break (Vlasenko and Stashchuk 2007). The resulting turbulence may mix subthermocline cold, nutrient-rich, sub-oxic and low-pH waters into shallow areas (Pineda 1991; Wolanski and Delesalle 1995; Leichter et al. 1998). The Andaman Sea features LAIW of exceptional amplitude (Perry and Schimke 1965; Osborne and Burch 1980). The Similan Islands, an island chain off the Thailand coast and close to the continental shelf break is located near the swash zone of LAIW generated near the Andaman-Nicobar island arc, some 400 – 600 km away (Jackson 2004). The west faces of the islands show large thermal oscillations of up to 10°C, on the scale of less than one

hour (Roder et al. accepted), corresponding with the passage of intense LAIW. The west sides, which are also exposed to seasonal storms during the SW monsoon period, lack true reefs (Chansang et al. 1999): corals growing in often flattened shapes occur in loose assemblages directly on the granite basement (Schmidt et al. submitted). In less than one km distance, on the sheltered east (E) sides of the Similan Islands, true reefs are found with dense cover of corals growing on a carbonate framework (Chansang et al. 1999). The immediate vicinity of such contrasting coral habitats raises the question if LAIW may have favored physiological acclimatization or perhaps even genetic adaptation within a given coral species (e.g. *Porites lutea*), or if the specimens growing along the W Similan Island sides only tolerate the combined effects of LAIW-introduced low-pH (Macyntire et al. 1993; Levitus 1994) and low-oxygenated (Gardella and Edmunds 1999) waters, high loads of inorganic nutrients (Muscatine et al. 1989b; Szmant 1997) and high fluxes of suspended or particulate organic material (Roder et al. accepted).

In this study, we use incubation experiments under normalized temperature, light and nutrient conditions to assess the coral metabolism (i.e. oxygen production, respiratory demand, calcification and exchange rates of particulate and dissolved organic matter) in response to the acclimatization history (or adaptation) to varying degrees of LAIW-exposure.

Material and Methods

To examine the metabolic potential of coral specimens from LAIW-affected and LAIW-sheltered sites under comparable conditions, incubations were conducted between 10 and 12 hours in the weeks from 08th and 18th of March 2007 under a shaded tent (Photosynthetic active radiation PAR of 35 and 45 $\mu\text{mol m}^{-2} \text{sec}^{-1}$, continuously monitored with the light-sensor of a DivingPAM (Waltz, Germany)) on land of Koh Miang Island (Similan Island # 4) with coral fragments freshly collected in deep (20 m) and shallow (7 m) waters of W and E island reef sites of Koh Miang (Fig. 1). The four chosen sites resemble decreasing LAIW impact from reefs of W deep > W shallow > E deep > E shallow (Schmidt et al. subm.).

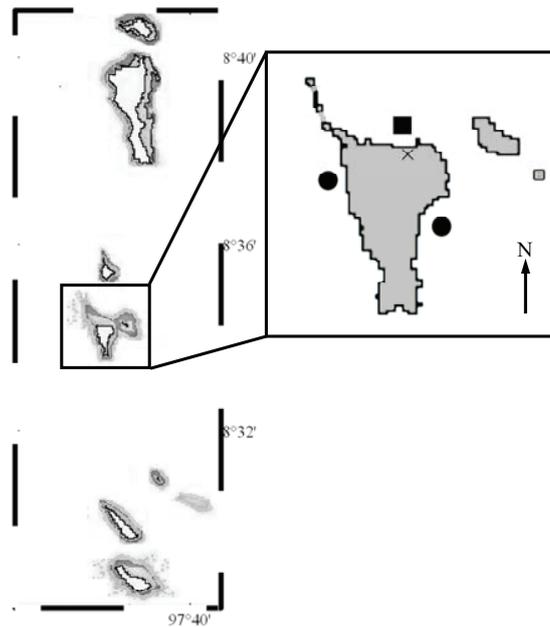


Figure 1: Koh Miang Island (extract), the fourth of the Similan Islands in the Andaman Sea, Thailand (left), with sampling sites (circles) in the reefs W and E of the island, incubation site (cross) on land and incubations water collection site (quadrat).

Incubation water was pumped (BADU Magic 8 Pump) from the Bay area in front of the incubation site from approximately 4 m depths and filled into a water tank housing four transparent and four opaque incubation beakers (three experimental chambers, one blank for monitoring purposes to guarantee consistent water quality) of 2 l volumes which could be gas-tight closed superimposing a cover plate outfitted with in- and outlets for tubes. Through these tubes, the water was rotated with a multi-channel peristaltic pump (521VK, Watson-Marlow, UK) after closure of the chambers to ensure constant motion of the water and moderate circulation. Every morning, fragments (two per colony, one for the transparent and one for the opaque chamber) of sizes from 20 – 50 cm² were chiseled off the upper surface of large *Porites lutea* (Milne-Edwards and Haime, 1860) colonies and transported immediately to the field laboratory where they were separately implanted into incubation chambers without exposing the fragments to air. After a short acclimatization time (~ 20 – 30 min), the oxygen content in the tank was measured using an optode (HQ40, Hach Lange), triplicate samples were taken for nutrient and alkalinity measurements (see below), the chambers were closed, taking care to avoid bubbles inside, and incubated for 118 to 124 minutes. After the incubation, the chambers were opened, the oxygen content recorded (HQ, Hach Lange) and 50 ml and 1 l aliquots of

incubation water taken for subsequent analyses of total alkalinity and dissolved or particulate organic matter respectively (see below). Net photosynthesis was calculated from the temporal difference in oxygen concentrations in the light chambers, respiration from the oxygen uptake in the dark chambers. Gross photosynthesis was calculated as the sum of net photosynthesis and dark respiration. Calcification was measured according to the alkalinity anomaly method (Schneider and Erez 2006). For calculation of calcification rates, 50 ml samples taken prior and after incubation were filtered (Whatman GF/F) by hand using a syringe and total alkalinity was immediately measured to the second end point (Gran 1952) using a solution of $0.01 \text{ mol l}^{-1} \text{ HCl} + 38 \text{ g l}^{-1} \text{ NaCl}$ (Titrisol, VWR) and a titration apparatus (Titrimo, Methrom). Further, 1 l samples taken prior and after incubation were filtered (Millipore Vacuum Pump, 200 mm Hg) over pre-combusted and pre-weighed Whatman GF/F filters for subsequent analyses of dissolved and particulate organic matter (DOM and POM respectively). Filters were desiccated (12 hours at 40°C) and cut in half for separate analysis of particulate organic carbon (POC) (after acidification with 0.1 M HCl to remove inorganic carbon) and particulate nitrogen (PN) using a NA2100 Protein Elemental Analyzer and an elemental CHNS standard (LECO). The filtrate was stored frozen until analysis of inorganic nitrogen compounds (nitrate, nitrite, ammonium) and total dissolved nitrogen (Parsons et al. 1998) using a spectrometer (GBC model UV/VIS918). Dissolved organic nitrogen (DON) was calculated by subtracting concentrations of inorganic nitrogen compounds from the total nitrogen content of the sample (Ferrier-Pagès et al. 1998). Dissolved organic carbon (DOC) was measured after acidification with phosphoric acid (20 %) to a pH of 2 in a DOC/DIC analyzer (Rosemount DC-190) using a 10-point calibration with TOC standards (ULTRA Scientific). To gain production / uptake rates, concentrations measured in the start samples taken prior to incubation were subtracted from final concentrations for all parameters. Blank chamber rates were calculated and verified to not exceed the range of standard deviation. All production / uptake rates were standardized per cm^{-2} and h^{-1} by accounting for the volumes of the coral fragments (measured in small beakers via displacement after) in the incubation chambers, normalizing for incubation time and calculating tissue area to the nearest 0.05 mm using a caliper and geometry as proposed by Naumann et al. (2009). After incubation, coral fragments were sacrificed

and tissue stripped off the skeleton using an artist's airbrush and filtered seawater. Tissue slurry was homogenized for 30 seconds (Ultra Turrax) and aliquots retained for the following analyses: Zooxanthellae densities were calculated by six replicate counts under the microscope (Leitz, Portugal, 260× magnification) using a Fuchs-Rosenthal haemocytometer. Five ml of the homogenate were filtered (Millipore Vacuum Pump, 200 mm Hg) on Whatman GF/F filters and frozen prior to chlorophyll-a extraction after standard procedures (Strickland and Parsons 1972) and analysis in a Shimadzu UV 1700 1nm Slit photometer at 750 nm and 664 nm (Lorenzen 1967). A known volume of the remaining tissue homogenate was centrifuged for separation of coral host tissue and zooxanthellae and each component was loaded (Millipore Vacuum Pump, ~100 mm Hg) separately onto pre-combusted glass fiber filters (Whatman) as described in Muscatine et al. (1989a). Filters were dried (24 hours at 40°C) and coral host and zooxanthellae organic carbon and nitrogen contents were determined in an Elemental Analyzer (NA2100 Protein) using an elemental CHNS standard (LECO). All coral parameters were correcting for homogenate volume and tissue surface area. Each site (W deep, W shallow, E deep, E shallow) was sampled twice; hence, in total, 8 incubations, each with 3 light-exposed and three shaded coral fragments were conducted. Due to non-normality of the data, nonparametric analyses of variance (Kruskal and Wallis 1952), followed by determination of differences between the groups (Wilcoxon and Wilcox 1964) were conducted.

Results

The highest zooxanthellae densities were found in W shallow corals, followed by W deep, E deep and E shallow specimens (Table 1). Coral host as well as zooxanthellae carbon and nitrogen concentrations followed the same pattern and were highest for the W side shallow water specimens. Only chlorophyll-a concentrations were highest in the deep corals of the W side, with second highest concentrations of the W shallow water specimens.

	10^6 zooxanthellae cm^{-2}	μg chlorophyll-a cm^{-2}	μg coral host carbon cm^{-2}	μg zooxanthellae carbon cm^{-2}	μg coral host nitrogen cm^{-2}	μg zooxanthellae nitrogen cm^{-2}
W deep	5.51 ± 0.58	11.50 ± 1.17	179.96 ± 10.79	638.00 ± 41.15	22.92 ± 1.54	83.68 ± 5.40
W shallow	9.92 ± 3.16	9.18 ± 1.42	241.76 ± 15.30	724.36 ± 83.68	32.28 ± 2.13	89.68 ± 8.47
E deep	5.64 ± 2.56	7.35 ± 0.85	172.32 ± 7.07	498.24 ± 29.02	22.88 ± 1.11	50.44 ± 3.66
E shallow	4.45 ± 0.92	4.33 ± 0.42	143.84 ± 4.99	397.32 ± 16.76	17.84 ± 0.56	43.72 ± 1.88

Table 1: Tissue parameters \pm SE of *Porites lutea* fragments from deep and shallow reef sites of W and E Koh Miang Island used in incubation experiments.

Overall, we found the highest net oxygen production (Fig. 2; $p < 0.05$) in the deep reef areas of the E island side ($33 \pm 5 \text{ mg cm}^{-2} \text{ h}^{-1}$). For shallow water corals, the net oxygen production was higher ($p < 0.05$) in the E ($16 \pm 3 \text{ mg cm}^{-2} \text{ h}^{-1}$) than in the W. Depth-related differences in net oxygen production were significant in the E but not on the W side of the island. Respiration rates (Fig. 2) were highest in deep W side specimens ($-30 \pm 2 \text{ mg cm}^{-2} \text{ h}^{-1}$) and significantly different ($p < 0.05$) from the other site specimens which did not differ from each other. Calcification (Fig. 3) in the transparent chambers ('light') was significantly higher than the corresponding dark calcification for all fragments ($p < 0.05$). Highest values were found for the shallow water corals from the E reef ($1.2 \pm 5 \mu\text{mol cm}^{-2} \text{ h}^{-1}$; $p < 0.05$).

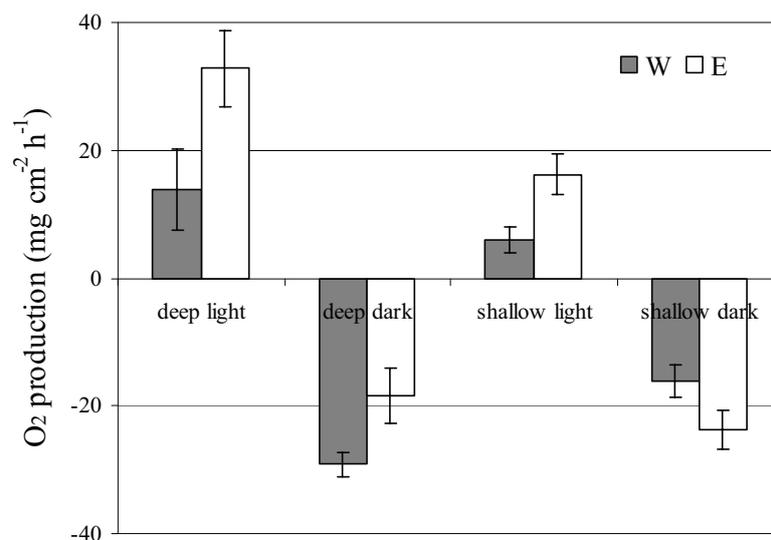


Figure 2: Net oxygen production and respiration rates \pm SE of *Porites lutea* from deep and shallow reef areas of W and E Koh Miang Island incubated under equal conditions.

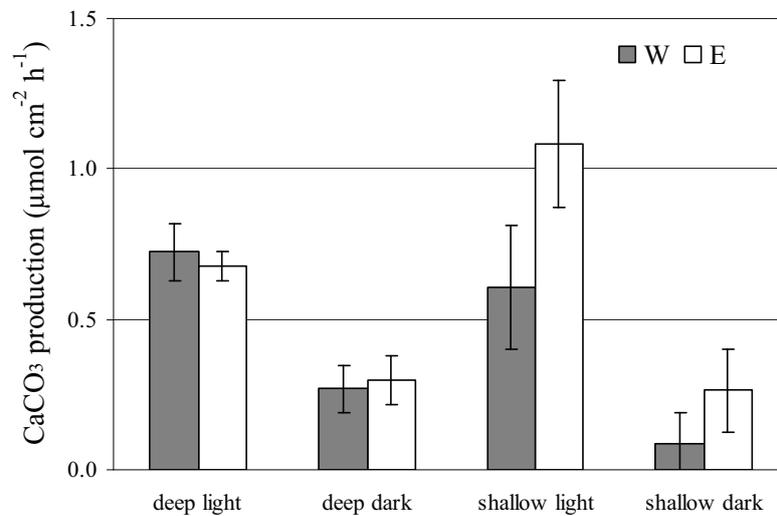


Figure 3: Calcium carbonate production rates \pm SE of *Porites lutea* from deep and shallow reef areas of W and E Koh Miang Island incubated under equal conditions.

Production and consumption rates of dissolved organic matter (DOM) were highly variable (Figs. 4 and 5). Dissolved organic carbon (DOC, Fig. 4) production occurred in light-exposed shallow water corals, both in E ($7.3 \pm 4 \mu\text{g cm}^{-2}\text{h}^{-1}$) and W ($11.8 \pm 8 \mu\text{g cm}^{-2}\text{h}^{-1}$). DOC uptake was observed in both, light incubated and dark deep water corals from E (-13.3 ± 6 and $-12.7 \pm 7 \mu\text{g cm}^{-2}\text{h}^{-1}$, respectively). The results from the other incubations were not significantly different from zero. Dissolved organic nitrogen (DON, Fig. 5) was produced exclusively by light-incubated shallow water corals from the E ($0.08 \pm 0.02 \mu\text{g cm}^{-2}\text{h}^{-1}$) whose production rates were significantly higher ($p < 0.05$) compared to their deep water counterparts, regardless of light exposure. DON was mainly taken up by deep water corals. Uptake in E deep water corals was higher ($p < 0.05$) in the light ($-0.18 \pm 0.07 \mu\text{g cm}^{-2}\text{h}^{-1}$) than in the darkness.

Particulate organic matter (POM) fluxes were almost exclusively positive (except for PN-measure of one fragment from the deep E reef site), indicating release of particulate organic carbon (POC, Fig. 6) and particulate nitrogen (PN, Fig. 7) into the incubation water. POC release rates (Fig. 6) were highest for deep corals ($p < 0.05$) in both, the light ($7.5 \pm 2.5 \mu\text{g cm}^{-2}\text{h}^{-1}$) and dark incubations ($5.6 \pm 1.7 \mu\text{g cm}^{-2}\text{h}^{-1}$). For deep and shallow water corals there were no significant differences between light and dark incubations. PN

release rates (Fig. 7) followed a similar pattern, with no significant differences in response to light treatment, nevertheless with a tendency of increased release under light for the W side coral fragments and a significantly higher ($p < 0.05$) release rate for corals from the deep W side reef incubated under light ($1.96 \pm 0.6 \mu\text{g cm}^{-2}\text{h}^{-1}$) as well as in opaque chambers ($1.2 \pm 0.4 \mu\text{g cm}^{-2}\text{h}^{-1}$).

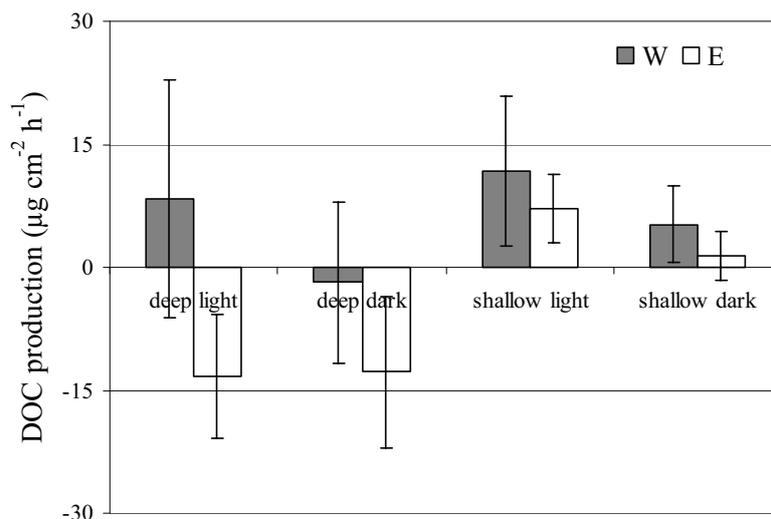


Figure 4: Dissolved organic carbon (DOC) production or uptake rates \pm SE of *Porites lutea* from deep and shallow reef areas of W and E Koh Miang Island incubated under equal conditions.

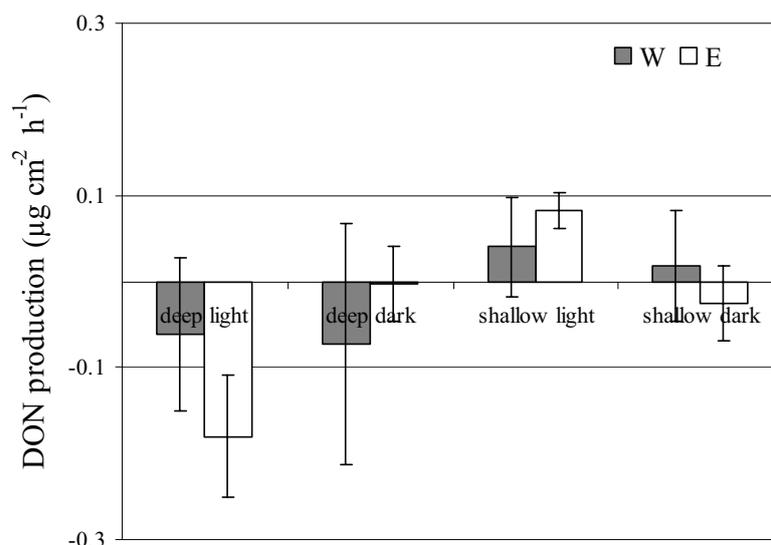


Figure 5: Dissolved organic nitrogen (DON) production or uptake rates \pm SE of *Porites lutea* from deep and shallow reef areas of W and E Koh Miang Island incubated under equal conditions.

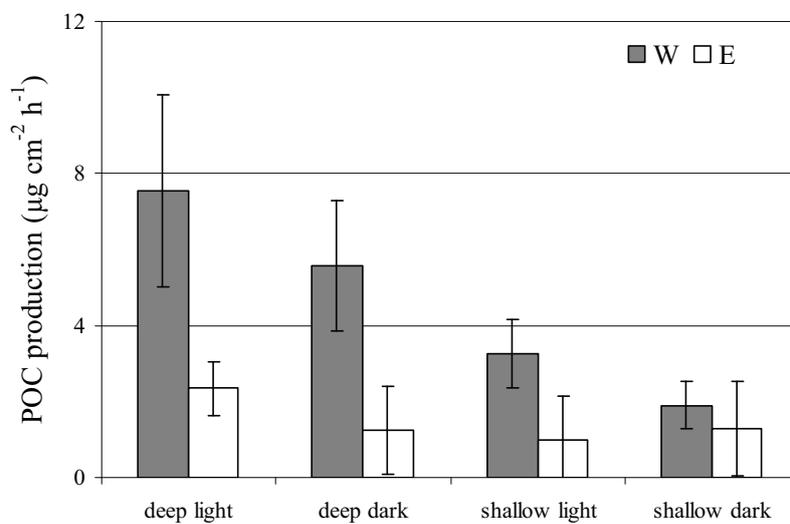


Figure 6: Particulate organic carbon (POC) production rates \pm SE of *Porites lutea* from deep and shallow reef areas of W and E Koh Miang Island incubated under equal conditions.

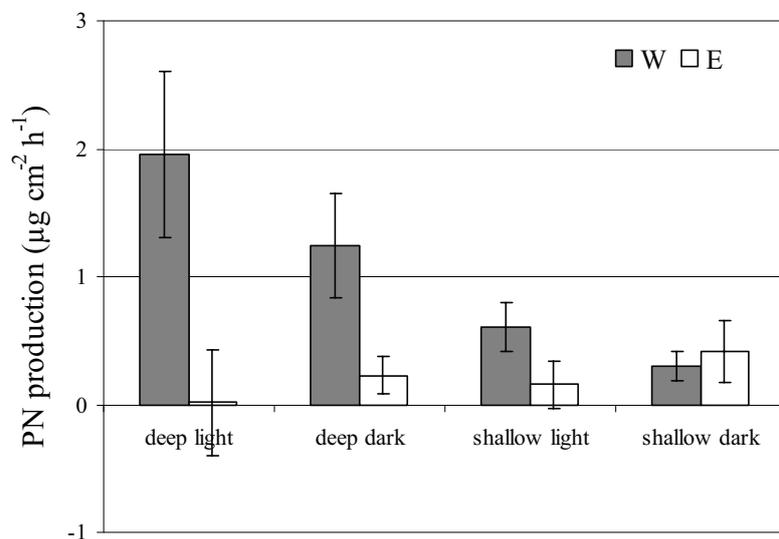


Figure 7: Particulate nitrogen (PN) production rates \pm SE of *Porites lutea* from deep and shallow reef areas of W and E Koh Miang Island incubated under equal conditions.

Discussion

This study shows pronounced lateral (W vs E) and vertical (shallow vs deep) differences in coral metabolism, suggesting different acclimatization histories (or perhaps adaptations) to LAIW in terms of photosynthesis, respiration and exchange of dissolved and particulate organic matter (DOM and POM).

Tissue conditions mirror the nutrient regimes of the corals' original environments with enhanced zooxanthellae densities and chlorophyll-a concentrations in response to large amplitude internal waves (LAIW). In the shallow water areas of the W side, the combined effects of high nutrient input and a high light environment (Schmidt et al. *subm.*) result in increased zooxanthellae densities (Brown et al. 1999) and biomass production (Fitt et al. 2000). In addition to strong currents resulting in higher food supplies coral host biomass production is also enhanced (Roder et al. *accepted*). The benefit of high biomass as an energy store (Fitt et al. 2000; Grottoli et al. 2004; Bachar et al. 2007) is counteracted by the respiratory demands of a thick tissue (Spence and Hynes 1971) resulting in lower net oxygen production of the holobiont. Therefore, specimens from less LAIW-impacted sites (E) are more effective oxygen producers dispensing higher rates of oxygen into the water column compared to W side fragments. Calculating the gross primary production by adding the absolute values of respiration and net oxygen production (McCloskey and Muscatine 1984) reveals still higher gross oxygen production rates for corals from the E reef sites despite higher zooxanthellae densities and pigment concentrations for W side corals suggesting a more costly photosynthesis under LAIW influence. Being light-enhanced because of the tight coupling with photosynthetic activity (Furla et al. 2000; Marubini et al. 2001), calcification was higher in the transparent chambers compared to dark incubated specimens. Calcification rates were highest in E shallow coral fragments indicating that other processes besides photosynthesis are involved as oxygen production was clearly higher in deep water specimens from the same side. Coral growth rates have been documented elsewhere to be higher in shallow waters (Falkowski et al. 1990; Furla et al. 2000; Marubini et al. 2001) as is seen for the E, but not for the W side fragments in our study. This might be due to their lower photosynthetic performance, but coral calcification is also determined by the

aragonite saturation state (Marubini et al. 2001) which is rather driven by the variable carbonate ion than by the nearly constant Ca^{2+} concentrations in the water column (Stumm and Morgan 1981). In upwelling deep sea water CO_2 concentrations are high (MacIntyre et al. 1993), resulting in low pH and low aragonite saturation state. As a result, calcium carbonate production is decreased as documented for the reefs in upwelling areas around Galapagos (Glynn 1988) or in the eastern Pacific (Cortés 1997). The exposure of W side coral specimens to corrosive (Feely et al. 2008) water might limit coral growth regardless of light availability.

Also DOC release rates are tightly coupled with the light regime, with high light adapted corals releasing more than low light adapted ones (Crossland 1987). Furthermore, DOC is released in increasing amounts when corals are exposed to increased nutrient concentrations and in even higher amounts when being fed (Ferrier-Pagès et al. 1998). High light and nutrient input plus an increased availability of organic material (Roder et al. accepted) due to LAIW-impact result in DOC release, especially in corals from the shallow W side. On the other hand, corals have also been documented to take up DOC mainly in oligotrophic environments using it as an additional food source (Sorokin 1973; Grover et al. 2008). With DON release corals tend to behave more conservatively, retaining higher amounts of DON in relation to DOC (Ferrier-Pagès et al. 1998). Ferrier-Pagès et al. (1998) found that the amount of DON released was equal in fed, starved and nutrient enriched experimental setups. POM by contrast was constantly excreted in all experimental setups and constantly higher than release rates of DOM as suggested before by (Tanaka et al. 2008). We attribute the release of POM to mucus production (Wild et al. 2004) which is generated by corals to i.e. remove high particle or sediment loads (Hubbard and Pocock 1972; Schuhmacher 1977). Even though resuspension in the area of high LAIW impact might be higher due to strong currents (Grant and Madsen 1979), smothering of corals by particles or sediments is unlikely for the same reason. Stronger currents, however, might be responsible for high flushing rates of mucus from the coral surface demanding quick mucus reproduction. Furthermore, the combination of high nutrient loads (Szmant 1997) and increased organic matter fluxes (Patterson 1992; Palardy et al. 2005, Roder et al. accepted) might constitute a nutritionally replete environment and hence increase mucus production as recycling is energetically not as

compellent as in more oligotrophic surroundings (Ferrier-Pagès et al. 1998). In contrary to the DOM release, the ratio of released POC to PN did not change between the various treatments. This suggests that the quality of the fresh mucus was similar (Coffroth 1990) regardless of the corals' origin and that nitrogenous compounds were not conserved in stringent amounts.

Production and consumption rates of *P. lutea* differ between the corals' origin, and hence history of LAIW-exposure, even though environmental conditions during time of measurement are equal. The interactive effects of high nutrient (Szmant 2002) and high organic matter fluxes (Roder et al. accepted) as well as the low light (Kleypas et al. 1999), low pH (Levitus 1994) and low temperature (Saxby et al. 2003) regime plus strong current conditions (Nakamura et al. 2003) on the metabolic performances such as photosynthesis, calcification or organic material release and uptake (Ferrier-Pagès et al. 1998) seem to be highly complex and extremely variable and need to be investigated in greater detail. The findings of this study suggest that production of a coral is dependent on its somatic state gained by exposure to its natural surrounding and that its behavior even under changed conditions represents to certain extent conditions of its origin. We presume that the corals' conditioning to LAIW has changed their metabolic response. What remains to be shown really is whether this conditioning is acclimatization – or rather adaptation.

Acknowledgements

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- Chapter IV -

**Benthic primary production in response to Large
Amplitude Internal Waves (LAIW) in coral reefs
at the Similan Islands, Thailand**

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Abstract

The Andaman Sea features Large Amplitude Internal Waves (LAIW) of exceptional amplitude (> 80 m), which may strongly affect environmental conditions within local coral reefs. The Similan Islands in the swash zone of LAIW offer the unique chance to explore small-scale variations in benthic primary production in response to these perturbations in temperature (cold bouts up to 4 °C below ambient), total inorganic nutrients (> 1.84 μ M) and light levels (~ 30 % below ambient). Here, we compare the relative cover and metabolism of the main primary producers (microphytobenthos in reef sands, turf algae, scleractinian corals) at LAIW-exposed and non-exposed sites at Koh Miang, Similan Islands. The LAIW-exposed Western (W) side of Koh Miang coincided with lower live coral (28 %), and higher turf algae (36 %) cover compared to the sheltered Eastern (E) reef (68 % and 8 % cover, respectively). Net photosynthesis and respiration by turf algae increased with rising LAIW influence, whereas sedimentary net photosynthesis and respiration exhibited the opposite pattern, despite similar chlorophyll concentrations in algae and sediment samples from both sides. The dominating reef-building coral *Porites lutea* showed similar net photosynthesis on both island sides, but 40 % higher pigment concentrations at W, likely due to the lower light availability and higher nutrient concentrations. Turf algae were the dominant primary producers on the rocky W side of Koh Miang, and the microphytobenthos on the sheltered E side, with corals contributing less than 15 % to the gross primary production on either side. In spite of the profound effects of LAIW on the metabolism of the various main primary producers, the overall primary production (i.e. microphytobenthos, turf algae and corals) was similar at both W and E, indicating high plasticity of primary production in LAIW-affected W side.

Introduction

Large Amplitude Internal Waves (LAIW) are ubiquitous in the ocean (Huthnance 1989, Apel 2006). They are formed through the interaction of tides and the undersea landscape in a density-stratified sea (Gerkema and Zimmerman 1995, Vlasenko and Hutter 2001). In the Andaman Sea, LAIW of exceptional amplitude are created by tidal currents across the shallow ridges near Sumatra, the Nicobar and Andaman Islands (Perry & Schimke 1965, Osborne and Burch 1980, Jackson 2004). When LAIW reach shallow water depths they may

transform and break delivering subthermocline water upslope (Vlasenko & Stashchuk 2007). Like pulsed upwellings in other coastal areas (Pineda 1991, Leichter et al. 2003, Leichter et al. 1996, Smith et al. 2004), they may deliver essential nutrients to the surface supporting primary production in otherwise nutrient-depleted waters. Arriving LAIW may be easily identified by divers as cold and turbid bores, which may occur once or twice during dives. The Similan Islands, located in the swash zone of LAIW (Vlasenko & Stashchuk 2007) feature dramatic differences in their benthic communities between the W and E sides: on the sheltered E sides where LAIW influence is weak, a typical tropical coral reef usually occurs. By contrast, on the W sides, where LAIW are much more pronounced, scattered corals encrust huge granite boulders or anchor on the sand floor, but a carbonate reef framework is lacking. This strikingly contrasting natural setting, only a few hundred meters apart, offers the unique opportunity to investigate coral reef primary production in dependence of pronounced variations in environmental conditions. Two opposed phenomena on the W side may affect primary production simultaneously: on the one hand the lowered light levels, which may decrease photosynthesis, and on the other hand the higher nutrient availability, which may enhance photosynthesis, e.g. via the increase of pigment concentrations, especially in deeper water (Dubinsky et al. 1990, Iglesias-Prieto and Trench 1994). Additionally, the higher temperature variability, due to short term temperature drops induced by incoming LAIW on the W side, may favour a different benthic community, adapted to these unstable conditions. The reef sands as biocatalytical filter systems (Wild et al. 2005, Rasheed et al. 2006) may be affected by elevated concentrations of inorganic nutrients and an enhanced load of organic material in the water column. This may strongly affect sedimentary primary production, which can importantly contribute to the high productivity of coral reef ecosystems (Bunt et al. 1972, Clavier and Garrigue 1999). Turf algae are likewise important primary producers within coral reefs (Rogers and Salesky 1981; Carpenter 1985), and the enhanced inorganic nutrient availability and concomitant lower light levels caused by the LAIW on the W sides, may affect their growth and photosynthetic output (Williams and Carpenter 1988, Smith et al. 2001, Smith et al. 2004). On the other hand, corals are usually adapted to oligotrophic environments and may have disadvantages under higher nutrient levels compared to algae (Hughes 1994, Lapointe 1997, Pandolfi et al. 2005).

