

Corals & Waves

Calcification and bioerosion in Large Amplitude Internal Wave (LAIW) affected coral reefs

Dissertation submitted by

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Zusammenfassung

Die Ergebnisse der vorliegenden Doktorarbeit tragen bei zu einem besseren Verständnis der Auswirkungen von starken natürlichen Schwankungen der physikalisch-chemischen Umweltbedingungen in Korallenriffen, die dem Einfluss von Internen Wellen großer Amplitude (englisch: Large Amplitude Internal Waves, LAIW) ausgesetzt sind. Der Einfluss dieser Wellen auf die benthische Korallenriff-Gemeinschaft verursacht unmittelbare Veränderungen und Anpassungen auf Ebene der einzelnen Organismen, funktioneller Gruppen und des gesamten Ökosystems.

LAIW sind ein weltweit auftretendes ozeanographisches Phänomen, das vor allem in tektonisch aktiven Gebieten wie Süd-Ost-Asien zu beobachten ist, in denen eine reiche Unterwasser-Topographie, Gezeitenströmungen und eine starke Dichtestratifizierung die Voraussetzung für ihre Entstehung und Ausbreitung schaffen. LAIW bewegen sich in Wellenpaketen mit Amplituden bis > 80 m und Geschwindigkeiten von etwa 2 m s^{-1} fort und bringen Wasser aus unterhalb der Dichtesprungschicht liegenden Bereichen mit sich in flachere Schelfbereiche, sobald sie sich aus dem Tiefwasserbereich den Schelfhang hinauf fortbewegen und dort brechen. Trotz ihrer langen Bekanntheit in der physikalischen Ozeanographie sind die möglicherweise extremen biologischen Auswirkungen von LAIW vor allem auf benthische Gemeinschaften und Ökosysteme, wie zum Beispiel Korallenriffe, die sich oberhalb des Schelfhangs im unmittelbaren Brechungsbereich dieser Wellen befinden, so gut wie unbekannt. In dieser Arbeit wird der Einfluss von LAIW auf Korallenriffe der Similan Inselkette untersucht, die 60 km östlich der thailändischen Küste und in der direkten Brechungszone der LAIW liegt. Die Wellen entstehen nahe Sumatra und an den Andamanen-Nikobaren-Inseln und breiten sich von dort in Richtung Westen und Nordwesten aus.

Es konnte gezeigt werden, dass die ungewöhnliche Riffverteilung an den Similan Inseln innerhalb der Inselkette konsistent und auf den Einfluss von LAIW zurückzuführen ist (Kapitel 1): Eine ausgeprägte Riffbildung zeigte sich nur auf den schelfzugewandten, geschützten Inselostseiten. Dem gegenüber beobachtete man einen kompletten Mangel an Riffentwicklung an den exponierten Westseiten. In Anbetracht der unmittelbaren Nähe zwischen Inselost- und -westseiten, waren die Unterschiede der physikalisch-chemisch-ozeanographischen Parameter erheblich: Die Temperaturlaufzeichnungen von zwei Jahren zeigten, dass LAIW ihren stärksten Einfluss an den tiefer liegenden Westhängen der Inseln ausübten, wo sie zahlreiche abrupte Temperaturabfälle verursachten (mehrmals pro Stunde, Schwankungen bis zu $10 \text{ }^\circ\text{C}$ innerhalb von Minuten). Ihre höchste Intensität erreichen die Temperaturschwankungen während des Nord-Ost-Monsoons (Januar bis April). LAIW brachten kaltes, nährstoffreiches, suboxisches Tiefenwasser mit geringem pH-Wert (bis zu 0.6 Einheiten unter Normalbedingungen) mit sich in flache Küstenbereiche, begleitet von starken Strömungsanstiegen. Dabei veränderten sie die Umweltbedingungen für die an den Westhängen lebenden benthischen Organismen grundlegend. Im Gegensatz zu einer relativ geringen Anzahl riffbildender Korallenarten auf den Ostseiten, waren die Westseiten durch einzeln verteilte, jedoch wesentlich diversere Korallengruppen charakterisiert, die direkt auf dem Granituntergrund wuchsen. Dies wird auf den sich im Westen abwechselnden Einfluss von Süd-West-Monsoon (Mai bis Oktober) und LAIW zurückgeführt. Dabei beeinflusst der Monsoon vor allem den flacheren und die LAIW den tieferen Hangbereich am stärksten. Dies führt zu einer räumlichen und zeitlichen Heterogenität, welche die Korallengemeinschaft in einem ständigen Wechsel der Umweltstörungen von letztlich gemäßigter Intensität hält und dadurch die Artenvielfalt erhöht.

Eine vergleichende Bestimmung der relativen Substratbedeckung und des Metabolismus der Haupt-Primärproduzenten (Mikrophytobenthos im Riffsediment, Turf-Algen und Korallen, untersucht am Beispiel von *Porites lutea*) auf West- und Ostseiten der Inseln ergab, dass Turf-Algen die dominanten Primärproduzenten im Westen darstellen. Im Osten

war dies das sedimentäre Mikrophytobenthos, während Korallen einen vergleichsweise geringen Anteil zur Gesamtprimärproduktion lieferten (Kapitel 2). Trotz der tiefgreifenden Auswirkungen von LAIW auf den Metabolismus der unterschiedlichen Primärproduzenten und der verschiedenen großen Beiträge der jeweiligen Organismengruppe zur Gesamtprimärproduktion, zeigte sich, dass die Gesamtprimärproduktionen im Westen und Osten ähnlich waren. Dies spiegelt eine hohe Plastizität der Primärproduktion an den von LAIW beeinflussten Westseiten wieder. Ebenso zeigte die dominierende riffbildende massive Koralle *Porites lutea* eine ähnliche Netto-Photosynthese auf beiden Inselseiten, jedoch mit um 40 % höheren Pigmentkonzentrationen im Westen, was auf eine Anpassung an die geringere Lichtversorgung bei höheren Nährstoffkonzentrationen im Wasser zurückzuführen ist.

Die an den Similan Inseln häufig vorkommende Koralle *Pocillopora meandrina* zeigte an den Inselwestseiten eine signifikant höhere Biomasse und Proteingehalt als Ostkorallen (Kapitel 3). Zudem zeichneten sich Westkorallen durch eine weit heterotrophere Ernährungsweise aus, die sich an der leichteren, stabilen Kohlenstoffsignatur im Korallengewebe erkennen ließ und bewiesen höhere Überlebensraten unter künstlicher Verdunklung. Die größeren Energiereserven von Westkorallen und die Unterschiede in ihrem trophischen Status, bedingt durch die LAIW-verursachte erhöhte Versorgung mit organischem Material, führten zu einem gesteigerten Anpassungspotential dieser Korallen an veränderte Umweltbedingungen.

Das Wachstum von *Porites lutea* wurde anhand von lebenden Korallenfragmenten und die Bioerosion an aus *P. lutea*-Skeletten geschnittenen Karbonatblöcken untersucht. Sowohl das Wachstum als auch die Bioerosion zeigten die jeweils geringsten Werte an den am stärksten LAIW-beeinflussten tieferen Westhängen und waren am ausgeprägtesten innerhalb der dichten Riffbereiche im flacheren Ostwasser (Kapitel 4). Das Korallenwachstum war unter LAIW-Einfluss vermutlich durch den kumulativen Effekt von kalter Temperatur, geringen pH- bzw. Aragonitsättigungs-Werten und erhöhten Nährstoffkonzentrationen gehemmt. Der Grad der Bioerosion ließ sich direkt auf die jeweilige Korallendichte beziehen. Ein für West- und Ostseiten berechnetes Karbonatbudget, das sowohl die jeweilige Lebend- und Totkorallenbedeckung mit einbezog, als auch die errechneten Korallenwachstums- und Bioerosionsraten, konnte die tiefgreifenden Unterschiede der Riffentwicklung vor allem zwischen flacheren West- und tieferen Ostbereichen nicht zufriedenstellend erklären. Stattdessen spielen die unterschiedlichen Überlebensraten von Jungkorallen und der Einfluss von Oberflächenwellen offenbar eine entscheidendere Rolle. Allerdings bestätigte sich im Karbonatbudget, dass sich unter extremem LAIW-Einfluss die reduzierten Wachstumsraten der Korallen, mit der entsprechend der Korallenbedeckung geringen Bioerosion knapp zugunsten des Wachstums regulierten.

Die Neuansiedlung von Jungkorallen auf natürlichem Riffsubstrat zeigte die signifikant höchsten Abundanzen in flacheren Westbereichen (Kapitel 5). Allerdings erhöhte sich die Anzahl von Jungkorallen auf experimentellen Besiedlungsplatten mit zunehmender Expositionszeit an den Ostseiten und nahm entlang der Westseiten ab. Dies spricht für das Unvermögen der Jungkorallen sich trotz der höheren anfänglichen Ansiedlungsdichte auf der Westseite permanent zu etablieren. Die Überlebensraten der Jungkorallen zeigten, dass frühe Stadien der Besiedlung unabhängig von LAIW-Einflüssen verliefen, vielmehr bestimmt von Prädation und Substratverfügbarkeit. Im Gegensatz dazu wurde die langfristige Etablierung sowie das Wachstum von Jungkorallen in zunehmendem Maße an den LAIW-beeinflussten Westseiten gehemmt. Dies könnte ein Hauptgrund sein für eine fehlende Riffentwicklung an den LAIW-exponierten Inselwestseiten.

Summary

The results of this work are a contribution to the understanding of the influence of dramatic natural variations of the physico-chemical environment in coral reef areas caused by Large Amplitude Internal Waves (LAIW) with direct relation to changes and adaptations within the benthic coral reef community on organism, functional group, and ecosystem level.

Large Amplitude Internal Waves (LAIW) are a worldwide oceanographic phenomenon, particularly in tectonically active areas such as South East Asia. A rich underwater topography, strong density stratification and tidal currents are prerequisite for their generation and propagation. These internal waves travelling in groups with amplitudes of > 80 m and speeds of about 2 m s^{-1} deliver sub-thermocline water upslope into shallow shelf regions when they propagate from a deep basin onto the shelf slope, transform, break and create further upslope propagating density intrusions. Despite their high profile in physical oceanography their possible biological impact especially on benthic communities and ecosystems located upslope in shallower shelf areas such as coral reefs is so far largely unknown. In this work the impact of LAIW on coral reefs was investigated at the Similan Island chain located 60 km east of the Thai coast in the Andaman Sea and in the swash zone of breaking LAIW generated near Sumatra and the Andaman-Nicobar Islands.

The unusual coral reef distribution with reefs flourishing only on the sheltered shelf sides east of the islands whereas the exposed west sides lack a true reef framework, was shown to be consistent among the islands and related to LAIW (Chapter 1). Given the close proximity of west and east sides, the differences in the physico-chemical oceanographic parameters were found to be striking: Two year temperature records revealed that LAIW have their strongest impact on the deeper west slopes where they may cause frequent (several events per hour) and abrupt (up to $10 \text{ }^{\circ}\text{C}$, in the order of minutes) drops in temperature with peak activity during the north-east monsoon (January through April). LAIW advected deep cold, nutrient rich, suboxic and low-pH waters (up to 0.6 units below ambient) coming with strong currents into the shallow near shore areas providing a dramatically altered growth environment for west slope benthic communities. In contrast to the low number of frame-building species in east, the west slopes were found to harbour only loose yet more diverse communities of scattered corals growing directly on the granite basement. This is suggested to be due to the alternating impact of south-west monsoon (May to October) and LAIW from above and below contributing to a spatio-temporal heterogeneity in west, maintaining the coral community in a non-equilibrium state of intermediate disturbances which enhances species diversity.

The relative cover and metabolism of the main primary producers (microphytobenthos in reef sands, turf algae and scleractinian corals, i.e. *Porites lutea*) was compared between LAIW-exposed west and non-exposed east side (Chapter 2). Turf algae were the dominant primary producers in west, whereas the sedimentary microphytobenthos communities contributed mostly to the primary production in east, and corals provided a smaller part in general. Despite the profound effects of LAIW on the metabolism of the various primary producers and the varying contributions of each group of primary producers, the overall primary production was similar at both west and east, indicating a high plasticity of primary production in the LAIW-affected west. Similarly the dominating reef building coral *Porites lutea* showed a similar net photosynthesis on both island sides yet with 40 % higher pigment concentrations in west, likely due to the adaptation to lower light availability and higher nutrient concentrations.

The investigation of the trophic response of the common coral *Pocillopora meandrina* (Chapter 3) showed that corals grown under LAIW-exposure revealed significantly higher biomass and protein content than sheltered east corals. Thereby west corals were more heterotrophic with lower stable carbon isotope signatures and showed higher survival in

artificial darkness. The higher energy reserves in west corals and the differences in trophic status due to LAIW-enhanced fluxes of organic matter resulted in an enhanced resilience of west corals to environmental stress.

Coral growth of *Porites lutea* investigated with living coral nubbins and bioerosion on carbonate blocks cut out of *P. lutea* skeletons revealed both, lowest rates at the site of highest LAIW-impact in west deep areas and highest rates within the dense coral reef of the sheltered east shallow sides (Chapter 4). Under LAIW-impact, coral growth is suggested to be hampered by the cumulative effects of low temperature, low pH, i.e. low aragonite saturation state and enhanced nutrient concentrations, while the rate of bioerosion in a healthy coral community seemed to be directly related to the particular amount of coral cover. A carbonate budget calculated for west and east implicating the in each case living and dead coral cover as well as coral growth and bioerosion rates could not satisfactorily explain the large differences in reef development especially between the shallow west sides and deeper east areas. This suggests that other factors, i.e. differential rates of early juvenile mortality and surface wave impact, play a more important role. However the budget confirmed that carbonate accretion by reduced coral growth and carbonate erosion by alike reduced grazing and boring organisms are balanced but only barely positive under highly variable LAIW conditions in west deep areas.

The investigation of coral recruitment on natural reef substrate revealed significantly higher abundances in shallow west areas than in east (Chapter 5). However with increasing exposure period of experimental settlement tiles, the proportion of juvenile corals increased in east but decreased in west, indicating a failure of recruits to establish permanently on the LAIW-exposed sides in spite of the higher initial spat fall. Survival analysis indicated that early stages of settlement and growth occurred independently of LAIW exposure, suggesting that initial recruitment is governed by predation, substrate suitability, and/or competition for space. The subsequent establishment of juvenile corals, by contrast, appeared to be related to LAIW intensity, reflecting the lack of true reefs on the LAIW-exposed west sides of the islands.

General introduction

Coral reef ecosystem – a balance of construction and destruction

Coral reefs are the biologically most diverse and species rich ecosystems in the oceans (Goreau et al. 1979, Birkeland 1997, Veron 2000). They are major geological features on the earth's surface covering about 15 % of the seabed in the 0 to 30 m depth range (Barnes & Chalker 1990), representing about 50 % of the net calcium carbonate accumulation precipitated in the ocean (Smith 1978, Birkeland 1997).

Coral reefs are built by anemone like coral polyps (Cnidarians, Anthozoa), which produce their skeletons of calcium carbonate (CaCO_3) faster than they are eroded by the sea (Smith & Buddemeier 1992, Gattuso et al. 1998, Marubini et al. 2001, 2003, Raven et al. 2005). Corals start their life as free living planula larvae which settle down to the substrate where the chemosensory recognition of morphogenic molecules often associated with the cell walls of specific crustose coralline algae (Raimondi & Morse 2000) or within biofilms (Webster et al. 2004) is required for the induction of their settlement and metamorphosis. After a successful settlement they immediately start to precipitate a CaCO_3 skeleton (Babcock & Mundy 1996, Babcock et al. 2003, Cohen et al. 2009). This skeletogenesis is a biologically highly controlled process in which alternating layers of organic matrix and mineral depositions mark seasonal to diurnal growth layers (Barnes & Lough 1993, Cuif et al. 1999, Cohen & McConnaughey 2003, Allemand et al. 2004, Cuif & Dauphin 2005, Tambutté et al. 2007). The calciblastic epithelium controls the process of calcification. It provides the peri-crystalline fluid with all parameters needed for calcification by secreting the organic matrix (Johnston 1980, Allemand et al. 1998a, Puvrel et al. 2005, Tambutté et al. 2007) and transporting calcium ions (Tambutté et al. 1996, Marshall 1996) and dissolved inorganic carbon (DIC) (Goreau 1961, Furla et al. 2000, Allemand et al. 2004). The peri-crystalline fluid is an extracellular fluid beneath the coral polyp between the epithelium of the ectodermal cells and the skeleton. It is the site of calcification where corals maintain a continuously high aragonite saturation state (Cohen & Holcomb 2009) and CaCO_3 crystals in the size range of micrometers are nucleated and grown incessantly (Cohen & McConnaughey 2003). The outcome of the assemblage of these crystals bundled and packed consecutively one on top of the other is a complex skeleton characteristic and unique for every coral species (Cohen & Holcomb 2009).

Most reef-building corals start as single polyps, as mentioned above, but continue to exist as colonies which are built by hundreds, sometimes even thousands of polyps and can reach imposing sizes of several metres in height. The variety of coral morphologies does not seem to be limited and there exist skeletons of encrusting, domed or branching, laminar and massive forms (Birkeland 1997, Veron 2000).

The reason for the build-up of such spectacular biological CaCO_3 depositions despite the associated high energetic costs for the coral polyps (Allemand et al. 2004, Kleypas & Yates 2009), is based on the symbiosis of corals with unicellular dinoflagellates (zooxanthellae) (Muller-Parker & D'Elia 1997, Gattuso et al. 1999). The photosynthetic carbon fixation by these algae accounts for the high productivity of corals (Hatcher 1988, Muscatine & Weis 1992) and is intimately linked to the CaCO_3 precipitation (Gattuso et al. 1999, Furla et al. 2000, Al-Horani et al. 2007). The majority of reef corals harbour zooxanthellae at densities of more than one million per square centimeter of coral surface (Falkowski & Dubinsky 1981, Edmunds & Davies 1986, Barnes & Chalker 1990). The acquisition of zooxanthellae by corals can take place in the early ontogeny of broadcast spawning corals from the environment (Little 2004) or by direct transfer from the parental colony of brooding species (Thornhill et al. 2006). The unicellular algae become established in the endodermal cells of the coral hosts as an endosymbiosis (Goreau et al. 1971, Muscatine et al. 1981). There exist different possible mechanisms which could explain the higher rate of calcification due to the presence of zooxanthellae: The algae maintain an oxic environment directly within the coral tissue (Rinkevich & Loya 1984, Rands et al. 1992). They produce photosynthates and provide them to the animal host and thus support active transport mechanisms (Chalker & Taylor 1975, Muscatine et al. 1981) or the generation of the organic matrix (Wainwright 1963, Allemand et al. 1998b). Metabolic waste products of the animal are absorbed by the zooxanthellae (Crossland & Barnes 1974, Crawley et al. 2010) as well as substances which could interfere with CaCO_3 precipitation (Simkiss 1964, Snidvongs & Kinzie 1994). The photosynthetic carbon dioxide (CO_2) fixation by the algae increases the CaCO_3 saturation and reduces the energetic costs of maintaining a high saturation state for the animal (Goreau 1959, Gattuso et al. 1999, Allemand et al. 2004). Although the significance of each of these mechanisms with respect to the link between calcification and symbiosis with zooxanthellae has not been determined so far (Gattuso et al. 1999, Allemand et al. 2004), it is nevertheless generally accepted that this delicate symbiosis is the essential trigger for the formation of the massive coral-reef frameworks.

Other calcifying benthic organisms, such as encrusting coralline algae (CCA) (Kuffner et al. 2007, Jokiel et al. 2008), bryozoans, bivalves, barnacles and polychaetes (Glynn 1997,

Hibino & van Woesik 2000) settling and growing in and upon bare coral skeleton, contribute to the consolidation of the reef framework, cementing carbonate fragments into massive reef structures (Adey 1998), closing gaps between colonies and connecting single stands (Goreau 1963, Glynn 1997).

The reef framework features various ecological habitats occupied and colonized by a multitude of organisms which all together constitute the reef community. The most specious fish assemblages known today are found within and between the outer framework ramifications (Choat and Bellwood 1991, Paxton 1995, Spalding et al. 2001). The extensive systems of cavities and crevices (Wunsch & Richter 1998, Richter et al. 2001) are inhabited by numerous filter feeders, prevalently sponges (Richter & Wunsch 1999, Richter et al. 2001).

Many of the organisms contributing to the high species diversity of coral reefs however normally weaken them and convert massive reef structures to rubble, sand and silt (Glynn 1997). This antagonistic process to carbonate bioaccretion is called bioerosion. Important external bioeroders are grazing organisms such as urchins (Bak 1990, 1994, Mokady et al. 1996) and excavating herbivores such as parrot fishes (Bellwood 1995). Internal bioeroders are endolithic sponges, bivalve molluscs, and polychaetes (Davies & Hutchings 1983, Scoffin 1992, Glynn 1997). Erosion of carbonate can also occur through physico-chemical processes, either by physical abrasion by waves or suspended sediment (Ball et al. 1967), or by geochemical shifts, when the addition of CO₂ causes ocean acidification, enhancing calcium carbonate dissolution (Gattuso et al. 1998; Kleypas et al. 1999). Indeed, carbonate budget studies have demonstrated that constructive and destructive processes are closely balanced on many reefs with a net reef accumulation barely ahead of the net reef loss (Scoffin et al. 1980, Glynn 1988).

Environmental conditions in coral reefs

Coral reefs in general flourish in nutrient poor, pristine, aragonite saturated, warm waters (Buddemeier & Kinzie 1976, Goreau et al. 1979, Hoegh-Guldberg 1999). These literally perfect environmental conditions however are rarely always fulfilled, and coral reefs are effectively forced to live under a wider range of environmental conditions, be it due to natural or due to anthropogenic disturbances (Kleypas et al. 2001, Hoegh-Guldberg 1999, Fabricius 2005).

Low nutrient concentrations – It seems to be contradictory that the highly productive coral reefs reside in a nutrient poor environment (Darwin 1842, Andrews & Gentien 1982). The solution for this alleged contradiction lies within the tight coupling and recycling of

nutrients between autotrophic and heterotrophic organisms both, within the individual symbiosis between coral host and zooxanthellae (Goreau et al. 1971, Muscatine et al. 1981) and within the whole reef ecosystem itself (e.g. Hatcher et al. 1997, Richter et al. 2001, Lesser et al. 2006).

Corals are heterotrophic, active filter feeders (Genin et al. 2005, Houlbreque & Ferrier-Pagès 2008), but they benefit from the autotrophic input coming from the zooxanthellae (Goreau et al. 1971, Muscatine et al. 1981). In a mutual exchange the endosymbiotic microalgae supply the coral with the main part of their photosynthates (Muscatine & Porter 1977, Muscatine et al. 1981), i.e. amino acids and sugars (Streamer et al. 1988), and receive the excretion products, i.e. re-mineralized nutrients, from the coral host (Rahav et al. 1989, Yellowlees et al. 2008).

Within the reef ecosystem, the contribution of particulate and dissolved organic matter coming from the surrounding water is crucial for the maintenance of the high productivity in coral reefs (Ferrier-Pagès & Gattuso 1998, Genin et al. 2002). Plankton input is thereby one of the most important allochthon resources (Genin et al. 2005, Yahel 2005). A variety of heterotrophic benthic filter feeders, including corals (Houlbrèque & Ferrier-Pagès 2008), sponges (Lesser 2006), tunicates (Ribes et al. 2005), actinians and bryozoans (Ribes et al. 2003) contribute to the processing of the organic input. The coral cavities and their biota, mainly sponges (Corredor et al. 1988, Richter & Wunsch 1999), but also tunicates, bryozoans, bivalves and polychaetes colonizing the inner reef framework (Ginsburg 1983) are actual sinks for dissolved organic matter extracting them effectively from the reef water (de Goeij & van Duyl 2007). The high abundance of heterotrophic microorganisms associated with the permeable, sandy reef sediments further supports the decomposition of organic material (Wild et al. 2004a, b). Organic material released within the coral reef itself such as for example coral mucus is not lost for the ecosystem, rather it gets rebound into the processing by descending to the ground and contributing to a close benthic-pelagic coupling (Wild et al. 2004a, Huettel et al. 2006).

All of these mechanisms contribute to an efficient processing of organic material until the stage of re-mineralized inorganic nutrients which are subsequently reintroduced into the nutrient cycle due to their usage by autotrophic primary producers. They provide the possibility to maintain high primary productivity and consequently the production of new biomass. This tight coupling between heterotrophic and autotrophic organisms and the efficient nutrient recycling within the reef community on organism level, contributes to the retention of nutrients such as nitrogen and phosphorus within the coral reef ecosystem, and results in a nearly autonomous system with respect to inorganic nutrient input.

However additional input of external nutrients can be delivered into the ecosystem either by natural events, i.e. internal tidal bores (Leichter et al. 2003, Smith et al. 2004), upwelling (Andrews & Gentien 1982), or river discharges (Bell 1991), or by anthropogenic events, i.e. terrestrial run-off or untreated waste waters (Hughes 1994, Fabricius 2005). Even though corals may benefit from enhanced nutrient supply due to increasing zooxanthellae densities (Muscatine et al. 1989, Muller-Parker 1994, Ferrier-Pagès et al. 2001) and photosynthetic efficiency (Muscatine et al. 1989, Houlbrèque et al. 2004), higher nutrient concentrations favour the growth of competitively superior macroalgae (McCook 1999) and may facilitate phase shifts from coral reefs to macroalgae-dominated systems as soon as a certain threshold of nutrient supply is exceeded (Lapointe 1997, McCook 1999, Smith et al. 2001). Enhanced bioerosion on CaCO₃ substrate may be an indirect effect of elevated nutrient concentrations, initially induced by external damage due to grazers which are attracted by the higher cover of macroalgae and algal turf (Steneck 1988), and further amplified by internal micro-bioeroders which benefit directly from the higher nutrient supply (Chazottes et al. 2002, Ward-Paige et al. 2005). Coral recruitment might be hampered directly by increased nutrient concentrations (Tomascik 1991, Wittenberg & Hunte 1992) or indirectly due to an enhanced competition for space with more abundant macroalgae (Belliveau & Paul 2002). Further it has been shown that coral growth rates may be reduced due to additional input of inorganic nutrients (Ferrier-Pagès et al. 2000, 2001).

Light environment - Pristine, clear water conditions are essential for the primary production within coral reefs because light provides the energy for the photosynthetic energy conversion (Yentsch et al. 2002). When light is attenuated, both in shade and at depth, adaptations by zooxanthellae permit a maximal absorption and utilization of the available light energy (Titlyanov 1991). For this reason amongst others benthic coral community compositions may be different in high light conditions of shallow waters compared to lower light conditions in deeper waters (Bak et al. 2005). Rates in primary productivity are closely related to relatively small changes in water transparency (Yentsch et al. 2002). The threat of high turbidity and accompanying enhanced particle loads as caused e.g. by terrestrial run off (Fabricius 2005) is therefore not only the additional nutrient input and sedimentation (Rogers 1990, Fabricius et al. 2003) but also the loss of a sufficient light and energy supply for the primary producers in the benthic reef community (Fabricius 2005). Furthermore as coral growth is directly linked to the photosynthesis of the endosymbiotic zooxanthellae (Gattuso et al. 1999), known as the process of light-enhanced calcification (Chalker & Taylor 1975), changes in the light environment do have an immediate effect on coral calcification (Al Horani et al. 2003).

Aragonite saturation state – Aragonite is the form of calcium carbonate that corals produce (Langdon et al. 2000, 2003). Coral growth and calcification are highly dependent on the aragonite saturation state (Ω_{arag}) of seawater. The definition for Ω_{arag} is the product of the concentrations of calcium (Ca^{2+}) and carbonate ions (CO_3^{2-}) measured in seawater divided by the product of the concentrations of Ca^{2+} and CO_3^{2-} under saturated conditions (in equilibrium) in seawater (Gattuso et al. 1999). Variations in Ω_{arag} are mainly assigned to changes in the CO_3^{2-} concentration as the Ca^{2+} concentration in seawater is generally very high and largely constant (Gattuso et al. 1999). The tropical surface ocean where most coral reefs are found is, in general, highly supersaturated with respect to aragonite with $\Omega_{\text{arag}} > 3$ (Levitus 1998). Nevertheless, neither calcite nor aragonite will form spontaneously because there are kinetic barriers that prevent nucleation and/or crystal growth (Cohen & Holcomb 2009). Studies with different scientific approaches indicated that corals presumably use seawater as the starting fluid for calcification (Cohen et al. 2001, 2009, Gaetani & Cohen 2006, Erez & Braun 2007, Holcomb et al. 2009), and that seawater is transported directly to the actual site of calcification, the peri-crystalline fluid (Erez & Braun 2004). Yet to enable CaCO_3 to precipitate, corals must modify and control the given conditions of the seawater chemical composition in their calcifying fluid (Al Horani et al. 2003, Cohen & McConnaughey 2003, Cohen et al. 2009). These regulations at the site of calcification are associated with high energetic costs (Dennison & Barnes 1988) constituting up to 30 % of the coral's energy budget (Allemand et al. in press). Under normal conditions of pH (around 8.2) and $\Omega_{\text{arag}} (> 1)$ corals can afford these energetic expenses. Yet in case of lowered pH conditions in the seawater due to higher concentrations of carbon dioxide (CO_2) and a shift in the carbonate chemistry to lower CO_3^{2-} concentrations, i.e. Ω_{arag} , the energetic demands for the maintenance of a high saturation state at the site of calcification might be too high (Cohen & Holcomb 2009). As a result coral calcification can be dramatically reduced (Schneider & Erez 2006, Marubini et al. 2008) or even shifted into dissolution processes (Andersson et al. 2009).

Temperature - Although tropical corals are known to exist 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)) and tolerate large annual temperature ranges (up to 25 °C), the sensitive association between coral host and endosymbiotic zooxanthellate is highly susceptible to uncommon changes in the surrounding seawater temperature (Gates et al. 1992). Thereby the tolerances seem to be less expandable towards thermal stress as already small increases in temperature of < 2 °C can cause coral bleaching (Gates et al. 1992, Brown 1997, Fitt et al. 2001), i.e. the detachment of zooxanthellae from their coral host. On the other hand corals may survive

severe cold periods (13 °C for several days, Coles & Fadlallah 1991), but periodic cold water influence may preclude hard-coral communities from attaining higher levels of cover and abundance (Burns 1985, Kleypas et al. 1999). Furthermore, temperature variations can have a delicate influence on the calcification process in corals (Al Horani 2005), and cold temperatures in particular with about 6 to 10 °C below ambient may have clearly negative effects on the symbiosis of corals with their zooxanthellae (Gates et al. 1992), coral health and survival (Coles & Fadlallah 1991).

Although it is altogether clear that the benthic coral reef community and its related primary production are likely adjusted to the prevailing environmental conditions, their feasibilities to adapt as a 'healthy' and balanced ecosystem are limited. Changes or disturbances of one or several environmental factors automatically affect single organisms, and can finally result in changes within the whole ecosystem. This can be especially dramatic when these changes or disturbances affect corals, i.e. the vital constructors of the reef framework which provides the basic foundation of the whole coral reef ecosystem.

Large Amplitude Internal Waves (LAIW)

Large Amplitude Internal Waves (LAIW) are a ubiquitous phenomenon in the world's oceans (Huthnance 1989, Apel et al. 2006), and a well known feature in physical oceanography (Vlasenko & Hutter 2001, 2002, Jackson 2004). They are generated by tidal fluctuations across shallow under water ridges in a density-stratified water column (Gerkema & Zimmerman 1995, Vlasenko and Hutter 2001). LAIW travel fast and over long distances (Osborne & Burch 1980) as waves of depression in groups or packages along the density separation layer, i.e. the pycnocline (Vlasenko & Hutter 2001). As the solitary waves encounter an obstruction, such as the shelf and start propagating from a deep basin onto the shelf slope, they gradually transform 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 larger than 40 % of the thickness of the pycnocline, the steepening and overturning of the rear wave faces causes wave breaking and the generation of upslope propagating density intrusions (Vlasenko & Hutter 2002, Vlasenko & Stashchuk 2007). Thereby deep sub-thermocline water is delivered upslope (Vlasenko & Stashchuk 2007) extending into shallow shelf regions (Nielsen et al. 2004). Further the passage of these waves of elevation causes turbulent mixing near the sea bed (De Silva et al. 1997), and can

lead to resuspension of bottom sediments raising them up to 30 m above the seafloor (Moum et al. 2007).

Despite their worldwide occurrence in all parts of the oceans LAIW are so far barely noticed by biologists and remain a phenomenon mainly studied by physical oceanographers. However their possible impacts especially on benthic communities and ecosystems located along the shelf break and upslope in shallower shelf areas might be of fundamental importance for their shaping and composition.

Large Amplitude Internal Waves and coral reefs

The Andaman Sea represents one of the most important coral reef regions in the Indian Ocean province harbouring more than 250 hard coral species along its Thai coasts (Yeemin et al. 2006). While only a few studies on coral reef conditions (e.g. Brown et al. 2002, Brown & Phongsuwan 2004, Brown 2007) and coral recruitment in this area have been published (Phongsuwan 1991, Thongtham & Chansang 1999, Chanmethakul 2001, Sawall et al. 2010) interest in Andaman Sea reefs of Thailand has increased significantly following the tsunami in 2004 (Allen et al. 2005, Plathong 2005, Yeemin 2006, Phongsuwan et al. 2006, Phongsuwan & Brown 2007). The Andaman basin is characterized by two major climatic and oceanographic features: the south-west (SW) monsoon from May to October (Dunne & Brown 1996, Wu & Zhang 1998) with intense rainfall and heavy swell, and the year-round occurrence of Large Amplitude Internal Waves (Perry & Schimke 1965, Osborne & Burch 1980, Jackson 2004).

LAIW have been known for decades in the Andaman Sea (Perry & Schimke 1965, Osborne & Burch 1980) and their extraordinary amplitudes of > 80 m have already been described in the 60ies (Perry & Schimke 1965). They are generated along the Andaman-Nicobar Island arc and at the shallow reefs northwest of Sumatra (Alpers et al. 1997, Jackson 2004), and travel eastward through the deep Andaman basin reaching speeds of > 2 m s⁻¹ (Osborne & Burch 1980). Satellite images show these dense wave packages as 'ripple bands' on the water surface (Fig 1), visible from their place of origin until far beyond the 200 m shelf break reaching the coasts of Thailand and Myanmar (Jackson 2004). As LAIW obviously expand until near coast regions (Nielsen et al. 2004, Jackson 2004) they may reach coral reefs residing in shallow waters. The closer coral reefs are located to the shelf break where LAIW strike the seafloor and start travelling upslope, the more presumable it is that LAIW secondary waves propagating from the shelf break reach these benthic ecosystems directly and largely undamped.

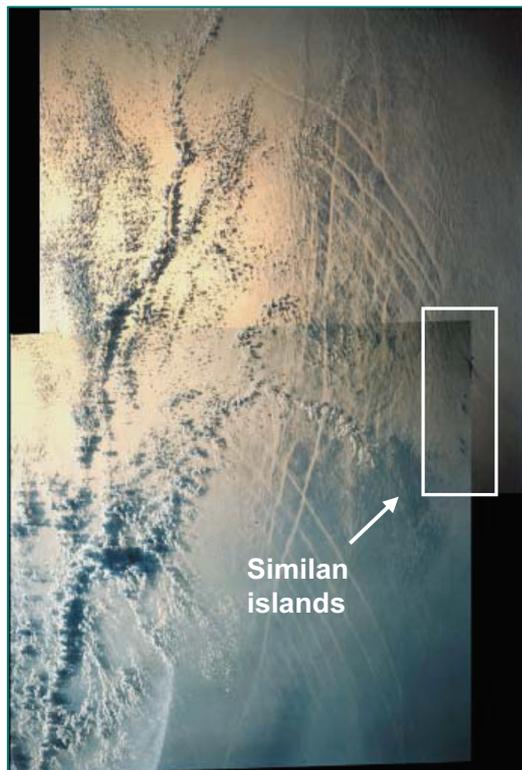


Figure 1 Astronaut photograph (STS075-709-55, 56) acquired on 27 February 1996 at 1030 UTC. The image shows the signature of internal wave packages in the Andaman Sea with the Similan island chain (marked). [Image courtesy of Earth Sciences and Image Analysis Laboratory, NASA Johnson Space Center (<http://eol.jsc.nasa.gov>)] (Modified after Jackson 2004)

The *chemical composition* of deep sub-pycnocline water, which might possibly reach shallow coral reef areas with the LAIW, is largely different from the surface water composition. It is characterized in general, by an enrichment of re-mineralized nutrients, i.e. nitrate and phosphorus due to decomposition processes of organic material (Jackson & Williams 1985), and can be largely poor or even depleted in oxygen concentrations due to biological combustion processes in areas isolated from additional oxygen supply (Levin et al. 1991). Further the considerable lower temperatures of sub-thermocline waters in contrast to warm surface waters entail an increased solubility of CO_2 and consequently a different carbon ion composition at the expense of CO_3^{2-} concentrations. This can result in a clearly reduced Ω_{arag} of deepwater (Levitus 1998).

The *physical impact* of LAIW on shallow coral reef regions might be characterized by the intense interactions of LAIW with the bottom while travelling upslope which are associated with large velocity shear, bottom turbulence and mixing (De Silva et al. 1997). LAIW may entrain interstitial material and bottom sediments from the deeper shelf slope areas up to shallow waters (cf. Moum et al. 2007). As a consequence the benthic reef community would have to deal with increased particle loads, reduced light levels and intense turbulences and current speeds.

Furthermore, LAIW might also entrain an enhanced phytoplankton biomass (Nielsen et al. 2004), and could act as a transport for plankton and larvae, similarly as it has been reported for tidal bores (Pineda 1991, Leichter et al. 1998).

In summary, coral reef areas which are passed and directly impacted by LAIW would presumably have to deal with a whole 'cocktail' of abrupt chemical and physical changes in their environment whose influences on the benthic coral reef community, framework development, primary production, coral nutrition, coral growth, bioerosion, and coral recruitment, just to mention some, remain so far speculation.



The Similan island group, located off the Andaman Sea coast of Thailand, near the 90 m isobath where most of the mixing due to LAIW is believed to take place (Jackson 2004, Vlasenko & Alpers 2005) turned out to be a predestined study area to examine the possible impact of LAIW on coral reefs. The nine granitic islands extend in a perfect north-south alignment over a distance of about 24 km located 60 km west of the Thai coast and 400 km east of the Andaman-Nicobar-Islands. Monitoring studies (Chansang et al. 1999, Phongsuwan et al. 2008) along the Similan islands and other offshore islands in the Andaman Sea and satellite images (www.reefbase.org/gis_maps) suggest that coral reef development is restricted to the sheltered eastern island sides, whereas the windward, ocean facing west sides are characterized by only scattered patchy reef assemblages but lack actual reef formations (Fig 2). This is in contrast to most other barriers or islands where reef growth is most developed at the ocean facing windward sides (Veron 2000), even in the storm areas of the open tropical Pacific (Spalding et al. 2001). It therefore stands to reason that LAIW might play an important role in explaining this unusual coral reef distribution.

Figure 2 Similan island chain in the Andaman Sea about 60 km west of the Thai coast and 400 km east of the Andaman-Nicobar-Islands [Image source: Google Earth, Data SIO, NOAA, U.S. Navy, NGA, GEBCO, 2007 Europa Technologies, US Dept of State Geographer, June 2007]

The aim of the present thesis was to answer some of the main questions arising from the above described relations within - and requirements of coral reefs and the possible impact of LAIW on these sensitive benthic ecosystems. The here from arised research questions and accordant hypotheses are listed below:

Research questions and hypotheses addressed

1. Are LAIW reaching the shallow reef areas of the Similan islands located within their supposed swash zone? (Chapter 1 – 5)
2. In case that LAIW reach the islands, how do they change the physico-chemical environment? (Chapter 1, 2, 3)
3. In case that LAIW reach the islands, are they an explanation for the existing coral reef distribution and coral community composition? (Chapter 1, 4, 5)
4. In case that LAIW reach the islands, how do they influence primary production within the reef community? (Chapter 2)
5. In case that LAIW reach the islands, how do they influence the trophic status of corals? (Chapter 3)
6. In case that LAIW reach the islands, how do they influence coral growth and bioerosion on dead coral skeletons? (Chapter 4)
7. In case that LAIW reach the islands, how do they influence coral recruitment? (Chapter 5)

The following hypotheses were formulated regarding the results:

In LAIW exposed reef areas,

1. the development of a dense coral reef framework is inhibited due to the cumulative effects of enriched nutrient concentrations, reduced light levels, low pH, i.e. low Ω_{arag} , and low temperatures hampering coral recruitment, coral skeletal growth and enhancing internal bioerosion processes on dead coral skeletons undermining the formation of permanently stable reef structures.
2. the primary production within the reef community is different from LAIW sheltered reef areas due to the influence of reduced light availability in combination with enhanced nutrient concentrations.
3. corals reveal a more heterotrophic performance than non-exposed corals due to the LAIW-enhanced supply of plankton and organic matter under light depleted conditions.

Literature

- Adey WH (1998) Coral reefs: Algal structured and mediated ecosystems in shallow, turbulent, alkaline waters. *J. Phycol* 34:393–406
- Al-Horani FA, Al-Moghrabi SM, de Beer D (2003) The mechanism of calcification and its relation to photosynthesis and respiration in the scleractinian coral *Galaxea fascicularis*. *Mar Biol* 142:419–426
- Al-Horani FA (2005) Effects of changing seawater temperature on the photosynthesis and calcification in the scleractinian coral *Galaxea fascicularis*, measured with O₂, Ca²⁺ and pH microsensors. *Scientia Marina* 69:347–354
- Al-Horani FA, Tambutté É, Allemand D (2007) Dark calcification and the daily rhythm of calcification in the scleractinian coral, *Galaxea fascicularis*. *Coral Reefs* 26:531–538
- Allemand D, Furla P, Bénazet-Tambutté S (1998a) Mechanisms of carbon acquisition for endosymbiont photosynthesis in Anthozoa. *Can J Bot* 76:925–941
- Allemand D, Tambutté É, Girard JP, Jaubert J (1998b) Organic matrix synthesis in the scleractinian coral *Stylophora pistillata*: Role in biomineralization and potential target of the organotin tributyltin. *J Exp Biol* 201:2001–2009
- Allemand D, Ferrier-Pagès C, Furla P, Houlbrèque F, Puverel S, Reynaud S, Tambutté É, Tambutté S, Zoccola D (2004) Biomineralisation in reef-building corals: from molecular mechanisms to environmental control. *Comptes Rendus Palevol* 3:453–467
- Allemand D, Tambutté É, Zoccola D, Tambutté S (in press) Coral calcification, cells to reefs. In Dubinsky Z (ed) *Coral and Coral Reefs*. Springer
- Allen GR, Stone GS (2005) Rapid assessment survey of tsunami-affected reefs of Thailand. New England Aquarium Technical Report 02-05, Boston, USA, 122 pp
- Alpers W, Wang-Chen H, Hock L (1997) Observation of internal waves in the Andaman Sea by ERS SAR. Proc 3rd ERS Symp on Space at Service of our Environment. Florence Italy
- Andersson AJ, Kuffner IB, Mackenzie FT, Jokiel PL, Rodgers KS, Tan A (2009) Net loss of CaCO₃ from coral reef communities due to human induced seawater acidification. *Biogeosci Discuss* 6:2163–2182
- Andrews JC, Gentien P (1982) Upwelling as a source of nutrients for the Great Barrier Reef Ecosystems: A solution to Darwin's question? *Mar Ecol Prog Ser* 8:257–269
- Apel JR, Ostrovsky LA, Stepanyants YA, Lynch JF (2006) Internal Solitons in the Ocean. Technical report WHOI-2006-04, Oceanographic Inst, Woods Hole
- Babcock RC, Mundy C (1996) Coral recruitment: Consequences of settlement choice for early growth and survivorship in two scleractinians. *J Exp Mar Biol Ecol* 206:179–201
- Babcock RC, Baird AH, Piromvaragorn S, Thomson DP, Willis BL (2003) Identification of Scleractinian Coral Recruits from Indo-Pacific Reefs. *Zool Std* 42:211–226
- Bak RP, G Nieuwland, EH Meesters. 2005. Coral reef crisis in deep and shallow reefs: 30 years of constancy and change in reefs of Curacao and Bonaire. *Coral Reefs* 24:475–479.
- Barnes DJ, Chalker BE (1990) Calcification and photosynthesis in reef-building corals and algae. In Dubinsky Z (ed) *Ecosystems of the world*, vol 25, Coral reefs, pp 109–131. Elsevier Science Publ, New York, 550 p
- Barnes DJ, Lough JM (1993) On the nature and causes of density banding in massive coral skeletons. *J Exp Mar Biol Ecol* 167:91–108
- Bell PRF (1991) Status of eutrophication in the Great Barrier Reef Lagoon. *Mar Poll Bull* 23:89–93
- Belliveau SA, Paul VJ (2002) Effects of herbivory and nutrients on early colonization of crustose coralline and fleshy algae. *Mar Ecol Prog Ser* 232:105–114
- Birkeland C (1997) *Life and death of coral reefs*. Chapman & Hall, Int Thomson Publishing, New York, pp 1–12
- Brown BE (1997) Coral bleaching: causes and consequences. *Coral Reefs* 16 Suppl:S129–S138
- Brown BE (2007) Coral reefs of the Andaman Sea - an integrated perspective. *Oceanogr Mar Biol Annu Rev* 45:173–194
- Brown BE, Phongsuwan N (2004) Constancy and change on shallow reefs around Leam Panwa, Phuket, Thailand over a twenty year period. *Phuket Mar Biol Cent Res Bull* 65:61–73
- Brown BE, Clarke KR, Warwick RM (2002) Serial patterns of biodiversity change in corals across shallow reef flats in Ko Phuket, Thailand, due to the effects of local (sedimentation) and regional (climatic) perturbations. *Mar Biol* 141:21–29
- Buddemeier, RW, Kinzie RA (1976) Coral growth. *Oceanogr mar Biol A Rev* 14:183–225
- Burns TP (1985) Hard-coral distribution and cold-water disturbances in South Florida: variation with depth and location. *Coral Reefs* 4:117–124
- Chalker BE, Taylor DL (1975) Light-enhanced calcification and the role of oxidative phosphorylation in calcification of the coral *Acropora cervicornis*. *Proc R Soc London B* 190:323–331
- Chanmethakul (2001) Spawning season of scleractinian corals on Phuket Island. M.Sc. thesis, Prince of Songkla University, Thailand, 82 pp.
- Chansang H, Satapoomin U, Poovachiranon S (1999) Maps of coral reefs in Thai waters. Vol 2, Coral Reef Resource Management Project, Department of Fisheries. Pp 198 (in Thai) Andaman Sea, Bangkok

- Chave KE (1962) Factors influencing the mineralogy of carbonate sediments. *Limnol Oceanogr* 7:218–223
- Chazottes V, Le Campion-Alsumard T, Peyrot-Clausade M, Cuet P (2002) The effects of eutrophication-related alterations to coral reef communities on agents and rates of bioerosion (Reunion Island, Indian Ocean). *Coral reefs* 21:375-390
- Choat JH, DR Bellwood (1991) Reef fishes: their history and evolution. In Sale PF (ed) *The Ecology of fishes on coral reefs*. Academic Press, San Diego and London pp 39-66
- Cohen AL, Layne GD, Hart SR, Lobel PS (2001) Kinetic control of skeletal Sr/Ca in a symbiotic coral: Implications for the paleotemperature proxy. *Paleoceanography* 16:20–26
- Cohen AL, McConnaughey TA (2003) Geochemical perspectives on coral mineralization. In: Dove PM, Weiner S, Yoreo JJ (eds) *Biom mineralization*. *Rev Mineral Geochem* 54:151–187
- Cohen AL, McCorkle DC, de Putron S, Gaetani GA, Rose KA (2009) Morphological and compositional changes in the skeletons of new coral recruits reared in acidified seawater: Insights into biomineralization response to ocean acidification. *Geochem Geophys Geosyst* 10(7), Q07005, doi:10.1029/2009GC002411
- Cohen AL, Holcomb M (2009) Why corals care about ocean acidification – uncovering the mechanism. *Oceanography* 22:118-127
- Coles SL, Fadlallah YH (1991) Reef coral survival and mortality at low temperatures in the Arabian Gulf: new species-specific lower temperature limits. *Coral Reefs* 9:231-237
- Corredor JE, Wilkinson CR, Vicente VP, Morell JM, Otero E (1988) Nitrate release by Caribbean reef sponges. *Limnol Oceanogr* 33:114-120
- Crawley A, Kline DI, Dunn S, Anthony K, Dove S (2010) The effect of ocean acidification on symbiont photorespiration and productivity in *Acropora Formosa*. *Global Change Biol* 16:851-863
- Crossland CJ, Barnes DJ (1974) The role of metabolic nitrogen in coral calcification. *Mar Biol* 28:325-332
- Cuif JP, Dauphin Y (2005) The environment recording unit in corals skeletons—a synthesis of structural and chemical evidences for a biochemically driven, stepping-growth process in fibres. *Biogeosciences* 2:61–73
- Cuif JP, Dauphin Y, Freiwald A, Gautret P, Zibrowius H (1999) Biochemical markers of zooxanthellae symbiosis in soluble matrices of skeleton of 24 Scleractinia species. *Comp Biochem Physiol* 123(A):269–278
- Darwin CJ (1842) *Coral reefs*. Smith Elder, London
- Dennison WC, Barnes DJ (1988) Effect of water motion on coral photosynthesis and calcification. *J Exp Mar Biol Ecol* 115:67–77.
- De Silva IPD, Imberger J, Ivey GN (1997) Localized mixing due to a breaking internal wave ray at a sloping bed. *J Fluid Mech* 350:1-27
- Dunne RP, Brown BE (1996) Penetration of solar UVB radiation in shallow tropical waters and its potential biological effects on coral reefs; results from the central Indian Ocean and Andaman Sea. *Mar Ecol Prog Ser* 144:109-118
- Edmunds PJ, Davies PS (1986) An energy budget for *Porites porites* (Scleractinia). *Mar Biol* 92:339-347
- Erez J, Braun A (2007) Calcification in hermatypic corals is based on direct seawater supply to the biomineralization site. *Geochim Cosmochim Acta*, 71(15, Supplement 1), A260
- Fabricius K., Wild, C., Wolanski, E., Abele, D (2003) Effects of transparent exopolymer particles (TEP) and muddy terrigenous sediments on the survival of hard coral recruits. *Estuarine, Coast Shelf Sci* 57:613–621
- Fabricius KE (2005) Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. *Mar Poll Bull* 50:125-146
- Falkowski PG, Dubinsky Z (1981) Light-shade adaptation of *Stylophora pistillata*, a hermatypic coral from the gulf of Eilat. *Nature* 289:172-174
- Ferrier-Pagès C, Gattuso JP (1998) Biomass, production and grazing rates of pico- and nanoplankton in coral reef waters (Miyako Island, Japan). *Microb Ecol* 3: 546-557
- Ferrier-Pagès C, Gattuso J P, Dallot S, Jaubert J (2000) Effect of nutrient enrichment on growth and photosynthesis of the zooxanthellate coral *Stylophora pistillata*. *Coral Reefs* 19: 103-113
- Ferrier-Pagès C, Schoelzke V, Jaubert J, Muscatine L, Hoegh-Guldberg O (2001) Response of a scleractinian coral, *Stylophora pistillata*, to iron and nitrate enrichment. *J Exp Mar Biol Ecol* 259:249-261
- Fitt WK, Brown BE, Warner ME, Dunne RP (2001) Coral bleaching: interpretation of thermal tolerance limits and thermal thresholds in tropical corals. *Coral Reefs* 20:51-65
- Furla P, Galgani I, Durand I, Allemand D (2000) Sources and mechanisms of inorganic carbon transport for coral calcification and photosynthesis. *J Exp Biol* 203:3445–3457
- Gaetani GA, Cohen AL (2006) Element partitioning during precipitation of aragonite from seawater: A framework for understanding paleoproxies. *Geochem Cosmochim Acta* 70:617-634
- Gates RD; Baghdasarian G, Muscatine L (1992) Temperature stress causes host cell detachment in symbiotic cnidarians: Implications for coral bleaching. *Biol Bull* 182:324-332
- Gattuso JP, Frankignoulle M, Bourge I, Romaine S, Buddemeier RW (1998) Effect of calcium carbonate saturation of seawater on coral calcification. *Global Planet Change* 18:37–46
- Gattuso JP, Allemand D, Frankignoulle M (1999) Photosynthesis and calcification at cellular, organismal and community levels in coral reefs: A review on interactions and control by carbonate chemistry. *Amer Zool* 39:160-183

- Genin A, Yahel G, Reidenbach MA, Monismith SG, Koseff JR (2002) Intense benthic grazing on phytoplankton in coral reefs revealed using the control volume approach. *Oceanography* 15:90–96
- Genin A, Jaffe JS, Reef R, Richter C, Franks PJS (2005) Swimming against the flow: a mechanism of zooplankton aggregation. *Science* 308:860–862
- Gerkema, Zimmerman (1995) Generation of nonlinear internal tides and solitary waves. *Amer Meteorol Soc* 25:1081-1094
- Ginsburf RN (1983) Geological and biological roles of cavities in coral reefs, p. 148–153. In Barnes D (ed) *Perspectives on coral reefs*. Australian Institute of Marine Science.
- Glynn PW (1988) El Niño warming, coral mortality and reef framework destruction by echinoid bioerosion in the eastern Pacific. *Galaxea* 7:129-160
- Glynn PW (1997) Bioerosion and coral reef growth: a dynamic balance. In: Birkeland C (ed) *Life and death of coral reefs*. Chapman and Hall, New York, pp 68-95
- Goreau TF (1959) The physiology of skeleton formation in corals. I. A method for measuring the rate of calcium deposition by corals under different conditions. *Biol Bull* 116:59-75
- Goreau TF (1961) Problèmes de croissance et de dépôt du calcium dans les coraux récifaux/Problems of growth and calcium deposition in reef corals. *Endeavour* 20:32–39
- Goreau TF (1963) Calcium carbonate deposition by coralline algae and corals in relation to their roles as reef builders: *Ann NY Acad Sci* 109:127-167
- Goreau TF, Goreau NI, Yonge CM (1971) Reefcorals: autotrophs or heterotrophs? *Biol Bull* 141:247-260
- Goreau TF, Goreau NI, Goreau TJ (1979) Corals and Coral Reefs. *Scientific American* 124-136
- de Goeij JM, van Duyl FC (2007) Coral cavities are sinks of dissolved organic carbon (DOC). *Limnol Oceanogr* 53:2608–2617.
- Hatcher BG (1988) The primary productivity of coral reefs: a beggar’s banquet. *Trends Ecol Evol* 3:106-111
- Hatcher BG (1997) Coral reef ecosystems: how much greater is the whole than the sum of the parts? *Coral Reefs* 16:77–91
- Heyward AJ, Negri AP (1999) Natural inducers for coral larval metamorphosis. *Coral Reefs* 18:273–279
- Hibino K, van Woessik R (2000) Spatial differences and seasonal changes of net carbonate accumulation on some coral reefs of the Ryukyu Islands, Japan. *J Exp Mar Biol Ecol* 252:1-14
- Hoegh-Guldberg O (1999) Climate change, coral bleaching and the future of the world’s coral reefs. *Mar Freshwater research* 50:839-866
- Holcomb M, Cohen AL, Gabitov R, Hutter J (2009) Compositional and morphological features of aragonite precipitated experimentally from seawater and biogenically by corals. *Geochim Cosmochim Acta* 73:166–179, doi:10.1016/j.gca.2009.04.015
- Houlbrèque F, Tambutte E, Allemand D, Ferrier-Pagès C (2004) Interactions between zooplankton feeding, photosynthesis and skeletal growth in the scleractinian coral *Stylophora pistillata*. *J Exp Biol* 207:1461–1469
- Houlbrèque F, Ferrier-Pagès C (2008) Heterotrophy in tropical Scleractinian corals. *Biol Rev* 2009 84:1-17
- Huettel M, Wild C, Gonelli S (2006) The mucus trap in coral reefs: formation and temporal evolution of aggregates caused by coral mucus. *Mar Ecol Progr Ser* 30769-84
- Hughes TP (1994) Catastrophes, phase shift, and large scale degradation of Caribbean coral reef. *Science* 265:1547-1551
- Hughes TP, Baird AH, Bellwood DR, Card M, Connolly SR, Folke C, Grosberg R, Hoegh-Guldberg O, Jackson JBC, Kleypas J, Lough JM, Marshall P, Nyström M, Palumbi SR, Pandolfi JM, Rosen B, Roughgarden J (2003) Climate Change, Human Impacts, and the Resilience of Coral Reefs. *Science* 301:929-933
- Huthnance (1989) Internal tides and waves near the continental shelf edge. *Geophys. Astrophys. Fluid dynamics*, 48:81-106
- Jackson CR (2004) An atlas of internal solitary-like waves and their properties. 2nd Ed. Office of Naval Research, Global Ocean Associates, Alexandria, VA, USA
- Jackson GA, Williams GM (1985) Importance of dissolved organic nitrogen and phosphorus to biological nutrient cycling. *Deep-Sea Res* 32:223-235
- Johnston IS (1980) The ultrastructure of skeletogenesis in zooxanthellate corals. *Int Rev Cytol* 67:171–214
- Jokiel PL, Rodgers KS, Kuffner IB, Andersson AJ, Cox EF, Mackenzie FT (2008) Ocean acidification and calcifying reef organisms: a mesocosm investigation. *Coral Reefs* 27:473-483
- Kleypas JA, McManus JW, Lambert Meñez AB (1999) Environmental limits to coral reef development: Where do we draw the line? *Amer Zool* 39:146-159
- Kleypas JA, Buddemeier RW, Gattuso JP (2001) The future of coral reefs in an age of global change. *Int J Earth Sci (Geol Rundsch)* 90:426-437, doi 10.1007/s005310000125
- Kleypas JA, Yates KK (2009) Coral reefs and ocean acidification. *Oceanography* 22:108-117
- Kuffner IB, Andersson AJ, Jokiel PL, Rodgers KS, Mackenzie FT (2007) Decreased abundance of crustose coralline algae due to ocean acidification. *Nature* 1:114-117
- Langdon C, Takahashi T, Sweeney C, Chipman D, Goddard J, Marubini F, Aceves H, Barnett H, Atkinson MJ (2000) Effect of calcium carbonate saturation state on the calcification rate of an experimental coral reef. *Global Biogeochem Cycles* 14:639–654
- Langdon C, Broecker WS, Hammond DE, Glenn E, Fitzsimmons K, Nelson SG, Peng TH, Hajdas I, Bonani G

