



Effects of simulated eutrophication and overfishing on algae and invertebrate settlement in a coral reef of Koh Phangan, Gulf of Thailand



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ABSTRACT

Coral reefs in the Gulf of Thailand are highly under-investigated regarding responses to anthropogenic stressors. Thus, this study simulated overfishing and eutrophication using herbivore enclosure cages and slow-release fertilizer to study the *in-situ* effects on benthic algae and invertebrate settlement in a coral reef of Koh Phangan, Thailand. Settlement of organisms and the development of organic matter on light-exposed and shaded tiles were quantified weekly/biweekly over a study period of 12 weeks. Simulated eutrophication did not significantly influence response parameters, while simulated overfishing positively affected dry mass, turf algae height and fleshy macroalgae occurrence on light-exposed tiles. On shaded tiles, settlement of crustose coralline algae decreased, while abundances of ascidians increased compared to controls. An interactive effect of both stressors was not observed. These results hint to herbivory as actual key controlling factor on the benthic community, and fleshy macroalgae together with ascidians as potential bioindicators for local overfishing.

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1. Introduction

The relative abundance of benthic organisms in a coral reef is largely influenced by two factors: resource availability (e.g. light, nutrients, substrate; bottom-up factors) and species interaction (especially competition and herbivory; top-down factors). The most important competitors of corals for resources on most reefs are seaweeds (Miller 1998; McCook et al. 2001) and within the last few decades, this competition between algae and corals increased due to anthropogenic pressures such as eutrophication and overfishing (e.g. Nyström et al. 2000; McCook et al. 2001; Smith et al. 2010). Eutrophication is caused by extensive coastal development and discharge of waste waters into the ocean (e.g. Nixon 1995). Untreated sewage water contains high concentrations of nutrients and, once reaching coastal waters, acts as fertilizer by enhancing primary production (Smith et al. 1981; Lapointe 1997; Paytan et al., 2006). If chronically enhanced, nutrients may alter the coral reef community through the promotion of macroalgae, bioeroders and suspension-feeding animals (Hallock and Schlager 1986, studies reviewed by Fabricius 2005). Overfishing is of concern as reef

ecosystems support a high proportion of local fisheries (Moberg and Folke 1999). As fisheries management is often inadequate, most target species are fully fished or overfished (Jackson et al. 2001; Myers and Worm 2003). Particularly the excessive removal of large algal-grazing fishes decreases reef resilience (Nyström et al. 2000; Hughes et al. 2007), as herbivores play an important role by limiting the establishment and growth of algal communities (Green and Bellwood 2009).

The relative importance of these bottom-up versus top-down factors in the degradation of reefs is vigorously discussed within the last 20 years of coral reef research. Bell (1992), Lapointe (1997), Littler et al. (2006a) and Vermeij et al. (2010) found significant increases in algae biomass after exposure to enhanced nutrient levels only. On the other hand, numerous studies have shown increases in algal abundance in response to herbivore reduction with no change in nutrient supply, demonstrating that enhanced nutrients are not necessary for phase shifts (Belliveau and Paul 2002; Diaz-Pulido and McCook 2005; Burkepille and Hay 2006, 2009; Rasher et al. 2012; Jessen and Wild 2013). Other studies concluded that nutrient overloads can contribute to reef degradation by algal proliferation, but are unlikely to lead to phase shifts unless herbivory is naturally or artificially low (McCook 1999; Burkepille and Hay 2006, 2009; Smith et al. 2010). For settlement of invertebrates, there are few studies investigating the individual or combined impacts of herbivore exclusion and nutrient enrichment. In

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general, results showed increases in small filter-feeding organisms in response to enhanced nutrient concentrations and decreases in crustose coralline algae (CCA) and coral recruit abundances in response to herbivore exclusion (Hunte and Wittenberg 1992; Abelson et al. 2005; Jessen et al. 2014). Reviews by Burkepile and Hay (2006), Gruner et al. (2008) and Teichberg et al. (2012) concluded that the relative role of bottom-up versus top-down controls in structuring benthic reef communities is obviously context-dependent, i.e. it may differ by type of habitat, latitude or functional groups of algae and herbivores. Available studies have rarely assessed the importance of these controls on reefs with varying levels of anthropogenic influence (Rasher et al. 2012). However, such studies are needed to better evaluate the context dependency of bottom-up versus top-down effects (Houk et al. 2010; Smith et al. 2010).