The aim of this study therefore was to comparatively evaluate O₂ fluxes (photosynthesis and respiration) induced by key primary producers (sedimentary microphytobenthos, turf algae and scleractinian corals) from LAIW-exposed and protected sites and how these organisms

contribute to overall primary production. Thereby primary production budgets were calculated combining respective benthic cover and oxygen fluxes.

Material and methods

Description of study site and background parameters

Samplings and measurements were carried out at Similan Island # 4 (Koh Miang) on the E (8° 33.593' N, 97° 38.237' E) and on the W (8° 34.254' N, 97° 37.957' E) side, in January-March 2008, in two water depths (shallow: 6-9 m; deep: 19-21 m), in the following referred to as sampling 'sites' (E shallow, E deep, W shallow, W deep). Large Amplitude Internal Waves (LAIW) occur in the Andaman Sea almost throughout the year (despite August and September, Jackson 2004), but they are most pronounced from February until April at the Similan Islands (Schmidt et al. *subm.*).

Light intensity (lx) and water temperature (°C) were recorded in-situ at all four sites using temperature (C°, TidbiT v2, Onset) and light loggers (0 - 320000 lx, Pendant, Onset) both with a temporal resolution of 1 minute. Light was calculated as a daily mean around noon (11-14 h, 02.02.-16.03.2008). As the spectral properties of the pendant loggers are unknown, the transformation of light intensity (lx) into photosynthetic active radiation (PAR [$\mu\text{mol quanta m}^{-2} \text{s}^{-1}$]) equivalents can only be considered as a coarse approximation. Light intensity (I [lx]) was measured during 4 shallow and 2 deep diurnal cycles in-situ with light loggers (lx, see also above), and PAR ($\mu\text{mol quanta m}^{-2} \text{s}^{-1}$) was recorded concomitantly with the internal light sensor of a Diving PAM (submersible fluorometer, pulse amplitude modulated, Heinz Walz GmbH, Germany). In spite of the mentioned limitations, we found a reasonable correlation ($I \text{ (lx)} = 76.684 \times \text{PAR} \text{ (}\mu\text{mol quanta m}^{-2} \text{s}^{-1}\text{)}$, $R^2 = 0.52$, Fig. 1 suppl. data) between the two measuring devices. Such PAR ($\mu\text{mol quanta m}^{-2} \text{s}^{-1}$) and light intensity (lx) correlations are widely used particularly in monitoring environmental conditions during mariculture of fish.

Autonomous upward-looking Acoustic Doppler Current Profilers (ADCP, RDI Teledyne Workhorse Sentinel, 600 kHz and 300 kHz) were deployed at the deep sites (20 m) at E and W. They measured the 3-D currents above the transducer at 1 m vertical and 1 min temporal resolution with an accuracy of 0.3 to 0.5 % of the water velocity ± 0.3 to 0.5 cm/s. Data were imported into Matlab (rdradcp.m by Rich Pawlowicz, U. of British Columbia,

<http://www2.ocgy.ubc.ca/~rich/>) and average current velocities for the E and W side were calculated.

Water samples for inorganic nutrient analysis (ammonium, nitrate plus nitrite, and phosphate) were collected during the sampling period using SCUBA (in total: E shallow, n = 11; E deep, n = 12; W shallow n = 8; W deep n = 9 samples). Water samples were filtered (GF/F filters, Ø 25 mm, nominal pore size: 0.7 µm), and the filtrate was conserved with 100 ml HgCl₂ (Kattner 1999).

For comparison, additional temperature loggers (TidpiT v2, Onset, triggered every 6 min) were deployed at some other Similan Islands (# 2, # 7, # 8 south and # 8 north), each at E and W and in the two water depths. There, the same consistent temperature characteristics were found as at Koh Miang (same time period 02.02.-16.03.2008), revealing ‘averaged daily temperature ranges’ (DTRs) displayed as mean of daily max – min, as a measure for LAIW impact at each site (for Koh Miang: Table 1, all: Table 1 suppl. data). This revealed increasing LAIW impact from E shallow, E deep, W shallow to W deep; therefore, sampling sites are aligned according to rising LAIW influence throughout this manuscript.

Furthermore, at Koh Miang nutrients, pH, oxygen, salinity, and current velocities correlated with temperature at each site (Schmidt et al. *subm.*). Schmidt et al. (*subm.*) also showed that temperature variations of similar magnitude recorded at W-exposed faces of the above mentioned islands over longer period (Feb 2007 to Nov 2008) were consistently higher than the variations recorded on the respective E island faces. This suggests that LAIW are impacting more or less equally on all W island slopes and are actually causing the recorded W-E differences in environmental regime. Similar W-E differences were found in coral communities (Schmidt et al. *subm.*). Both environmental and biological data suggest that the W and E faces of Koh Miang, an island in the middle of the Similans (Schmidt et al. *subm.*), can be considered representative of a LAIW-beaten and LAIW-sheltered tropical island, respectively.

Benthic community composition analyses

Line point intercept transects (50 m length, Hodgson et al. 2004), were conducted along isobaths on the E and W sides of the island, at two depths (7m and 20 m). Two to three replicate transects were carried out spaced 10 m apart. Within each transect, the benthic community was sampled every 0.5 m. Hard substrate (live and dead coral cover and rock), sediment and turf algae cover (on all substrates and on hard substrate), and coral growth form (used for the 2D to 3D factors, see below) were determined.

Sampling and preparation of investigated primary producers

To investigate photosynthesis related parameters and sediment composition, mini-corers to obtain 1.2 cm long, 6.4 ml volume and 3.9 cm² surface area samples were used. Only the top layer of the sediment was considered as photosynthetically active, as light can only penetrate a few mm into the sediment (Kühl et al. 1994). The samples were processed within one h after collection and used either for incubation experiments (E shallow, n = 15; E deep, n = 15; W shallow, n = 14, W deep, n = 20, see below), pigment determinations of chl-a and pheophytin content (n = 10 for each site) or to analyse sediment grain sizes (12 samples pooled for each site) as described below.

Additionally, small-cores of 5.6 cm sediment depth (33.4 ml) were taken for pore water nutrient analysis (n = 4 for each site). Within one h after sampling, the small cores were washed with 10 ml distilled water, centrifuged and then the supernatant was filtered through pre-combusted GF/F filters; this procedure was repeated two more times and 100 µl HgCl₂ were added to the final filtrate for conservation (Kattner 1999). Filters were frozen for later determination of particulate organic carbon (POC) and particulate total nitrogen (PN).

Turf algae were defined as a conglomerate of various diminutive and filamentous algae growing up to a height of about 1 cm. Turf algae occasionally appeared on sediment, but only the ones on hard substrate were used for turf algae analysis. Small pieces of coral rubble and rock were sampled and processed within one hour; algae were removed using a scalpel and an airbrush filled with filtered seawater. The algae-seawater suspension was used for incubations and later filtered on GF/F Filters and frozen for pigment analysis (E shallow, n = 5; E deep, n = 15; W shallow, n = 10; W deep, n = 15). Surface area was calculated using the best fitting geometrical form(s) of each scraped rubble piece. Only the light-exposed surfaces of the rubble fragments were considered. To determine algae growth rates, microscope slides (later referred to as algae tiles) were fixed on holders and deployed at each site. Algae tiles were sampled and displaced in a random order after 1-3 weeks (E shallow, n = 15; E deep, n = 15; W shallow, n = 10; W deep, n = 17); then they were scraped with a scalpel and airbrushed with filtered seawater. The algae-seawater suspension was treated as above. Daily growth rates were calculated as amount of chl-a (µg, see pigment determination below) per algae tile area (cm²) and unit time (d⁻¹).

Five colonies of the massive stony coral *Porites lutea*, the most common coral genus at Koh Miang, and one of the most abundant species at the Similan Islands (Schmidt et al. subm.), were sampled at each site, and two fragments were chiselled from each colony; fragments were left at the appropriate site on racks to heal for two weeks. One replicate of each colony

was used for light and the other one for dark incubations, five fragments for each chamber (light or dark). Coral surfaces were calculated according to Naumann et al. (2009) with the best fitting geometric shape (half-ellipsoid). Tissue was removed with an airbrush and filtered seawater, and homogenized with a tissue grinder. A subsample was filtered on GF/F filters and frozen for later pigment analysis.

Measurement of oxygen fluxes by main primary producers

Sedimentary microphytobenthos and turf algae were incubated in Winkler bottles (~ 60 ml) with natural sea water in a water bath on land. Short-term incubations (1-2 h) were conducted around noon to obtain maximum photosynthetic rates. Five independent light and dark incubations, either sediment or algae, were conducted simultaneously for each site. Varying layers of net cloth were used to adjust, on a daily basis, PAR to 105 ± 16 and 39 ± 13 ($\mu\text{mol quanta m}^{-2} \text{ s}^{-1}$), corresponding to the average ambient E light levels at 7 m and 20 m, respectively. Light and temperature were recorded every minute by the corresponding sensor of a Diving PAM and temperature loggers (see above), respectively. Incubation temperature was 31 ± 1 °C, 1 °C higher than the maximum temperature at E shallow in-situ. This lack of temperature control may be a weakness of this study. However, the same conditions during the incubations yielded in overall valid primary production rates independent from short-term interferences caused by the relatively unpredictable, brief temperature drops in-situ (Schmidt et al. *subm.*).

Oxygen concentrations were determined before and after each incubation using an optode (HQ 40, Hach Lange). Repeated incubations with seawater only (i.e. controls) in light and dark (each $n = 10$), at simulated shallow water light conditions revealed no measurable differences between start and end oxygen values after 2h and were therefore not considered in the calculations. A submersible flow-respirometer was used for coral incubations on four occasions (clear skies), one at each site in-situ. Light was measured concomitantly with pendant loggers (see above). The respirometer consisted of three incubation chambers - light, dark and light control (each 2.1 L) -, a CTD multisensor-probe (Seabird SBE 19plusV2 with oxygen sensor and terminal 5T pump), plumbing between valves and a programmable control unit. The unit was programmed to perform a measuring cycle as follows: (1) simultaneous flushing of chambers with ambient water, (2) consecutive measurements of initial temperature and oxygen concentrations in each of the chambers (measurements of each chamber took 40 s, chambers were always analysed in the same order), (3) incubations (20 min) with intermittent stirring of chambers with external pumps (Reich submersible pump 511-0110), and (4) consecutive measurement of final temperature and oxygen concentrations in each of the

chambers (intervals as initial values). This cycle lasted 30 min and was repeated 10 – 15 times during the course of a day. The corals were likely not exposed to variations in water temperature during incubations in-situ, as the volume of the chambers (2.1 l) likely prevented short-term LAIW to have a considerably influence of the enclosed water. Therefore, the measured oxygen fluxes were obtained under relatively stable conditions, similar to those during sediment and turf algae incubations. Gross photosynthesis for each site was calculated as: net production of each cycle + respiration mean for each dark chamber. A 2nd order polynomial curve showed the best fit to the data ($y = ax^2 + bx + c$). The new incubation device offered the possibility to obtain several incubation measurements autonomously during the course of a day in-situ, however the before and after handling, as well as the deploying of the quite huge device in the field is still very time consuming and requested a team of at least four people. Therefore only few runs could be obtained during this study.

Sample analyses

Nutrient concentrations (from water column and pore water) were determined photometrically after Grasshof et al. (1999) with an autoanalyser (Evolution III, Alliance Instruments, France). Nutrient pore water results were related to the water volume of small sediment cores using the water content of the sediment at each site (see below). Two extreme values of pore water ammonium were removed from the data set due to an outlier test (criteria of multiple SD).

For pigment concentration measurements, samples (either filters or sediment) were unfreezed, added with a certain volume of acetone (90%), shaken thoroughly, then placed in an ultrasonic bath for 15 min and stored afterwards for 24h at 4°C in the dark to extract pigments. Accordingly samples were shaken thoroughly again and then centrifuged at high speed for 15 min. The supernatant was measured in a photometer (Shimadzu UV 1700, 1nm slit). For sediment and turf algae chl-a and pheophytin was calculated using the equations after Lorenzen (1967). For pigment calculations of corals the equations of Jeffrey and Humphrey (1975) were used. Pigment data were normalized by sediment area sampled, growth area of turf algae (on hard substrate) or coral surface area.

For sediment characteristics grain size fraction was analysed using the pipette method (to separate the fine fraction) and wet sieving (to separate the coarse fraction; both Tucker 1988); the different grain size fractions were dried, afterwards weighted and the proportion of weight calculated. Carbonate content was determined using a Schleicher-Apparatus and precipitated lime as a standard (Schlichting et al. 1995). Water content was estimated by weighing wet and dry sediment to recompute pore water nutrient concentrations of the small-cores (see above). Microscopic investigations on untreated sediment revealed pennate and centric diatoms as the

by far dominating micro-algae in all sediments. The visual sediment characteristics are illustrated in Fig. 2 suppl. data, which also indicates much lower bio-turbation on the W side. Filters for POC and PN analysis were unfreezed and dried at 40 °C. HCl (1N, 100-200 µl), was added to one half of each filter, in order to remove inorganic carbon, and dried again. POC and PN content was determined using an Elemental Analyzer (NA2100 Protein) calibrated against an elemental CHNS standard (LECO).

Primary production budget calculations

The daily net and gross primary production (P_{net} and P_{gross}), as well as respiration (R) of sedimentary microphytobenthos and turf algae were calculated using the results of the short term incubations (maximum rates around noon, see above) and the start and end time points of photosynthetic activity by corals obtained via the 2nd order polynomial curves (see above) to conduct likewise quadratic extrapolations. P_{gross} = P_{net} + R, for each incubation, all values in (µg cm⁻² h⁻¹). For investigated primary producers, integral area of the daily curves was computed using Mathematica 5.2 (Wolfram Research, Inc. 2005), resulting in an actual net and gross primary production (d⁻¹). To gain daily primary production and respiration per reef and benthic community area, respectively, the daily actual rates were then multiplied with the relative proportion of each primary producer at each site; then a 2D to 3D conversion for turf algae, i.e. the surface area on which the turf algae grew, and corals, i.e. coral surface area, was applied. This factor was determined for turf algae by relating the area measured on photos (using ImageJ, 2-D area) to the area measured via geometry (see above, 3-D); actual rock surface colonized by turf algae/projected benthic surface = 1.5. For corals the in-situ conversion factors after Alcalá and Vogt (1997) were used. A coral 2D to 3D factor for each site was estimated using the mean of all factors for each coral growth form (branching, massive, encrusting or foliose), weighted by the percentage cover of each coral growth form found. Gross photosynthesis is given over the period of photosynthetic active radiation per day (12 h, see also above) and respiration for 24 h (calculated from dark incubations).

Statistical analyses

Light, temperature and water currents were compared between E and W sides using a two-tailed T-test, adapted to unequal variances (Ruxton 2006); for all other parameters, a two-tailed U-test after Wilcoxon, Mann and Whitney was applied, either to compare E or W, or shallow and deep sites. To test for correlations of the DTRs with other parameters, the non-parametric Spearman correlation was used, setting the DTRs as ordinal ranks.

Results

Environmental background conditions on E and W

At Koh Miang, temperature was significantly lower on W and in the deep in general (Table 1) when compared to E and shallow (both: t-Test, $p \ll 0.001$). Therefore, mean daily temperature ranges (DTRs, daily max – min), as a measure for the impact of Large Amplitude Internal Waves (LAIW), were less pronounced at E shallow and increased from E deep to W shallow, to W deep (Table 1), where LAIW are most pronounced. Temperature loggers deployed at three other islands, at 16 sites (Islands (# 2, # 7 and # 8 south and # 8 north; each E and W, shallow and deep) revealed similar variations (Table 1 suppl. data) with the highest DTRs at island # 2. An all-site average (including island # 4) yielded in DTRs of 0.9 ± 0.06 °C at E shallow, 1.34 ± 0.13 °C at E deep, 2.19 ± 0.28 °C at W shallow, and 3.7 ± 0.14 °C at W deep.

Table 1: Environmental characteristics. Measured water parameters were temperature, light intensity, current velocity, nutrient concentration; measured sediment parameters were grain size fractions, carbonate content, water content, nutrient concentration, POC, PN; all were determined at Koh Miang.

<i>Parameter</i>	<i>E shallow</i>	<i>E deep</i>	<i>W shallow</i>	<i>W deep</i>
Water				
<i>Temperature (C°, modal)</i>	28.84	28.59	28.82	28.77
<i>Temperature (C°, mean±SE)</i>	28.89 ± 0.0013	28.66 ± 0.0015	28.75 ± 0.0018	28.23 ± 0.0035
<i>DTR, daily max-min (C°, mean±SE)</i>	1.03 ± 0.07	1.5 ± 0.10	2.44 ± 0.16	3.94 ± 0.16
<i>PAR 11:00-14:00h (µmol quanta m⁻² s⁻¹, mean±SE)</i>	103.2 ± 0.48	36.2 ± 0.18	76.0 ± 0.59	23.7 ± 0.17
Current velocity (m s ⁻¹ , mean±SE)		0.078 ± 0.0002		0.1068 ± 0.0003
Ammonium, water (µmol, mean±SE)	1.04 ± 0.094	1.19 ± 0.11	1.14 ± 0.12	1.45 ± 0.27
Nitrate + nitrite, water (µmol, mean±SE)	0.42 ± 0.062	0.57 ± 0.072	0.70 ± 0.14	1.19 ± 0.32
Phosphate, water (µmol, mean±SE)	0.22 ± 0.018	0.25 ± 0.013	0.26 ± 0.0092	0.37 ± 0.12
Sediment characteristics				
Clay and silt (% , pooled samples)	4.33	3.85	4.03	0.29
Fine sand (% , pooled samples)	25.25	26.5	1.57	16.23
Medium sand (% , pooled samples)	42.59	46.41	47.42	35.92
Coarse sand (% , pooled samples)	18.03	20.21	41.02	33.86
Carbonate content, (% , pooled samples)	86.7	83.4	72.6	78
Water content, (% , pooled samples)	35.2	34.7	38.7	37.9
Ammonium (pore water, mean±SE)	8.3 ± 2.47	11.09 ± 3.01	10.91 ± 1.49	16.15 ± 1.56
Nitrate + nitrite (pore water, mean±SE)	0.82 ± 0.24	2.77 ± 0.81	1.59 ± 0.53	7.84 ± 1.58
Phosphate (pore water, mean±SE)	3.18 ± 0.48	3.89 ± 0.53	3.35 ± 0.92	4.98 ± 0.72
POC content (µg mg ⁻¹ pore water, mean±SE)	2.10 ± 0.072	2.06 ± 0.075	2.33 ± 0.067	2.21 ± 0.068
PN content (µg mg ⁻¹ pore water, mean±SE)	0.13 ± 0.0071	0.057 ± 0.0096	0.18 ± 0.025	0.11 ± 0.017

Light intensity was significantly lower on W compared to E in general (for each depth, t-Test, $p \ll 0.001$) and revealed $\sim 30\%$ lower values around noon (11:00-14:00 h, W shallow: 26.4 %, W deep: 34.5 %, Table 1). The diurnal cycles of light (Fig. 3 suppl. data) clearly exhibited the lower light regime for the W side. Furthermore, a slightly shifted course of sun light between E and W, caused by a shading effect of the island itself, could be observed.

Overall current velocities were significantly higher on the W compared to the E side (t-Test, $p \ll 0.001$), reflecting an enhanced water exchange due to the incoming LAIW.

Nutrients in the water column, nitrate pooled together with nitrite (nitrate + nitrite) and phosphate, showed an increase with LAIW impact (DTRs, Table 1 and Table 2), but Ammonium on the other hand did not. Pore water nutrients yielded in a different result as again nitrate + nitrite, but also ammonium was correlated with LAIW impact (Table 1 and Table 2), whereas phosphate was not.

Particulate organic carbon (POC) and total particulate nitrogen (PN) amounts within the sediment (Table 1, as $\mu\text{g mg}^{-1}$ sediment), were significantly higher on the W side (both depths pooled together: U-test, $p < 0.05$) with an increase of 8 % and 43 % for POC and PN concentrations, respectively.

Grain size of the sediments showed different characteristics for each site (Table 1). Almost no clay and silt was found for W deep and little fine sand for both W sites (fewest on W shallow) contrasting finer sediments on the E. Therefore, more coarse sand could be found on the W sites, due to the elevated current regime. Accordingly water content within the sediments was higher for the W sites than for E. Carbonate content was $\sim 10\%$ lower on the W side (Table 1) compared to E.

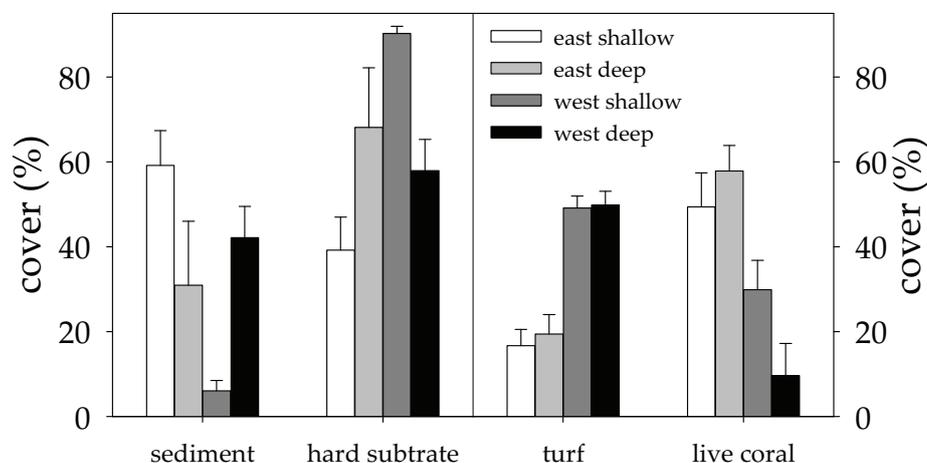


Figure 1: Benthic cover. Line transects on benthic cover at Koh Miang (E shallow, E deep, W shallow, W deep) in %; live coral cover as a fraction of hard substrate.

Benthic community composition

A summary of the results obtained by the line-intercept transects is given in Figure 1. Sediment cover was highest at E shallow due to extensive sandy patches, medium at the deep sites and lowest at W shallow. Hard substrate (live coral cover, dead coral cover and rock) on the W side was mainly determined by the presence of rocks. Accordingly, the highest rock cover (granite boulders) was found on W shallow, few in W deep and 0 % at both E sites. W sites showed in general enhanced turf algae cover on any substrate and reduced coral cover as a fraction of hard substrate compared to E sites. The main primary producers, according to percent cover, were the microphytobenthos (the sediment associated micro-algae), turf algae and corals.

Growth rate of turf algae and pigment content of primary producers

Algae growth rates as chl-a increase, displayed in Figure 2, were higher on the W side when compared to E (U-test, both depths pooled together per side: $p > 0.0001$). Higher growth rates mostly occurred in deeper water, nevertheless highest individual values were found for two algae tiles on W shallow (up to $0.025 \mu\text{g Chl a cm}^{-2} \text{d}^{-1}$). Growth rates were highly correlated with LAIW impact despite lowest values found on E deep (and not E shallow, presumably evoked by higher light levels).

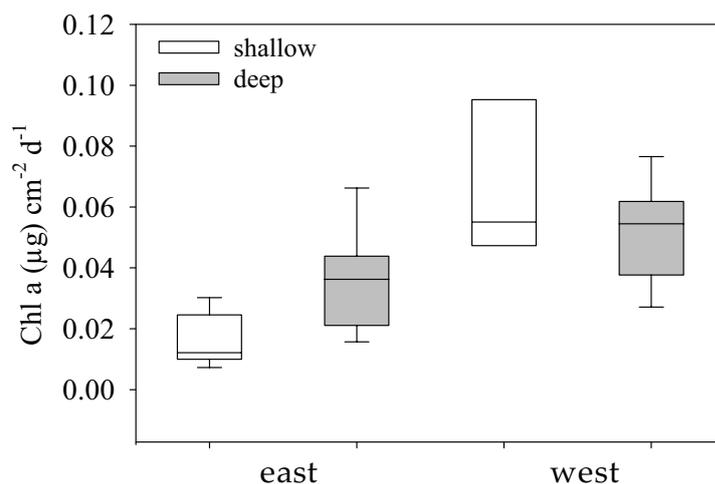


Figure 2: Growth rates of turf algae. Microscopic slides (algae tiles) were deployed in-situ at all investigation sites at Koh Miang and displaced in random order after 1-3 weeks (E shallow, n:15; E deep, n:15; W shallow, n:10; W deep, n:17); algal growth was determined as chl-a ($\mu\text{g cm}^{-2} \text{d}^{-1}$).

The sediment showed similar chl-a values for all sites (Fig. 3 left panel, U-test, $p \gg 0.05$), but pheophytin was coupled to LAIW impact (Fig. 3 right panel, Table 2) and was therefore significantly higher on the W side (U-test, both depths pooled together per side: $p < 0.02$). A similar pattern was observed for the turf algae on hard substrate; with no difference in chl-a content for either site (Fig. 4 left panel, U-test, $p \gg 0.05$), an increase of pheophytin with rising LAIW impact (Fig. 4 right panel, Table 2) and accordingly significant more pheophytin on the W side in general (U-test, both depths pooled together per side: $p < 0.02$).

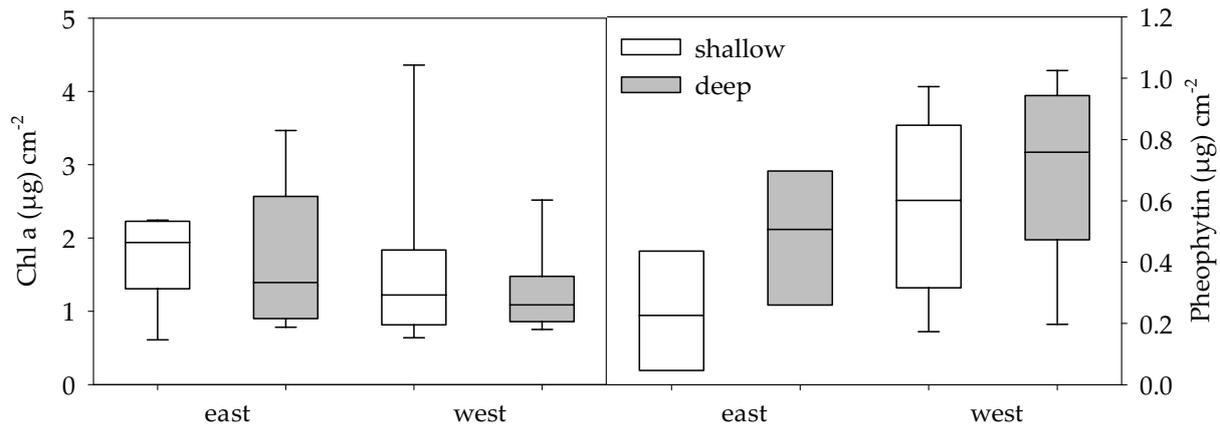


Figure 3: Pigment content of sediment. Chl-a and Pheophytin content of sediment from all investigation sites at Koh Miang, normalised to sediment surface area ($\mu\text{g cm}^{-2}$).

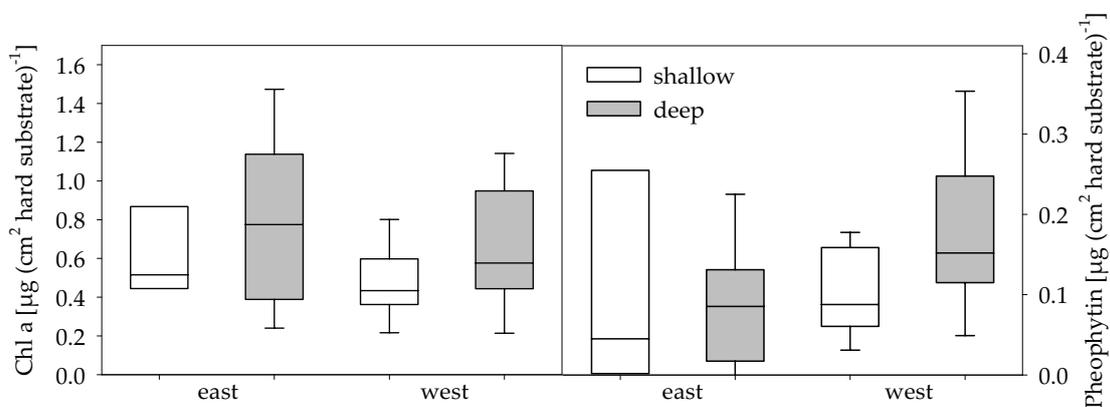


Figure 4: Pigment content of turf algae. Chl-a and Pheophytin content of turf algae from all investigation sites at Koh Miang, normalised to growth area [$\mu\text{g (cm}^2 \text{ hard substrate)}^{-1}$].

Coral pigments as chl-a rose with increasing LAIW impact (Table 2) and exhibited lowest values for E shallow, medium values for E deep and W shallow and highest values for W deep (Fig. 5). Chl-a content was higher on W (both depth pooled together per side, U-test, $p < 0.02$) and at deep sites (both sides pooled together per depth: U-test, $p < 0.02$), compared to E and shallow sites.

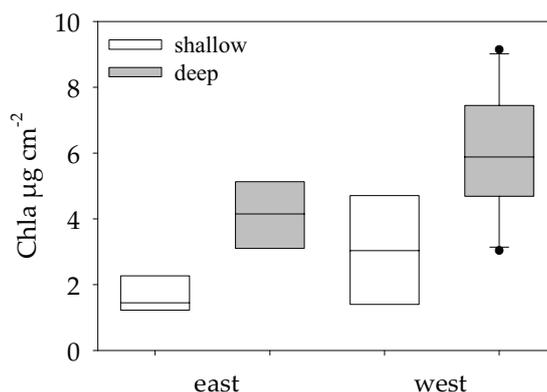


Figure 5: Pigment content of corals. Chl-a content of *P. lutea* from all investigation sites at Koh Miang, normalised to coral surface area ($\mu\text{g cm}^{-2}$).

Table 2: Correlations to daily temperature ranges (DTRs). Various measures (see also results) were correlated to DTRs at Koh Miang.