- (2003) Effect of elevated CO₂ on the community metabolism of an experimental coral reef. *Global Biogeochem Cycles* 17:1011, doi:10.1029/2002GB001941
- Lapointe BE (1997) Nutrient thresholds for bottom-up control of macroalgal blooms on coral reefs in Jamaica and southE Florida. *Limnol Oceanogr* 42:1119-1131
- Leichter JJ., Shellenbarger G, Genovese SJ, Wing SR (1998) Breaking internal waves on a Florida (USA) coral reef: A plankton pump at work? *Mar Ecol Prog Ser* 166:83-97
- Leichter J J, Stewart H L, Miller S L (2003) Episodic nutrient transport to Florida coral reefs. *Limnol Oceanogr* 8:1394–1407
- Lesser MP (2006) Benthic-pelagic coupling on coral reefs: feeding and growth of Caribbean sponges. *J Exp Mar Biol Ecol* 328:277–288. doi:10.1016/j.jembe.2005.07.010
- Levin LA, Huggett CL, Wishner KF (1991) Control of deep-sea benthic community structure by oxygen and organic-matter gradients in the eastern Pacific Ocean. *J Mar Res* 49:763-800(38)
- Levitus S, Boyer T, Conkright M et al. (1998) World ocean atlas. Ocean climate laboratory, National Oceanographic Data Center, Washington, DC
- Little AF (2004) Flexibility in algal endosymbiosis shapes growth in reef corals. *Science* 304:1492-1494
- Marshall AT (1996) Calcification in hermatypic and ahermatypic corals. *Science* 271:637–639
- Marubini F, Barnett H, Langdon C, Atkinson MJ (2001) Dependence of calcification on light and carbonate ion concentration for the hermatypic coral *Porites compressa*. *Mar Ecol Prog Ser* 220:153–162
- Marubini F, Ferrier-Pagés C, Cuif JP (2003) Suppression of growth scleractinian corals by decreasing ambient carbonate ion concentration: a cross-family comparison. *Proc R Soc Lond B* 270:179–184
- Marubini F, Ferrier-Pagés C, Furla P, Allemand D (2008) Coral calcification responds to seawater acidification: a working hypothesis towards a physiological mechanism. *Coral reefs* 27:491-499
- Mc Cook (1999) Macroalgae, nutrients and phase shifts on coral reefs: scientific issues and management consequences for the Great Barrier Reef, *Coral Reefs* 18:357-367
- Morse DE, Hooker N, Morse ANC, Jensen RA (1988) Control of larval metamorphosis and recruitment in sympatric agariciid corals. *J Exp Mar Biol Ecol* 116:193–217
- Moum JN, Klymak JM, Nash JD, Perlin A, Smyth WD (2007) Energy transport by nonlinear internal waves. *J Phys Oceanogr* 37:1968-1988
- Muller-Parker G, McCloskey LR, Hoegh-Guldberg O, McAuley PJ (1994) Effect of ammonium enrichment on animal and algal biomass of the coral *Pocillopora damicornis*. *Pacific Science* 48:273-283
- Muller-Parker G, D'Elia CF (1997) Interactions between corals and their symbiotic algae. In Birkeland C (ed) *Life and death of coral reefs*. Chapman & Hall, Int Thomson Publishing, New York, pp 96-113
- Muscantine L, Porter JW (1977) Reef corals: mutualistic symbiosis adapted to nutrient-poor environments. *Bio Sci* 27:454-460
- Muscantine L, McCloskey L R, Marian R E (1981) Estimating the daily contribution of carbon from zooxanthellae to coral animal respiration. *Limnol Oceanogr* 26:601-611
- Muscantine L, Falkowski P G, Dubinsky Z, Cook P A, McCloskey L R (1989) The effect of external nutrient resources on the population dynamics of zooxanthellae in a reef coral. *Proc R Soc Lond* 236:311-324
- Muscantine L, Weis VM (1992) Productivity of ooxanthellae and biogeochemical cycles
- Nielsen TG, Bjørnsen PK, Boonruang P, Fryd M, Hansen PJ, Janekarn V, Limtrakulvong V, Munk P, Hansen OS, Satapoomin S, Sawangraruks S, Thomsen HA, Østergaard JB (2004) Hydrography, bacteria and protist communities across the continental shelf and shelf slope of the Andaman Sea (NE Indian Ocean). *Mar Ecol Prog Ser* 274:69-86
- Osborne AR, Burch TL (1980) Internal solitons in the Andaman Sea. *Science (Wash.)* 208(4443):457-460
- Paxton JR (1995) Habitats and adaptations. In Paxton JR, Eschmeyer WN(eds): *Encyclopedia of Fishes*. Academic Press, New York, USA pp 32-41
- Perry RB, SchMike GR (1965) Large amplitude internal waves observed off the northwest coast of Sumatra. *J Geophys Res* 70:2319-2324
- Phongsuwan N (1991) Recolonization of a coral reef damaged by a storm on Phuket Island, Thailand. *Phuket Mar Biol Cent Res Bull* 56:75-83
- Phongsuwan N, Yeemin T, Worachananant S, Duangawasdi M, Chotiyaputta C, Comley J (2006) Post-tsunami status of coral reefs and other coastal ecosystems on the Andaman Sea coast of Thailand. In *Status of coral reefs in tsunami affected countries: 2005*. Australian Institute of Marine Science pp 63-77.
- Phongsuwan N, Brown BE (2007) The influence of the Indian ocean tsunami on coral reefs of western Thailand, Andaman Sea, Indian Ocean. In Stoddart DR (ed) *Tsunamis and coral reefs*. Atoll Research Bulletin No. 544
- Phongsuwan N, Yamarunpattana C, Paokanta Y, Areechon P (2008) Status of Coral Reefs in the Surin and Similan Archipelagos, Thailand. In Obura DO, Tamelander J, Linden O (ed) *Ten years after bleaching -facing the consequences of climate change in the Indian Ocean*. CORDIO Status report 2008, Mombasa
- Pineda J. (1991) Predictable upwelling and the shoreward transport of planktonic larvae by internal tidal bores. *Science* 253(5019):548-551
- Plathong S (2005) Survey of tsunami impact on coral reef and the reef recovery project for Similan islands marine national park. *Coral Reef and Benthos Res Unit, Centre Biod Penins Thailand, Dep Biol, Prince of Songkla University Had Yai, Songkla, Thailand*

- Puverel S, Tambutté É, Pereira-Mouries L, Zoccola D, Allemand D, Tambutté S (2005) Soluble organic matrix of two Scleractinian corals: partial and comparative analysis. *Comp Biochem Physiol B* 141:480–487
- Rahav O, Dubinsky Z, Achituv Y, Falkowski PG (1989) Ammonium metabolism in the zooxanthellate coral *Stylophora pistillata*. *Proc R Soc Lond* 236: 325-337
- Raimondi PT, Morse NC (2000) The consequences of complex larval behaviour in a coral. *Ecology* 81:3193-3211
- Rands ML, Douglas AE, Loughman BC, Ratcliffe RG (1992) Avoidance of hypoxia in a cnidarian symbiosis by algal photosynthetic oxygen. *Biol Bull* 182:159-162
- Raven J, Caldeira K, Elderfield H, Hoegh-Guldberg O, Liss P, Riebesell U, Shepherd J, Turley C, Watson A (2005) Ocean acidification due to increasing atmospheric carbon dioxide. Policy Document 12/05. Royal Society, London
- Ribes M, Coma R, Atkinson MJ, Kinzie RA III (2003) Particle removal by coral reef communities: picoplankton is a major source of nitrogen. *Mar Ecol Prog Ser* 257:13–23
- Ribes M, Coma R, Atkinson MJ, Kinzie RA (2005) Sponges and ascidians control removal of particulate organic nitrogen from coral reef water. *Limnol Oceanogr* 50:1480–1489
- Richter C, Wunsch M (1999) Cavity-dwelling suspension feeders in coral reefs—a new link in reef trophodynamics. *Mar Ecol Prog Ser* 188:105–116
- Richter C, Wunsch M, Rasheed M, Koetter I, Badran MI (2001) Endoscopic exploration of Red Sea coral reefs reveals dense populations of cavity dwelling sponges. *Nature* 413: 726–730
- Rinkevich B, Loya Y (1984) Does light enhance calcification in hermatypic corals ? *Mar Biol* 80:1-6
- Rogers CS (1990) Responses of coral reefs and reef organisms to sedimentation. *Mar Ecol Prog Ser* 62:185–202.
- Sawall Y, Phongsuwan N, Richter C (2010) Coral recruitment and recovery after the 2004 Tsunami around the Phi Phi Islands (Krabi Province) and Phuket, Andaman Sea, Thailand. *Helgol Mar Res* doi:10.1007/s10152-010-0192-5
- Schneider K, Erez J (2006) The effect of carbonate chemistry on calcification and photosynthesis in the hermatypic coral *Acropora eurystoma*. *Limnol Oceanogr* 51:1284-1293
- Scoffin TP, Stearn CW, Boucher D, Frydl P, Hawkins CM, Hunter IG, MacGeachy JK (1980) Calcium carbonate budget of a fringing reef on the west coast of Barbados. Part II – Erosion, sediments and internal structure. *Bull Mar Sci* 30:475-508
- Simkiss K (1964) Phosphates as crystals poisons of calcification. *Biol Rev* 39:487-505
- Smith SV (1978) Coral reef area and contributions to processes and resources of the world's oceans. *Nature* 273:225-226
- Smith SV, Buddemeier RW (1992) Global change and coral-reef ecosystems. *Annu Rev Ecol Syst* 23:89–118
- Smith JE, Smith CM, Hunter CL (2001) An experimental analysis of the effects of herbivory and nutrient enrichment on benthic community dynamics on a Hawaiian reef. *Coral Reefs* 19:332-342
- Smith JE, Smith CM, Vroom P, Beach KL, Miller S (2004) Nutrient and growth dynamics of *Halimeda tuna* on Conch Reef, Florida Keys: Possible influence of internal tides on nutrient status and physiology. *Limnol Oceanogr*, 49:1923–1936
- Snidvongs A, Kinzie RA (1994) Effects of nitrogen and phosphorus enrichment on in vivo symbiotic zooxanthellae of *Pocillopora damicornis*. *Mar Biol* 118:705-711
- Spalding MD, Ravilious C, Green EP (2001) World atlas of coral reefs. UNEP World Conservation Monitoring Centre, University of California Press, Berkeley, USA pp 424
- Steneck PS (1988) Herbivory on coral reefs: a synthesis. *Proc 6th Int Coral Reef Symp* 1:37-49
- Streamer M, Griffiths DJ, Thinh L (1988) The products of photosynthesis by zooxanthellae (Symbiodinium microadriaticum) of *Tridacna gigas* and their transfer to the host. *Symbiosis* 6:237-252.
- Tambutté É, Allemand D, Mueller E, Jaubert J (1996) A compartmental approach to the mechanism of calcification in hermatypic corals. *J Exp Biol* 199:1029–1041
- Tambutté S, Tambutté É, Zoccola D, Allemand D (2007) Organic matrix and biomineralization of scleractinian corals. In: Baeuerlein E (ed) *Handbook of biomineralization*, Vol 1. Wiley-VCH Verlag GmbH & Co, Weinheim, pp 243–259
- Thongtham N, Chansang H (1999) Influence of surface complexity on coral recruitment at Maiton island, Phuket, Thailand. *Phuket Mar Biol Cent Special Publ* 20:93-100
- Thornhill DJ, Fitt WK, Schmidt GW (2006) Highly stable symbioses among western Atlantic brooding corals. *Coral Reefs* 25:515-519
- Titlyanov EA (1991) The stable level of coral primary production in a wide light range. *Hydrobiol* 216/217:383-387
- Tomascik T (1991) Settlement patterns of Caribbean scleractinian corals on artificial substrata along a eutrophication gradient, Barbados, West Indies. *Mar Ecol Prog Ser* 77:261-269
- Veron JEN (2000) *Corals of the World*. Australian Institute of Marine Science, Townsville, Australia
- Vlasenko V, Alpers W (2005) Generation of secondary internal waves by the interaction of an internal solitary wave with an underwater bank. *Journal of Geophysical Research* 110:doi:10.1029/2004JC002467
- Vlasenko V, Hutter K (2001) Numerical experiments on the breaking of solitary internal waves over a slope–shelf topography. *Am Meteorol Soc* 32:1781-1793
- Vlasenko V, Hutter K (2002) Numerical experiments on the breaking of solitary internal waves over a slope–shelf topography. *J Phys Oceanogr* 32:1779–1793

- Vlasenko V, Stashchuk N (2007) Amplification and suppression of internal waves by tides over variable bottom topography. *J Phys Oceanogr* 36:1959–1973
- Wainwright SA (1963) Skeletal organization in the coral *Pocillopora damicornis*. *Quart J Micros Sci* 104:164-183
- Ward-Paige CA, Risk MJ, Sherwood OA, Jaap WC (2005) Clionid sponge surveys on the Florida reef tract suggest land-based nutrient inputs. *Mar Pol Bul* 51:570–579
- Webster NS, Smith LD, Heyward AJ, Watts JEM, Webb RI, Blackall LL, Negri AP (2004) Metamorphosis of a scleractinian coral in response to microbial biofilms. *Appl Environm Microbiol* DOI: 10.1128/AEM.70.2.1213–1221.2004, pp 1213-1221
- Wild C, Rasheed M, Werner U, Franke U, Johnstone R, Huettel M (2004a) Degradation and mineralization of coral mucus in reef environments. *Mar Ecol Prog Ser* 267:159–171
- Wild C, Huettel M, Klueter A, Kremb SG, Rasheed M, Jorgensen BB (2004b) Coral mucus functions as an energy carrier and particle trap in the reef ecosystem. *Nature* 428: 66–70
- Wittenberg M, Hunte W (1992) Effects of eutrophication and sedimentation on juvenila corals. *Mar Biol* 112:131-138
- Wu G, Zhang Y (1998) Tibetan Plateau Forcing and the Timing of the Monsoon Onset over South Asia and the South China Sea. *American Meteorol Soc* 126:913-927
- Wunsch M, Richter C (1998) The CaveCam - an endoscopic underwater videosystem for the exploration of cryptic habitats *Mar Ecol Progr Ser* 169: 277-282
www.reefbase.org/gis_maps
- Yahel R, Yahel G, Genin A (2005) Diel pattern with abrupt crepuscular changes of zooplankton over a coral reef. *Limnol Oceanogr* 50(3): 930–944
- Yellowlees D, Rees TAV, Leggat W (2008) Metabolic interactions between algal symbionts and invertebrate hosts. *Plant Cell Environ* 31: 679-694
- Yeemin T, Sutthacheep M, Pettongma R (2006) Coral reef restoration projects in Thailand. *Ocean & Coastal Management* 49:562-575
- Yentsch CS, Yentsch CM, Cullen JJ, Lapointe B, Phinney DA, Yentsch SW (2002) Sunlight and water transparency: cornerstones in coral research. *J Exp Mar Biol Ecol* 268:171-183

Manuscript and publication outline

The present thesis is based on three paper manuscripts, one submitted manuscript and one accepted publication listed below. The specific contributions of the authors on study idea, concept, data acquisition and analysis, as well as the writing of the manuscript are explained. The order of the chapters corresponds to the design of this thesis and the level of knowledge described in the introduction.

1. **Schmidt** GM, Phongsuwan N, Roder C, Jantzen C, Khokiattiwong S, Richter C
(submitted) Coral community and physico-chemical characteristics in response to
Large Amplitude Internal Waves

Contributions: The idea of a project on studying the influence of internal waves on coral reefs was initiated by C Richter. The particular idea of this study was developed by GM Schmidt, N Phongsuwan and C Richter. Data sampling and analysis was mainly conducted by GM Schmidt and N Phongsuwan, C Roder and C Jantzen with the logistical help of S Khokiattiwong. Data analysis was conducted by GM Schmidt with support of C Richter. The manuscript was written by G Schmidt with improvements by C Richter, C Roder and C Jantzen.

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

Contributions: The idea of a project on studying the influence of internal waves on coral reefs was initiated by C Richter. The particular idea of this study was developed by C Jantzen, with input from C Wild and C Richter. Data sampling and analysis was carried out by C Jantzen with the help of GM Schmidt and C Roder. The manuscript was written by C Jantzen with support of C Wild and C Richter, GM Schmidt and C Roder.

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

Contributions: The idea of a project on studying the influence of internal waves on coral reefs was initiated by C Richter. The particular idea of this study was developed by C Roder and C Richter. Data sampling and analysis was mainly conducted by C Roder with support of L Fillinger, GM Schmidt, and C Jantzen. The manuscript was written by C Roder and C Richter, with support of GM Schmidt and C Jantzen.

4. **Schmidt** GM, Phongsuwan N, Richter C (in preparation) Carbonate accretion and
erosion on the scleractinian coral *Porites lutea* in response to Large Amplitude Internal
Waves

Contributions: The idea of a project on studying the influence of internal waves on coral reefs was initiated by C Richter. The particulate idea of this study was created by GM Schmidt and further developed together with C Richter. Data sampling and

analysis was conducted by GM Schmidt and N Phongsuwan. Data analysis was conducted by GM Schmidt with support of C Richter. The manuscript was written by GM Schmidt with improvements by C Richter.

5. **Schmidt** GM, Phongsuwan N, Richter C (in preparation) Spatio-temporal variation of coral recruitment along Similan Islands, Thailand

Contributions: The idea of a project on studying the influence of internal waves on coral reefs was initiated by C Richter. The particulate idea of the study was created by GM Schmidt and further developed together with C Richter. Data sampling and analysis was conducted by GM Schmidt and N Phongsuwan. Data analysis was conducted by GM Schmidt with support of C Richter. The manuscript was written by GM Schmidt with improvements by C Richter.

Chapter 1

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 reef 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. 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

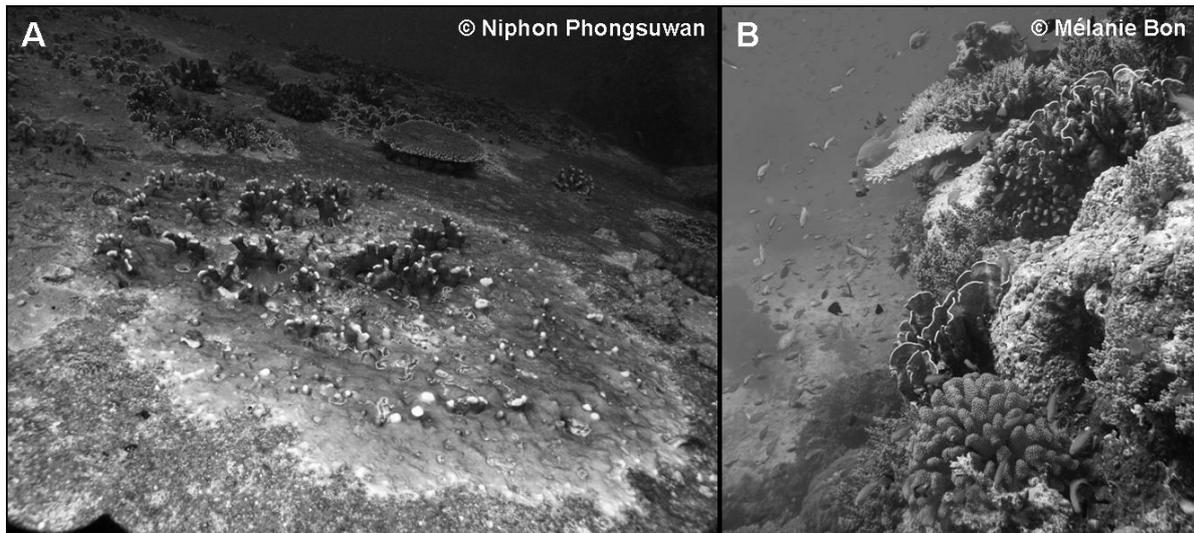


Figure 1 Typical substrate conditions at Similan Islands in about 12 m depth: **A)** at West W 4.1 and **B)** East E 7.1.

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.

Material & 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).

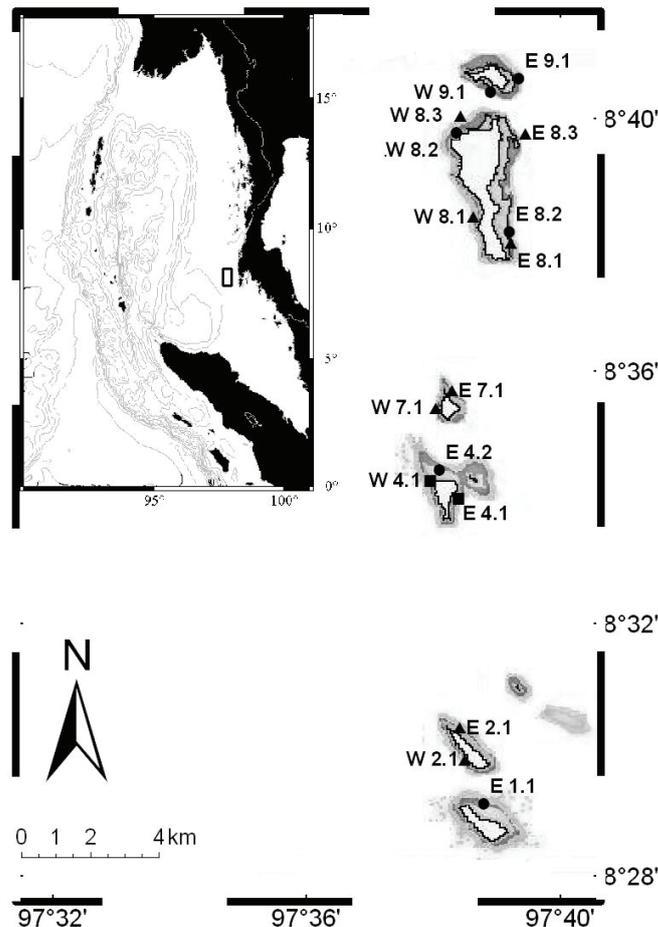


Figure 2 Similan Islands with biological and environmental samplings: (●) transects only; (▲) transects and temperature; (■) all parameters at central island Koh Miang (W 4.1 and E 4.1). (Figure modified after Jackson (2004)).

The islands consist of granite and have been built in the tertiary about 65 million years ago by volcanic activity (Mu Koh Similan National Park administration 2009). 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 (Mu Koh Similan National Park administration 2009).

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, fifteen 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).

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 two Acoustic Doppler Current Profiler (600 kHz Workhorse Sentinel ADCP, Teledyne RD Instruments) were placed in the same depths at the W (right next to the CTD) and E side of island Koh Miang 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 percentaged 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 Woosik 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 (m_y) and residuals (r_y) on the basis of the time-series (y); (2) splitting of residuals into cold (r_{yc}) and warm residuals (r_{yw}); 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 r_y . Degree days cooling was calculated by replacing the positive values in the residuals time

series r_y with zeros, yielding r_{yc} , summing the values $[\sum(r_{yc})]$, 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. $F = sp_y \times [sp(r_y)]^{-1}$ }. The corresponding equation is:

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

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

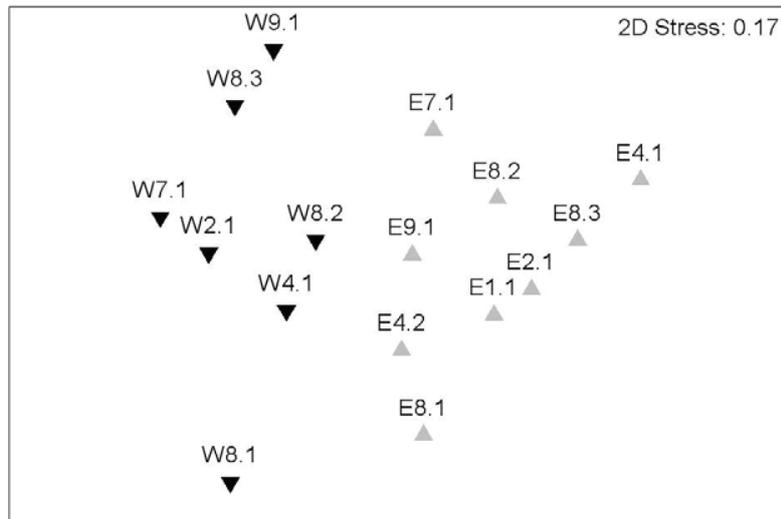
Reef data

Coral community composition – Overall 144 hermatypic coral species were recorded, belonging to 40 genera and 17 families (suppl. Table 2, suppl. 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. Coral species composition differed clearly between island sides (ANOSIM, one-way-analysis: W versus E: global $R = 0.585$, $p < 0.001$, suppl. 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

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

27.33 \pm 3.45 in the E, and evenness revealed 0.74 \pm 0.04 in the W and 0.63 \pm 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

**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.

species richness and evenness in W, the species compositions in W differed among sites (suppl. 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) (suppl. Table 2).

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

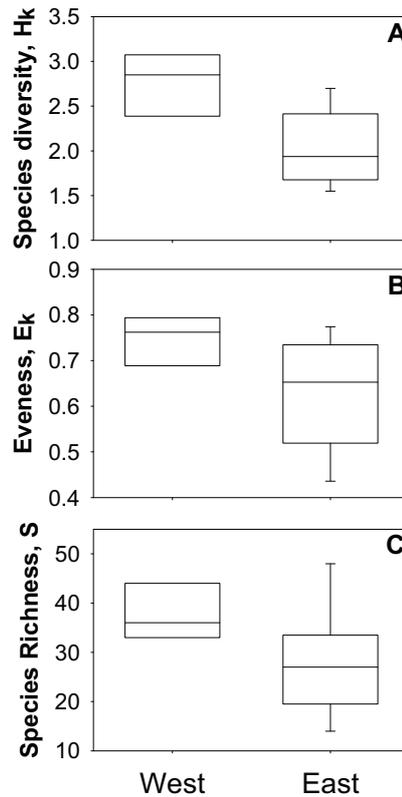


Figure 4 Coral diversity (Shannon index, **A**), evenness (**B**), and species richness (**C**) at LAIW-exposed (West), and sheltered (East) sides of Similan Islands.

7 m: global $R = 0.37$, $p < 0.05$) (Fig 5). Living coral cover was the second most powerful contributor to the dissimilarity of 72.50 % 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 $R = 0.079$, $p = 0.22$).

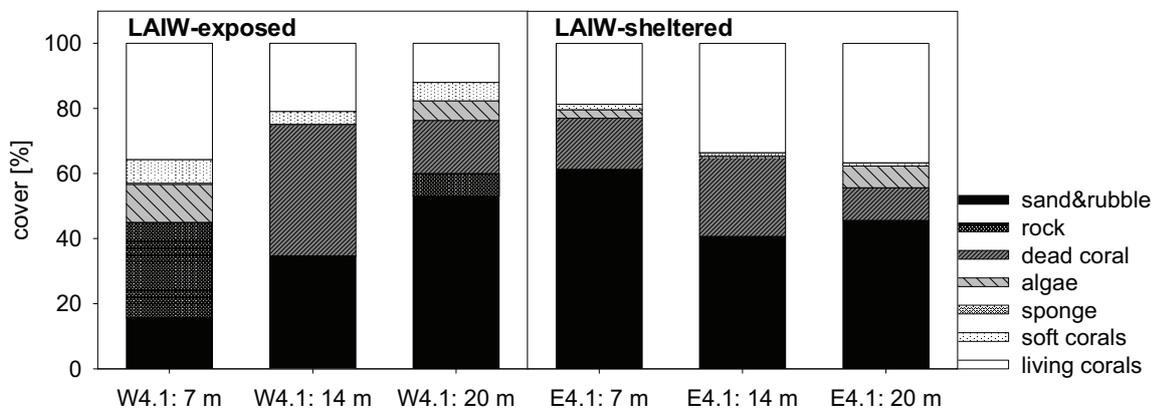


Figure 5 Benthic composition at Koh Miang on LAIW-exposed (W 4.1) and sheltered (E 4.1) side, grouped by depth: 7, 14 and 20 m.

In detail, for the intermediate depth at all 16 sites living coral cover averaged $25.57 \pm 4.22\%$ in W and $35.95 \pm 4.62\%$ 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 $67.71 \pm 6.59\%$ in W and $72.83 \pm 3.34\%$ in E, sand and rubble $29.75 \pm 6.89\%$ in W and $25.88 \pm 3.29\%$ in E. Rock structures were only found in W, while in E hard substrate consisted exclusively of dead coral (Fig 6, suppl. Table 1).

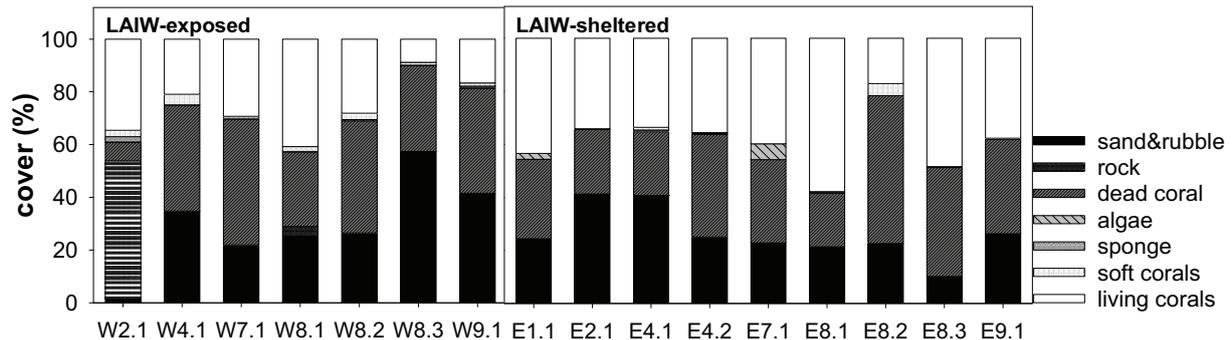


Figure 6 Benthic composition at Similan Islands on LAIW-exposed west (W), and east (E) sides (12 to 16 m depth, grouped by N-S orientation).

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).

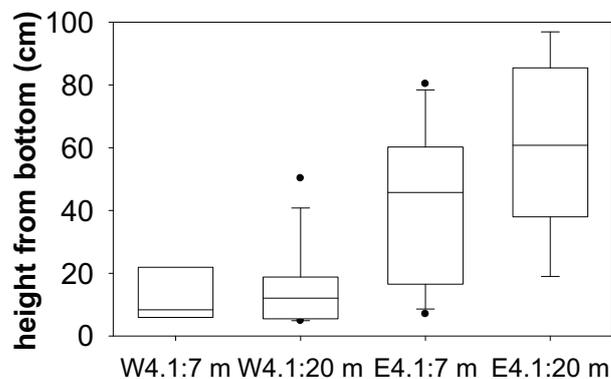


Figure 7 Coral framework at Koh Miang on LAIW-exposed (W 4.1) and sheltered (E 4.1) side, grouped by depth: 7 and 20 m.

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).

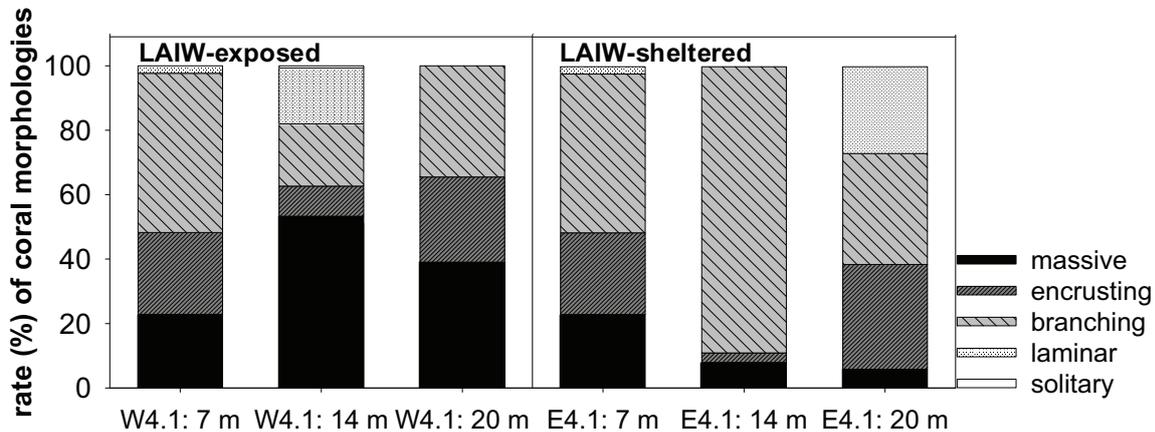


Figure 8 Coral morphologies as fractions of total number of colonies studied at Koh Miang on LAIW-exposed (W 4.1) and sheltered (E 4.1) side, grouped by depth: 7, 14, and 20 m.

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 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

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

°C below modal) water motion stayed stable at $0.13 \pm 0.001 \text{ ms}^{-1}$ (suppl. Fig 2) Oxygen concentrations, pH and salinity were highly correlated with temperature. The impact of LAIW in W (5 to 10 °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 increases in salinity of up to 5 % to values of 34.52 PSU. Neither optical backscatter nor fluorescence showed temperature dependent variations. Yet a tendency of lower chlorophyll concentrations up to 40 % in LAIW-water of $20 \pm 0.5 \text{ °C}$ 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, suppl. 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 .

Nutrient concentrations 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.

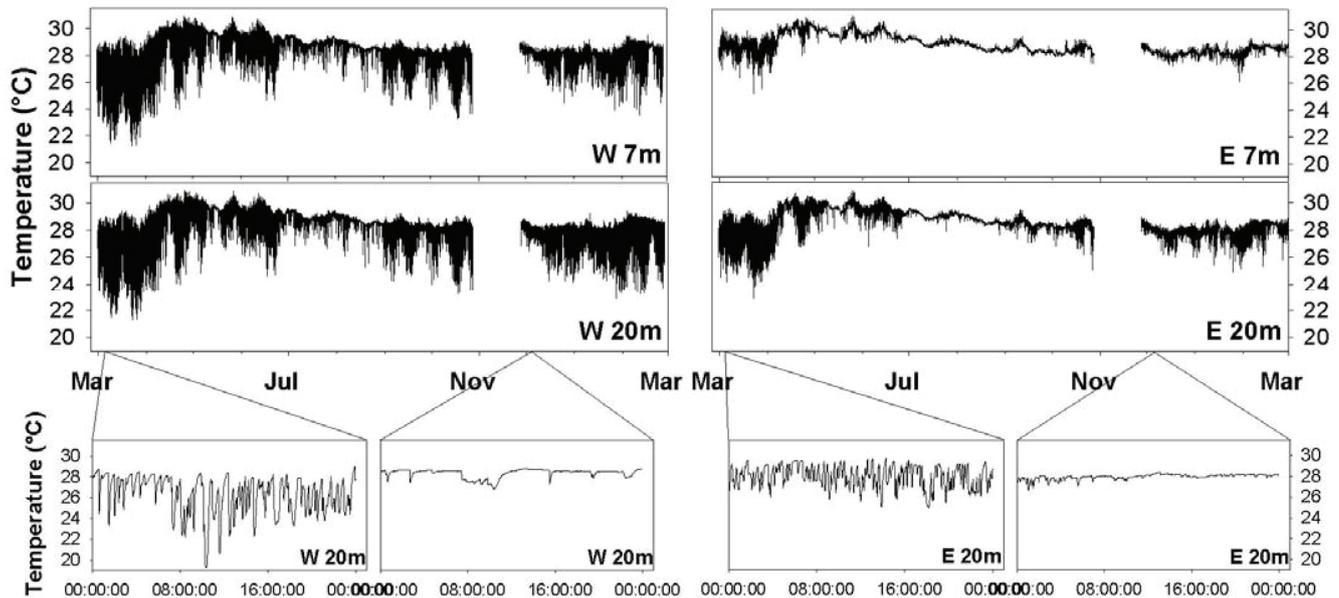


Figure 9 Large Amplitude Internal Wave (LAIW) associated temperature variations on W (left panels) and E (right panels) sides of Similan Islands. Examples are given for temperature logger readings from LAIW-exposed (W 4.1) and sheltered (E 4.1) side of Koh Miang in 20 m and 7 m depth. Upper panels show 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.

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, suppl. 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 (suppl. Table 3).

Correlations and relationships of coral community parameters and cumulative temperature anomalies

Diversity (Shannon index) and species richness exhibited a clearly positive relationship with 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 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	PSU	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)				

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 exceeded by far the moderate and lower-frequency variations reported earlier elsewhere (Leichter et al. 1996, 2003, Leichter & Genovese 2006), and ranked 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 caused 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

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 ≥ 0.01, **0.01 > P ≥ 0.001, ***P < 0.001)

		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

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 al. 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 PSU, 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.

Sub-thermocline waters transported into shallow areas with LAIW-arrival were low in pH and oxygen depleted. 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

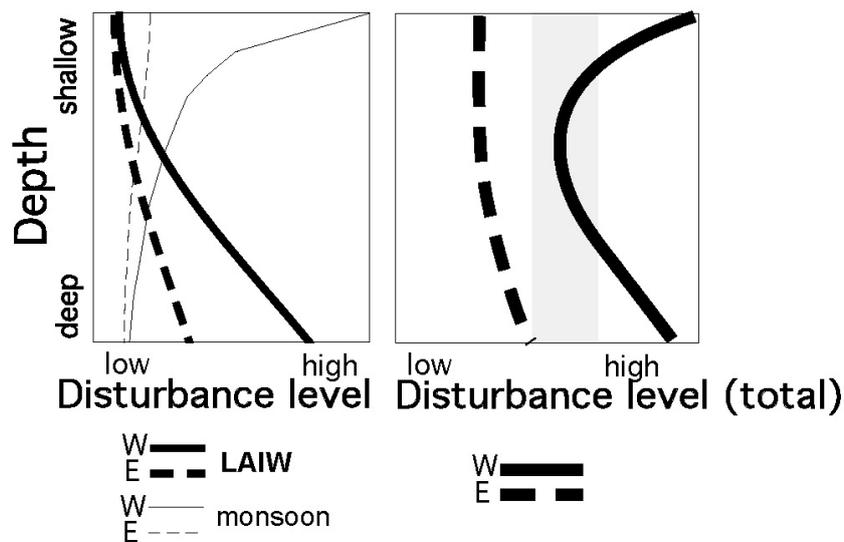


Figure 10 Graphic description of the separated (left panel) and cumulative effects of the disturbance by LAIW-impact, and by monsoon waves at W and E sides of Similan islands.

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 DDC, Table 3 and temperature record suppl. Fig 4).

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 arises if disturbances 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 along the W sides.

The composition of a coral community reflects the net result of the governing physical, chemical and biological drivers (Fishelson 1973, Loya 1976, 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 (Jackson et al. 2003) 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.

Supplementary data is given in Annex 1

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Literature

- Abram NJ, Gagan MK, McCulloch MT, Chappell J, Hantoro WS (2003) Coral Reef Death During the 1997 Indian Ocean Dipole Linked to Indonesian Wildfires. *Science (Washington)* 301(5635):952-955
- Al-Horani FA (2005) Effects of changing seawater temperature on the photosynthesis and calcification in the scleractinian coral *Galaxea fascicularis*, measured with O₂, Ca²⁺ and pH microsensors. *Scientia Marina* 69:347-354
- Alpers W (1985) Theory of radar imaging of internal waves. *Nature* 314:245-247
- Alpers W, Wang-Chen H, Hock L (1997) Observation of internal waves in the Andaman Sea by ERS SAR. Proc 3rd ERS Symp on Space at Service of our Environment. Florence Italy
- Andrews JC, Gentien P (1982) Upwelling as a source of nutrients for the Great Barrier Reef ecosystem: A solution to Darwin's question? *Mar Ecol Prog Ser* 8:257-269
- Aronson RB, Precht WF (1995) Landscape patterns of reef coral diversity: a test of the intermediate disturbance hypothesis. *J Exp Mar Biol Ecol* 192:1-14
- Birkeland C (1997) Life and death of coral reefs. Chapman & Hall, Int Thomson Publishing, New York, pp 1-12
- Brown BE (2007) Coral reefs of the Andaman Sea : An integrated perspective. In Gibson RN, Atkinson RJA, Gordon JDM (ed) *Oceanography and marine biology. An annual review. Volume 45*, Aberdeen University Press, Aberdeen
- Buddemeier, RW, Kinzie RA (1976) Coral growth. *Oceanogr mar Biol A Rev* 14:183-225
- Burns TP (1985) Hard-coral distribution and cold-water disturbances in South Florida: variation with depth and location. *Coral Reefs* 4:117-124
- Chansang H, Satapoomin U, Poovachiranon S (1999) Maps of coral reefs in Thai waters, Andaman Sea. Coral Reef Resource Management Project, Department of Fisheries, Bangkok Vol 2, pp 198
- Charuchinda M, Hylleberg J (1984) Skeletal extension of *Acropora formosa* at a fringing reef in the Andaman Sea. *Coral reefs* 3:215-219
- Chazottes V, Le Campion-Alsumard T, Peyrot-Clausade M, Cuet P (2002) The effects of eutrophication-related alterations to coral reef communities on agents and rates of bioerosion (Reunion Island, Indian Ocean). *Coral reefs* 21:375-390
- Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. *Austr J Ecology* 18:117-143
- Clarke KR, Warwick RM (1994) Similarity-based testing for community pattern: the two-way layout with no replication. *Mar Biol* 118:167-176
- Clarke KR, Warwick RM (2001) Change in marine communities: an approach to statistical analysis and interpretation. 5 Primer - E Ltd, Plymouth Marine Laboratory, Plymouth
- Cole C (2003) Dishing the dirt on coral reefs. *Nature* 421:705-706
- Coles SL, Jokiel PL (1976) Synergistic Effects of Temperature, Salinity and Light on the Hermatypic Coral *Montipora verrucosa**. *Mar Biol* 49:187-195
- Coles SL, Fadlallah YH (1991) Reef coral survival and mortality at low temperatures in the Arabian Gulf: new species-specific lower temperature limits. *Coral Reefs* 9:231-237
- Connell JH (1978) Diversity in tropical rain forests and coral reefs. *Science* 199:1302-1310
- Connell JH (1979) Tropical rain forests and coral reefs as open non-equilibrium systems. In: Anderson R, Turner B, Taylor L (eds) *Population dynamics*. Blackwell, Oxford, pp 141-163
- Connell JH (1997) Disturbance and recovery of coral assemblages. *Coral Reefs* 16 (Suppl):101-113
- Dennison WC, Barnes DJ (1988) Effect of water motion on coral photosynthesis and calcification. *J Exp Mar Biol Ecol* 115:67-77

- De Silva IPD, Imberger J, Ivey GN (1997) Localized mixing due to a breaking internal wave ray at a sloping bed. *J Fluid Mech* 350:1-27
- De Vantier LM, Death G, Done TJ, Turak E (1998) Ecological assessment of a complex natural system: a case study from the Great Barrier Reef. *Ecol Appl* 8(2):480-96
- Dunne RP, Brown BE (1996) Penetration of solar UVB radiation in shallow tropical waters and its potential biological effects on coral reefs; results from the central Indian Ocean and Andaman Sea. *Mar Ecol Prog Ser* 144:109-118
- Eppley RW, Renger EH, Harrison WG (1979) Nitrate and phytoplankton production in southern California coastal waters. *Limnol Oceanogr* 24:483-494
- Fabricsius KE (2005) Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. *Mar Pol Bull* 50:125-146
- Falkowski PG, Jokiel PL, Kenzie RAI (1990) Irradiance and corals. *Ecosyst World* 25:89-107
- Ferrier-Pages C, Schoelzke V, Jaubert J, Muscatine L, Hoegh-Guldberg O (2001) Response of a scleractinian coral, *Stylophora pistillata*, to iron and nitrate enrichment. *J Exp Mar Ecol* 259:249-261
- Fishelson L (1973) Ecology of coral reefs in the Gulf of Aqaba (Red Sea) influenced by pollution. *Oecologia* 12:55-67
- Garrett C, Munk W (1979) Internal waves in the ocean. *Ann Rev Fluid Mech* 11:339-369
- Gates RD, Baghdasarian G, Muscatine L (1992) Temperature stress causes host cell detachment in symbiotic cnidarians: Implications for coral bleaching. *Biol Bull* 182:324-332
- Gattuso JP, Allemand D, Frankignoulle M (1999) Photosynthesis and calcification at cellular, organismal and community levels in coral reefs: A review on interactions and control by carbonate chemistry. *American Zool* 39:160-183
- Glynn PW (1997) Bioerosion and Coral Reef Growth: A Dynamic Balance. In Birkeland C (ed) *Life and death of coral reefs*. Chapt 4. Chapman and Hall, ITP, New York
- Goreau TF, Goreau NI, Goreau TJ (1979) Corals and Coral Reefs. *Scientific American* 124-136
- Hallock P, Schlager W (1986) Nutrient excess and the demise of coral reefs and carbonate platforms. *Palaios* 1:389-398
- Hearn C, Atkinson M, Falter J (2001) A physical derivation of nutrient-uptake rates in coral reefs: effects of roughness and waves. *Coral Reefs* 20:347-356
- Hoegh-Guldberg O (1999) Climate change, coral bleaching and the future of the world's coral reefs. *Mar Freshwater research* 50:839-866
- Hughes TP, Baird AH, Bellwood DR, Card M, Connolly SR, Folke C, Grosberg R, Hoegh-Guldberg O, Jackson JBC, Kleypas J, Lough JM, Marshall P, Nyström M, Palumbi SR, Pandolfi JM, Rosen B, Roughgarden J (2003) Climate Change, Human Impacts, and the Resilience of Coral Reefs. *Science* 301:929-933
- Jackson JBC, Kleypas J, Lough JM, Marshall P, Nyström M, Palumbi SR, Pandolfi JM, Rosen B, Roughgarden J (2003) Climate Change, Human Impacts, and the Resilience of Coral Reefs. *Science* 301:929-933
- Jackson CR (2004) *An atlas of internal solitary-like waves and their properties*. 2nd Ed. Office of Naval Research, Global Ocean Associates, Alexandria, VA, USA
- Kattner G (1999) Storage of dissolved inorganic nutrients in seawater: poisoning with mercuric chloride. *Marine Chemistry* 67:61-66
- Kleypas JA, McManus JW, Lambert Meñez AB (1999) Environmental limits to coral reef development: Where do we draw the line? *Amer Zool* 39:146-159
- Leichter JJ, Wing SR, Miller SL, Denny MW (1996) Pulsed delivery of subthermoline water to Conch Reef (Florida Keys) by internal bores. *Limnol Oceanogr* 41:1490-1501
- Leichter JJ, Shellenbarger G, Genovese SJ, Wing SR (1998) Breaking internal waves on a Florida (USA) coral reef: A plankton pump at work? *Mar Ecol Prog Ser* 166:83-97
- Leichter JJ, Stewart HL, Miller SL (2003) Episodic nutrient transport to Florida coral reefs. *Limnol Oceanogr* 48:1394-1407
- Leichter JJ, Genovese SJ (2006) Intermittent upwelling and subsidized growth of the scleractinian coral *Madracis mirabilis* on the deep fore-reef slope of Discovery Bay, Jamaica. *Mar Ecol Prog Ser* 316:95-103
- Lesser MP, Slattery M, Leichter JJ (2009) Ecology of mesophotic coral reefs, *J Exp Mar Biol Ecol* doi:10.1016/j.jembe.2009.05.009
- Loya Y (1972) Community structure and species diversity of hermatypic corals at Eilat, Red Sea. *Mar Biol* 13:100-123
- Loya Y (1976) Effects of water turbidity and sedimentation on the community structure of Puerto Rican corals. *Bull Mar Science* 26:450-466
- Loya Y, Slobodkin LB (1971) The coral reefs of Eilat (Gulf of Eilat, Red Sea). In: Stoddart DR, Yonge M (ed) *Regional Variation in Indian Ocean Coral Reefs*. pp:117-139. Academic Press, New York
- Marubini F, Barnett H, Langdon C, Atkinson MJ (2001) Dependence of calcification on light and carbonate ion concentration for the hermatypic coral *Porites compressa*. *Mar Ecol Prog Ser* 20:153-162
- Massel SR, Done TJ (1993) Effects of cyclone waves on massive coral assemblages on the Great Barrier Reef: meteorology, hydrodynamics and demography. *Coral Reefs* 12:153-166
- McCook LJ (1999) Macroalgae, nutrients and phase shifts on coral reefs: scientific issues and management consequences for the Great Barrier Reef. *Coral Reefs* 18:357-367

- Moum JN, Klymak JM, Nash JD, Perlin A, Smyth WD (2007) Energy transport by nonlinear internal waves. *J Phys Oceanogr* 37:1968-1988
- Mu Koh Similan National Park administration (2009) Thaplamu, Phetkasem rd, Lamkaen Sub-district, Amphur Thai, Muang Phangnga, Thailand, www.dnp.go.th/parkreserve
- Muller-Parker G, McCloskey LR, Hoegh-Guldberg O, McAuley PJ (1994) Effect of ammonium enrichment on animal and algal biomass of the coral *Pocillopora damicornis*. *Pacific Science* 48:273-283
- Mumby PJ, Dahlgren CP, Harborne AR, Kappel CV, Micheli F, Brumbaugh DR, Holmes KE, Mendes JM, Broad K, Sanchirico JN, Buch K, Box S, Stoffle RW, Gill AB (2006) Fishing, trophic cascades, and the process of grazing on coral reefs. *Science* 311:98-101
- Muscantine L, Falkowski PG, Dubinsky Z, Cook PA, McCloskey LR (1989) The effect of external nutrient resources on the population dynamics of zooxanthellae in a reef coral. *Proc R Soc Lond Ser B* 236, 1284:311-324
- Nielsen TG, Bjørnsen PK, Boonruang P, Fryd M, Hansen PJ, Janekarn V, Limtrakulvong V, Munk P, Hansen OS, Satapoomin S, Sawangraruks S, Thomsen HA, Østergaard JB (2004) Hydrography, bacteria and protist communities across the continental shelf and shelf slope of the Andaman Sea (NE Indian Ocean). *Mar Ecol Prog Ser* 274:69-86
- Osborne AR, Burch TL (1980) Internal solitons in the Andaman Sea. *Science (Wash.)* 208(4443):457-460
- Parsons TR, Maita Y, Palli CM (1989) A manual of chemical and biological methods for seawater analysis. Pergamon Press. New York
- Perry RB, Schmike GR (1965) Large amplitude internal waves observed off the northwest coast of Sumatra. *J Geophys Res* 70:2319-2324
- Phongsuwan N (1991) Recolonization of a coral reef damaged by a storm on Phuket island, Thailand. *Phuket Mar Biol Cent Res Bull* 56:75-83
- Phongsuwan N, Chansang H (1986) Coral reef resources of the Tarutao national park, Thailand. *Proc Symp Coral Reef Manag Southeast Asia, Bogor, Indonesia*. *Biotrop Spec Publ* 29:141-156
- Phongsuwan N, Yeemin T, Worachananant S, Duangsawasdi M, Chotiyaputta C, Comley J (2006) Post-tsunami status of coral reefs and other coastal ecosystems on the Andaman Sea coast of Thailand. In *Status of coral reefs in tsunami affected countries: 2005*. Australian Institute of Marine Science pp 63-77.
- Phongsuwan N, Brown BE (2007) The influence of the Indian ocean tsunami on coral reefs of western Thailand, Andaman Sea, Indian Ocean. In Stoddart DR (ed) *Tsunamis and coral reefs*. Atoll Research Bulletin No. 544
- Phongsuwan N, Yamarunpattana C, Paokanta Y, Areechon P (2008) Status of Coral Reefs in the Surin and Similan Archipelagos, Thailand. In Obura DO, Tamelander J, Linden O (ed) *Ten years after bleaching - facing the consequences of climate change in the Indian Ocean*. CORDIO Status report 2008, Mombasa
- Pineda J. (1991) Predictable upwelling and the shoreward transport of planktonic larvae by internal tidal bores. *Science* 253(5019):548-551
- Pineda J. (1995) An internal tidal bore regime at nearshore stations along western U.S.A.: Predictable upwelling within the lunar cycle. *Cont Shelf Research* 15(8):1023-1041
- Plathong S (2005) Survey of tsunami impact on coral reef and the reef recovery project for Similan islands marine national park. *Coral Reef and Benthos Res Unit, Centre Biod Penins Thailand, Dep Biol, Prince of Songkla University Had Yai, Songkla, Thailand*
- Rogers CS (1993) Hurricanes and coral reefs: The intermediate hypothesis revisited. *Coral Reefs* 12:127-137
- Sammarco PW, Risk MJ (1990) Large-scale patterns in internal bioerosion of Porites: Cross continental shelf trends on the Great Barrier Reef. *Mar Ecol Prog Ser* 59:145-156
- Saxby T, Dennison WC, Hoegh-Guldberg O (2003) Photosynthetic response of the coral *Montipora digitata* to cold temperature stress. *Marine Ecology Progress Series* 248:85-97
- Schneider K, Erez J (2006) The effect of carbonate chemistry on calcification and photosynthesis in the hermatypic coral *Acropora eurystoma*. *Limnol Oceanogr* 51:1284-1293
- Shanks AL (1983) Surface slicks associated with tidally forced internal waves may transport pelagic larvae of benthic invertebrates and fishes shoreward. *Mar Ecol Prog Ser* 13:311-315
- Shashar N, Cohen Y, Loya Y (1993) Extreme diel fluxes of oxygen in diffusive boundary layers surrounding stony corals. *Biological Bulletin* 185:455-461
- Sheppard C (2009) Large temperature plunges recorded by data loggers at different depths on an Indian Ocean atoll: comparison with satellite data and relevance to coral refuges. *Coral Reefs* 28:399-403
- Sokal RR, Rohlf FJ (1995) *Biometry: the principles and practice of statistics in biological research*. W. H. Freeman. New York.
- Spalding MD; Ravilious C, Green EP (2001) *World atlas of coral reefs*. University of California Press, Berkeley, California, USA.
- Storlazzi CD, Brown EK, Field ME, Rodgers K, Jokiel PL (2005) A model for wave control on coral breakage and species distribution in the Hawaiian Islands. *Coral Reefs* 24:43-55
- Szmant AM (2002) Nutrient enrichment on coral reefs: Is it a major cause of coral reef decline? *Estuaries* 25:743-766
- Thorpe SA (2007) *An introduction to ocean turbulence*. Cambridge University Press, Cambridge, USA
- Tomascik T, Sander F (1987) Effects of eutrophication on reef-building corals II. Structure of scleractinian coral communities on fringing reefs, Barbados, West Indies. *Mar Biol* 94:53-75

- Veron JEN (2000) Corals of the World. Australian Institute of Marine Science, Townsville, Australia
- Vlasenko V, Hutter K (2002) Numerical experiments on the breaking of solitary internal waves over a slope-shelf topography. *J Phys Oceanogr* 32:1779–1793
- Vlasenko V, Stashchuk N (2007) Amplification and suppression of internal waves by tides over variable bottom topography. *J Phys Oceanogr* 36:1959–1973
- Ward-Paige CA, Risk MJ, Sherwood OA, Jaap WC (2005) Clionid sponge surveys on the Florida reef tract suggest land-based nutrient inputs. *Mar Pol Bul* 51:570–579
- van Woerik R, Tomascik T, Blake S (1999) Coral assemblages and physico-chemical characteristics of the Whitsunday Islands: evidence of recent community changes. *Mar Freshwater Res* 50:427–440
- Williams SL, Carpenter RC (1988) Nitrogen-limited primary productivity of coral reef algal turfs: potential contribution of ammonium excreted by *Diadema antillarum**. *Mar Ecol Prog Ser* 47:145–152
- Wolanski E, Delesalle B (1995) Upwelling by internal waves, Tahiti, French Polynesia. *Continental Shelf Research* 15:357–368
- Wolanski E, Fabricius K, Spagnol S, Brinkman R (2005) Fine sediment budget on an inner-shelf coral-fringed island, Great Barrier Reef of Australia. *Estuarine, Coastal and Shelf Science* 65:153–158
- Wu G, Zhang Y (1998) Tibetan Plateau Forcing and the Timing of the Monsoon Onset over South Asia and the South China Sea. *American Meteorol Soc* 126:913–927
- www.reefbase.org/gis_maps
- Yeemin T, Sutthacheep M, Pettongma R (2006) Coral reef restoration projects in Thailand. *Ocean & Coastal Management* 49:562–575

Chapter 2

Benthic primary production in response to Large Amplitude Internal Waves in coral reefs

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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 μM) 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.