Among all coral reef regions, local pressure on coral reefs is highest in Southeast Asia, where nearly 95% of reefs are threatened from overfishing and pollution (Knight et al. 2012). As many Southeast Asian countries are lacking effective water treatment facilities, over 80% of sewage is discharged untreated into the sea (Cheevaporn and Menasveta 2003; Todd et al. 2010). Besides pressure from increasing coastal development and pollution, overfishing exacerbates the problems for coral reefs in Asia, as this region supplies nearly 60% of the global fish production (Stobutzki et al. 2006; FAO 2011). Often, intensive fisheries are fishing down the food webs and thereby continue to alter the functioning of the ecosystems in the Gulf of Thailand (Pauly and Chuenpagdee 2003). However, despite the high anthropogenic pressures in this region, there are few studies investigating their impacts on coral reefs. Some information is available from reef survey programs carried out in 1998 and 2004, indicating declines in live coral coverage in response to poorly managed tourism in the Gulf of Thailand (Yeemin et al., 2006). It is further known that coastal development and jetty construction on the west coast of the Gulf of Thailand have resulted in seagrass and coral reef degradation (Yeemin et al., 2001; Chou et al. 2002). Discharge of untreated sewage water and eutrophication are listed as highest pollution problems in the Gulf causing bacterial contamination and red tides (Cheevaporn and Menasveta 2003). Nevertheless, understanding of coral reef resilience in the Indo-Pacific is still in its infancy (Roff and Mumby 2012), and studies in the Gulf of Thailand have been exclusively observational.

Therefore, this experimental study aimed to assess linkages between anthropogenic influences and ecosystem functioning in a reef of Koh Phangan, Thailand. The simulation of eutrophication and overfishing *in situ* allowed the assessments of direct responses in algae community composition and growth as well as in invertebrate settlement patterns to bottom-up and top-down controls.

2. Methods

2.1. Study site

The study was conducted in Mae Haad (9.796733 N, 99.978300E) on the northwest coast of Koh Phangan, an island in the lower Gulf of Thailand (Fig. 1). The bay hosted some bungalow resorts and experienced frequent dive and snorkel tourism. Fishing vessels were observed in front of the reef occasionally during nighttime despite its status as protected area. In the center of the bay, a small river framed by bungalows discharged into the water by seeping through the sand. Thereby, the reef in Mae Haad represents a typical coral reef of South East Asia, impacted by tourism, fishing and run-off from land.

To evaluate benthic community composition and to quantify the influence of herbivores at the study site, underwater surveys

were conducted in 4 m water depth using SCUBA. Benthic cover was determined along three 50 m Line-Point-Intercept-transects in 0.5 m steps and grouped into 'hard coral' (identified to genus level and pooled to 'hard coral'), 'soft coral', 'turf algae', 'fleshy macroalgae', 'crustose coralline algae' (CCA), 'rubble', 'sand' and 'other sessile invertebrates'. Coral cover ($20 \pm 4\%$ hard coral, and $4 \pm 6\%$ soft coral) was dominated by big boulders of the coral *Porites* spp.. Massive carbonate structures alternated with natural sand pools ($29 \pm 9\%$). Turf algae cover was high ($42 \pm 6\%$) while macroalgal as well as CCA cover in the reef were low (4 ± 6 and $1 \pm 2\%$ respectively). Abundances of sea urchins of the species *Diadema setosum* and *Echinotrix calamaris* counted in three 50 m belt-transects of 5 m width were low (0.002 ± 0.003 ind. m^{-2}). All observed fish except cryptic species and pelagic damselfish along three 50 m belt transects of 5 m width were identified to species level, counted and assigned to size classes (10–35 cm in 5 cm intervals). Fish biomass was then calculated from abundance, mid length of respective size class and species or genus specific Bayesian length-weight coefficients available on FishBase.org (Froese and Pauly, 2012). Fish species were classified as herbivore or carnivore according to Green and Bellwood (2009) to estimate herbivorous biomass. Total fish abundance was low (0.137 ± 0.040 ind. m^{-2} respectively). The most frequent groups observed were rabbitfish (Siganidae; 29%) followed by parrotfish (Scaridae; 28%), wrasses (Labridae; 16% carnivorous species, 7% herbivorous species) and butterflyfish (Chaetodontidae; 20%). Total fish biomass was low (21.3 ± 9.2 g m^{-2}) but herbivorous fish accounted for a high share of total fish abundance and biomass (64%).