<i>Daily temperature range (DTR) versus</i>		<i>level of significance</i>	<i>p</i>	<i>Rsp</i>
Nitrate + nitrite	water (μmol)	**	0.003	0.453
Phosphate	water (μmol)	(*)	0.068	0.295
Ammonium	water (μmol)		0.454	0.122
Nitrate + nitrite	pore water (μmol)	**	0.001	0.759
Phosphate	pore water (μmol)		0.113	0.412
Ammonium	pore water (μmol)	*	0.02	0.613
Algae tiles	growth rate ($\text{Chl a cm}^{-2} \text{d}^{-1}$)	**	< 0.001	0.698
Sediment	chl a ($\mu\text{g cm}^{-2}$)		0.115	-0.257
Sediment	pheophytin ($\mu\text{g cm}^{-2}$)	**	0.006	0.457
Algae	chl a ($\mu\text{g cm}^{-2}$)		0.73	-0.051
Algae	pheophytin ($\mu\text{g cm}^{-2}$)	*	0.013	0.368
Coral	chl a ($\mu\text{g cm}^{-2}$)	**	<0.001	0.657
Sediment	net photosynthesis ($\text{O}_2 [\mu\text{g cm}^{-2} \text{min}^{-1}]$)	**	<0.001	-0.456
Sediment	gross photosynthesis ($\text{O}_2 [\mu\text{g cm}^{-2} \text{min}^{-1}]$)	**	<0.001	-0.471
Sediment	respiration ($\text{O}_2 [\mu\text{g cm}^{-2} \text{min}^{-1}]$)		0.198	0.165
Algae	net photosynthesis ($\text{O}_2 [\mu\text{g cm}^{-2} \text{min}^{-1}]$)	(*)	0.078	0.275
Algae	gross photosynthesis ($\text{O}_2 [\mu\text{g cm}^{-2} \text{min}^{-1}]$)		0.596	-0.084
Algae	respiration ($\text{O}_2 [\mu\text{g cm}^{-2} \text{min}^{-1}]$)	**	0.002	0.444
Corals (max. rate)	net photosynthesis ($\text{O}_2 [\mu\text{g cm}^{-2} \text{min}^{-1}]$)		0.379	0.211
Corals (max. rate)	gross photosynthesis ($\text{O}_2 [\mu\text{g cm}^{-2} \text{min}^{-1}]$)		0.97	0.01
Corals (max. rate)	respiration ($\text{O}_2 [\mu\text{g cm}^{-2} \text{min}^{-1}]$)	**	<0.001	0.528
Sediment	net photosynthesis ($\text{O}_2 [\mu\text{g cm}^{-2} \text{min}^{-1}]$ Chl a [μg^{-1}])	*	0.015	-0.307
Sediment	gross photosynthesis ($\text{O}_2 [\mu\text{g cm}^{-2} \text{min}^{-1}]$ Chl a [μg^{-1}])	*	0.022	-0.289
Sediment	respiration ($\text{O}_2 [\mu\text{g cm}^{-2} \text{min}^{-1}]$ Chl a [μg^{-1}])		0.763	0.033
Algae	net photosynthesis ($\text{O}_2 [\mu\text{g cm}^{-2} \text{min}^{-1}]$ Chl a [μg^{-1}])		0.11	0.242
Algae	gross photosynthesis ($\text{O}_2 [\mu\text{g cm}^{-2} \text{min}^{-1}]$ Chl a [μg^{-1}])		0.343	-0.146
Algae	respiration ($\text{O}_2 [\mu\text{g cm}^{-2} \text{min}^{-1}]$ Chl a [μg^{-1}])	**	0.001	0.466
Corals (max. rate)	net photosynthesis ($\text{O}_2 [\mu\text{g cm}^{-2} \text{min}^{-1}]$ Chl a [μg^{-1}])	**	<0.001	-0.792
Corals (max. rate)	gross Photosynthesis ($\text{O}_2 [\mu\text{g cm}^{-2} \text{min}^{-1}]$ Chl a [μg^{-1}])	**	<0.002	-0.745
Corals (max. rate)	respiration ($\text{O}_2 [\mu\text{g cm}^{-2} \text{min}^{-1}]$ Chl a [μg^{-1}])	**	<0.003	0.861

Primary production

Sedimentary microphytobenthos showed higher net photosynthetic rates in the shallow, which were accompanied by higher respiration rates compared to deep (Fig. 6 left panel). Nevertheless, respiration was reduced on the W side in general (Fig. 6 left panel, U-test, both depth pooled together per side, $p < 0.02$). Net and gross photosynthetic rates as well as both photosynthetic rates related to pigment content (chl-a^{-1}), were negatively correlated with LAIW impact (Table 2).

Turf algae, by contrast, showed a positive coupling of net photosynthetic and respiration rates to LAIW impact (Fig. 6 right panel), also when relating both rates to pigment content (chl-a^{-1} , Table 2). Furthermore, respiration rates were significantly higher on the W side (U-test, both water depths pooled per side: $p = 0.015$). Gross photosynthetic rates were constant, irrespective of side, depth or LAIW impact.

Corals on the shallow W site were slightly more productive than the ones on the respective E side, whereas in deeper water there was no difference, in spite of lower light intensities on the W side (Fig. 7). Respiration rates were similar, except for E shallow with twice the value compared to the other sites (Fig. 4 suppl. data). Chl-a specific net photosynthetic rates were much lower for the W side (either depth, Fig. 5 suppl. data), reflecting the higher chl-a content. The photosynthetic rates of corals around noon (net and gross, 11 - 14 h) related to pigment content (chl-a^{-1}) were negative coupled with the LAIW impact, suggesting a more costly photosynthesis on the W side (Table 2).

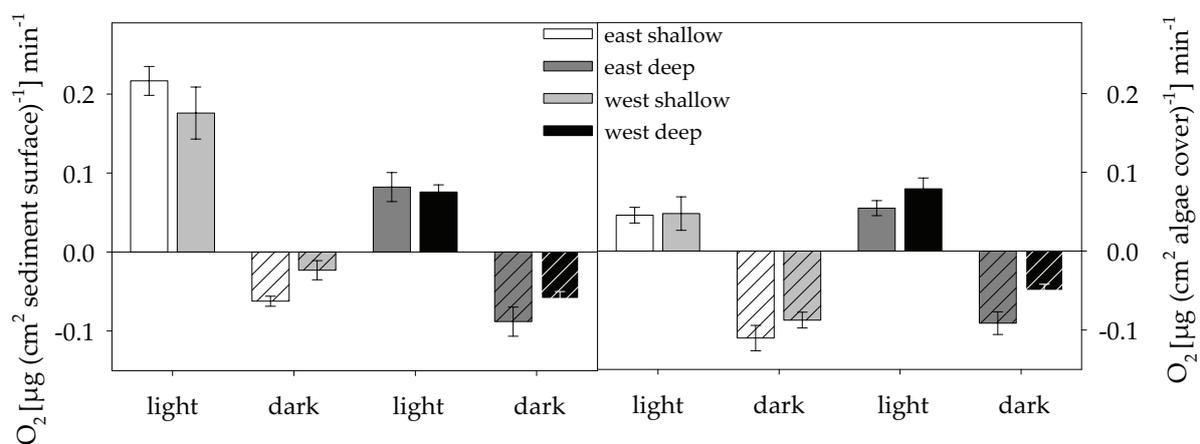


Figure 6: Oxygen fluxes of sediment and turf algae. Sediment and turf algae were incubated in a water bath on land to determine oxygen fluxes (net photosynthesis and respiration); values were normalised to surface area of sediment or turf algae growth substrate ($\mu\text{g cm}^{-2} \text{min}^{-1}$).

Primary production budgets

Actual net and gross primary production rates, i.e. rates attributed to photosynthetic active surface area d^{-1} , showed highest values for the sedimentary microphytobenthos, followed by turf algae, whereas corals only achieved a relatively low productivity (Table 3). The sediments showed by far the highest photosynthetic activity on E and W shallow, with almost 50 % higher photosynthetic rates than algae or corals at any site. Taking into account the different proportions of benthic cover and the conversion factors (2D to 3D) for each site, the sediments were still the major primary producers on the E side, especially in the shallow (Table 3). At the W sites, on contrast, the turf algae were the major primary producers, only then followed by the sediments (Table 3). Corals contributed a relatively small amount to the primary production on W deep, but a rather considerable quantity on all other sites.

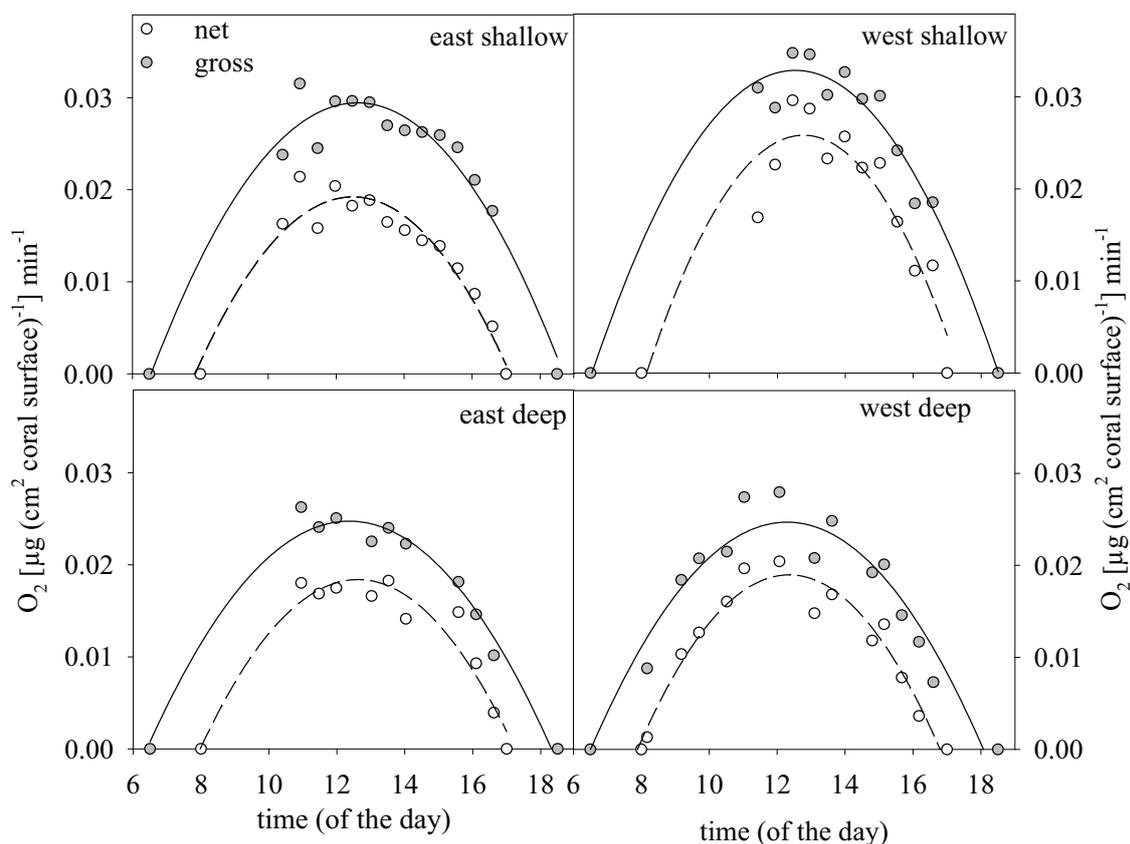


Figure 7: Oxygen fluxes of corals. Incubations of *P. lutea* in-situ with an automated respirometer during one day at each site at Koh Miang to determine oxygen fluxes, i.e. net and gross photosynthesis, values were normalised to surface area ($\mu\text{g cm}^{-2}$).

Discussion

This study revealed that turf algae benefited mostly from the LAIW nutrient input, and budget calculations showed that these organisms were also the quantitatively most important primary producers on the exposed W side. However, although growth, net photosynthesis and respiration rates of turf algae were higher on the LAIW-impacted side, the sedimentary microphytobenthos experienced reduced overall productivity on the W side. LAIW impact did obviously not affect primary production rates of corals, but supported investment into pigmentation as reflected by the higher chlorophyll a tissue content.

Primary production rates

Even though it is reported that the sediment associated microalgae are capable to effectively take up nutrients from pore water and the water column (Miyajima et al. 2001), no fertilising effect on the primary production of the sedimentary microphytobenthos could be observed at the W side. Indeed, net and gross photosynthetic rates were reduced - and correspondingly respiration showed lower values - when compared to the E side, despite the fact that similar chl-a contents were measured in sediments collected from both sides. This generally reduced sedimentary activity on the W side may be crucial for the overall benthic metabolism as the permeable reef sediments are usually places of high productivity and important places for recycling (Hatcher 1990, Rasheed et al. 2004, Wild et al. 2005). Higher concentrations of organic material and inorganic nutrients (ammonium and nitrate + nitrite) in sedimentary pore water samples from the W side may be due to a higher particle load in the water column, detectable as an increased turbidity (i.e. reduced light levels), and may be further enhanced by N-fixing cyanobacteria, which can reach higher abundances under enhanced nutrient levels (Miller et al. 1999). Roder et al. (submitted) demonstrated that although there were no enhanced plankton abundances and suspended particulate organic matter (POM) concentrations in waters at the W side, the elevated water currents contributed to a 30 % higher plankton and POM supply to the W ecosystem compared to E.

Table 3: Primary production budget. A primary production budget was estimated using actual gross photosynthetic rates (actual PP [$\mu\text{g oxygen cm}^{-2} 12\text{h}^{-1}$]) weighted by transect data (% cover) and conversion factors (2D to 3D, sediment: none; algae: own, see material and methods; corals: Alcalá and Vogt 1997).

<i>affiliation</i>	<i>compartement</i>	<i>Actual PP net</i> ($\mu\text{g O}_2 \text{ cm}^{-2} 12\text{h}^{-1}$)	<i>Actual PP gross</i> ($\mu\text{g O}_2 \text{ cm}^{-2} 12\text{h}^{-1}$)	<i>3D factors</i>	<i>cover</i> (%)	<i>PP gross</i> ($\text{mg O}_2 \text{ m}^{-2} 12\text{h}^{-1}$)	<i>respiration</i> ($\text{mg O}_2 \text{ m}^{-2} 24\text{h}^{-1}$)
E shallow	Sediment	78.1	133.8	1	59.1	791.41	-529.93
	Algae	17.8	72.0	1.5	16.6	218.89	-483.16
	Corals	7.8	13.9	4.47	18.9	118.00	-134.06
E deep	Sediment	35.2	92.9	1	30.8	286.73	-427.87
	Algae	21.2	66.5	1.5	19.4	278.07	-590.56
	Corals	7.0	11.5	2.97	40.3	137.16	-120.55
W shallow	Sediment	68.0	101.6	1	6.1	61.58	-19.82
	Algae	27.4	79.3	1.5	49.2	753.29	-1196.74
	Corals	10.6	15.7	3.24	26.9	133.21	-91.45
W deep	Sediment	29.4	70.3	1	42.6	299.85	-372.51
	Algae	31.0	66.5	1.5	50.3	521.91	-595.14
	Corals	7.0	11.4	3.45	6.1	24.02	-21.59

These higher water currents are also reflected in the coarser grain size of the sediments at the W side. Although sedimentary grain size usually correlates negatively with organic matter content, and positively with permeability and oxygen penetration (Rusch et al. 2000, Huettel & Webster 2001, Huettel et al. 2003, Rasheed et al. 2003, Rusch et al. 2006), incompletely degraded organic matter accumulated within the sediments, as evidenced by high concentrations of pheophytin. Permeable (reef) sediments are major places for the recycling of organic material (Hansen et al. 1992, Rasheed et al. 2006), and their efficiency relies on the microbial diversity and abundance, which in turn is determined by the sediment properties and mineralogy (Wild et al. 2005, Wild et al. 2006). Therefore, the reduced sedimentary metabolism on the W side may be partly explained by different sediment characteristics. The lower carbonate content and the more coarse grain size may lead to a reduced surface area for microbial colonisation (Wild et al. 2005, Wild et al. 2006). This may imply further consequences for the sedimentary meiofauna and the associated intensity of bioturbation (Schlacher 1991), which was less pronounced on the W side (pers. observations, also visible at Fig. 2 suppl. data).

Turf algae are likewise important primary producers within the benthic reef community (Borowitzka et al. 1978, Carpenter 1985, Hatcher 1990), and their photosynthesis may be enhanced under elevated nutrient levels (Williams and Carpenter 1988), but related studies are rare. Still, as net photosynthesis and respiration co-varied in response to LAIW impact, gross photosynthesis of turf algae remained constant. A study by Klumpp and McKinnon (1992)

revealed an inverse relationship of turf algae biomass and primary productivity, possibly due to self-shading. The same relation may apply here as the turf algae obviously benefit from the LAIW caused nutrient input in terms of enhanced growth rates, further supported by a higher observed cover, but they showed similar gross photosynthetic rates on E and W.

A dense algal turf is not uncommon in coral reefs and may constitute up to 80 % of total benthic cover (Klumpp and McKinnon 1992). The growth of these algae is limited by nutrient availability, especially inorganic nitrogen, but also by grazing (Hatcher and Larkum 1983, William and Carpenter 1988, Smith et al. 2001). Although grazers were present on both sides, no apparent grazing traces could be observed on any of the algae tiles (E or W). Some of the turf algae on the W side may also have died or were fading as indicated by their high pheophytin content.

For corals (here *Porites lutea*), the two environmental factors, reduced light intensities and enhanced nutrient concentrations may have balanced each other, because the massive *Porites lutea* at the W side could sustain its photosynthetic rates when compared to specimens on the E. On W shallow, *P. lutea* may have benefited particularly from the elevated nutrient availability and relatively high light intensities, as corals revealed the (slightly) highest photosynthesis rate compared to all other sites. Corals on the W side exhibited a higher investment into pigmentation, likely facilitated by the enhanced nutrient levels (Muscatine et al. 1989, Dubinsky et al. 1990) enabling them to maintain high productivity under reduced light intensities., which suggests efficient use of available light intensities (Dubinsky et al. 1990, Titlyanov 1991, Iglesias-Prieto and Trench 1994). This implies a high cellular investment by the zooxanthellae as increased chl-a contents are more likely caused by elevated chl-a concentrations than by multiplication of zooxanthellae within the host tissue, because zooxanthellae abundances are reported to stay relatively constant within the range of nutrient concentrations and light intensities measured in the present study (see review by Leletkin 2000). This is further supported by similar zooxanthellae abundances in the tissue of *P. lutea* irrespective of side or water depth (own unpublished data, two-tailed U-test, $p \gg 0.05$).

Net and gross primary production of the investigated corals were similar on all sites, which is in accordance with the study by Titlyanov (1991), who found a stable level of corals' primary production in a wide range of light intensities (i.e. water depths), mainly caused by reduced respiration under lower light levels. Still, *P. lutea*'s respiration rates were relatively similar, despite the ones at E shallow, where elevated respiration rates may reflect an enhanced metabolism, due to a high-light history (Edmunds and Davies 1988, Hoogenboom et al.

2006). Generally, a surplus of solar energy, which cannot be used for photochemical energy conversion, is mainly dissipated as heat, but causes also reversible photodamage, which in turn requires enzymatic reparation of photosystem II and consequently raises respiration rates (Edmunds and Davies 1988, Hoegh-Guldberg and Jones 1999, Gorbunov et al. 2001).

Primary production budget

A primary production budget per reef area for all sites was estimated by combining incubation with transect data. It should be noted that no light respiration could be measured, which may be considerably higher than the dark respiration (Titlyanov 1991, Anthony and Hoegh-Guldberg 2003). Therefore, gross primary production may be underestimated and may explain P:R ratios lower than 1 for each site.

Both sediments and algae exceeded the productivity of corals, which was mainly caused by a higher absolute cover, but also by an elevated photosynthetic activity. Corals contributed a rather small amount to primary production, especially at W deep. This was supported by a study of Rogers and Salesky (1981), which revealed turf algae as more photosynthetically productive than *Acropora palmata*. The total gross primary production budgets for each site yielded in similar results – although somewhat higher in the shallow – leading to the conclusion that the overall gross primary production was relatively independent of the side, but the contribution of each compartment varied under the different environmental conditions. Although different incubation approaches were applied for corals in contrast to sediment and turf algae, oxygen fluxes were consistent with published rates from other reef areas, however at the lower end for turf algae and corals (sediment: Hansen et al. 1992, Clavier and Garrigue 1999, Wild et al. 2005; turf algae: Williams and Carpenter 1988, Carpenter et al. 1991, Klumpp and McKinnon 1992; corals: Falkowski and Dubinsky 1981, Hatcher 1990, Titlyanow 1991). Still, metabolic characteristics of *P. lutea* may not be valid for all scleractinian coral species. According to Ralph et al. (2002), who investigated photosynthetic efficiency and productivity of six coral species, a massive species (*Cyphastrea serialia*) and corals of the genus *Porites* (*P. cylindrica*) showed lowest values.

Ecological implications and outlook

Elevated nutrient levels are usually assumed to be rather unfavourable for corals in contrast to algae and therefore play an important role during phase shifts from coral- towards algae-dominated reef ecosystems (Hughes 1994, Lapointe 1997, Pandolfi et al. 2005). Turf algae were the dominant algae at Koh Miang and there is evidence that they may not be efficient

competitors for corals, even under eutrophic conditions (Mc Cook 1999, Jompa and McCook 2003), particularly not for the massive growing genus *Porites* (McCook 2001). However, it must be considered that – as in most studies – the species composition of turf algae was not determined and may change considerably over time or space. Therefore, on the one hand coral cover was reduced on the W side and some coral species like *Stylophora pistillata* may suffer under enhanced nutrient levels (Ferrier-Pages et al. 2000), but on the other hand, *P. lutea* may also benefit from the elevated nutrient levels, maintaining high photosynthetic performance under low light levels.

Huge *Porites lutea* colonies in-situ were regularly observed covered with mucus sheets to get rid of the sedimentation, especially on the W side, and *Porites* sp. is known to be even abundant in areas with high particle load (Morelock et al. 1983, Cortes and Risk 1984). But generally, sedimentation of corals can cause a decrease in photosynthesis and respiration rates as well as a decline of several other metabolic features (Rogers et al. 1990, Philipp and Fabricius 2003). In contrast, the higher water currents on the W side may increase photosynthesis of the investigated organisms in-situ as indicated by the studies of Carpenter et al. (1991) for turf algae, Cook and Røy (2006) for sedimentary microphytobenthos, and Dennison and Barnes (1988) for corals.

The Similan Islands as a study site offer a unique opportunity to investigate coral reef ecosystem functioning and resilience in response to different environmental conditions. This is particularly important in order to understand potential consequences of global climate change on the reef ecosystem level. An alteration in coral reef benthic community composition as reported from many reef locations world-wide (Hughes 1994, Bellwood et al. 2006, Hoegh-Guldberg et al. 2007, Hughes et al. 2007) also potentially implies changes in ecosystem-wide primary productivity. The present study showed that this does not have to be the case, as it revealed high plasticity of benthic primary production under different environmental factors. However, further investigations on benthic primary production, as fundament of the trophic cascade, are needed, particularly with focus on changing coral reef ecosystems.

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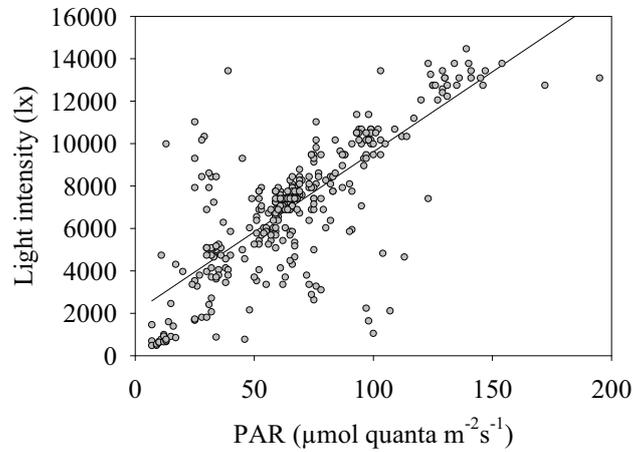
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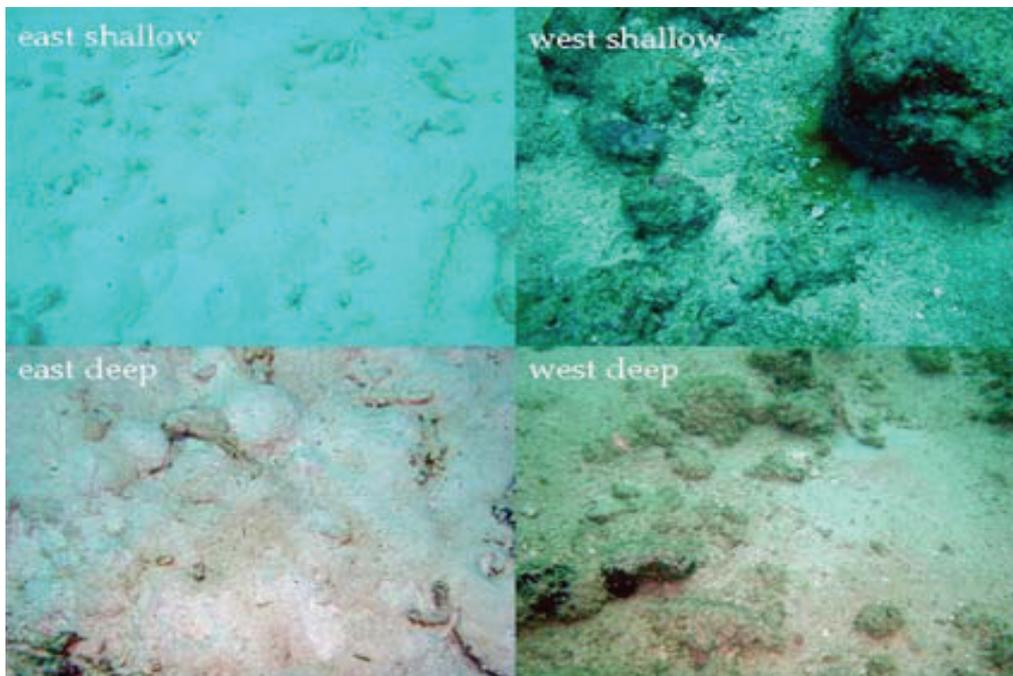
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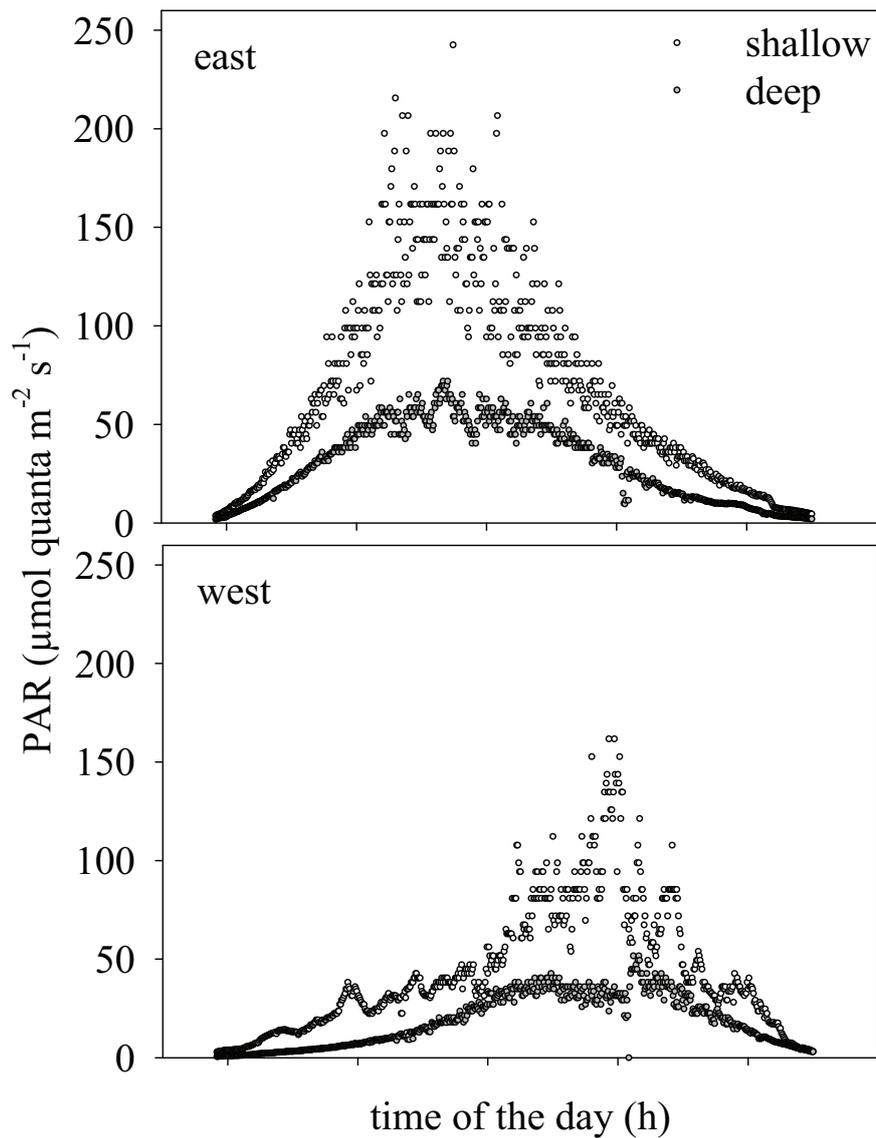
Supplemental data Chapter IV



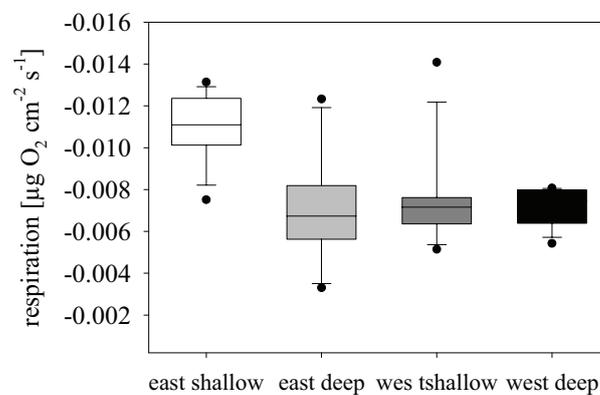
Supplemental figure 1: Light (lx) - PAR correlation. A light intensity (I, lx) to photosynthetic active radiation (PAR) correlation was obtained by comparing pendant loggers and the light sensor of the Diving PAM during 6 days (4 shallow and 2 deep); $R^2: 0.52$, $I \text{ (lx)} = 76.684 * \text{PAR} \text{ (}\mu\text{mol quanta m}^{-2} \text{s}^{-1}\text{)}$.



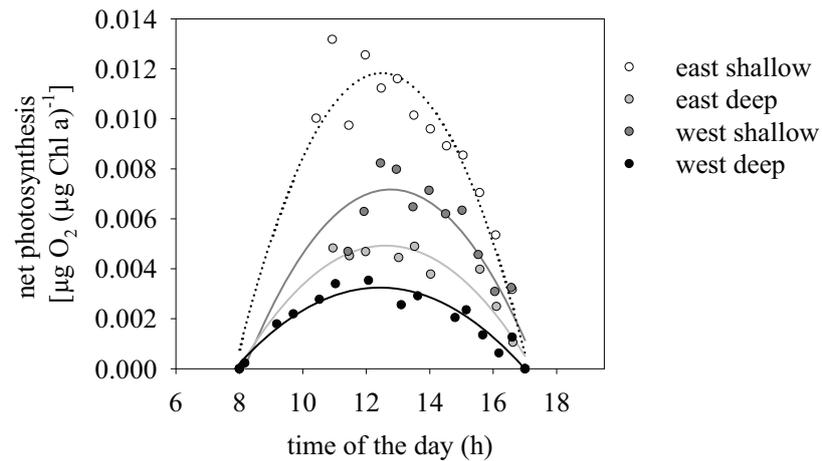
Supplemental figure 2: Visual sediment characteristics. Exemplary photos of sediment surfaces at all investigation sites at Koh Miang (~ 30cm above bottom).