Key words

Large Amplitude Internal Wave - Soliton - primary production - benthic community – nutrients – sediment - turf algae - coral

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 & 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: suppl. Table 1). 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 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 μ l HgCl 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 (μ g, see pigment determination below) per algae tile area (cm^{-2}) 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 ($\mu\text{g cm}^{-2} \text{ h}^{-1}$). 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 (suppl. Table 1) 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				
Temperature (C°, modal)	28.84	28.59	28.82	28.77
Temperature (C°, mean±SE)	28.89 ± 0.0013	28.66 ± 0.0015	28.75 ± 0.0018	28.23 ± 0.0035
DTR, daily max-min (C°, mean±SE)	1.03 ± 0.07	1.5 ± 0.10	2.44 ± 0.16	3.94 ± 0.16
PAR 11:00-14:00h ($\mu\text{mol quanta m}^{-2} \text{s}^{-1}$, mean±SE)	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 ($\mu\text{g mg}^{-1}$ pore water, mean±SE)	2.10 ± 0.072	2.06 ± 0.075	2.33 ± 0.067	2.21 ± 0.068
PN content ($\mu\text{g mg}^{-1}$ 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 ~ 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 (suppl. Fig 3) 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, $p < 0.001$), 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.

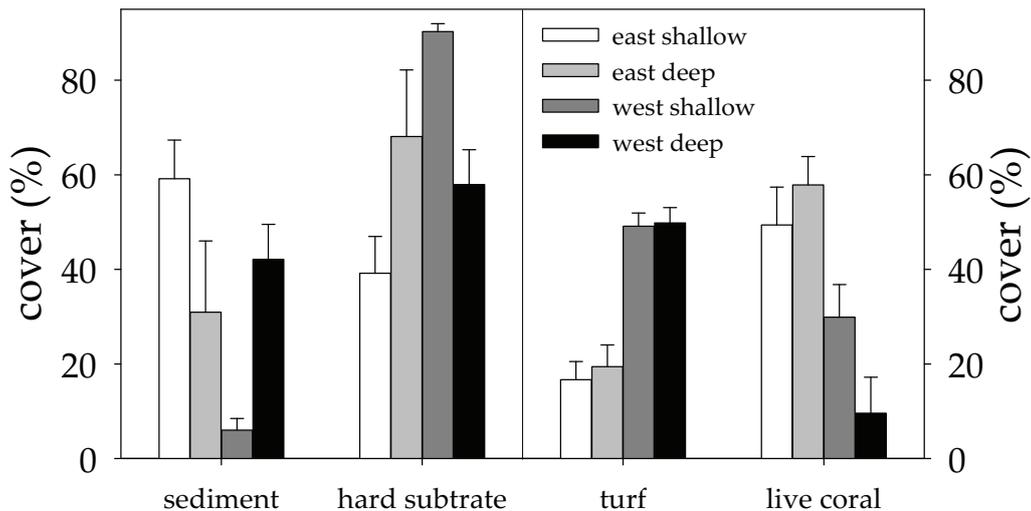


Figure 1 Benthic cover. Line transects on benthic cover at Koh Miang (E shallow, E deep, W shallow, W deep) in %; live coral cover as a fraction of hard substrate.

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 ~ 10% lower on the W side (Table 1) compared to E.

Benthic community composition

A summary of the results obtained by the line-intercept transects is given in Fig 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.

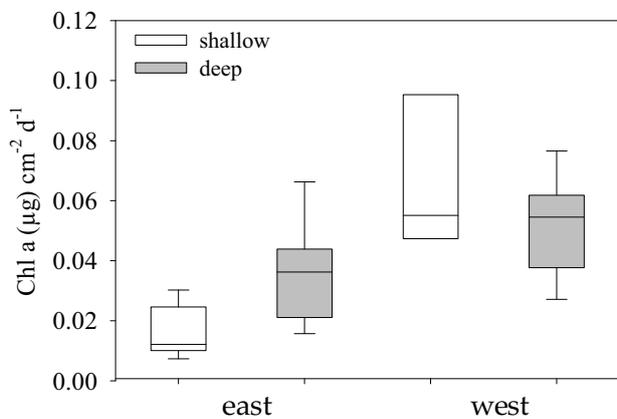


Figure 2 Growth rates of turf algae. Microscopic slides (algae tiles) were deployed in-situ at all investigation sites at Koh Miang and displaced in random order after 1-3 weeks (E shallow, n:15; E deep, n:15; W shallow, n:10; W deep, n:17); algal growth was determined as chl-a ($\mu\text{g cm}^{-2}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

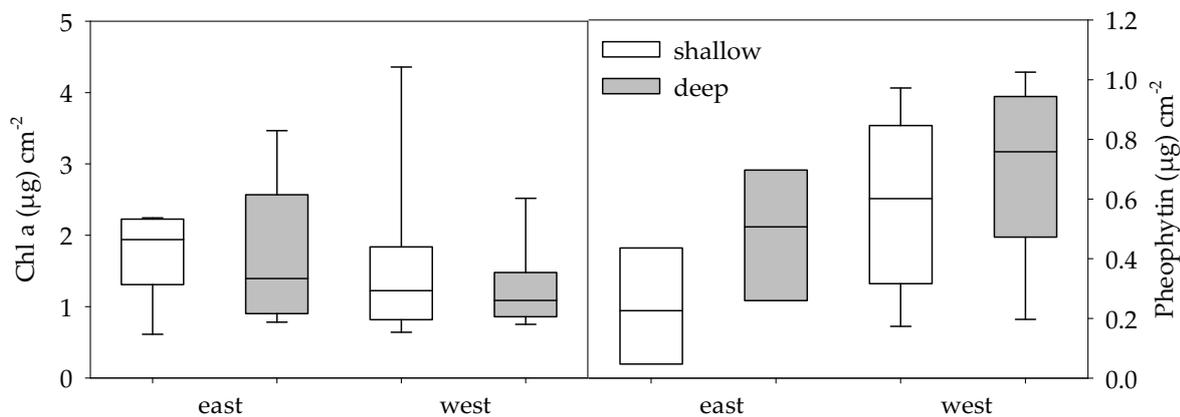


Figure 3 Pigment content of sediment. Chl-a and Pheophytin content of sediment from all investigation sites at Koh Miang, normalised to sediment surface area ($\mu\text{g cm}^{-2}$).

Growth rate of turf algae and pigment content of primary producers

Algae growth rates as chl-a increase, displayed in Fig 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 were found on E deep (and not E shallow, presumably evoked by higher light levels).

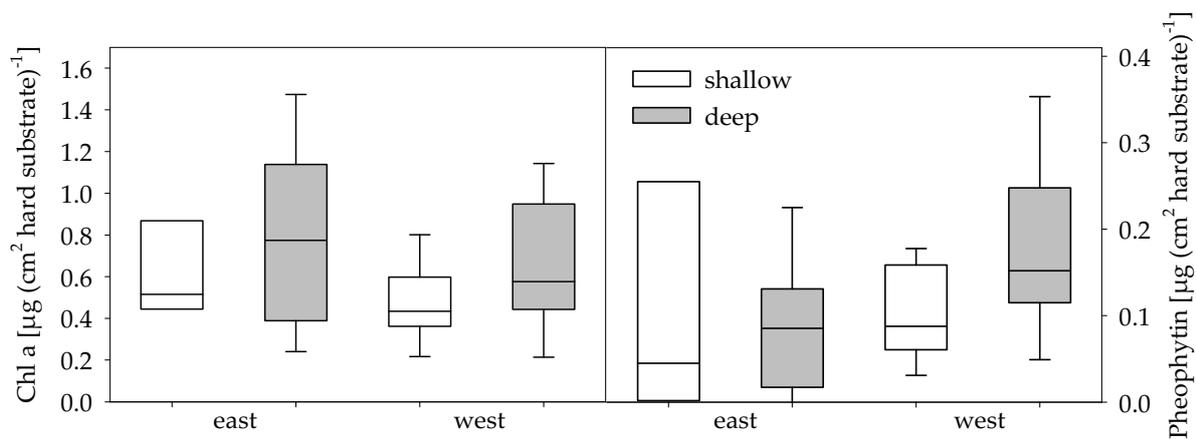


Figure 4 Pigment content of turf algae. Chl-a and Pheophytin content of turf algae from all investigation sites at Koh Miang, normalised to growth area [$\mu\text{g (cm}^2 \text{ hard substrate)}^{-1}$].

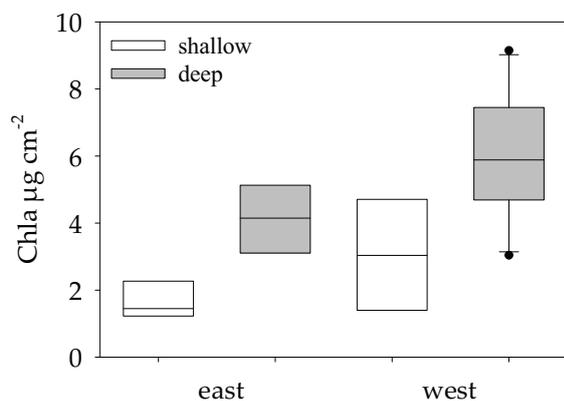


Figure 5 Pigment content of corals. Chl-a content of *P. lutea* from all investigation sites at Koh Miang, normalised to coral surface area ($\mu\text{g cm}^{-2}$).

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: $p < 0.02$).

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

Daily temperature range (DTR) versus		level of significance	p	Rsp
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 (Chl a $\text{cm}^{-2} \text{d}^{-1}$)	**	< 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 (O_2 [$\mu\text{g cm}^{-2} \text{min}^{-1}$])	**	<0.001	-0.456
Sediment	gross photosynthesis (O_2 [$\mu\text{g cm}^{-2} \text{min}^{-1}$])	**	<0.001	-0.471
Sediment	respiration (O_2 [$\mu\text{g cm}^{-2} \text{min}^{-1}$])		0.198	0.165
Algae	net photosynthesis (O_2 [$\mu\text{g cm}^{-2} \text{min}^{-1}$])	(*)	0.078	0.275
Algae	gross photosynthesis (O_2 [$\mu\text{g cm}^{-2} \text{min}^{-1}$])		0.596	-0.084
Algae	respiration (O_2 [$\mu\text{g cm}^{-2} \text{min}^{-1}$])	**	0.002	0.444
Corals (max. rate)	net photosynthesis (O_2 [$\mu\text{g cm}^{-2} \text{min}^{-1}$])		0.379	0.211
Corals (max. rate)	gross photosynthesis (O_2 [$\mu\text{g cm}^{-2} \text{min}^{-1}$])		0.97	0.01
Corals (max. rate)	respiration (O_2 [$\mu\text{g cm}^{-2} \text{min}^{-1}$])	**	<0.001	0.528
Sediment	net photosynthesis (O_2 [$\mu\text{g cm}^{-2} \text{min}^{-1}$] Chla [μg^{-1}])	*	0.015	-0.307
Sediment	gross photosynthesis (O_2 [$\mu\text{g cm}^{-2} \text{min}^{-1}$] Chla [μg^{-1}])	*	0.022	-0.289
Sediment	respiration (O_2 [$\mu\text{g cm}^{-2} \text{min}^{-1}$] Chla [μg^{-1}])		0.763	0.033
Algae	net photosynthesis (O_2 [$\mu\text{g cm}^{-2} \text{min}^{-1}$] Chla [μg^{-1}])		0.11	0.242
Algae	gross photosynthesis (O_2 [$\mu\text{g cm}^{-2} \text{min}^{-1}$] Chla [μg^{-1}])		0.343	-0.146
Algae	respiration (O_2 [$\mu\text{g cm}^{-2} \text{min}^{-1}$] Chla [μg^{-1}])	**	0.001	0.466
Corals (max. rate)	net photosynthesis (O_2 [$\mu\text{g cm}^{-2} \text{min}^{-1}$] Chla [μg^{-1}])	**	<0.001	-0.792
Corals (max. rate)	gross Photosynthesis (O_2 [$\mu\text{g cm}^{-2} \text{min}^{-1}$] Chla [μg^{-1}])	**	<0.002	-0.745
Corals (max. rate)	respiration (O_2 [$\mu\text{g cm}^{-2} \text{min}^{-1}$] Chla [μg^{-1}])	**	<0.003	0.861

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.

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's 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 (suppl. Fig 4). Chl-a specific net photosynthetic rates were much lower for the W side (either depth, suppl. Fig 5), 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).

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.

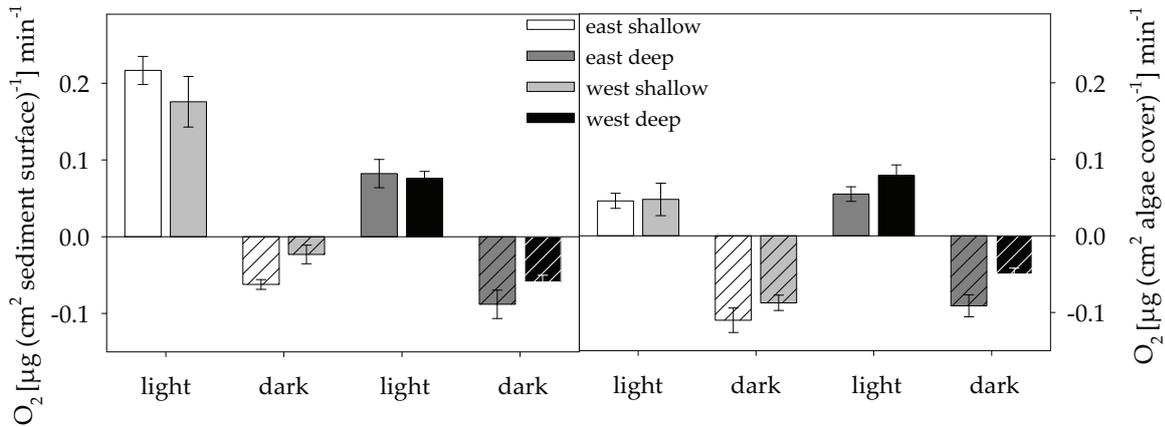


Figure 6 Oxygen fluxes of sediment and turf algae. Sediment and turf algae were incubated in a water bath on land to determine oxygen fluxes (net photosynthesis and respiration); values were normalised to surface area of sediment or turf algae growth substrate ($\mu\text{g cm}^{-2} \text{min}^{-1}$).

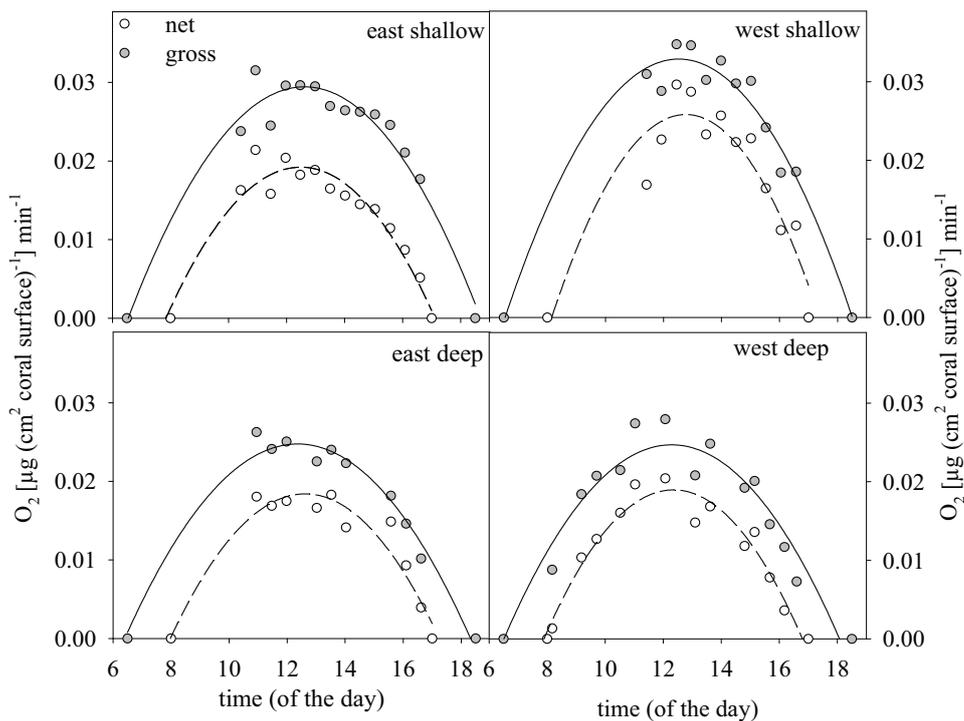


Figure 7 Oxygen fluxes of corals. Incubations of *P. lutea* in-situ with an automated respirometer during one day at each site at Koh Miang to determine oxygen fluxes, i.e. net and gross photosynthesis, values were normalised to surface area ($\mu\text{g cm}^{-2}$).

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).

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

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. (accepted) 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.

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 suppl. Fig 2).

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, Titlyanov 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.

Supplementary data is given in Annex 2

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References

- Alcala MLR, Vogt E (1997) Approximation of coral reef surfaces using standardised growth forms and video courts. 8th int. Coral Reef Sym 2:1452-1458
- Anthony KRN, Hoegh-Guldberg O (2003) Variation in coral photosynthesis, respiration and growth characteristics in contrasting light microhabitats: an analogue to plants in forest gaps and understoreys? *Functional Ecology* 17:246–259
- Apel JR, Ostrovsky LA, Stepanyants YA, Lynch JF (2006) Internal Solitons in the Ocean. Technical report WHOI-2006-04, Oceanographic Inst, Woods Hole
- Bellwood DR, Andrew SH, Ackerman JH, Depczynski M (2006) Coral bleaching, reef fish community phase shifts and the resilience of coral reefs. *Global Change Biology* 12:1587-1594
- Borowitzka MA, Larkum AWD, Borowitzka LJ (1978) A preliminary study of algal turf communities of a shallow coral reef lagoon using an artificial substratum. *Aquatic Botany* 5(4):365-381
- Bunt JS, Lee CC, Lee E (1972) Primary Productivity and Related Data from Tropical and Subtropical Marine Sediments. *Marine Biology* 16:28-36
- Carpenter RC, Hackney JM, Adey WH (1991) Measurements of primary productivity and nitrogenase activity of coral reef algae in a chamber incorporating oscillatory flow. *Limnol Oceanogr*, 36:40-49
- Carpenter RC (1985) Relationship between primary production and irradiance in coral reef algal communities. *Limnol Oceanogr* 30(4):784-793
- Clavier J, Garrigue C (1999) Annual sediment primary production and respiration in a large coral reef lagoon (SW New Caledonia). *Mar Ecol Prog Ser* 191:79-89
- Cook P, Røy H (2006) Advective relief of CO₂ limitation in microphytobenthos in highly productive sandy sediments. *Limnol Oceanogr* 51:1594–1601.
- Cortés J, Risk MJ (1984) El arrecife coralino del Parque Nacional Cahuita, Costa Rica. *Revista de Biología Tropical*, 32(1) pp.109-121
- Dennison WC, Barnes DJ (1988) Effect of water motion on coral photosynthesis and calcification. *J Exp Mar Biol Ecol* 115:67-77
- Dubinsky Z, Stambler N, Ben-Zion M, McCloskey LR, Muscatine L, Falkowski PG (1990) The effect of external nutrient resources on the optical properties and photosynthetic efficiency of *Stylophora pistillata*. *Proc R Soc Lond* 239:231-246
- Edmunds PJ, Davies PS (1988) Post-illumination stimulation of respiration rate in the coral *Porites porites*. *Coral Reefs* 7:7-9
- Falkowski PG, Dubinsky Z (1981) Light-shade adaptation of *Stylophora pistillata*, a hermatypic coral from the Gulf of Eilat. *Nature* 289:172-174
- Ferrier-Pages C, Gattuso JP, Dallot S, Jaubert J (2000) Effect of nutrient enrichment on growth and photosynthesis of the zooxanthellate coral *Stylophora pistillata*. *Coral Reefs* 19:103-113
- Gerkema and Zimmerman (1995) Generation of nonlinear internal tides and solitary waves. *American Meteorological Society Vol. 25:1081-1094*
- Gorbunov MY, Kolber ZS, Lesser MP, Falkowsky PG (2001) Photosynthesis and photoprotection in symbiotic corals. *Limnol Oceanogr* 46(1):75–85
- Grasshoff K, Ehrhardt M, Kremling K (1999) *Methods of Seawater Analysis*. 3rd Edition Verlag Chemie, Weinheim
- Hansen JA, Klumpp DW, Alongi DM, Dayton PK, Riddle MJ (1992) Detrital pathways in a coral reef lagoon II. Detritus deposition, benthic microbial biomass and production. *Mar Biol* vol 113:363-372
- Hatcher BG, Larkum AWD (1983) An experimental analysis of factors controlling the standing crop of the epilithic algal community on a coral reef. *J Exp Biol Mar Ecol*, 69(1):61-84
- Hatcher BG (1990) Coral Reef primary productivity: a hierarchy of pattern and processes. *TREE* (5):149-155
- Hoegh-Guldberg O, Jones RJ (1999) Photoinhibition and photoprotection in symbiotic dinoflagellates from reef-building corals. *Mar Ecol Prog Ser*, 183:73-86
- Hoegh-Guldberg O, Mumby PJ, Hooten AJ, Steneck RS, Greenfield P, Gomez E, Harvell CD, Sale PF, Edwards AJ, Caldeira K, Knowlton N, Eakin CM, Iglesias-Prieto R, Muthiga N, Bradbury RH, Dubi A, Hatzioiols ME (2007) Coral reefs under rapid climate change and ocean acidification. *Science* 318:1737-1742
- Hodgson G, Kiene W, Mihaly J, Liebeler J, Shuman C, Maun L (2004) Reef check instruction manual: a guide to reef check coral reef monitoring. Reef Check, Los Angeles
- Hoogenboom MO, Anthony KRN, Connolly SR (2006) Energetic cost of photoinhibition in corals. *Mar Ecol Prog Ser*, 313:1–12
- Huettel M, Røy H, Precht E, Ehrenhauss S (2003) Hydrodynamical impact on biogeochemical processes in aquatic sediments. *Hydrobiologia* 494:231-236
- Huettel M, Webster IT (2001) Porewater flow in permeable sediments. In: Boudreau BP, Jørgensen BB (eds) *The benthic boundary layer*. Oxford University Press
- Hughes T P (1994) Catastrophes, phase shift, and large scale degradation of Caribbean coral reef. *Science*, 265:1547-1551
- Hughes T, Rodrigues M, Bellwood D, Ceccarelli D, Hoegh-Guldberg O, McCook L, Moltschaniwskyj N, Pratchett

- M, Steneck R, Willis B (2007) Phase shifts, herbivory, and the resilience of coral reefs to climate change. *Current Biology* 17:360-365
- Huthnance (1989) Internal tides and waves near the continental shelf edge. *Geophys. Astrophys. Fluid dynamics*, 48:81-106
- Iglesias-Prieto R, Trench RK (1994) Acclimation and adaptation to irradiance in symbiotic dinoflagellates. I. Responses of the photosynthetic unit to changes in photon flux density. *Mar Ecol Prog Ser* 113:163-175
- Jackson CR (2004) Andaman Sea. In *An Atlas of Oceanic Internal Solitary-like Waves and their Properties*, pages 485–500. Global Ocean Associates, 2nd edition. Prepared under contract with the Office of Naval Research-Code 322PO
- Jeffrey S W, Humphrey GF (1975) New spectrophotometric equations for determining chlorophylls a, b, c, and c2 in higher plants, algae and natural phytoplankton. *Biochem Physiol Pflanz*, 167:191-194
- Jompa J, McCook LJ (2003) Contrasting effects of turf algae on corals: massive *Porites* spp. are unaffected by mixed-species turfs, but killed by the red alga *Anotrichium tenue*. *Mar Ecol Prog Ser* 258:79-86
- Kattner G (1999) Storage of dissolved inorganic nutrients in seawater: poisoning with mercury chloride. *Mar Chem* 67:61-66
- Klumpp DW, McKinnon AD (1992) Community structure, biomass and productivity of epilithic algal communities on the Great Barrier Reef: dynamics at different spatial scales. *Mar Ecol Prog Ser* 86:77-89
- Kühl M, Lassen C, Jørgen BB (1994) Light penetration and light intensity in sandy marine sediments measured with irradiance and scalar irradiance fiber-optic microprobes. *Mar Ecol Progr Ser* 105:139-148
- Lapointe BE (1997) Nutrient thresholds for bottom-up control of macroalgal blooms on coral reefs in Jamaica and south E Florida. *Limnol Oceanogr* 42:1119-1131
- Leichter JJ, Wing SR, Miller SL, Denny MW (1996) Pulsed delivery of subthermoline water to Conch Reef (Florida Keys) by internal bores. *Limnol Oceanogr* 41:1490-1501
- Leichter JJ, Stewart HL, Miller SL (2003) Episodic nutrient transport to Florida coral reefs. *Limnol Oceanogr* 48(4):1394–1407
- Leletkin VA (2000) Trophic status and population density of zooxanthellae in hermatypic corals. *Russian J Mar Biol* 26(4):231-240
- Lorenzen CJ (1967) Determination of Chlorophyll and Pheo-Pigments: Spectrophotometric Equations. *Limnol Oceanogr* 12(2):343-346
- McCook LJ (1999) Macroalgae, nutrients and phase shifts on coral reefs: scientific issues and management consequences for the Great Barrier Reef. *Coral Reefs* 18:357-367
- McCook LJ (2001) Competition of corals and algae turf along a gradient of terrestrial influence in the near shore central Great Barrier Reef. *Coral Reefs* 19:419-425
- Miller MW, Hay ME, Miller SL, Malone D, Sotka E, Szmant AM (1999) Effects of nutrients versus herbivores on reef algae: a new method for manipulating nutrients on coral reefs. *Limnol Oceanogr* 44:1847–1861
- Miyajima T, Suzumura M, Umezawa Y, Koike I (2001) Microbiological nitrogen transformation in carbonate sediments of a coral-reef lagoon and associated seagrass beds. *Mar Ecol Prog Ser* 217:273–286
- Morelock J, Grove K, Hernandez M (1983). *Oceanography and patterns of shelf sediments, Mayaguez, Puerto Rico*. *J Sedim Petrol* 53:371-381
- Muscantine L, Falkowski PG, Dubinsky Z, Cook PA, McCloskey LR (1989) The effect of external nutrient resources on the population dynamics of zooxanthellae in a reef coral. *Proc R Soc Lond* 236:311-324
- Naumann MS, Niggli W, Laforsch C, Glaser C, Wild C (2009) Coral surface area quantification-evaluation of established techniques by comparison with computer tomography. *Coral Reefs* 28:109–117
- Osborne AR, Burch TL (1980) Internal Solitons in the Andaman Sea. *Science* 208(4443):451-460
- Pandolfi JM, Jackson JBC, Baron N, Bradbury RH, Guzman HM, Hughes TP, Kappel CV, Micheli F, Ogden JC, Possingham HP, Sala E (2005) Are U.S. Coral Reefs on the slippery Slope to Slime? *Science* 307:1725-1726
- Perry RB, Schimke GR (1965) Large-Amplitude Internal Waves observed off the Northwest coast of Sumatra. *J Geophys Res* 70:2319-2324
- Philipp E, Fabricius K (2003) Photophysiological stress in scleractinian corals in response to short-term sedimentation. *J Exp Mar Biol Ecol* 287:57– 78
- Pineda J (1991) Predictable upwelling and the shoreward transport of planktonic larvae by internal tidal bores. *Nature* 253:548-551
- Ralph PJ, Gademann R, Larkum AWD, Kühl M (2002) Spatial heterogeneity in active chlorophyll fluorescence and PSII activity of coral tissues. *Mar Biol* 141:639–646
- Rasheed M, Badran M, Huettel M (2003) Particulate matter filtration and seasonal nutrient dynamics in permeable carbonate and silicate sands of the Gulf of Aqaba, Red Sea. *Corals Reefs* 22:167-177
- Rasheed M, Wild C, Franke U, Huettel M (2004) Benthic photosynthesis and oxygen consumption in permeable carbonate sediments at Heron Island, Great Barrier Reef, Australia. *Est Coast Shelf Sc* 59(1):139-150, doi:10.1016/j.ecss.2003.08.013
- Rasheed M, Wild C, Jantzen C, Badran M (2006) Mineralization of particulate organic matter derived from coral-reef organisms in reef sediments of the Gulf of Aqaba. *Chem Ecol* 22:13–20
- Roder C, Fillinger L, Jantzen C, Schmidt GM, Khokiattiwong S, Richter C (accepted) Trophic response of corals to Large Amplitude Internal Waves. *Mar Ecol Prog Ser*

- Rogers CS (1990) Responses of coral reefs and reef organisms to sedimentation. *Mar Ecol Prog Ser* 62:185-202
- Rogers CS, Salesky NH (1981) Productivity of *Acropora palmata* (Lamarck), macroscopic algae, and algal turf from Tague Bay Reef St. Croix, U.S. Virgin Islands. *J Exp Mar Biol Ecol* 49:179-187
- Rusch A, Huettel M, Forster S (2000) Particulate organic matter in permeable marine sands – dynamics in time and depth. *Estuar Coast Shelf Sci* 51:399-414
- Rusch A, Huettel M, Wild C, Reimers CE (2006) Benthic oxygen consumption and organic matter turnover in organic-poor, permeable shelf sands. *Aqu Geochem*
- Ruxton, GD (2006) The unequal variance t-test is an underused alternative to Student's t-test and the Mann-Whitney U-test. *Behav Ecol* 17:688-690.
- Saxby TA, Denniso, WC, Hoegh-Guldberg O (2003) Photosynthetic responses of the coral *Montipora digitata* to cold temperature stress. *Mar Ecol Prog Ser* 248:85–97
- Schlacher TA, Newell P, Clavier J, Schlacher-Hoenlinger, Chevillon C, Britton (1998) Soft-sediment benthic community structure in a coral reef lagoon - the prominence of patch heterogeneity and 'spot endemism'. *Mar Ecol Progr Ser* 174:159-174
- Schlichting E, Blume H-P, Stahr K (1995) *Bodenkundliches Praktikum*. Pareys Studentexte Blackwell, 2. Aufl. Berlin
- Schmidt GM, Phongsuwan N, Roder C, Jantzen C, Khokiattiwong S, Richter C (submitted) Coral community and physico-chemical characteristics in response to Large Amplitude Internal Waves. *Mar Ecol Prog Ser*
- Smith JE, Smith CM, Hunter CL (2001) An experimental analysis of the effects of herbivory and nutrient enrichment on benthic community dynamics on a Hawaiian reef. *Coral Reefs* 19:332-342
- Smith JE, Smith CM, Vroom P, Beach KL, Miller S (2004) Nutrient and growth dynamics of *Halimeda* tuna on Conch Reef, Florida Keys: Possible influence of internal tides on nutrient status and physiology. *Limnol Oceanogr* 49(6):1923–1936
- Titlyanov EA (1991) The stable level of coral primary production in a wide light range. *Hydrobiol* 216/217:383-387
- Tucker M, (1988) *Techniques in Sedimentology*. Blackwell Scientific Publication
- Vlasenko Vland Hutter K (2001) Numerical experiments on the breaking of solitary internal waves over a slope–shelf topography. *Am Meteorol Soc* 32:1781-1793
- Vlasenko V, Stashchuk N (2007) Three-dimensional shoaling of large-amplitude internal waves. *J Geophys Res* 112:doi:10.1029/2007JC004107
- Wild C, Rasheed M, Jantzen C, Cook P, Struck U, Huettel M, Boetius A (2005) Benthic metabolism and degradation of natural particulate organic matter in carbonate and silicate reef sands of the northern Red Sea. *Mar Ecol Prog Ser* 298:69–78
- Wild C, Laforsch C, Huettel M (2006) Detection and enumeration of microbial cells within highly porous calcareous reef sands. *Mar Freshw Res* 57:415-420
- Williams SL, Carpenter RC (1988) Nitrogen-limited primary productivity of coral reef algal turfs: potential contribution of ammonium excreted by *Diadema antillarum*. *Mar Ecol Prog Ser* 47:145-152

Chapter 3

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

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 & Grottooli 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 & Cernichiarri 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 & Grotoli 2006).

Materials & 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 &

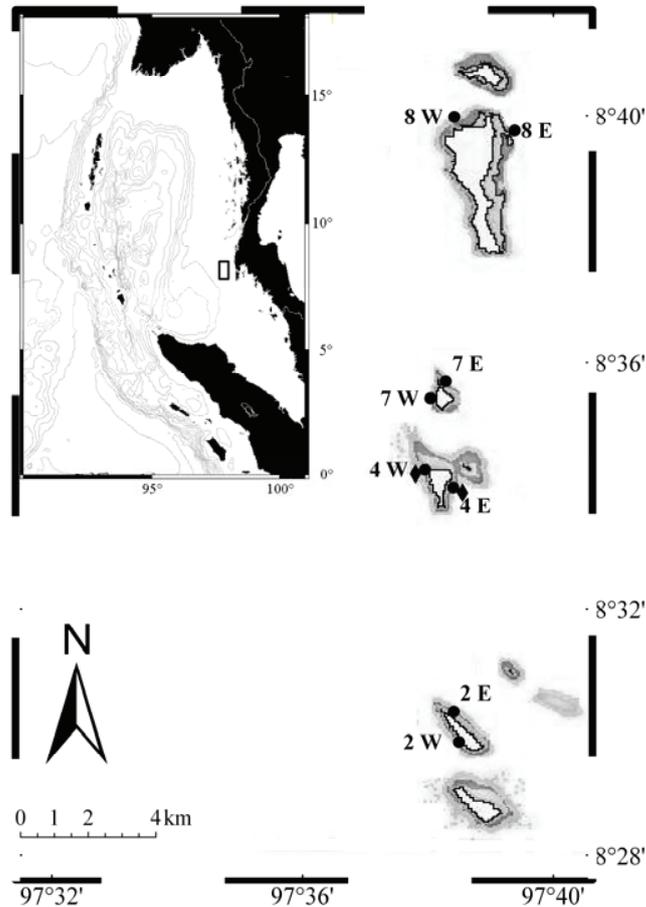


Figure 1 Map of the Similan Islands in the Andaman Sea off the coast of Thailand. Experimental sites (circles) on W (LAIW+) and E (LAIW-) of Island # 4 (Koh Miang Island) are also locations of water and near-reef plankton sampling. Off-reef plankton sampling sites (on Island # 4) are indicated with diamonds.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

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.).

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 2 A) 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.

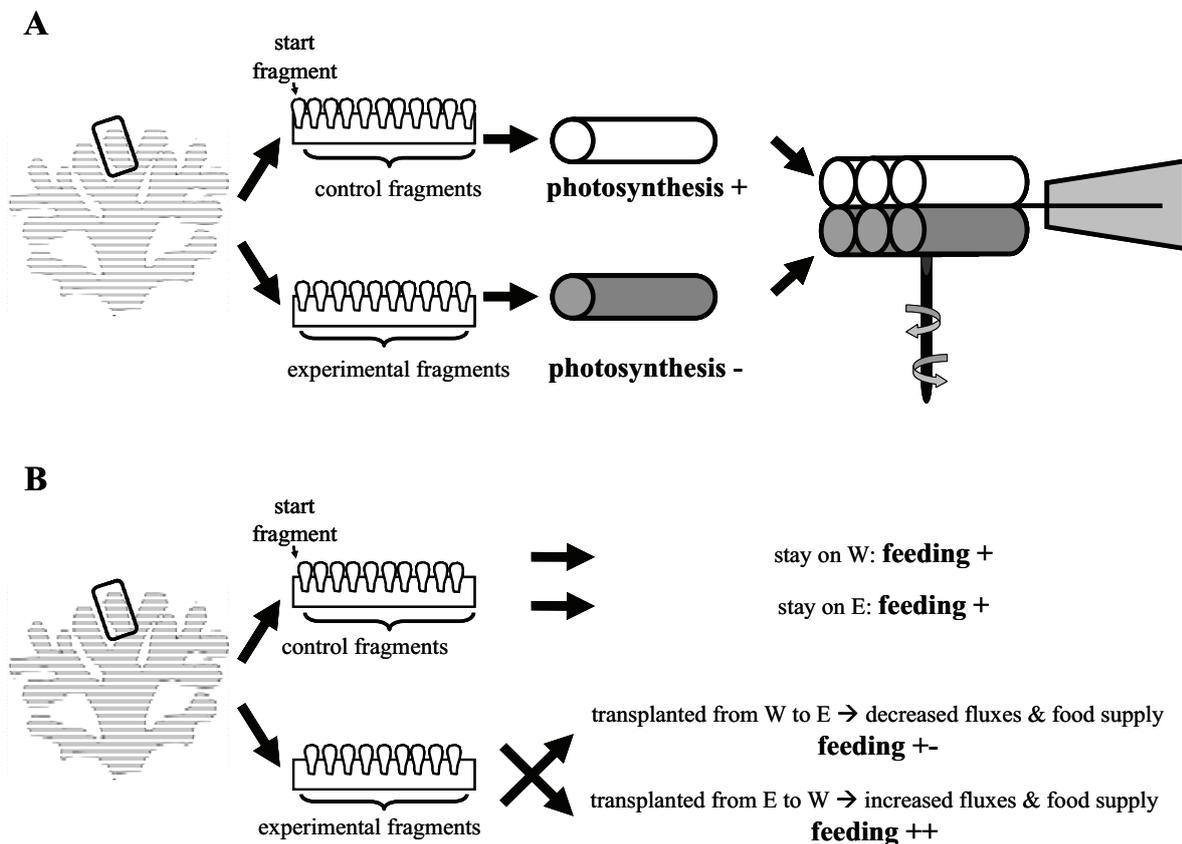


Figure 2 Schematic representation of the experimental designs: A) Light-exclusion experiment: 3 donor colonies per island side, each colony providing 21 fragments (1 start, 10 control and 10 light-deprived fragments). One chamber set-up on each island side (W/LAIW+ and E/LAIW-). B) Transplantation experiment: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

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 3 x 2

stack of these flow pipes (Fig 2 A) 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 2 B) 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.

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 °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 °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 m³) 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 °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 $< 0.2 \text{ }^\circ\text{C}$ over 0 to $50 \text{ }^\circ\text{C}$) 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 ($\Delta T < 0.2$ °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 3 A 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, $p < 0.001$).

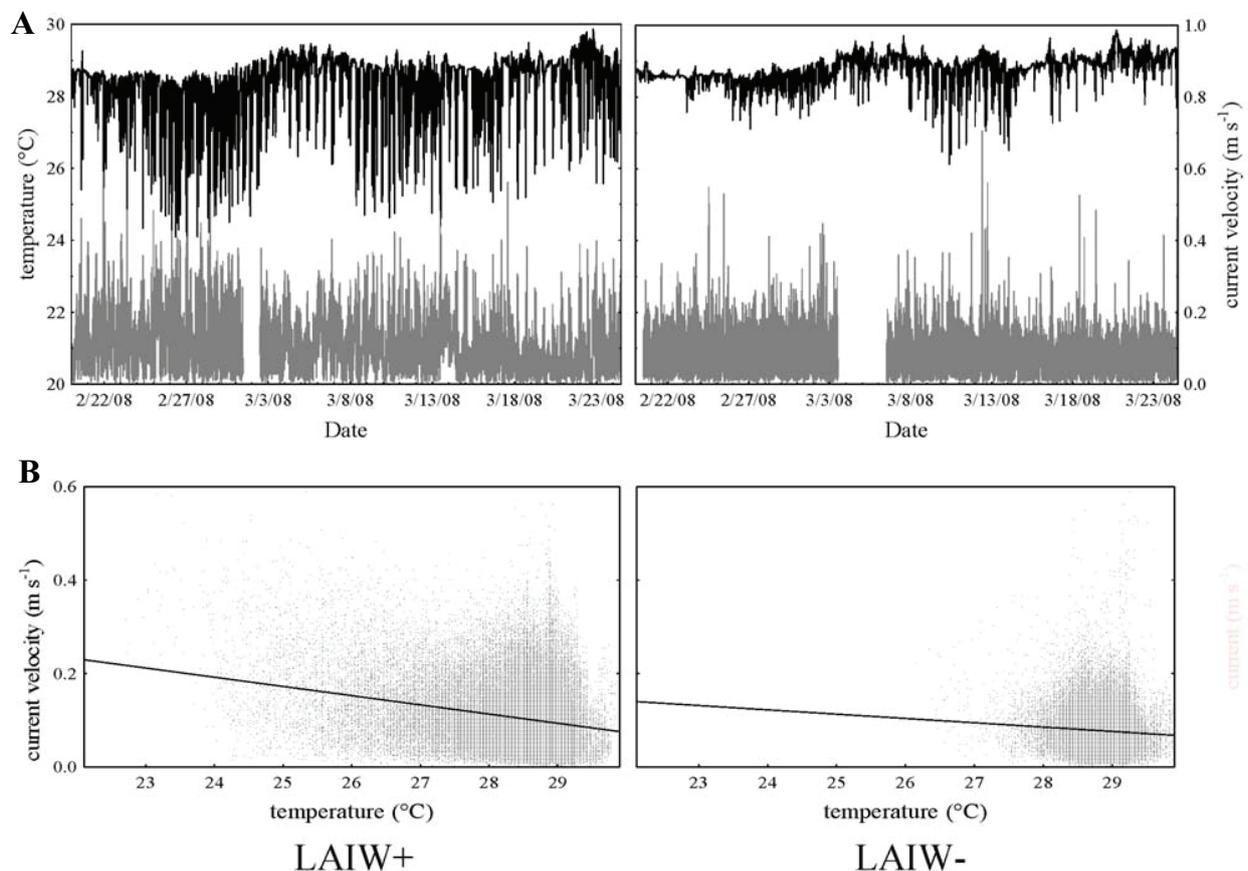


Figure 3 Temperature and currents on the W LAIW-exposed (left panels) and E LAIW-sheltered face of Koh Miang. A) Time series of temperature (black) and current velocity (gray) over the study period. Blank periods in the current data are due to recovery, cleaning and redeployment of the current meters. 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).

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- (suppl. Fig 1) and the

concentrations alone (means \pm SE in suppl. Table 1), of both near- or off-reef plankton and POC (suppl. Fig 1 and 2), TSM, TPOC or DOC (suppl. Fig 3), 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.

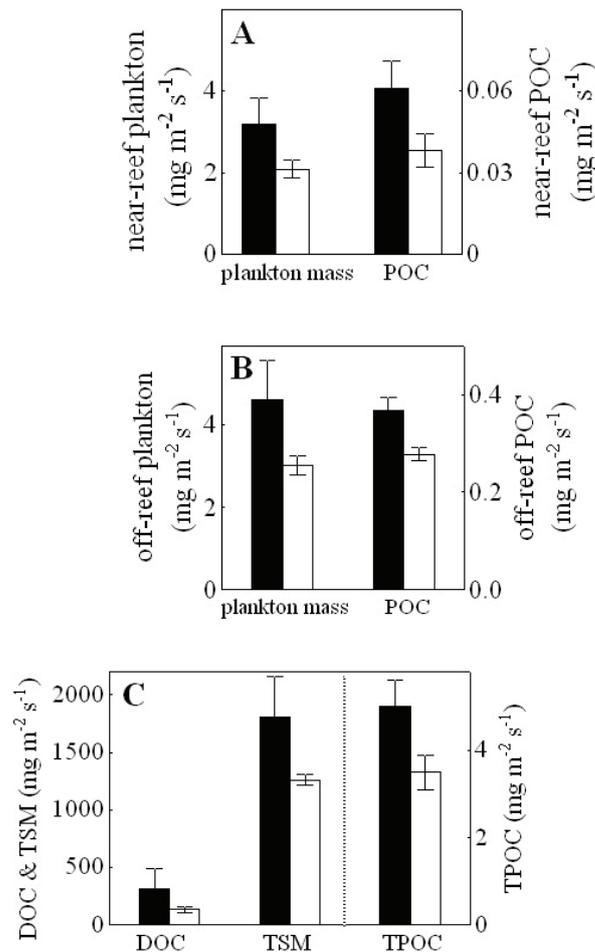


Figure 4 Daily mean fluxes (\pm SE) of **A**) near-reef plankton and its organic carbon fraction **B**) off-reef plankton and its organic carbon fraction and **C**) reef water DOC, TSM and TPOC from LAIW+ (black) and LAIW- (white) Koh Miang. All LAIW+ and LAIW- side samples are statistically significant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

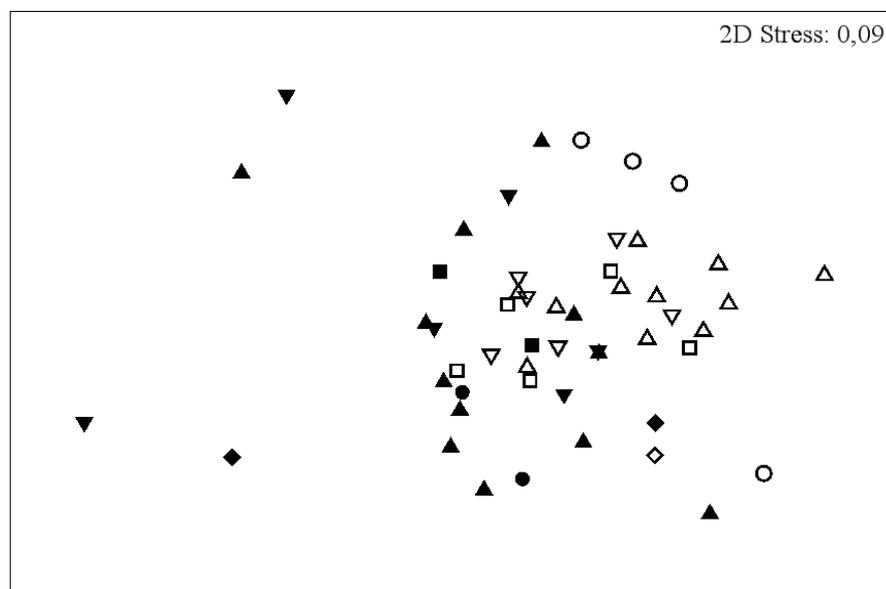


Figure 5 MDS ordination of fragments from LAIW+ (n = 18 plus 6 start fragments from both experiments) and LAIW- (n = 21 plus 6 start fragments from both experiments) sides of all islands to illustrate the multidimensional similarities in coral tissue composition (in terms of zooxanthellae densities, 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 (Fig 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 (Table 3 and 5).

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 %

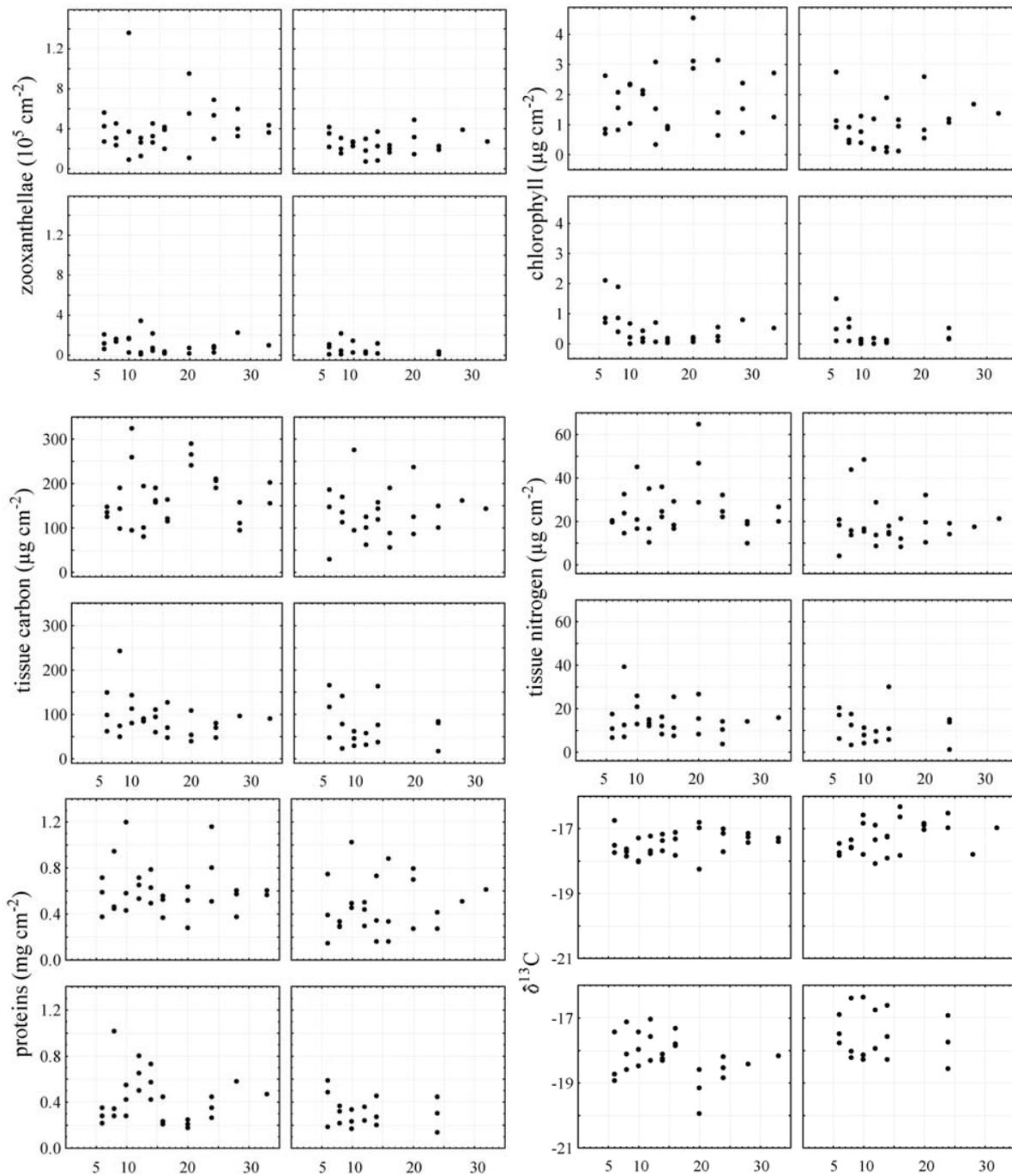


Figure 6 Time-series of all tissue parameters (from top to bottom: zooxanthellae densities, chlorophyll content, carbon tissue content, nitrogen tissue content, protein concentrations and isotopic carbon ratios) measured in controls and light-deprived fragments from W (LAIW+) and E (LAIW-) over experimental 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-).

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

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.

light-exclusion experiment	LAIW+				LAIW-			
	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)

of the control host tissue were not significantly different between LAIW+ and LAIW- reefs (Table 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 (Table 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).