To investigate the eutrophication status of the reef and estimate land-based pollution in the bay, stations on an ocean-land-transect from experimental plots at the reef border into the small river discharging into the bay were investigated for phosphate and chlorophyll *a* concentrations. The river was not directly connected to the sea but water seeped through the part of the beach separating river and bay, which was evidenced by the observation of infiltrating water channels during low tide and lower salinity in seawater close to the beach. From each of the six sampling stations (two stations in the river, two close to the beach and two on the reef; Fig. 1b), one water sample was taken in a 5 L canister at each of three sampling times in June, resulting in 6 data points for river and 12 for bay stations. Samples were filtered through VWR glass microfiber filters (particle retention 1.6 μm) and analyzed for phosphate concentrations within 4 h after sampling using spectrophotometric analysis (Biochrom Libra S12) following the standard protocol of Murphy and Riley (1962) described in Grasshoff et al. (1999). For analyses of water chlorophyll *a* concentrations, 3 L of seawater or 0.5 L of river-water was filtered on pre-combusted VWR glass microfiber filters ($\varnothing = 47$ mm, particle retention 1.6 μm) with an electric vacuum pump (max. pressure < 200 mbar) and incubated in 10 mL 90% Acetone for 24 h at 4 °C before analyzed with a spectrophotometer (Biochrom Libra S12). Chlorophyll *a* concentrations were then calculated according to ESS Method 150.1 (Wisconsin State Lab of Hygiene 1991). Inorganic phosphate concentrations in the river stations ($1.70 \pm 0.33 \mu mol PO_4^{3-} L^{-1}$) were more than ten times higher than in the bay stations ($0.14 \pm 0.08 \mu mol PO_4^{3-} L^{-1}$; Mann-Whitney $T = 93.00$, $n_1 = 6$, $n_2 = 12$, $p < 0.001$). Chlorophyll *a* concentrations were also significantly higher in the river ($2.43 \pm 0.21 \mu g Chl a L^{-1}$) than in the bay ($0.92 \pm 0.08 \mu g Chl a L^{-1}$; Mann-Whitney $T = 93.00$, $n_1 = 6$, $n_2 = 12$, $p < 0.001$).

2.2. Manipulation experiments

Experiments to test the impact of nutrient supply and herbivore exclusion were run from February to May 2012 (12 weeks). The study used two levels of nutrients (ambient and enriched)

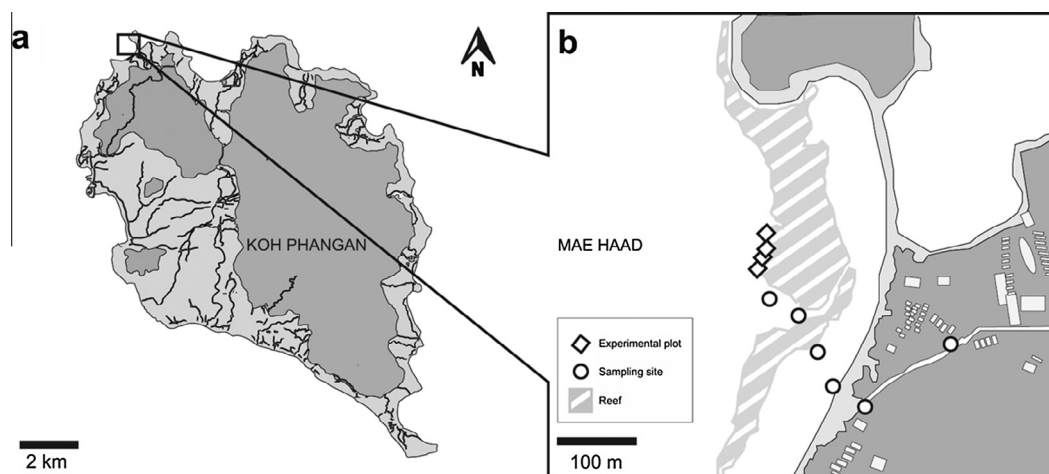


Fig. 1. Study site. (a) Location of the study site Mae Haad (9.796733 N, 99.978300E) at the northwestern coast of the island Phangan. (b) Diamonds indicate locations of experimental plots along the reef border. Each of the four plots contained four set-ups with settlement tiles under different treatment conditions. Dots indicate the sampling sites for phosphate and chlorophyll *a* concentrations within the bay and in the river.