Supplemental figure 3: Diurnal cycles of PAR. The diurnal cycles of ambient light intensity (I_x) during in-situ incubation of *P. lutea* at each of the incubation days were converted into PAR (photosynthetic active radiation [$\mu\text{mol quanta m}^{-2} \text{s}^{-1}$]) using the correlation from Fig. 1 suppl. data.



Supplemental figure 4: Oxygen fluxes of corals. Incubations of *P. lutea* in-situ with an automated respirometer during one daily cycle at each investigation site to determine oxygen fluxes, i.e. mean respiration rates.



Supplemental figure 5: Oxygen fluxes of corals related to chl-a content. Incubations of *P. lutea* in-situ with a new automated device during one daily cycle at each investigation site to determine oxygen fluxes, i.e. net photosynthesis, values were normalised to chl-a content ($\mu\text{g O}_2 [\mu\text{g chl-a}]^{-1}$).

Supplemental table 1: Daily temperature variation ranges. DTRs as max – min (mean \pm SE) at four of the Similan Islands (# 4, #2, #7, #8 south, # 8 north), each at four sites: E shallow, E deep, W shallow, W deep; n.a. values were not available.

<i>Site</i>	<i>Koh #4</i>	<i>Koh #2</i>	<i>Koh #7</i>	<i>Koh #8 south</i>	<i>Koh #8 north</i>	<i>Overall mean</i>
			max-min ($^{\circ}\text{C}$)			
E shallow	1.03 \pm 0.07	0.75 \pm 0.06	0.94 \pm 0.04	0.88 \pm 0.46	n.a.	0.9 \pm 0.06
E deep	1.50 \pm 0.10	1.61 \pm 0.11	1.04 \pm 0.07	n.a.	1.20 \pm 0.07	1.34 \pm 0.13
W shallow	2.44 \pm 0.16	3.06 \pm 0.18	2.18 \pm 0.18	1.33 \pm 0.11	1.95 \pm 0.15	2.19 \pm 0.28
W deep	3.94 \pm 0.16	3.98 \pm 0.17	3.84 \pm 0.16	3.22 \pm 0.18	3.52 \pm 0.18	3.70 \pm 0.14

- Chapter V -

**Coral community and physico-chemical
characteristics in response to Large Amplitude
Internal Waves**

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Abstract

The Similan Islands (Thailand), Andaman Sea, feature an unusual coral reef distribution: reefs flourish on the sheltered shelf sides east of the islands (E) whereas the ocean-facing west (W) sides lack a true reef framework. Here, we show that the striking differences in reef development, occurring at spatial scales of only tens to hundreds of metres, are consistent among the islands and related to Large Amplitude Internal Waves (LAIW). Two year temperature records show that LAIW have their strongest impact on the deeper parts of the W Similans where they may cause frequent (several events per hour) and abrupt (up to 10°C, in the order of minutes) drops in temperature with peak activity during the NE monsoon (January through April). Physical and chemical oceanographic analyses show that LAIW advect deep cold, nutrient-rich, suboxic and low-pH waters (0.6 pH units below ambient) into shallow near shore areas, and provide a dramatically altered growth environment for W slope benthic communities. In contrast to E reefs, which are dominated by a low number of frame-building species, the W slopes harbour only loose, however more diverse communities of scattered corals growing directly on the granite basement, often with modified phenotypes (broadened bases, reduced ramification). LAIW, which are ubiquitous in SE Asia and beyond, provide a so far understudied source of physico-chemical-biological disturbance operating at different spatio-temporal scales compared to the well-known physical effects of storms. In the light of the wide range and complex nature of environmental variability involved, LAIW may hold a clue to coral resilience in an era of global change.

Key words

Large Amplitude Internal Waves - benthic-pelagic coupling - coral community - Similan Islands - Andaman Sea – solitons

Introduction

Coral reefs are highly productive benthic ecosystems thriving in clear, warm, nutrient poor tropical waters (Buddemeier & Kinzie 1976, Goreau et al. 1979, Veron 2000, Birkeland 1997, Hoegh-Guldberg 1999). Many reefs, however, are subjected to natural disturbances which affect light,

temperature, nutrient and aragonite saturation state on various scales, e.g. monsoon driven rainfalls, mixing by storms, and upwelling of cold deep waters (Buddemeier & Kinzie 1976, Charuchinda & Hylleberg 1984, Leichter et al. 1996, Lesser et al. 2009). Tidally recurring internal waves have been shown to play a potentially important role in the cross-shore exchange of larvae, nutrients and particulate food (Shanks 1983, Pineda 1991) and can be a source of nutrients for coral reefs (Leichter et al. 1998, 2003). However, Large Amplitude Internal Waves (LAIW) causing temperature drops of up to 6 – 9 °C (Wolanski & Delesalle 1995, Sheppard 2009), could be a mixed blessing, where the positive effects of an enhanced exchange of material may be offset by the cumulative negative effects of periodic low temperature, low aragonite saturation state and high nutrient content of the upwelled LAIW waters. The Andaman Sea features internal solitary waves of extraordinary amplitude (> 80 m, Perry & Schimke 1965, Osborne & Burch 1980, Jackson 2004) generated by the waxing and waning of the tides across the shallow ridges of the Andaman-Nicobar island arc and the shallow reefs northwest of Sumatra (Alpers et al. 1997, Jackson 2004). These LAIW travel as waves of depression in groups eastward across the deep Andaman Sea at speeds of 2 m s⁻¹. As the solitary waves propagate from the basin onto the shelf, interaction with the bottom leads to a gradual transformation into waves of elevation with secondary waves of dispersion evolving from the trailing edge of the LAIW (Vlasenko & Stashchuk 2007). For intense LAIW with amplitudes exceeding 40 % of the thickness of the layer below the pycnocline, (Vlasenko & Hutter 2002), the steepening and overturning of the rear wave faces cause wave breaking and generation of upslope propagating density intrusions (Vlasenko & Hutter 2002, Vlasenko & Stashchuk 2007). Although the passage of LAIW leads to turbulent mixing near the sea bed (De Silva et al. 1997), with resuspension of sediments up to 30 m above bottom (Moum et al. 2007), it is so far largely unknown to what extent they may affect coral communities.

The Similan Islands are an offshore group of coral islands in the Andaman Sea located in the swash zone of Andaman Sea LAIW (Jackson 2004, Vlasenko & Stashchuk 2007). In contrast to most other reefs, where reef growth is most vigorous on the exposed (or windward) face of a barrier or island (Veron 2000, Spalding et al. 2001), satellite images (www.reefbase.org/gis_maps) and monitoring studies (Chansang et al. 1999) suggest that reef development along the Similan Islands and other offshore islands in the Andaman Sea is restricted to the sheltered E sides (Fig. 1 B) (Phongsuwan et al. 2008). The W sides, by contrast, appear to be conspicuously devoid of reef formations and corals occur only in scattered colonies and sheltered areas along the coastline (Fig. 1 A). The reasons for the Andaman Sea paradox of coral reef distribution are so far unknown.

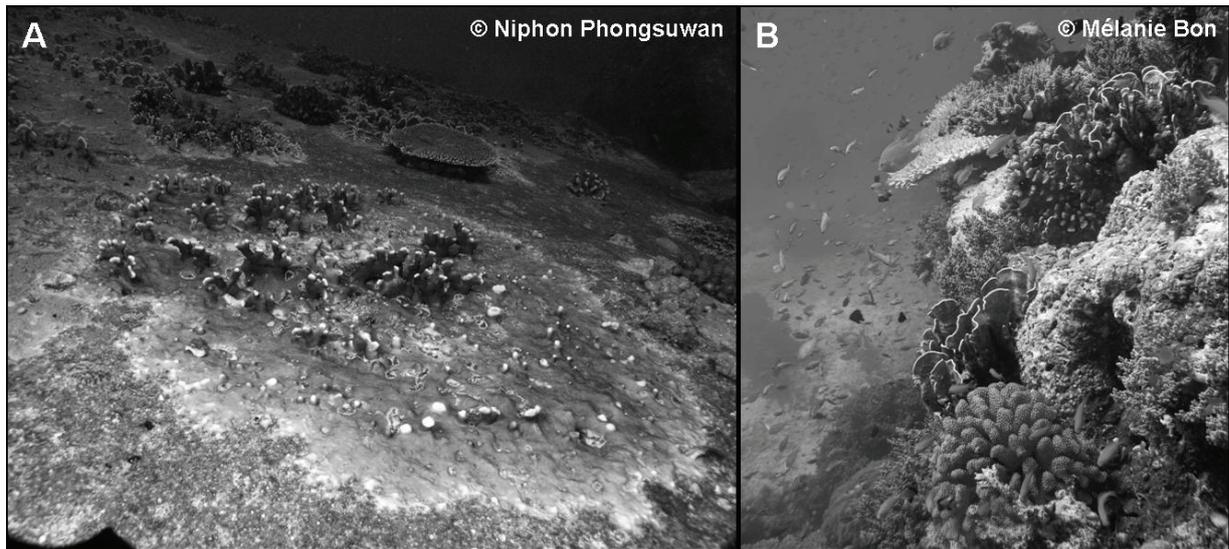


Figure 1: Typical substrate conditions at Similan Islands in about 12 m depth: A) at West W 4.1 and B) at East 7.1

Although hydro-dynamical forcing by surface gravity waves may be important for structuring coral communities in shallow W-facing areas exposed to the south-west (SW) monsoon (Dunne & Brown 1996, Wu & Zhang 1998), ocean swell and storms in the Andaman Sea are less severe than e.g. in the cyclone tracks of the open tropical Pacific, where coral communities flourish on the windward sides (Spalding et al. 2001). Here, we suggest that LAIW-induced upwelling undermines reef-generating processes by the cumulative effects of low temperatures, low aragonite saturation state and elevated nutrient concentrations of the upwelled water. Low temperatures have been shown to limit reef development (Kleypas et al. 1999), low aragonite saturation state reduces coral growth and calcification (Schneider & Erez 2006), elevated nutrient concentrations affect the delicate association of corals with their endosymbiotic zooxanthellae (Muscatine et al. 1989, Muller-Parker 1994, Ferrier-Pages et al. 2001), favour the growth of competitively superior phytoplankton and macroalgae (Abram et al. 2003, McCook 1999) and enhance bioerosion (Sammarco & Risk 1990, Chazottes et al. 2002, Ward-Paige et al. 2005). Tropical shallow platforms subjected to intense wind-driven upwelling are thus devoid of coral reefs (Hallock & Schlager 1986) but moderate and/or intermittent upwelling may allow for moderate to extensive reef development (Andrews & Gentien 1982). The magnitude and potential role of upwelling near Andaman Sea coral reefs and adjacent upper slope communities is so far unknown.

The present study explores the relationship between environmental variability and coral abundance and diversity in relation to LAIW. The objective was to examine the fringing reef communities and the physico-chemical characteristics of the Similan Islands which are under the influence of a strong

SW-monsoon regime and tidally recurring LAIW. We hypothesize that monsoon and LAIW differentially affect shallow and deep, E and W coral communities. This was tested by (1) quantifying and comparing coral community and coral cover patterns, (2) assessing W - E and shallow - deep physico-chemical differences and (3) relating the characteristics of coral communities to the existing environmental conditions.

Methods

Study area

The Similan Islands belong to the National Park “Mu Koh Similan” with a total area of 140 km² in the Andaman Sea, Thailand, about 60 km west of the Thai coast and 400 km east of the Andaman-Nicobar-Islands. The 9 islands are located in a North-South alignment over a distance of about 24 km between 8°40'54.49"N, 97°38'56.41"E and 8°28'28.45"N, 97°38'56.85"E (Fig. 2). The islands consist of granite and have been built in the tertiary about 65 million years ago by volcanic activity (Thai National Park administration). Their topography and surrounding bathymetry are characterized by a generally steep slope (> 45°) down to 20 m depth along the western sides and a slightly gentler slope (< 40°) in the east with broad sandy beaches and shallow reefs. Under water the substrate in the west is shaped by granite boulders along the steep slope until about 16 m depth before passing into sand and coral rubble and continuing to gently drop down to 60 – 80 m depth around and between the islands (Fig. 2). Annual rainfall is 3560 mm and mostly restricted to the South-West monsoon between May and October with strong winds, occasional storms and high waves (Thai National Park administration).

Reef sampling

Representative study localities were established along the eastern (E) and western (W) sides of Similan Islands (nine in the east: E 1.1 – E 9.1 and seven in the west: W 2.1 – W 9.1, Fig. 2). To explore W-E differences in coral communities, single 100 m line transects were established at each of the 16 localities and marked with steel stakes, one at either end. Transect sites were positioned along isobaths at a depth of 12 – 16 m, i.e. beyond the reach of storms (Wolanski et al. 2005). The line-intercept method (Loya and Slobodkin 1971; Loya 1972, 1976) was adopted to quantify the coral communities. The intercept of each benthic component (i.e. scleractinian corals, soft corals, macroalgae, sand and rubble) under each line transect was recorded to the nearest centimetre and the

number of colonies recorded. Scleractinian corals were identified to species level. To establish vertical differences in coral communities, additional triplicate transects of 50 m length were established in 20 and 7 m at Koh Miang on both sides, west (W 4.1) and east (E 4.1). Transect lines were positioned along isobaths spaced 10 m apart. Wherever in these latter transects coral cover was detected the height of its skeletal framework was determined every 5 m across the whole transect distance. Therefore a measuring stick of known length was placed perpendicular to the isobath in front of the coral framework and a picture taken displaying the complete framework with its basement (sediment or rock) and the measuring stick. The height of the framework was calculated from later picture analysis with the software ImageJ. A total of 42 framework measurements was carried out, 15 and six in W 20 and 7 m respectively, and nine and twelve each in 20 and 7 m E. Logistic constraints precluded the extension of this work to all sites, but the lack of differences among and the consistency and significance of differences between W and E sides of the islands justified to restrict the vertical analysis to this central Similan island (see results, below).

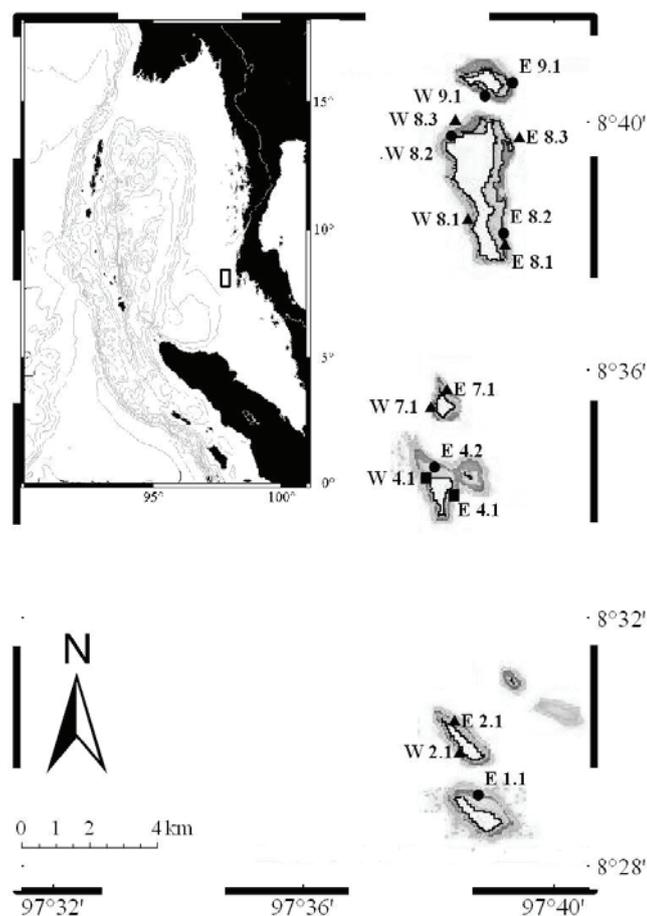


Figure 2: Similan Islands with biological and environmental samplings: (●) transects only; (▲) transects and temperature; (■) all parameters at central island Koh Miang (W 4.1 and E 4.1). (Figure modified after Jackson (2004)).

Physico-chemical sampling

Broad-scale temperature measurements - Temperature recorders (TidbiT v2, Onset computers; resolution 0.2 °C within a range of 0 to 50 °C) were deployed in two depths (20 and 7 m) at 5 study sites, both in W (W 2.1, W 4.1, W 7.1, W 8.1, W 8.3) and in the opposing E face (E 2.1, E 4.1, E 7.1, E 8.1, E 8.3). Loggers were attached about 20 cm above the substrate recording temperature values at 6 min intervals from February 2007 to November 2008.

Fine-scale temperature measurements - Additional temperature loggers were established in the reefs at island Koh Miang (W 4.1 and E 4.1) in 5, 10, 15 and 20 m depth logging every minute from December 2007 through March 2008.

Light-, current- and CTD-measurements – Temperature, salinity, pressure, oxygen, pH, chlorophyll-a fluorescence and optical backscatter was measured with a CTD (Seacat SBE 19plus, Sea-Bird Electronics) deployed in 20 m depth at the W side (W 4.1) of island Koh Miang in March 2007 for four weeks. At the same time an Acoustic Doppler Current Profiler (600 kHz Workhorse Sentinel ADCP, Teledyne RD Instruments) was placed right next to the CTD to determine the current field at 2 m vertical (bins) and 1 min temporal resolution. Current speeds were determined by averaging the 3-D current measurements from three vertical bins for deep (20 m: 20 to 16 m depth) and shallow (7 m: 10 to 6 m depth). Light loggers (Onset pendant light logger: 0 - 320000 lux [lm m^{-2}], typical to 90%) were deployed on both sides of island Koh Miang (W 4.1, E 4.1) in two depths (20 and 7 m) about 20 cm above the substrate recording light values every minute from December 2007 till April 2008. The loggers were cleaned daily to avoid fouling organisms to interfere with light measurements. Additionally a photosynthetic active radiation (PAR, $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$) sensor (Biospherical Instruments) was mounted on a CTD (SEACAT, SBE 19plus, Sea-Bird Electronics) in January 2008 over a period of 20 days on the W of island Koh Miang (W 4.1) in 20 m depth.

Chemical measurements – A total of 40 water samples was collected by SCUBA about 1 m above the reef substrate using sterile 1-litre PE-bottles at island Koh Miang at both sides (W 4.1, E 4.1) in two depths (20 and 7 m) between February and March 2007. Right after collection water samples were filtered through pre-combusted and pre-weighed glass-fibre filters (Whatman GF/F, 45 μm). The filtrate was stored in sterile polypropylene bottles for further nutrient analysis and in pre-combusted DOC-vials spiked with phosphoric acid for further determination of dissolved organic carbon. The filters were kept for the determination of suspended particulate matter. Water samples for dissolved inorganic nutrient analysis were poisoned with mercuric chloride after Kattner (1999). All samples were stored on ice and frozen. Nutrient samples were analyzed after Parsons et al. 1989

for nitrate, nitrite, ammonium, phosphate and silicate using a spectrometer, GBC model UV/VIS981 with an autosampler model FS3000 at Phuket Marine Biological Center (PMBC) in Phuket. Dissolved organic carbon samples were analyzed by means of high temperature catalytic oxidation using a Dohrman DC-190 Total Organic Carbon Analyzer equipped with a platinum catalyst. Before injection into the furnace, the acidified samples were decarbonated by purging with oxygen. The evolving CO₂ was purified, dried and detected by a non-dispersive infrared detection system. Suspended particulate matter was determined by weighing the filters after drying them over night at 50°C on a microbalance (Mettler, AT21 Comparator, 1 µg accuracy).

Data processing and statistical analysis

Before applying parametric or non-parametric analyses, as the data required, both biological and environmental data were tested for the assumption of normality and homogeneity of variances using Kolmogorov-Smirnov and Levene's tests, respectively.

Transect data were processed as percentage abundances per site and analysed with the software PRIMER v6 for non-parametric multivariate datasets (see Clarke 1993, Clarke & Warwick 1994). ANOSIM permutation tests based on Bray-Curtis similarities were used to detect spatial differences in substrate cover and species compositions between island sides (one-way-analysis with 25 iteration steps) as well as to clarify depth dependent cover and distribution patterns at the W and E site of island Koh Miang (two-way-crossed design implicating the differing impact of LAIW depending on orientation: W versus E, and depth: 20 versus 7 m). ANOSIM calculates a global R statistic that reflects the differences in variability between groups as compared to within groups (so R values are proportional to differences between the groups) and checks for the significance of R using permutation tests (Clarke and Warwick 2001). Nonmetric multidimensional scaling (MDS) was also used to further analyze benthic communities. Based on a similarity matrix, MDS generates plots in which the distance between points is proportional to their degree of similarity (Clarke and Warwick 2001). SIMPER analyses were consulted to assess the respective contributions of substrate types and coral species to the similarities and dissimilarities within and among the W and E sites studied. Descriptive coral community factors as Shannon index, evenness and species richness (Rogers 1993, van Woesik et al. 1999) were calculated for every site and tested for LAIW-exposure (W versus E) using Student's t-tests.

Degree days cooling (DDC) was calculated for every temperature time-series. The calculation involved three steps: (1) calculation of moving modes (my) and residuals (ry) on the basis of the time-series (y); (2) splitting of residuals into cold (ryc) and warm residuals (ryw); and (3) integrating

cold and warm anomalies into DDC and degree days warming (DDW). The moving modes were calculated using a slide function (by Jos van der Geest; <http://www.mathworks.com/matlabcentral/fileexchange/12550>) to a moving 1-day window of elements of the time-series y and smoothing the output by a 1-day moving average, yielding ry . Degree days cooling was calculated by replacing the positive values in the residuals time series ry with zeros, yielding ryc , summing the values [$\text{sum}(ryc)$], dividing by the number of samples per day (spd), and normalizing to the full year with F {samples per year, divided by the number of samples of the time series, i.e. $F = \text{spd} \times [\text{sp}(ry)]^{-1}$ }. The corresponding equation is:

$$\text{DDC} = \text{sum}(ry) \times (\text{spd})^{-1} \times F \quad (1)$$

Because not all loggers were logging continuously without failure at all sites, the calculation of the DDC was done for the period when data were available from all sites and depths (20 weeks, February 2007 to July 2007). The resulting degree days cooling (DDC) displayed as ($^{\circ}\text{Cd}$) were used as site specific indicators of LAIW exposure. Their relationship with the descriptive coral community factors and living coral cover of every site was tested using linear-regression analyses. Nutrient concentrations, current and light recordings were statistically tested for LAIW-exposure using non-parametric Kruskal-Wallis ANOVA by ranks. Linear-regression analyses were undertaken to test the relationships between both chemical and physical parameters in the water as the dependent variables with temperature as the independent variable (see Sokal & Rohlf 1995) followed by Student's t-test to examine their statistical significance. If not stated otherwise data are always displayed as mean \pm SE.

Results

Reef data

Coral community composition – Overall 144 hermatypic coral species were recorded, belonging to 40 genera and 17 families (supplemental Table 2, supplemental Fig. 1). Ten genera could be detected as the mayor players along the island chain containing exactly half of the number of species found at all sites studied (Table 1). *Porites* was the overall dominant genus, especially in E, followed by *Acropora*, *Hydnophora* and *Pocillopora*, all of them with comparatively larger appearances in W.

Table 1: Cover composition of the most abundant genera at all sites studied along Similan Islands. Percentage of total coral cover calculated as mean (\pm SE).

genus	# species found	percentage of total coral cover [%] all sites	percentage of total coral cover [%]		# sites of appearance	
			West	East	West	East
<i>Porites</i>	6	42.97 (7.16)	15.69 (3.81)	64.19 (5.81)	7	9
<i>Acropora</i>	36	18.99 (4.12)	28.64 (7.55)	11.49 (2.68)	7	9
<i>Hydnophora</i>	3	8.25 (4.77)	8.51 (8.16)	8.06 (6.08)	3	6
<i>Pocillopora</i>	4	4.48 (1.56)	6.92 (3.11)	2.58 (1.20)	7	8
<i>Pavona</i>	8	3.23 (1.40)	6.35 (2.85)	0.81 (0.36)	6	7
<i>Millepora</i>	4	2.23 (1.04)	3.94 (2.23)	0.90 (0.43)	6	5
<i>Diploastrea</i>	1	1.98 (0.58)	2.65 (1.06)	1.46 (0.62)	5	6
<i>Echinopora</i>	3	1.43 (0.58)	0.74 (0.41)	1.96 (0.97)	3	5
<i>Heliopora</i>	1	1.40 (0.85)	1.22 (0.90)	1.53 (1.38)	2	3
<i>Goniopora</i>	6	0.80 (0.35)	0.77 (0.33)	0.83 (0.59)	4	4
other	72	14.23 (2.97)	24.57 (3.86)	6.19 (1.54)	7	9

Coral species composition differed clearly between island sides (ANOSIM, one-way-analysis: W versus E: global $R = 0.585$, $p < 0.001$, supplemental Table 2) resulting in a distinct clustering in the MDS plot of the W and E sites, respectively (Fig. 3, see also Table 2). In the W higher species diversity (t-test, $p < 0.01$) and richness (t-test, $p < 0.02$) along with a more homogeneous distribution pattern were found compared to the E (evenness: t-test, $p < 0.04$; Fig. 4): Shannon index was 2.69 ± 0.15 in the W and 2.03 ± 0.13 in the E, species richness showed 38.34 ± 2.35 species in the W and 27.33 ± 3.45 in the E, and evenness revealed 0.74 ± 0.04 in the W and 0.63 ± 0.04 in the E. The similarities calculated on the basis of species compositions were relatively low among W and E sites, respectively (Table 2). This can be explained by the fact that besides the high species richness and evenness in W, the species compositions in W differed among sites (supplemental Table 2). Whereas the E sites were characterized by a lower number of species, and a higher dominance by a variable subset of species, including two species of *Porites* (*P. lutea* dominating in five out of nine E locations; and *P. rus*, dominating in four locations) and *Hydnophora rigida* (dominating in one E location) (supplemental Table 2).

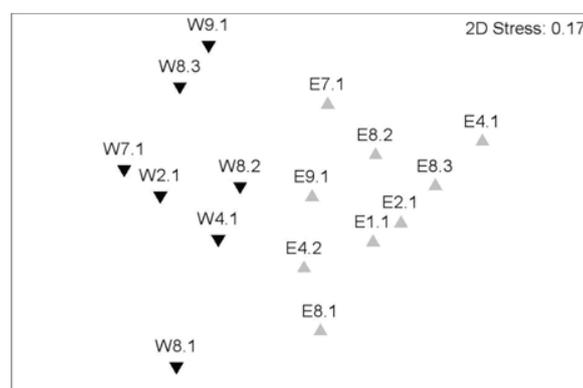
**Figure 3:** MDS ordination of coral communities in the Similan Islands based on the species abundance data (%) and Bray-Curtis Similarities. LAIW-exposed (\blacktriangledown) and sheltered (\blacktriangle) sites are grouped in separate clusters.

Table 2: Inter-site comparison of coral communities with the top 10 coral species contributing most to (A) the dissimilarities (diss) between LAIW-exposed (West) and LAIW-sheltered (East), (B) similarities (sim) within LAIW-exposed (West), and (C) similarities within LAIW-sheltered (East) sides of the Similan Islands. Values denote mean (\pm SE) percentage of total living coral cover, SD: standard deviation of dissimilarity and similarity, respectively.

A average dissimilarity [%]: 83.16							
genus	species	percentage of living coral [%]		average diss	diss/SD	contrib diss [%]	cum contrib diss [%]
		West	East				
<i>Porites</i>	<i>lutea</i>	12.68 (3.58)	25.17 (6.59)	12.39	1.11	14.9	14.9
	<i>rus</i>	1.40 (0.58)	22.37 (5.15)	11.71	2.55	14.08	28.98
<i>Hydnophora</i>	<i>rigida</i>	8.13 (8.13)	8.02 (6.08)	8.85	0.61	10.64	39.62
<i>Porites</i>	<i>nigrescens</i>	0.37 (0.27)	11.13 (4.11)	6.77	0.94	8.14	47.76
<i>Acropora</i>	<i>clathrata</i>	10.83 (5.21)	0.86 (0.53)	4.7	0.73	5.65	53.41
<i>Porites</i>	<i>cylindrica</i>	0.00 (0.00)	4.79 (3.28)	2.96	0.47	3.56	56.97
<i>Acropora</i>	<i>palifera</i>	6.63 (4.95)	0.69 (0.35)	2.37	0.58	2.85	59.82
<i>Pocillopora</i>	<i>eydouxi</i>	5.46 (2.76)	0.23 (0.16)	2.31	0.7	2.78	62.60
<i>Millepora</i>	<i>exaesa</i>	2.94 (1.43)	0.09 (0.07)	1.38	0.74	1.66	64.26
<i>Pavona</i>	<i>clavus</i>	2.57 (2.57)	0.00 (0.00)	1.17	0.4	1.41	65.67

B average similarity [%]: 24.27							
genus	species	percentage of living coral [%]		average sim	sim/SD	contrib sim [%]	cum contrib sim [%]
		West	East				
<i>Porites</i>	<i>lutea</i>	12.68 (3.58)		6.44	1.31	26.52	26.52
<i>Acropora</i>	<i>clathrata</i>	10.83 (5.21)		3.27	0.57	13.49	40.01
<i>Cyphastrea</i>	<i>sp.</i>	2.55 (0.70)		1.47	2.68	6.06	46.07
<i>Pocillopora</i>	<i>eydouxi</i>	5.46 (2.76)		1.38	0.79	5.68	51.75
<i>Pavona</i>	<i>varians</i>	2.82 (0.95)		1.29	1.05	5.3	57.05
<i>Acropora</i>	<i>palifera</i>	6.63 (4.95)		0.98	0.63	4.04	61.09
<i>Millepora</i>	<i>exaesa</i>	2.94 (1.43)		0.89	1.01	3.68	64.77
<i>Diploastrea</i>	<i>heliopora</i>	2.65 (1.06)		0.88	0.72	3.63	68.40
<i>Acropora</i>	<i>austera</i>	1.90 (1.08)		0.54	0.58	2.21	70.61
<i>Porites</i>	<i>stephensoni</i>	1.21 (0.38)		0.51	0.93	2.08	72.69

C average similarity [%]: 31.91							
genus	species	percentage of living coral [%]		average sim	sim/SD	contrib sim [%]	cum contrib sim [%]
		West	East				
<i>Porites</i>	<i>lutea</i>		25.17 (6.59)	12.28	1.05	38.49	38.49
	<i>rus</i>		22.37 (5.15)	11.19	2.43	35.08	73.57
	<i>nigrescens</i>		11.13 (4.11)	4.11	0.53	12.88	86.45
	<i>cylindrica</i>		4.79 (3.28)	0.53	0.47	1.66	88.11
<i>Diploastrea</i>	<i>heliopora</i>		1.52 (0.61)	0.44	0.51	1.38	89.49
<i>Hydnophora</i>	<i>rigida</i>		8.02 (6.08)	0.42	0.22	1.3	90.79

Benthic substrate composition – Comparing the benthic cover compositions in shallow (monsoon-impact), mid and deep (LAIW-impact) depths, the clearly lowest living coral cover was found in W deep (ANOSIM, two-way-crossed analysis: W 4.1 versus E 4.1: global $R = 0.639$, $p < 0.02$). Significantly higher living coral cover was found in shallow W (35.67 ± 5.61 % in 7 m versus 12 ± 4.36 % in 20 m depth) and in deeper and mid-waters in E (36.67 ± 4.63 % in 20 m depth and 33.57 % in 14 m depth versus 18.67 ± 5.49 % in 7 m depth; 20 m versus 7 m: global $R = 0.37$, $p < 0.05$) (Fig. 5). Living coral cover was the second most powerful contributor to the dissimilarity of 72.5 % between W and E with a contribution of 25.06 %. The most important contribution was achieved by sand and rubble with 35.86 %, thirdly followed by rock (17.93 %). In the mid-depths located in

between the direct impact of LAIW and monsoon waves differences in the overall benthic composition failed to be significant between W and E sides (ANOSIM, one-way analysis: global $R = 0.079$, $p = 0.22$). In detail, for the intermediate depth at all 16 sites living coral cover averaged 25.57 ± 4.22 % in W and 35.95 ± 4.62 % in E. Total hard substrate and sand including rubble also showed similar compositions at W and E. Total hard substrate consisting of dead coral, living coral and rock averaged 67.71 ± 6.59 % in W and 72.83 ± 3.34 % in E, sand and rubble 29.75 ± 6.89 % in W and 25.88 ± 3.29 % in E. Rock structures were only found in W, while in E hard substrate consisted exclusively of dead coral (Fig. 6, supplemental Table 1).