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,

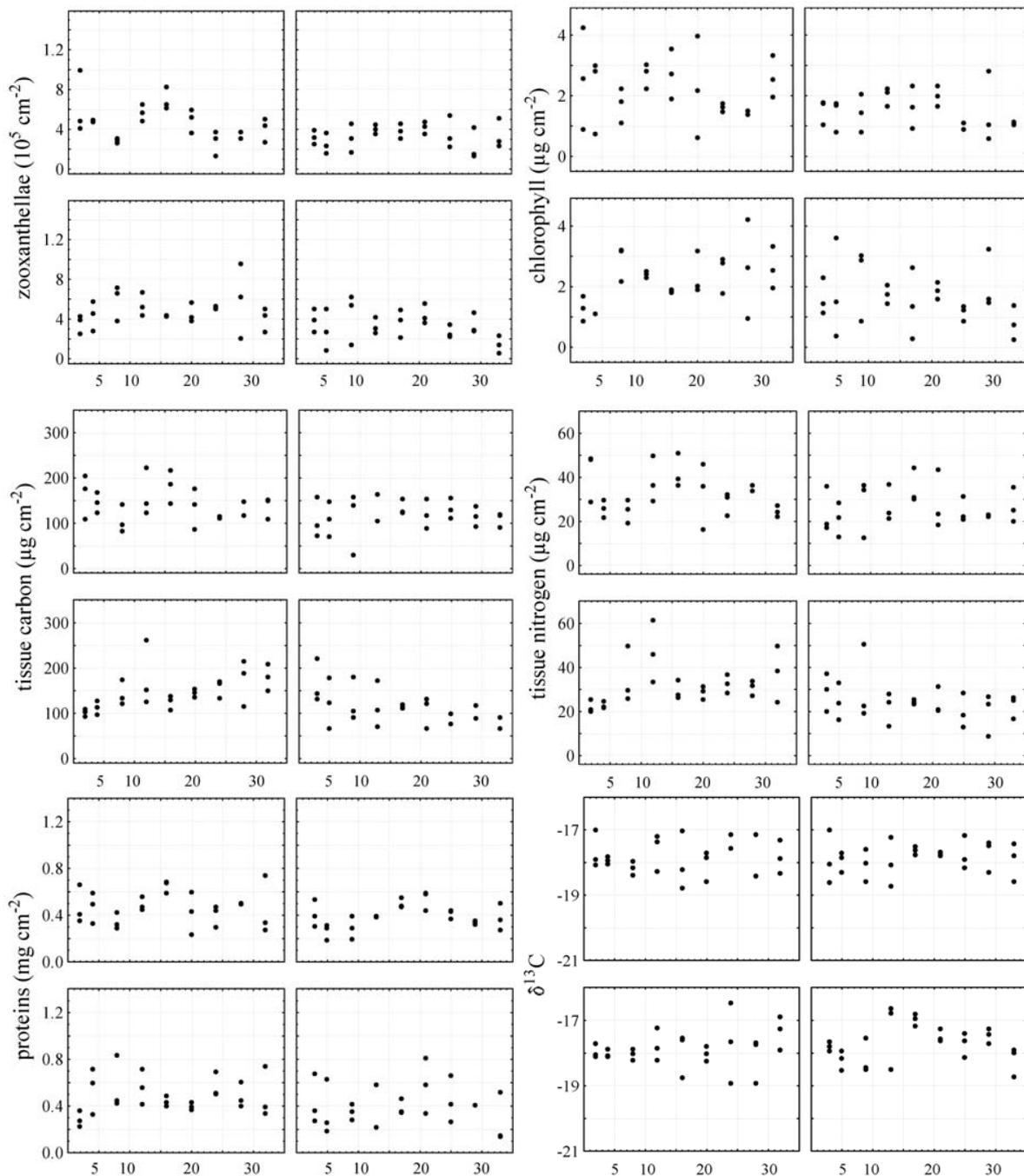


Figure 7 Time-series of all tissue parameters (from top to bottom: zooxanthellae densities, chlorophyll content, carbon tissue content, nitrogen tissue content, protein concentrations and isotopic carbon ratios) measured in controls and feed-altered fragments from W (LAIW+) and E (LAIW-) over experimental 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-).

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 ($p < 0.001$).

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		

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, Table 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).

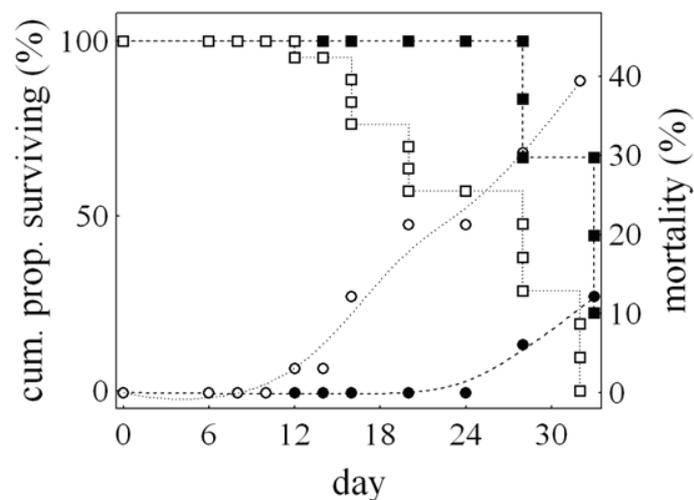


Figure 8 Survival analysis of *Pocillopora meandrina* in the light-exclusion experiment. Kaplan Meier cumulative proportion survival curves (left y-axis, squares) of corals from LAIW+ (closed symbols) and LAIW- (open symbols) reefs of Koh Miang over experiment time (x-axis), showing the cumulative proportion 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.

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

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*

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

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		

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

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

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-affected 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 (Tregnier 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 *Pocillopora* (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.

Supplementary data is given in Annex 3

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Literature

- Abe N (1938) Feeding behaviour and the nematocyst of *Fungia* and 15 other species of corals. Palau Tropical Biology Station Studies 3:469-521
- Al-Horani FA (2005) Effects of changing seawater temperature on the photosynthesis and calcification in the scleractinian coral *Galaxea fascicularis*, measured with O₂, Ca²⁺ and pH microsensors. *Scientia Marina* 69:347-354
- Al-Moghrabi SM, Allemann D, Couret JM, Jaubert J (1995) Fatty acids of the scleractinian coral *Galaxea fascicularis*: effect of light and feeding. *Journal of Comparative Physiology B: Biochemical* 165:183-192
- Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. *Australian Journal of Ecology* 26:32-46
- Anderson MJ, Gorley RN, Clarke KR (2008) PERMANOVA+ for PRIMER: guide to software and statistical methods. Plymouth, UK: PRIMER-E
- Anderson MJ, Ter Braak CJF (2003) Permutation tests for multi-factorial analysis of variance. *Journal of Statistical Computation and Simulation* 73:85-113

- Andrews JC, Gentien P (1982) Upwelling as a source of nutrients for the Great Barrier Reef ecosystems: A solution to Darwin's question? *Marine Ecology Progress Series* 8:257-269
- Anthony KR (2000) Enhanced particle-feeding capacity of corals on turbid reefs (Great Barrier Reef, Australia). *Coral Reefs* 19:59-67
- Anthony KR, Fabricius KE (2000) Shifting roles of heterotrophy and autotrophy in coral energetics under varying turbidity. *Journal of Experimental Marine Biology and Ecology* 252:221-253
- Anthony KR, Hoogenboom MO, Maynard JA, Grottoli AG, Middlebrook R (2009) Energetics approach to predicting mortality risk from environmental stress: a case study of coral bleaching. *Functional Ecology* doi: 10.1111/j.1365-2435.2008.01531.x
- Anthony KRN (2006) Enhanced energy status of corals on coastal, high-turbidity reefs. *Marine Ecology Progress Series* 319:111-116
- Bachar A, Achituv Y, Pasternak Z, Dubinsky Z (2007) Autotrophy versus heterotrophy: The origin of carbon determines its fate in a symbiotic sea anemone. *Journal of Experimental Marine Biology and Ecology* 349:295-298
- Bak R, Joenje M, de Jong I, Lambrechts D, Nieuwland G (1998) Bacterial suspension feeding by coral reef benthic organisms. *Marine Ecology Progress Series* 175:285-288
- Borell E, Yuliantri A, Bischof K, Richter C (2008) The effect of heterotrophy on photosynthesis and tissue composition of two scleractinian corals under elevated temperature. *Journal of Experimental Marine Biology and Ecology* 364:116-123
- Brown BE (1997) Coral bleaching: causes and consequences. *Coral Reefs* 16:129-138
- Chansang H, Satapoomin U, Poovachiranon S (1999) Maps of coral reefs in Thai waters, Andaman Sea. *Coral Reef Resource Management Project, Department of Fisheries, Bangkok* 2:pp 198
- Clarke KR, Gorley RN (2006) PRIMER v6: User Manual/Tutorial. Plymouth, UK: PRIMER-E
- Cortés J (1997) Biology and geology of eastern Pacific coral reefs. *Coral Reefs* 16:Suppl.: S39-S46
- Cushing DH (1989) A difference in structure between ecosystems in strongly stratified waters and in those that are only weakly stratified. *Journal of Plankton Research* 11:1-13
- Dennison WC, Barnes DJ (1988) Effect of water motion on coral photosynthesis and calcification. *Journal of Experimental Marine Biology and Ecology* 115:67-77
- Feely RA, Sabine CL, Hernandez-Ayon M, Ianson D, Hales B (2008) Evidence for upwelling of corrosive "acidified" water onto the continental shelf. *Science* 320:1490-1492
- Ferrier-Pagès C, Allemand D, Gattuso J, Jaubert J, Rassoulzadegan F (1998) Microheterotrophy in the zooxanthellate coral *Stylophora pistillata*: Effects of light and ciliate density. *Limnology and Oceanography* 43:1639-1648
- Ferrier-Pagès C, Witting J, Tambutté E, Sebens KP (2003) Effect of natural zooplankton feeding on the tissue and skeletal growth of the scleractinian coral *Stylophora pistillata*. *Coral Reefs* 22:229-240
- Fine M, Tchernov D (2007) Scleractinian coral species survive and recover from decalcification. *Science* 315:1811
- Fitt WK, Gates RD, Hoegh-Guldberg O, Bythell JC, Jatkar A, Grottoli AG, Gomez M, Fisher P, LaJeunesse T, Pantos O, Iglesias-Prieto R, Franklin DJ, Rodrigues LJ, Torregiani JM, van Woesik R, Lesser MP (2009) Response of two species of Indo-Pacific corals, *Porites cylindrica* and *Stylophora pistillata*, to short-term thermal stress: The host does matter in determining the tolerance of corals to bleaching. *Journal of Experimental Marine Biology and Ecology* 373:102-110
- Fitt WK, McFarland F, Warner M, Chilcoat G (2000) Seasonal patterns of tissue biomass and densities of symbiotic dinoflagellates in reef corals and relation to coral bleaching. *Limnology and Oceanography* 45:677-685
- Franzisket L (1969) Riffkorallen können autotroph leben. *Naturwissenschaften* 3:144
- Gardella DJ, Edmunds PJ (1999) The oxygen microenvironment adjacent to the tissue of the scleractinian *Dichocoenia stokesii* and its effects on symbiont metabolism. *Marine Biology* 135:289-295
- Genin A, Jaffe JS, Reef R, Richter C, Franks PJS (2005) Swimming against the flow: a mechanism of zooplankton aggregation. *Science* 308:860-862
- Glynn P (1973) Ecology of a Caribbean coral reef. The *Porites* reef-flat biotope: Part II. Plankton community with evidence for depletion. *Marine Biology* 22:1-21
- Gonzalez L, Manly BFJ (1998) Analysis of variance by randomization with small data sets. *Environmetrics* 9:53-65
- Grottoli AG (1999) Variability of stable isotopes and maximum linear extension in reef-coral skeletons at Kaneohe Bay, Hawaii. *Marine Biology* 135:437-449
- Grottoli AG (2002) Effect of light and brine shrimp on skeletal $\delta^{13}\text{C}$ in the Hawaiian coral *Porites compressa*: a tank experiment. *Geochimica et Cosmochimica Acta* 66:1955-1967
- Grottoli AG, Rodrigues LJ, Juarez C (2004) Lipids and stable carbon isotopes in two species of Hawaiian corals, *Porites compressa* and *Montipora verrucosa*, following a bleaching event. *Marine Biology* 145:621-631
- Grottoli AG, Rodrigues LJ, Palardy JE (2006) Heterotrophic plasticity and resilience in bleached corals. *Nature* 440:1186-1189
- Grottoli AG, Wellington GM (1999) Effect of light and zooplankton on skeletal $\delta^{13}\text{C}$ values in the eastern Pacific corals *Pavona clavus* and *Pavona gigantea*. *Coral Reefs* 18:29-41
- Grover R, Maguer J, Allemand D, Ferrier-Pagès C (2008) Uptake of dissolved free amino acids by the scleractinian coral *Stylophora pistillata*. *Journal of Experimental Biology* 211:860-865

- Hearn C, Atkinson M, Falter J (2001) A physical derivation of nutrient-uptake rates in coral reefs: effects of roughness and waves. *Coral Reefs* 20:347-356
- Heidelberg KB, Sebens KP, Purcell JE (2004) Composition and sources of near reef zooplankton on a Jamaican forereef along with implications for coral feeding. *Coral Reefs* 23:263–276
- Helmuth B, Sebens KP (1993) The influence of colony morphology and orientation to flow on particle capture by the scleractinian coral *Agaricia agaricites* (Linnaeus). *Journal of Experimental Marine Biology and Ecology* 165:251-278
- Hoegh-Guldberg O (1999) Climate change, coral bleaching and the future of the world's coral reefs. *Marine Freshwater Research* 50:839-866
- Houlbrèque F, Ferrier-Pagès C (2009) Heterotrophy in tropical scleractinian corals. *Biological Reviews*:1-17
- Houlbrèque F, Tambutté E, Allemand D, Ferrier-Pagès C (2004a) Interactions between zooplankton feeding, photosynthesis and skeletal growth in the scleractinian coral *Stylophora pistillata*. *Journal of Experimental Biology* 207:1461-1469
- Houlbrèque F, Tambutté E, Ferrier-Pagès C (2003) Effect of zooplankton availability on the rates of photosynthesis, and tissue and skeletal growth in the scleractinian coral *Stylophora pistillata*. *Journal of Experimental Marine Biology and Ecology* 296:145-166
- Houlbrèque F, Tambutté E, Richard C, Ferrier-Pagès C (2004b) Importance of a micro-diet for scleractinian corals. *Marine Ecology Progress Series* 282:151-160
- Jackson CR (2004) An atlas of Internal Solitary-like Waves and their Properties. Global Ocean Association Second edition:560 pp.
- Jantzen C, Wild C, Schmidt GM, Roder C, Khokiattiwong S, Richter C (in preparation) Benthic primary production in response to Large Amplitude Internal Waves in coral reefs
- Johannes RE, Tepley L (1974) Examination of feeding of the reef coral *Porites lobata* in situ using time lapse photography. *Proceedings of the Second International Coral Reef Symposium* 1:127-131
- Kinsey DW (1988) Coral reef system response to some natural and anthropogenic stresses. *Galaxea* 7:113-128
- Leichter J, J., Genovese S, J. (2006) Intermittent upwelling and subsidized growth of the scleractinian coral *Madracis mirabilis* on the deep fore-reef slope of Discovery Bay, Jamaica. *Marine Ecology Progress Series* 316:95-103
- Leichter J, J., Shellenbarger G, Genovese S, J., Wing S, R. (1998) Breaking internal waves on a Florida (USA) coral reef: a plankton pump at work? *Marine Ecology Progress Series* 166:83-97
- Leichter JJ, Paytan A, Wankel S, Hanson K, Miller SL, Altabet MA (2007) Nitrogen and oxygen isotopic signatures of subsurface nitrate seaward of the Florida Keys reef tract. *Limnology and Oceanography* 52:1258-1267
- Leichter JJ, Wing SR, Miller SL, Denny MW (1996) Pulsed delivery of subthermoline water to Conch Reef (Florida Keys) by internal bores. *Limnology and Oceanography* 41:1490-1501
- Lewis JB (1976) Experimental tests of suspension feeding in Atlantic reef corals. *Mar Biol* 36:147-150
- Lewis JB, Price WS (1975) Feeding mechanisms and feeding strategies of Atlantic reef corals. *Journal of Zoology* 276:527-545
- Ljung GM, Box GEP (1978) On a measure of lack of fit in time series models. *Biometrika* 65:297-303
- Lorenzen CJ (1967) Determination of chlorophyll and phaeo-pigments: Spectrophotometric equations. *Limnology and Oceanography* 12:343-346
- Lowry OH, Rosebrough NJ, Farr AL, Randall RJ (1951) Protein measurement with the Folin phenol reagent. *Journal of Biological Chemistry* 193:265-275
- Madhu NV, Jyothibabu R, Ramu K, Sunil V, Gopalakrishnan TC, Nair KKC (2003) Vertical distribution of mesozooplankton biomass in relation to oxygen minimum layer in the Andaman Sea. *Indian Journal of Fisheries* 50:533-538
- Mirto S, Bianchelli S, Gambi C, Krzelj M, Pusceddu A, Scopa M, Holmer M, Danovaro R (2009) Fish-farm impact on metazoan meiofauna in the Mediterranean Sea: Analysis of regional vs. habitat effects. *Marine Environmental Research*:doi:10.1016/j.marenvres.2009.1007.1005
- Muscatine L, Cerniichiari E (1969) Assimilation of photosynthetic products of zooxanthellae by a reef coral. *Biological Bulletin* 137:506-523
- Muscatine L, Porter JW (1977) Reef corals: Mutualistic symbioses adapted to nutrient-poor environments. *BioScience* 27:454-460
- Muscatine L, Porter JW, Kaplan IR (1989) Resource partitioning by reef corals as determined from stable isotope composition. *Marine Biology* 100:185-193
- Nakamura T, van Woesik R (2001) Water-flow rates and passive diffusion partially explain differential survival of corals during the 1998 bleaching event. *Marine Ecology Progress Series* 212:301-304
- Nakamura T, Yamasaki H, van Woesik R (2003) Water flow facilitates recovery from bleaching in the coral *Stylophora pistillata* *Marine Ecology Progress Series* 256:287-291
- Naumann M, Niggel W, Laforsch C, Glaser C, Wild C (2009) Coral surface area quantification—evaluation of established techniques by comparison with computer tomography. *Coral Reefs* 28:109-117
- Nielsen TG, Bjørnsen PK, Boonruang P, Fryd M, Hansen PJ, Janekarn V, Limtrakulvong V, Munk P, Hansen OS, Satapoomin S, Sawangraruks S, Thomsen HA, Østergaard JB (2004) Hydrography, bacteria and protist communities across the continental shelf and shelf slope of the Andaman Sea (NE Indian Ocean). *Marine Ecology Progress Series* 274:69–86

- Osborne AR, Burch TI (1980) Internal solitons in the Andaman Sea. *Science* 208:451-460
- Palardy JE, Grottoli AG, Matthews KA (2005) Effects of upwelling, depth, morphology and polyp size on feeding in three species of Panamanian corals. *Marine Ecology Progress Series* 300:79-89
- Palardy JE, Grottoli AG, Matthews KA (2006) Effect of naturally changing zooplankton concentrations on feeding rates of two coral species in the Eastern Pacific. *Journal of Experimental Marine Biology and Ecology* 331:99-107
- Palardy JE, Rodrigues LJ, Grottoli AG (2008) The importance of zooplankton to the daily metabolic carbon requirements of healthy and bleached corals at two depths. *Journal of Experimental Marine Biology and Ecology* 367:180-188
- Patterson MR (1992) A chemical engineering view of cnidarian symbioses. *American Zoologist* 32:566-582
- Perry RB, Schimke GR (1965) Large-Amplitude Internal Waves observed off the Northwest coast of Sumatra. *Journal of Geophysical Research* 70:2319-2324
- Pineda J (1991) Predictable upwelling and the shoreward transport of planktonic larvae by internal tidal bores. *Science* 253:548-551
- Porter JW, Porter KG (1977) Quantitative sampling of demersal plankton migrating from different coral reef substrates. *Limnology and Oceanography* 22:553-556
- Rodrigues LJ, Grottoli AG (2006) Calcification rate and the stable carbon, oxygen, and nitrogen isotopes in the skeleton, host tissue, and zooxanthellae of bleached and recovering Hawaiian corals. *Geochimica et Cosmochimica Acta* 70:2781-2789
- Rodrigues LJ, Grottoli AG, Pease TK (2008) Lipid class composition of bleached and recovering *Porites compressa* Dana, 1846 and *Montipora capitata* Dana, 1846 corals from Hawaii. *Journal of Experimental Marine Biology and Ecology* 358:136-143
- Satterthwaite FE (1946) An approximate distribution of estimates of variance components. *Biometrics Bulletin* 2:110-114
- Saxby T, Dennison WC, Hoegh-Guldberg O (2003) Photosynthetic response of the coral *Montipora digitata* to cold temperature stress. *Marine Ecology Progress Series* 248:85-97
- 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. *Mar Ecol Prog Ser*
- Sebens KP, DeRiemer K (1977) Diel cycles of expansion and contraction in coral reef anthozoans. *Marine Biology* 43:247-256
- Sebens KP, Grace SP, Helmuth B, Maney Jr E, Miles J (1998) Water flow and prey capture by three scleractinian corals, *Madracis mirabilis*, *Montastrea cavernosa* and *Porites porites* in a field enclosure. *Mar Biol* 131:347-360
- Sebens KP, Johnson AS (1991) Effects of water movement on prey capture and distribution of reef corals. *Hydrobiologia* 226:91-101
- Sebens KP, Vandersall K, Savina L, Graham K (1996) Zooplankton capture by two scleractinian corals, *Madracis mirabilis* and *Montastrea cavernosa*, in a field enclosure *Marine Biology* 127:303-317
- Sebens KP, Witting J, Helmuth B (1997) Effects of water flow and branch spacing on particle capture by the reef coral *Madracis mirabilis* (Duchassaing and Michelotti). *Journal of Experimental Marine Biology and Ecology* 211:1-28
- Shashar N, Cohen Y, Loya Y (1993) Extreme diel fluxes of oxygen in diffusive boundary layers surrounding stony corals. *Biological Bulletin* 185:455-461
- Sheppard C (2009) Large temperature plunges recorded by data loggers at different depths on an Indian Ocean atoll: comparison with satellite data and relevance to coral refuges. *Coral Reefs* 28:399-403
- Skirving W, Guinotte J (2001) The sea surface temperature story on the Great Barrier Reef during the coral bleaching event of 1998. In: Wolanski E (ed) *Oceanographic processes of coral reefs: physical and biological links in the Great Barrier Reef*. CRC Press LLC, p 301-310
- Smith PE, Counts RC, Clutter RI (1968) Changes in filtering efficiency of plankton nets due to clogging under tow. *ICES - Journal of Marine Science* 32:232-248
- Sorokin YI (1973) On the feeding of some scleractinian corals with bacteria and dissolved organic matter. *Limnology and Oceanography* 18:380-385
- Strickland JDH, Parsons TR (1972) A practical handbook of seawater analysis, Vol. *Bulletin of Fisheries Research Board of Canada* 167
- Swart PK, Saied A, Lamb K (2005) Temporal and spatial variation in the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of coral tissue and zooxanthellae in *Montastrea faveolata* collected from the Florida reef tract. *Limnology and Oceanography* 50:1049-1058
- Szmant A (2002) Nutrient enrichment on coral reefs: is it a major cause of coral reef decline? *Estuaries* 25:743-766
- Szmant A, Gassman NJ (1990) The effects of prolonged "bleaching" on the tissue biomass and reproduction of the reef coral *Montastrea annularis*. *Coral Reefs* 8:217-224
- Treignier C, Grover R, Ferrier-Pagès C, Tolosa I (2008) Effect of light and feeding on the fatty acid and sterol composition of zooxanthellae and host tissue isolated from the scleractinian coral *Turbinaria reniformis*. *Limnology and Oceanography* 53:2702-2710

- Vlasenko V, Alpers W (2005) Generation of secondary internal waves by the interaction of an internal solitary wave with an underwater bank. *Journal of Geophysical Research* 110:doi:10.1029/2004JC002467
- Vlasenko V, Hutter K (2002) Numerical experiments on the breaking of solitary internal waves over a slope-shelf topography. *Journal of Physical Oceanography* 32:1779-1793
- Vlasenko V, Stashchuk N (2007) Three-dimensional shoaling of large-amplitude internal waves. *Journal of Geophysical Research* 112:doi:10.1029/2007JC004107
- Wellington GM (1982) An experimental analysis of the effects of light and zooplankton on coral zonation. *Oecologia* 52:311-320
- Witman JD, Leichter JJ, Genovese S, J., Brooks DA (1993) Pulsed phytoplankton supply to the rocky subtidal zone: Influence of internal waves. *Proceedings of the National Academy of Sciences* 90:1686-1690
- Yahel R, Yahel G, Genin A (2005) Near- bottom depletion of zooplankton over coral reefs: I: diurnal dynamics and size distribution. *Coral Reefs* 24:75-85
- Yonge CM (1930) Studies on the physiology of corals. I. Feeding mechanisms and food. *Scientific Reports on the Great Barrier Reef expedition 1928-29* 1:1-57

Chapter 4

Carbonate accretion, bioerosion and growth of the scleractinian coral *Porites lutea* in response to Large Amplitude Internal Waves

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Abstract

The Similan Islands (Thailand) in the Andaman Sea are subjected to Large Amplitude Internal Waves (LAIW). Two-year temperature recordings document their year-round occurrence with highest activity-periods at the end of the NE monsoon (January to April) and at the end of the SW monsoon (October to November). The deep western (*W*) slopes of the nine islands are most heavily affected with highly frequent (several events per hour) and severe temperature drops of up to 10 °C, whereas the E sides are protected. Cooling, expressed as degree days cooling (°C d) below the depth specific daily modal temperature increase from -33.7 °C d in east (*E*) shallow (7 m) to -152.0 °C d in *W* deep (20 m). Two consecutive transplant experiments (one yr duration each) with living coral nubbins of the massive coral *Porites lutea* were carried out to assess coral growth rates between the LAIW-exposed *W* and sheltered *E* island sides. Two bio-fouling experiments (12 and 21 months duration) with carbonate blocks cut out of *P. lutea* skeletons were conducted to explore the carbonate bioaccretion and bioerosion on both sides of the islands. Coral growth and bioerosion were lowest at the site of highest LAIW-impact in *W* deep and highest within the dense coral reef of the sheltered *E* shallow. Bioaccretion rates were negligible compared to bioerosion. A carbonate budget calculated for *E* and *W* partially reflected the existing reef and coral distributions and indicated that carbonate accretion by reduced coral growth and carbonate erosion by alike reduced grazing and boring organisms are balanced but only barely positive under highly variable LAIW conditions in *W* deep. However the findings do not satisfactorily explain the large differences in reef development especially between *W* shallow and *E* Similans, suggesting that other factors (e.g. differential rates of early juvenile mortality or surface wave impact) may play a larger role.

Key words

Porites lutea – coral growth – bioaccretion – bioerosion – Large Amplitude Internal Waves – benthic-pelagic coupling – Similan islands – Andaman Sea

Introduction

The primary framework of coral reefs is built by the *in situ* deposition of CaCO₃ in coral skeletons (Goreau 1963, Bak 1976). However the constructive or destructive influences of other organisms, e.g. calcareous algae or boring sponges, play important roles (Scoffin et al.

1980, Hutchings 1986, McClanahan 1994, Glynn 1997, Tribollet & Golubic 2005), modifying the composition of coral reef communities (Glynn 1997, van Woesik et al. 1999), and the skeletal composition of the coral colonies (e.g. Davies & Hutchings 1983, Sammarco & Risk 1990, Osorno et al. 2005). Various processes of construction and destruction of carbonate occur simultaneously with the coral skeleton growth itself all of which are in a permanent dynamic equilibrium determining the carbonate balance in the reef. As long as a coral reef community exists within a stable and undisturbed environment with clear, nutrient poor, tropical waters, it is able to maintain a sustainable system in which carbonate accretion exceeds erosion and the reef carbonate framework grows (Scoffin et al. 1980, Davies & Hutchings 1983, Hutchings 1986, Glynn 1997). This carbonate balance can get destabilized easily to the advantage of eroding organisms as soon as the environment changes permanently to for example consistently higher nutrient loads and sedimentation (Hallock 1988, Montaggioni et al. 1993, Edinger et al. 2000, Pari et al. 1998, Pari et al. 2002, Carriero-Silva et al. 2005) or is afflicted by long-term disturbances such as recurring El Niño events or storms with high wave energy (Glynn & Colgan 1992, Riegl 2001). But little is known so far about the influence of episodic notorious short-term disturbances, such as internal waves, on coral skeleton growth and on carbonate precipitation and bioerosion on dead coral skeleton.

The Andaman Sea is characterized by two major climatic and oceanographic features: the south-east (SE) monsoon from May to October (Dunne & Brown 1996, Wu & Zhang 1998) with intense rainfall and heavy swell, and the year-round occurrence of Large Amplitude Internal Waves (LAIW) (Perry & Schimke 1965, Osborne & Burch 1980, Jackson 2004). LAIW are created as packets of solitary waves of depression by tidal fluctuations along the Andaman-Nicobar island arc and northwest of Sumatra (Alpers et al. 1997, Jackson 2004). They travel eastward through the Andaman basin with speeds of 2 m s^{-1} (Osborne & Burch 1980), reaching amplitudes of more than 80 m (Perry & Schimke 1965). When they reach the shelf, LAIW transform into waves of elevation interacting with the bottom, which results in resuspension of sediments (Moum et al. 2007), and mixing of deep waters to shallow areas (Vlasenko & Hutter 2002, Vlasenko & Stashchuk 2007), which are cold, nutrient-rich, oxygen-poor and likely also low in aragonite saturation state.

The Similan island group is located near the 90 m isobath where most of the mixing is believed to take place (Jackson 2004), off the Andaman Sea coast of Thailand. Although measurements are so far lacking, satellite images and modelling results suggest the Similan islands are within the direct impact area of Andaman Sea LAIW (Jackson 2004, Vlasenko & Stachuk 2007). The island chain features an unusual coral reef distribution: Monitoring studies (Chansang et al. 1999, Phongsuwan et al. 2008) and satellite images

(www.reefbase.org/gis_maps) suggest that reef development is restricted to the sheltered eastern island sides, whereas the windward (or exposed) western sides appear to lack any actual reef formations. This is in contrast to most other barriers or islands where reef growth is most developed at the ocean facing windward sides (Veron 2000), even in the storm areas of the open tropical Pacific (Spalding et al. 2001). We therefore suggest that LAIW may play an important role in explaining this unusual reef development at the western island sides: the cumulative effects of low temperature, low aragonite saturation state and elevated nutrient concentrations in the upwelled water may undermine reef development by both, depressing the growth of calcifying organisms and enhancing the development of bioeroding organisms.

The massive coral *Porites lutea* (Milne Edwards & Haime 1851) is one of the most abundant species along the Andaman Sea coast of Thailand (Scoffin et al. 1992, Yeemin et al. 2006, Tanzil et al. 2009). It is also a coral of choice for numerous physiological and ecological investigations in the Andaman Sea (Brown et al. 1986, Scoffin et al. 1992, Allison et al. 1996) and elsewhere (e.g. Harriott 1983, Moberg et al. 1997, Titlyanov et al. 2007), because of its robustness to experimental handling and high commonness in most South-East Asian coral reefs (Veron 2000). Several studies on bioerosion have been using the coral skeleton of *Porites lutea* as experimental substrate and found it to be a very suitable material for this purpose (Sammarco & Risk 1990, Pari et al. 1998, Osorno et al. 2005, Tribollet & Golubic 2005).

The goal of this study was to assess the episodic impact of Large Amplitude Internal Waves (LAIW) on the carbonate production, erosion and accretion in coral reefs. *Porites lutea* was used as a model organism for carbonate production on the *organism* level (bioerosion of healthy living corals considered negligible compared to growth). Blocks of dead coral skeleton were used as a surrogate for erosion and accretion of carbonate on the *system* level (organism growth of corals only part of the whole) due to the combined action of bioeroding and CaCO₃ precipitating organisms.

We hypothesise that (1) the W and E sides of the Similan Islands are exposed to differential impacts of LAIW, and that the deep slopes are more strongly affected than the shallow areas. Given any significant differences in LAIW impact, we further postulate (2) reduced carbonate growth due to the negative influence of cold temperatures (Coles & Fadlallah 1991), low pH, i.e. low aragonite saturation state (Marubini & Atkinson 1999, Marubini et al. 2001, Schneider & Erez 2006), and enhanced nutrient concentrations (Ferrier-Pagès et al. 2000, 2001); (3) enhanced internal bioerosion due to nutrient enhanced boring filter-feeders (Chazottes et al. 2002, Ward-Paige et al. 2005), and (4) reduced external bioerosion due to reduced framework and hence reduced excavating herbivore shelter in the

LAIW-impacted sites. The aragonite-precipitating members of the fouling communities may on the one hand benefit from LAIW-upwelling, but also suffer from reduced CaCO_3 precipitation rates.

Material & methods

The general approach was to measure near-bottom temperature at multiple locations along the Similan island chain in conjunction with two consecutive transplant experiments with living coral nubbins and a succession experiment with dead skeleton blocks of *P. lutea* to assess coral growth, bioaccretion, and bioerosion rates in LAIW-exposed W and sheltered E island slopes. Therefore coral nubbins and dead skeleton blocks were prior collected at LAIW protected sites to be thereupon transplanted to presumably differentially LAIW-impacted exposure sites (detailed description below).

Study site

The study was conducted at the Similan Islands in the Andaman Sea, Thailand (between $8^{\circ}40'40.12''\text{N}$, $97^{\circ}38'54.70''\text{E}$ and $8^{\circ}28'45.92''\text{N}$, $97^{\circ}38'54.08''\text{E}$, Fig 1) from February 2007 to November 2008 in depths of 7 and 20 m at 5 sites in the west (W) and 5 sites vis-à-vis to their western counterparts along the east (E) sides of the islands.

Temperature record

Benthic temperature recorders (TidbiT v2, Onset computers; resolution 0.2°C within a range of 0 to 50°C) were deployed at each study site attached to the experimental setups about 20 cm above the reef substrate recording temperature values at 6 min intervals. Monthly and yearly values of the temperature modal, minimum, and maximum were calculated for all sites and depths recorded. The calculation of degree days cooling and warming ($^{\circ}\text{C d}$), respectively, 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 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 one-day window of elements of the time-series (y) and smoothing the output by a one-day moving average, yielding the residuals time series (ry). Degree days cooling (DDC) was calculated by replacing the positive values in the residuals time series (ry) with zeros, yielding ryc, summing the values [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. $F = \text{spy}/\text{sp}(\text{ry})$]. The corresponding equation is:

$$DDC = \frac{\text{sum}(ry) * F}{\text{spd}} \quad (1)$$

Degree days warming (DDW) was calculated in the same way, only by replacing the negative values. Due to scattered failures of single loggers at different sites, the calculation of the degree days cooling and warming was confined to a 20 week period (February 2007 to July 2007) when data were available from all sites and depths.

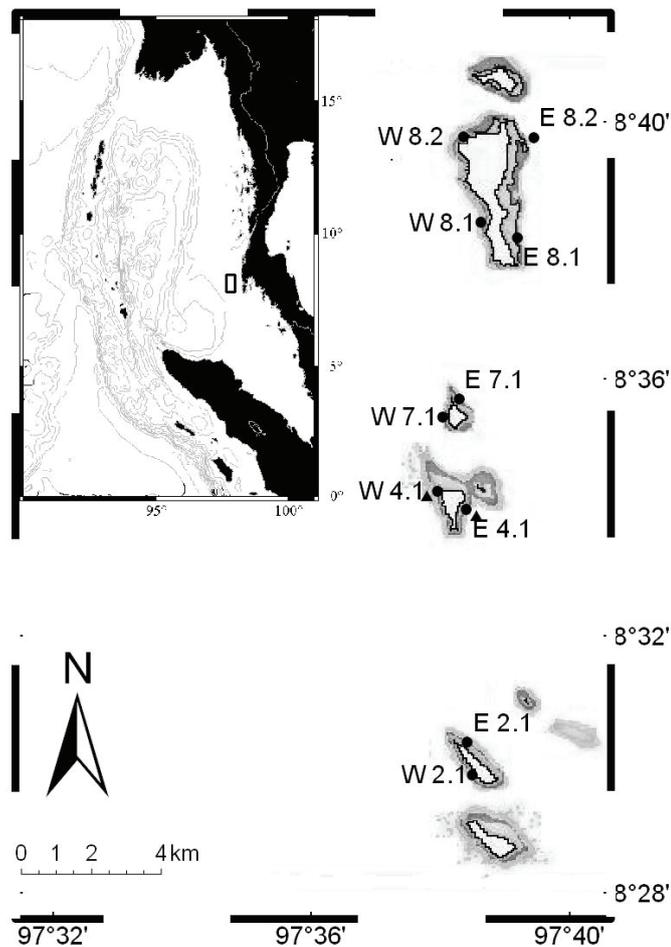


Figure 1 Locations of study sites along Similan Islands, Andaman Sea, Thailand. Five sites in W and E, respectively, for temperature record and growth rate experiments (●). W and E site for bioerosion experiment were located at central island Koh Miang (W4.1, E4.1) (▲). (Figure modified after Jackson (2004)).

Coral growth rate

Growth rates of *Porites lutea* were investigated in two transplant experiments of 12 months (Feb 2007 to Feb 2008 and Nov 2007 and Nov 2008). Coral nubbins were collected from ten colonies at a LAIW protected common site in the south east of the largest central island (Koh Similan, 8°38'21.43"N 97°38'59.73"E) in about 7 m depth along the shallow reef

slope and held in a laboratory flow-through reef water system for a maximum of 1 d for measurements prior to transplantation back to the reef slope. The buoyant weight technique according to Davies (1989) was applied to determinate the nubbins' wet weight with a high precision microbalance (Sartorius ME-235S, suppl. Fig 1) before attaching them to individual numbered holders using fast drying concrete (after Phongsuwan, pers. communication, suppl. Fig 2) and reweighing them. The wet weight of each nubbin and of the nubbin with its transplant holder and concrete were recorded, and nubbins were randomly assigned to the different exposure sites. The skeletal density of *P. lutea* was determined using the method described by Davies (1989) to 2.31 g cm^{-3} and used for calculating the dry weight of each nubbin. Initial sizes of the coral nubbins were approximately 3 to 5 cm in diameter, ranging in mass from 3.46 to 31.12 g, with a mean of 15.76 g. An equivalent range of nubbin sizes was assigned to each exposure site. For each experiment, 10 individual nubbins were transplanted to each depth per exposure site (5*10 nubbins, i.e. 50 nubbins per experimental side and depth: W 7 m and 20 m and E 7 m and 20 m). The nubbins on their individual holders were attached to racks made of acrylic glass (suppl. Fig 2) which were fixed on dead coral substrate within 1 to 4 m of the temperature recorder at each depth per site. The first experiment was started between 20 and 24 Feb 2007 and terminated between 22 and 27 Feb 2008, and the second experiment was started between 22 and 27 Nov 2007 and terminated between 11 and 14 Nov 2008, when the corals were retrieved and returned to the laboratory. Epiphytes growing on the transplant holders were removed, and the wet weights of all corals that were alive at the end of the experiment were measured with the holders. The corals and holders were then dried at $60 \text{ }^{\circ}\text{C}$ for 24 h and reweighed. The constant weight of each holder was subtracted to yield a change in weight of the corals. Growth rate (g yr^{-1}) was calculated as change in mass over the 1 year duration of both experiments, normalized to the initial weight of every fragment and displayed as $\% \text{ yr}^{-1}$.

Rates of bioerosion and bioaccretion

For the investigation of bioerosion and bioaccretion rates a total of 72 rectangular blocks of approximately $8 \times 8 \times 1.5 \text{ cm}^3$ were cut out of the interior unscathed skeleton part of a dead *P. lutea* colony (suppl. Fig 4) collected from the fringing reef close to Phuket Marine Biological Centre at the southern tip of Phuket peninsula ($7^{\circ}47'58.76''\text{N}$, $98^{\circ}24'31.14''\text{E}$, Fig.1). The blocks were soaked in running fresh water, dried, weighed to the closest 0.01 g and the dimensions measured to the closest 0.1 cm. At each time 6 of these coral blocks were attached in a distance of 15 cm to each other to a PVC tube by stainless steel screws passing through their centres ensuring a constant distance of 2 cm of each block to the tube (suppl. Fig 3). Three tubes per research depth in a distance of 1 to 10 m to the temperature

recorder were attached directly to dead coral substrate at the reef slope on the W and E side of Similan Island Koh Miang (Fig 1). The experiment started mid of March 2007 followed by two recollection events of nine replicate samples from each side and depth (3 blocks per tube) after 12 months (mid of March 2008) and 21 months (mid of November 2008), respectively. The samples were chosen randomly before diving to avoid personal bias. After recollection the blocks were bleached to remove any organic material, rinsed in fresh water, dried and then weighed as above. Care was taken not to loose any material during handling. Values were expressed as $\text{kg m}^{-2} \text{yr}^{-1}$. Carbonate accretion was estimated from precise geometric measurements under a stereomicroscope of the skeletal volumes (cm^3) of all individuals grown on each block (suppl. Fig 5). Tubes of serpulids were constituted as cylinder with continuously reducing diameter and the tube wall accounting for 40 % of the tube volume (Hassan 1997). Bivalves were measured as ellipse and balanids as truncated cone with accordingly measured shell thickness. The corals' geometry was determined in detail according to their massive (hemisphere) or branching (cylinder) habit. Skeletal densities of serpulids, balanids and bivalves were assessed as an approximate density of 2.7 g cm^{-3} (Hassan 1997), approximate corals' density as 2.6 g cm^{-3} (after Davies 1989). Total bioaccretion was determined as the sum of bioaccretion of serpulids, bivalves, balanids and corals and standardised to $\text{kg m}^{-2} \text{yr}^{-1}$.

Statistical analysis

For statistical analyses the software Statistica v 9 was used. Data were tested for normal distribution and homogeneity of variances with Kolmogorov-Smirnov and Levene's test, and square root transformed. The effect of LAIW-exposure (exposed W, sheltered E) and depth (7 and 20 m) on rates of coral growth and bioerosion was analyzed using analysis of covariance (ANCOVA), with side and depth as the treatment factors and the initial weight of coral nubbins and dead skeleton blocks as the respective covariate. Posthoc, pair wise comparisons of the adjusted group means were performed via Tukey HSD-tests. Possible site or rack effects between coral fragments exposed at the same site on the same rack were considered by implicating the factor site (named: island) as random factor into the analysis. This factor could be excluded as statistically significant (see results) and data were pooled for graphical presentation. Bioaccretion data did not achieve normal distribution of the residuals and were therefore analysed with a non-parametric Kruskal-Wallis ANOVA and median test followed by multiple comparisons of mean ranks in order to measure differences of accretion rates between side (W versus E) and depth (7 versus 20 m). If not stated otherwise data are always displayed as mean (\pm SE).

Results

Temperature record

Periods of high frequency deviation from the seasonal modal value were evident throughout the year with decreasing intensity between island faces and depths showing a declining LAIW-impact between $W\ 20\ m > W\ 7\ m > E\ 20\ m > E\ 7\ m$ (cf. Fig 2 as a representative example for all experimental sites).

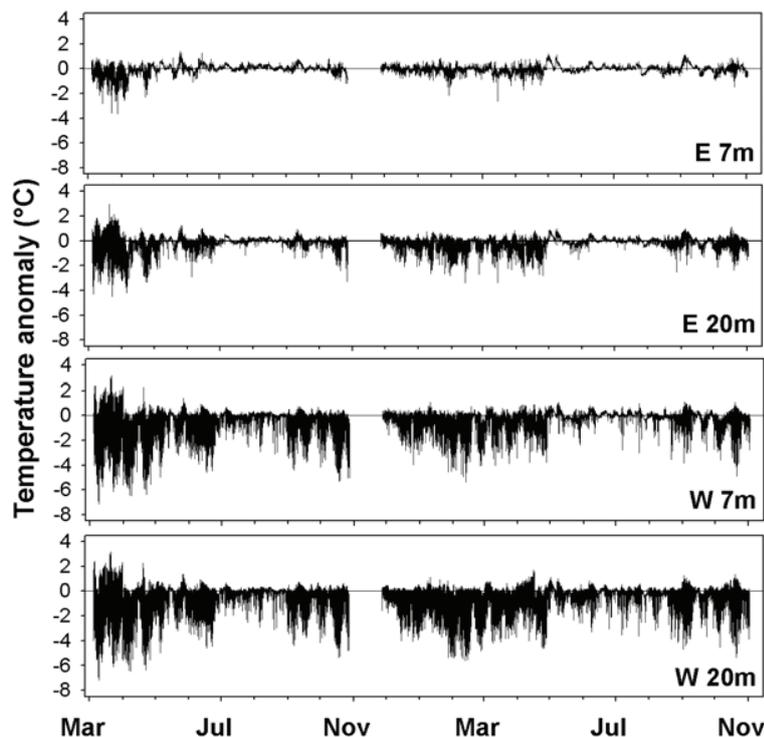


Figure 2 LAIW induced temperature anomalies (negative deviations of weekly modal value of temperature) at Similan Island Koh Miang (study sites: E 4.1, W 4.1) for period March 2007 to November 2008. Individual data points recorded at 6 min sampling intervals.

Periodograms showed a typical red noise pattern due to the overall high variability and non-stationary nature of the signal, especially at high LAIW-impact sites, masking the detection of peaks in any of the frequency bands (data not shown). Fig 3 clearly shows that the high variability in the high frequency region was primarily composed of episodes of very rapid cooling (within minutes) relative to the site specific modal value, with up to 10 °C during extreme LAIW-events in W compared to < 5 °C in sheltered E (Fig 3). The high-frequency variance was especially predominant in February through March and October through November in both years (Fig 2). The pattern of high and low variability periods and order of magnitude in amplitude in the temperature time series was consistent among all sites of the same depth and orientation (Fig 3). Summaries of the temperature patterns comparing the

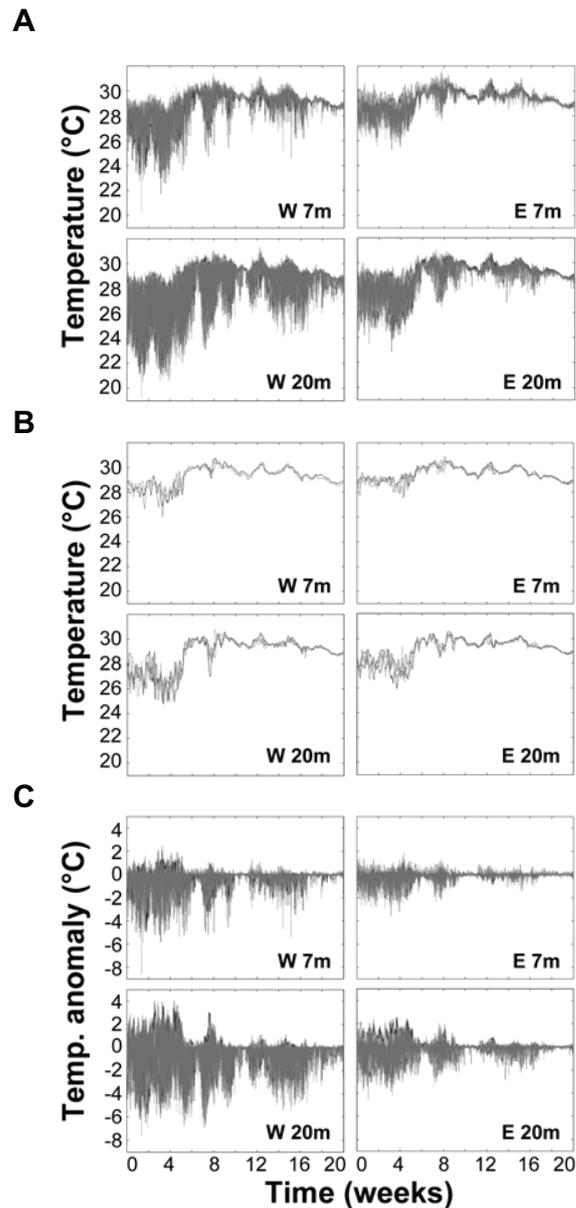
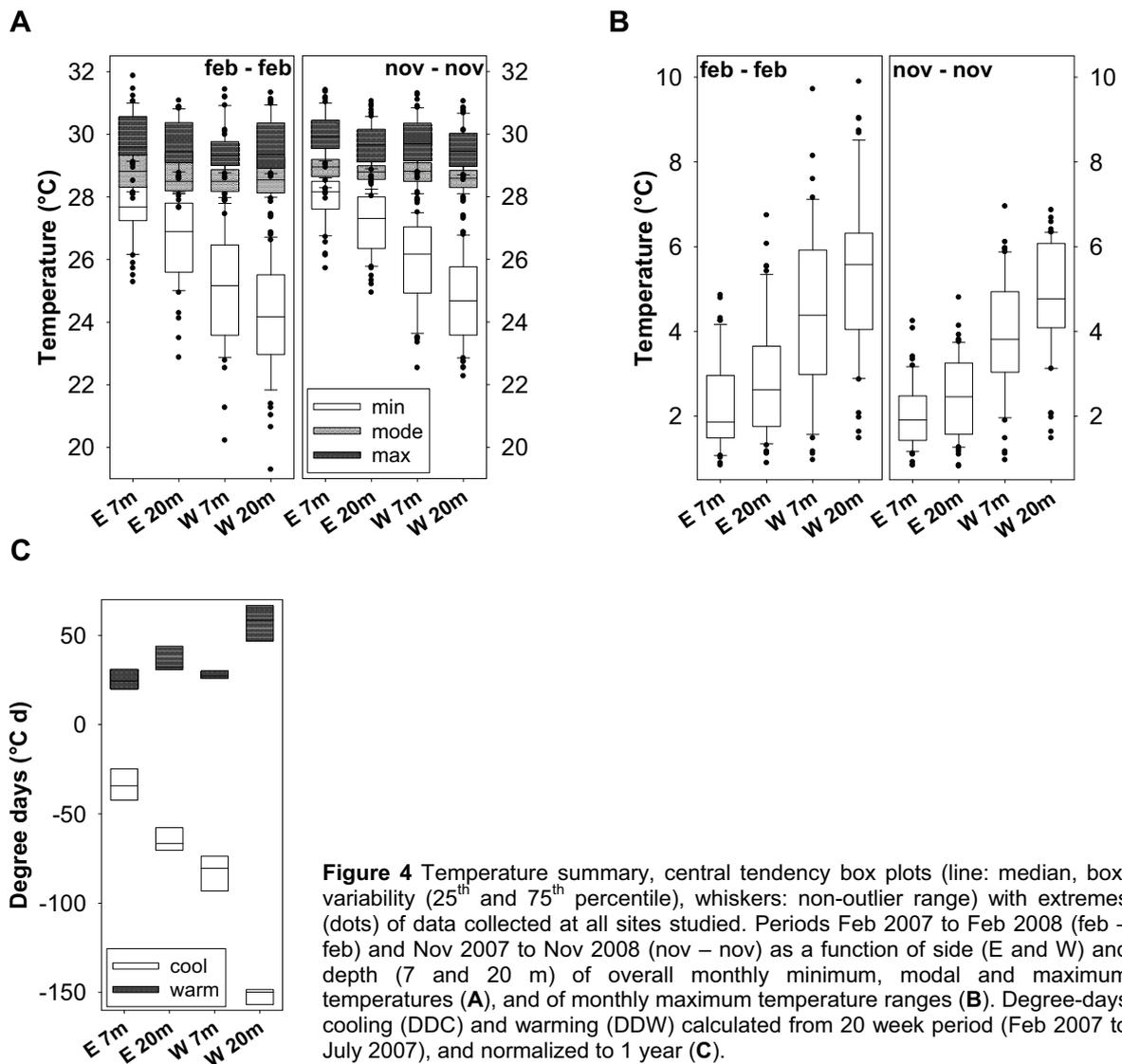


Figure 3 Temperature record of all sites studied at LAIW-exposed W and sheltered E in two depths (7 and 20 m) for period of 20 weeks (February 2007 to July 2007): Continuous temperature record of raw data (A), daily running mode (B), and deviations from daily running mode (positive and negative anomalies) (C).

study periods in 2007 and 2008 as a function of exposure side (LAIW-exposed W vs. sheltered E) and depth (7 and 20 m) are shown in Fig 4 A and B. Monthly modal and maximum values were consistent across the entire study period irrespective of side and depth (modal values: $\Delta T < 3.6$ °C, maximum values: $\Delta T < 3.0$ °C). Monthly minima showed decreasing values with LAIW-exposure and considerably lower values in the period of Feb 2007 to Feb 2008 compared to the period Nov 2007 to Nov 2008. The maximum temperature ranges increased with depth and exposure, and again were more pronounced in the first half of the study period (February 2007 to February 2008). The cool degree days below the site

averaged daily running mode temperature increased with depth and LAIW-exposure revealing in W 20 m double the value of W 7 m and fivefold of E 7 m (Fig 4 C). The warm degree days above the site averaged daily mode were highest in W (Fig 4 C) due to a descending daily mode during intensive LAIW-impact which led to an increase in the positive anomalies (Fig 3).



Mortality rate of coral nubbins

Mortality of coral nubbins was high in both transplant experiments with rates below 50 % only in E after the first, and exceeding 90 % in W after the second growth experiment (Fig 5 B).

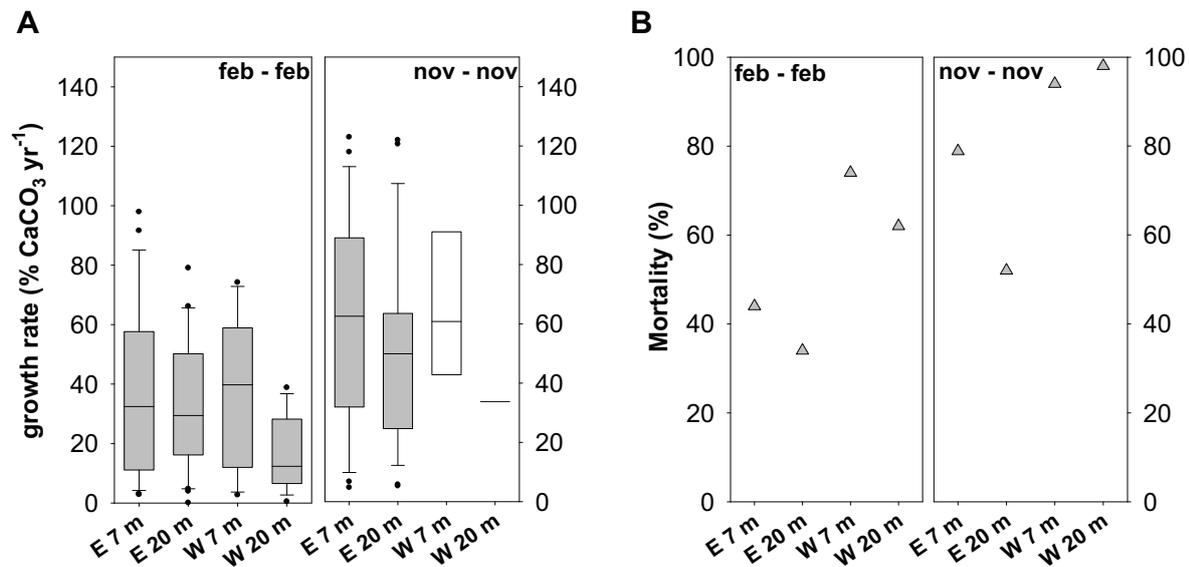


Figure 5 Comparison of coral growth rates of *Porites lutea* nubbins transplanted from LAIW sheltered E 7 m to 7 and 20 m depth at E and W sides of Similan Islands (Central tendency box plots (line: median, box: variability 25th and 75th percentile, whiskers: non-outlier range, with extremes: dots) (A), and mortality of coral nubbins out of $n = 50$ transplanted individuals per side (E and W) and depth (7 and 20 m) (B). Left panels show experimental period from Feb 2007 to Feb 2008 (feb – feb) and right panels from Nov 2007 to Nov 2008 (nov – nov) respectively. Note: white marked plot in (A) right panel for W 7 m and straight line for W 20 m comprise only data from 4 and 1 survived coral nubbins, respectively. Data shown for sake of completeness but not involved in statistical analysis.

Coral growth rate

ANCOVA results for *Porites lutea* growth rates revealed significant effects of side and depth for the first exposure period (Feb 2007 to Feb 2008, $p < 0.038$, Table 1 A). In the second growth experiment (Nov 2007 to Nov 2008), too few nubbins survived in W for statistical analysis (only 4 in W 7 m and 1 in W 20 m), and no differences of growth rates were detected between depths in E (Table 1 B, Fig 5). As the initial nubbins weights of both growth experiments were equally distributed across the exposure treatments (side and depth, see Student's t-tests, suppl. Table 1) mean growth rates were normalized to their initial weights and are shown in units of % yr⁻¹ in Fig 5.