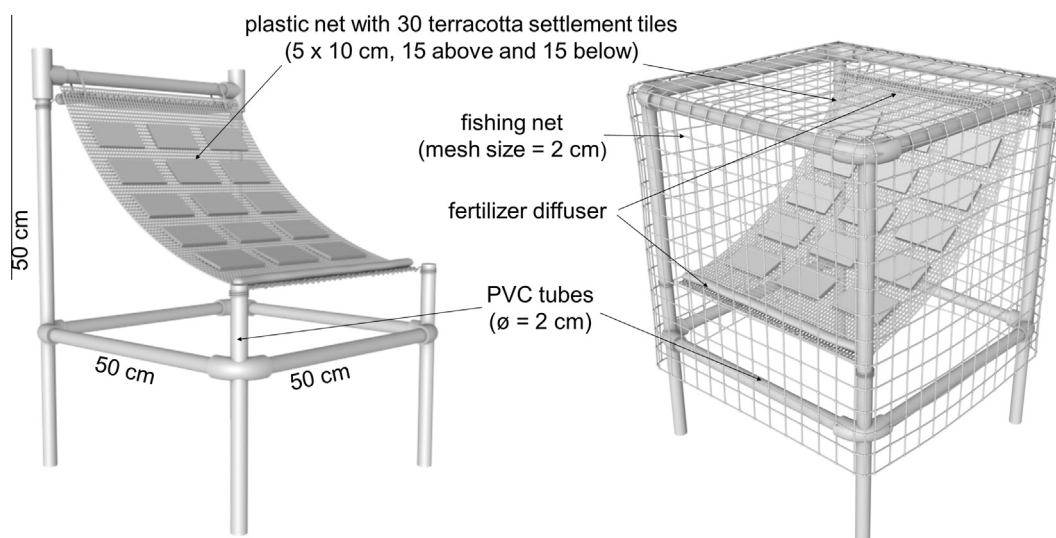


Fig. 2. Visualization of cage design. Control (left) and combined treatment (right). Overfishing was simulated by covering assigned set-ups with fishing net; eutrophication was simulated by adding two fertilizer diffusers to assigned set-ups. Tubes below lower frames protruded into the sand to secure the set-ups in the ground.

and herbivory (open and caged) with a crossed design that allowed testing the interaction between the two factors. Thus, each of the 16 set-ups was randomly assigned to one of four treatments: A: control – no manipulation, B: nutrient enrichment, C: herbivore exclusion or D: both nutrient enrichment and herbivore exclusion. Replication of each treatment was 4. Set-ups simulating eutrophication and overfishing were deployed in sand pools surrounded by coral structure in 5 m water depth with at least 1.5 m distance to each other and 10–30 m distance between plots of replicates (Fig. 1). Cage frames ($0.5 \times 0.5 \times 0.5$ m) were constructed from PVC-tubes (Fig. 2). Plastic net was fixed to the vertical tubes in an angle of 45° to serve as basis for settlement tiles while avoiding sedimentation on their surface. Of the 30 terracotta tiles fixed to each net with cable ties, 15 were facing upwards (light-exposed, algae growth) and 15 were facing downwards (shaded, invertebrate settlement). The tiles (standardized to 50 cm^2 from customary floor terracotta tiles) were preconditioned in buckets with seawater for 24 h prior to deployment.