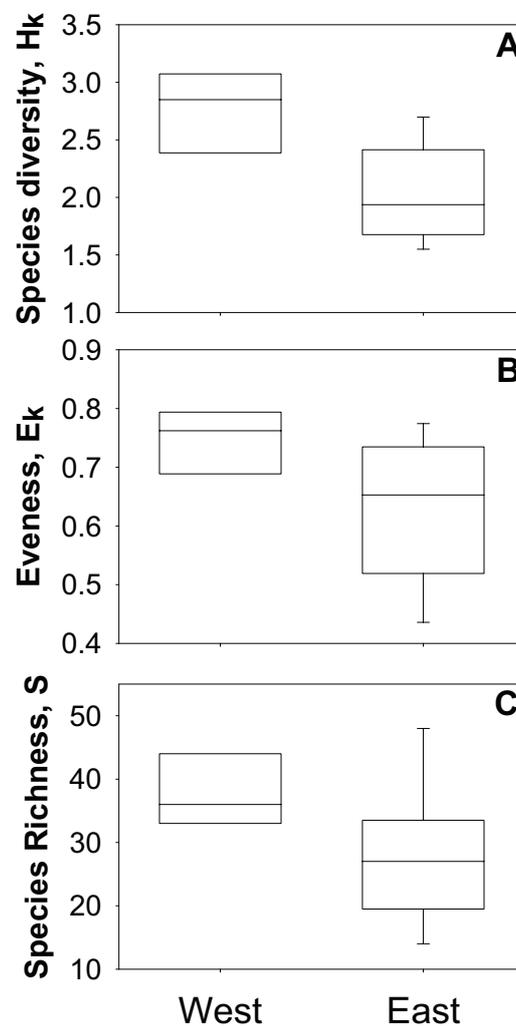


Figure 4: Coral diversity (Shannon index, A), evenness (B), and species richness (C) at LAIW-exposed (West), and sheltered (East) sides of Similan Islands.

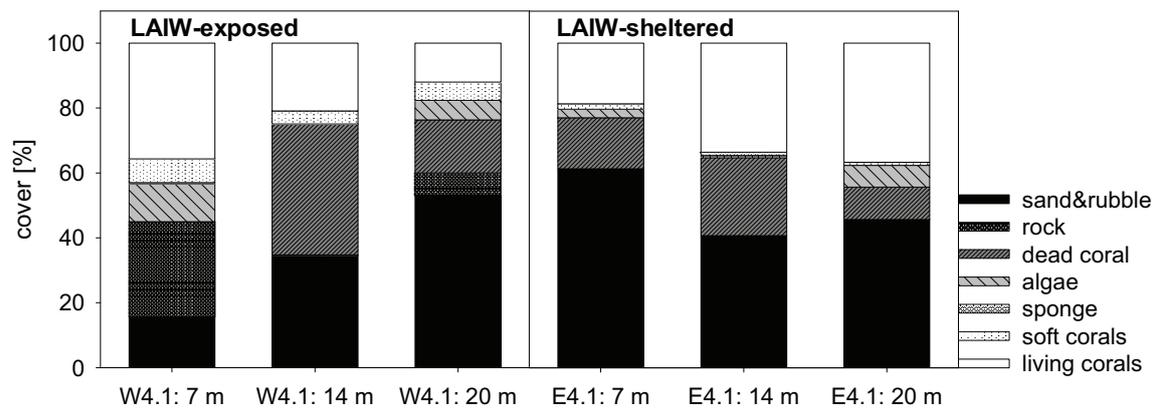


Figure 5: Benthic composition at Koh Miang on LAIW-exposed (W 4.1) and sheltered (E 4.1) side, grouped by depth: 7, 14 and 20 m.

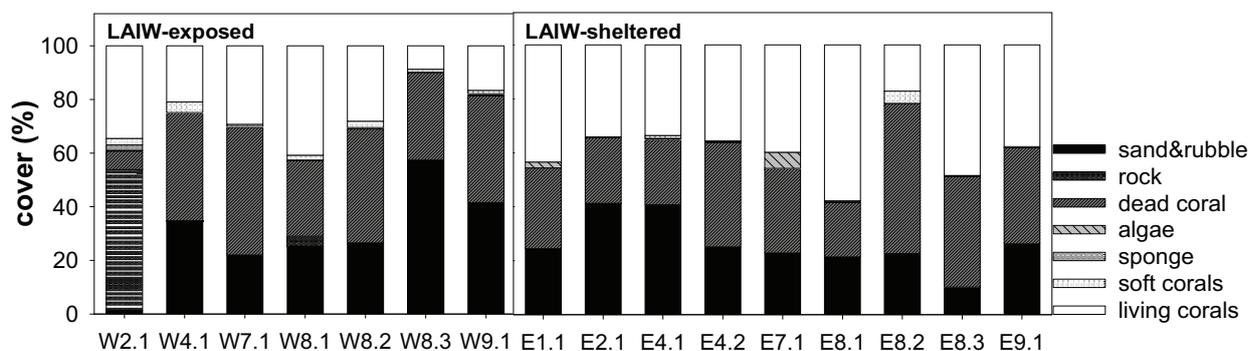


Figure 6: Benthic composition at Similan Islands on LAIW-exposed west (W), and east (E) sides (12 to 16 m depth, grouped by N-S orientation).

Coral framework and morphologies – A dense and complex coral framework characterized the E whereas in the W hard corals were distributed as solitary colonies without developing any actual framework (W 4.1 versus E 4.1, depths pooled: $p < 0.001$) (Fig. 7). Coral morphologies differed significantly between sides (ANOSIM two-way-crossed analysis: W versus E, global $R = 0.311$, $p < 0.05$) and depths (7 vs. 20 m, global $R = 0.253$, $p < 0.05$) (Fig. 8). Although the dominance of massive and encrusting colonies in W and of branching species in E of Koh Miang fell short of being significant (t-test, $p = 0.064$ and $p = 0.1$, respectively) Fig. 8 shows clear tendencies towards this pattern. Large massive and encrusting hard coral species sparsely covered deeper areas in the W, and small often densely thronged colonies of all morphological types nestled to the rocks in shallower waters. Here, branching hard corals, especially within the genera *Millepora* and *Acropora* often displayed flattened morphologies with pancake-like broadened bases and strongly reduced ramification (Fig. 1 A).

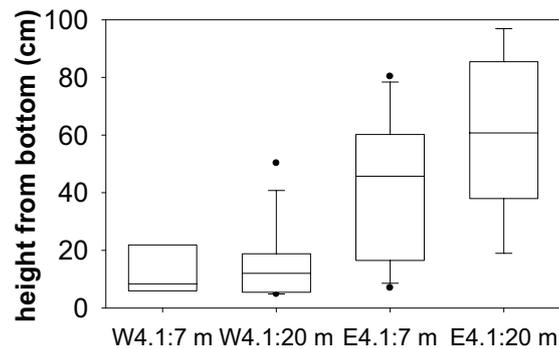


Figure 7: Coral framework at Koh Miang on LAIW-exposed (W 4.1) and sheltered (E 4.1) side, grouped by depth: 7 and 20 m.

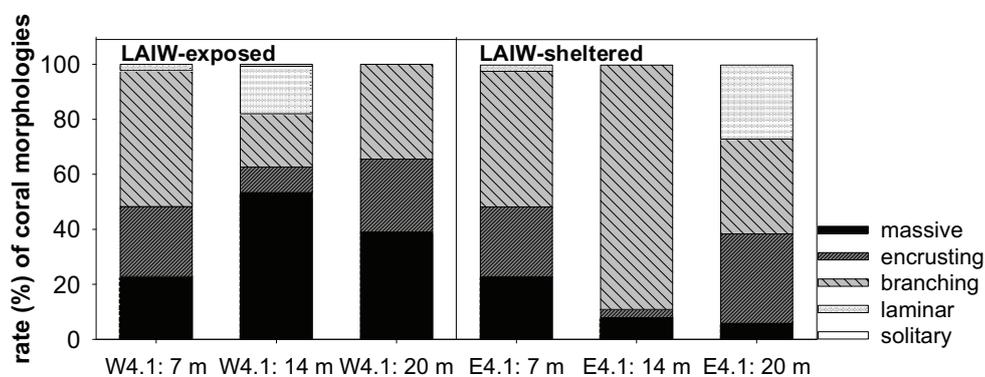


Figure 8: Coral morphologies as fractions of total number of colonies studied at Koh Miang on LAIW-exposed (W 4.1) and sheltered (E 4.1) side, grouped by depth: 7, 14, and 20 m.

Physico-chemical environment

Temperatures were barely lower (modal values, $\Delta T < 0.3$ °C) in the W than in the E, but characterized by very high variability with up to 10 °C drops during extreme LAIW-events in the W, as opposed to < 5 °C in the sheltered E. Corresponding degree days cooling (DDC) averaged -125.94 ± 12.94 °Cd and -49.10 ± 5.74 °Cd for W and E both depths pooled, respectively (Student's t-test, $p < 0.001$). Table 3 represents the summary of the temperature data recorded. Fig. 9 shows the complete temperature record for Koh Miang. Superimposed on the lower frequency variations (diurnal tides, spring-neap tides cycles, seasons) were periods of high-frequency oscillations which were most pronounced from February to April and October to November. Temperature drops as large as 10 °C were observed in spring in 20 m depth at the W sites. Less pronounced oscillations occurred in the shallower and sheltered E sites. The temperature record at W Koh Miang (December 2007 to April 2008) reveals also that the magnitude and duration of cool water events increased significantly with depth. This was less obvious in the E, underscoring the importance of LAIW for the W slope of the island (Table 3).

Table 3: Summary of temperature (°C) and degree days cooling, DDC (°Cd), of all sites recorded along Similan Islands and of Koh Miang in detail. Temperature values calculated as mean, modal, and range (\pm SE), respectively, of complete time period recorded (all sites: Feb 2007 to Nov 2008, Koh Miang: Dec 2007 through March 2008); DDC calculated from complete data set of 20 week period for all sites (Feb 2007 to July 2007) and of 16 week period at Koh Miang (Dec 2007 through March 2008).

all sites	West		East			
	20 m	7 m	20 m	7 m		
mean	28.46 (0.07)	28.79 (0.07)	28.82 (0.05)	29.05 (0.05)		
modal	28.71 (0.06)	28.85 (0.07)	28.84 (0.06)	28.99 (0.06)		
monthly range	5.20 (0.17)	4.25 (0.20)	2.69 (0.13)	2.08 (0.09)		
DDC	-152.03 (2.22)	-82.45 (5.70)	-64.53 (2.90)	-33.68 (4.57)		
Koh Miang	West W4.1			East E4.1		
	20 m	14 m	7 m	20 m	14 m	7 m
mean	27.98 (0.84)	28.31 (0.67)	28.56 (0.50)	28.40 (0.49)	28.40 (0.38)	28.58 (0.47)
modal	28.20	28.10	28.39	28.15	28.25	28.10
weekly range	4.65 (0.80)	3.22 (1.81)	3.42 (1.04)	2.29 (0.91)	1.69 (0.90)	1.85 (0.78)
DDC	-184.04	-101.61	-42.54	-60.03	-24.14	-24.16

Table 4 shows the statistics summary of the further physical and chemical parameters measured at Koh Miang. Mean current velocities were twice as high in W as in E (Kruskal-Wallis test, $p < 0.001$) with maximum speeds reaching 0.65 and 0.73 ms^{-1} in W deep and shallow opposed to 0.58 and 0.56 ms^{-1} in E deep and shallow respectively. Higher velocities coincided with lower temperature, while under constant temperature conditions (at most $0.5 \text{ }^{\circ}\text{C}$ below modal) water motion stayed stable at $0.13 \pm 0.001 \text{ ms}^{-1}$ (supplemental Fig. 2) Oxygen concentrations, pH and salinity were highly correlated with temperature. The impact of LAIW in W (5 to $10 \text{ }^{\circ}\text{C}$) caused drops in oxygen concentration of up to 88% (down to $21.80 \mu\text{molL}^{-1}$), in pH of up to 0.6 units (down to 7.75) and increased in salinity up to 5% to values of 34.52 . Neither optical backscatter nor fluorescence showed temperature dependent variations. Yet a tendency of lower chlorophyll concentrations up to 40% in LAIW-water of $20 \pm 0.5 \text{ }^{\circ}\text{C}$ was noted when compared to constant modal temperature conditions.

Highest light intensities were found in E shallow and lowest in W deep. Light conditions were significantly different on W and E in both depths (7 and 20 m) (Kruskal-Wallis test, $p < 0.001$, supplemental Table 3 B), with over three times higher light values in E during the main part of the day and a longer lasting light environment in W at the end of the day (Table 4 C, supplemental Fig. 3). During a period of turgescence LAIW-impact in January 2007 photosynthetic active radiation (PAR) never exceeded $141.5 \mu\text{mol quanta m}^{-2} \text{ s}^{-1}$ in W 20 m with a mean of 102.5 ± 3.4 (Fig. 9).

Table 4: Environmental parameters at Koh Miang (W 4.1 and E 4.1) displayed as mean (\pm SE). Linear regression model with each environmental parameter as dependent and water temperature as independent variable: **(A)** Parameters measured continuously every minute and **(B)** parameters determined from water samples. **(C)** Averaged light values (lux [lm m^{-2}]) over a period of 4 months from December 2007 to April 2008. (Significance levels are $*0.05 > P \geq 0.01$, $**0.01 > P \geq 0.001$, $***P < 0.001$)

		Units			N	Intercept a	Slope b \pm s.e.	R ²	P
A		West W4.1							
Dependent variable		20 m							
Oxygen	$\mu\text{mol L}^{-1}$	146.53 (0.20)		13682	-295.50	16.70 \pm 0.03	0.95	0.001***	
pH	-	8.14 (0.00)		13682	6.93	0.05 \pm 0.00	0.72	0.001***	
Salinity	ppm	33.18 (0.00)		13682	38.13	-0.19 \pm 0.00	0.97	0.001***	
Fluorescence (Chla)	$\mu\text{g L}^{-1}$	0.50 (0.00)		13682	-0.51	0.04 \pm 0.00	0.04	0.001***	
Optical backscatter	free units	0.09 (0.00)		13682	0.10	-0.00 \pm 0.00	0.06	0.001***	
		20 m	7 m						
Current velocity	m s^{-1}	0.13 (0.00)	0.14 (0.00)	15551	0.20	0.01 \pm 0.00	0.01	0.001***	
		East E4.1							
Current velocity	m s^{-1}	0.07 (0.00)	0.06 (0.00)	16021	-0.08	0.01 \pm 0.00	0.01	0.001***	
B		West W 4.1							
		20 m	7 m						
Si(OH) ₄	$\mu\text{mol L}^{-1}$	11.14 (1.83)	5.07 (1.20)	18	77.93	-2.58 \pm 0.47	0.66	0.001***	
PO ₄ ³⁻	$\mu\text{mol L}^{-1}$	0.48 (0.11)	0.17 (0.05)	18	3.98	-0.14 \pm 0.02	0.72	0.001***	
NO ₂ ⁻ +NO ₃ ⁻	$\mu\text{mol L}^{-1}$	3.81 (0.89)	0.77 (0.26)	19	28.46	-0.98 \pm 0.19	0.62	0.001***	
NH ₄ ⁺	$\mu\text{mol L}^{-1}$	0.64 (0.32)	0.62 (0.20)	18	0.43	0.01 \pm 0.10	0.00	0.88	
Dissolved organic carbon	ppm	0.86 (0.09)	0.79 (0.06)	16	1.08	-0.01 \pm 0.03	0.01	0.26	
Suspended particulate matter	mg L^{-1}	10.41 (0.52)	11.08 (1.14)	19	16.68	-0.22 \pm 0.37	0.02	0.12	
		East E 4.1							
Si(OH) ₄	$\mu\text{mol L}^{-1}$	5.13 (0.49)	3.90 (0.55)	22	49.77	-1.59 \pm 0.39	0.45	0.001***	
PO ₄ ³⁻	$\mu\text{mol L}^{-1}$	0.37 (0.12)	0.25 (0.09)	14	5.31	-0.18 \pm 0.07	0.41	0.02**	
NO ₂ ⁻ +NO ₃ ⁻	$\mu\text{mol L}^{-1}$	1.30 (0.30)	0.37 (0.11)	22	23.91	-0.80 \pm 0.27	0.31	0.006**	
NH ₄ ⁺	$\mu\text{mol L}^{-1}$	0.44 (0.11)	0.53 (0.05)	14	-1.90	0.08 \pm 0.08	0.13	0.44	
Dissolved organic carbon	ppm	0.94 (0.14)	0.83 (0.11)	21	3.58	-0.09 \pm 0.12	0.03	0.32	
Suspended particulate matter	mg L^{-1}	10.39 (0.64)	10.26 (0.95)	20	-3.75	0.50 \pm 0.77	0.02	0.87	
C		West W 4.1		East E 4.1					
part of day	time intervall	20 m	7 m	20 m	7 m				
morning	07:00 - 10:00	272.55 (11.86)	766.65 (28.53)	967.33 (47.39)	2575.73 (129.46)				
midday	10:00 - 15:00	1381.61 (25.47)	5493.29 (169.31)	2442.87 (32.21)	6931.51 (81.90)				
afternoon	15:00 - 18:00	879.99 (36.96)	3559.43 (156.68)	565.30 (23.95)	1863.83 (78.67)				

Nutrients revealed significant differences between W and E for nitrate and nitrite, as well as for silicate (Kruskal-Wallis test, $p < 0.009$ and $p < 0.002$, respectively). Mean concentrations of silicate were more than 100 % higher in W 20 m than in E 20 m, supported by an increase of nitrate and nitrite (almost 200 %) and of phosphate (30 %) concentrations. In shallow waters the differences were still noticeable but far less pronounced and statistically not significant. Thereby concentrations exhibited a clearly negative relationship with temperature when correlating to the in-situ temperature during sampling (Table 4 B, supplemental Table 3). Ammonium showed 45 % higher mean concentrations in W than in E but did not clearly correlate negatively with water temperature. No significant differences were found between sides in dissolved organic carbon and suspended particulate matter concentrations which varied independent from temperature variations (supplemental Table 3).

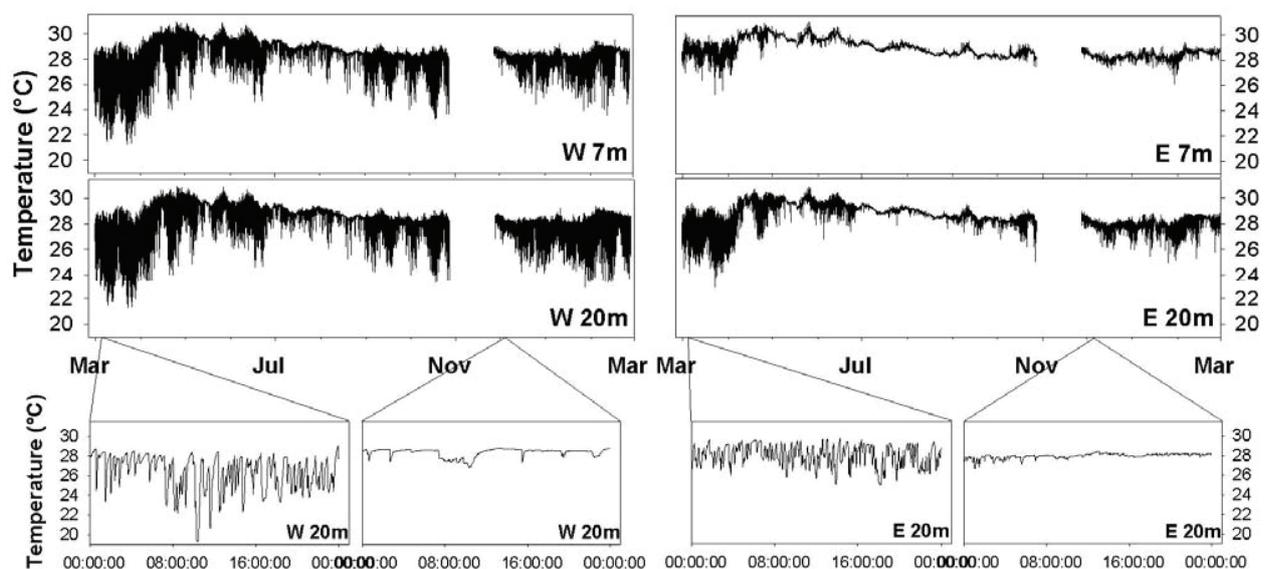


Figure 9: Large Amplitude Internal Wave (LAIW) associated temperature variations on W (left panels) and E sides of Similan Islands. Examples are given for temperature logger readings from LAIW-exposed (W 4.1) and sheltered (E 4.1) side of Koh Miang in 20 m and 7 m depth. Upper panels show full temperature record (March 2007 - March 2008; blank periods are missing values). Insets (lower panels) highlight 24 h-periods of high (March 2007) and low LAIW activity (December 2007), respectively, showing the frequency, intensity and duration of cold swells associated with LAIW.

Correlations and relationships of coral community parameters and cumulative temperature anomalies

Diversity (Shannon index) and species richness exhibited a clearly positive relationship with degree days cooling (DDC). Living coral cover as a fraction of the available hard substrate was inversely, but only weakly, related to DDC. This negative correlation became clearer after considering the depth gradient of DDC and living coral cover in the calculation comparing W and E (island Koh Miang, Table 5).

Table 5: Relationship between coral diversity and LAIW intensity. Linear regression model with Shannon index, Evenness, species richness and coral cover as dependent and degree days cooling (DDC in °Cd) as independent variables.

(Significance levels are $*0.05 > P \geq 0.01$, $**0.01 > P \geq 0.001$, $***P < 0.001$)

	Dependent variable	N	Intercept a	Slope b ± s.e.	R ²	P
all sites	Shannon Index, H _k	10	1.55	-0.007 ± 0.003	0.40	< 0.05*
	Evenness, E _k	10	0.61	-0.001 ± 0.000	0.07	0.46
	Species richness, S	10	10.39	-0.197 ± 0.053	0.63	< 0.01**
	coral cover as fraction of hard substrate	10	0.58	0.001 ± 0.000	0.13	0.29
Koh Miang	coral cover as fraction of hard substrate	6	0.65	0.002 ± 0.001	0.42	0.08

Discussion

Although non-linear Large Amplitude Internal Waves (LAIW, or solitons) have been known for decades from the Andaman Sea (Perry & Schimke 1965, Osborne & Burch 1980) and many other tropical oceans (Jackson 2004), our report is the first to date to establish their existence in islands bordering the Andaman basin, and the first to investigate their relation with coral communities. The frequency and severity of the temperature variations in our study exceed by far the moderate and lower-frequency variations reported earlier elsewhere (Leichter et al. 1996, 2003, Leichter & Genovese 2006), and rank among the largest short-term variations so far reported in tropical reef areas (Sheppard 2009). Although some of the LAIW's energy was found to wrap around the islands, evidenced by the dampened oscillations in our deep E temperature loggers, the deep ocean-facing W sides of the islands were most profoundly affected. Superimposed on the violent short-term

variations in the temperature time-series were lower-frequency variations (spring-neap time and seasonal) revealing highest LAIW-activities after spring tides and during the late NE monsoon (March, Fig. 9). These modulations are related to variations in both, LAIW-generating and -propagating factors, i.e. tidal current variations at the generation sites, which vary with the lunar cycle (Pineda 1995) and the depth and strength of the seasonal pycnocline, where the shallow pycnocline during the NE monsoon (Nielsen et al. 2004) corresponds with strongest LAIW activity. While many of the internal waves reported in the literature are linear phenomena raising and depressing the thermocline over tidal periods (Garrett & Munk 1979, Alpers 1985), the non-linear LAIW recorded in this study cause much larger temperature variations on much smaller time-scales. The source depth of the coldest water reaching the reef (up to 10 °C below ambient) can be estimated from the 18 °C isotherm in the Andaman Sea, which oscillates between 100 and 150 m (Nielsen et al. 2004). The actual depth may be much deeper, depending on the degree of turbulent mixing of the cold bores with above-thermocline waters (Vlasenko & Hutter 2002).

Tropical hermatypic corals are known to occur over a wide geographical range of temperatures (e.g. up to 12 °C differences in maximum summer temperatures for species co-occurring in the Arabian Sea and Lord Howe Island, Australia (Hughes et al. 2003), tolerate large annual ranges of temperature (up to 25 °C) and survive severe cold periods (13 °C for several days; Coles and Fadlallah 1991)). Yet it has been shown in several studies that cold water stress (starting with 6 to 10 °C under normal conditions) has a strongly negative influence on the outward appearance of corals and their physiology (Coles & Fadlallah 1991), on the sensitive association with their endosymbiotic zooxanthellae (Gates et al. 1992), that it can decrease the photosynthetic performance of a coral (Saxby et al. 2003), and undermine the development of dense coral reef formations (Burns 1985, Kleypas et al. 1999). These reports support the assumption that the reduced coral cover in W 20 m depth and the absence of reef framework in W may be partly due to the observed temperature oscillations.

However the cold temperatures in our study are only one stressor out of many co-occurring environmental factors: Temperature was related to the other environmental parameters in a conservative way with a strong positive correlation with oxygen and pH, negative correlation with several nutrients and salinity, and concomitant increases in current speeds (Table 4).

Dennison & Barnes (1988) have shown that high current speeds enhance photosynthesis and calcification by scaling down the boundary layer adjacent to the coral surface and increasing gas exchange. The combination of higher current velocities and nutrient concentrations can enhance

coral nutrient uptake (Hearn et al. 2001) and photosynthesis (Szmant 2002). The latter can be highest in cooler water (23 to 26 °C, Al Horani 2005) suggesting that the negative effect of low oxygen concentrations in LAIW waters could be counterbalanced by the photosynthetic oxygen production by the corals (Shashar et al. 1993). The nutrient concentrations measured at the Similan islands during a typical high LAIW-period (February, March 2007) led to mean concentrations for nitrate, nitrite and phosphate in W clearly above the averaged concentrations of most tropical reefs and close to or even above the extreme values assessed for coral reef communities (Table 4 B; Kleypas et al. 1999). Increased concentrations of these nutrients entail neutral or positive effects on coral nutrition (as mentioned above), physiology and zooxanthellae numbers (Muscatine et al. 1989, Ferrier-Pages et. 2001). However, they are likely dwarfed by the negative indirect effect of nutrients on the balance between corals and space-competing macroalgae. Raised nutrient concentrations in the water can favour growth and expansion of turf- and macroalgae, known to be competitors of corals in the struggle for light and space (Williams and Carpenter 1988, McCook 1999). Nutrient-enhanced pelagic productivity may further enhance internal bioerosion of coral skeletons and the reef framework, since the majority of endolith bioeroders are suspension or filter feeders (Glynn 1997, Chazottes et al. 2002, Ward-Paige et al. 2005).

The abrupt drops in pH and oxygen concentrations delivered with the cold water were found to create short-term conditions in W with decreased pH-values of 0.2 to 0.6 units and frequently more than half of the common oxygen concentrations (Table 4 A). These effects in combination with reduced light intensities in W (Table 4 C) may limit or at least strongly reduce coral growth, i.e. calcification and photosynthesis compared to their eastern counterparts as photosynthesis and calcification are tightly coupled in zooxanthellate scleractinian corals and suffer from reduced aragonite saturation states (lowered pH) and light levels (Gattuso et al. 1999, Marubini et al. 2001). Laboratory experiments on coral calcification and photosynthesis by Schneider & Erez (2006) revealed that pH reduced by only 0.2 units might implicate a 30 % reduction of CO_3^{2-} and decrease calcification by 50 %. On the other hand especially the reduced light intensities in W deep might favour the successful toleration of the low temperatures by corals as Coles & Jokiel (1978) already demonstrated the highly negative effects of combined low temperatures and high light intensities leading to a substantial deterioration of the coral host metabolism and to significantly higher mortality rates.

Salinity concentrations, although highly correlated with temperature, always stayed within a range of 32.6 and 34.4 ppm, which is normal for tropical reef conditions (Kleypas et al. 1999), and therefore was not estimated as an important community shaping factor in our study.

The lack of difference in suspended particulate matter concentrations (Table 4 B) between W and E and the apparent independence of temperature variations (see also optical backscatter, Table 4 A) appears inconsistent with the pronounced differences in the physical oceanographic variables, suggesting other processes than mixing to be involved.

Higher concentrations of chlorophyll transported into shallow areas with LAIW-arrival were found in our study and also stated by Leichter et al. (1996) to come from thermocline waters. However sub-thermocline layers contain low pH and oxygen depleted waters. This could possibly lead to a mutual compensation of depletion processes (low oxygen) and production processes (plankton production due to higher nutrient concentrations (Eppley et al. 1979)) and could be a reason for the lack of difference in dissolved organic matter concentrations between W and E.

As almost all LAIW-induced changes in seawater properties (i.e. cold, low-oxygen, low-pH waters with high nutrient loads) are reported to have adverse effects on corals, both directly, by stressing their physiological and metabolic conditions, and indirectly, by promoting coral competitors such as algae and bioeroders, these potential stressors may act synergistically to exert a cumulative pulsed disturbance on the LAIW-exposed coral communities.

While light and hydrodynamics are known as the most prominent physical factors shaping coral morphologies, species distributions and reef structures across depth (Falkowski et al 1990, Massel & Done 1993), it is important to note that the LAIW-impact represents a vertical gradient in the opposite direction. Both, SW monsoon and LAIW impart their strongest impact on the W faces of the islands; but the force of monsoonal surface waves declines exponentially with increasing depth (Thorpe 2007), while the impact of LAIW increases. The cumulative impact of SW monsoon and LAIW-disturbances on the Similan islands coral communities is conceptualized in Fig. 10. Although surface and internal waves are only two out of numerous environmental and biological disturbances affecting benthic communities on various spatial and temporal scales (i.e. disturbances caused by grazing and trophic cascades (Mumby et al. 2006) terrestrial runoff and sedimentation (Cole 2003, Fabricius 2005), or eutrophication (Tomascik & Sander 1987, Szmant 2002), they provide a useful framework for understanding the rather striking differences in coral community composition and reef development in our study. Overall levels of wave disturbances are higher on the W faces of the islands than on the E, and higher on the upper and lower margins of the depth gradient. As a result,

low levels of disturbance are found on the E, intermediate levels in intermediate depths of W, and high levels of disturbance on W-shallow and W-deep (see also cooling rates, CRs, Table 3 and temperature record supplemental Fig. 4).