Positive growth rates were measured at all sites with very similar mean growth in E 7 m (36.65 ± 0.19 %), E 20 m (36.48 ± 0.18 %) and W 7 m (36.17 ± 0.38 %), and clearly reduced growth rates in W 20 m (16.33 ± 0.19 %) in the period Feb 2007 to Feb 2008 (Fig 5 A). Pair wise comparisons showed that the growth rates at W 20 m were significantly slower than at E 20 m and 7 m (Tukey HSD, Table 1 A). Fig 5 B shows the growth results for nubbins exposed from Nov 2007 to Nov 2008 with growth rates of W nubbins for the sake of completeness, as they were generated from only 4 (W 7 m) and 1 (W 20 m) nubbins respectively. Nubbins from E 7 m revealed significantly faster growth rates compared to eastern nubbins of the first

Table 1 Analysis of covariance (ANCOVA) for coral growth (data square-root-transformed) at E and W of Similan Islands. Side (E and W) and depth (7 and 20 m) were used as treatment factors, and the initial weight of coral nubbins as covariate; the factor site (named: islands) was implicated as random factor; posthoc, pair wise comparisons of the adjusted group means were performed via Tukey HSD-tests. (df = degrees of freedom; MS = means square; F = F-value; p = probability level, significance levels are *0.05 > P ≥ 0.01, **0.01 > P ≥ 0.001, ***P < 0.001). Results for experimental period from Feb 2007 to Feb 2008 (A), and from Nov 2007 to Nov 2008 (B).

A Feb 2007 - Feb 2008				
Factor	df	MS	F	p
initial weight	1	3.296	3.829	< 0.05*
side & depth	3	4.172	1.192	< 0.001***
island	4	0.684	0.197	0.932
side & depth*island	7	3.614	4.120	0.379
Error	76	0.861		
Tukey HSD, significantly different, pairwise comparisons:				p
W 20 m < E 20 m				< 0.003**
W 20 m < E 7 m				< 0.002**
B Nov 2007 - Nov 2008				
Factor	df	MS	F	p
initial weight	1	4.805	4.276	< 0.05*
side & depth	1	1.108	0.819	0.427
island	3	4.089	2.996	0.196
side & depth*island	3	1.365	1.215	0.318
Error	37	1.124		
Tukey HSD, no significant results detected				

exposure period from Feb 2007 to Feb 2008 (Table 2) with 50.10 ± 6.51 % in E 20 m and 61.53 ± 7.42 % in E 7 m.

Rates of bioerosion

ANCOVA results for bioerosion rates revealed significant effects of side and depth for both exposure periods (net bioerosion B_{net} , Table 3). Irrespective of exposure time bioerosion was highest in E 7 m (Tukey HSD, Table 3 A and B, and Fig 6). After 12 months exposure carbonate erosion revealed 90 % higher rates in E 7 m than in E 20 m (-3.67 ± 0.56 kg $\text{CaCO}_3 \text{ m}^{-2}$ in 7 m compared to -0.39 ± 0.19 kg $\text{CaCO}_3 \text{ m}^{-2}$ in 20 m), and over 100 % higher rates than in W 7 m and 20 m, where erosion was close to zero (0.07 ± 0.36 kg $\text{CaCO}_3 \text{ yr}^{-1}$ in W 7 m and -0.01 ± 0.12 kg $\text{CaCO}_3 \text{ yr}^{-1}$ in W 20 m). After 21 months exposure erosion rates were clearly increased at all sites compared to the 12 months period with 59 % higher rates in E 7 m (-8.97 ± 0.81 kg $\text{CaCO}_3 \text{ m}^{-2}$), 90 % in E 20 m (-3.94 ± 1.01 kg $\text{CaCO}_3 \text{ m}^{-2}$) and almost 100 % higher rates in W 7 m and 20 m (-5.65 ± 1.14 kg $\text{CaCO}_3 \text{ m}^{-2}$ and -1.63 ± 0.38 kg

Table 2 Analysis of covariance (ANCOVA) for coral growth (data square-root-transformed) at E of Similan Islands. Experimental period (Feb 2007 to Feb 2008: feb – feb and Nov 2007 to Nov 2008: nov – nov; named: year) and depth (7 and 20 m) were used as treatment factors, and the initial weight of the coral nubbins as covariate; the factor site (named: island) was implicated as random factor; posthoc, pair wise comparisons of the adjusted group means were performed via Tukey HSD-tests. (df = degrees of freedom; MS = means square; F = F-value; p = probability level, significance levels are *0.05 > P ≥ 0.01, **0.01 > P ≥ 0.001, ***P < 0.001).

Factor	df	MS	F	p
initial weight	1	9.114	8.169	< 0.005**
year & depth	3	2.751	0.935	0.004**
island	4	1.552	0.515	0.727
year & depth*island	10	3.206	2.874	0.457
Error	87	1.116		

Tukey HSD, significantly different, pairwise comparisons:				p
nov - nov 7 m	>	feb - feb 20 m		< 0.001***
nov - nov 7 m	>	feb - feb 7 m		< 0.002**

CaCO₃ m⁻², respectively). Thereby again E 7 m revealed highest erosion rates (56 % higher than in E 20 m and 81 % than in W 20 m, respectively), followed by W 7 m with significantly higher erosion compared to W 20 m (71 % and Tukey HSD, Table 3 B). Compared to the total erosion which is corrected for bioaccretion, the net carbonate change (weight difference between start and end weight) revealed no significantly different values irrespective of exposure time except for W 20 m after 12 months (net erosion versus total erosion: Student's t-test: p < 0.01, suppl. Table 2 and Fig 6). After the first 12 months of exposure the negligible

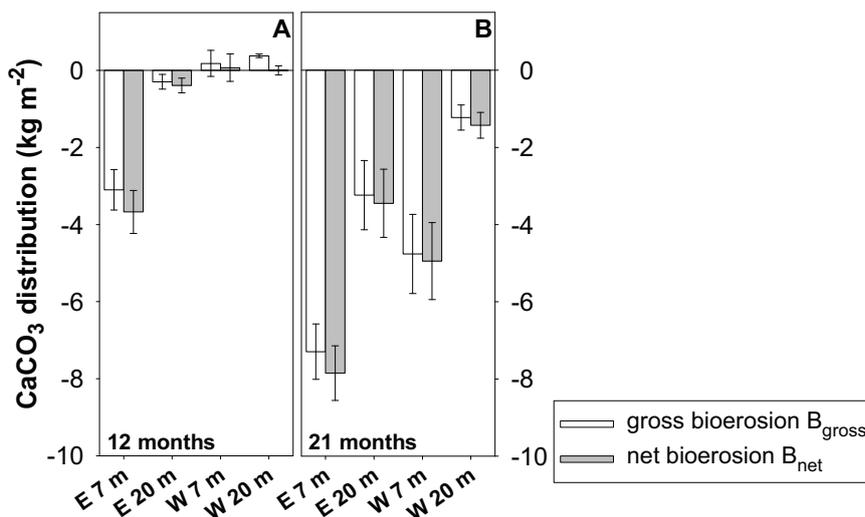


Figure 6 Comparison of the gross bioerosion on dead skeletal substrates and net bioerosion (corrected for bioaccretion) at E and W side of Similan Island Koh Miang. Error bars: ± 1 SE of mean. Results from 12 months exposure (Feb 2007 to Feb 2008) (A), and 21 months exposure (Feb 2007 to Nov 2008) (B). Values are replicates of 9 samples.

erosion rates in W led to comparatively high accretion values of 100 % in W 20 m and 60 % in W 7 m. By contrast in all other cases the differences between net carbonate change and total bioerosion stayed under 25 % (24.3 % in E 20 m after 12 months), in most cases around 4 – 7 % (in E 7 and 20 m and W 7 m after 21 months exposure, Fig 6).

Table 3 Analysis of covariance (ANCOVA) for net bioerosion B_{net} (data square-root-transformed) at E and W of Similan Island Koh Miang. Side (E and W) and depth (7 and 20 m) were used as treatment factors, and the initial weight of the skeletal substrates as covariate; posthoc, pair wise comparisons of the adjusted group means were performed via Tukey HSD-tests. (df = degrees of freedom; MS = means square; F = F-value; p = probability level, significance levels are *0.05 > P ≥ 0.01, **0.01 > P ≥ 0.001, ***P < 0.001). Results for experimental period from Feb 2007 to Feb 2008, 12 months (**A**), and from Feb 2007 to Nov 2008, 21 months (**B**).

A 12 months exposure					B 21 months exposure			
Factor	df	MS	F	p	df	MS	F	p
initial weight	1	19.498	91.636	< 0.001***	1	36.112	33.604	< 0.001***
side	1	5.901	27.732	< 0.001***	1	12.215	11.367	< 0.002**
depth	1	2.933	13.785	< 0.001***	1	20.267	18.859	< 0.001***
side*depth	1	3.794	17.830	< 0.001***	1	0.526	0.489	0.489
Error	31	0.213			31	1.075		

Tukey HSD, significantly different, pairwise comparisons:

E 7 m < E 20 m	< 0.001***	E 7 m < E 20 m	< 0.001***
E 7 m < W 7 m	< 0.001***	E 7 m < W 20 m	< 0.001***
E 7 m < W 20 m	< 0.001***	W 7 m < W 20 m	< 0.003**

Rates of bioaccretion

Kruskal Wallis ANOVA results for total bioaccretion revealed significant effects of side and depth for the first 12 months exposure (Feb 2007 to Feb 2008, p < 0.02, Table 4). Highest accretion rates were found in E 7 m (0.58 ± 0.35 kg CaCO₃ m⁻²) followed by W 20 m (0.38 ± 0.10 kg CaCO₃ m⁻²) (Fig 7). Pair wise comparisons showed that the accretion rates in E 7 m were significantly higher than in E 20 m and W 7 m. On the latter only 0.11 ± 0.04 kg CaCO₃ m⁻² and 0.10 ± 0.03 kg CaCO₃ m⁻² respectively had grown upon the experimental substrates. After 21 months the pattern of accretion between sides and depths was very similar to the first 12 months exposure (Fig 7), and not even the amount of accretion rates had changed detectably for statistical analysis (see suppl. Table 3). Corals were practically only found in E 7 m on the skeletal substrates were they provided the main contribution to the carbonate accretion with 64.4 % after 12 months and 61.3 % after 21 months exposure. Serpulids were more common and showed quite similar growth rates in W and E and both depths (Fig 7) with carbonate productions between 30.0 % (in E 20 m after 12 months exposure) an even 91.3 % (in W 7 m after 21 months exposure) of the in each case total bioaccretion. Bivalves revealed between zero accretion in E 7 m after 21 months and

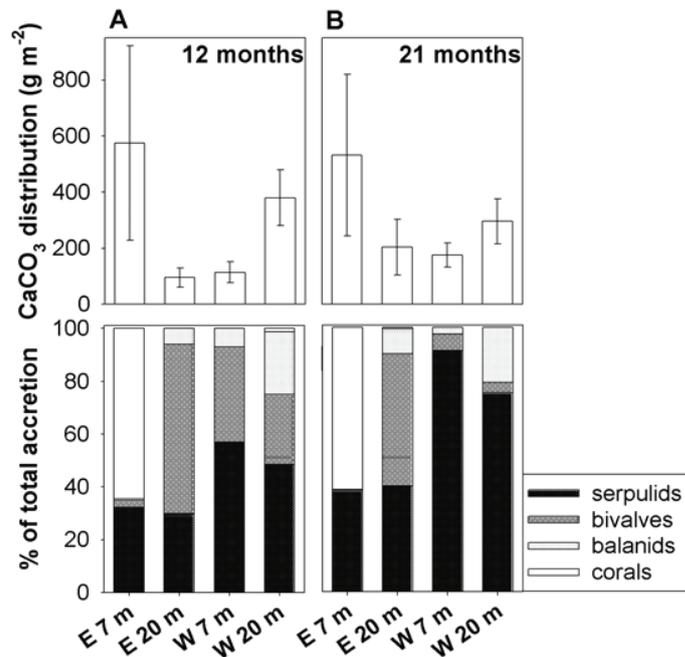


Figure 7 Comparison of total bioaccretion (upper panels) and bioaccretion by different groups of carbonate producers (lower panels, as fractions of total bioaccretion) on dead coral substrates at island Koh Miang. Error bars: ± 1 SE of mean. Results from 12 months exposure (Feb 2007 to Feb 2008) (A), and 21 months exposure (Feb 2007 to Nov 2008) (B). Values are replicates of 9 samples.

maximum accretion in W 20 m after 12 months and E 20 m after 21 months (0.1 ± 0.08 kg $\text{CaCO}_3 \text{ m}^{-2}$ in both cases). They contributed up to even 63.9 % of the total bioaccretion in E 20 m after 12 months exposure. Balanids showed significantly higher accretion rates in W 20 m after 12 months than at all other sites (pair wise comparisons: Table 4) but they achieved a comparatively minor carbonate production with a maximum contribution to the total accretion of 23.5 % in W 20 m after 12 months.

Discussion

Temperature variations

The temperature variations at the exposed W sides along Similan Islands are among the largest short-term variations so far reported in tropical reef areas (Sheppard 2009) and support our first hypothesis that LAIW are present in the Similan Islands and exert a differential effect on LAIW-exposed and LAIW-sheltered faces of the islands. Their frequency and severity exceeds by far variations which have been reported earlier for considerably deeper reef depths than 20 m (Leichter et al. 1996, 2003, Leichter & Genovese 2006). Although the Andaman Sea has been known for long to feature non-linear Large Amplitude Internal Waves (LAIW, or solitons) (Perry & Schimke 1965, Osborne & Burch 1980), this

study is one of the first to ascertain their presence in shallow reef areas and impact on coral growth, bioerosion and bioaccretion of CaCO₃. Although some temperature variations were also measured on the E side of the islands, the much larger oscillations along the W sides show that the ocean facing island slopes are most severely affected. The intense short-term variations during highest LAIW-activities after spring tides and during the late NE monsoon (February, March), alternate with lower-frequency variations (spring-neap tide, seasonal) (Fig 2), which is due to several factors: Tidal currents at the generation sites of LAIW vary with the lunar cycle (Pineda 1995), and the seasonal pycnocline varies in depth and strength, with the shallow pycnocline corresponding to strongest LAIW activity during the NE monsoon (Nielsen et al. 2004). According to the findings of Nielsen et al. (2004) the source depth of the coldest water reaching the reef (up to 10 °C below ambient) can be related to the 18 °C isotherm which is oscillating between 100 and 150 m depth in the Andaman Sea. Implicating the degree of turbulent mixing of the cold water masses above the thermocline (Vlasenko & Hutter 2002), the actual depth may be even much deeper.

We know from other studies that temperature co-varies with other physical and chemical parameters: the temperature drops are accompanied by comparable drops in oxygen concentrations and pH, which may decrease down to 12 % saturation and 0.6 units below ambient, respectively. Nutrient concentrations can increase to up to 12-fold for nitrate and nitrite, 5-fold for silicate and over 20-fold for phosphate, and current speeds increase to up to 6-fold (Schmidt et al. *subm.*). These environmental contrasts are reflected also in the reef development with complex, dense reef framework along the sheltered E sides and only

Table 4 Comparison of bioaccretion at E and W side of Similan Island Koh Miang. Non-parametric Kruskal-Wallis ANOVA and median test followed by multiple comparisons of mean ranks with side (E and W) and depth (7 and 20 m) as treatment factors. (p = probability level, significance levels are *0.05 > P ≥ 0.01, **0.01 > P ≥ 0.001, ***P < 0.001, n.s.: not significant). Results for experimental period from Feb 2007 to Feb 2008, 12 months (**A**), and from Feb 2007 to Nov 2008, 21 months (**B**).

A 12 months exposure						
significance levels		total bioaccretion	bioaccretion by			
			serpulids	bivalves	balanids	corals
Kruskal-Wallis test		< 0.015*	n.s.	n.s.	< 0.001***	< 0.02*
W 20 m	vs E 7 m	n.s.	n.s.	n.s.	< 0.018*	n.s.
W 20 m	vs E 20 m	< 0.033*	n.s.	n.s.	< 0.008**	n.s.
W 20 m	vs W 7 m	< 0.049*	n.s.	n.s.	< 0.022*	n.s.
B 21 months exposure						
Kruskal-Wallis test		n.s.	n.s.	n.s.	< 0.05*	< 0.05*

scattered communities of single coral colonies along the LAIW-exposed W (Schmidt et al. subm.).

Coral growth rates

The coral growth rates in our study support our second hypothesis: Growth rates of *Porites lutea* were significantly reduced in W deep whereas growth rates in W shallow and E were barely different (Fig 5 A, Table 1 A). This suggests that coral growth measured here does not only follow a simple pattern corresponding to light availability and depth (Falkowski et al. 1990, Yentsch et al. 2002) but is the result of a far more complex set of processes.

Temperature variations have been shown to have a delicate influence on calcification processes in corals (Al Horani 2005), and cold temperatures in particular can have clearly negative effects on coral health and survival (Coles & Fadlallah 1991). Several studies showed that cold water stress 6 to 10 °C below ambient conditions has a strongly negative influence on the sensitive association between coral host and endosymbiotic zooxanthellae (Gates et al. 1992). The cold water pulses in W 20 m frequently reach similar ranges of cold temperatures and might therefore be responsible for deleterious changes in the symbiosis of zooxanthellae and coral host which could result in reduced calcification rates (Gattuso et al. 1999, Furla et al. 2000).

Other studies demonstrated that corals grown under LAIW-influence revealed a high plasticity with respect to their primary production (Jantzen et al. in prep.) and energy status (Roder et al. subm.), yet obviously at the expense of their growth performance. Accordingly Jantzen et al. (in prep.) showed that area-specific photosynthetic rates of *Porites lutea* were similar in W and E Similan, due to the adaptation of W corals to lower light levels and higher nutrient concentrations with 40 % higher pigment concentrations. Thereby the lower light levels in deeper slope areas in W might even be advantageous to W corals alleviating damage to the photosynthetic apparatus during cold water stress (Jokiel & Coles 1977, Saxby et al. 2003). Roder et al. (accepted) demonstrated that the branching coral species *Pocillopora meandrina* reveals significantly higher biomass and protein content when exposed to LAIW, with a more intense heterotrophic performance and higher energy reserves, compared to sheltered corals. However these obvious metabolic adaptations of coral host and zooxanthellae to LAIW impact seem to be required for a general viability in W 20 m, but do not support skeletal growth.

Besides coral growth and calcification depend directly on the carbonate concentration in seawater (Schneider & Erez 2006, Marubini et al. 2008, Andersson et al. 2009, Kleypas & Yates 2009). Assuming that the drops in pH coming with deep LAIW waters (Schmidt et al. subm.) are related to an accordantly decreased aragonite saturation state and carbon ion

concentration, the frequently occurring pH values of 0.2 to 0.5 units below ambient would correspond to short-term conditions of 30 to 60 % decreased carbonate concentrations. This exceeds by far natural swings of pH which were reported to occasionally occur on a diurnal basis for coral reef waters (e.g. 7.9 – 8.1, Bates et al. 2001, Suzuki & Kawahata 2003). Corals maintain a high saturation state at the site of calcification, but at low pH this requires extra energy that they possibly do not readily divert from other energy demands (Cohen & Holcomb 2009). Therefore conditions as reported here for the Similan Islands should be highly obstructive for coral calcification and possibly even lead to dissolution processes of the coral skeleton (Schneider & Erez 2006, Andersson et al. 2009). Yet *P. lutea* revealed positive growth rates even at the sites of highest LAIW-impact in W deep, leading to the assumption that the short-termed, pulsed occurrence of LAIW-impacts possibly permits a time-delayed compensation of the periodic corrosive water conditions during the calcification process, as the uptake of carbon ions (potentially under normal pH conditions) and their incorporation into the skeleton (potentially during LAIW-impact) do not occur at the same time (Erez & Braun 2007). Or coral growth in LAIW-exposed sites is mainly restricted to the transition periods between high LAIW- and SW monsoon seasons, as during the latter, growth rates of *P. lutea* had been shown to be reduced due to the constantly higher turbidity and lower light regime caused by the strong swell (Scoffin et al. 1992).

The lack of a possible comparison between W growth rates of the first (February 2007 to February 2008) and second (November 2007 to November 2008) exposure period leaves the answer open, if the significantly higher growth of the actual control fragments in E 7 m during the second transplant experiment (Table 2) would have been supported by a similar pattern in W. The growth rates calculated from the few fragments survived in W after the second exposure period definitely indicate also extremely higher growth rates compared to the first period. But these data have to be treated with caution, of course. The differences in the temperature regime between the two study periods strongly indicate more gentle environmental conditions from November 2007 to November 2008 (Fig 4) with less variability due to comparatively attenuated LAIW-periods in 2008 compared to 2007 (February, March and October, November) (Fig 2) and could be a reason for the increased growth rates.

Mortality of coral nubbins and bioerosion

The mortality rate of *Porites lutea* nubbins was generally very high on both sides, E and W, but always higher in W where it even reached an almost complete extinction of nubbins during the second exposure period (Nov 2007 to Nov 2008, Fig 5 B). This was obviously caused by grazing damage (bite marks) and the subsequent overgrowth by filamentous algal turf. Turf algae are generally not more successful competitors in more

nutrient rich conditions than corals as long as the corals are healthy and undamaged, yet a damaged coral skeleton triggers an immediate takeover of space by turf algae and can then be overgrown (McCook 2001, Titlyanov et al. 2007). Already little grazing can cause enough damage to stimulate algal growth (McCook 2001) and start the degenerating process of coral tissue at the algal interface (Titlyanov et al. 2007). Due to LAIW-conditions in W the coral nubbins there might not have been strong enough to effectively detain the take-over by the algae (McCook 2001) as it has been described for corals elsewhere (Bak et al. 1977) and might have been done with more success by E nubbins.

The extreme mortality induced by grazing in W stands in contrast to the findings of the bioerosion experiments and to our forth hypothesis, because the significantly highest bioerosion or rather grazing rates on dead skeleton blocks were found in E 7 m and not in W (Fig 6, Table 3), which supports our predictions. Intense bioerosion has been shown to concur with high coral reef cover as the reef framework harbours numerous eroding and grazing organisms (Hallock 1988, Glynn 1997). The dense coral reef framework in E shallow (Schmidt et al. *subm.*) could therefore be an explanation for the higher bioerosion rates in E. The obvious delay in detectable bioerosion in W between the first 12 months and the 21 months exposure periods (Fig 6) might be due to the lack of a dense coral reef assemblage (Schmidt et al. *subm.*) including a well-established community of bioeroders. This indicates however, that the grazing induced mortality of coral nubbins in W must have been caused by non-residential grazers, which are not permanently bound to one fix reef area, such as shoals of parrot fishes (family Scaridae) appearing in indefinite time intervals at W *browsing* and grazing through the patchy reef assemblages (Schmidt, *pers. observations*).

External versus internal bioerosion

The hypothesized higher grazing rates in E are supported by our findings and so are obviously also the enhanced internal bioerosion rates for W (third hypothesis):

The fact that external grazing was the predominant agent of bioerosion in E after the comparatively short exposure periods of 12 and 21 months, is consistent with other studies elsewhere (cf. Bak 1990, Chazottes et al. 2002, Tribollet et al. 2002). The fouling by epilithic algal biomass on newly exposed clean substrates generally occurs within a short period of time (McCook 2001), whereas endolithic microorganisms and internal bioeroders require a longer initial time of conditioning and settlement (Hutchings 1986). The external conditioning of the newly exposed skeletal substrates followed by intense grazing occurred within the first 12 months of exposure in E shallow. Thereby the rates of carbonate loss were within the range of rates measured elsewhere in coral reefs denoted as healthy and balanced in their carbonate budget (Tribollet et al. 2002, Chazottes et al. 2002, Osorno et al. 2005). After the

almost doubled exposure time (21 months) bioerosion rates in E shallow expectedly doubled as there were no further erosion supportive factors (Fig 6).

In W however bioerosion was close to zero after 12 months and had increased extremely and disproportionally after the second exposure period (Fig 6). This could be explained by a delayed establishment of an internal bioeroding community and the almost complete lack of external bioerosion: Skeletal blocks recollected from W after 12 months were virtually free of grazing traces and bite marks, and blocks collected after 21 months showed still far less external damage than eastern blocks. However, evidence was found for an infestation with macro-boring sponges and bivalves (macroscopic observations), the most important agents of internal bioerosion (Sammarco & Risk 1990, Moran & Reaka-Kudla 1988, Kiene & Hutchings 1994, Pari et al. 1998, Tribollet & Golubic 2005). Internal bioeroders in general excavate far less than external grazers (Reaka-Kudla et al. 1996), which could again explain the extreme differences between the erosion rates on E and W. However since the majority of internal bioeroders are filter feeders (Glynn 1997), the periodic and intense increases in nutrient concentrations in W (Schmidt et al. *subm.*) could have favoured their growth and number as soon as they were established on the skeletal blocks (Chazottes et al. 2002, Ward-Paige et al. 2005). This could have increased the porosity of the substrates (Osorno et al. 2005), and thereby supported the following clearly increased internal bioerosion, which was then measured after 21 months.

Although erosion rates were accordantly also increased in W deep after 21 months compared to the first 12 months, they were significantly lower than the rates in W shallow (Table 3 B). This could be due to a concomitant decrease of reef associated bioeroders and living coral cover with depth in W (Schmidt et al. *subm.*), and the possible attraction of even if not many but at least more eroding grazers in W shallow by the abundant cover of up to 36 % algal turf (Jantzen et al. *in prep.*).

Bioaccretion

Biological carbonate precipitation on skeletal blocks was negligible as soon as bioerosion was in progress (Fig 6, Osorno et al. 2005, Tribollet & Golubic 2005), and is therefore not used as an indicator for carbonate accumulation versus bioerosion but as a specification and correction of the measured bioerosion.

Nevertheless, compared to other studies, where bioaccretion was confined to carbonate accretion by calcifying coralline algae (CCA) which resulted in barely detectable accretion rates close to zero or of < 5 % of the accordant bioerosion (Osorno et al. 2005, Tribollet & Golubic 2005) rates of bioaccretion were high if not very high in our study.

Schmidt et al. (subm.) showed that CCA occurred in only low abundances (< 12 % cover), with no difference in their distribution between W and E sides at Similan Islands. We therefore confined the measurements of carbonate precipitation by fouling organisms on the four organism groups found on the skeletal substrates (serpulids, bivalves, balanids, and corals, Davies & Hutchings 1983) to achieve actual weight differences of carbonate accretion between exposed W and sheltered E sides.

A clear depth profile for bioaccretion was found in W after the first 12 months exposure, which was replaced by an almost balanced distribution over sides and depths after 21 months (Fig 7, Table 2). Higher densities of serpulids and bivalves in W deep can be attributed to the competition for space with other epibionts which are benefiting from higher light intensities in shallow (Vine & Bailey-Brock 2008). Filamentous algae and algal turf are among the first colonizers of newly available substrates (McCook 2001, Titlyanov et al. 2007) and were therefore initially the most important competitors in W shallow (Jantzen et al. in prep). Further the periodically high current speeds increasing fluxes of plankton and particulate organic matter in W (Roder et al. accepted) enhanced living conditions for filter feeding calcifiers compared to E (Glynn 1997, Fabricius 2005). Accordingly the abundances of the mostly calcite precipitating serpulids, bivalves and balanids did not seem to be affected negatively by the frequently pulsed cold and low-pH waters in W, compared to the positive effects of less competition for space and higher food supply. Bioaccretion by corals was exclusively constricted to E yet coming along with a very high standard deviation (Fig 7) indicating the very scattered distribution of some few individuals which definitely benefited from the sheltered conditions in E but lack the comparatively homogenous within site distribution of serpulids as the second most abundant group in E (Fig 7).

Carbonate budget

To combine and summarize our findings in this study and to achieve an estimate of the relation between coral skeleton growth and bioerosion on dead coral substrate in the reefs at Similan Islands, we made a 'back-of-the-envelope' calculation for a simple carbonate budget. The aim was to find out if coral growth (data from exposure: Feb 2007 to Feb 2008) and net bioerosion data (21 months exposure) in our study combined with cover data of living coral substrate and non-living calcareous (dead coral) substrate in Schmidt et al. (subm.) could reflect the existing coral reef distribution at Similan Islands (using island Koh Miang as representative example, Fig 1: W 4.1, E 4.1): A highly developed reef framework in E with 19 % living versus 16 % dead coral cover in E 7 m and 37 % living versus 10 % dead coral cover in E 20 m compared to no reef framework but patchy coral assemblages in W with 36 % living versus 3 % dead coral cover in W 7 m and 12 % living versus 16 % dead coral cover in W 20

m (Schmidt et al. subm.). The calculation implicated a conservative estimation of coral growth as *Porites lutea* is a slowly growing massive coral (Scoffin et al. 1992).

The carbonate budget (CB) calculation involved the following four steps: (1) calculation of mean coral growth rate (G) in kg CaCO₃ m⁻² yr⁻¹ for E 7 m, E 20 m, W 7 m, and W 20 m by using an estimated mean nubbin surface of 16.7 cm² (deriving from initial surface measurements on the nubbins before transplantations), (2) applying the particular coral growth rate (G) to the in each case corresponding percent living coral cover (A_{LC}, as fraction of one, dimensionless), (3) applying the net bioerosion (B_{net}) in kg CaCO₃ m⁻² yr⁻¹ for E 7 m, E 20 m, W 7 m, and W 20 m to the in each case corresponding percent dead coral cover (A_{DC}, as fraction of one, dimensionless); and (4) combining these calculations to the corresponding carbonate budget equation:

$$CB = G * A_{LC} - B_{net} * A_{DC} \quad (2)$$

The preliminary hypothesis was that CB is positive (> 0) in E 7 m and E 20 m, but different in W 7 m and W 20 m. The results are shown in Table 5: The carbonate budget was positive at all sites, with highest rates in E 20 m and W 7 m, both characterized by the highest living coral cover (Schmidt et al. subm.) but clear differences in reef framework development (highly developed in E, not existent in W) and bioerosion rates (high in E, low in W). In E 7 m, both skeletal growth and bioerosion were well developed resulting in a more tightly balanced carbonate budget. The low net coral skeleton accumulation in W 20 m was barely ahead the alike low net bioerosion.

Carbonate accretion by coral growth and carbonate erosion by grazing and boring organisms are obviously balanced (Hallock 1988, Scoffin et al. 1980, Glynn 1997), even under the highly variable conditions of LAIW. However the findings here do not satisfactorily

Table 5 'Back-of-the-envelope' calculation of a carbonate budget (CB) at Similan Islands; $CB = G * A_{LC} - B_{net} * A_{DC}$ with (G): coral growth rate in kg CaCO₃ m⁻² yr⁻¹, (B_{net}): net bioerosion in kg CaCO₃ m⁻² yr⁻¹, (A_{LC}): living coral cover (as fraction of one, dimensionless), and (A_{DC}): non-living calcareous (dead coral) substrate (as fraction of one, dimensionless).

	E 7 m	E 20 m	W 7 m	W 20 m
A _{LC}	0.19	0.37	0.36	0.12
A _{DC}	0.16	0.10	0.03	0.16
G * A_{LC}	0.86	1.62	1.42	0.22
B_{net} * A_{DC}	-0.70	-0.20	-0.08	-0.13
CB	0.16	1.43	1.33	0.09

explain the large differences in reef and framework development especially between W shallow and E deep (Schmidt et al. subm.) suggesting that there are other factors, such as early juvenile mortality (Schmidt et al. in prep.) or the framework hampering impact of surface gravity waves during the monsoon seasons (Schmidt et al. subm.) responsible for the lack of an actual reef framework in W shallow. The findings in our study however confirm that as long as corals are healthy and intact, i.e. undamaged, in a balanced system the accordant bioerosion does not necessarily menace the persistence of positive carbonate precipitation. Yet as soon as a disturbance such as grazing rates (in the case of our study in particular due to non-residential grazers) exceed the potential of compensation by coral defense and growth, the competitive advantage of overgrowing algae and bioeroding heterotrophs in W becomes unconquerable. Low coral cover (Schmidt et al., subm.) due to high LAIW-impact entails low residential bioerosion due to the lack of a complex reef community and thus guarantees the own persistence.

Supplementary data is given in Annex 4

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Literature

- Al-Horani FA (2005) Effects of changing seawater temperature on the photosynthesis and calcification in the scleractinian coral *Galaxea fascicularis*, measured with O₂, Ca²⁺ and pH microsensors. *Scientia Marina* 69:347-354
- Allison N, Tudhope AW, Fallick AE (1996) Factors influencing the stable carbon and oxygen isotopic composition of *Porites lutea* coral skeletons from Phuket, South Thailand. *Coral Reefs* 15:43-57
- Alpers W, Wang-Chen H, Hock L (1997) Observation of internal waves in the Andaman Sea by ERS SAR. Proc 3rd ERS Symp on Space at Service of our Environment. Florence Italy
- Andersson AJ, Kuffner IB, Mackenzie FT, Jokiel PL, Rodgers KS, Tan A (2009) Net loss of CaCO₃ from coral reef communities due to human induced seawater acidification. *Biogeosci Discuss* 6:2163-2182
- Bak RPM (1976) The growth of coral colonies and the importance of crustose coralline algae and burrowing sponges in relation with carbonate accumulation. *Netherlands J Sea Res* 10:285-337
- Bak RPM (1990) Patterns of echinoid bioerosion in two Pacific coral reef lagoons. *Mar Ecol Prog Ser* 66:267-372
- Bak RPM, Brouns JJWM, Heys FML (1977) Regeneration and aspects of spatial competition in the scleractinian corals *Agaricia agaricites* and *Montastrea annularis*. In Proc 3rd Int Coral Reef Symp Publ 1:143-148
- Bates NR, Samuels L, Merlivat L (2001) Biogeochemical and physical factors influencing seawater fCO₂, and air-

- sea CO₂ exchange on the Bermuda coral reef. *Limnol Oceanogr* 46:833–846
- Brown B, Le Tissier M, Howard LS, Charuchinda M, Jackson JA (1986) Asynchronous deposition of dense skeletal bands in *Porites lutea*. *Mar Biol* 93:83–89
- Chansang H, Satapoomin U, Poovachiranon S (1999) Maps of coral reefs in Thai waters. Vol 2, Coral Reef Resource Management Project, Department of Fisheries. Pp 198 (in Thai) Andaman Sea, Bangkok
- Carriero-Silva M, McClanahan T, Kiene W (2005) The role of inorganic nutrients and herbivory in controlling microbioerosion of carbonate substrate. *Coral Reefs* 24:214–221
- Chazottes V, Le Campion-Alsumard T, Peyrot-Clausade M, Cuet P (2002) The effects of eutrophication-related alterations to coral reef communities on agents and rates of bioerosion (Reunion Island, Indian Ocean). *Coral reefs* 21:375–390
- Cohen AL, Holcomb M (2009) Why corals care about ocean acidification – uncovering the mechanism. *Oceanogr* 22:118–127
- Coles SL, Fadlallah UH (1991) Reef coral survival and mortality at low temperatures in the Arabian Gulf: new species specific lower temperature limits. *Coral Reefs* 9:231–237
- Davies PS (1989) Short-term growth measurements of corals using an accurate buoyant weighing technique. *Mar Biol* 101:389–395
- Davies PS, Hutchings PA (1983) Initial colonization, erosion and accretion on coral substrate. *Coral Reefs* 2:27–35
- Dunne RP, Brown BE (1996) Penetration of solar UVB radiation in shallow tropical waters and its potential biological effects on coral reefs; results from the central Indian Ocean and Andaman Sea. *Mar Ecol Prog Ser* 144:109–118
- Edinger EN, Limmon GV, Jompa J, Widjatmoko W, Heikoop JM, Risk MJ (2000) Normal coral growth rates on dying reefs: are coral growth rates good indicators for reef health? *Mar Pol Bull* 40:404–425
- Erez J, Braun A (2007) Calcification in hermatypic corals is based on direct seawater supply to the biomineralization site. *Geochim Cosmochim Acta*, 71(15, Supplement 1), A260
- Fabricius KE (2005) Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. *Mar Poll Bull* 50:125–146
- Falkowski PG, Jokiel PL, Kenzie RAI (1990) Irradiance and corals. *Ecosyst World* 25:89–107
- Ferrier-Pagès C, Gattuso J P, Dallot S, Jaubert J (2000) Effect of nutrient enrichment on growth and photosynthesis of the zooxanthellate coral *Stylophora pistillata*. *Coral Reefs* 19: 103–113
- Ferrier-Pagès C, Schoelzke V, Jaubert J, Muscatine L, Hoegh-Guldberg O (2001) Response of a scleractinian coral, *Stylophora pistillata*, to iron and nitrate enrichment. *J Exp Mar Biol Ecol* 259:249–261
- Furla P, Galgani I, Durand I, Allemand D (2000) Sources and mechanisms of inorganic carbon transport for coral calcification and photosynthesis. *J Exp Biol* 203:3445–3457
- Gates RD; Baghdasarian G, Muscatine L (1992) Temperature stress causes host cell detachment in symbiotic cnidarians: Implications for coral bleaching. *Biol Bull* 182:324–332
- Gattuso JP, Allemand D, Frankignoulle M (1999) Photosynthesis and calcification at cellular, organismal and community levels in coral reefs: A review on interactions and control by carbonate chemistry. *Amer Zool* 39:160–183
- Glynn PW (1997) Bioerosion and coral reef growth: a dynamic balance. In: Birkeland C (ed) *Life and death of coral reefs*. Chapman and Hall, New York, pp 68–95
- Glynn PW, Colgan MW (1992) Sporadic disturbances in fluctuating coral reef environments: El Niño and coral reef development in the Eastern Pacific. *Amer Zool* 32:707–718
- Goreau TF (1963) Calcium carbonate deposition by coralline algae and corals in relation to their roles as reef builders. *Ann NY Acad Sci* 109:127–167
- Hallock P (1988) The role of nutrient availability in bioerosion: consequences to carbonate buildups (1988) *Palaeogeogr Palaeoclimat Palaeoecol* 63:275–291
- Hassan M (1997) Modification of carbonate substrata by bioerosion and bioaccretion on coral reefs of the Red Sea. PhD Thesis, University of Kiel, Germany, pp 1–126
- Hutchings PA (1986) Biological destruction of coral reefs. *Coral Reefs* 4:239–252
- Jackson CR (2004) *An atlas of internal solitary-like waves and their properties*. 2nd Ed. Office of Naval Research, Global Ocean Associates, Alexandria, VA, USA
- Jantzen C, Wild C, Schmidt GM, Roder C, Khokiattiwong S, Richter C (in preparation) Benthic primary production in response to Large Amplitude Internal Waves in coral reefs
- Jokiel PL, Coles SL (1977) Effects of temperature on the mortality and growth of Hawaiian reef corals. *Mar Biol* 43:201–208
- Kleypas JA, Yates KK (2009) Coral reefs and ocean acidification. *Oceanography* 22:108–117
- Kiene WE, Hutchings PA (1994) Bioerosion experiments at Lizard Island, Great Barrier Reef. *Coral reefs* 13:91–98
- Leichter JJ, Wing SR, Miller SL, Denny MW (1996) Pulsed delivery of subthermoline water to Conch Reef (Florida Keys) by internal bores. *Limnol Oceanogr* 41:1490–1501
- Leichter JJ, Stewart HL, Miller SL (2003) Episodic nutrient transport to Florida coral reefs. *Limnol Oceanogr* 48:1394–1407
- Leichter JJ, Genovese SJ (2006) Intermittent upwelling and subsidized growth of the scleractinian coral *Madracis mirabilis* on the deep fore-reef slope of Discovery Bay, Jamaica. *Mar Ecol Prog Ser* 316:95–103
- Marubini F, Atkinson MJ (1999) Effects of lowered pH and elevated nitrate on coral calcification. *Mar Ecol Prog*

- Ser 188:117-121
- Marubini F, Bernett H, Langdon C, Atkinson MJ (2001) Dependence of calcification on light and carbonate ion concentration for the hermatypic coral *Porites compressa*. *Mar Ecol Prog Ser* 220:153-162
- Marubini F, Ferrier-Pagès C, Furla P, Allemand D (2008) Coral calcification responds to seawater acidification: a working hypothesis towards a physiological mechanism. *Coral reefs* 27:491-499
- McClanahan TR (1994) Kenyan coral reef lagoon fish: effects of fishing, substrate complexity, and sea urchins. *Coral Reefs* 13:231-241
- McCook LM, Jompa J, Diaz-Pulido G (2001) Competition between corals and algae on coral reefs: a review of evidence and mechanisms. *Coral Reefs* 19:400-419
- Moberg F, Nyström M, Kautsky N, Tedengren M, Jarayabhand P (1997) Effects of reduced salinity on the rates of photosynthesis and respiration in the hermatypic corals *Porites lutea* and *Pocillopora damicornis*. *Mar Ecol Prog Ser* 157:53-59
- Montaggioni LF, Cuet P, Naim O, Walton Smith FG (1993) Effect of nutrient excess on a modern fringing reef (Reunion Island, Western Indian Ocean) and its geological implications. *Global Aspects of Coral Reefs: Health, Hazards and History*. University of Miami, Miami, pp 27–33
- Moran DP, Reaka-Kudla ML (1988) Bioerosion and availability of shelter for benthic reef organisms. *Mar Ecol Prog Ser* 44:249–263
- Moum JN, Klymak JM, Nash JD, Perlin A, Smyth WD (2007) Energy transport by nonlinear internal waves. *J Phys Oceanogr* 37:1968-1988
- Nielsen TG, Bjørnsen PK, Boonruang P, Fryd M, Hansen PJ, Janekarn V, Limtrakulvong V, Munk P, Hansen OS, Satapoomin S, Sawangraruks S, Thomsen HA, Østergaard JB (2004) Hydrography, bacteria and protist communities across the continental shelf and shelf slope of the Andaman Sea (NE Indian Ocean). *Mar Ecol Prog Ser* 274:69-86
- Osborne AR, Burch TL (1980) Internal solitons in the Andaman Sea. *Science (Wash.)* 208(4443):457-460
- Osorno A, Peyrot-Clausade M, Hutchings PA (2005) Patterns and rates of erosion in dead *Porites* across the Great Barrier Reef (Australia) after 2 years and 4 years of exposure. *Coral Reefs* 24:292–303
- Pari N, Peyrot-Clausade M, Le Campion-Alsumard T, Hutchings PA, Chazottes V, Golubic S, Le Campion J, Fontaine MF (1998) Bioerosion of experimental substrates on high islands and on atoll lagoons (French Polynesia) after two years of exposure. *Mar Ecol Prog Ser* 166:119-130
- Pari N, Peyrot-Clausade M, Hutchings PA (2002) Bioerosion of experimental substrates on high islands and atoll lagoons (French Polynesia) during 5 years of exposure. *J Exp Mar Biol Ecol* 276:109–127
- Perry RB, Schmike GR (1965) Large amplitude internal waves observed off the northwest coast of Sumatra. *J Geophys Res* 70:2319-2324
- Phongsuwan N, Yamarunpattana C, Paokanta Y, Areechon P (2008) Status of Coral Reefs in the Surin and Similan Archipelagos, Thailand. In Obura DO, Tamelander J, Linden O (ed) Ten years after bleaching -facing the consequences of climate change in the Indian Ocean. CORDIO Status report 2008, Mombasa
- Pineda J. (1995) An internal tidal bore regime at nearshore stations along western U.S.A.: Predictable upwelling within the lunar cycle. *Cont Shelf Research* 15(8):1023-1041
- Reaka-Kudla M, Feinglod JS, Glynn W (1996) Experimental studies of rapid bioerosion of coral reefs in the Galapagos Islands. *Coral Reefs* 15:101-107
- Riegl B (2001) Inhibition of reef framework by frequent disturbance: examples from the Arabian Gulf, South Africa, and the Cayman Islands. *Palaeo* 175:79-101
- Roder C, Fillingner L, Jantzen C, Schmidt GM, Khokiattiwong S, Richter C (accepted) Trophic response of corals to Large Amplitude Internal Waves. *Mar Ecol Prog Ser*
- Saxby T, Dennison WC, Hoegh-Guldberg O (2003) Photosynthetic response of the coral *Montipora digitata* to cold temperature stress. *Mar Ecol Prog Ser* 248:85-97
- Sammarco PW, Risk MJ (1990) Large-scale patterns in internal bioerosion of *Porites*: cross continental shelf trends on the Great Barrier Reef. *Mar Ecol Prog Ser* 59:145-156
- Schneider K, Erez J (2006) The effect of carbonate chemistry on calcification and photosynthesis in the hermatypic coral *Acropora eurystoma*. *Limnol Oceanogr* 51:1284-1293
- Schmidt GM, Phongsuwan N, Roder C, Jantzen C, Khokiattiwong S, Richter C (submitted) Coral community and physico-chemical characteristics in response to Large Amplitude Internal Waves. *Mar Ecol Prog Ser*
- Scoffin TP, Stearn CW, Boucher D, Frydl P, Hwakins CM, Hunter IG, MacGeachy JK (1980) Calcium carbonate budget of a fringing reef on the west coast of Barbados. *Bull Mar Sci* 30(2):475-508
- Scoffin TP, Tudhope AW, Brown BE, Chansang H, Cheeney RF (1992) Coral Reefs (1992) Patterns and possible environmental controls of skeletogenesis of *Porites lutea*, South Thailand. *Coral reefs* 11:1-11
- Sheppard C (2009) Large temperature plunges recorded by data loggers at different depths on an Indian Ocean atoll: comparison with satellite data and relevance to coral refuges. *Coral Reefs* 28:399-403
- Spalding MD; Ravilious C, Green EP (2001) World atlas of coral reefs. University of California Press, Berkeley, California, USA.
- Suzuki A, Kawahata H (2003) Carbon budget of coral reef systems: An overview of observations in fringing reefs, barrier reefs and atolls in the Indo-Pacific regions. *Tellus Ser B-Chem Phys Meteorol* 55:428–444
- Tanzil JTI, Brown BE, Tudhope AW, Dunne RP (2009) Decline in skeletal growth of the coral *Porites lutea* from

- the Andaman Sea, South Thailand between 1984 and 2005. *Coral Reefs* 28:519-528
- Titlyanov EA, Yakovleva IM, Titlyanova TV (2007) Interaction between benthic algae (*Lyngbya bouillonii*, *Dictyota dichotoma*) and scleractinian coral *Porites lutea* in direct contact. *J Exp Mar Biol Ecol* 342:282-291
- Tribollet A, Decherf G, Hutchings PA, Peyrot-Clausade M (2002) Large-scale spatial variability in bioerosion of experimental coral substrates on the Great Barrier Reef (Australia): importance of microborers. *Coral Reefs* 21:424-432
- Tribollet A, Golubic S (2005) Cross-shelf differences in the pattern and pace of bioerosion of experimental carbonate substrates exposed for 3 years on the northern Great Barrier Reef, Australia. *Coral Reefs* 24:422-434
- van Woesik R, Tomascik T, Blake S (1999) Coral assemblages and physico-chemical characteristics of the Whitsunday Islands: evidence of recent community changes. *Mar Freshwater Res* 50:427-440
- Veron JEN (2000) *Corals of the World*. Australian Institute of Marine Science, Townsville, Australia
- Vine PJ, Bailey-Brock JH (2008) Taxonomy and ecology of coral reef tube worms (Serpulidae, Spirorbidae) in the Sudanese Red Sea. *Zool J Linn Soc* 80:135-156
- Vlasenko V, Hutter K (2002) Numerical experiments on the breaking of solitary internal waves over a slope-shelf topography. *J Phys Oceanogr* 32:1779-1793
- Vlasenko V, Stashchuk N (2007) Amplification and suppression of internal waves by tides over variable bottom topography. *J Phys Oceanogr* 36:1959-1973
- Ward-Paige CA, Risk MJ, Sherwood OA, Jaap WC (2005) Clionid sponge surveys on the Florida reef tract suggest land-based nutrient inputs. *Mar Pol Bul* 51:570-579
- Wu G, Zhang Y (1998) Tibetan Plateau Forcing and the Timing of the Monsoon Onset over South Asia and the South China Sea. *American Meteorol Soc* 126:913-927
- www.reefbase.org/gis_maps
- Yeemin T, Sutthacheep M, Pettongma R (2006) Coral reef restoration projects in Thailand. *Ocean & Coastal Management* 49:562-575
- Yentsch CS, Yentsch CM, Cullen JJ, Lapointe B, Phinney DA, Yentsch SW (2002) Sunlight and water transparency: cornerstones in coral research. *J Exp Mar Biol Ecol* 268:171-183

Chapter 5

Spatio-temporal variation of coral recruitment along Similan Islands, Thailand

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Abstract

The Similan Islands, Thailand, are characterized by Large Amplitude Internal Waves (LAIW) bringing periodically cold deep waters into shallower reef areas. Highest LAIW activity was found during the NE monsoon (January through April) and with strongest impact in deeper water at the west (*W*) sides of the islands. The Similans are also exposed to an intense SW monsoon (May to October) affecting the shallower parts of the *W* sides of the islands. Recruitment of scleractinian corals was studied at ten locations in the *W* and east (*E*) sides of the islands at the shallow (7 m) and deep (20 m) fore-reef slope. Coral juveniles were counted on experimental limestone tiles exposed successively for 21, 12 and 9 months and on natural reef substrate by random quadrat sampling. On natural substrate, the abundances of coral recruits were significantly higher in *W* shallow than in *E* deep, whereas on settlement tiles the *W* vs. *E* differences were not significant. With increasing exposure period, the proportion of juvenile corals increased in *E* but decreased in *W*, indicating a failure of recruits to establish on the LAIW-exposed sides in spite of the higher initial spat fall. Recruitment to settlement tiles was dominated by *Pocilloporidae* and *Poritidae* but only 262 corals were settling on 114 tiles. Survival analysis indicates that early stages of settlement and growth occur independently of LAIW exposure, suggesting that initial recruitment is governed by predation, substrate suitability, and/or competition for space. Subsequent establishment of juvenile corals, by contrast, appears to be related to LAIW intensity, reflecting the lack of true reefs on LAIW-exposed *W* sides of the islands.

Key words

Coral recruitment – settlement - survivorship - Large Amplitude Internal Waves - benthic-pelagic coupling - Similan islands - Andaman Sea

Introduction

Coral recruitment represents the reproductive success of both, sexual and asexual propagules in scleractinian corals. It is one of the fundamental processes structuring coral reefs. Numerous studies have been reported on coral recruitment from various regions and scales (i. a. Richmond & Hunter 1990: review, Soong et al. 2003: Taiwan, Fisk & Harriott 1990: N GBR, Hughes et al. 1999: mid GBR, Dunstan & Johnson 1998: S GBR, Banks & Harriott 1996, Harriott 1999: SE Australia, Tomascik 1991: Barbados, Caribbean, Glassom et

al. 2004, Abelson et al. 2005: Eilat, N Red Sea). These studies emphasise the importance of biotic factors, such as predation and competition, but also abiotic factors like environmental variability and disturbance (Richmond & Hunter 1990, Mumby 1999). For sexual propagules, recruitment is a function of several parameters including the timing of reproduction (Richmond & Hunter 1990), competency periods of planula larvae (Babcock & Heyward 1986), currents (Sammarco & Andrews 1988), availability of substrates (Babcock & Mundy 1996, Heyward & Negri 1999, Norström et al. 2006, Vermeij & Sandin 2008, Lee et al. 2009), and densities of predators and competitors (Maida et al. 1995, Kuffner et al. 2006). The spatial scales of coral recruitment have been explored on the Great Barrier Reef (GBR) (e.g. Hughes et al. 1999), and it has been suggested that self-seeding of reefs there is a common phenomenon (Baggett & Bright 1985, Harriott and Banks 1995, Sammarco & Andrews 1988, 1989, Andrews et al. 1989). Yet this scale of self-seeding is unlikely for many other reefs that are relatively isolated and small, and several studies have found evidence for 'open populations' with non-localized sources of coral planulae (Wallace 1985, Babcock 1989, Richmond & Hunter 1990, Kojis and Quinn 2001). Recruitment rates have been shown to be cyclic over decades (Coles & Brown 2007), to exhibit seasonal peaks and partly strong annual fluctuations (Wallace 1985: GBR).

The Andaman Sea represents one of the most important coral reef regions in the Indian Ocean province harbouring more than 250 hard coral species along its Thai coasts (Yeemin et al. 2006). While only a few studies on coral reef conditions (e.g. Brown et al. 2002, Brown & Phongsuwan 2004, Brown 2007) and coral recruitment in this area have been published (Phongsuwan 1991, Thongtham & Chansang 1999, Chanmethakul 2001, Sawall et al. 2010) interest in Andaman Sea reefs of Thailand has increased following the tsunami in 2004 (Allen et al. 2005, Plathong 2005, Yeemin et al. 2006, Phongsuwan et al. 2006, Phongsuwan & Brown 2007).

Two major features are characteristic for the Andaman Sea: intense rainfall and heavy swell during the south-west (SW) monsoon from May to October (Dunne & Brown 1996, Wu & Zhang 1998), and the year-round occurrence of Large Amplitude Internal Waves (LAIW) (Perry & Schimke 1965, Osborne & Burch 1980, Jackson 2004). The LAIW are generated by tidal fluctuations along the Andaman-Nicobar island arc and northwest of Sumatra (Alpers et al. 1997, Jackson 2004) creating packets of solitary waves of depression travelling eastward across the Andaman basin. Near the shelf, the LAIW transform into waves of elevation. Near the 90 m isobath (Jackson 2004), interactions with the bottom lead to strong current shear, resuspension of sediments (Moum et al. 2007), and breaking of waves with turbulent mixing of warm surface and cold deep waters (Vlasenko & Hutter 2002, Vlasenko & Stashchuk

2007). To what extent the offshore swash zone of LAIW, or secondary waves emanating from this area (cf. Jackson 2004, Vlasenko & Stashchuk 2007), may affect adjacent reefs near the shelf break is so far unknown.

The Similan Islands are an offshore group of granite islands located in a north-south alignment in the eastern Andaman Sea near the swash zone of Andaman Sea LAIW (Jackson 2004, Vlasenko & Stachuk 2007). Monitoring studies (Chansang et al. 1999, Phongsuwan 2008) and satellite images (www.reefbase.org/gis_maps) show that reefs have developed only on the sheltered E sides of the islands, whereas the W sides lack a coral reef framework. This is surprising in view of the paradigm predicting the most vigorous reef growth on the exposed, ocean-facing sides of coral islands (Veron 2000, Spalding et al. 2001). LAIW-induced mixing of sub-thermocline waters into shallow areas may potentially hamper reef development due to the combined effects of low temperatures, low aragonite saturation state, and elevated nutrient levels in the upwelled water, but possibly also due to lower densities of coral propagules or the negative effects of environmental variability on the survival of coral recruits. Accordingly, even though the W sides are exposed to the south-west (SW) monsoon as well, the lack of reef development suggests that LAIW may be involved in the reef-forming process.

Edmunds et al. (2001) showed that lowered temperatures, compared to ambient conditions, increased the rates of mortality and metamorphosis in *Porites astreoides* larvae, while reducing gross photosynthesis. In several studies raised nutrient concentrations along eutrophication gradients were always accompanied by reduced recruit numbers (Tomascik 1991, Wittenberg & Hunte 1992, Abelson et al. 2005) and higher juvenile mortality by supporting competitively stronger fleshy and turf algae (Wittenberg & Hunte 1992). Although there are several studies which demonstrated the negative influence of reduced pH on adult coral calcification and growth (Marubini & Atkinson 1999, Marubini et al. 2001, Schneider & Erez 2006), studies on juvenile corals under reduced aragonite saturation states and their impact on coral recruitment were missing until quite recently (Albright et al. 2008, Kurihara 2008, Cohen et al. 2009). These studies suggest that coral spat, due to the putatively smaller energy reserves and larger surface to volume ratio (Cohen et al. 2009) may be even more susceptible to corrosive upwelling waters. Recruitment depends on three components: (1) the rate of arrival of competent larvae to the site; (2) the probability that larvae will settle on the reef once they arrive, and (3) the probability that new settlers will survive after settling to a size where they can be detected (Keough & Downes 1982, Connell 1985).