2.2.1. Simulated overfishing

Overfishing was simulated by covering assigned frames with fishing net (mesh size 2 cm), which was exchanged weekly to avoid light attenuation by overgrowth. To evaluate the effectiveness of herbivore exclusion, fish-bites on settlement tiles were counted on one occasion on two open and two closed set-ups for 30 min each. Simulated overfishing decreased fish bites on caged ($0.0\text{--}0.5 \text{ bites min}^{-1}$) compared to open plots ($6\text{--}12 \text{ bites min}^{-1}$). Different species of fish were observed to graze on settlement tiles, mainly individual adult parrotfish or groups of juvenile parrotfish, but also some wrasses and few damselfish. Besides, small and medium sized hermit crabs were frequently observed feeding on tiles. Possible caging artifacts were assessed by monitoring light availability in closed and open set-ups with HOBO® Pendant Temperature/Light Data loggers. Mean daily light availabilities within experimental plots ranged from 400 to 2200 lux and were on average $23 \pm 9\%$ lower in caged set-ups. However, this difference was considered negligible due to the general high light availability in 5 m water depth. Water movement, as a proxy for water currents

and flow exposure, was measured in open and caged set-ups on two occasions in March and May using the clod-card technique. Small objects of fine plaster were standardized to 20.0 ± 0.2 g, glued to tiles and exposed to *in situ* conditions for 24 h. The diffusion factor (DF) was then calculated from weight-loss of clods *in situ* relative to controls in buckets of seawater without water flow (Jokiell and Morrissey 1993). Water movement was not significantly reduced in caged ($DF = 2.34 \pm 0.15$) compared to open plots ($DF = 2.17 \pm 0.17$; $t(10) = 1.960$, $p = 0.093$).

2.2.2. Simulated eutrophication

Eutrophication was simulated by using bags of polyethylen mesh, each filled with 40 g Osmocote® controlled release fertilizer pellets (13% N, 13% P_2O_5 and 13% K_2O), which is one of the most commonly used nutrient sources for enrichment studies (Littler et al. 2006b). Two bags were fixed to the plastic net in each cage assigned to nutrient enrichment, facing land and ocean side to ensure the supply with nutrients independent of water current direction. Fertilizer diffusers were exchanged weekly to ensure constant supply with nutrients. The remaining fertilizer was dried and re-weighed to estimate daily nutrient release. The mean total mass of fertilizer lost from the diffusers was not different in caged (4.52 ± 1.14 g) and open plots (4.37 ± 1.19 g; $t(62) = -0.524$, $p = 0.602$). Fertilizer loss averaged 4.4 ± 1.2 g per diffuser after 7 days of exposure which corresponds to a daily release of around 164 mg N and 164 mg P in nutrient-enriched plots. To evaluate the success of nutrient enrichment, water was sampled from 5 cm above the central tiles in all 16 set-ups with 60 mL syringes on three occasions in April/May 2012, resulting in 24 data points for unenriched and 21 (3 samples lost) for enriched plots. The samples were filtered and analyzed for inorganic phosphate concentrations within 4 h after sampling as described above. Determination of nitrate and nitrite was attempted using a simplified Resorcinol method (Zhang and Fischer 2006) but results are excluded due to impurity of analytical compounds and resulting low precision of data. The release of nutrients from diffusers was confirmed by nutrient concentrations above upper detection limits in direct proximity (0.5–1 cm distance) to the diffusers. However, phosphate water concentrations in the center of nutrient enriched plots ($0.17 \pm 0.05 \mu\text{mol PO}_4^{3-} \text{L}^{-1}$) were not significantly elevated compared to controls ($0.16 \pm 0.04 \mu\text{mol PO}_4^{3-} \text{L}^{-1}$; Mann–Whitney $T = 531.00$, $n_1 = 21$, $n_2 = 24$, $p = 0.277$).

2.3. Sampling and processing of settlement tiles

A random pair of tiles (light-exposed and shaded) was collected weekly from each cage over 12 weeks using SCUBA. Tiles were stored in ziplock bags for transportation, rinsed with seawater to remove sediment and mobile invertebrates and analyzed for following parameters in the Center for Oceanic Research and Education, South East Asia (COREsea) on Koh Phangan, Thailand, on the day of sampling:

- (1) Light-exposed tiles were submerged in boxes with seawater, and pictures were taken from above in about 20 cm distance with a digital camera. The relative cover of organisms on tiles was then observed below 50 random grid points projected on each tile picture with the software CPCe 4.1 (Kohler and Gill 2006). Groups were bare substrate, turf algae (assemblages of filamentous algae and cyanobacteria up to 3 cm height), fleshy macroalgae and sessile invertebrates. For statistical analyses, turf algae and fleshy macroalgae were grouped to total algal cover as fleshy macroalgae cover was too low to be tested statistically as individual algal group.