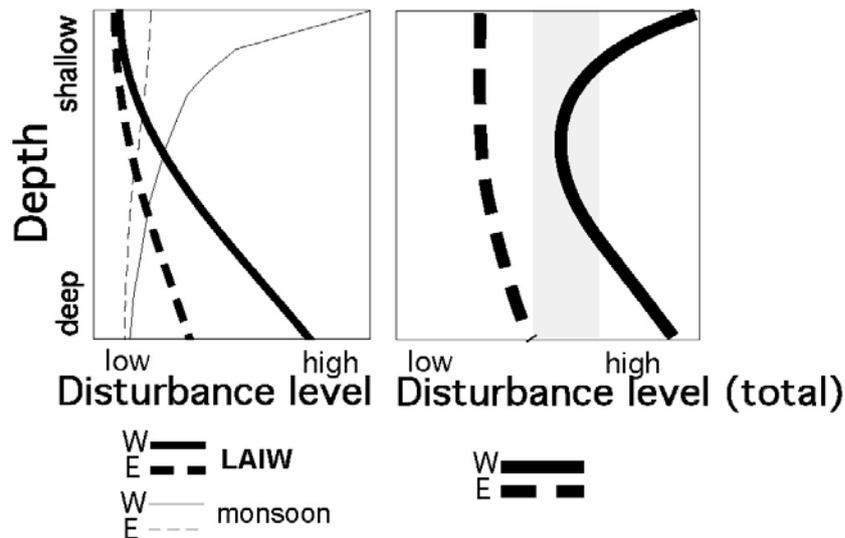


Figure 10: Graphic description of the separated (left panel) and cumulative effects of the disturbance by LAIW-impact, and by monsoon waves at W and E sides of Similan islands.

The highest level of coral diversity in our study corresponds to intermediate levels of disturbance as theory predicts: Connell (1978, 1979) suggested that highest number of coral species will be reached at intermediate levels (frequency and size) of natural disturbance. Lower diversity results if disturbances which are either too frequent or too infrequent, or too large or too small. Accordingly he found (Connell 1997) that coral communities exposed to acute pulsed short-term disturbances rather than to chronic long-term ones are able to recover faster and more completely and develop highly diverse communities. The observed extreme conditions in the chemical and physical environment in our study concurring with the pulsed LAIW-impacts are replaced each time within 15 to 30 min by again moderate water conditions (lower panels Fig. 9; nearly identical modal temperature values on W and E: Table 3). These acute disturbances are likely to be stressful to the corals, as discussed above, but their intermittent and short-termed character seems to prevent physiological damage and mortality observed for longer-term disturbances following cold spells (Coles & Fadlallah 1991) or eutrophication (Szmant 2002). The alternation of storm and LAIW impact during the SW (May to October, Phongsuwan & Chansang 1986) and NE monsoon (February, March, see Fig. 9) periods, respectively, may also create seasonal periods of recovery for

the affected shallow and deep fore-reef areas, respectively. We therefore propose that in intermediate depths in W, the alternating impact of SW monsoon and LAIW from above and below, respectively, contribute to a spatio-temporal heterogeneity maintaining the community in a non-equilibrium state, resetting succession and enhancing species diversity. The sheltered E reefs which are only some hundred meters apart from their western counterparts reside in sheltered tropical reef conditions, where the lack of environmental disturbances prevents the destruction or removal of species monopolizing the space, and diversity is lowered (Fig. 4). Similarly Rogers (1993) and Aronson & Precht (1995) found that there is need of i.e. storm-generated disturbances to possibly reduce the cover of dominant coral species allowing competitively subordinate species to increase.

The hampered reef development in W shallow and deep contrasting the areas in E (Fig. 7) reflects apparently too high levels of disturbance to build and maintain an actual reef framework. Based on regional climatology (Brown 2007) and previous investigations in the area (Phongsuwan & Chansang 1986, Phongsuwan 1991) the impact of strong surface gravity waves during the SW-monsoon periods is strongest along W shallow reef areas. Corals there grow nestled and disjointed directly to the granite basement to shelter from the waves' impact and to reduce physical damage (Storlazzi et al. 2005). In deeper W, the greater distance between single coral stands and the reduced number of branching species as framework spacers and builders lead to the lack of reef development (Fig. 8) due to the strongest impact of combined negative stressors (reduced light, temperature, oxygen, pH and increased nutrient concentrations, discussed above) coinciding with the frequently strong swell-like currents of LAIW-arrivals. Although it was possible, for logistic limitations, to quantify these findings for only one of the nine islands, the same pattern was evident throughout the Similans (N. Phongsuwan, G. Schmidt, pers. observations). Hence high levels of disturbance by surface waves in shallow W and LAIW in deep W inhibit reef framework building due to their chronically disturbing character. It is noteworthy that this lack of destructible reef formations was the reason for the comparatively low destructive impact of the Indian Ocean tsunami in 2004 on Similan island reefs (Phongsuwan et al. 2006, Phongsuwan & Brown 2007). The tsunami struck the island chain from the SW and caused only small scale and patchy destruction patterns in E reefs with an initial total of 31.6 % damage (high damage (> 50 %): 18.4 %, moderate damage (31 – 50 %): 13.2 %, Plathong 2005, Yeemin 2006).

In this context it needs to be mentioned that these striking W-E differences in reef development (Fig. 1, Fig. 7) were not fully captured in the line intercept transects (LIT, Loya and Slobodkin 1971, Loya 1972, 1976). The LIT's original strength to reduce the complexity of a three-dimensional coral

community into a two-dimensional measure is not convenient when organisms expand in a two-dimensional plane as in our study.

The composition of a coral community reflects the net result of the governing physical, chemical and biological drivers (Fishelson 1973, Loya 1975, De Vantier et al. 1998). Corals growing along the W of Similan islands are exposed to an extraordinary stressful physico-chemical environment to which they obviously adapted. We therefore propose that these coral assemblages could provide a clue to coral resilience in an era of global temperature increase and ocean acidification due to their successful and potentially variegated adaptation processes to this cocktail of LAIW-pulsed low temperature, low pH, low oxygen and high nutrient conditions. LAIW are a ubiquitous phenomenon in SE Asia and beyond (Jackson 2004), yet they have not been considered with the so far adequate attention regarding their strong effects on coral reef communities.

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Supplemental data Chapter V

Supplemental table 1: Benthic composition at Similan islands on LAIW-exposed (West), and sheltered (East) sides in 12 to 16 m depth. Data displayed as mean (\pm SE).

substrate	cover [%]		
	all sites	West	East
hard substrate			
living coral, dead coral, rock	67.73 (3.18)	67.71 (6.59)	72.83 (3.34)
living coral	26.35 (3.25)	25.57 (4.22)	35.95 (4.62)
dead coral	36.58 (2.94)	34.06 (5.51)	36.87 (3.44)
rock	4.81 (3.27)	8.09 (8.00)	0.00 (0.00)
sand and loose coral fragments	30.15 (3.25)	29.75 (6.89)	25.88 (3.29)
algae	0.43 (0.14)	0.20 (0.07)	0.50 (0.24)
sponge	0.31 (0.13)	0.39 (0.30)	0.10 (0.07)
other	0.32 (0.22)	0.00 (0.00)	0.39 (0.37)

Supplemental table 2: Summary of presence and absence of hard coral species with an approximate quantitative assessment of the proportion of the total substrate cover measured with one 100 m line intercept transect in 12 to 16 m depth on LAIW-exposed (West), and sheltered (East) sides.

(cover [%]): • 0 - 1, ● 1.01 - 5, ● 5.01 - 10, ● 10.01 - 20, ● >20

coral taxa	West								East								
	W2.1	W4.1	W7.1	W8.1	W8.2	W8.3	W9.1		E1.1	E2.1	E4.1	E4.2	E7.1	E8.1	E8.2	E8.3	E9.1
<i>Acropora austera</i>	•		•	•	•		•						•				•
<i>Acropora clathrata</i>	●	•	●	•	•	•	•		•				•		•	•	•
<i>Acropora cytheria</i>	•																
<i>Acropora divaricata</i>	•										•		•				
<i>Acropora danei</i>	•		•		•				•				•				•
<i>Acropora echinata</i>											•		•				•
<i>Acropora elseyi</i>														•	•		
<i>Acropora formosa</i>							•		•							•	
<i>Acropora florida</i>		•							•				•				•
<i>Acropora gemmifera</i>	•				•						•						
<i>Acropora grandis</i>									•						•		
<i>Acropora granulosa</i>												•					
<i>Acropora hoeksemai</i>																	
<i>Acropora humilis</i>	•	•	•		•	•	•				•						•
<i>Acropora hyacinthus</i>								•									
<i>Acropora kosurini</i>					•												
<i>Acropora longicyathus</i>											•						
<i>Acropora microphthalma</i>								•									
<i>Acropora monticulosa</i>																	
<i>Acropora nasuta</i>														•			
<i>Acropora nobilis</i>					•		•										•
<i>Acropora palifera</i>	•	•	•		•	•	•		•			•	•				•
<i>Acropora robusta</i>					•												
<i>Acropora rudis</i>		•															
<i>Acropora samoensis</i>																	•
<i>Acropora secale</i>											•						
<i>Acropora selago</i>															•		
<i>Acropora subglabra</i>												•					
<i>Acropora subulata</i>										•							•
<i>Acropora tenuis</i>		•	•	•		•					•		•			•	•
<i>Acropora yongei</i>				•				•									
<i>Acropora</i> sp. (casepitose form)																	
<i>Acropora</i> sp.1 (corymbo-tabulate)	•	•	•														
<i>Acropora</i> sp.2 (corymbo-tabulate)	•	•															
<i>Acropora</i> sp. (juvenile)												•		•	•		
<i>Acropora</i> sp.																	
<i>Astreopora myriophthalma</i>														•			
<i>Astreopora</i> sp.		•	•														
<i>Coeloseris mayeri</i>			•	•	•	•	•		•	•		•	•	•			•
<i>Cyphastrea</i> sp.	•	•	•	•	•	•	•		•	•	•	•	•	•			•
<i>Diploastrea heliopora</i>	•			•	•	•	•		•	•	•	•	•			•	•
<i>Echinophyllia aspera</i>		•															
<i>Echinopora horrida</i>																	•
<i>Echinopora lamellosa</i>					•				•	•			•				
<i>Echinopora gemmacea</i>						•	•		•		•						
<i>Favia amicornum</i>							•										
<i>Favia helianthoides</i>	•																

Supplemental table 2 continued

coral taxa	West								East								
	W2.1	W4.1	W7.1	W8.1	W8.2	W8.3	W9.1	E1.1	E2.1	E4.1	E4.2	E7.1	E8.1	E8.2	E8.3	E9.1	
<i>Favia matthaii</i>		
<i>Favia pallida</i>				.									.				
<i>Favia pallifera</i>		.															
<i>Favia speciosa</i>		.															
<i>Favia stelligera</i>													.		.	.	
<i>Favia</i> sp.	
<i>Favites abdita</i>	•	
<i>Favites pentagona</i>	.	.		.													
<i>Favites</i> sp.	.						.										
<i>Fungia echinata</i>												.		.			
<i>Fungia fungites</i>											.					.	
<i>Fungia paumotensis</i>												.					
<i>Fungia repanda</i>												.					
<i>Fungia scutaria</i>								.									
<i>Fungia</i> sp.				.			.										
<i>Galaxea fascicularis</i>				.													
<i>Gardineroseris planulata</i>	
<i>Goniastrea pectinata</i>			.	•	
<i>Goniastrea retiformis</i>								.				.		.			
<i>Goniopora burgosi</i>														.			
<i>Goniopora lobata</i>						.	.						.				
<i>Goniopora stutchburyi</i>					.							.					
<i>Goniopora</i> sp. -massive								.									
<i>Goniopora</i> sp -soft med									.								
<i>Goniopora</i> sp.			.		.												
<i>Heliopora coerulea</i>						.	.				•	•			.		
<i>Herpetoglossa simplex</i>															.		
<i>Herpolitha limax</i>			.									.					
<i>Hydnophora exesa</i>					.												
<i>Hydnophora microconos</i>						
<i>Hydnophora rigida</i>				•				•		.		•		.	.	.	
<i>Leptastrea</i> sp.	
<i>Leptoria phrygia</i>	
<i>Leptoseris mycetoseroides</i>		
<i>Leptoseris</i> sp.																	
<i>Merulina ampliata</i>		
<i>Millepora tenella</i>	•													.		•	
<i>Millepora exaesa</i>	•			
<i>Millepora platyphylla</i>				
<i>Millepora</i> sp. - encrust										.						.	
<i>Montastrea valenciennesi</i>				.												.	
<i>Montastrea</i> sp.	.			.				.									
<i>Montipora aequituberculata</i>			.		.				.								
<i>Montipora calculata</i>	
<i>Montipora corbettensis</i>						.											
<i>Montipora danae</i>		.															
<i>Montipora efflorescens</i>				
<i>Montipora foveolata</i>		.															
<i>Montipora hispida</i>	.		.		•						.						
<i>Montipora informis</i>		
<i>Montipora peltiformis</i>				.	.												
<i>Montipora tuberculosa</i>	

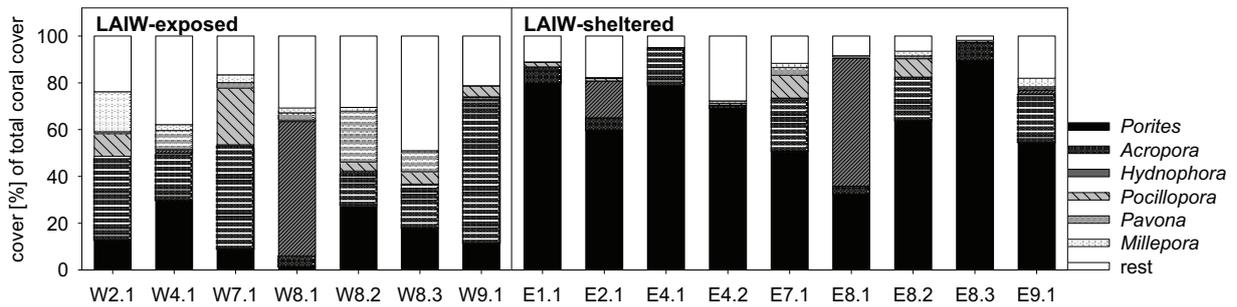
Supplemental table 2 continued

coral taxa	West								East								
	W2.1	W4.1	W7.1	W8.1	W8.2	W8.3	W9.1	E1.1	E2.1	E4.1	E4.2	E7.1	E8.1	E8.2	E8.3	E9.1	
<i>Montipora venosa</i>							•										
<i>Montipora</i> sp. -encrust	•	•	•	•	•	•	•	•			•					•	
<i>Montipora</i> sp.2 encrust							•									•	
<i>Montipora</i> sp.3 - encrust							•									•	
<i>Montipora</i> sp.4 - encrust							•									•	
<i>Montipora</i> sp. -massive					•			•		•			•				
<i>Montipora</i> sp.		•		•												•	
<i>Pachyseris speciosa</i>							•							•			
<i>Pavona clavus</i>					•												
<i>Pavona decussata</i>		•			•	•											
<i>Pavona duerdeni</i>				•													
<i>Pavona explanulata</i>		•			•			•						•			
<i>Pavona madivensis</i>					•												
<i>Pavona minuta</i>	•		•				•										
<i>Pavona varians</i>	•	•	•	•	•	•	•	•	•		•	•	•	•		•	
<i>Pavona venosa</i>	•			•	•												
<i>Pectinia</i> sp.												•					
<i>Physogyra litchtensteini</i>										•							
<i>Platygyra daedalea</i>	•	•		•	•	•					•						
<i>Platygyra lamellina</i>		•														•	
<i>Platygyra sinensis</i>		•					•										
<i>Pleasiastrea versipora</i>		•															
<i>Pocillopora damicornis</i>			•				•		•				•	•			
<i>Pocillopora eydouxi</i>	•	•	•	•	•	•	•	•			•	•					
<i>Pocillopora meandrina</i>	•		•		•	•	•	•	•			•	•			•	
<i>Pocillopora verrucosa</i>	•						•	•	•					•	•		
<i>Podabacia crustacea</i>																	
<i>Polyphyllia talpina</i>				•													
<i>Porites annae</i>					•											•	
<i>Porites cylindrica</i>								•	•					•	•	•	
<i>Porites lobata</i>																•	
<i>Porites lutea</i>	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	
<i>Porites nigrescens</i>					•	•		•	•	•	•	•			•		
<i>Porites stephensoni</i>	•	•	•		•	•	•	•	•		•	•	•	•	•	•	
<i>Porites</i> sp. -massive								•									
<i>Porites (Synaraea) rus</i> - branching	•		•		•	•		•	•	•	•	•	•	•	•	•	
<i>Porites (Synaraea) rus</i> - columnar						•		•	•	•		•		•	•	•	
<i>Psammocora digitata</i>					•			•			•						
<i>Psammocora profundacella</i>		•															
<i>Seriatopora hystrix</i>																	
<i>Stylocoeniella quentheri</i>		•														•	
<i>Stylocoeniella</i> sp.																	
<i>Stylophora pistillata</i>	•	•	•	•		•					•	•					
<i>Symphyllia agaricia</i>	•				•												
<i>Symphyllia radians</i>	•	•		•			•										
Total	42	44	32	36	48	33	29	32	18	14	30	27	35	21	18	48	

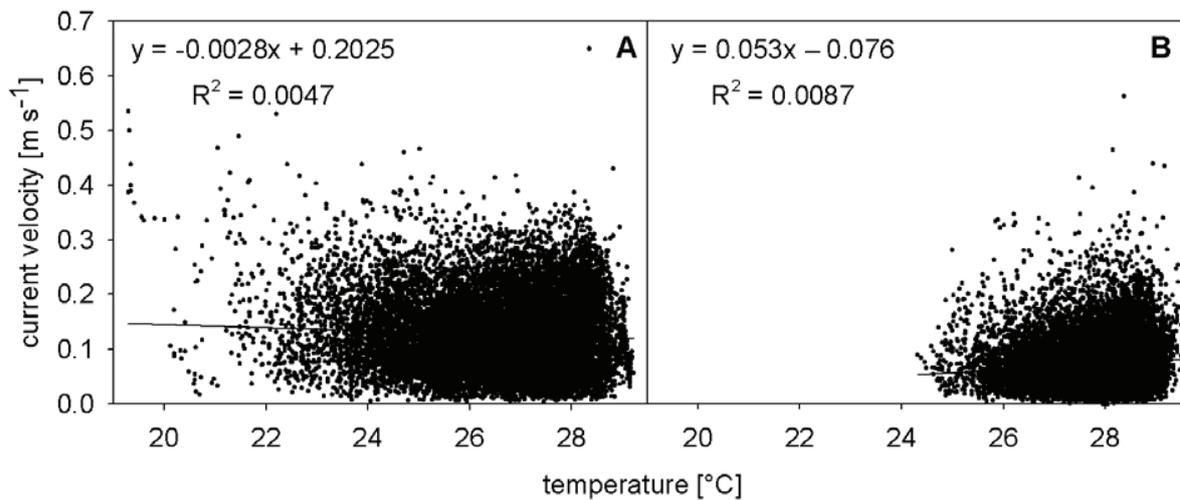
Supplemental table 3: Environmental parameters at Koh Miang (W 4.1, E 4.1). Results of non-parametric Kruskal-Wallis ANOVA by ranks (p-values, significance levels). **(A)** Water current measured continuously every minute over period of 4 weeks (February, March 2007), **(B)** light values (lux [lm m^{-2}]) recorded over period of 4 months (December 2007 to April 2008), and **(C)** parameters determined from water sample analyses collected in February, March 2007.

(Significance levels are $*0.05 > P \geq 0.01$, $**0.01 > P \geq 0.001$, $***P < 0.001$)

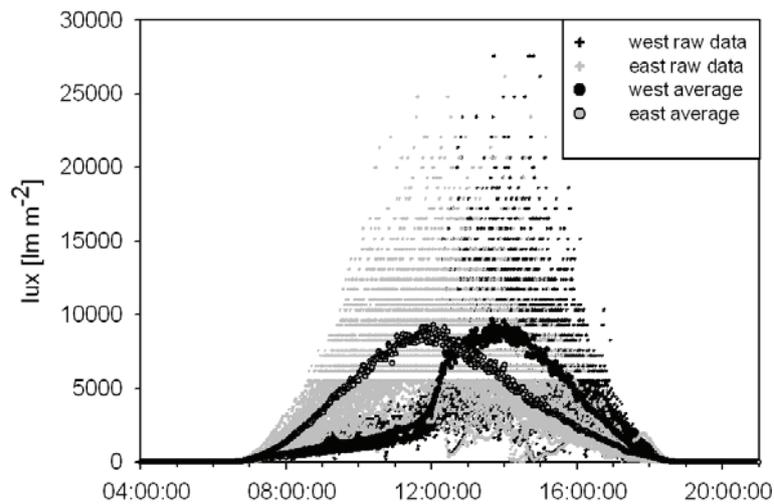
A Current velocity [m s^{-1}]					B lux [lm m^{-2}]				
Kruskal-Wallis test					Kruskal-Wallis test				
	W 20 m	W 7 m	E 20 m	E 7 m		W 20 m	W 7 m	E 20 m	E 7 m
W 20 m					W 20 m				
W 7 m	n.s.				W 7 m	0.000***			
E 20 m	0.000***	0.000***			E 20 m	0.000***	0.000***		
E 7 m	0.000***	0.000***	0.000***		E 7 m	0.000***	0.000***	0.000***	
C Si(OH)_4 [$\mu\text{mol L}^{-1}$]					PO_4^{3-} [$\mu\text{mol L}^{-1}$]				
Kruskal-Wallis test					Kruskal-Wallis test				
	W 20 m	W 7 m	E 20 m	E 7 m		W 20 m	W 7 m	E 20 m	E 7 m
W 20 m					W 20 m				
W 7 m	n.s.				W 7 m	n.s.			
E 20 m	0.04**	n.s.			E 20 m	n.s.	n.s.		
E 7 m	0.000***	n.s.	n.s.		E 7 m	n.s.	n.s.	n.s.	
$\text{NO}_2^- + \text{NO}_3^-$ [$\mu\text{mol L}^{-1}$]					NH_4^+ [$\mu\text{mol L}^{-1}$]				
Kruskal-Wallis test					Kruskal-Wallis test				
	W 20 m	W 7 m	E 20 m	E 7 m		W 20 m	W 7 m	E 20 m	E 7 m
W 20 m					W 20 m				
W 7 m	n.s.				W 7 m	n.s.			
E 20 m	n.s.	n.s.			E 20 m	n.s.	n.s.		
E 7 m	0.007**	n.s.	n.s.		E 7 m	n.s.	n.s.	n.s.	
Dissolved organic carbon [ppm]					Suspended particulate matter [mg L^{-1}]				
Kruskal-Wallis test					Kruskal-Wallis test				
	W 20 m	W 7 m	E 20 m	E 7 m		W 20 m	W 7 m	E 20 m	E 7 m
W 20 m					W 20 m				
W 7 m	n.s.				W 7 m	n.s.			
E 20 m	n.s.	n.s.			E 20 m	n.s.	n.s.		
E 7 m	n.s.	n.s.	n.s.		E 7 m	n.s.	n.s.	n.s.	



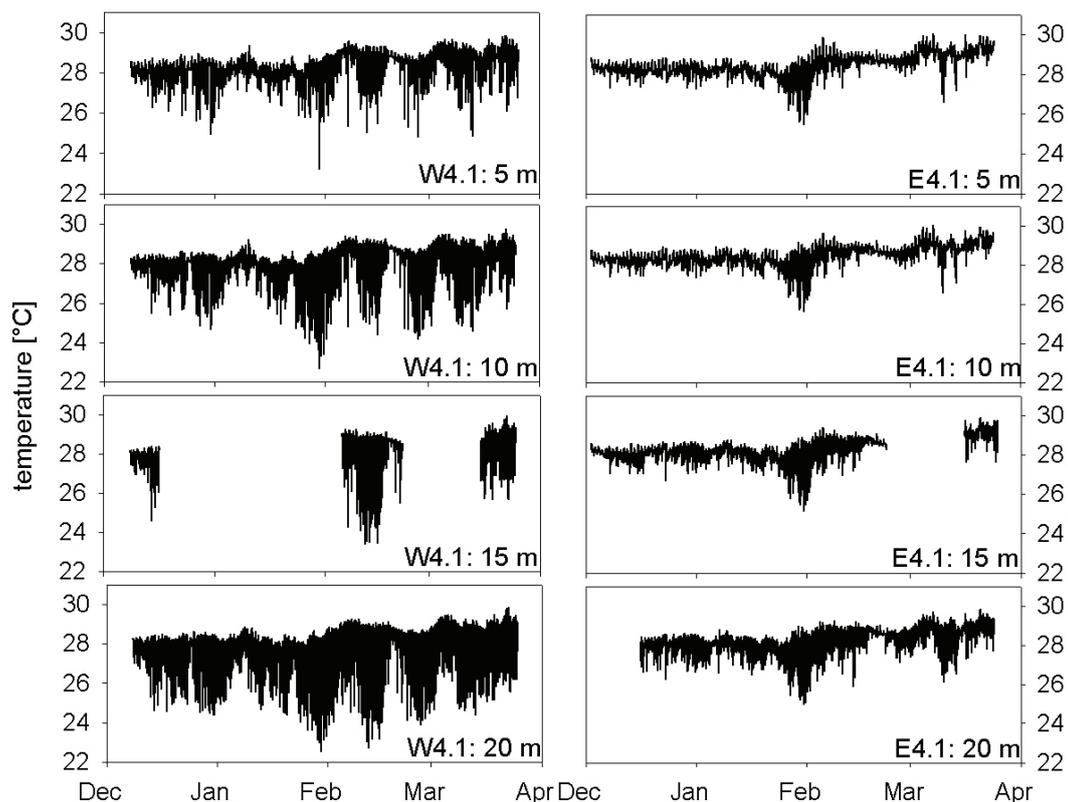
Supplemental figure 1: Most abundant genera of stony corals as percentage of living coral cover on LAIW-exposed west (W), and east (E) sides (12 to 16 m depth, grouped by N-S orientation).



Supplemental figure 2: Relationship between current velocity and temperature. Linear regression model with current velocity as the dependent, and temperature as the independent variable ($p < 0.001$): **A**) West and **B**) East, both in 20 m depth.



Supplemental fig 3 Daily light curve at Koh Miang. Loggers were fixed in 7 m depth on W and E side (W 4.1, E 4.1) over period of 30 days in February, March 2007; sample interval 1 min, raw data in background, mean values calculated for every daily analogue minute over whole sample period.



Supplemental fig 4 Large Amplitude Internal Wave (LAIW) associated temperature variations at the Similan Islands. Examples are given for temperature logger readings from LAIW-exposed (W 4.1) and sheltered (E 4.1) sides of Koh Miang in 20 m (within LAIW swash depth) 15 m and 10 m (intermediate LAIW exposure) and 7 m (beyond the reach of LAIW swash zone) depth. Panels show full temperature record (December 2007 - April 2008; blank periods are missing values).

- Chapter VI -

1A

**Riverine input of particulate material and
inorganic nutrients to a coastal reef ecosystem at
the Caribbean coast of Costa Rica**

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1B

**Tracing the extend of fertilizer input on coral
metabolism**

Additional information on Roder et al., 2009

- chlorinated hydrocarbons in sediments and tissues using accelerated solvent extraction and gas chromatography/mass spectrometry. In: Ostrander, G.K. (Ed.), *Techniques in Aquatic Toxicology*, vol. 2. CRC Press, Boca Raton, FL (Chapter 35).
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1A

Riverine input of particulate material and inorganic nutrients to a coastal reef ecosystem at the Caribbean coast of Costa Rica

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Reasons for the alarming global coral reef destruction can often be found on land (ISRS, 2004). Agricultural activities accompanied by land clearing, fertilization, use of pesticides, and urbanization or tourism expansion along with enhanced sewage and waste production are of concern (ISRS, 2004). Rivers and groundwater carry high loads of sediment, nutrients and other pollutants to the sea, where they can have serious impacts on nearshore ecosystems such as coral reefs (Cortés and Risk, 1985; Guzmán and Jiménez, 1992; Rogers, 1990; Fabricius, 2005).

While nutrients enhance coral growth in lower amounts, they inhibit it when highly concentrated (Tomascik and Sander, 1985; Koop et al., 2001), and accelerate the progress and severity of coral disease (Bruno et al., 2003; Voss and Richardson, 2006). Nutrients fuel algal growth and, combined with reduced herbivory, can be responsible for shifts from coral- to algal-dominated reefs (Díaz-Pulido and McCook, 2003; Hughes et al., 2003). Also bioeroders such as algae, sponges, worms or bivalves profit from nutrient and organic matter increase (Risk and MacGeachy, 1978). Bored

sediments and corals are less resistant to storms and waves, resulting in reef erosion (Hallock, 1988; Chazottes et al., 2002).

Suspended matter in the water column decreases transparency and light availability. While organic material may initially be used as an additional food source by corals, this benefit is outweighed in turbid water, where photosynthesis and calcification are reduced (Rogers, 1983; Anthony and Fabricius, 2000). Smothering by particulate material forces the coral to clean its surface using energy needed for growth or reproduction (Tomascik and Sander, 1987; Edmunds and Davies, 1989). Terrestrial runoff can become a serious threat for reef communities and even small rivers have been shown to influence reefs within a few kilometers distance to their mouths (West and van Woesik, 2001; Fabricius, 2005).

The aim of this study was to evaluate the present influence of a heavily anthropogenic impacted river on the distribution of particulate material and dissolved inorganic nutrients in the waters of a nearby coral reef area in Costa Rica.

The Caribbean coast of Costa Rica is characterized by humid, hot climate with year-round rains of about 6000 mm (Cortés and Jiménez, 2003). Precipitation between December and February and between June and August is higher compared to the rest of the year. The largest, best-developed and most diverse reef in the area is found in the Cahuita National Park (Cortés and León, 2002;

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Cortés and Jiménez, 2003), which is located next to the village of Cahuita, 43 km south of Limón. It consists of three barriers arranged around the peninsula of the national park, the outer crest around the tip, the inner crest along the eastern, and a small barrier on the western side of the peninsula (Cortés and Risk, 1985).

North of Cahuita lays the Valle La Estrella, one of the largest banana cultivation areas of Costa Rica. The Estrella River, with a length of 61 km and a watershed of 745 km², is one of the longest rivers in this region (Mora-Cordero, 2005). It meanders through the cultivation areas and discharges about 10 km north of the Cahuita National Park (Fig. 1). The main current along the coast from the river to the national park runs from northwest to southeast (Cortés and Jiménez, 2003).

Water sampling took place in October 2004 (dry season) and in January 2005 (rainy season). Water transparency was measured using a Secchi disk. Samples for total suspended matter (TSM) and nutrient analyses were collected in 50 cm depth in the river station (1 km inland) and at each coastal station (Fig. 1). After filtration, TSM quantity was determined gravimetrically using dried (24 h at 40 °C), pre-weighed filters (Whatman GF/F). Total particulate carbon (PC) and nitrogen (PN) content and (after acidification with 0.1 M HCl) organic carbon (POC) content of TSM were determined with an Elemental Analyzer (NA2100 Protein). Nutrient samples were preserved with HgCl₂ (Kattner, 1999) and nitrite–nitrate (NO_x), silicate and phosphate concentrations measured using standard colorimetric methods (Grasshoff et al., 1983).