The aim of the present study was to examine coral recruitment along the Similan Islands and to relate variations in settlement to the main physical factors governing reef

development in this offshore location at seasonal and tidal scales - monsoon and LAIW. This was assessed by (1) measuring the temporal variability of W – E and deep – shallow recruitment rates, (2) comparing the size structure and growth rate of coral recruits, (3) determining the cover of other sessile organisms and their relationship among each other and with coral recruit densities, and (4) relating the composition of coral recruits to the adult coral community.

Material & methods

Field work was conducted at the Similan Islands in the Andaman Sea about 60 km west of Phuket, Thailand from February 2007 to November 2008. Recruitment of scleractinian corals, the encrustation by benthic organisms like bryozoans, bivalves, polychaetes, sponges, calcifying crustose coralline algae (CCA), fleshy algae (fleshy or filamentous macro-algae > 1 cm) and turf (filamentous algae < 1 cm), and external bioerosion via bite marks was examined on the upper- and under-surfaces of limestone tiles (150*150 mm). Ten sites along the island chain were chosen as study areas, 5 in the LAIW- and monsoon-exposed west (W 2.1, W 4.1, W 7.1, W 8.1, and W 8.2) and 5 along their opposite sheltered eastern faces (E 2.1, E 4.1, E 7.1, E 8.1, and E 8.2) (Fig 1). Racks constructed of PVC-tubes and metal bars, were deployed in the same position along the reef slopes at all sites. At each site two racks were fixed in 7 m (monsoon exposure) and 20 m (LAIW-exposure) depth respectively in a distance of approximately 10 m to each other. Every rack supported five juxtaposed tiles fixed with stainless steel screws passing through the tile-centres to ensure a constant distance of 2 cm of each tile to the rack and about 15 cm to the substrate (see suppl. Fig 1). Tiles were attached at a 45° angle, since coral recruitment has been positively correlated with the angle of recruitment surface (after Carleton and Sammarco 1987; English et al. 1997), and were facing directly west at the W sites and east at the E sites, respectively. Untreated limestone tiles consisting of pure calcium carbonate deriving from a limestone quarry near Phuket were used as settlement substrate as limestone is the most similar material to the generally common natural coral reef substrate, the carbonate skeletons of dead scleractinian corals. Besides these plates offered identical settlement facilities on both upper and under-surfaces unlike the commonly used bathroom tiles with only one side unglazed and suitable for assessing coral recruitment (Harriott and Fisk 1987; Maida et al. 1995). The tiles were deployed successively: one tile per rack in February 2007 and two tiles per rack each time in November 2007 and February 2008.

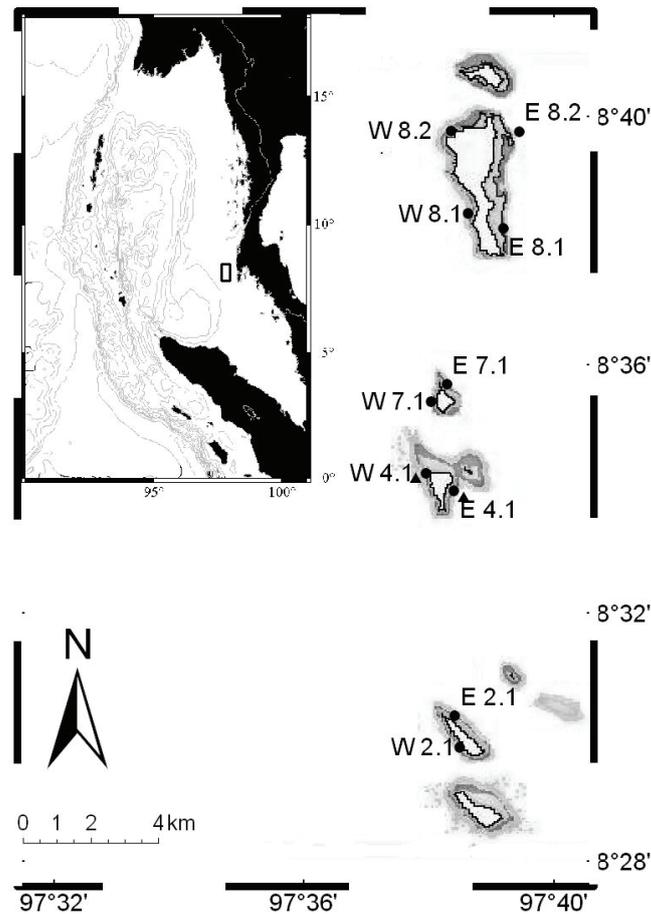


Figure 1 Similan Islands with study sites in W and E (●). Recruitment on natural substrate was examined at central island Koh Miang (W 4.1, E 4.1) (▲). (Figure modified after Jackson (2004)).

The recollection of all tiles took place in November 2008, thus yielding three different exposure periods of 21 (Feb 2007 to Nov 2008), 12 (Nov 2007 to Nov 2008) and 9 (Feb 2008 to Nov 2008) months, respectively. Some tiles were lost from the racks through breakage, and analyses are based on one tile per rack for each exposure period. These tiles were selected randomly from the plates collected. High-resolution photographs were taken with a Nikon D200 camera of both upper and underside-surfaces of every tile right after collection and again after two weeks of air-drying for later picture analyses. Settlement tiles were then bleached in a 10 % chlorine solution to remove any organic material, rinsed and dried. Microscopic examinations were conducted with a binocular microscope (Leica, Wild M3B) and an integrated measuring ocular. Coral recruits were identified to family level (Babcock et al. 2003, suppl. Fig 2). Unidentifiably recruits (i.e. those that lacked distinguishable features) were designated as 'others'. Coral spats were measured and the number of polyps counted. Percent cover of other sessile organisms on the tiles was determined by picture analysis with the coral point count method (CPCe) of Kohler & Gill (2006). For this purpose a matrix of 100

randomly distributed points was overlaid exactly on the upper- and under-surface area of every tile-picture, and the organism or substrate-type lying beneath each point was visually identified (suppl. Fig 3). To verify determinations of sessile organisms on the tile-pictures taken right after collection, the dried tile pictures were consulted as well. All analyses comprised both the upper and underside-surface of any tile.

For direct comparisons of the recruit composition on tiles with the natural adult coral community composition single 100 m line transects were established at each of the study sites at a depth of 12 – 16 m. The line-intercept method (Loya and Slobodkin 1971; Loya 1972, 1976) was adopted to quantify the coral communities to family level.

Recruitment to natural reef substrates in the field was quantified at island Koh Miang W (W 4.1) and E (E 4.1) (Fig 1) in 20 and 7 m depth from 64 50*50 cm quadrates, 16 quadrates per site and depth. These quadrates were chosen haphazardly in the reef on suitable substrate for possible settlers (i.e. dead coral and rock) and scanned for new recruits using 10*10 cm grids and a magnifying lens. All visible coral recruits from 0.5 to 5 cm in diameter were counted.

Coral recruitment to tiles and natural substrate is displayed per m² for reasons of comparability.

Temperature recorders (TidbiT v2, Onset computers; resolution 0.2 °C within a range of 0 to 50 °C) were attached to one of the racks at each site and depth and exchanged in 3 to 9 month intervals to retrieve the temperature records collected in 6 min intervals for the whole experimental period (i.e. February 2007 through November 2008).

Temperature recordings were used to calculate monthly modal, maximum and minimum values for every site and depth.

Statistical analyses were conducted using Statistica v 9. Site effects between temperature values (monthly minima, maxima and modal values) of the same side (W or E), and depth (20 or 7 m) were excluded by paired Student's t-tests (see suppl. Table 1) and the data pooled afterwards for further analysis. Data sets were tested for normal distribution and homogeneity of variances and log+1-transformed before analysis. A non-parametric Kruskal-Wallis ANOVA and median test followed by multiple comparisons of mean ranks was used to measure differences in coral recruit densities on natural substrate and temperature values (minima, maxima and modal values) between side (W versus E) and depth (20 versus 7 m) at island Koh Miang (W 4.1, E 4.1). A General Linear Model (GLM) analysis followed by pairwise comparisons of significant effects with the Fisher LSD post-hoc test was used to estimate differences in coral recruitment and cover of benthic organisms on tiles between side (W versus E), depth (20 versus 7 m), and time (exposure periods of 21, 12 and 9

months, respectively). For direct comparison of LAIW-exposed deep and monsoon-exposed shallow sites, a hierarchical nested design was applied in the GLM analysis with depth nested in side. Possible site effects between tiles of the same exposure period, side, and depth collected at the different island sites were considered by implicating the factor site (named: island) as random factor into the GLM analysis. As the factor site (island) could be excluded as statistically significant (see results) data were pooled for graphical presentation. The relationship between density of coral recruits, density of the different benthic organisms and the abundance of bite marks determined on the tiles was examined using Pearson's correlation. Linear correlation analysis was used to determine the relationship between the density of recruits and adult corals from the same taxa in the established coral community. The software PRIMER v6 was used to analyze differences in the communities of benthic organisms and coral recruits found on the tiles as a function of side (W versus E), depth (20 versus 7 m), and time (exposure periods of 21, 12 and 9 months, respectively) (Clarke and Warwick 2001). Log-transformed cover data were used to calculate a Bray–Curtis similarity matrix, and analysis of similarities (ANOSIM) was used to test for differences in community structure across sides, depths, and time. Therefore a two-way crossed ANOSIM was used with depth (20 or 7 m) nested in side (W or E). The global R value calculated by the ANOSIM statistic reflects the differences in variation between groups compared to within groups and its significance was checked by permutation tests (Clarke and Warwick 2001). Non-metric multidimensional scaling (MDS) was used to illustrate the similarities between tiles on the basis of their fouling communities. An exploratory similarity breakdown using the SIMPER procedure was used to quantify the relative contribution of each organism to the community structure (Clarke and Warwick 2001). If not stated otherwise data are displayed as mean (\pm SE).

Results

Temperature record

Monthly modal, minimum and maximum temperatures were synchronous among all sites of the same depth and orientation (Fig 2: W deep, W shallow, E deep, and E shallow respectively; Student's t-tests: no significant differences, suppl. Table 1). Only small (< 3.5 °C) seasonal differences were found in the monthly modal and maximum values, irrespective of side or depth. Highest values were measured in April 2007, the lowest in March 2007. Significant differences in modal and maximum temperatures were found only between the LAIW-exposed W deep and the sheltered E shallow sites, all other differences were

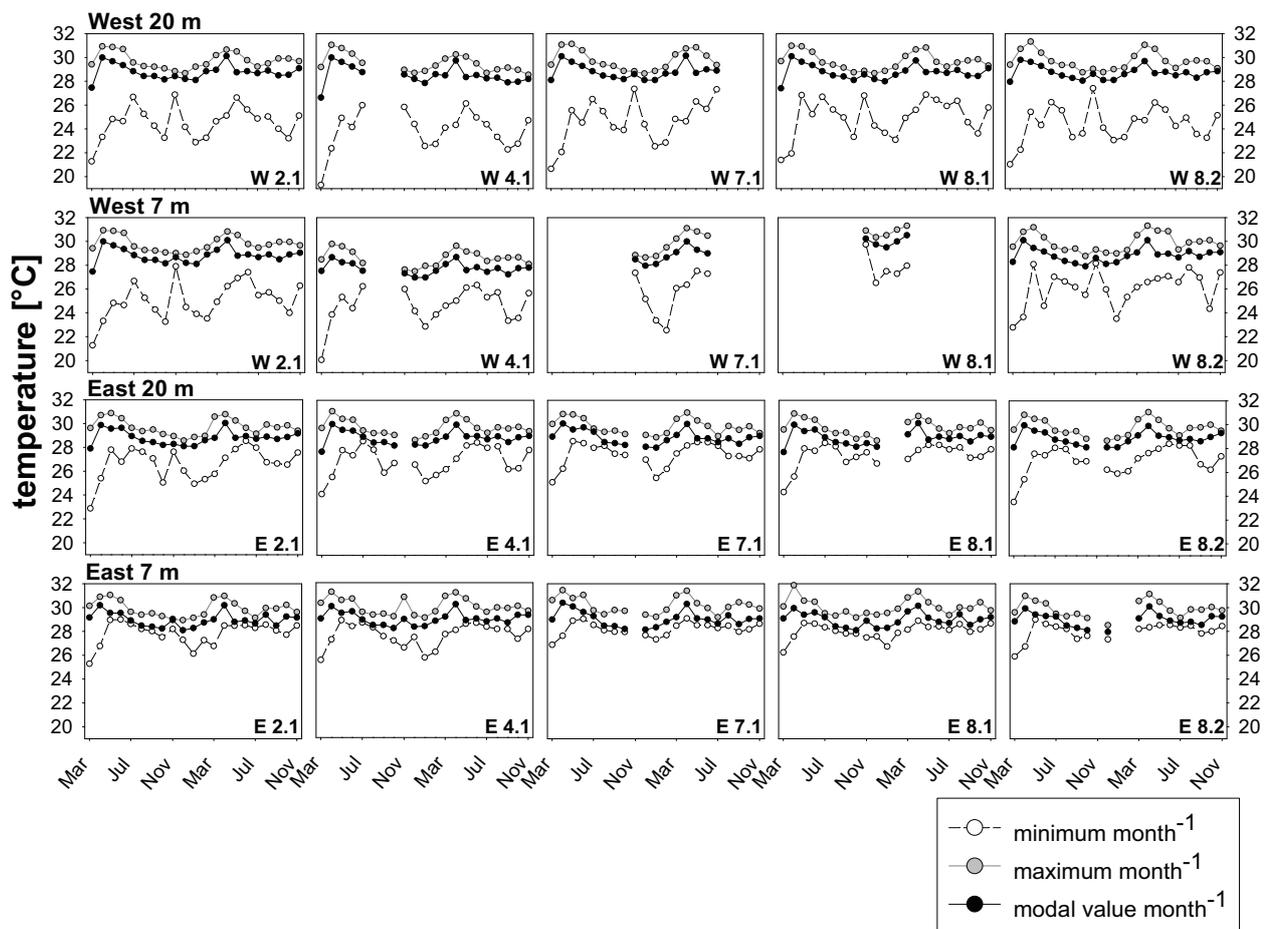


Figure 2 Large Amplitude Internal Wave (LAIW) associated temperature variations in the Similan Islands. Monthly minimum, maximum and modal values of temperature from LAIW-exposed W and sheltered E sides at all study sites in 20 m (within LAIW swash depth) and 7 m (beyond the reach of LAIW swash zone) depth for the complete experimental period of February 2007 to November 2008. Blank periods are missing values due to lost or broken loggers.

insignificant (Table 1). The low seasonal variability contrasts dramatically with the high variability found at higher frequencies, as reflected by the large differences between modal and minima values. The largest variability was found in February through April (W deep: $\Delta T = 8.6 \pm 0.2$ °C in 2007 and 6.0 ± 0.1 °C in 2008), the lowest variability between July and November (W deep: $\Delta T = 3.8 \pm 0.3$ in 2007 and 4.5 ± 0.3 in 2008). Negative deviations from the modal values were much larger than the positive. The monthly minima, averaged over the whole study period, revealed clear differences between W and E, deep and shallow sites (Table 1) with consistently lowest values at W deep sites (24.5 ± 0.2 °C compared to 25.6 ± 0.2 °C for W shallow, 27.1 ± 0.1 °C for E deep, and 27.9 ± 0.1 °C for E shallow, Fig 2). These findings indicate that LAIW are strongest during the late NE monsoon and weakest during the SW monsoon. In other words: internal waves are strongest when surface waves are weakest.

Total abundances of coral recruits

A total of 262 coral spats (with 12621 polyps) were counted on all settlement plates over the whole exposure time, 140 in W and 122 in E (Table 2). Recruitment of spat was dominated by the family *Pocilloporidae* which accounted for 52.3 % (137 colonies: 80 in W and 57 in E, depths pooled) of all recruits recorded, followed by *Poritidae* with 17.9 % (47 colonies: 16 in W and 31 in E) and *Acroporidae* with 10.3 % (27 colonies: 24 in W and 3 in E). Fewer percentage cover was reached for the families *Fungiidae*, *Faviidae*, *Helioporaceae* and *Agariciidae* which amounted to 6.5 % (17 colonies: 9 in W and 8 in E), 3.4 % (9 colonies: 1 in W and 8 in E), 3.4 % (9 colonies: 0 in W and 9 in E), and 0.8 % (2 colonies: 1 in W and 1 in E) respectively. Colonies lacking distinguishable features (referred to as “others”) totalled 5.3 % (14 colonies: 9 in W and 5 in E) of all recruits observed.

Spatio-temporal patterns in recruitment

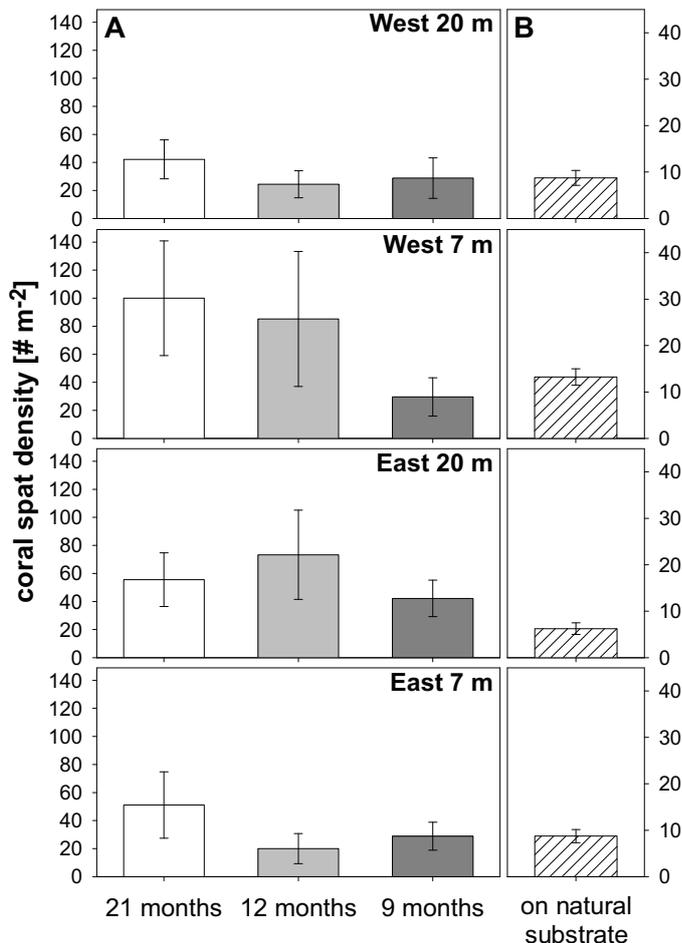


Figure 3 Spatial and temporal variations of coral recruitment at Similan Islands: Mean density (\pm SE) of coral recruits on settlement plates along W (West) and E (East) (all study sites) in two depths (20 and 7 m) after twenty-one (\square) Feb 2007 to Nov 2008), twelve (\blacksquare) Nov 2007 to Nov 2008) and nine (\blacksquare) Feb 2008 to Nov 2008) months deployment (A); recruitment on natural substrate (Koh Miang) in Feb 2008 (B). Note the different scaling of the y-axis of (A) and (B).

Recruitment of scleractinian corals on natural substrate revealed significantly higher recruit colonies in W shallow than E deep (Kruskal Wallis, multiple comparisons, $p < 0.03$) with 7.1 ± 1.8 recruits m^{-2} in W shallow and 5.1 ± 1.3 recruits m^{-2} in E deep (Fig 3). The same pattern of recruit distribution was observed on settlement tiles exposed for the longest period of 21 months with higher recruit numbers calculated per m^2 in W shallow (100.0 ± 40.9) compared to all other sites (E deep: 55.6 ± 19.1 ; E shallow: 51.1 ± 23.7 , and W deep: 42.2 ± 13.8), but statistical tests failed to be significant. The same trend of recruit distribution but less pronounced could be observed on tiles exposed for 12 months with the highest recruit density per m^2 in W shallow (85.2 ± 48.1) and E deep (73.3 ± 31.8), followed by W deep (24.4 ± 9.6) and E shallow (20.0 ± 10.7). On tiles exposed for 9 months, recruit numbers were distributed quite homogeneously between sides and depths with slightly higher densities in E deep (W deep: 28.9 ± 14.5 , W shallow: 29.6 ± 13.7 , E deep: 42.2 ± 13.0 , E shallow: 28.9 ± 10.0) (Fig 3).

Size structure and survival of coral recruits

Small recruits in the size classes 1 – 5 and 6 – 10 polyps dominated coral recruitment on settlement tiles irrespective of side (exposed W or sheltered E), depth (LAIW-exposed deep: 20 m or monsoon-exposed shallow: 7 m) or time of exposure (Fig 4, suppl. Table 3). They constituted between 90 % (in W deep after 21 months and in E shallow after 9 months) and at least 68 % (in E deep after 21 months) of the total number of recruits per side and depth. Thereby the only significant difference in the abundances of small recruits between island sides was detected after 12 months exposure with clearly higher densities on W shallow tiles compared to W deep and E shallow (Fisher LDS test: $p < 0.05$ and $p < 0.03$, respectively). The growth rate of recruits (*sensu* rate of addition of new polyps) was faster in W than in E on tiles exposed at last for 9 months (Feb to Nov 2008): 7 % (in W shallow) to 17 % (in W deep) exceeded 30 polyps per colony compared to only 8 % reaching a maximum of 25 polyps on tiles in E shallow (Fig 4). Tiles exposed earlier and for a longer period revealed increasingly higher abundances of larger colony sizes in E compared to W: 12 months after exposure colonies exceeding 30 polyps were still more common in W with unchanged proportions (7 % in shallow and 18 % in deep), yet in E the number of recruits reaching this size class had clearly increased (11 % in E shallow and 3 % in E deep); after 21 months exposure the relation had turned over completely and large recruit colonies with over 30 polyps were more common in E (22 % in E shallow and 28 % in E deep) than in W (13 % in W shallow and 10 % in W deep) (Fig 4). Largest colony sizes exceeding 150 polyps were found only on tiles exposed for 12 and 21 months with similar numbers in W and E after 12 months (4 % in W shallow, 9 % in W deep and 11 % in E shallow) and clearly increased

Table 2 Total abundances of corals settled on tiles: Total number of recruit spats and polyps (in parentheses) of present coral families for each time period: twenty-one (Feb 2007 to Nov 2008), twelve (Nov 2007 to Nov 2008) and nine (Feb 2008 to 2008) months.

Time period deployment	Site	# Tiles removed	<i>Pocilloporidae</i>	<i>Acroporidae</i>	<i>Fungiidae</i>	<i>Poritidae</i>	<i>Faviidae</i>	<i>Agaricidae</i>	<i>Helicoporaceae</i>	Other	Total
21 months	Feb 07 -	10	6 (14)	1 (329)	5 (5)	3 (5)	1 (1)	1 (210)	0 (0)	3 (3)	20 (570)
	Nov 08	6	17 (348)	1 (1)	2 (2)	5 (56)	0 (0)	0 (0)	0 (0)	2 (2)	27 (412)
	East 20 m	10	12 (730)	1 (1313)	5 (5)	4 (149)	2 (40)	0 (0)	0 (0)	1 (1)	25 (2238)
	East 7 m	10	8 (6328)	0 (0)	0 (0)	3 (3)	1 (1)	1 (5)	9 (14)	1 (1)	15 (6352)
	total:	36	43 (7420)	3 (1644)	12 (12)	15 (213)	4 (42)	2 (215)	9 (14)	7 (7)	95 (9572)
	% of total		45.3 (77.5)	3.2 (17.2)	12.6 (0.1)	15.8 (2.2)	4.2 (0.4)	2.1 (2.3)	9.5 (0.2)	7.4 (0.1)	100 (100)
12 months	Nov 07 -	10	8 (906)	1 (1)	2 (2)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	11 (910)
	Nov 08	10	34 (969)	17 (123)	0 (0)	2 (2)	0 (0)	0 (0)	0 (0)	2 (2)	55 (1101)
	East 20 m	10	18 (106)	1 (9)	2 (2)	10 (10)	0 (0)	0 (0)	0 (0)	2 (2)	33 (138)
	East 7 m	10	6 (489)	0 (0)	0 (0)	2 (2)	0 (0)	0 (0)	0 (0)	1 (1)	9 (493)
	total:	40	66 (2470)	19 (133)	4 (4)	14 (14)	0 (0)	0 (0)	0 (0)	5 (5)	108 (2642)
	% of total		61.1 (93.5)	17.6 (5.1)	3.7 (0.2)	13.0 (0.5)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	4.6 (0.2)	100 (100)
9 months	Feb 08 -	10	5 (92)	1 (1)	0 (0)	5 (98)	0 (0)	0 (0)	0 (0)	1 (1)	12 (192)
	Nov 08	8	10 (98)	3 (21)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1 (1)	14 (120)
	East 20 m	10	9 (43)	0 (0)	1 (1)	4 (4)	5 (5)	0 (0)	0 (0)	0 (0)	19 (54)
	East 7 m	10	4 (32)	1 (1)	0 (0)	8 (8)	0 (0)	0 (0)	0 (0)	0 (0)	13 (41)
	total:	38	28 (265)	5 (23)	1 (1)	17 (110)	5 (5)	0 (0)	0 (0)	2 (2)	58 (407)
	% of total		48.3 (63.7)	8.6 (5.5)	1.7 (0.2)	29.3 (26.6)	8.6 (1.2)	0.0 (0.0)	0.0 (0.0)	3.4 (0.5)	100 (100)

numbers in E compared to again unchanged proportions in W after 21 months (4 % in W shallow, 10 % in W deep and 17 % in E shallow, 16 % in E deep). It is remarkable that only few recruits in the intermediate size classes of 11 – 25 polyps were counted (less than 14 % for all exposure periods and sites).

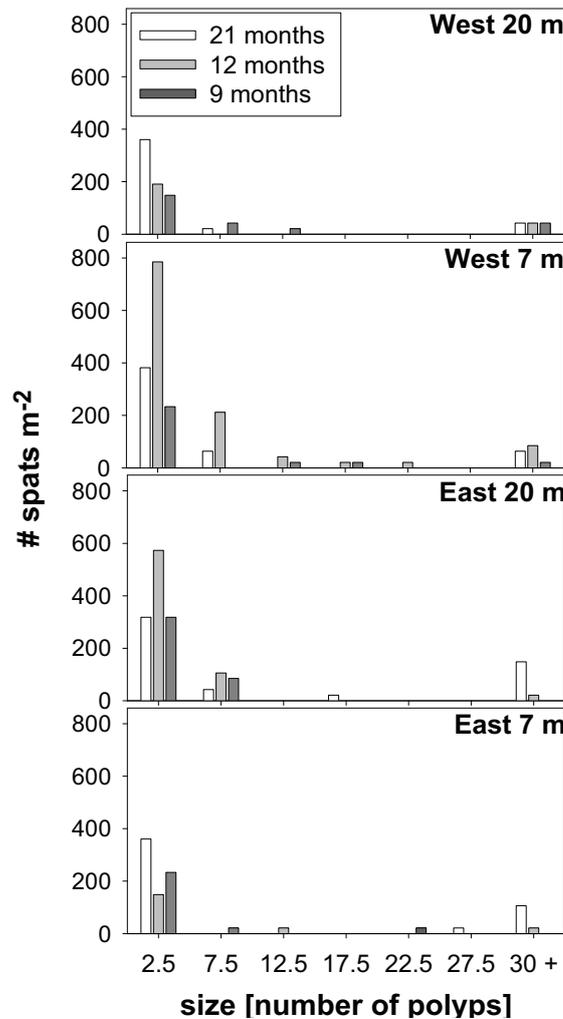


Figure 4 Size frequency distribution (size class mid point) of coral recruits on settlement tiles in W (West) and E (East) of Similan islands in two depths (20 and 7 m). Plates exposed for twenty-one (\square) Feb 2007 to Nov 2008), twelve (\blacksquare) Nov 2007 to Nov 2008) and nine (\blacksquare) Feb 2008 to Nov 2008) months.

The mean settling rate of recruits (successfully settled individuals per month) was estimated for each exposure period, side and depth by comparing the mean densities of recruits divided by the number of exposure-months. The relation of settling rate and exposure period was similar for W deep and E shallow, as well as for W shallow and E deep, respectively. The former exhibited highest settling rates on tiles after 21 months exposure (for W deep: 42 % higher settling than on 12 month-tiles and 32 % higher than on 9 month-tiles, and for E shallow: 39 % higher settling than on 12 month-tiles and 57 % higher than on 9

month-tiles). In W shallow and E deep the 12 month-exposure period revealed highest settling rates, followed by the 21 month-exposure period (with 18 % less settling for W shallow, and 24 % less for E deep), and the 9 month-exposure period (with 68 % less settling for W shallow, and 42 % for E deep) (see also Fig 4).

Cover of other sessile organisms on tiles

After 21 months the total composition of sessile organisms on settlement tiles failed to be significantly different between W and E (ANOSIM, two-way analysis, nested design: W versus E: global $R = 0$, $p = 0.667$, Fig 5 A) but differed clearly between depths (ANOSIM, two-way analysis, nested design: Deep versus shallow: global $R = 0.211$, $p < 0.039$) resulting in a quite distinct clustering in the MDS plot of deep (LAIW-exposed) and shallow (monsoon-exposed) sites (Fig 5 B). Algal turf was the most powerful contributor to this dissimilarity of 24.2 % between deep and shallow with a contribution of 16.50 %, followed by fleshy macroalgae with 14.62 %, bivalves with 13.97 %, and crustose coralline algae with 13.78 %. Further statistical analyses on the total cover-composition of sessile organisms on tiles after 12 and 9 months exposure revealed no significant differences between side (W versus E) and depth (20 m versus 7 m).

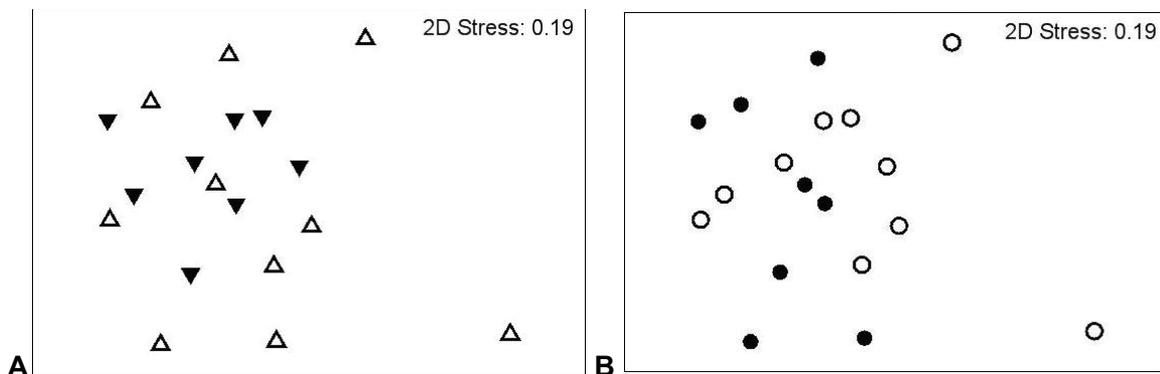


Figure 5 Multidimensional scaling (MDS): substrate cover (of benthic organisms and coral recruits) on tiles after twenty-one months exposure; same plots labelled according to side, West (▼) and East (▲) (A), and depth 20 m (○) and 7 m (●) (B).

Fig 6 shows a summary overview of the different groups of sessile organisms and bite marks on settlement tiles with the statistical analysis summarized in Table 3. Bryozoans were the most common group on tiles varying between 18.5 ± 4.5 % (W shallow after 21 months) and 40.2 ± 7.6 % (E shallow after 21 months) cover. They were more prevalent in E compared to W irrespective of exposure time (Table 3). Conversely, fleshy macroalgae and filamentous algal turf were more abundant in W than in E (Table 3), constituting between 5.8 ± 1.7 % (W deep after 21 months) and 31.7 ± 6.7 % (W shallow after 21 months) cover for macroalgae, and 2.0 ± 0.9 % (W shallow after 12 months) and 18.2 ± 3.2 % (W deep after 9

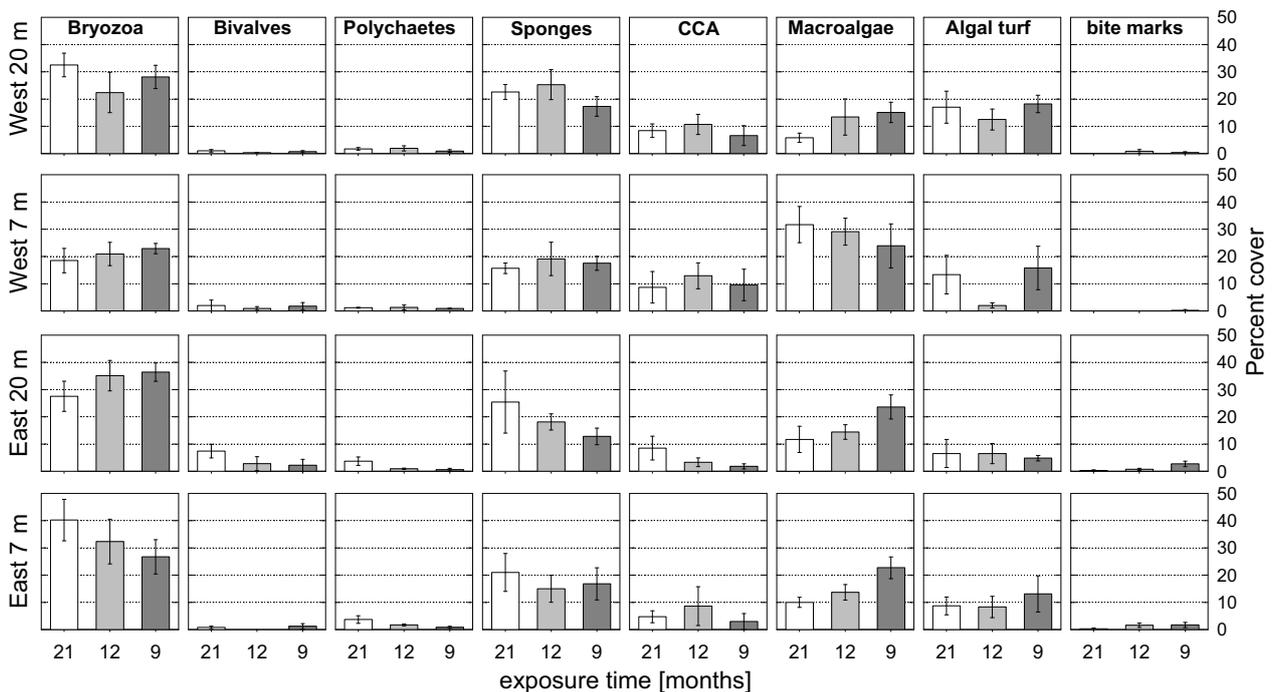


Figure 6 Percentage cover (mean \pm SE) of most abundant benthic organisms and bite marks on settlement tiles in W (West) and E (East) of Similan islands in two depths (20 and 7 m). Plates exposed for twenty-one (\square) Feb 2007 to Nov 2008, twelve (\blacksquare) Nov 2007 to Nov 2008 and nine (\blacksquare) Feb 2008 to Nov 2008 months.

months) for algal turf. Fleshy macroalgae showed highest densities on tiles from W shallow contrasting algal turf with higher cover in LAIW-exposed W deep (Table 3). Crustose coralline algae (CCA) were more common in W compared to E when looking at all exposure periods pooled (Table 3), and revealed between 1.8 ± 0.9 % (E deep after 9 months) and 12.9 ± 4.8 % cover (W shallow after 12 months). Cover of sponge species varied between 12.8 ± 3.0 % and 25.3 ± 5.5 % and was relatively evenly distributed between sides and depths irrespective of exposure time. Bivalves and polychaetes reached their low maximum cover rates with 7.4 ± 2.5 % for bivalves in E deep, and 3.7 ± 1.5 % for polychaetes in E deep and shallow, respectively, after 21 months exposure (Table 3). Thereby bivalves revealed their highest abundances in E deep (Table 3) whereas densities of polychaetes were too low to perform reliable statistics between sides and depths. Bite marks as a measure for external bioerosion by herbivores revealed highest densities in E deep after 9 months exposure (2.7 ± 1.0 %). They were generally more prevalent in E than in W (Table 3). Showing a decrease with increasing exposure time no bite marks were detected at all any more on tiles collected in W after 21 months exposure (Fig 6).

Relationships between sessile taxa and coral recruit densities on tiles

There were significant negative correlations between coral spat densities and total cover of bryozoans after 21 months (sides and depths pooled), and between coral spat and

Table 3 Cover distribution of most abundant benthic organisms and bite marks on settlement tiles along Similan Islands. General Linear Model (GLM) analysis (data log +1 transformed) for all exposure periods pooled and separate, with side (W and E) and depth (20 and 7 m) as fixed factors in a nested design (depth nested in side), and exposure site (named: island) as random factor. Fisher LSD post-hoc test for pairwise comparisons of significant effects. Only significant results are shown here. (Significance levels are *0.05 > P ≥ 0.01, **0.01 > P ≥ 0.001, ***P < 0.001).

	Treatment	df	MS	F	p	Fisher LSD, pairwise comparisons:	p
exposure periods pooled							
Bryozoa	intercept	1	598.428	1006.864	< 0.001***	<u>side</u>	
	side	1	1.381	4.457	< 0.05*	E > W	< 0.04*
	depth (side)	2	0.075	0.241	0.787		
	exposure	2	0.274	0.884	0.420		
	island	4	0.598	1.930	0.121		
	Error	47	0.310				
Bivalves	intercept	1	20.556	20.124	< 0.02*	<u>depth (side)</u>	
	side	1	0.372	0.741	0.394	E 20 m > E 7 m	< 0.007**
	depth (side)	2	2.150	4.282	< 0.02*	> W 20 m	< 0.02*
	exposure	2	1.798	3.582	< 0.04*	<u>exposure</u>	
	island	4	1.028	2.048	0.103	21 months > 12 months	< 0.02*
	Error	47	0.502				
Polychaetes	intercept	1	34.710	53.041	< 0.002**		
	side	1	0.115	0.412	0.524		
	depth (side)	2	0.165	0.589	0.559		
	exposure	2	1.891	6.763	< 0.003**	<u>exposure</u>	
	island	4	0.659	2.357	0.067	21 months > 12 months	< 0.04*
	Error	47	0.280			21 months > 9 months	< 0.001***
CCA	intercept	1	134.247	72.321	< 0.001***	<u>side</u>	
	side	1	7.511	7.263	< 0.01**	W > E	< 0.007**
	depth (side)	2	0.050	0.049	0.953		
	exposure	2	2.148	2.077	0.137		
	island	4	1.867	1.805	0.144		
	Error	47	1.034				
fleshy Macroalgae	intercept	1	413.247	666.670	< 0.001***	<u>depth (side)</u>	
	side	1	0.223	0.580	0.450	W 7 m > W 20 m, E 20 m, E 7 m	< 0.01**
	depth (side)	2	3.741	9.734	< 0.001***		
	exposure	2	2.002	5.210	< 0.009**	<u>exposure</u>	
	island	4	0.623	1.621	0.185	9 months > 12 months	< 0.04*
	Error	47	0.384			9 months > 21 months	< 0.001***
Algal turf	intercept	1	213.175	65.675	< 0.002**	<u>depth (side)</u>	
	side	1	2.413	3.805	0.057	W 20 m > W 7 m	< 0.004**
	depth (side)	2	4.476	7.060	< 0.003**	> E 20 m	< 0.001***
	exposure	2	1.257	1.982	0.149	> E 7 m	< 0.03*
	island	4	3.279	5.172	0.124		
	Error	47	0.634				
Bite marks	intercept	1	6.541	20.011	< 0.02*	<u>side</u>	
	side	1	3.163	13.514	< 0.001***	E > W	< 0.002**
	depth (side)	2	0.178	0.761	0.473		
	exposure	2	1.302	5.562	< 0.007**	<u>exposure</u>	
	island	4	0.328	1.401	0.248	9 months > 21 months	< 0.004**
	Error	47	0.234				

Table 3 continued

Treatment	df	MS	F	p	Fisher LSD, pairwise comparisons:	p	
21 months exposure							
Algal turf	intercept	1	12.529	29.360	< 0.006**	<u>side</u>	
	side	1	0.650	5.977	< 0.04*	W > E	< 0.02*
	depth (side)	2	0.157	1.440	0.282		
	island	4	0.449	4.125	0.314		
	Error	10	0.109				
Bivalves	intercept	1	2.648	20.945	< 0.009**	<u>depth (side)</u>	
	side	1	0.271	4.069	0.071	E 20 m > E 7 m	< 0.003**
	depth (side)	2	0.535	8.034	< 0.009**	> W 20 m	< 0.005**
	island	4	0.131	1.959	0.177	> W 7 m	< 0.02*
	Error	10	0.067				
12 months exposure							
fleshy Macroalgae	intercept	1	27.963	218.528	< 0.001***	<u>depth (side)</u>	
	side	1	0.029	0.568	0.465	W 7 m > W 20 m	< 0.008**
	depth (side)	2	0.265	5.150	< 0.02**	> E 7 m	< 0.05*
	island	4	0.128	2.485	0.099		
	Error	12	0.051				
Algal turf	intercept	1	10.921	61.146	< 0.001***	<u>depth (side)</u>	
	side	1	0.002	0.018	0.896	W 20 m > W 7 m	< 0.01**
	depth (side)	2	0.547	4.633	< 0.03*		
	island	4	0.179	1.513	0.260		
	Error	12	0.118				
9 months exposure							
Bite marks	intercept	1	1.207	16.285	< 0.01**	<u>side</u>	
	side	1	0.426	6.590	< 0.02*	E > W	< 0.02*
	depth (side)	2	0.036	0.550	0.592		
	island	4	0.074	1.149	0.384		
	Error	11	0.065				

macroalgae in E (exposure periods and depths pooled) (Table 4). No other significant linear correlations between coral spat density and cover of other sessile taxa at the level of $\alpha = 0.05$ were found. Competition for space was obvious among the most common sessile taxa on the tiles: Bryozoans, macroalgae, algal turf, crustose coralline algae and sponges competed for settlement area in different constellations depending on exposure time, side and depth (Table 4). Bite marks of herbivorous fishes were found to be negatively correlated with bryozoans in W and polychaetes in E (exposure times and depths pooled in both cases, Table 4).

Relationship and composition of most abundant taxa in adult coral community and recruits on tiles

Correlation analyses showed that for each taxon there was no significant relationship between the relative density of coral recruits on tiles after 21 months exposure and the cover of corals from the same taxa in the established coral community (Table 5). The most striking

Table 4 Pearson's correlations between groups of most abundant benthic organisms, coral recruits, and bite marks on tiles at Similan islands. Only significant correlations are shown here. A further 111 tests, in which no significant correlation was detected, were excluded for the sake of clarity. Loss of some tiles resulted in differences in sample size (N). (Significance levels are *0.05 > P ≥ 0.01, **0.01 > P ≥ 0.001, ***P < 0.001)

Organisms correlated	Data source	N	R	p
Sponge & CCA	21 months exposure sides & depths pooled	18	-0.494	0.037*
Sponge & bryozoa	12 months exposure	20	-0.480	0.032*
Macroalgae & turf	sides & depths pooled	20	-0.647	0.002**
Sponge & bryozoa	West	27	-0.411	0.033*
Macroalgae & turf	exposure periods & depths pooled	27	-0.444	0.020*
Bryozoa & bite marks		27	-0.382	0.049*
Coral spats & macroalgae	East	30	-0.379	0.039*
Sponge & bryozoa	exposure periods & depths pooled	30	-0.436	0.016*
Bryozoa & turf		30	-0.416	0.022*
Polychaetes & bite marks		30	-0.388	0.034*

features were the rather contrary distributions of adult colony abundances and recruit numbers within the families *Pocilloporidae*, *Poritidae*: While the adult distributions were clearly different between W and E, recruit abundances on both sides were very similar. In the case of the family *Faviidae*, higher adult cover was found in W, yet without accordant recruit numbers (Table 5).

Table 5 Coral cover (%) and coral colony abundances (#) as a mean of five 100 m line intercept transects in W and E (at each experimental site) in 12 to 16 m depth, and density and surface area of recruit spats per m⁻² (calculated from tiles recollected after 21 months exposure from 20 and 7 m depth, depths pooled). Data given as mean (±SE).

		<i>Pocilloporidae</i>	<i>Acroporidae</i>	<i>Fungiidae</i>	<i>Poritidae</i>	<i>Faviidae</i>	<i>Agariciidae</i>	total hard corals	
West	per 100 m	coral colony [#]	16.0 (8.5)	19.2 (5.9)	0.6 (0.4)	20.2 (5.1)	36.6 (7.2)	16.0 (2.5)	121.6 (19.5)
		coral cover [%]	2.63 (1.33)	6.71 (2.24)	0.15 (0.12)	3.15 (0.91)	5.72 (1.37)	1.37 (0.18)	26.85 (4.98)
	per m ⁻²	recruit spats [#]	25.56 (10.73)	2.22 (1.53)	7.78 (2.43)	8.89 (3.75)	1.11 (1.11)	2.22 (1.53)	53.33 (15.16)
		spat cover [%]	0.03 (0.03)	0.05 (0.05)	0.01 (0.00)	0.01 (0.00)	0.00 (0.00)	0.07 (0.07)	0.17 (0.09)
East	per 100 m	coral colony [#]	4.2 (2.8)	11.2 (3.4)	1.0 (0.8)	65.2 (6.7)	8.6 (3.6)	4.0 (1.2)	109.8 (11.6)
		coral cover [%]	0.55 (0.29)	3.55 (0.56)	0.20 (0.09)	23.46 (5.07)	2.07 (0.67)	0.44 (0.18)	37.96 (6.19)
	per m ⁻²	recruit spats [#]	22.22 (6.03)	1.11 (1.11)	5.56 (2.73)	8.89 (4.08)	3.33 (1.82)	1.11 (1.11)	44.44 (12.59)
		spat cover [%]	0.64 (0.51)	0.15 (0.14)	0.02 (0.01)	0.02 (0.02)	0.00 (0.00)	0.00 (0.00)	0.83 (0.52)

The community composition on family level of adult corals revealed significant differences between W and E (ANOSIM, one-way analysis, cover (%) W versus E: global R = 0.424, p < 0.016; see also suppl. Fig 4). This dissimilarity in community composition was mainly generated by the family *Poritidae* (29.8 % contribution), followed by undefined coral

families (20.2 %), *Faviidae* (14.4 %), *Pocilloporidae* (12.2 %), *Acroporidae* (11.1 %), and *Agariciidae* (9.1 %). Coral recruits on settlement tiles revealed no statistically detectable difference in their community structure between W and E, irrespective of exposure time.

Discussion

Environmental factors or LAIW impact on coral reef performance

The monthly temperature values shown in our study must be regarded as conservatively summarized outcome of highly frequent and severe short term variations along Similan Islands caused by Large Amplitude Internal Waves (LAIW), ranking among the largest temperature variations so far reported for coral reef regions (Leichter et al. 1996, 2003, Leichter & Genovese 2006, Sheppard 2009). The comparison of temperature variance between the W-, E-, shallow- and deep records are a strong indication that the temperature drops are caused by ocean-travelling LAIW impinging on the deeper parts of the ocean facing W sides of the islands (Table 1, Fig 2). Highest LAIW-impacts occurred during the late NE monsoon (Fig 2) and varied with the lunar cycle (cf. also Pineda 1995) and the depth and strength of the seasonal pycnocline (Nielsen et al. 2004). Other studies showed (Schmidt et al. *subm.*) that the temperature variations coincide with variations in other physico-chemical characteristics of the water column, including pH (with drops of up to 0.6 units below ambient), oxygen (drops down to 12 % saturation), currents (up to 6-fold increases), and nutrient concentrations (up to 12-fold increases in nitrate and nitrite concentrations, 5-fold increases in silicate and over 20-fold increases in phosphate) (Schmidt et al. *subm.*).

These environmental contrasts are reflected also in the coral species richness and reef development (Schmidt et al. *subm.*). The E reefs are composed of relatively low numbers of species, whereas in the W the scattered communities of corals show a higher species-richness and evenness. Schmidt et al. (*in prep.*) further demonstrated that LAIW contributed to a 44 % decrease in the net carbonate production of the massive coral *Porites lutea* in the deeper parts of the W Similans. Similar photosynthetic rates of *P. lutea* between W and E are achieved at the expense of adaptations to lower light intensities, shown as 40 % higher pigment concentrations at W (Jantzen et al. *in prep.*). Similarly, Roder et al. (*accepted*) showed that the branching coral species *Pocillopora meandrina* exposed to LAIW reveals significantly higher biomass and protein content compared to sheltered corals, with a more intense heterotrophic performance and higher energy reserves. All of this indicates a high plasticity of corals grown under LAIW-influence with respect to their primary production and energy status, yet obviously at the expense of their growth performance.

Coral recruitment patterns

In summary abundances of coral recruits on natural substrate were significantly higher in W shallow than in E deep, but the W vs. E differences were not significant on the settlement tiles. The proportion of juvenile corals increased in E with increasing exposure period, yet decreased in W, indicating a failure of recruits to establish permanently on the LAIW-exposed sides in spite of the higher initial recruitment. The families *Pocilloporidae* and *Poritidae* dominated recruitment to settlement tiles but in comparison to other studies recruitment was low with only 262 corals settling on 114 tiles. The analysis of recruit survival indicated that early stages of settlement and growth occur independently of LAIW exposure, suggesting that initial recruitment is governed by predation, substrate suitability, and/or competition for space, while the subsequent establishment of juvenile corals, by contrast, appears to be related to LAIW impact.

Coral recruitment on natural substrate was significantly higher in W shallow compared to E deep (Fig 3). Although Jantzen et al. (in prep.) found turf algae to be the dominant primary producers on the rocky W side of Similan Islands (36 % cover compared to 8 % in E), which are known to inhibit coral settlement (Rogers et al. 1984, Vermeij & Sandin 2008), coral larvae must have found adequate substrate where they can settle and metamorphose (Richmond 1988). According to Becerro et al. (2006) monsoon-driven surface wave action is able to expose suitable substrate for coral recruitment like CCA (Heyward & Negri 1999) by mechanically removing cyanobacteria. It is therefore plausible that the ocean swell during the monsoon season in W shallow along Similan Islands (Phongsuwan, pers communication) may have enhanced the availability of suitable substrate on the granite basement for coral larvae settlement. Surface gravity waves thus have an antagonistic effect on the young corals, by removing the major competitors and thus providing settlement space, and enhancing mixing and the supply of nutrients favouring fleshy macroalgae and algal turf (Littler et al. 1983, Belliveau & Paul 2002, Walker & Ormond 1982, Tomascik 1991, Wittenberg & Hunte 1992). The lower recruit numbers within the dense coral framework of the sheltered E deep (Schmidt et al. subm.) could be the result of the actual lack of suitable settling substrate which is highly competitive by any benthic organisms and occupied the moment it gets available (Jackson 1977). Without the regular exposure of new suitable substrate by environmental disturbances, like ocean swell, the first settlers, mostly turf algae and cyanobacteria, determine the subsequent settling stages, and often inhibit the settling of coral larvae (Kuffner & Paul 2004, Kuffner et al. 2006). Further, besides the fact that the abundances of young corals generally decrease with depth (Rogers et al. 1984), coral larvae

have been described as depth dependent in their habitat selection according to the community composition of the parental reef (Baird et al. 2003), which in our case is dominated by a relatively small number of framework building species in E deep. In addition Vermeij & Sandin (2008) showed that early post-settlement survivorship of young corals decreased with increasing adult cover, revealing structuring density dependence in coral settlers.

On the settlement tiles coral recruitment showed a similar distribution as found on natural substrate, yet the high variability did not allow detecting statistically significant differences (Fig 3). The clearly higher abundances of recruits on tiles compared to the numbers found on natural substrate are presumably due to the fact that the early stages of corals are very small and difficult to see in their natural habitat, especially in high relief areas with a high cover of encrusting organisms (Miller et al. 2000). Thus, obtaining accurate estimates of in situ coral settlement and recruitment rates on natural substrates is far more difficult and might lead to underestimations compared to counting recruit numbers on tiles under the microscope (Smith 1997, Miller et al. 2000). The comparison of settlement rates on tiles between the different exposure periods revealed highest rates on both, the highly exposed W deep and completely sheltered E shallow tiles after the longest exposure period (21 months), whereas tiles exposed in W shallow and E deep were colonized by the highest numbers of coral recruits already after 12 months exposure. This coincides with the differing living coral cover in W and E along Similan Islands (Schmidt et al. *subm.*). Areas with higher coral cover (W shallow and E deep) revealed higher recruit abundances within a shorter period of time than areas with comparatively lower coral cover (W deep and E shallow) (Wallace & Bull 1982). The general lack of difference in recruitment rates on settlement tiles between W and E indicates that there are factors other than LAIW-induced environmental variations, responsible for the initial coral recruit abundances. Although LAIW bring enormous changes in temperature, pH, and nutrient concentrations (Schmidt et al. *subm.*), and all of these factors have been shown to have a significantly negative influence on coral recruitment and/or coral growth (low temperature: Edmunds et al. (2001), increased nutrients: Tomascik (1991), Wittenberg & Hunte (1992), Abelson et al. (2005), reduced pH or rather aragonite saturation state: Albright et al. (2008), Kurihara (2008), Cohen et al. (2009)), in our case these changes seem to be too short-termed (in the order of minutes) to cause long-term reactions in young coral recruits, which seem to be rather dealing with their biological competitors.

Competition for space

Competition for space in reef communities is intense (Connell 1978, Littler & Littler 1984), and thus the organisms that initially colonize new and open substrata may play a key role in influencing the structure of reef communities by dictating the success of coral recruitment (Done 1992). In this respect conditions are even more constricted on settlement tiles (Belliveau & Paul 2002). A prerequisite for coral settlement is the pre-conditioning of the tiles' surfaces, as chemical cues have been shown to be necessary to induce metamorphosis in coral larvae when establishing contact with the substrate (Morse et al. 1996). Although the chemical and physical cues for settlement of larvae are still poorly understood (Morse et al. 1988) the common approach still is to use artificial settlement tiles which can be removed from the reef for microscopic examination (e.g. Rogers et al. 1984, Smith 1992, Miller et al. 2000, Abelson et al. 2005, Lee et al. 2009). In our study a wide variety of organisms besides corals recruited to the settlement tiles. The dominant space occupants were bryozoans, which was also found during a study by Dunstan & Johnson (1998), followed by sponges, fleshy and turf algae, crustose coralline algae (CCA), bivalves and polychaetes. The community composition was similar on both, W and E tiles, but revealed significant differences between depths on the longest exposed tiles (Fig 5). Algal turf and fleshy algae were the main contributors to these differences, due to their abundance: turf algae on W deep, fleshy algae on W shallow tiles (Table 3). This was also reflected in the occasional abundance in W of shoals of herbivorous fish (family Scaridae) which was much higher on W shallow (Schmidt, pers. observation), suggesting that possibly grazing governs the selective removal of turf algae versus the less palatable and better defended fleshy algae (Steneck 1988, Hay 1991). The generally elevated grazing pressure at E (bite marks on settlement tiles, Table 3) could also be an explanation for the reduced cover of algae on E tiles compared to W (Fig 6, Table 3). Yet the provision of additional settlement space by herbivores did not lead to an enhanced coral recruitment on E tiles compared to W (Fig 3), suggesting that coral recruits were outcompeted by superior pioneer colonizers, such as bryozoans and bivalves (Dunstan & Johnson 1998) which were more abundant on heavily fouled tiles in E than in W (Fig 6, Table 3). During later stages of succession the high cover of bryozoans, sponges and bivalves may have prevented coral recruitment by occupying and defending settling space (Birkeland 1977, Dunstan & Johnson 1998, Abelson et al. 2005). Although biofouling is generally known to inhibit settlement and reduce the survival of newly settled coral recruits (e.g. Walker & Ormond 1982, Tomascik 1991), the calcareous tubes of serpulid worms may have provided a suitable secondary substrate for coral settlement in this study. On our plates, several coral recruits were observed to settle on serpulid tubes (see

also Glassom et al. 2004), rarely on bivalves yet never on bryozoans (see also Dunstan & Johnson 1998) or sponges. Overall, there was a weak negative correlation between the number of coral recruits per plate and the percent cover of bryozoans and fleshy algae (Table 4, Glassom et al, 2004, Kuffner et al. 2006). However this pattern was not consistent between sides (W and E) and exposure periods, so that the biological significance should be treated with caution. It is likely that the relatively low numbers of corals (between 1.6 recruits per plate after 9 months and 2.7 after 12 months) compared with other studies (e.g. to 15 recruits per plate in Tomascik (1991) or to 18 in Dunstan & Johnson (1998), and the high densities of bryozoans, fleshy algae, algal turf and sponges led to interactions between the main groups of sessile organisms which obscured any clear effects of competition for space with coral recruits along Similan Islands. These effects could have been found with higher recruit abundances (see also Dunstan & Johnson 1998, Glassom et al. 2004).