- (2) Light-exposed tiles were rinsed with fresh water to remove salt. Organisms were scraped off the surface completely with razor blades and collected in pre-combusted tinfoil. The samples were dried for 7 days in a solar-powered dry oven ensuring $40\text{--}48^\circ\text{C}$ for at least 5 h per day before dry mass was determined with a digital precision scale (accuracy: 0.001 g). As a desiccator was not available, some remaining moisture in the samples cannot be ruled out. However, all samples were treated equally and quantitative differences in biomass were therefore considered reliable.
- (3) Shaded tiles were submerged in boxes with seawater, and abundances of invertebrate settlers as well as CCA were recorded on the tile surface using a stereomicroscope (Carton DSZ44, magnification 10x – 44x). Identified groups were *Asciidiidae*, *Balanidae*, *Bivalvia*, *Membraniporidae*, *Bugulidae*, *Folliculina* sp. (a ciliate of the class Heterotrichea), *Serpulidae*, *Spirorbinae*, *Sabellidae*, *Scleractinia*, *Actiniidae* and *Desmospongiae* which were later assigned to the groups ascidians (*Asciidiidae*), polychaetes (*Serpulidae*, *Spirorbinae*, *Sabellidae*), bryozoans (*Membraniporidae*, *Bugulidae*), ciliates (*Folliculina* sp.), bivalves (*Bivalvia*), barnacles (*Balanidae*), corals (*Scleractinia*, *Actiniidae*) and sponges (*Desmospongiae*) for further analyses.

While shaded tiles were only assessed for qualitative changes in settler communities, organisms on light-exposed tiles were additionally analyzed for inorganic carbon (C_{inorg}) and organic carbon contents (C_{org}) along with nitrogen (N) contents.

- (1) Dried samples of light-exposed tiles were transported to the Leibniz Center for Tropical Marine Ecology (ZMT), Bremen, Germany and again dried for 24 h at 40°C before homogenized with mortar and pestle. Elemental analyses of subsamples were performed for sampling weeks 2, 4, 6, 8, 10 and 12 in three replications for each treatment (samples from plots 2, 3, 4) with a CHN elemental analyzer (Eurovector Euro EA 3000). Analyzed parameters were total carbon (C) and N content (1 mg sample in tin cups) as well as C_{org} content after acidification with HCl to remove inorganic calcium carbonate (100 μL 1 N HCl added to 1 mg sample in silver cups, dried for 24 h at 40°C before analysis). Development of C, C_{org} or N on tile surfaces was then calculated by multiplying the percent of proportion values resulting from the analysis with the dry mass on respective tiles. C_{inorg} was calculated by subtracting C_{org} from C.

2.4. Statistical data analysis

Values are given as mean $\pm$ standard deviation if not stated otherwise. Caging artifacts were evaluated using two-tailed unpaired *t*-tests, nutrient enrichment success and comparisons of phosphate and chlorophyll *a* concentrations in bay and river stations were evaluated using non-parametric Mann–Whitney Rank Sum Tests in SigmaPlot 12.3.

Total dry mass, algal cover, C_{inorg} , C_{org} and N content as well as C_{org} /N ratio on light-exposed tiles were analyzed using 3-factorial GLMs in R (R Development Core Team, 2012), containing cage (present/absent), nutrients (present/absent), time (12 or 6 sampling times), and their interactions as fixed factors to test for single and interactive effects of treatments. The assumptions of normality and equality of variance were evaluated through graphical analyses of residuals. GLMs with gamma distribution and link-functions ‘log’ or ‘identity’ were used as they fitted available data best. One sample (time 2, treatment D, plot 2) was excluded from the analyses as its C and N values were 10 times higher than those from

other samples, likely due to contamination of that sample prior to analysis.