Sedimentation rates in the reefs were assessed by exposure of monthly-replaced sediment traps. Three vertically oriented PVC tubes (opening area of 24 cm² each) were placed in each reef at depths of 3.5–4 m. Grain size distribution (gravel >2 mm, coarse

sand >200 µm, fine sand >63 µm, silt and clay <63 µm) was determined by wet sieving. The barrier reef on the western side exposed to the river plume (Fig. 1, I) and the sheltered reef on the eastern side of the peninsula (Fig. 1, II) were sampled.

For the graphical display of the data the Ocean Data View program (Schlitzer, 2008) was used. After testing for normality and homogeneity of variance, *t*-tests were conducted to reveal significant differences of water transparency, TSM, PC, PN, POC, NO_x, silicate and phosphate between dry and rainy season at a level of $p < 0.05$. Linear regressions were conducted to reveal significant spatial trends (indicated by salinity). In the rainy season not all stations could be reached and only those sampled in both seasons were included in the calculations. One-way ANOVAs followed by Tukey's post hoc test at a level of $p < 0.05$ were used to detect differences in sedimentation rates over time.

Both water sampling periods (October 2004 and January 2005) coincided with extreme weather conditions in the region (data provided by the Instituto Meteorológico Nacional, Limón station). In October (dry season), rainfall was extremely low (80.7 mm) compared to average conditions (mean rainfall in October 1941–2005: 212 ± 109 mm). Precipitation in January (rainy season) reached a total of 907 mm, much higher than the mean rainfall in January during the period 1941–2005 (310 ± 126 mm).

Water transparency during the dry season (Fig. 2a) was low close to the mouth of the Estrella River, and lower close to the shore than further offshore. The increase in transparency with salinity was only significant in the dry season, as in the rainy season it only increased slightly with distance to the river mouth (Fig. 3). Compared to the dry season, transparency was significantly decreased in the rainy season and <4 m at all sampling stations ($p < 0.0001$).

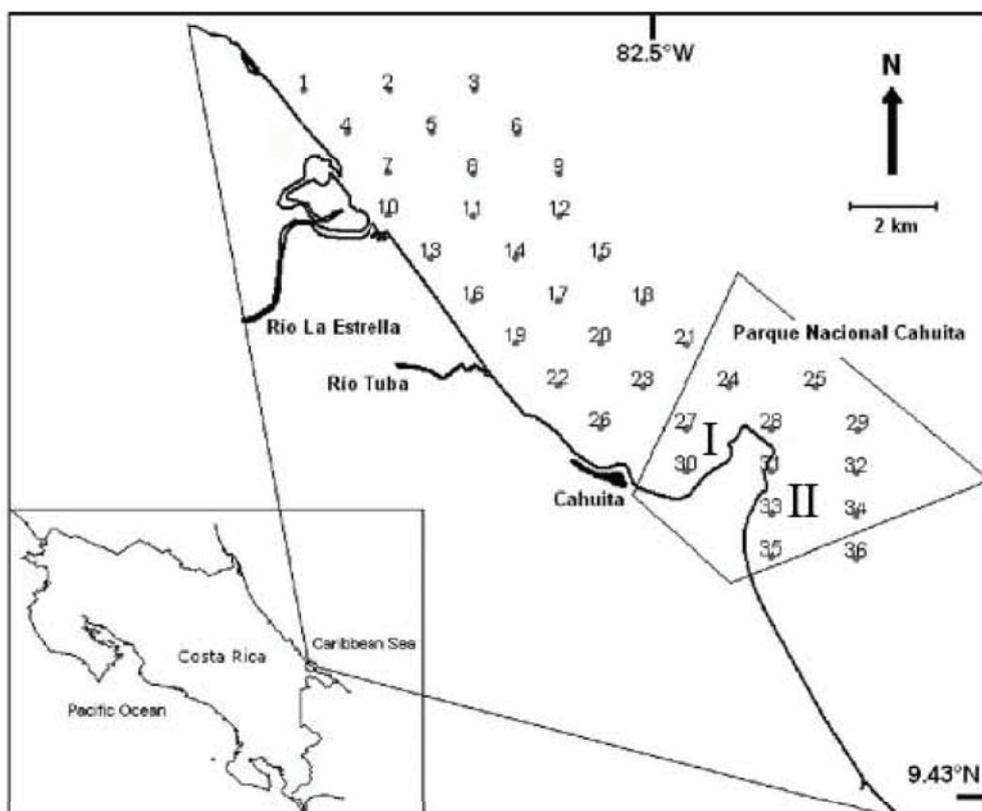


Fig. 1. Sampling area water sampling stations (1–36) and sediment sampling stations, (I) at the exposed side of the reef and (II) the sheltered side of the reef of the National Park Cahuita.

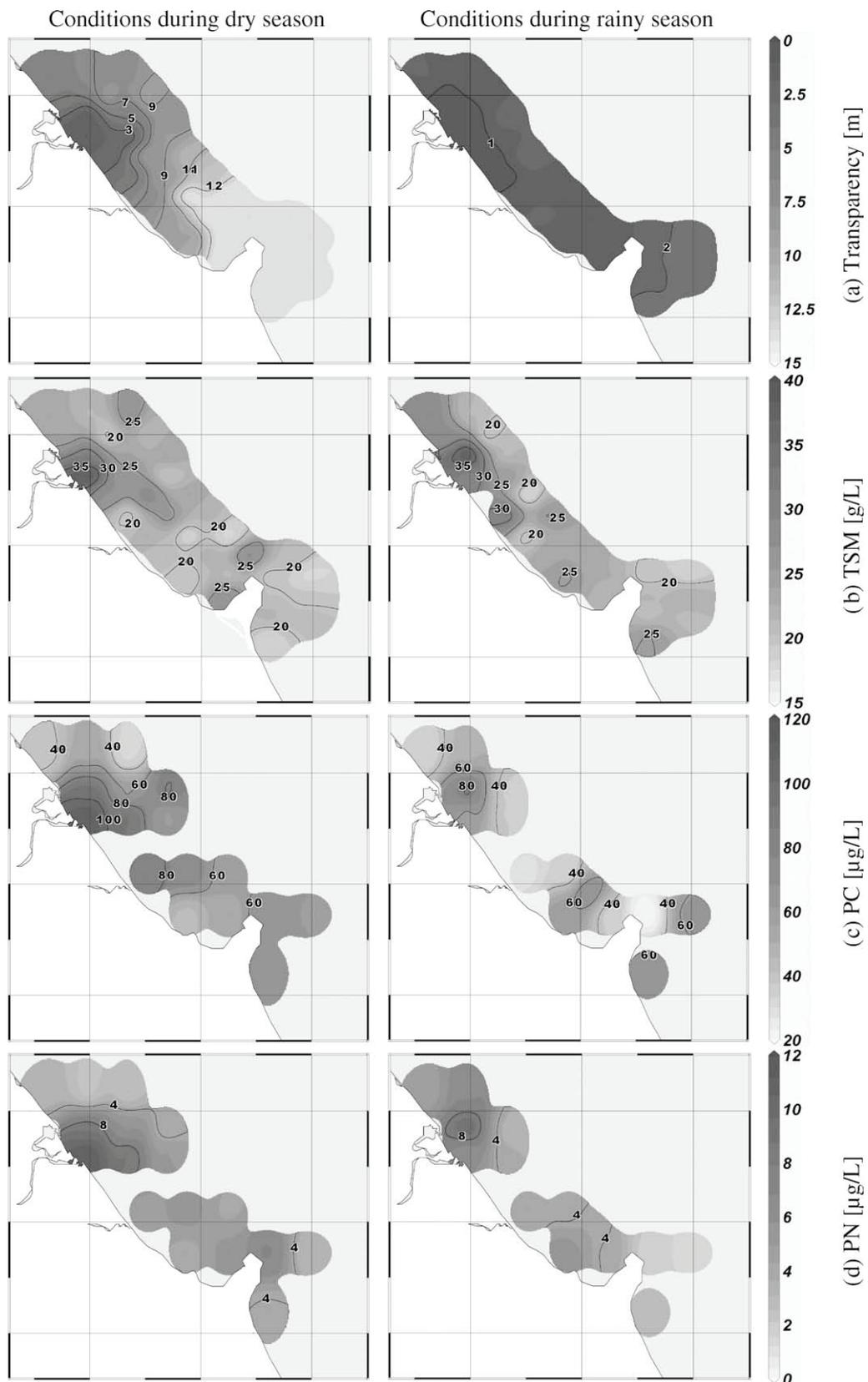


Fig. 2. Transparency and distribution of suspended material and dissolved inorganic nutrients in the study area.

TSM concentrations (Fig. 2b) in the dry season were highest in front of the river mouth and decreased significantly with distance along the coast and offshore (Fig. 3). In the rainy season, TSM con-

centrations again were highest at the river mouth (Fig. 2b) and generally higher than in the dry season (Table 1), but a significant difference to dry season values was not detected. PC, PN and POC

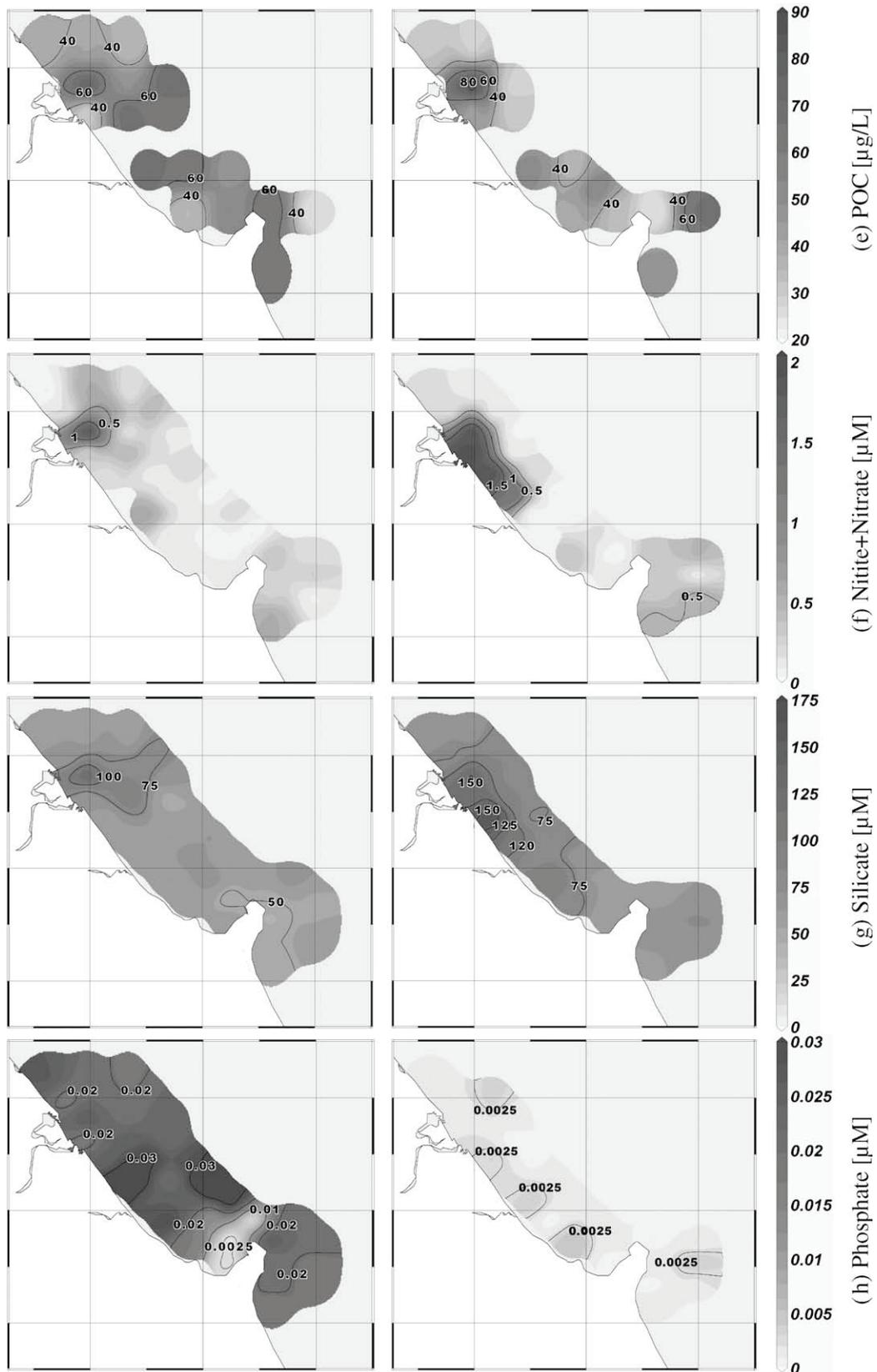


Fig. 2 (continued)

values were also highest in front of the river mouth in both seasons (Figs. 2c–e), but significant seasonal or spatial differences were not observed. Increased irradiation and water transparency with dis-

tance to the river mouth or during dry season enhance primary production and hence are likely to mask the input of particulate material to the coastal area. In the water samples taken at the river

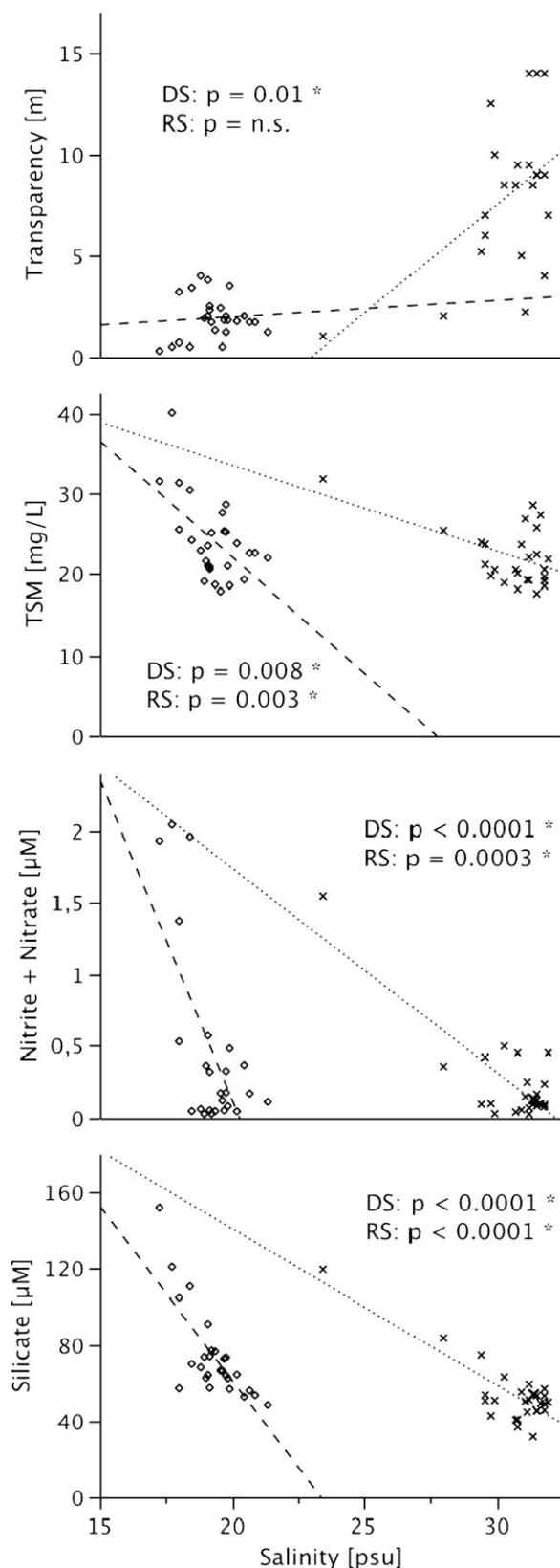


Fig. 3. Correlation of each parameter with salinity for spatial comparisons during dry (DS: crosses, dotted lines) and rainy season (RS: diamonds, dashed lines). Significant differences are marked with an asterisk; n.s., not significant.

station during rainy season, TSM concentrations were ~ 30 times, PC ~ 3 , PN ~ 2 and POC ~ 4 times higher than during dry season (Tables 1 and 2).

TSM concentrations in Cahuita National Park waters have previously been measured in the rainy season in 1979 and 1980 (Cortés and Risk, 1985), and in 1981 and 1993 (Cortés, 1993). Values at the outer reef crest, east of the peninsula, and in the Estrella River in 1979/1980 are lower than those observed in this study (Table 1). In 1981 and 1993, Cortés (1993) reported TSM concentrations $< 10 \text{ mg L}^{-1}$ in the stations near Cahuita town (stations 23, 26, 27 and 30), while in this study for both seasons, concentrations were found to be more than twice as high (Table 1). The increase over the years is likely to be the result of increased erosion of soils in the Caribbean hinterland, where banana plantations between 1987 and 1993 were expanded from a cultivated area of 28,000 ha to the size of 52,000 ha (Foro Emaús, 2008).

Concentrations of all measured parameters were highest in the water taken directly from the Estrella River and most of them were elevated during rainy season. Because of the large physico-chemical gradient that develops in the salt-wedge productivity and flocculation are high resulting in rapid settling of flocs (Eisma and Cadeé, 1991; Szekielda and McGinnis, 1991), hence trapping much of the suspended material within the estuary region of the Estrella River. As the rate of flocculation of suspended material and inorganic nutrients is dependent on the amount of TSM in the water (Kranck, 1981), TSM and most nutrient concentrations outside the river plume were still elevated during the rainy season, however not as much as in the river water further inland.

The highest concentrations of NO_x and silicate in the coastal waters were found in the mouth area of the Estrella River in the dry as well as in the rainy season (Figs. 2f and g). Compared to the dry season (Table 3), NO_x and silicate concentrations were significantly higher during rainy season ($p = 0.02$ and 0.001 , respectively) and the significant inverse correlations with salinity (Fig. 3) revealed the Estrella River as the main source of nitrogen and silicon to the coastal waters. Silicate concentrations were found to be twice as high (Table 3), compared to concentrations measured during the rainy season 100 km south of Cahuita, in the runoff affected Chiriquí Lagoon at the Caribbean coast of Panama (D'Croz et al., 2005). High concentrations of silicate are found in waters close to deforested areas (Hillbricht-Ilkowska et al., 1995) and the high amounts found here may be another consequence of erosion of the Caribbean hinterland deforested for agricultural purposes (Mora-Cordero and Chavarría, 2008). In the river stations, NO_x and silicate concentrations during the rainy season were 3.5 and 2.5 times higher than during dry season (Table 3).

In contrast, phosphate concentrations were evenly distributed in the coastal area (Fig. 2h), significantly lower ($p < 0.001$) in the rainy than in the dry season, and as the only parameter measured in higher concentrations during the dry than during rainy season in river water (Table 3). Even though values in river water were high during dry and still elevated during rainy season, they did not show concentration peaks in the river mouth area. Additionally, phosphate concentrations were lower during the rainy season, indicating dilution rather than increased output during times of high precipitation. As phosphorus concentrations in Caribbean marine environments are generally low (Szmant and Forrester, 1996; McClanahan et al., 2002), and fertilizer used for bananas and other fruits contains only small amounts of phosphorus, but is high in nitrogen (Beaton et al., 1995), the river is not the main source of phosphate. Also phosphate concentrations measured by Muller-Parker and Cortés (2001) in the rainy season 1997 (precipitation: 147.1 mm) were in between those sampled in the extreme weather conditions of this study. However, compared to Panamanian waters (D'Croz et al., 2005), phosphate concentrations in the Cahuita area are much higher (Table 3).

Due to increasing rain over the sampling time, sedimentation increased in both reefs and there is a significant increase (difference

Table 1
Mean concentrations of total suspended matter (TSM) during dry season (DS) 2004 and rainy season (RS) 2005 in the river water and the coastal area and the comparison with TSM concentrations measured in the river, the reef areas and close to Cahuita during previous studies.

	TSM [mg/L]				
	This study		Cortés and Risk (1985)	Cortés (1993)	
	DS 2004	RS 2005	RS 1979/1980	RS 1981	RS 1993
River station	30.29 ± 6.08	1046.05 ± 179.96	450		
Coastal stations	22.54 ± 0.96	24.10 ± 0.92			
Cahuita region	25.28 ± 4.13	24.1 ± 4.88		8.4 ± 1.6	9.1 ± 2.8
Outer reef	19.37 ± 1.77	18.95 ± 0.49	2.6		
Eastern Reef	21.04 ± 1.95	21.75 ± 1.63	5.1		

Table 2
Mean concentrations of particulate carbon (PC), particulate nitrogen (PN) and particulate organic carbon (POC) during dry season (DS) 2004 and rainy season (RS) 2005 in the river water and the coastal area of Cahuita.

	PC [µg/L]		PN [µg/L]		POC [µg/L]	
	This study		This study			
	DS 2004	RS 2005	DS 2004	RS 2005	DS 2004	RS 2005
River station	202.58 ± 10.8	588.84 ± 4.22	15.47 ± 5.81	34.55 ± 5.21	175.79 ± 12.46	700.02 ± 3.82
Coastal stations	67.37 ± 5.47	47.8408 ± 5.10	5.26 ± 0.64	4.43 ± 0.60	52.22 ± 5.15	42.36 ± 4.79

Table 3
Mean concentrations of dissolved inorganic nutrient concentrations during dry season (DS) and rainy season (RS) in the river water and the coastal area of Cahuita and their comparison with concentrations measured in Caribbean waters of Panama affected by terrestrial freshwater runoff.

	Nitrate + Nitrite [µM]			Silicate [µM]			Phosphate [µM]		
	This study		D'Croz et al. (2005)	This study		D'Croz et al. (2005)	This study		D'Croz et al. (2005)
	DS 2004	RS 2005	RS 1997	DS 2004	RS 2005	RS 1997	DS 2004	RS 2005	RS 1997
River station	6.26 ± 0.16	22.58 ± 0.16		207.43 ± 5.88	501.84 ± 13.36		0.095 ± 0.017	0.034 ± 0.02	
Coastal stations	0.39 ± 0.09	0.46 ± 0.09	1.14 ± 0.29	51.79 ± 3.67	73.97 ± 3.54	24.56 ± 2.86	3.22 ± 0.39	0.89 ± 0.37	0.10 ± 0.02

Table 4
Mean daily sedimentation rates of total particulate matter (PM) and the share of its different grain sizes with standard deviations in the coral reefs west and east of Cahuita National Park's peninsula between October 2004 and January 2005.

Sampling date	mg PM/cm ² /day	Gravel [mg]	Coarse sand [mg]	Fine sand [mg]	Silt and clay [mg]
<i>West of peninsula*</i>					
15.10.2004–14.11.2004	26.94 ± 2.84	0	11.93 ± 2.42	8.92 ± 2.37	6.09 ± 1.85
14.11.2004–12.12.2004	42.65 ± 6.52	0	12.72 ± 0.96	16.30 ± 3.59	13.62 ± 4.42
12.12.2004–16.01.2005	141.53 ± 24.04	3.58 ± 3.09	94.54 ± 38.71	27.53 ± 12.14	15.89 ± 10.42
<i>East of peninsula**</i>					
15.10.2004–14.11.2004	19.75 ± 5.66	0	7.39 ± 4.56	5.78 ± 2.69	6.58 ± 0.50
14.11.2004–12.12.2004	133.68 ± 82.71	6.62 ± 0.4	54.95 ± 30.32	35.20 ± 14.18	36.90 ± 3.49
12.12.2004–16.01.2005	521.80 ± 289.76	210.59 ± 152.77	249.09 ± 148.40	23.70 ± 7.20	38.42 ± 15.36

Significance levels for increase of sedimentation rates over time.

* $p < 0.01$.

** $p < 0.001$.

between the months) within each reef (Table 4). Barnes and Lough (1999) recorded sedimentation rates in a reef in Papua New Guinea before and after the excavation of a gold mine. Pre-excavation concentrations were below $1 \text{ mg cm}^{-2} \text{ day}^{-1}$, and the heaviest impacted reef with sedimentation rates of $680 \text{ mg cm}^{-2} \text{ day}^{-1}$ completely died off. The highest sedimentation rate recorded within our study was above $800 \text{ mg cm}^{-2} \text{ day}^{-1}$. All size fractions of settling material increased in amount over time, especially coarse sand and gravel were abundant in times of heavy rain and rough sea conditions (Table 4). Sedimentation rates of $>100 \text{ mg cm}^{-2} \text{ day}^{-1}$ over

periods of only a few days severely harm coral tissue (Riegl and Branch, 1995) and especially small grain sizes increase the damage (Weber et al., 2006). This impact poses the highest threat to the reef ecosystem in the Cahuita National Park as coral organisms will have to increase their metabolic cost for sediment removal, which would otherwise be needed for growth or reproduction (Telesnicki and Goldberg, 1995; Edmunds and Davies, 1989).

The Cahuita National Park reef already shows a decline in live coral cover and species diversity (Cortés and Risk, 1985) and the ongoing chronic exposure to a combination of high nutrient and

sediment loads is likely to further persist. Due to siltation, combined with eutrophication, algal growth and bioerosion (McCook, 1999; Díaz-Pullido and McCook 2003), the loss of the coral reef ecosystem and a shift to an algal-dominated reef will continue.

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1B - Tracing the extend of fertilizer input on coral metabolism

The waters within the coral reef ecosystem of the National Park in Cahuita, Costa Rica, are subjected to nutrient and suspended solid loads introduced by the Estrella River and presumably originating from excessive land use in the Carribean hinterland of Costa Rica (Cortés 1993, Roder et al. 2009).

Synthetic fertilizer used for excessive fruit crop cultivation is mainly composed of N-derivates (Beaton et al. 1995), which - being obtained from atmospheric nitrogen fixed under high temperatures - represent isotopic nitrogen ratios of -2 to 2‰ (Clark & Fritz 1997, McClelland & Valiela 1998), close to those of atmospheric nitrogen (0‰). Natural isotopic values for N-derivates in water and soils on the other hand - having undergone various steps of fractionation after fixation (Yamamuro et al. 1995, McCutchan et al. 2003) - display isotopic signatures ranging between 4 and 15‰ (Clark & Fritz 1997, Sigman et al. 1997, Leichter et al. 2007). As the signature of consumers is only slightly heavier compared to their diet (Yamamuro et al. 1995), $\delta^{15}\text{N}$ can indicate possible sources of nitrogen (Sammarco et al. 1999) and serve as a good tracer of nitrogenous compounds such as sewage (Heikoop et al. 2000), fertilizer (McClelland & Valiela 1998) or synthetically labeled feed (Hoegh-Guldberg et al. 2004).

To investigate the uptake of fertilizer-derived nitrogen in the Cahuita National Park, coral fragments (total n = 12) of randomly chosen massive starlet corals *Siderastrea siderea* (Ellis and Solander, 1786) were collected at 4 m depth on the exposed W and the rather sheltered E side of the national park's peninsula in the rainy and the dry season using SCUBA. Pieces of about 10 cm² were chiseled off the non-shaded upper surface of the coral head. The samples were transferred into pre-labeled plastic bags (max. 4 ml supernatant) and transferred to the laboratory for immediate processing. The tissue was separated from the skeleton with an artist's airbrush using a buffer (0.4 M NaCl, 20 mM EDTA and 20 mM Tris-HCl, pH = 7.6, 4°C) (Seutin et al. 1991), centrifuged at maximum speed to pellet all tissue and zooxanthellate components for subsequent desiccation (40°C), grinding and analysis of nitrogen isotopic composition in a gas isotope ratio mass spectrometer (Flash 1112 Analyzer) relative to atmospheric nitrogen using an Apple Leaf standard (HEKAtech SRM 1515) for calibration.

The coral samples displayed $\delta^{15}\text{N}$ ratios of $1.19 \pm 0.3 \text{ ‰}$ (W) and $0.72 \pm 0.3 \text{ ‰}$ (E) in the dry and of even as low as $0.35 \pm 0.2 \text{ ‰}$ (W) and $1.48 \pm 0.2 \text{ ‰}$ (E) in the rainy season (Fig. S1). These ratios are depleted compared to previously published results of $\sim 5 \text{ ‰}$ from other areas (Heikoop et al. 1998, Sammarco et al. 1999, Heikoop et al. 2000, Swart et al. 2005, Titlyanov et al. 2008) and strongly suggest, that *S. siderastrea* colonies from the national park reefs are well influenced by the river, taking up the introduced nitrogen compounds (Roder et al. 2009), and with them possibly further deleterious things such as heavy metals (Guzmán & Jimenez 1992, Guzmán & García 2002), common components for example in fungicides (Tabora et al. 1997), leading to a further weakening of the corals' health (Harland & Brown 1989, Esslemont 2000).

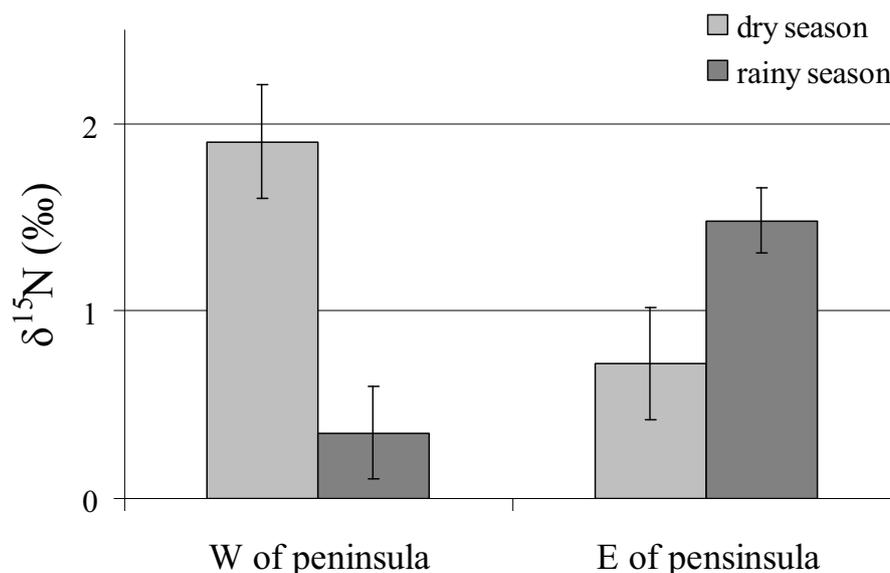


Figure S1: Nitrogen isotopic ratios of *Siderastrea siderea* (holobiont) samples collected at 4 m depth from the reefs W and E of the peninsula within the Cahuita National Park. Differences between sites or seasons are not significant.

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- Chapter VII -

**Field observations and preliminary notes on the
status of NE-Hainan coral reefs**

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In preparation

Abstract

Hainan's coast provides unique climatic, geochemical and biogeographic conditions for the development of luxurious coral reefs in China. Observations in five reefs along the NE coast of Hainan however showed that the overall densities of mobile macrofauna is low and key functional groups such as browsing, scarping or excavating fish are missing altogether. Coral diseases, partial mortality, tissue degradation or fission are abundant and algal growth extensive. Signs of eutrophication, siltation and destructive fishing practices are evident resulting in a strongly altered environment unfavorable for coral survival and recruitment success, e.g. larval settlement. Even though corals that are still extant in the affected areas seem to have acclimated to the prevailing conditions, a shift from a coral to algae dominated reef may occur if land-based disturbance prevails unabated.