Larger recruits (> 30 polyps) with a good chance to develop a permanent coral colony, were increasingly more common on eastern than on western settlement tiles with increasing exposure period (Fig 4). This suggests that in spite of successful settlement in W, the subsequent development and growth of young corals was hampered, most likely by the strong variations in the physico-chemical environment due to LAIW and the resulting competitive advantage of algae and fouling organisms. Coral-coral competition, by contrast, is likely to have been negligible in W due to low adult coral cover compared to fully developed coral reefs (Vermeij & Sandin 2008), e.g. in E.

Species composition of recruits

Pocilloporid corals clearly dominated recruitment on settlement tiles at the Similan Islands followed by recruits of the family *Poritiae* and acroporid corals (Table 2). This pattern is consistent with observations made in other Andaman Sea coral reefs (Thongtham & Chansang 1999, Sawall et al. 2010). In the case of the Similan Islands however, the domination by recruits of corals which release brooded larvae (pocilloporids, *Poritidae*), as opposed to spawning taxa (acroporids) with external fertilisation could be due to the rather isolated position of the Similan reef community. With increasing distances between reefs, rates of recruitment of spawning corals are likely to decline to recruitment of brooding corals (Preece & Johnson 1993) as brooded larvae can travel large distances and survive the journey to an isolated reef (Harrison & Wallace 1990), or by contrast have a shorter period before they are competent to settle and are therefore more likely to be retained on the parental reef (Fadlallah 1983, Harrison & Wallace 1990, Harriott 1992). The lack of a direct relationship between adult coral community and recruit community structure in our study

(Table 5) supports the assumption that reproduction strategies and larval settlement behaviour are more important for successful recruitment than the parental coral community. This lack of correlation between juvenile abundance and adult coral cover has also been found in several other studies and seems to be rather the rule than the exception (Harriott 1985, Babcock & Mundy 1996, Banks & Harriott 1996, Vermeij & Sandin 2008).

Recruitment of corals is often seasonal with strong interannual fluctuations (Wallace 1985, Miller et al. 2000) and can be highly variable and cyclic on decadal time scales, often correlated with species and site-specific recruitment intervals (Coles & Brown 2007). The two year period of our study thus opens only a short time window into a long-term biological process governing the recruitment of corals in reefs. However although we might not be able to draw final conclusions with respect to recruitment patterns of scleractinian corals along Similan Islands, our results do reveal new indications concerning coral recruitment: We found an initial non-sensibility of young coral stages towards severe environmental variations such as LAIW-disturbance related to their larval search for suitable substrates, their settlement preferences, and early growth successes. However the subsequent establishment of young corals revealed an increasing sensibility to LAIW-impact, and reflected the lack of true reefs along the exposed western island sides.

LAIW are a widespread phenomenon especially in south-east Asia and may therefore also play an important yet so far unexplored role concerning the initial shaping and composition of coral reef communities in a variety of other coral reef regions.

Supplementary data is given in Annex 5

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Literature

- Abelson A, Olinky R, Gaines S (2005) Coral recruitment to the reefs of Eilat, Red Sea: temporal and spatial variation, and possible effects of anthropogenic disturbances. *Mar Pol Bull* 50:576-582
- Alpers W, Wang-Chen H, Hock L (1997) Observation of internal waves in the Andaman Sea by ERS SAR. Proc 3rd ERS Symp on Space at Service of our Environment. Florence Italy
- Albright R, Mason B, Langdon C (2008) Effect of aragonite saturation state on settlement and post-settlement growth of *Porites astreoides* larvae. *Coral Reefs* 27:485-490
- Allen GR, Stone GS (2005) Rapid assessment survey of tsunami-affected reefs of Thailand. New England Aquarium Technical Report 02-05, Boston, USA, 122 pp
- Andrews JC, Gay SL, Sammarco PW (1989) Models of dispersal and recruitment of coral larvae around an isolated reef (Helix Reef) in the central Great Barrier Reef. Proc 6th Int Coral Reef Congr, Townsville
- Babcock RC (1989) Fine-scale spatial and temporal patterns in coral settlement. Proc 6th Int Coral Reef Symp Aust 2:635-639
- Babcock RC, Heyward AJ (1986) Larval development of certain gamete-spawning scleractinian corals. *Coral Reefs* 5:111-116
- Babcock RC, Mundy C (1996) Coral recruitment: Consequences of settlement choice for early growth and survivorship in two scleractinians. *J Exp Mar Biol Ecol* 206:179-201
- Babcock RC, Baird AH, Piromvaragorn S, Thomson DP, Willis BL (2003) Identification of scleractinian coral recruits from Indo-Pacific Reefs. *Zool Stud* 42:211-226
- Baggett LS, Bright TJ (1985) Coral recruitment at the East Flower Garden Reef. Proc 5th Int Coral Reef Congr, Tahiti 4:379-384
- Baird AH, Babcock RC, Mundy CP (2003) Habitat selection by larvae influences the depth distribution of six common coral species. *Mar Ecol Prog Ser* 252:289-293
- Banks SA, Harriott VJ (1996) Patterns of coral recruitment at the Gneering Shoals, southeast Queensland, Australia. *Coral Reefs* 15:225-230
- Becerro MA, Bonito V, Paul VJ (2006) Effects of monsoon-driven wave action on coral reefs of Guam and implications for coral recruitment. *Coral Reefs* 25:193-199
- Belliveau SA, Paul VJ (2002) Effects of herbivory and nutrients on early colonization of crustose coralline and fleshy algae. *Mar Ecol Prog Ser* 232:105-114
- Birkeland C (1977) The importance of biomass accumulation in early successional stages of benthic communities to the survival of coral recruits. In: Taylor DL (ed) Proc 3rd Int Coral Reef Symp, Miami School of Mar Atmosph Sc University of Miami, Miami, pp 15-21
- Brown BE (2007) Coral reefs of the Andaman Sea - an integrated perspective. *Oceanogr Mar Biol Annu Rev* 45:173-194
- Brown BE, Phongsuwan N (2004) Constancy and change on shallow reefs around Leam Panwa, Phuket, Thailand over a twenty year period. *Phuket Mar Biol Cent Res Bull* 65:61-73
- Brown BE, Clarke KR, Warwick RM (2002) Serial patterns of biodiversity change in corals across shallow reef flats in Ko Phuket, Thailand, due to the effects of local (sedimentation) and regional (climatic) perturbations. *Mar Biol* 141:21-29
- Carleton JH, Sammarco PW (1987) Effects of substratum irregularity on success of coral settlement: quantification by geomorphological techniques. *Bull Mar Sci* 40:85-98
- Chanmethakul (2001) Spawning season of scleractinian corals on Phuket Island. M.Sc. thesis, Prince of Songkla University, Thailand, 82 pp.
- Chansang H, Satapoomin U, Poovachiranon S (1999) Maps of coral reefs in Thai waters. Vol 2, Coral Reef Resource Management Project, Department of Fisheries. Pp 198 (in Thai) Andaman Sea, Bangkok
- Clarke KR, Warwick RM (2001) Change in marine communities: an approach to statistical analysis and interpretation. 5 Primer - E Ltd, Plymouth Marine Laboratory, Plymouth
- Cohen AL, McCorkle DC, de Putron S, Gaetani GA, Rose KA (2009) Morphological and compositional changes in the skeletons of new coral recruits reared in acidified seawater: Insights into biomineralization response to ocean acidification. *Geochem Geophys Geosyst* 10(7), Q07005, doi:10.1029/2009GC002411
- Coles SL, Brown BE (2007) Twenty-five years of change in coral coverage on a hurricane impacted reef in Hawaii: the importance of recruitment. *Coral Reefs* 26:705-717
- Connell JH (1978) Diversity in tropical rainforests and coral reefs. *Science* 199:1302-1309
- Connell JH (1985) The consequences of variation in initial settlement vs. post-settlement mortality in rocky intertidal communities. *J Exp Mar Biol Ecol* 93:11-45
- Done TJ (1992) Phase shifts in coral reef communities and their ecological significance. *Hydrobiologia* 247:121-132
- Dunne RP, Brown BE (1996) Penetration of solar UVB radiation in shallow tropical waters and its potential biological effects on coral reefs; results from the central Indian Ocean and Andaman Sea. *Mar Ecol Prog Ser* 144:109-118
- Dunstan PK, Johnson CR (1998) Spatio-temporal variation in coral recruitment at different scales on Heron Reef,

- southern Great Barrier Reef. *Coral Reefs* 17:71-81
- Edmunds PJ, Gates RD, Gleason DF (2001) The biology of larvae from the reef coral *Porites astreoides*, and their response to temperature disturbances. *Mar Biol* 139:981-989
- English S, Wilkinson C, Baker V (eds) (1997) Survey manual for tropical marine resources, 2nd edn., Australian Institute for Marine Science, Townsville
- Fadlallah YH (1983) Sexual reproduction, development and larval biology in scleractinian corals. *Coral Reefs* 2:129-150
- Fisk DA, Harriott VJ (1990) Spatial and temporal variation in coral recruitment on the Great Barrier Reef: implications for dispersal hypothesis. *Mar Biol* 107:485-490
- Glassom D, Zakai D, Chadwick-Furman NE (2004) Coral recruitment: a spatio-temporal analysis along the coastline of Eilat, northern Red Sea. *Mar Biol* 144:641-651
- Hay ME (1991) Fish-seaweed interactions on coral reefs: effects of herbivorous fishes and adaptation of their prey. In: Sale PF (ed) *The ecology of reef fish*. Meade Press, San Diego, pp 96-117
- Harrison PL, Wallace CC (1990) Reproduction, dispersal and recruitment of scleractinian corals. In: Dubinsky Z (ed) *Coral Reefs*. Elsevier Science, Amsterdam pp 133-207
- Harriott VJ (1985) Recruitment patterns of scleractinian corals at Lizard Island, Great Barrier Reef. *Proc 5th Int Coral Reef Cong* 4:367-372
- Harriott VJ, Fisk DA (1987) A comparison of settlement plate types for experiments on the recruitment of scleractinian corals. *Mar Ecol Prog Ser* 37:201-208
- Harriott VJ (1992) Recruitment patterns of scleractinian corals in an isolated sub-tropical reef system. *Coral Reefs* 11:215-219
- Harriott VJ (1999) Coral recruitment at a high latitude pacific site: a comparison with Atlantic reefs. *Bull Mar Sci* 65:881-891
- Harriott VJ, Banks SA (1995) Recruitment of scleractinian corals in the Solitary Islands Marine Reserve, a high latitude coral-dominated community in eastern Australia. *Mar Ecol Prog Ser* 123:155-161
- Heyward AJ, Negri AP (1999) Natural inducers for coral larval metamorphosis. *Coral Reefs* 18:273-279
- Hughes TP, Baird AH, Dinsdale EA, Moltschanivskyi NA, Pratchett MS, Tanner JE, Willis BL (1999) Patterns of recruitment and abundance of corals along the Great Barrier Reef. *Nature* 397:59-63
- Jackson CR (2004) *An atlas of internal solitary-like waves and their properties*. 2nd Ed. Office of Naval Research, Global Ocean Associates, Alexandria, VA, USA
- Jackson JBC (1977) Competition on marine hard substrata: The adaptive significance of solitary and colonial strategies. *Am Nat* 111: pp 743
- Jantzen C, Schmidt GM, Roder C, Wild C, Khokiattiwong S, Richter C (in preparation) Benthic primary production in response to Large Amplitude Internal Waves in coral reefs
- Keough MJ, Downes BJ (1982) Recruitment and marine invertebrates: the role of active larval choices and early mortality. *Oecologia* 54:348-352
- Kohler KE, Gill SM (2006) Coral Point Count with Excel extensions (CPCe): A Visual Basic program for the determination of coral and substrate coverage using random point count methodology. *Computers & Geosciences* 32:1259-1269
- Kojis BL, Quinn NJ (2001) The importance of regional differences in hard coral recruitment rates for determining the need for coral restoration. *Bull Mar Sci* 69:967-974
- Kuffner IB, Paul VJ (2004) Effects of the cyanobacterium *Lyngbya majuscula* on larval recruitment of the reef corals *Acropora surculosa* and *Pocillopora damicornis*. *Coral Reefs* 23:455-458
- Kuffner IB, Walters LJ, Becerro MA, Paul VJ, Ritson-Williams R, Beach KS (2006) Inhibition of coral recruitment by macroalgae and cyanobacteria. *Mar Ecol Prog Ser* 323:107-117
- Kurihara H (2008) Effects of CO₂-driven ocean acidification on the early developmental stages of invertebrates. *Mar Ecol Prog Ser* 373:275-284
- Lee CS, Walford J, Goh BPL (2009) Adding coral rubble to substrata enhances settlement of *Pocillopora damicornis* larvae. *Coral Reefs* 28:529-533
- Leichter JJ, Wing SR, Miller SL, Denny MW (1996) Pulsed delivery of subthermoline water to Conch Reef (Florida Keys) by internal bores. *Limnol Oceanogr* 41:1490-1501
- Leichter JJ, Stewart HL, Miller SL (2003) Episodic nutrient transport to Florida coral reefs. *Limnol Oceanogr* 48:1394-1407
- Leichter JJ, Genovese SJ (2006) Intermittent upwelling and subsidized growth of the scleractinian coral *Madracis mirabilis* on the deep fore-reef slope of Discovery Bay, Jamaica. *Mar Ecol Prog Ser* 316:95-103
- Littler MM, Littler DS (1984) Models of tropical reef biogenesis: the contribution of algae. *Prog Phycol Res* 3:322-365
- Littler MM, Taylor PR, Littler DS (1983) Algal resistance to herbivory on a Caribbean barrier reef. *Coral Reefs* 2:111-118
- Loya Y (1972) Community structure and species diversity of hermatypic corals at Eilat, Red Sea. *Mar Biol* 13:100-123
- Loya Y (1976) Effects of water turbidity and sedimentation on the community structure of Puerto Rican corals. *Bull Mar Science* 26:450-466
- Loya Y, Slobodkin LB (1971) The coral reefs of Eilat (Gulf of Eilat, Red Sea). In: Stoddart DR, Yonge M (ed)

- Regional Variation in Indian Ocean Coral Reefs. pp:117-139. Academic Press, New York
- Maida M, Sammarco PW, Coll JC (1995) Effect of soft corals on scleractinian coral recruitment. I: Directional allelopathy and inhibition of settlement. *Mar Ecol Prog Ser* 121:191-202
- Marubini F, Atkinson MJ (1999) Effects of lowered pH and elevated nitrate on coral calcification. *Mar Ecol Prog Ser* 188:117-121
- Marubini F, Bennett H, Langdon C, Atkinson MJ (2001) Dependence of calcification on light and carbonate ion concentration for the hermatypic coral *Porites compressa*. *Mar Ecol Prog Ser* 220:153-162
- Miller MW, Weil E, Szmant AM (2000) Coral recruitment and juvenile mortality as structuring factors for reef benthic communities in Biscayne National Park, USA. *Coral Reefs* 19:115-123
- Morse DE, Hooker N, Morse ANC, Jensen RA (1988) Control of larval metamorphosis and recruitment in sympatric agariciid corals. *J Exp Mar Biol Ecol* 116:193-217
- Morse ANC, Iwao K, Baba M, Shimoike K, Hayashibara T, Omori M (1996) An ancient chemosensory mechanism brings new life to coral reefs. *Biol Bull (Woods Hole)* 191:149-154
- Moum JN, Klymak JM, Nash JD, Perlin A, Smyth WD (2007) Energy transport by nonlinear internal waves. *J Phys Oceanogr* 37:1968-1988
- Mumby PJ (1999) Bleaching and hurricane disturbance to populations of coral recruits in Belize. *Mar Ecol Prog Ser* 190:27-35
- Nielsen TG, Bjørnsen PK, Boonruang P, Fryd M, Hansen PJ, Janekarn V, Limtrakulvong V, Munk P, Hansen OS, Satapoomin S, Sawangraruks S, Thomsen HA, Østergaard JB (2004) Hydrography, bacteria and protist communities across the continental shelf and shelf slope of the Andaman Sea (NE Indian Ocean). *Mar Ecol Prog Ser* 274:69-86
- Norström AV, Lokrantz J, Nyström M, Yap HT (2006) Influence of dead coral substrate morphology on patterns of juvenile coral distribution. *Mar Biol DOI* 10.1007/s00227-006-0458-2
- Osborne AR, Burch TL (1980) Internal solitons in the Andaman Sea. *Science (Wash.)* 208(4443):457-460
- Perry RB, Schmike GR (1965) Large amplitude internal waves observed off the northwest coast of Sumatra. *J Geophys Res* 70:2319-2324
- Phongsuwan N (1991) Recolonization of a coral reef damaged by a storm on Phuket Island, Thailand. *Phuket Mar Biol Cent Res Bull* 56:75-83
- Phongsuwan N, Yeemin T, Worachananant S, Duangsawadi M, Chotiyaputta C, Comley J (2006) Post-tsunami status of coral reefs and other coastal ecosystems on the Andaman Sea coast of Thailand. In *Status of coral reefs in tsunami affected countries: 2005*. Australian Institute of Marine Science pp 63-77.
- Phongsuwan N, Brown BE (2007) The influence of the Indian ocean tsunami on coral reefs of western Thailand, Andaman Sea, Indian Ocean. In Stoddart DR (ed) *Tsunamis and coral reefs*. Atoll Research Bulletin No. 544
- Phongsuwan N, Yamarunpattana C, Paokanta Y, Areechon P (2008) Status of Coral Reefs in the Surin and Similan Archipelagos, Thailand. In Obura DO, Tamelander J, Linden O (ed) *Ten years after bleaching -facing the consequences of climate change in the Indian Ocean*. CORDIO Status report 2008, Mombasa
- Pineda J. (1995) An internal tidal bore regime at nearshore stations along western U.S.A.: Predictable upwelling within the lunar cycle. *Cont Shelf Research* 15(8):1023-1041
- Plathong S (2005) Survey of tsunami impact on coral reef and the reef recovery project for Similan islands marine national park. Coral Reef and Benthos Res Unit, Centre Biod Penins Thailand, Dep Biol, Prince of Songkla University Had Yai, Songkla, Thailand
- Preece A, Johnson CR (1993) Recovery of model coral communities: complex behaviours from interaction of parameters operating at different spatial scales. In: Green D, Bossomaier T (eds) *Complex systems*. IOS Press, Amsterdam, pp 69-81
- Richmond RH (1988) Competency and dispersal potential of planula larvae of a spawning versus a brooding coral. In: *Proc 6th Int Coral Reef Symp* 2:827-832
- Richmond RH, Hunter CL (1990) Reproduction and recruitment of corals: comparisons among the Caribbean, the tropical Pacific, and the Red Sea. *Mar Ecol Prog Ser* 60:185-203
- Roder C, Fillingner L, Jantzen C, Schmidt GM, Khokiattiwong S, Richter C (accepted) Trophic response of corals to Large Amplitude Internal Waves. *Mar Ecol Prog Ser*
- Rogers CS, Fitz HC, Gilnack M, Beets J, Hardin J (1984) Scleractinian coral recruitment patterns at Salt River Submarine Canyon, St. Croix, U.S. Virgin Islands. *Coral Reefs* 3:69-76
- Sammarco PW, Andrews JC (1988) Localized dispersal and recruitment in Great Barrier Reef corals: The Helix Experiment. *Science* 239:1422-1424
- Sawall Y, Phongsuwan N, Richter C (2010) Coral recruitment and recovery after the 2004 Tsunami around the Phi Phi Islands (Krabi Province) and Phuket, Andaman Sea, Thailand. *Helgol Mar Res doi:10.1007/s10152-010-0192-5*
- Schmidt GM, Phongsuwan N, Roder C, Jantzen C, Khokiattiwong S, Richter C (submitted) Coral community and physico-chemical characteristics in response to Large Amplitude Internal Waves. *Mar Ecol Prog Ser*
- Schmidt GM, Phongsuwan N, Richter C (in preparation) Carbonate-accretion and erosion on the scleractinian coral *Porites lutea* in response to Large Amplitude Internal Waves
- Schneider K, Erez J (2006) The effect of carbonate chemistry on calcification and photosynthesis in the hermatypic coral *Acropora eurystoma*. *Limnol Oceanogr* 51:1284-1293

- Sheppard C (2009) Large temperature plunges recorded by data loggers at different depths on an Indian Ocean atoll: comparison with satellite data and relevance to coral refuges. *Coral Reefs* 28:399-403
- Smith SR (1992) Patterns of coral recruitment and post-settlement mortality on Bermuda's reefs: comparisons to Caribbean and Pacific reefs. *Am Zool* 32:663-673
- Smith SR (1997) Patterns of coral settlement, recruitment, and juvenile mortality with depth at Conch Reef, Florida. *Proc 8th Int Coral Reef Symp* 2:1197-1202
- Soong K, Chen M, Chen, C, Dai C, Fan T, Li J, Fan H (2003) Spatial and temporal variation of coral recruitment in Taiwan. *Coral Reefs* 22:224-228
- Spalding MD; Ravilious C, Green EP (2001) *World atlas of coral reefs*. University of California Press, Berkeley, California, USA.
- Steneck PS (1988) Herbivory on coral reefs: a synthesis. *Proc 6th Int Coral Reef Symp* 1:37-49
- Thongtham N, Chansang H (1999) Influence of surface complexity on coral recruitment at Maiton island, Phuket, Thailand. *Phuket Mar Biol Cent Special Publ* 20:93-100
- Tomascik T (1991) Settlement patterns of Caribbean scleractinian corals on artificial substrata along a eutrophication gradient, Barbados, West Indies. *Mar Ecol Prog Ser* 77:261-269
- Vermeij MJA, Sandin SA (2008) Density-dependent settlement and mortality structure. The earliest life phases of a coral population. *Ecology* 89:1994-2004
- Veron JEN (2000) *Corals of the World*. Australian Institute of Marine Science, Townsville, Australia
- Vlasenko V, Hutter K (2002) Numerical experiments on the breaking of solitary internal waves over a slope-shelf topography. *J Phys Oceanogr* 32:1779-1793
- Vlasenko V, Stashchuk N (2007) Amplification and suppression of internal waves by tides over variable bottom topography. *J Phys Oceanogr* 36:1959-1973
- Walker DI, Ormond RFG (1982) Coral death from sewage and phosphate pollution at Aquaba, Red Sea. *Mar Poll Bull* 13:21-25
- Wallace CC (1985) Seasonal peaks and annual fluctuations in recruitment of juvenile scleractinian corals. *Mar Ecol Prog Ser* 21: 289-298
- Wallace CC, Bull GD (1982) Patterns of juvenile coral recruitment on a reef front during a spring-summer spawning period. *Proc. 4th Int. Coral Reef Symp. Manila* 2:345-350
- Wittenberg M, Hunte W (1992) Effects of eutrophication and sedimentation on juvenila corals. *Mar Biol* 112:131-138
- Wu G, Zhang Y (1998) Tibetan Plateau Forcing and the Timing of the Monsoon Onset over South Asia and the South China Sea. *American Meteorol Soc* 126:913-927
- www.reefbase.org/gis_maps
- Yeemin T, Sutthacheep M, Pettongma R (2006) Coral reef restoration projects in Thailand. *Ocean & Coastal Management* 49:562-575

General thesis discussion and conclusions

Feedback to the initially proposed research questions

1. This thesis showed that LAIW reach islands bordering the eastern Andaman Sea basin with their strongest impact in the deeper slope areas of the exposed western island sides which declines with declining depth in west and increasing shelter in east up to complete LAIW-shelter in eastern shallow areas. (Chapter 1 – 5)
2. LAIW implicated dramatic high-frequency variations (in the order of minutes) in the physico-chemical environment at the impacted island sides, including abrupt drops in temperature (up to 10 °C below ambient), pH (up to 0.6 units below ambient), and oxygen concentration (down to 12 % saturation), coming with concomitant increases in current speeds (up to 6-fold), and inorganic nutrient concentrations (up to 12-fold for nitrate and nitrite, 5-fold for silicate and over 20-fold for phosphate). (Chapter 1 – 5)
3. The formation of an actual coral reef framework was restricted to the sheltered east; however the communities of scattered corals growing directly on the granite basement in the exposed west were more diverse and species rich. This is likely due to the alternating impact of south-west monsoon (May to October) and LAIW from above and below contributing to a spatio-temporal heterogeneity, maintaining the coral community in a non-equilibrium state of intermediate disturbances which enhances species diversity. (Chapter 1)
4. Despite the profound effects of LAIW on the metabolism of the various primary producers and the varying contributions of the different functional groups of primary producers, the overall primary production was similar at both west and east, indicating a high plasticity of primary production in the LAIW-affected west. Similarly the dominating reef building coral *Porites lutea* showed similar net photosynthesis in exposed west and sheltered east island sides but with 40 % higher pigment concentrations in west, likely due to the adaptation to lower light availability and enhanced nutrient concentrations. (Chapter 2)
5. The common coral *Pocillopora meandrina* revealed significantly higher biomass and protein content together with a more heterotrophic status in the exposed west compared to east corals due to LAIW-enhanced fluxes of organic matter. This resulted in higher energy reserves in west corals and a higher resilience to environmental stress (artificial darkness). (Chapter 3)

6. The growth rates of the massive coral *Porites lutea* and bioerosion on its' dead skeleton, both were lowest in the highly LAIW-impacted western deep slopes and highest within the dense coral framework in east shallow. Growth was likely reduced due to the cumulative effects of low temperature, low pH, i.e. low Ω_{arag} , and enhanced nutrient concentrations, whereas bioerosion rates seemed to be directly related to the particular amount of coral cover. A carbonate budget calculated for west and east implicating the in each case living and dead coral cover as well as coral growth (of *Porites lutea*) and bioerosion rates (on dead coral skeleton of *P. lutea*), could not satisfactorily explain the extreme differences in reef development especially between west shallow and east deep areas. This suggests that other factors, i.e. differential rates of early juvenile mortality and surface wave impact, play a more important role. However the budget confirmed that reduced coral growth and alike reduced bioerosion were balanced but only barely positive under the highly variable conditions in west deep (Chapter 4)
7. On natural reef substrate the abundances of coral recruits were highest in west shallow. However with increasing exposure period of experimental settlement tiles, the proportion of juvenile corals increased in east but decreased in west, indicating a failure of recruits to establish permanently on the LAIW-exposed sides in spite of the higher initial spat fall. Early recruitment seemed to be independent of LAIW-exposure and rather determined by larval behaviour, predation and substrate availability, while the subsequent establishment of young corals appeared to be related to LAIW intensity, reflecting the lack of true reefs on the LAIW-exposed west sides of the islands.

Corals and coral communities under LAIW-impact

The present thesis contributes to a better understanding of basic relations between the physico-chemical impact of LAIW and the biological reactions and adaptations within exposed reef areas on organism- (corals), functional group- (turf algae, microphytobenthos in reef sediments, internal and external bioeroders), and ecosystem levels (coral community composition, primary production- and carbonate-budget, framework development).

As initially proposed, this thesis showed that LAIW are entraining a whole 'cocktail' of abrupt environmental changes in frequently recurring short-term events into coral reef areas (Chapter 1). The findings of the present work suggest that corals are able to adapt and live

under these highly stressful conditions yet at the expense of the development of true coral reefs.

The tight coupling of scleractinian corals and their symbiotic zooxanthellae enables them to adapt to a wide range of environmental conditions such as different light intensities (Falkowski et al. 1990, Falkowski and Dubinsky 1981, Titlyanov 1991). They are able to compensate reduced light availability via the uptake of inorganic nutrients by the zooxanthellae, which may increase the cell-specific density of the algae (Ferrier-Pagès et al. 2001) and the efficiency of the photosynthetic process (Muscatine et al. 1989, Ferrier-Pagès et al. 2000). In this context, the present work showed that the coral *Porites lutea* is able to achieve high photosynthetic efficiency under LAIW influence with low light conditions due to the enhanced inorganic nutrient supply (Chapter 2). The resulting primary production was similar to that of corals not exposed to LAIW. At the same time the combination of reduced light intensity and cold water intrusions was obviously advantageous for LAIW-exposed corals mitigating damage to the photosynthetic apparatus during cold water stress (Jokiel & Coles 1977, Saxby et al. 2003).

Corals with sufficient food supply in contrast to starved corals, have been shown to reveal better physiological conditions and higher survival rates when put under artificial bleaching conditions (Grottoli et al. 2006, Borell et al. 2008) and to be able to sustain their energy supply under reduced light intensities (Houlbrèque et al. 2004). The in-situ investigations on *Pocillopora meandrina* in the present thesis support these laboratory findings (Chapter 3). This coral was shown to reveal higher energetic reserves in terms of biomass and protein content when grown under LAIW influence and to be able to shift to a more heterotrophic status when put under environmental stress, such as artificial darkness, when exposed to enhanced fluxes of particulate organic matter and plankton entrained by LAIW. These findings support the initially proposed third hypothesis, which predicted a higher heterotrophic status of LAIW-exposed corals due to the enhanced supply of plankton and organic matter under light-depleted conditions.

These metabolic adaptations of corals grown under the influence of LAIW, their plasticity in photosynthesis and heterotrophic status, as well as their enhanced resilience to stress seemed to be either mainly or completely used for their general viability under LAIW conditions. No supportive effect of higher pigment concentrations (Chapters 2 and 3), biomass and protein content (Chapter 3) could be observed on the growth performance of corals (Chapter 4).

Previous investigations on coral growth demonstrated that calcification can be reduced under low light (Falkowski et al. 1990, Lough & Barnes 2000) and enhanced nutrient

concentrations (Ferrier-Pagès et al. 2000, 2001), is highly sensitive to low temperatures (Coles & Fadlallah 1991, Gates et al. 1992, Al Horani 2005), and dependent on a sufficient aragonite saturation state Ω_{arag} of the seawater (Marubini & Atkinson 1999, Marubini et al. 2001, Schneider & Erez 2006, Cohen & Holcomb 2009). The significantly reduced growth rates of *Porites lutea* exposed to LAIW influence supported these findings and confirmed that the cumulative negative effects of reduced light, temperature and pH (Chapter 4) could not be compensated by metabolic adaptations, which themselves benefited from enhanced nutrient concentrations (Chapters 2 and 3). The findings of other studies (Schneider & Erez 2006, Andersson et al. 2009) suggest that corals under reduced pH-conditions similar to those reported here for the Similan Islands during strong LAIW-impacts should actually reveal a net loss of skeleton due to carbonate dissolution at the site of calcification (Cohen & Holcomb 2009). However in the present thesis the studied corals revealed positive, even though small growth rates even at the sites of high LAIW influence. There are two possible explanations for this result: (1) The short-termed, pulsed occurrence of LAIW-impacts might permit a time-delayed compensation of the periodic corrosive water conditions during the calcification process, as the uptake of carbon ions and their incorporation into the skeleton do not occur at the same time (Erez & Braun 2007), and/or (2) coral growth in LAIW-exposed sites is mainly restricted to the transition periods between high LAIW- and south-east monsoon seasons, as during the latter, growth rates of *Porites lutea* had been shown to be reduced due to the constantly higher turbidity and lower light regime caused by the strong swell (Scoffin et al. 1992).

In this context the high initial settlement rates of coral recruits at the shallow LAIW-exposed west sides of the islands as found in this thesis (Chapter 5) presumably occurred particularly during low LAIW- and high south-east monsoon seasons. The coral recruits likely took advantage of the newly exposed substrates due to the impact of surface gravity waves (Becerro et al. 2006). Further during these seasons they had to deal mainly with biological factors, such as substrate suitability (Morse et al. 1988, Raimondi & Morse 2000), predation and competitors for space (Maida et al. 1995, Kuffner et al. 2006), but they were relatively undisturbed by the influence of LAIW. The subsequent failure of young corals to establish permanently under high LAIW influence is in accordance with other studies which demonstrated the negative influence of low temperature (Edmunds et al. 2001), increased inorganic nutrient concentrations (Tomascik 1991, Wittenberg & Hunte 1992, Abelson et al. 2005), and reduced pH, i.e. Ω_{arag} (Albright et al. 2008, Kurihara 2008, Cohen et al. 2009) on the growth of especially young corals.

Chapter 1 however demonstrates that despite the extreme environmental conditions in western areas entrained by LAIW especially in the deep and by surface gravity waves during the monsoon periods into shallow areas, there has been the establishment of a more diverse coral community in intermediate depths than in the non-impacted sheltered east. This is in accordance with the intermediate disturbance hypothesis (Connell 1978, 1979), which has been specified also to coral reef ecosystems (Connell 1997). The spatio-temporal heterogeneity in intermediate depths at western island slopes maintains the coral community in a non-equilibrium state of intermediate disturbance due to the alternating effects of LAIW from below and monsoon waves from above. Newly settled coral recruits in this area therefore obviously cope successfully with the prevailing environmental conditions and contribute to an especially species rich community.

Yet although individual corals are able to get along with the environmental challenges at the exposed west sides and even accomplish a relatively high living coral cover in shallow west areas, the formation of a typical coral reef, including the reef framework, is suppressed, which emphasizes the environmental limits for coral reef development (Chapter 1).

Two budget studies have been conducted on the functional group-level for a direct comparison of LAIW-exposed west and sheltered east island sides, one for the overall primary production (Chapter 2) and one more roughly calculated for the overall carbonate budget (Chapter 4).

The total primary production budgets revealed similar values for exposed west and sheltered east sides. This is in contrast to the initially proposed second hypothesis, which predicted different primary production rates for LAIW-exposed and sheltered reef communities, but it highlights the extreme plasticity within the benthic ecosystem to adapt to different environmental conditions and to take advantage of given opportunities such as an enhanced inorganic nutrient supply. The main beneficiaries of the enhanced inorganic nutrient concentrations under LAIW conditions were turf-algae (cf. Williams & Carpenter 1988), revealing higher photosynthetic capacities and growth levels compared to their sheltered counterparts and contributing most to the overall primary production in west. In contrast to that, on the LAIW-sheltered east the microphytobenthic community exhibited the highest productivity emphasizing the importance of the sedimentary microorganisms for the primary production within coral reef communities under non-impacted low-nutrient conditions.

According to several other carbonate budget calculations (Scoffin et al. 1980, Glynn 1988) carbonate accretion by coral growth and carbonate erosion by grazing and boring organisms were positively balanced in this thesis, even at the site of highest LAIW-impact (Chapter 4). Thereby highest rates of both, coral growth and bioerosion were found within the

dense reef areas at the sheltered east sides. This coincides with the general assumption that intense bioerosion concurs with high coral reef cover as the reef framework also harbours its own destructive, eroding and grazing dwellers (Hallock 1988, Glynn 1997). According to that the budget also confirmed that the highly reduced coral cover and the lack of a coral reef framework in west deep areas implicated a proportionally reduced rate of bioerosion. In this context however the high mortality rates of coral nubbins due to intense grazing in west which were found in Chapter 4 were not compatible with a general low bioerosion in this area. The solution for this inconsistency is thought to be the sporadic yet acute impact by non-residential grazers which was not captured in the budget but still had a highly remarkable effect on coral health and survival.

As the lack of a true coral reef framework could not be adequately explained by the carbonate budget calculated from coral growth and bioerosion rates, other factors than these are thought to play a more important role. The apparently too high levels of disturbance in west undermine the formation of contiguously connected coral reef formations from the start: The high mortality rates of young corals failing to establish permanently in west deep and shallow (Chapter 5) prevent the possibility to form bigger skeletal reef structures. Moreover the physical impact by monsoon waves from above (Storlazzi et al. 2005) and the negative stressors (reduced light, temperature, oxygen, pH and increased nutrient concentrations, discussed above) entrained with the frequently strong swell-like currents of LAIW-arrivals directly hamper any attempts of framework construction. These findings widely support the initially proposed first hypothesis, which predicted the inhibition of the development of coral reef frameworks due to the impact of LAIW-entrained stressors, reduced recruitment and enhanced bioerosion. The residential bioerosion was not shown to be disproportionately enhanced under LAIW conditions, but unexpected factors such as bioerosion caused by non-residential grazers might be of importance.

In summary, both budget studies together with the findings in Chapter 1 demonstrated the ability of an ecosystem to develop entirely different community compositions (west versus east), despite their spatial proximity due to the adaptation to highly different environmental conditions.

Conclusions and prospects

The developmental stage and composition of a coral community reflects the net results of the governing physical, chemical and biological factors influencing it (Fishelson 1973, Loya 1976, De Vantier et al. 1998). Corals growing along the western sides of the Similan Islands are

exposed to an extraordinary stressful physico-chemical environment to which they obviously adapted successfully due to their high metabolic plasticity (Chapters 2 and 3). Although the environmental disturbances in west exceed the possibility to develop true coral reef formations, corals are still able to recruit (Chapter 5), grow and develop (Chapter 4). These coral assemblages could therefore provide a clue to coral resilience in an era of global temperature increase and ocean acidification due to their potentially diverse adaptation processes to the steadily entrained 'cocktail' of LAIW-pulsed stressors.

Furthermore LAIW are ubiquitous in South-East Asia and beyond (Jackson 2004, Apel et al. 2006), as already mentioned several times, but they have so far not been considered with an adequate attention regarding their obviously strong effects on corals and coral reef communities. For this reason, the present thesis hopefully contributes to an attraction of further intensive studies in this highly interesting and important field of research.

Literature

- Abelson A, Olinky R, Gaines S (2005) Coral recruitment to the reefs of Eilat, Red Sea: temporal and spatial variation, and possible effects of anthropogenic disturbances. *Mar Pol Bull* 50:576-582
- Albright R, Mason B, Langdon C (2008) Effect of aragonite saturation state on settlement and post-settlement growth of *Porites astreoides* larvae. *Coral Reefs* 27:485-490
- Al-Horani FA (2005) Effects of changing seawater temperature on the photosynthesis and calcification in the scleractinian coral *Galaxea fascicularis*, measured with O₂, Ca²⁺ and pH microsensors. *Scientia Marina* 69:347-354
- Andersson AJ, Kuffner IB, Mackenzie FT, Jokiel PL, Rodgers KS, Tan A (2009) Net loss of CaCO₃ from coral reef communities due to human induced seawater acidification. *Biogeosci Discuss* 6:2163-2182
- Apel JR, Ostrovsky LA, Stepanyants YA, Lynch JF (2006) Internal Solitons in the Ocean. Technical report WHOI-2006-04, Oceanographic Inst, Woods Hole
- Becerro MA, Bonito V, Paul VJ (2006) Effects of monsoon-driven wave action on coral reefs of Guam and implications for coral recruitment. *Coral Reefs* 25:193-199
- Borell EM, Yuliantri AR, Bischof K, Richter C (2008) The effect of heterotrophy on photosynthesis and tissue composition of two scleractinian corals under elevated temperature. *J Exp Mar Biol Ecol* 364:116-123
- Cohen AL, Holcomb M (2009) Why corals care about ocean acidification – uncovering the mechanism. *Oceanogr* 22:118-127
- Cohen AL, McCorkle DC, de Putron S, Gaetani GA, Rose KA (2009) Morphological and compositional changes in the skeletons of new coral recruits reared in acidified seawater: Insights into biomineralization response to ocean acidification. *Geochem Geophys Geosyst* 10(7), Q07005, doi:10.1029/2009GC002411
- Coles SL, Fadlallah UH (1991) Reef coral survival and mortality at low temperatures in the Arabian Gulf: new species specific lower temperature limits. *Coral Reefs* 9:231-237
- Connell JH (1978) Diversity in tropical rain forests and coral reefs. *Science* 199:1302-1310
- Connell JH (1979) Tropical rain forests and coral reefs as open non-equilibrium systems. In: Anderson R, Turner B, Taylor L (eds) *Population dynamics*. Blackwell, Oxford, pp 141-163
- Connell JH (1997) Disturbance and recovery of coral assemblages. *Coral Reefs* 16 (Suppl):101-113
- De Vantier LM, Death G, Done TJ, Turak E (1998) Ecological assessment of a complex natural system: a case study from the Great Barrier Reef. *Ecol Appl* 8(2):480-96
- Edmunds PJ, Gates RD, Gleason DF (2001) The biology of larvae from the reef coral *Porites astreoides*, and their response to temperature disturbances. *Mar Biol* 139:981-989
- Falkowski PG, Dubinsky Z (1981) Light-shade adaptation of *Stylophora pistillata*, a hermatypic coral from the Gulf of Eilat. *Nature* 289:172-174
- Falkowski PG, Jokiel PL, Kenzie RAI (1990) Irradiance and corals. *Ecosyst World* 25:89-107
- Ferrier-Pagès C, Gattuso J P, Dallot S, Jaubert J (2000) Effect of nutrient enrichment on growth and photosynthesis of the zooxanthellate coral *Stylophora pistillata*. *Coral Reefs* 19: 103-113
- Ferrier-Pagès C, Schoelzke V, Jaubert J, Muscatine L, Hoegh-Guldberg O (2001) Response of a scleractinian

- coral, *Stylophora pistillata*, to iron and nitrate enrichment. *J Exp Mar Biol Ecol* 259:249-261
- Fishelson L (1973) Ecology of coral reefs in the Gulf of Aqaba (Red Sea) influenced by pollution. *Oecologia* 12:55-67
- Gates RD; Baghdasarian G, Muscatine L (1992) Temperature stress causes host cell detachment in symbiotic cnidarians: Implications for coral bleaching. *Biol Bull* 182:324-332
- Glynn PW (1997) Bioerosion and coral reef growth: a dynamic balance. In: Birkeland C (ed) *Life and death of coral reefs*. Chapman and Hall, New York, pp 68-95
- Grottoli AG, Rodrigues LJ, Palardy JE (2006) Heterotrophic plasticity and resilience in bleached corals. *Nature* 440:1186-1189
- Hallock P(1988) The role of nutrient availability in bioerosion: consequences to carbonate buildups (1988) *Palaeogeogr Palaeoclimat Palaeoecol* 63:275-291
- Houlbrèque F, Tambutte E, Allemand D, Ferrier-Pages C (2004) Interactions between zooplankton feeding, photosynthesis and skeletal growth in the scleractinian coral *Stylophora pistillata*. *J Exp Biol* 207:1461-1469
- Jackson CR (2004) *An atlas of internal solitary-like waves and their properties*. 2nd Ed. Office of Naval Research, Global Ocean Associates, Alexandria, VA, USA
- Jokiel PL, Coles SL (1977) Effects of temperature on the mortality and growth of Hawaiian reef corals. *Mar Biol* 43:201-208
- Kuffner IB, Walters LJ, Becerro MA, Paul VJ, Ritson-Williams R, Beach KS (2006) Inhibition of coral recruitment by macroalgae and cyanobacteria. *Mar Ecol Prog Ser* 323:107-117
- Kurihara H (2008) Effects of CO₂-driven ocean acidification on the early developmental stages of invertebrates. *Mar Ecol Prog Ser* 373:275-284
- Lough JM, Barnes DJ (2000) Environmental controls on growth of the massive coral *Porites*. *J Exp Mar Biol Ecol* 245:225-243
- Loya Y (1976) Effects of water turbidity and sedimentation on the community structure of Puerto Rican corals. *Bull Mar Science* 26:450-466
- Maida M, Sammarco PW, Coll JC (1995) Effect of soft corals on scleractinian coral recruitment. I: Directional allelopathy and inhibition of settlement. *Mar Ecol Prog Ser* 121:191-202
- Marubini F, Atkinson MJ (1999) Effects of lowered pH and elevated nitrate on coral calcification. *Mar Ecol Prog Ser* 188:117-121
- Marubini F, Bennett H, Langdon C, Atkinson MJ (2001) Dependence of calcification on light and carbonate ion concentration for the hermatypic coral *Porites compressa*. *Mar Ecol Prog Ser* 220:153-162
- Morse ANC, Iwao K, Baba M, Shimoike K, Hayashibara T, Omori M (1996) An ancient chemosensory mechanism brings new life to coral reefs. *Biol Bull (Woods Hole)* 191:149-154
- Muscatine L, Falkowski PG, Dubinsky Z, Cook PA, McCloskey LR (1989) The effect of external nutrient resources on the population dynamics of zooxanthellae in a reef coral. *Proc R Soc Lond* 236:311-324
- Raimondi PT, Morse NC (2000) The consequences of complex larval behaviour in a coral. *Ecology* 81:3193-3211
- Saxby T, Dennison WC, Hoegh-Guldberg O (2003) Photosynthetic response of the coral *Montipora digitata* to cold temperature stress. *Mar Ecol Prog Ser* 248:85-97
- Schneider K, Erez J (2006) The effect of carbonate chemistry on calcification and photosynthesis in the hermatypic coral *Acropora eurystoma*. *Limnol Oceanogr* 51:1284-1293
- Scoffin TP, Stearn CW, Boucher D, Frydl P, Hwakins CM, Hunter IG, MacGeachy JK (1980) Calcium carbonate budget of a fringing reef on the west coast of Barbados. *Bull Mar Sci* 30(2):475-508
- Storlazzi CD, Brown EK, Field ME, Rodgers K, Jokiel PL (2005) A model for wave control on coral breakage and species distribution in the Hawaiian Islands. *Coral Reefs* 24:43-55
- Titlyanov EA (1991) The stable level of coral primary production in a wide light range. *Hydrobiologia* 216/217:383-387
- Tomascik T (1991) Settlement patterns of Caribbean scleractinian corals on artificial substrata along a eutrophication gradient, Barbados, West Indies. *Mar Ecol Prog Ser* 77:261-269
- Williams SL, Carpenter RC (1988) Nitrogen-limited primary productivity of coral reef algal turfs: potential contribution of ammonium excreted by *Diadema antillarum*. *Mar Ecol Prog Ser* 47:145-152
- Wittenberg M, Hunte W (1992) Effects of eutrophication and sedimentation on juvenila corals. *Mar Biol* 112:131-138

Annex 1

Supplementary 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)

Supplementary 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 microphthalmalma</i>							•										
<i>Acropora monticulosa</i>																	
<i>Acropora nasuta</i>													•				
<i>Acropora nobilis</i>					•		•									•	
<i>Acropora pallifera</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 heliopera</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>	•																

Supplementary Table 2 continued

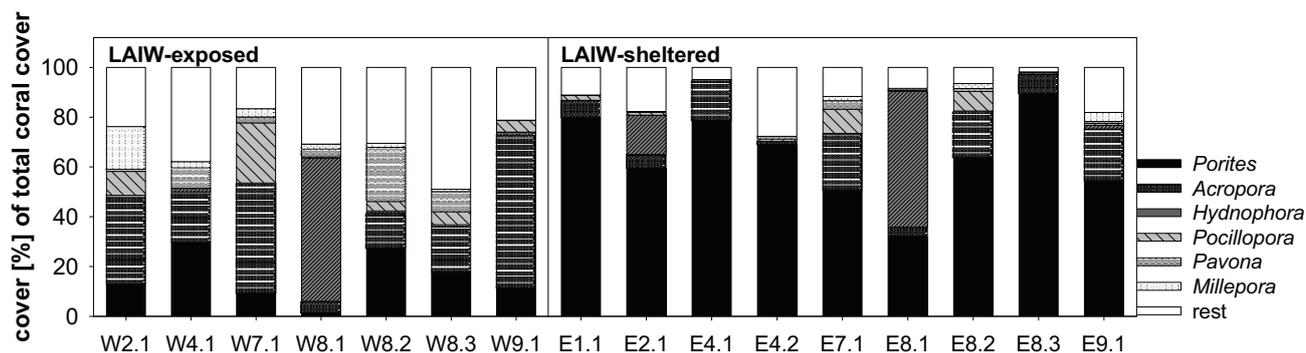
coral taxa	West								East								
	W2.1	W4.1	W7.1	W8.1	W8.2	W8.3	W9.1		E1.1	E2.1	E4.1	E4.2	E7.1	E8.1	E8.2	E8.3	E9.1
<i>Favia matthaii</i>	
<i>Favia pallida</i>				.										.			
<i>Favia pallifera</i>		.															
<i>Favia speciosa</i>		.															
<i>Favia stelligera</i>														.		.	.
<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 caliculata</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>

Supplementary Table 2 continued

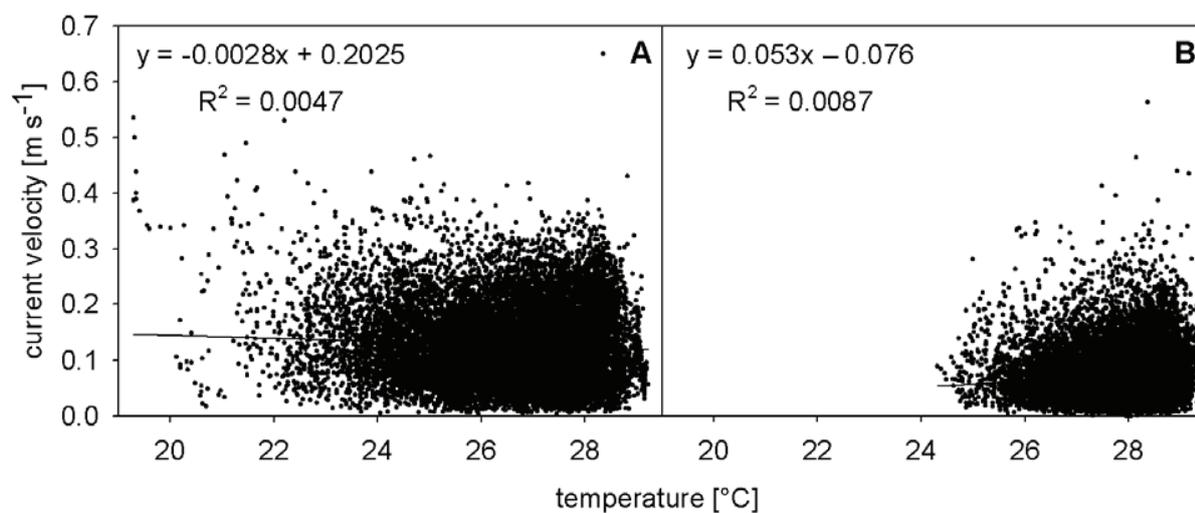
coral taxa	West								East								
	W2.1	W4.1	W7.1	W8.1	W8.2	W8.3	W9.1	E1.1	E2.1	E4.1	E4.2	E7.1	E8.1	E8.2	E8.3	E9.1	
<i>Montipora venosa</i>							•										
<i>Montipora</i> sp. -encrust	•	•	•	•	•	•	•	•		•						•	
<i>Montipora</i> sp.2 encrust							•									•	
<i>Montipora</i> sp.3 - encrust							•									•	
<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 lichtensteini</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	

Supplementary 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 $*0.05 > P \geq 0.01$, $**0.01 > P \geq 0.001$, $***P < 0.001$)

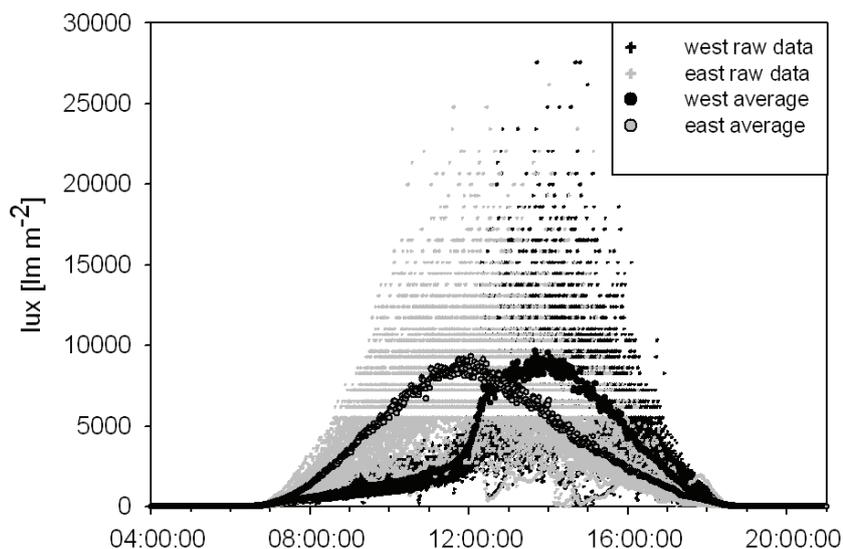
A Current velocity [m s^{-1}]					B lux [lm m^{-2}]				
Kruskal-Wallis test					Kruskal-Wallis test				
0.000***					0.000***				
	W 20 m	W 7 m	E 20 m	E 7 m		W 20 m	W 7 m	E 20 m	E 7 m
W 20 m					W 20 m				
W 7 m	n.s.				W 7 m	0.001***			
E 20 m	0.001***	0.001***			E 20 m	0.001***	0.001***		
E 7 m	0.001***	0.001***	0.001***		E 7 m	0.001***	0.001***	0.001***	
C $\text{Si}(\text{OH})_4$ [$\mu\text{mol L}^{-1}$]					PO_4^{3-} [$\mu\text{mol L}^{-1}$]				
Kruskal-Wallis test					Kruskal-Wallis test				
0.002**					n.s.				
	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	0.001***	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				
0.009**					n.s.				
	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				
n.s.					n.s.				
	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.	



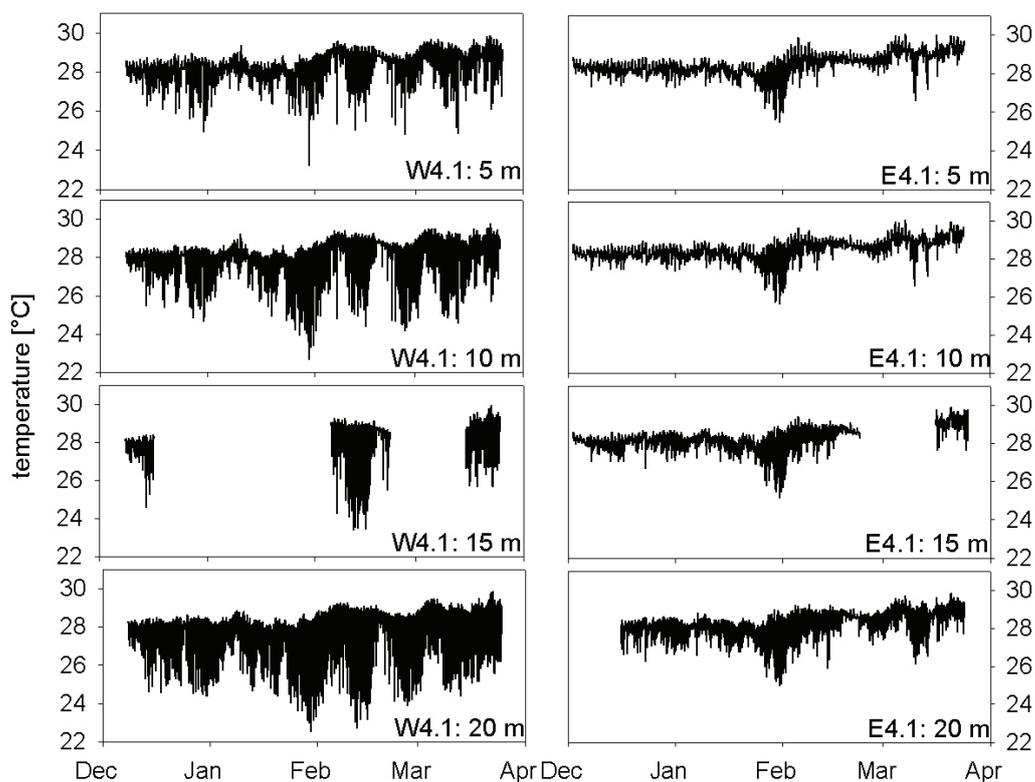
Supplementary Figure 1 Most abundant genera of stony corals as percentage of living coral cover on LAIW-exposed west (W), and east (E) sides (12 to 16 m depth, grouped by N-S orientation).