Abundances of CCA on shaded tiles were analyzed using a 3-factorial GLM with function 'quasi' and link 'identity'. Invertebrate settlers on shaded tiles were analyzed using 2-factorial GLMs with fixed factors treatments (A, B, C and D) and time (1–12) and either negative binomial or quasi-distributions (depending which model fit the data better based on graphical analyses of residuals) to cope with over- and underdispersion of count data. Tukey post hoc tests (function 'glht' of 'multcomp' package in R) were performed for groups with significant influence of treatments.

3. Results

Light exposure had a strong influence on the communities developing on settlement tile surfaces. Cover on light-exposed tiles was almost exclusively composed of turf algae and some fleshy brown macroalgae. Shaded tiles were covered by CCA, turf algae, and invertebrate settlers, which in general did not occur on light-exposed tiles (Fig. 3). Many invertebrates tended to cluster on individual tiles (up to 1000 individuals), independent of treatment conditions.

3.1. Effects of simulated eutrophication

Simulated eutrophication did not have an effect on optical diversity of algal assemblages (Fig. 3) and total algae cover (Fig. 5) on light-exposed tiles or on the abundance of CCA (Table 1) and invertebrate groups (Tables 2 and 3) on shaded tiles.

C_{org} contents, N contents and C_{org}/N ratios on light-exposed tiles were not affected by simulated eutrophication (Fig. 4, Table 1). Only C_{inorg} content was significantly higher on tiles exposed to simulated eutrophication compared to controls ($p < 0.001$, Table 1).

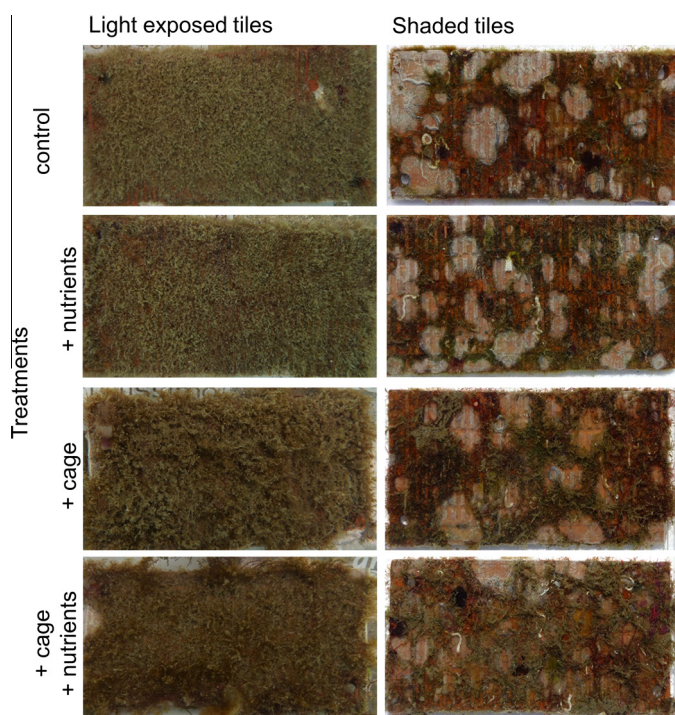


Fig. 3. Settler communities. Photographs show representative communities on light-exposed (left column) and shaded tiles (right column) of each treatment after 10 weeks of exposure. Please note short, dense turf algae and high abundances of crustose coralline algae on open plots (rows 1 & 2) and longer turf algae filaments as well as fleshy macroalgae on caged plots (rows 3 & 4).

Total dry mass was not affected by simulated eutrophication as a single factor, but showed a significant response to the interaction of nutrients and time ($p = 0.008$, Table 1), i.e. nutrients increased dry mass on simulated eutrophication tiles compared to controls at some of the sampling times (week 4 and week 12, Fig. 4).

3.2. Effects of simulated overfishing

Simulated overfishing affected turf algae height and fleshy macroalgal cover on light exposed tiles. Assemblages of turf algae on caged tiles were 3–4 times taller than dense, but very short, turf algae on uncaged tiles (Fig. 3). From week 7 onwards, small individuals of fleshy brown macroalgae occurred on caged tiles, most frequently of the genus *Padina* sp., but also some *Sargassum* sp. and one large individual of *Dictyota* sp.. Cover of fleshy macroalgae on light exposed tiles was highest after 12 weeks of exposure with 12–17% relative cover in caged and 0% in open treatments (Fig. 5b). On shaded tiles, simulated overfishing significantly reduced abundances of CCA ($p = 0.001$, Table 1), whereas abundances of total settlers and ascidians were significantly higher in caged compared to control treatments ($p < 0.001$ and $p = 0.004$ respectively, Tables 2 and 3).