Introduction

Corals and algae are important primary producers co-occurring in tropical shallow water reefs (Crossland et al. 1991; Hatcher 1997). Whilst they have to compete for space (Littler and Littler 1985; Lapointe et al. 1997), their co-existence is balanced by nutrient supply (bottom-up control) and grazing (top-down control), whereas the competitive advantage of algae for a more efficient utilization of inorganic nutrients is opposed by their greater grazing susceptibility. Changes in nutrient status and grazing can therefore have deleterious effects to coral dominated reefs (Hughes 1994; Bellwood et al. 2004), however rates and kinds of change are difficult to predict, as the interplay of direct and indirect effects is complex (Glynn 1988) and coral- or algal dominated communities are only two out of several possible reef conditions (Bellwood et al. 2004; Pandolfi et al. 2005). Corals have been shown to persist in eutrophied waters, when sufficient grazing pressure on algae is present (Aronson and Precht 2001; Aronson et al. 2002). Sometimes, the original grazers might not even be present any more, but replaced by other species such as sea urchins (McClanahan and Muthiga 1988; Steneck 1998). They can in cases of

extensive overfishing become the only grazing control of algae (Ogden et al. 1973; Levitan 1988) and may, when not antagonized by predators, become themselves a pest not only grazing on macroalgae, but finally also on corals and rock, and so eroding the total reef base (Bellwood et al. 2004). When these grazers die off or migrate, they leave barren substrate behind which may be the base for extensive algal growth due to their efficient resettlement capabilities compared to that of corals (Hughes 1994; Gardner et al. 2003) and especially when coral recruitment is low (Aronson et al. 2002). Coral reefs threatened by eutrophication together with overfishing which moreover may be by means of destructive techniques (McManus et al. 1997), are hence at high risk of imminent phase shift (Hughes 1994; Bellwood et al. 2004).

The coral reefs of Hainan are yet poorly investigated ecosystems. Descriptions from the 1950s focus on distribution and diversity of coral communities (Yu and Zou 1996a,b), while later studies on coral diversity were conducted concerning anthropogenic effects (Yu and Zou 1996a,b; Shi and Zhang 2004) as the rapid economic exploitation in combination with heavy fishing and land-based agricultural as well as aquacultural development, both sources for heavy eutrophication and pollution, has taken the coral reefs to the borderline of tolerance. Studies from reefs on the south coast have been reporting decreases in live coral cover from 60% in 1983, to 41.5% in 1998, and to 21.51% in 2002 (Yu and Zou 1996a,b), despite the foundation of the Sanya National Coral Reef Reserve in 1990. During a reef and seagrass monitoring project in 2002 (Status of China Marine Ecology Report, 2002), coral, seagrass and fish species distribution, biomass and recruitment was assessed along the east coast of Hainan. The results revealed that live coral cover and coral recruitment, as well as coral reef associated fish and invertebrate density was very low, while macro-algal abundance, especially that of the brown algae *Sargassum* spp. was high (Hainan east coast coral reef and seagrass monitoring report, 2005). Therefore further information on the status of Hainan's coral reefs and their potential threats is urgently needed to provide the base for a more sustainable coastal management, benefiting or even recovering adjacent coral reefs.

Material and Methods

In 2007 and 2008 field trips were conducted to the NE reef sites of Hainan (Fig. 1). Five reefs were chosen to be sampled (from north to south): Tonggulin, Coconut Bay, Chang qi gan, Longwan and Tanmen. Photographs of site characteristics at each reef are given in Figs. 2-6. Due to time and logistic limits along with sampling constraints, the status of each reef could only be evaluated on a descriptive basis in rapid assessment, thereby taking pictures and notes on first impressions, including the independent estimations of live coral cover by two divers. At each site, five corals were investigated in terms of photosynthetic performance (see below, $n =$ minimum of 3 per colony) and tissue samples (see below, $n = 3$ per colony) for biogeochemical analyses were taken using hammer and chisel. Photosynthetic performance was analysed in situ with rapid light curves (RLC, Ralph et al. 1999; Ralph and Gademann 2005) of the massive coral *Porites lutea* (Milne-Edwards and Haime, 1860), between 11 and 12 hrs of days with 0 % cloud cover as photosynthetic output changes with cloudiness or over day (Brown et al. 1999). RCLs were conducted using a submersible pulse amplitude modulated fluorometer (DivingPAM, Heinz Waltz Ltd., Germany) with a universal sample holder ('DIVING-USH') to assess the coral surface with a standardized distance of 1 cm (Schreiber 1986). Thereby, RLCs were conducted using the internal settings of the diving PAM applying increasing light intensities (photosynthetic active radiation, PAR, 0-2896 $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$) and recording electron transport rates (ETR) (Ralph et al. 1999; Ralph and Gademann 2005). Ambient light intensities were measured concomitantly with the light sensor of the DivingPAM. The resulting light curves are a good measure of the present photosynthetic performance and the short-term light history of the investigated colony (Schreiber et al. 1997). The ETR is calculated as $\Delta F/F_m' \times \text{PAR} \times 0.5 \times \text{ETR factor}$, where $\Delta F/F_m'$ is the effective PSII quantum yield, a dimensionless value representing the photosynthetic effectiveness of photosystem II in the given light state, 0.5 constitutes for the assumed equal distribution of electrons between the two photosystems (Ralph et al. 1999), and the ETR factor, reflecting the light absorbance by the sample, as being unknown for *P. lutea*, was set to unity. Therefore only the commonly used relative ETR (rETR) (Hoegh-Guldberg and Jones 1999) could be obtained, still allowing comparisons

between different coral colonies of one species (Schreiber 1986). Chiseled samples were transported in ziplock plastic bags (< 3 ml residual water) to the laboratory for storage on ice and further processing. Furthermore at the reef site of Coconut Bay, three colonies of the branching species *Pocillopora verrucosa* (Ellis and Solander, 1986) were examined as described above, but only one sample per colony was taken for tissue analyses.

Descriptions of the reefs were accomplished prior to examinations of light curves or analyses of collected fragments in order to get unprejudiced records.

Due to limiting authority regulations, only few coral tissue parameters could be evaluated, comprising zooxanthellae density, pigment determinations and dry weights of coral and zooxanthellae. Two square centimeters of coral tissue were removed from the skeleton using an artist's airbrush and filtered seawater. The tissue slurry was subsequently homogenized and aliquots retained for zooxanthellae density counts using a Fuchs-Rosenthal haemocytometer and a microscope (Leitz, Portugal, 260x magnification). 5 ml were filtered on Whatman glass fiber filters (F) for pigment analysis using the standard procedure of (Strickland and Parsons 1972) and frozen for later processing. For chlorophyll-a determinations filters were added with a certain volume of Acetone (90 %), incubated for 24h in the dark at 4° and pigment concentrations were determined spectrophotometrically (Lorenzen 1967) using a handphotometer. Due to dissimilar storage times of the samples (up to one year), which may increase pheophytin content in longer stored samples (Hill et al. 1995; Hill et al. 2000), not only chlorophyll-a content but also the amount of pheophytin was determined (using the acidification method of Lorenzen (1967)), and both summed up to obtain the initial chlorophyll-a content of the coral tissue. Additionally, 15 ml of the slurry were centrifuged to separate coral host components from zooxanthellae (Muscatine et al. 1989; Swart et al. 2005) and (after several washing steps) separately loaded on precombusted glass fiber filters (Whatman GF/F) for further desiccation and determination of coral host and zooxanthellate dry weights on a microbalance (Mettler Toledo AB204-S, accuracy 0.1 mg).

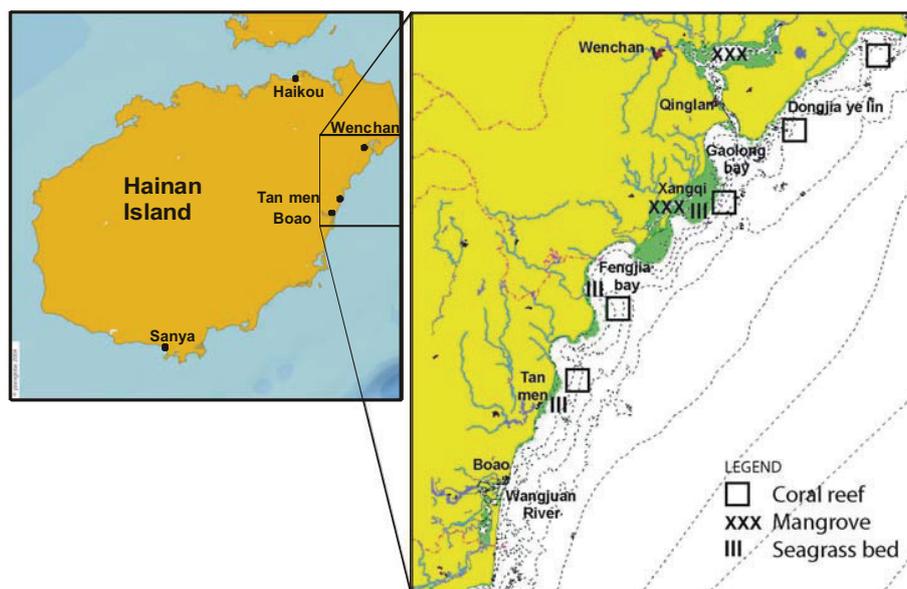


Figure 1: Hainan Island located in the South China Sea and a close-up of the NE-coast indicating the five reef sampling sites (squares), from N to S: Tonggulin, Coconut Bay, Chang qi gan, Longwan and Tanmen.

Results

Descriptions of study sites

All fringing reefs along the NE-coast of Hainan are located in shallow waters (2 – 8 m) relatively close to shore (200 – 1000 m) and consist of a reef flat, crest and slope. The first inspection of the working areas revealed at best algae dominated, fragmentary reefs with extensive coral rubble fields and only remote live coral cover (often less than 1 %, sometimes up to 15 %), but higher and more divers cover (up to 60 %) of mainly small colonies along the reef crests where wave and surge action was strongest resulting in constant removal of sediments. Living colonies were often partly affected by disease, mortality or fission and often threatened by algal overgrowth or snail predation. In contrast, we documented a high abundance of coralline and macro-algae, the latter especially on the reef slopes, but almost a total lack of mobile macrofauna, especially herbivorous and predatory fish, as well as echinoderms. Visibility was low (between 0.5 and 8 m) and coral rubble fields were in general covered with thick layers of sediment. A more detailed description of each site is given in the following:

Tonggulin - The shallow reef flat of Tonggulin (2 – 5 m) consisted of extensive coral rubble fields presumably originating from destructive bomb fishing (Fig. 2). The coral rubble, however, was already mostly cemented together by encrusting algae, indicating that the destruction of the reef has not happened recently. Life coral cover was low (5 – 10 %), but increased to 40% on the reef crest and diversity was highest compared to all other reefs observed. In the area of low cover, mainly small branching species could be observed, and diversity rose with increasing coverage. Algae were present, but were less abundant than at other reef sites. Fish abundances was low and most individuals were juvenile.



Figure 2: Tonggulin reef

Coconut Bay - The coral reef of Coconut Bay (Fig. 3) was likewise shallow (2 – 4 m) and close to shore (~ 400 m). The widespread coral rubble fields on the reef flat, likely originating from destructive fishing methods, were mainly covered and clotted by silt. Fleshy green algae were abundant, but large *Sargassum* spp. specimens dominated the area. Only few small individuals of massive coral colonies could be observed, many of them diseased, damaged or encroached by algae. Close to the reef crest, where currents were stronger and waves present, the structure of the original reef still remained intact in great parts and featured many recruits of mainly branching coral species. There were only few fish, even along the reef crest.



Figure 3: Coconut Bay reef

Chang qi gan - The reef area of Chang qi gan (Fig. 4) was further offshore (~ 800 m) and depth ranged from 4 – 8 m. The site seemed to be heavily fished, especially during dry season as indicated by high amounts of fishing boats in the reef area and audible as well as visible reoccurring explosions. Few large massive *Porites* colonies several meters in diameter still strengthening the damaged reef framework represented the main part of live coral cover. However, many of them were affected by disease, partial mortality or in direct competition with algae. Mucus excretion in most of these colonies was high with thick flats covering the colonies, presumably to get rid of the sediment load. Branching species could only be rarely found as small recruits. Again, only low numbers of fish were present, most of them being juveniles.



Figure 4: Chang qi gan reef

Longwan – In Longwan (Fig. 5) the reef was close to the shore (~ 200 m) and depth did not exceed 4 m. Coral rubble, cemented together by encrusting algae, dominated the reef area. Further offshore, a mix of branching and foliose coral recruits and mid-sized massive colonies built the reef framework. Diversity in this reef was second highest (after Tonggulin) of all investigated reef sites, however, live coral cover was low and most colonies were rather small. Algae were present in high amounts, but not as abundant as in Coconut Bay, Chang qi gan or Tanmen. As in all other reefs, only few juvenile fish could be observed.



Figure 5: Longwan reef

Tanmen - The reef of Tanmen (Fig. 6) further offshore (~ 1000 m) than the others, was located directly outside the river estuary and the Tanmen harbor. It was slightly deeper than the other reefs (5 – 8 m) and characterized by heavy algal growth. As in Chang qi gan, the living part of the coral reef consisted of mainly massive boulder colonies (predominantly *Porites*), which showed strong mucus secretion and were often affected by disease. The intense ship traffic not only exposes the reef to pollution or mechanical destruction, but is likewise, regarding the many fishing boats and floating houses, evidence for the extensive fishing pressure in this area. Accordingly, the reef lacked almost completely any fishfauna.



Figure 6: Tanmen reef

Metabolic investigations

An overview of investigated tissue parameters is given in Fig. 7. None of the investigated parameters (coral host and zooxanthellae dry weight, zooxanthellae densities or pigment concentrations) in samples from *Porites lutea* differed significantly (Kruskal-Wallis: $p > 0.05$) within samples from one colony or between the five reef sites. Coral host dry weights ranged from 0.3 (Coconut Bay) to 15.25 mg cm⁻² (Tonggulin) with a mean of 6.25 ± 0.34 mg cm⁻². Zooxanthellae dry weights were in the range of 3.85 ± 0.18 mg cm⁻² with a minimum of 1.3 mg cm⁻² in Coconut Bay and a maximum of 8.14 mg cm⁻² in Tonggulin. On average, $3.6 \pm 1.6 * 10^6$ zooxanthellae cm⁻² were counted, with highest abundances of $7.6 * 10^6$ cm⁻² in Tanmen and lowest abundances of just fewer than one million in Tonggulin. Pigment concentrations (chlorophyll-a) were lowest in Tonggulin (2.42 µg cm⁻²), but highest in samples from Coconut Bay (29.52 µg cm⁻²) and on average 14.27 ± 0.77 µg cm⁻². The three samples of *Pocillopora verrucosa* collected in the reef of Coconut Bay were similar in tissue composition to *P. lutea* samples, with coral host tissue dry weight being in the higher range, while zooxanthellae dry weight, zooxanthellae densities or pigment concentrations were in the lower range of the values computed for *P. lutea*.

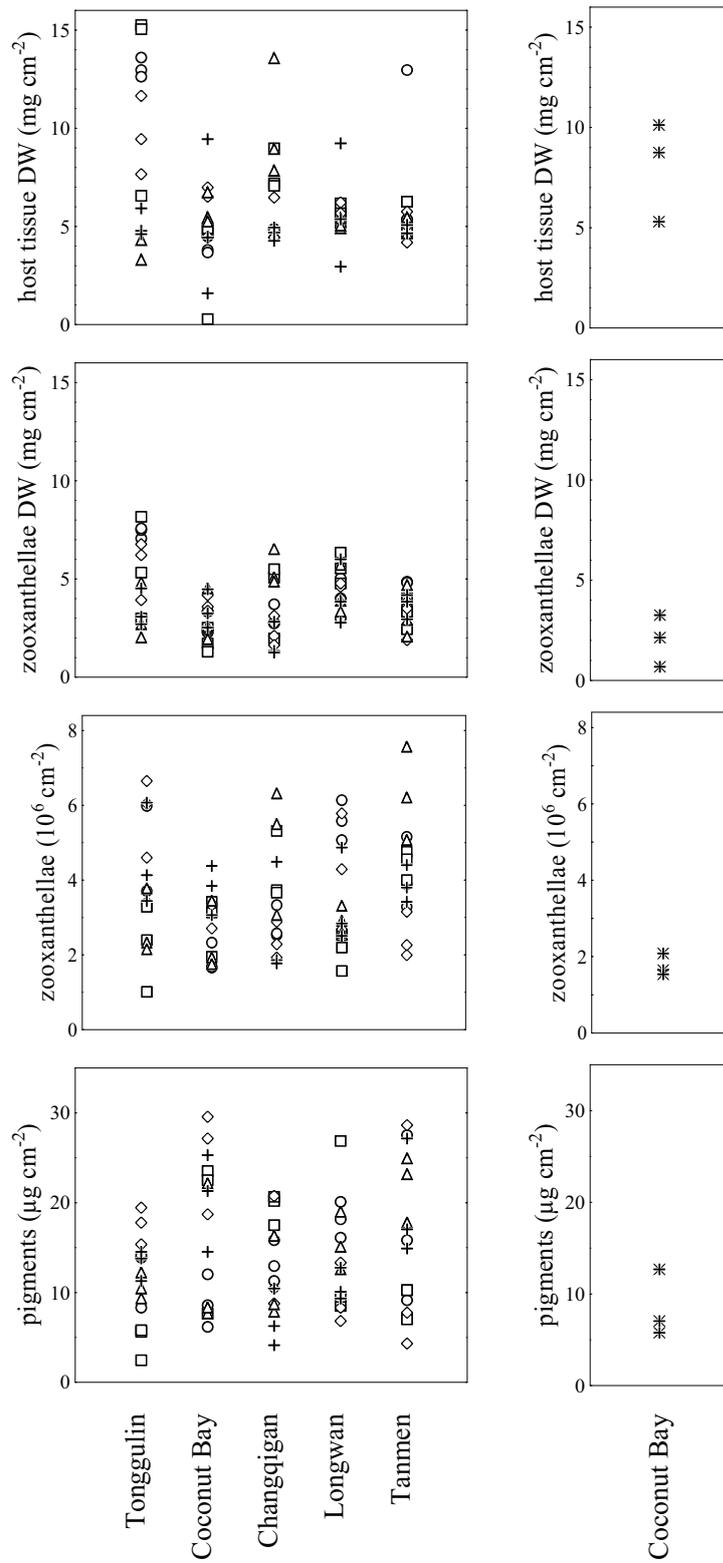


Figure 7: Host tissue and zooxanthellae dry weights, zooxanthellae densities and pigment concentrations of *Porites lutea* from NE-Hainan reefs and from *Pocillopora verrucosa* from Coconut Bay.

The general photosynthetic performance as illustrated by the rapid light curves (RLCs, Fig. 8) is similar for all reefs except Coconut Bay where colonies of *P. lutea* reached only rETR maximum rates of < 100 ($\mu\text{mol electrons m}^{-2}\text{s}^{-1}$) and was less efficient under the same irradiance levels. Most colonies (*Porites lutea* and *Pocillopora verrucosa* specimens) reached a saturation plateau with maximum rETR of 50 – 150 $\mu\text{mol electrons m}^{-2}\text{s}^{-1}$ at a photosynthetic active radiation (PAR) of about 1000 $\mu\text{mol quanta m}^{-2}\text{s}^{-1}$. While all curves stagnated at a certain saturation level or even decrease due to exposure to supra-optimal irradiance (% over ambient max PAR intensities), coral colonies from Tonggulin also leveled out, but did not reach their saturation limit.

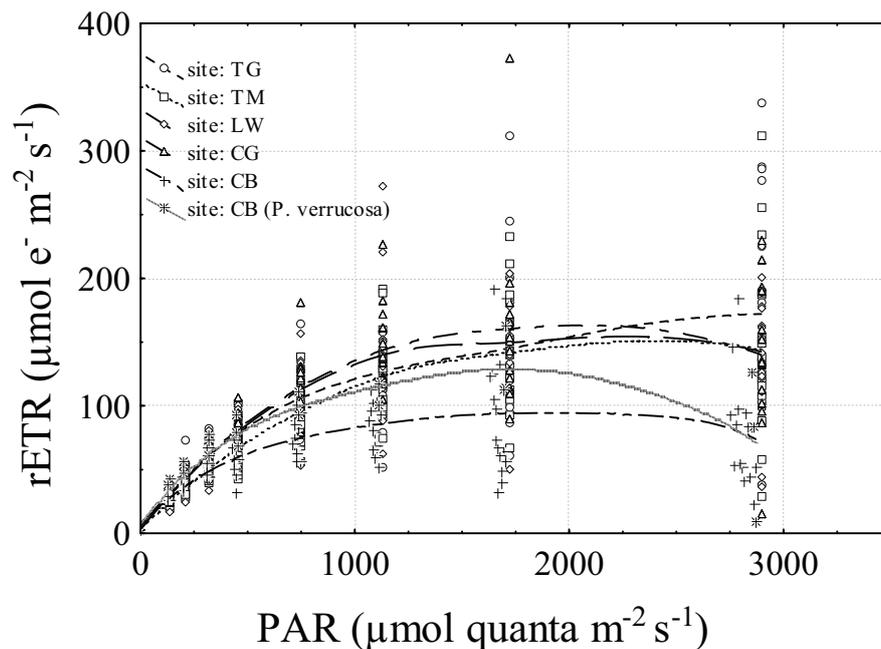


Figure 8: Rapid light curves of *Porites lutea* colonies from various reefs along NE-Hainan (TG: Tonggulin, TM: Tanmen, LW: Longwan, CG: Chang qi gan, CB: Coconut Bay) and from *Pocillopora verrucosa* specimens from Coconut Bay.

Discussion

The conducted surveys along the NE-coast of Hainan revealed a degraded status of coral reefs in this area, almost certainly due to extensive anthropogenic impact. This is in congruence with studies of You and Zou (1996 a, b), who described that the once flourishing coral reefs of Luhuitou, in the southern part of Hainan, have suffered combined impacts of fishing, mining and land-based sources of pollution. This includes in particular severe sediment run-off via rivers to coastal waters, construction and alteration of land use near the coastline, comprising discharge of untreated human sewage, agriculture fertilizers and heavily polluted and eutrophied wastewater from land based aquaculture during the last two decades. Furthermore coastal waters along the NE-coast of Hainan are contaminated with high loads of total suspended matter and nutrient concentrations, reaching up to 42 mg l⁻¹ (TSM) and up 40 µM inorganic nitrogenous compounds or 3 µM phosphate, especially during times of high precipitation (Krupp et al. in prep.). The nitrogenous compounds suspended in the water column revealed high δ¹⁵N values and could accordingly be ascribed to shrimp ponds as nitrogen sources (Krupp et al. in prep.). Highest amounts of TSM and nutrient loads were found at the reefs of Coconut Bay and Tanmen (Krupp et al in prep.), directly outside the river plumes of the Wenchang and the Wangjuan river. This is further manifested by the low visibility at the investigated reefs, caused by the chronic nutrient- and sediment-loaded runoff and resulting in reduced light availability and stress caused by sedimentation (Fabricius 2005). The high abundance of thallose macroalgae and the dark coloration of the scattered living corals are further indicators of reduced light levels and eutrophication. Additionally the extensive mucus flats excreted by many corals in the area are known to be a cost-intensive technique of sediment removal (Schuhmacher 1977) or bio-fouling (Ducklow and Mitchell 1979) as well as a general particle load protection (Ruble et al. 1980). Further human induced stresses are overfishing and the use of destructive fishing techniques (McManus et al. 1997). Altogether this indicates strong fertilization and degradation of all reef sites along the NE-coast of Hainan as a result of an anthropogenic altered coastal system.

Biomasses of coral host tissue and zooxanthellae, even though not statistically significant, are lowest in the most affected reefs and may indicate reduced health of the present corals (Fabricius 2005), while zooxanthellae densities and chlorophyll concentrations are highest suggesting energetic costly adaptations to a low-light environment (Falkowski and Dubinsky 1981; Iglesias-Prieto and Trench 1994). This is further supported by the fact that coral colonies from Coconut Bay had lowest photosynthetic capacities which is typical for corals (or colony parts) chronically exposed to reduced light levels (Beer et al. 1998). On the other hand, the reef of Tonggulin gave the impression of being the most intact one in this area which is supported by highest biomasses of coral host and zooxanthellae as well as by its enhanced photosynthetic performance and the indication that specimens are adapted to higher light environments compared to all other reefs.

While zooxanthellae densities of *Porites lutea* as well as *Pocillopora verrucosa* are in the range of those shown for the same species in Chinese waters of Sanya (South Hainan) and Daya Bay (Guangdong Province, South China mainland) (Li et al. 2008), the investigated photosynthetic performance with saturation potentials are in the lower range of those reported (i.e. Beer et al. 1998; Ralph et al. 1999). The latter incidence dissents from the fact that all corals were shallow water specimens (< 6 m), but rather resembled efficiencies of deep or turbid water, i.e. low light specimens (Iglesias-Prieto and Trench 1994; Jantzen et al. 2008).

In general it seems that corals that still outlive these unfavorable conditions have arranged to respond to the mentioned eutrophication and reduced light levels by adjusting their metabolic performance to the given conditions. Nevertheless, it can further be expected that their fitness is momentarily impacted to a degree where their own survival may still be possible, but, if conditions prevail or even deteriorate, the energetic costs necessary to keep pace with the disturbance are too high and accordingly may result in mortality of the coral community (Kirkwood 1992).

A glimmer of hope for the NE coral reefs of Hainan are the frequently noticed small sized coral colonies, mainly occurring along the reef crests which may signify a high recovery potential (Dustan 1977), however, their survival may be uncertain because coral rubble, being the main substrate, especially on the reef flats, poses unfavorable conditions for

settling and longer-term persistence (Hodgson 1990) as it is easily turned by waves or surge and hence extremely unstable.

It appears that in the subsequent decades, particularly during the rapid economic development in the 90's, human activities have taken their toll on the coastal marine environment and at present all coral reefs along the NE-coast of Hainan are suffering from eutrophication, siltation as well as disease to greater or lesser extent. The subsistence of scleractinian corals nevertheless indicates that reproduction is existent and at least in parts the top-down control of algae still holds and that reproduction is existent. Data on the abundance and grazing activity of herbivores or on coral reproduction is however wanting. Obviously, the importance to gain insights on the interactive consequences of high nutrient and sediment inputs from land-based runoff, the low fish and invertebrate grazer abundances and the altered environment due to destructive fishing on coral health and reef status is crucial in the area to implement proper management strategies for the coral reefs of NE Hainan.

Aknowledgements

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Discussion

This thesis has demonstrated the characteristics of the natural disturbance of Large Amplitude Internal Waves (LAIW) (Chapters I to V) and of the anthropogenic disturbances of river runoff (Chapter VI) and combined effects of destructive fishing, coastal development and aquaculture (Chapter VIII). Herein, the responses of corals to the respective disturbance have been investigated.

LAIW introduce cold, oxygen depleted, low pH and nutrient rich water into the reef ecosystem of the Similan Islands, Thailand, located close to the continental shelf break in the Andaman Sea. Even though some LAIW energy is also found to wrap around the islands to the east (E) side, the main impact is experienced by the deep reef sites along the west (W) coasts.

It is shown that corals along the W reef sides of the Similan Islands are strongly influenced by the prevailing LAIW conditions (Chapter I). The amount of impact is regulated by the frequency and the intensity of the LAIW and differs on spatial (W deep highly influenced > W shallow > E deep > E shallow least influenced) as well as on temporal scales (yearly differences between 2007 and 2008, Chapter I), however never between equally exposed reefs of the various islands. The potential of acclimatization is also highly species specific with some species (such as *D. heliopora*) responding stronger to LAIW impact (Chapter I).

The high input of nutrients fuels pigment concentrations in corals (Muscatine et al. 1989) (Chapter I, IV). However, coral primary production is similar in situ (Chapter IV) between exposed W and sheltered E side corals, and even lower in W when incubated under equal conditions (Chapter III) indicating an energy costly photosynthesis due to acclimatization to low light levels (Iglesias-Prieto and Trench 1994). Corals from the W reefs of the Similans also feature higher biomasses and protein contents, most likely due to higher heterotrophic input (Bachar et al. 2007; Rodrigues et al. 2008) as a result of strong currents (Sebens and Johnson 1991) and increased organic matter fluxes (Chapter I, II). The combination of photo- and heterotrophy enhances the energy stores of the W side corals and increases their resilience potential to disturbance (Chapter II).

The high availability of nutrients and organics in the W side reefs might also be the trigger for a less conservative behavior in retaining organic material in dissolved or particulate form (Ferrier-Pagès et al. 1998) leading to an increased release of dissolved organics or mucus (Chapter III). Corals under LAIW impact are furthermore poorer calcifiers compared to their

sheltered E counterparts (Chapter III) which might be attributed to the frequent exposure to low pH water (Marubini et al. 2001) or acclimatization to low light levels (Crossland 1984).

The gross primary production in W and E side reefs is similar, however with contrary contributions of the various compartments. While the sediments are stronger producers in the E, turf algae contribute stronger to primary production under LAIW influence most likely due to elevated nutrient availability (Hatcher and Larkum 1983) with increasing LAIW impact and due to their higher abundance on W compared to E (Chapter III).

The combined effects of low coral photosynthesis and calcification might be in large parts responsible for the reduced reef formation, especially in the deeper reef waters along the western Similan Islands (Chapter V). While the E reefs form a dense and complex framework, the W side is characterized by scattered corals lacking a true three-dimensional structure (Chapter V). While in the shallow waters of the W the altered morphologies of corals growing closely attached to the granite boulders can be explained by a strong SW monsoon impact (Nielsen et al. 2004), the lack of reef framework in deeper water is attributed to LAIW (Chapter V). There is indication, that the potential of the coral species to respond to the stressful physico-chemical environment of LAIW determines its fate in abundance along the Similan Islands (Chapter I). Those able to exploit the benefits of nutrient enrichment and organic matter fluxes (Chapter I) are more likely to colonize the W Similan reefs.

What remains to be determined is whether the responses to disturbance that we see in LAIW affected corals, namely costly photosynthesis and reduced calcification on the one hand, but increased energy uptake and release and a higher resilience on the other, is within the frame of genotypic acclimatization or if it might even be genetic adaptation. The reefs of the Similan Islands provide a clue to understanding coral resilience in the face of climate change and ocean acidification due their successful and versatile acclimatization to pulsed low temperature, low oxygen, low pH, and high nutrient conditions.

The situation is different in the examples from Costa Rica (Chapter VI) and Hainan (Chapter VII), where the reefs are exposed to chronic and not pulsed disturbance. The main impacts of eutrophication (Szmant 2002) and sedimentation (Anthony 2006) at either investigation site drive the ecosystems to their borderlines. While the reef of the National Park Cahuita on the Caribbean coast of Costa Rica (Chapter VI) suffers heavy sedimentation and is at risk of being suffocated (Weber et al. 2006), the extensive algal growth along the NE-Hainan coast (Chapter VII) indicates a shift towards an algal dominated ecosystem (Lapointe 1997). The

causes of disturbance are obvious: excessive land use of the Caribbean hinterland has altered the coastline leading to strong erosion and fertilizer pollution. The eutrophication gradient from river mouth to coral reef is clearly traceable and evidence on direct impact is given by the active uptake of fertilizer derived nitrogen by the corals of the national park reef (Chapter VI). In the reefs of NE-Hainan, destruction from explosive fishing is visible by widespread fields of coral rubble and lack of coral as well as fish fauna. The turbid water column has strongly reduced photosynthetic efficiency of the corals possibly leading to decreased coral growth (Rodolfo-Metalpa et al. 2006) that might not be able to keep up with the rate of destruction. In Costa Rica as well as on Hainan, it is crucial to develop and enforce proper conservation strategies, as the disturbances are likely to remain high or even further increase.

Coral reef ecosystems are very complex, nevertheless extremely flexible systems and due to their high productivity and biodiversity of high conservation value. Gaining information on coral reef functioning under disturbances is important to assess necessary management implications and to predict future coral reef scenarios in a rapidly changing world. This thesis contributes to the baseline of understanding reef functioning and acclimatization potentials of corals in disturbed environments.

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Bremen, 20. Februar 2009

Cornelia Roder