Supplementary 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.



Supplementary Figure 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.

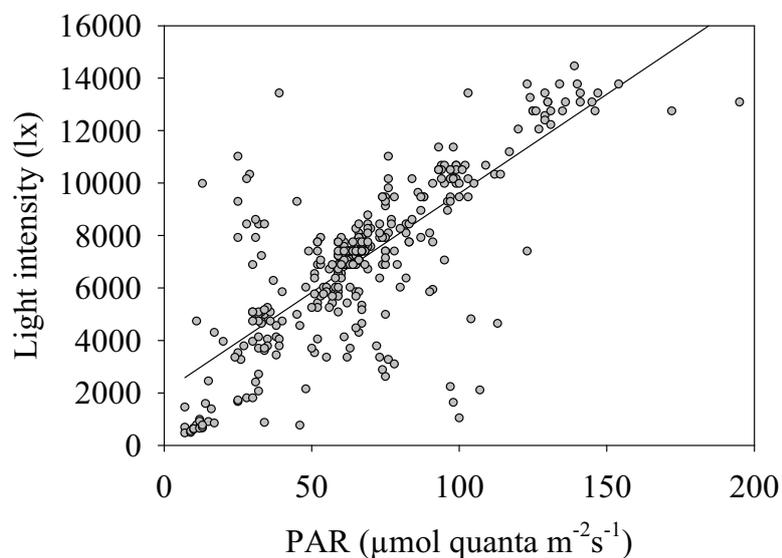


Supplementary Figure 4 Large Amplitude Internal Wave (LAIW) associated temperature variations at the Similan Islands. Examples are given for temperature logger readings from LAIW-exposed (W 4.1) and sheltered (E 4.1) sides of Koh Miang in 20 m (within LAIW swash depth) 15 m and 10 m (intermediate LAIW 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).

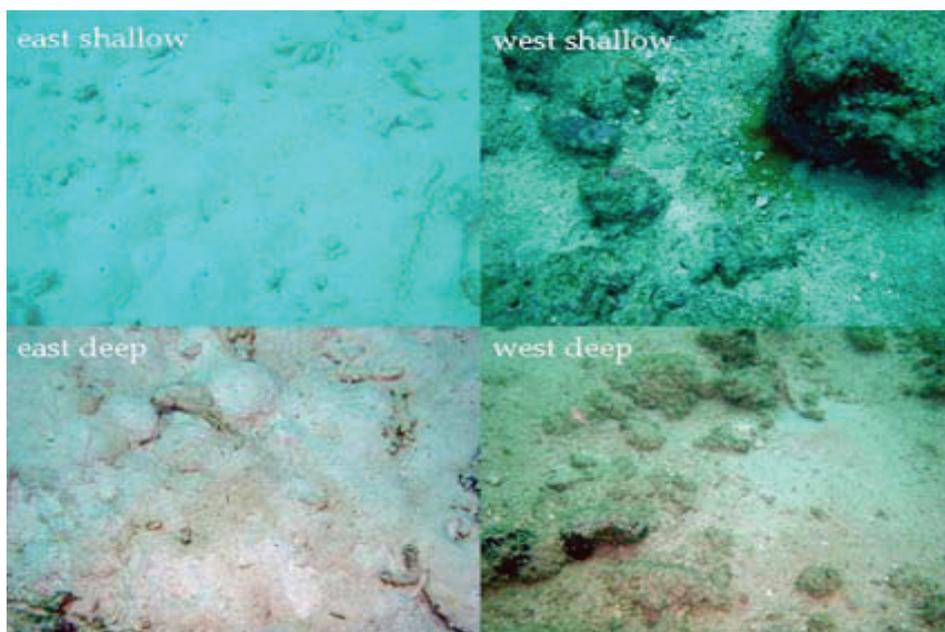
Annex 2

Supplementary 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.

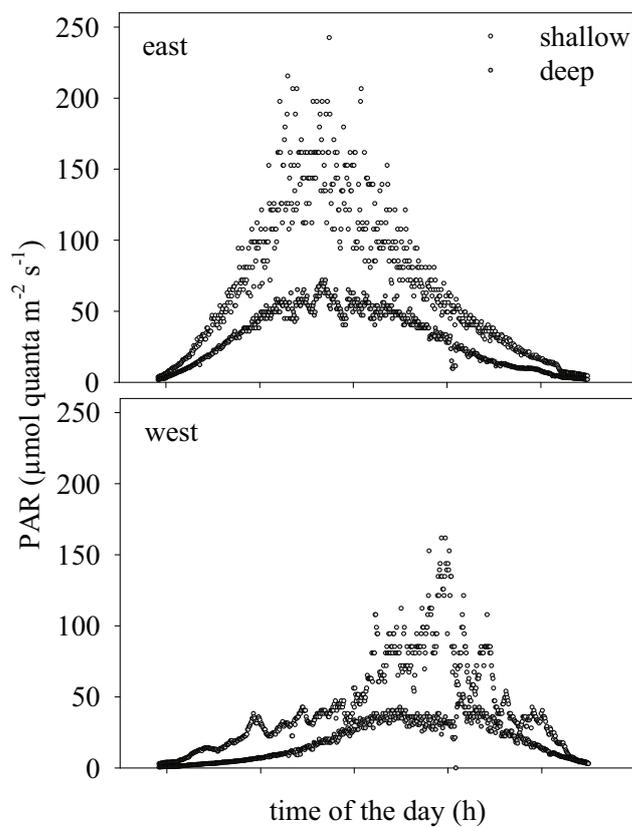
Site	Koh #4	Koh #2	Koh #7	Koh #8 south	Koh #8 north	Overall mean
			max-min ($^{\circ}$ C)			
E shallow	1.03 \pm 0.07	0.75 \pm 0.06	0.94 \pm 0.04	0.88 \pm 0.46	n.a.	0.9 \pm 0.06
E deep	1.50 \pm 0.10	1.61 \pm 0.11	1.04 \pm 0.07	n.a.	1.20 \pm 0.07	1.34 \pm 0.13
W shallow	2.44 \pm 0.16	3.06 \pm 0.18	2.18 \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



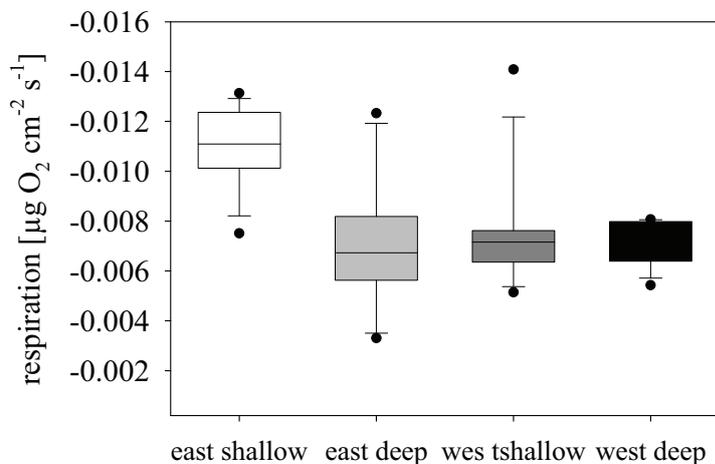
Supplementary Figure 1 Light (lx) - PAR correlation. A light intensity (l, lx) to photosynthetic active radiation (PAR) correlation was obtained by comparing pendant loggers and the light sensor of the Diving PAM during 6 days (4 shallow and 2 deep); R^2 : 0.52, l (lx) = 76.684 * PAR ($\mu\text{mol quanta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



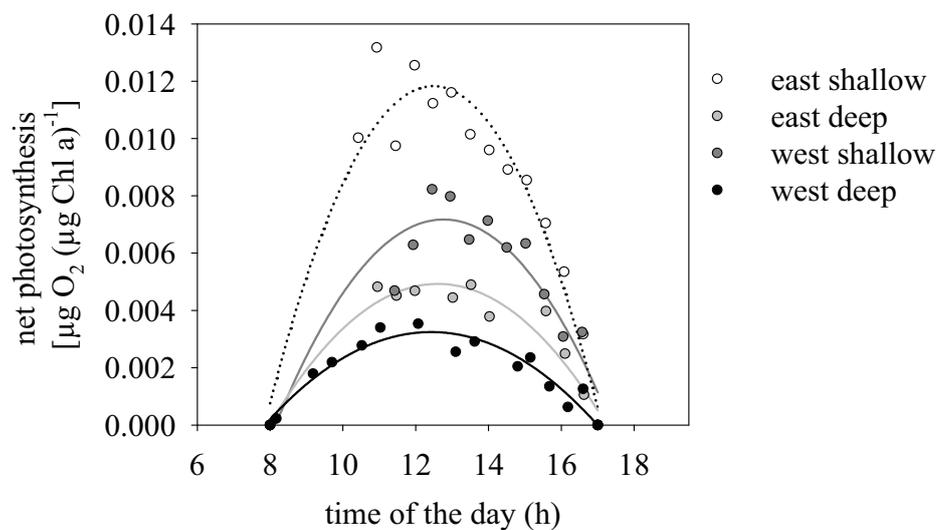
Supplementary Figure 2 Visual sediment characteristics. Exemplary photos of sediment surfaces at all investigation sites at Koh Miang (~ 30cm above bottom).



Supplementary Figure 3 Diurnal cycles of PAR. The diurnal cycles of ambient light intensity (lx) 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.



Supplementary 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.

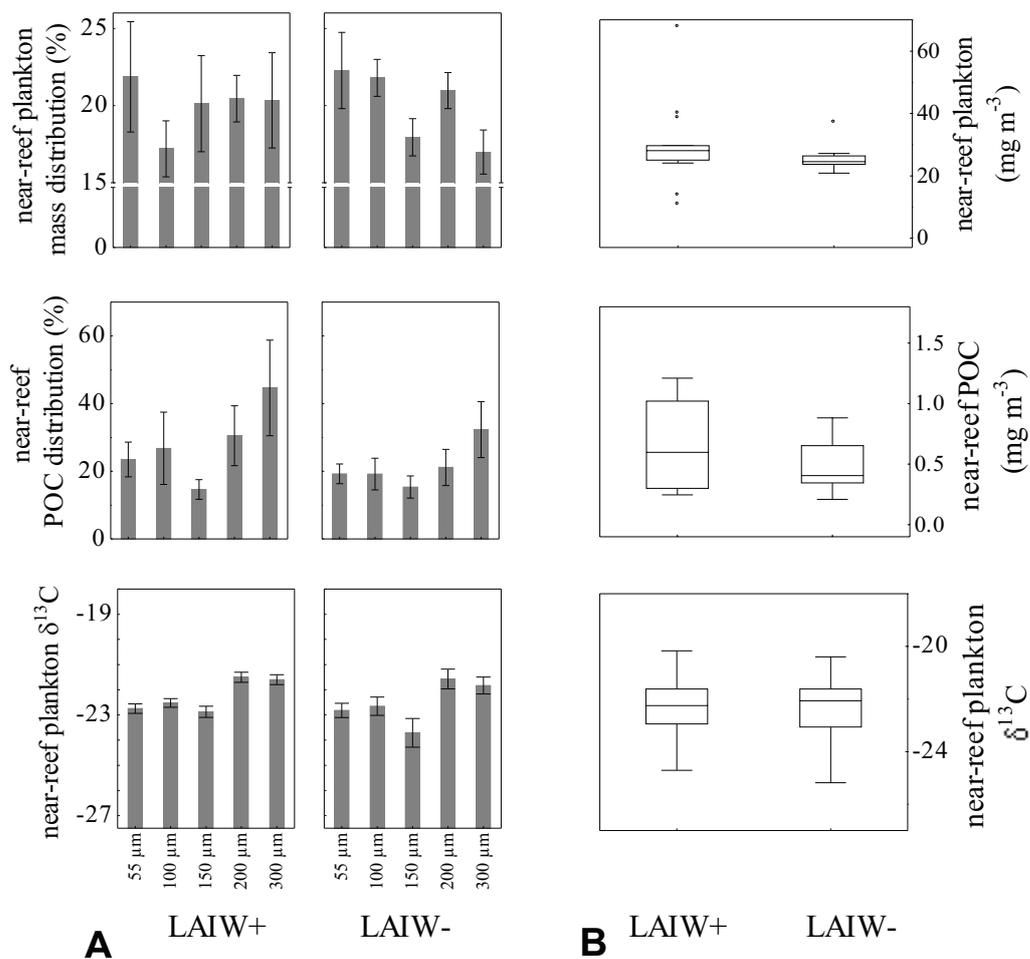


Supplementary Figure 5 Oxygen fluxes of corals related to chl-a content. Incubations of *P. lutea* in-situ with a new automated device during one daily cycle at each investigation site to determine oxygen fluxes, i.e. net photosynthesis, values were normalised to chl-a content ($\mu\text{g O}_2 [\mu\text{g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

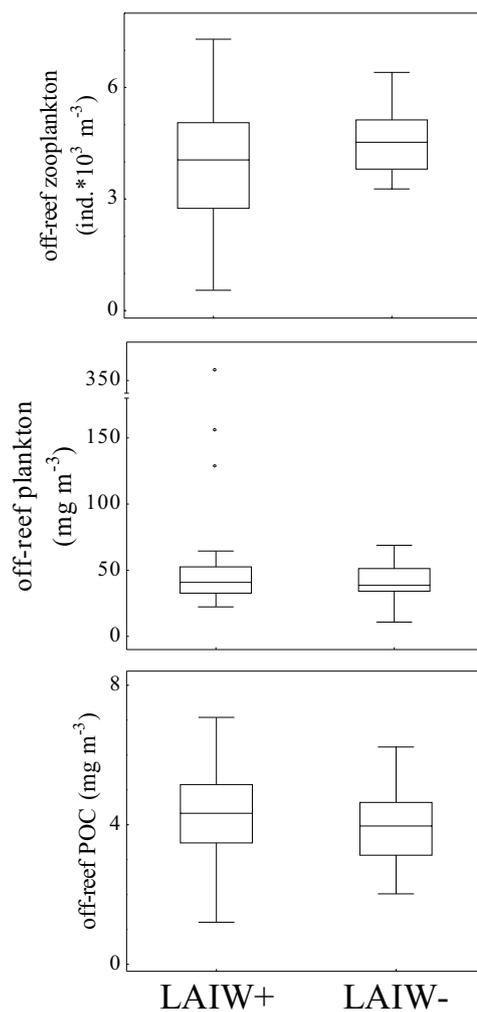
Annex 3

Supplementary Table 1 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.

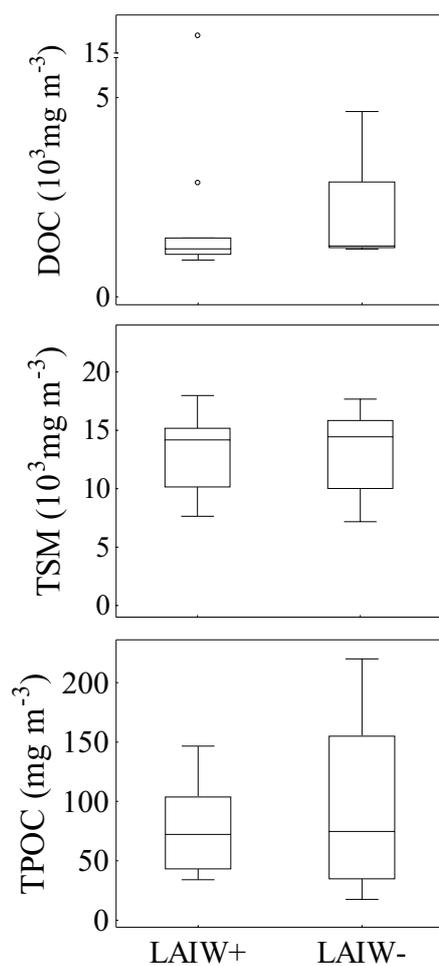
	LAIW-	LAIW+
near-reef plankton mass (mg m^{-3})	33.9 ± 5.5	26.9 ± 2.6
near-reef POC (mg m^{-3})	0.63 ± 0.09	0.49 ± 0.07
near-reef $\delta^{13}\text{C}$ (‰)	-22.3 ± 0.11	-22.52 ± 0.21
off-reef zooplankton numbers (individuals m^{-3})	$4.0 \times 10^3 \pm 0.4 \times 10^3$	$4.5 \times 10^3 \pm 0.4 \times 10^3$
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



Supplementary Figure 1 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.



Supplementary Figure 2 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.



Supplementary Figure 3 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.

Annex 4

Supplementary Table 1 Comparison of initial weights of coral nubbins (data square-root-transformed) between different sides (E and W) and depths (7 and 20 m) at Similan Islands. Student's t-test results of nubbins from experimental period Feb 2007 to Feb 2008 with all sides and depths included (**A**), and Nov 2007 to Nov 2008 with only E sides included because of high mortality in W (**B**). (df = degrees of freedom; N = number of samples; t = t-value; p = probability level, significance levels are *0.05 > P ≥ 0.01, **0.01 > P ≥ 0.001, ***P < 0.001).

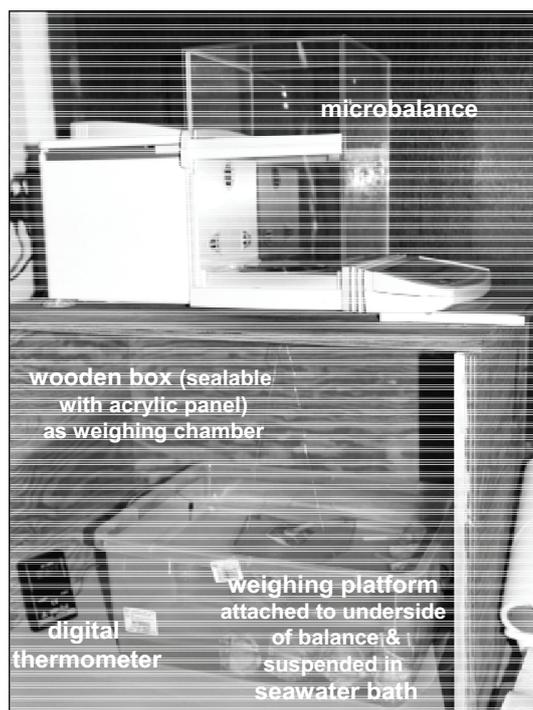
group 1 versus group 2	t-value	N group 1	N group 2	df	p
A Feb 2007 - Feb 2008					
W 20 m versus W 7 m	1.10	19	13	30	0.281
W 20 m versus E 20 m	-0.64	19	33	50	0.524
W 20 m versus E 7 m	-0.30	19	27	44	0.767
W 7 m versus E 20 m	-2.08	13	33	44	0.065
W 7 m versus E 7 m	-1.49	13	27	38	0.143
E 20 m versus E 7 m	0.33	33	27	58	0.740
B Nov 2007 - Nov 2008					
E 20 m versus E 7 m	-1.70	24	22	44	0.098

Supplementary Table 2 Comparison of gross bioerosion (B_{gross}) and net bioerosion (B_{net} , corrected for bioaccretion) on dead skeletal substrates exposed in E and W of Similan Island Koh Miang in 7 and 20 m depth. Student's t-test results skeletal substrates exposed for 12 months (**A**) and 21 months (**B**); (df = degrees of freedom; t = t-value; p = probability level, significance levels are *0.05 > P ≥ 0.01, **0.01 > P ≥ 0.001, ***P < 0.001; N = 9 for all variables compared, mean values given as kg CaCO₃ distribution m⁻²).

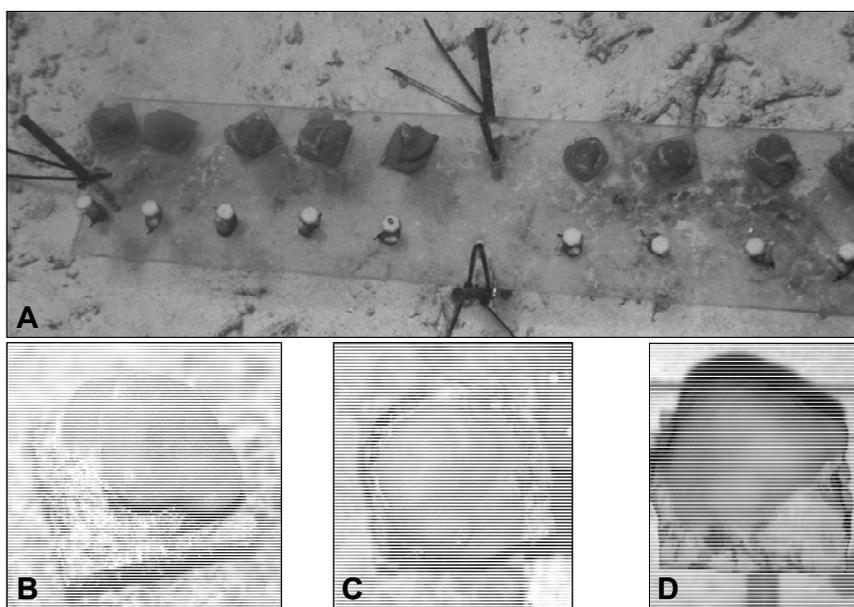
B_{gross} versus B_{net}	t-value	B_{gross}	B_{net}	df	p
A 12 months exposure					
E 7 m	0.749	-3.098	-3.672	16	0.465
E 20 m	0.254	-0.296	-0.391	16	0.728
W 7 m	0.226	0.18	0.069	16	0.824
W 20 m	2.948	0.377	-0.002	16	< 0.01**
B 21 months exposure					
E 7 m	0.552	-8.333	-8.969	16	0.589
E 20 m	0.169	-3.699	-3.941	16	0.868
W 7 m	0.127	-5.442	-5.651	16	0.900
W 20 m	0.435	-1.401	-1.633	16	0.669

Supplementary Table 3 Comparison of bioaccretion on dead skeletal substrates between 12 (Feb 2007 to Feb 2008) and 21 months (Feb 2007 to Nov 2008) exposure at Similan Island Koh Miang at E and W side in 7 m and 20 m depth. Mann-Whitney-U test results of total bioaccretion rates and bioaccretion rates by different groups of carbonate producers. (U = U-value; p = probability level, significance levels are *0.05 > P ≥ 0.01, **0.01 > P ≥ 0.001, ***P < 0.001). (N = 9 for all variables compared, mean values given as kg CaCO₃ distribution m⁻²).

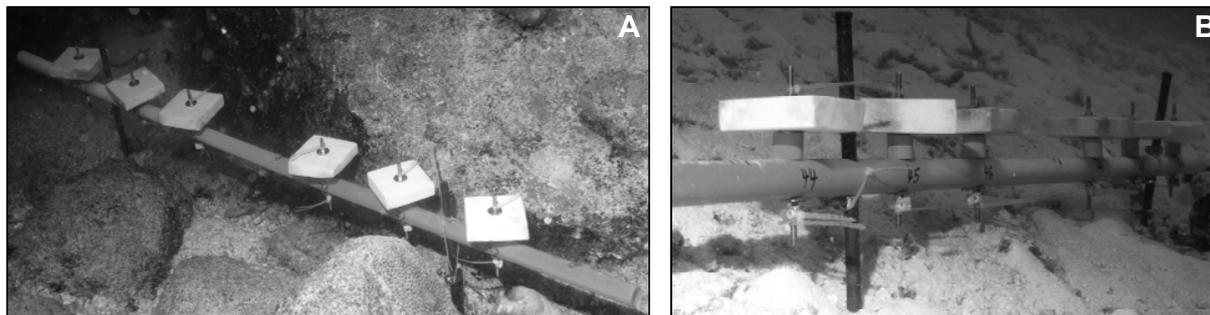
12 months versus 21 months	z-value	12 months	21 months	U	p
E 7 m					
total bioaccretion	0.309	0.575	0.532	44	0.757
serpulids	0.662	0.185	0.204	48	0.508
bivalves	0.574	0.014	0.000	47	0.566
balanids	0.386	0.005	0.002	46	0.627
corals	0.000	0.370	0.326	40	1.000
E 20 m					
total bioaccretion	0.839	0.095	0.204	50	0.402
serpulids	0.751	0.029	0.082	49	0.453
bivalves	0.574	0.061	0.102	47	0.566
balanids	0.397	0.006	0.019	45	0.691
corals	0.000	0.000	0.000	40	1.000
W 7 m					
total bioaccretion	1.280	0.114	0.175	55	0.200
serpulids	1.987	0.065	0.160	63	0.046
bivalves	0.839	0.041	0.011	50	0.402
balanids	0.397	0.008	0.004	45	0.691
corals	0.691	0.000	0.000	40	1.000
W 20 m					
total bioaccretion	1.104	0.380	0.296	53	0.270
serpulids	0.397	0.184	0.223	45	0.691
bivalves	0.662	0.101	0.012	48	0.508
balanids	1.236	0.089	0.061	54	0.216
corals	0.397	0.005	0.000	45	0.691



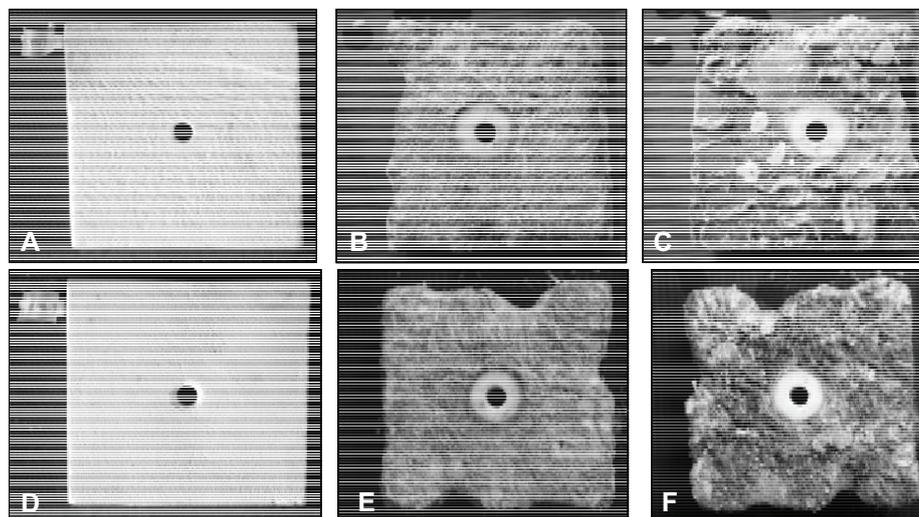
Supplementary Figure 1 Microbalance and weighing construction for buoyant weight technique after Davies (1989).



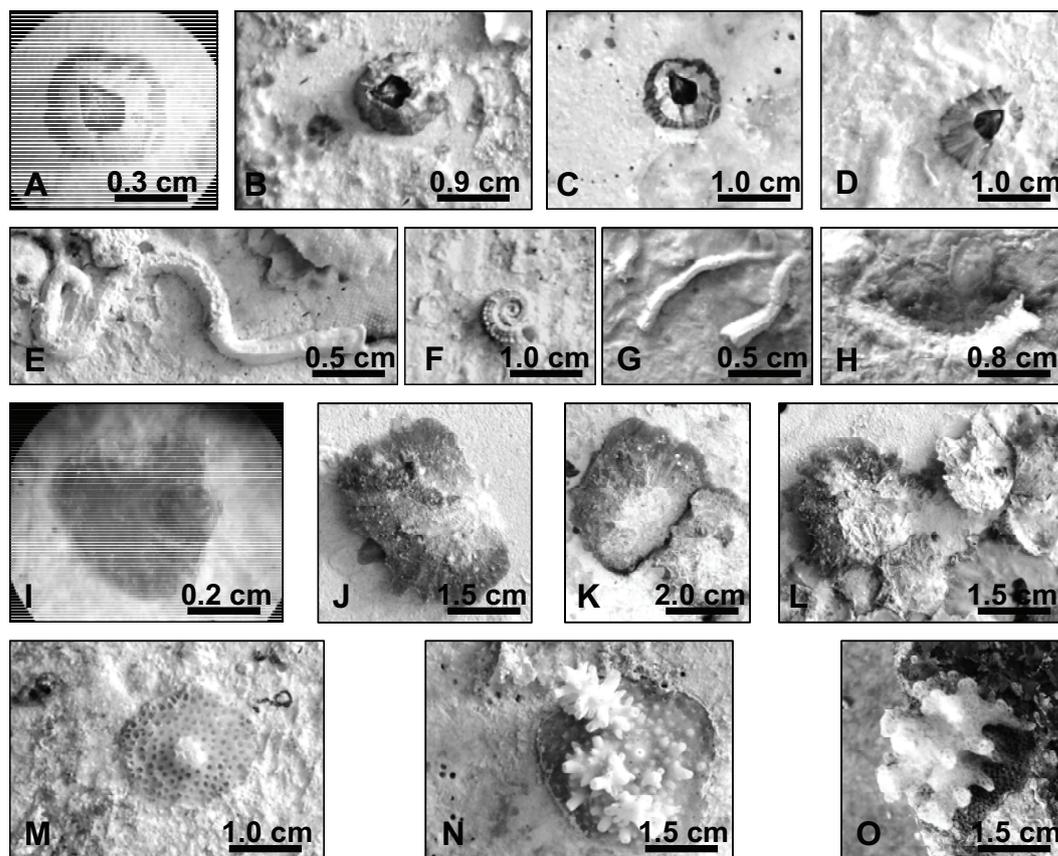
Supplementary Figure 2 Coral nubbins of *Porites lutea* on individual transplant holders attached to racks built of acrylic glass and metal rocks (A), and coral nubbins on holders right after recollection with un-growing epiphytes (B, C) and with epiphytes removed (D).



Supplementary Figure 3 Bioerosion racks made of PVC-tubes and metal bars each with six dead coral blocks of *Porites lutea* attached. View from above the setup (A), and from diagonally below (B).



Supplementary Figure 4 Two different rectangular blocks (one in upper and second in lower panel) of dead coral skeleton of *Porites lutea* before (A, D) and right after exposure for 12 months (upper side: B, E and under side: C, F).



Supplementary Figure 5 Calcium carbonate precipitating organisms on the dead skeletal blocks: from top to bottom: Balanids (A – D), serpulids (E – H), bivalves (I – L), and corals (M – O).

Annex 5

Supplementary Table 1 Monthly temperature values (modal, maxima and minima) at all study sites along Similan Islands: Paired student's t-tests for testing of variability within replicate island sites. (df = degrees of freedom; p = probability level, significance levels are *0.05 > P ≥ 0.01, **0.01 > P ≥ 0.001, ***P < 0.001).

group 1 vs group 2	modal					maxima					minima				
	t-value	N	N	df	p	t-value	N	N	df	p	t-value	N	N	df	p
West 20 m															
W2.1 vs W4.1	1.17	21	18	37	0.25	1.11	21	18	37	0.273	1.38	21	18	37	0.18
W2.1 vs W7.1	-0.19	21	17	36	0.85	-0.18	21	17	36	0.858	-0.21	21	17	36	0.84
W2.1 vs W8.1	0.19	21	21	40	0.85	0.23	21	21	40	0.819	-0.93	21	21	40	0.36
W2.1 vs W8.3	0.37	21	21	40	0.71	0.16	21	21	40	0.873	0.30	21	21	40	0.77
W4.1 vs W7.1	-1.25	18	17	33	0.22	-1.10	18	17	33	0.279	-1.31	18	17	33	0.20
W4.1 vs W8.1	-1.02	18	21	37	0.32	-0.86	18	21	37	0.396	-2.08	18	21	37	0.04*
W4.1 vs W8.3	-0.94	18	21	37	0.35	-0.90	18	21	37	0.373	-1.07	18	21	37	0.29
W7.1 vs W8.1	0.37	17	21	36	0.71	0.37	17	21	36	0.715	-0.57	17	21	36	0.57
W7.1 vs W8.3	0.55	17	21	36	0.58	0.31	17	21	36	0.761	0.44	17	21	36	0.66
W8.1 vs W8.3	0.17	21	21	40	0.87	-0.06	21	21	40	0.950	1.17	21	21	40	0.25
West 7 m															
W2.1 vs W4.1	-1.26	21	18	37	0.22	-1.32	21	18	37	0.19	-0.77	21	18	37	0.45
W2.1 vs W7.1	0.01	21	8	27	0.99	-0.01	21	8	27	0.99	-0.99	21	8	27	0.33
W2.1 vs W8.1	1.77	21	5	24	0.09	2.63	21	5	24	0.01*	-1.92	21	5	24	0.07
W2.1 vs W8.3	-0.05	21	21	40	0.96	-0.51	21	21	40	0.61	-2.16	21	21	40	0.04*
W4.1 vs W7.1	0.96	18	8	24	0.34	0.83	18	8	24	0.41	-0.35	18	8	24	0.73
W4.1 vs W8.1	2.83	18	5	21	0.01*	3.05	18	5	21	0.01*	-1.20	18	5	21	0.24
W4.1 vs W8.3	1.26	18	21	37	0.22	0.76	18	21	37	0.45	-1.16	18	21	37	0.25
W7.1 vs W8.1	1.59	8	5	11	0.14	1.74	8	5	11	0.11	-0.80	8	5	11	0.44
W7.1 vs W8.3	-0.05	8	21	27	0.96	-0.31	8	21	27	0.76	-0.51	8	21	27	0.61
W8.1 vs W8.3	-1.93	5	21	24	0.07	-2.56	5	21	24	0.02*	0.55	5	21	24	0.59
East 20 m															
E2.1 vs E4.1	-0.13	21	20	39	0.90	-0.12	21	20	39	0.90	-0.65	21	20	39	0.52
E2.1 vs E7.1	-0.40	21	20	39	0.69	-0.44	21	20	39	0.67	-2.15	21	20	39	0.04*
E2.1 vs E8.1	-0.16	21	19	38	0.87	-0.14	21	19	38	0.89	-1.95	21	19	38	0.06
E2.1 vs E8.3	-0.12	21	20	39	0.90	-0.12	21	20	39	0.90	-0.89	21	20	39	0.38
E4.1 vs E7.1	-0.27	20	20	38	0.79	-0.32	20	20	38	0.75	-1.53	20	20	38	0.13
E4.1 vs E8.1	-0.04	20	19	37	0.97	-0.02	20	19	37	0.99	-1.34	20	19	37	0.19
E4.1 vs E8.3	0.01	20	20	38	0.99	0.00	20	20	38	1.00	-0.25	20	20	38	0.81
E7.1 vs E8.1	0.22	20	19	37	0.82	0.30	20	19	37	0.77	0.18	20	19	37	0.86
E7.1 vs E8.3	0.29	20	20	38	0.78	0.31	20	20	38	0.76	1.28	20	20	38	0.21
E8.1 vs E8.3	0.05	19	20	37	0.96	0.01	19	20	37	0.99	1.09	19	20	37	0.28
East 7 m															
E2.1 vs E4.1	-0.02	21	21	40	0.98	-0.62	21	21	40	0.54	0.73	21	21	40	0.47
E2.1 vs E7.1	-0.41	21	20	39	0.68	-1.33	21	20	39	0.19	-1.41	21	20	39	0.17
E2.1 vs E8.1	-0.10	21	21	40	0.92	-0.74	21	21	40	0.47	-0.66	21	21	40	0.51
E2.1 vs E8.3	0.02	21	18	37	0.99	0.09	21	18	37	0.93	-0.53	21	18	37	0.60
E4.1 vs E7.1	-0.41	21	20	39	0.69	-0.73	21	20	39	0.47	-2.28	21	20	39	0.03*
E4.1 vs E8.1	-0.08	21	21	40	0.93	-0.12	21	21	40	0.90	-1.52	21	21	40	0.14
E4.1 vs E8.3	0.04	21	18	37	0.97	0.68	21	18	37	0.50	-1.30	21	18	37	0.20
E7.1 vs E8.1	0.32	20	21	39	0.75	0.60	20	21	39	0.55	0.95	20	21	39	0.35
E7.1 vs E8.3	0.41	20	18	36	0.68	1.36	20	18	36	0.18	0.93	20	18	36	0.36
E8.1 vs E8.3	0.11	21	18	37	0.91	0.79	21	18	37	0.44	0.08	21	18	37	0.93

Supplementary Table 2 Total surface-area [mm²] of corals settled on tiles: Total surface area of recruit spats of present coral families for each time period: twenty-one (Feb 2007 to Nov 2008), twelve (Nov 2007 to Nov 2008) and nine (Feb 2008 to Nov 2008) months.

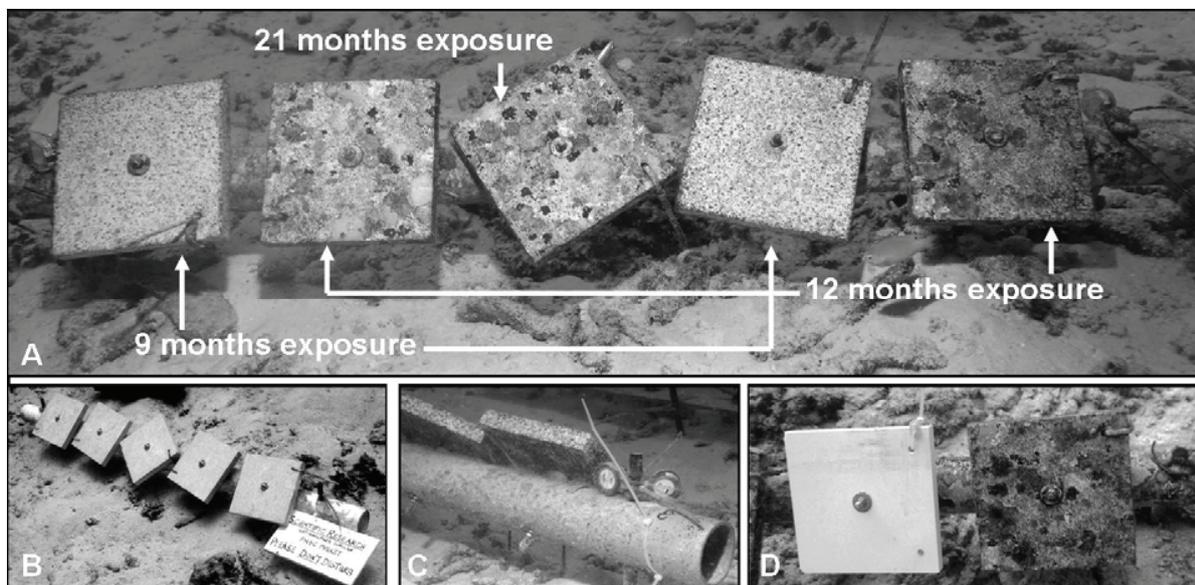
Time period deployment	Site	# Tiles removed	<i>Pocilloporidae</i>	<i>Acroporidae</i>	<i>Fungidae</i>	<i>Poritidae</i>	<i>Favidae</i>	<i>Agariciidae</i>	<i>Helioporaceae</i>	Other	Total
Feb 07 - Nov 08 21 months	West 20 m	10	7.67	471.44	56.07	8.55	0.57	622.04	0.00	4.42	1170.75
	West 7 m	6	387.57	2.87	19.58	36.50	0.00	0.00	0.00	2.05	448.58
	East 20 m	10	631.75	1305.33	139.83	145.58	36.36	0.00	0.00	0.25	2259.10
	East 7 m	10	5128.65	0.00	0.00	1.21	0.46	18.16	18.63	1.63	5168.74
	total:	36	6155.64	1779.64	215.48	191.85	37.39	640.19	18.63	8.35	9047.17
	% of total		68.04	19.67	2.38	2.12	0.41	7.08	0.21	0.09	100
Nov 07 - Nov 08 12 months	West 20 m	10	893.52	1.20	10.20	0.00	0.00	0.00	0.00	0.00	904.93
	West 7 m	10	970.17	101.27	0.00	2.17	0.00	0.00	0.00	1.03	1074.64
	East 20 m	10	53.30	11.20	16.31	12.25	0.00	0.00	0.00	0.78	93.84
	East 7 m	10	482.83	0.00	0.00	0.67	0.00	0.00	0.00	0.41	484.36
	total:	40	2399.82	113.67	26.51	15.09	0.00	0.00	0.00	2.22	2557.77
	% of total		93.82	4.44	1.04	0.59	0.00	0.00	0.00	0.09	100
Feb 08 - Nov 08 9 months	West 20 m	10	43.94	1.25	0.00	159.84	0.00	0.00	0.00	0.92	205.94
	West 7 m	8	28.51	15.87	0.00	0.00	0.00	0.00	0.00	0.25	44.62
	East 20 m	10	23.87	0.00	0.70	2.76	2.45	0.00	0.00	0.00	29.78
	East 7 m	10	25.64	1.12	0.00	3.78	0.00	0.00	0.00	0.00	30.54
	total:	38	121.96	18.23	0.70	166.38	2.45	0.00	0.00	1.16	310.89
	% of total		39.23	5.86	0.23	53.52	0.79	0.00	0.00	0.37	100

Supplementary Table 3 Size distribution of coral recruits on settlement tiles along Similan Islands. Shown are results of General Linear Model (GLM) analysis (data log +1 transformed) for all exposure periods with data of sides (W and E) and depths (20 and 7 m) pooled and separated. Size class (2.5, 7.5, 12.5, 17.5, 22.5, 27.5, and 30+) used as fixed factor and site (named: island) as random factor nested in size class. Fisher LSD post-hoc test followed for pairwise comparisons of significant effects. Only significant results are shown here. (df = degrees of freedom; MS = means square; F = F-value; p = probability level, significance levels are *0.05 > P ≥ 0.01, **0.01 > P ≥ 0.001, ***P < 0.001).

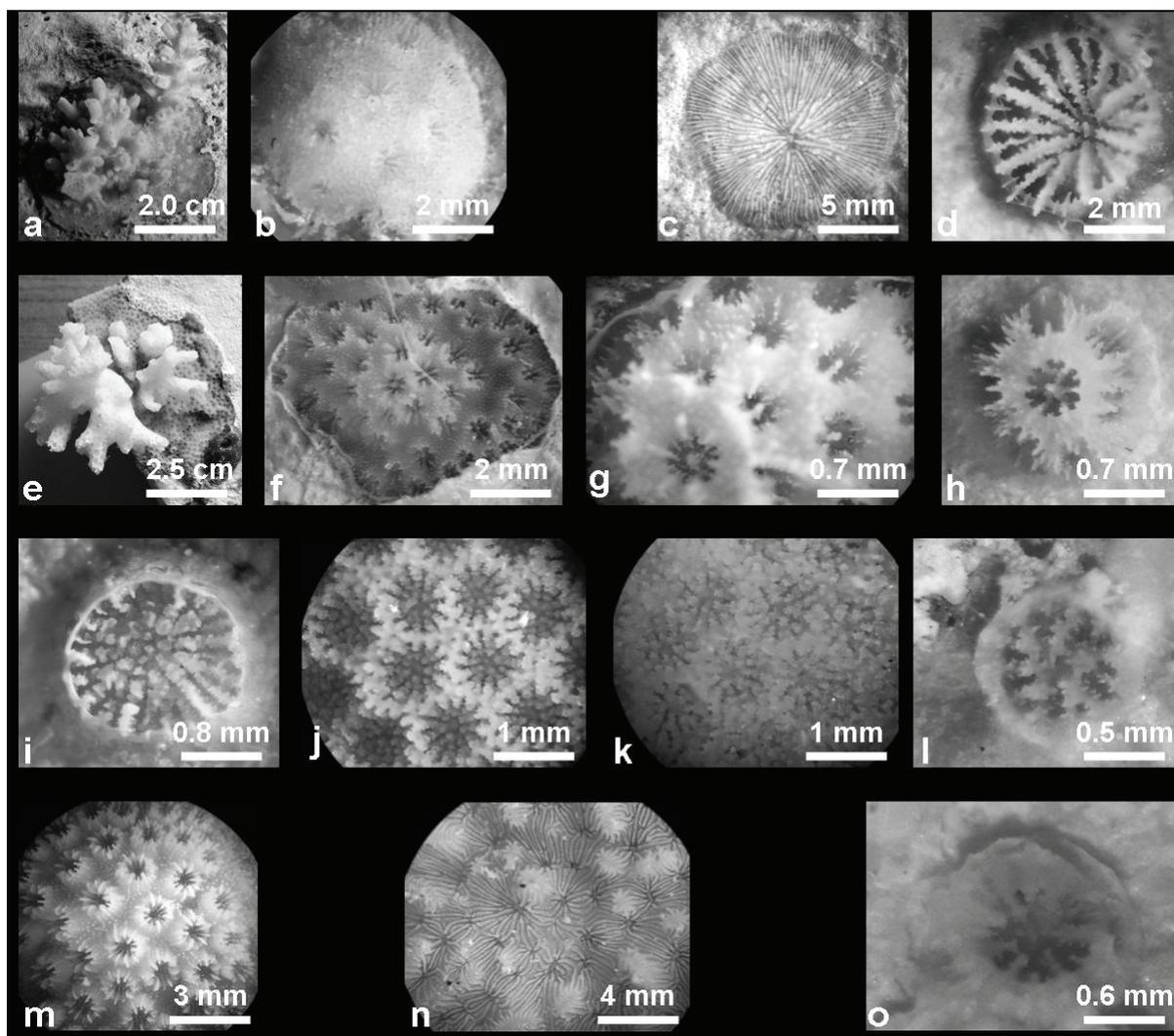
Treatment		df	MS	F	p	Fisher LSD, pairwise comparisons:	p
21 months exposure							
sides & depths pooled	intercept	1	11.185	38.669	< 0.001***	2.5 > 7.5, 12.5, 17.5, 22.5, 27.5, 30+	< 0.001***
	island (sizeclass)	28	0.289	2.092	0.061	7.5 > 12.5, 17.5, 22.5, 27.5	< 0.04*
	sizeclass	6	3.589	12.409	< 0.001***	30+ > 12.5, 17.5, 22.5, 27.5	< 0.005**
	Error	245	0.138	1.545	0.216		
West 20 m	intercept	1	1.560	29.705	< 0.001***	2.5 > 7.5, 12.5, 17.5, 22.5, 27.5, 30+	< 0.001***
	island (sizeclass)	28	0.053	0.481	0.975		
	sizeclass	6	0.948	18.048	< 0.001***		
	Error	35	0.109				
West 7 m	intercept	1	1.812	6.798	0.014*	2.5 > 7.5, 12.5, 17.5, 22.5, 27.5, 30+	< 0.001***
	island (sizeclass)	28	0.267	4.174	0.773	7.5 > 12.5, 17.5, 22.5, 27.5	< 0.04*
	sizeclass	6	0.668	2.505	0.046*		
	Error	35	0.064				
East 20 m	intercept	1	8.229	23.040	< 0.001***	2.5 > 7.5, 12.5, 17.5, 22.5, 27.5	< 0.002**
	island (sizeclass)	28	0.357	0.543	0.950		
	sizeclass	6	2.795	7.827	< 0.001***		
	Error	35	0.657				
East 7 m	intercept	1	41.657	15.429	< 0.001***	2.5 > 7.5, 12.5, 17.5, 22.5, 27.5, 30+	< 0.001***
	island (sizeclass)	28	2.700	1.152	0.342		
	sizeclass	6	13.790	5.108	< 0.001***		
	Error	35	2.343				
12 months exposure							
sides & depths pooled	intercept	1	37.889	12.194	< 0.002**	2.5 > 7.5, 12.5, 17.5, 22.5, 27.5, 30+	< 0.001***
	island (sizeclass)	28	3.107	2.410	0.465		
	sizeclass	6	18.373	5.913	< 0.001***		
	Error	245	1.289				
West 20 m	intercept	1	1.729	8.067	< 0.008**	2.5 > 7.5, 12.5, 17.5, 22.5, 27.5	< 0.004**
	island (sizeclass)	28	0.214	0.517	0.962	2.5 > 30+	< 0.02*
	sizeclass	6	1.129	5.267	< 0.001***		
	Error	35	0.414				
West 7 m	intercept	1	35.714	12.755	< 0.001***	2.5 > 7.5, 12.5, 17.5, 22.5, 27.5, 30+	< 0.001***
	island (sizeclass)	28	2.800	1.181	0.318		
	sizeclass	6	13.148	4.696	< 0.002**		
	Error	35	2.371				
East 20 m	intercept	1	15.557	3.889	0.059	2.5 > 7.5, 12.5, 17.5, 22.5, 27.5	< 0.001***
	island (sizeclass)	28	4.000	3.733	0.421		
	sizeclass	6	9.990	2.498	< 0.046*		
	Error	35	1.071				

Supplementary Table 3 continued

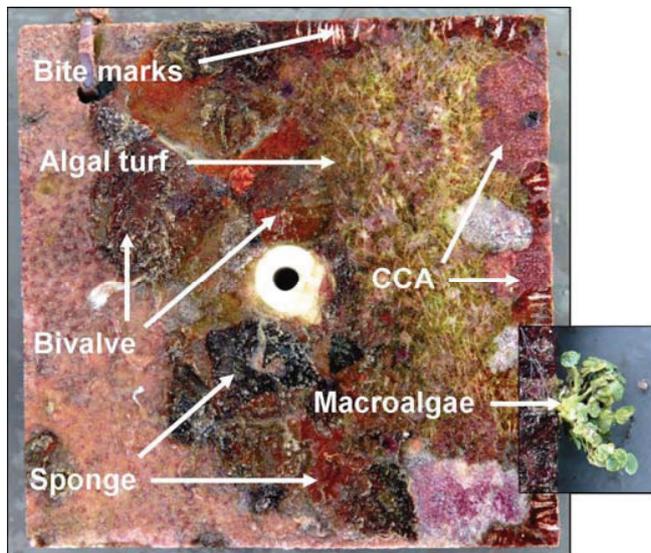
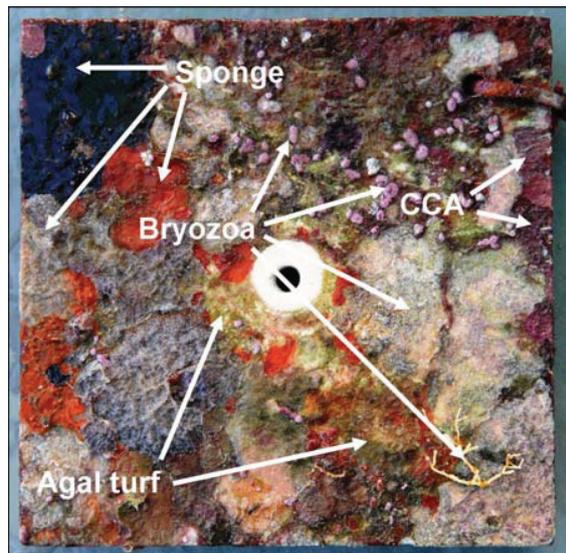
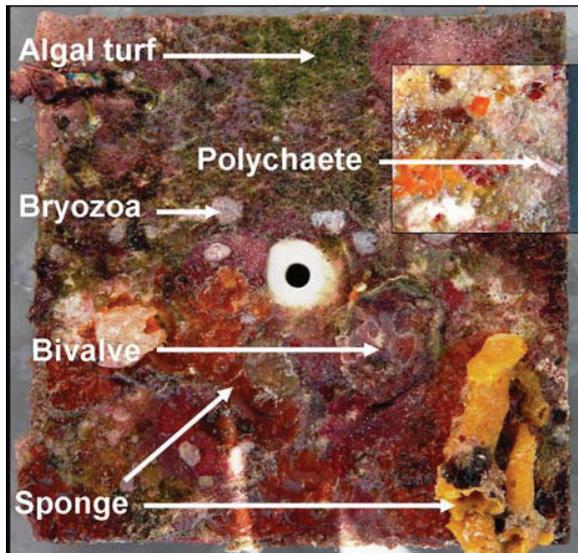
Treatment		df	MS	F	p	Fisher LSD, pairwise comparisons:	p
9 months exposure							
sides & depths pooled	intercept	1	15.557	34.165	< 0.001***	2.5 > 7.5, 12.5, 17.5, 22.5, 27.5, 30+	< 0.001***
	island (sizeclass)	28	0.455	0.773	0.789		
	sizeclass	6	8.574	18.829	< 0.001***		
	Error	245	0.589				
West 7 m	intercept	1	1.729	7.118	< 0.013*	2.5 > 7.5, 12.5, 17.5, 22.5, 27.5, 30+	< 0.001***
	island (sizeclass)	28	0.243	1.545	0.111		
	sizeclass	6	0.829	3.412	< 0.012*		
	Error	35	0.157				
East 20 m	intercept	1	12.014	8.126	< 0.008**	2.5 > 7.5, 12.5, 17.5, 22.5, 27.5, 30+	< 0.001***
	island (sizeclass)	28	1.479	1.190	0.310		
	sizeclass	6	8.681	5.871	< 0.001***		
	Error	35	1.243				
East 7 m	intercept	1	2.414	8.244	< 0.008**	2.5 > 7.5, 12.5, 17.5, 22.5, 27.5, 30+	< 0.01**
	island (sizeclass)	28	0.293	0.820	0.703		
	sizeclass	6	1.648	5.626	< 0.001***		
	Error	35	0.357				



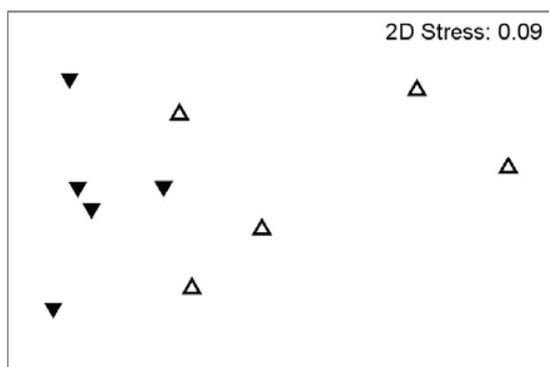
Supplementary Figure 1 Under water pictures of racks for settlement tiles. **A)** Frontal view with clearly distinguishable settlement tiles of different exposure periods. **B)** Lateral view on rack. **C)** Back view of rack with temperature loggers attached (TidbiT v2, Onset computers). **D)** Newly attached tile (left side) and tile exposed for 12 months (right side).



Supplementary Figure 2 Photographs of coral recruits on settlement tiles with different stages of development. *Acroporidae* (a, b); *Fungiidae* (c, d); *Pocilloporidae* (e – h), *Poritidae* (i: *Goniopora* sp., j – l: *Porites* sp.), *Faviidae* (m: *Cyphastrea* sp.), *Agariciidae* (n: *Pavona* sp.), and 'other' (o).



Supplemental fig 3 Determination of benthic organisms and bite marks on settlement tiles by picture analysis of tiles photographed right after collection.



Supplementary Figure 4 Multidimensional scaling (MDS) of family composition of adult coral colonies along one 100 m line intercept transect at each site, 5 in West (▼) and East (▲), respectively.