Simulated overfishing significantly increased total dry mass on light-exposed tiles ($p < 0.001$, Table 1), whereas C_{inorg} , C_{org} and N contents as well as C_{org}/N ratio were not affected (Table 1, Fig. 4). C_{inorg} showed a significant response to the interaction of caging and time ($p = 0.008$, Table 1), i.e. simulated overfishing increased C_{inorg} compared to controls at some of the sampling times (week 10, Fig. 4).

3.3. Combined effects

The combined simulation of herbivore exclusion and nutrient enrichment did not influence any response parameters on light-exposed tiles (Fig. 4, Table 1). On shaded tiles, the combined simulation significantly decreased abundances of barnacles compared to controls and simulated eutrophication treatments (Tables 2 and 3). Communities developing on tiles exposed to combined treatments resembled those exposed to simulated overfishing optically on light-exposed and shaded tiles (Fig. 3).

4. Discussion

Herbivory seemed to have a greater control on local benthic communities and their variables than nutrient enrichment, or the interaction of the two. While a limited number of previous studies showed that nutrients can drive macroalgal production in some locations (Smith et al. 2001; Lapointe et al. 2004; Littler et al., 2006a), the majority of field experiments identified herbivory as the key controlling factor for algal growth (Miller et al. 1999; Thacker et al. 2001; Belliveau and Paul 2002; Diaz-Pulido and McCook 2003; McClanahan et al. 2003; Sotka and Hay 2009; Burkepile and Hay 2009; Rasher et al. 2012; Jessen et al. 2013). The conflicting results from field experiments may be due to complex interactions between herbivory and nutrients that may vary with productivity, latitude, algal group and duration of study (Burkepile and Hay 2006; Houk et al. 2010; Smith et al. 2010).

4.1. Effects of simulated eutrophication

The lack of organism responses to simulated eutrophication and the relatively low C_{org}/N ratio in algal biomass from all treatments suggest, that ambient nutrient concentrations were already satisfying algal growth, and thereby masked the effects of further nutrient input. Several studies showed increased algal growth in

Table 1
Results of 3-factorial generalized linear models (GLMs): influence of simulated eutrophication and overfishing on response parameters. Independent factors (1st column) are caging (C), nutrients (N), and time (T) and their interactions. Response variables are displayed in first rows with C = carbon and N = nitrogen. GLMs were performed in R and used quasi distribution (CCA abundance) or gamma distribution (other response parameters) with link functions 'log' (dry mass) or 'identity' (other response parameters). Significant results are indicated by asterisks and displayed in bold.

	Dry mass			Inorganic C on tiles			Organic C on tiles		
	df	Chi ²	p	df	Chi ²	p	df	Chi ²	p
C	1	12.24	*<0.001	1	0.92	0.338	1	0.34	0.557
N	1	1.21	0.270	1	11.14	*<0.001	1	1.44	0.231
T	11	779.61	*<0.001	5	184.11	*<0.001	5	497.77	*<0.001
C x N	1	1.30	0.254	1	0.32	0.574	1	2.01	0.157
C x T	11	11.04	0.440	5	15.56	*0.008	5	4.24	0.516
N x T	11	25.52	*0.008	5	4.44	0.488	5	4.86	0.434
	N on tiles			C _{org} /N ratio on tiles			CCA abundance		
	df	Chi ²	p	df	Chi ²	p	df	Chi ²	p
C	1	0.02	0.899	1	1.72	0.189	1	30.67	*<0.001
N	1	1.28	0.260	1	0.01	0.912	1	0.74	0.391
T	5	568.19	*<0.001	5	31.50	*<0.001	11	32.86	*<0.001
C x N	1	1.68	0.195	1	0.02	0.889	1	0.00	0.947
C x T	5	5.57	0.351	5	3.32	0.651	11	17.89	0.084
N x T	5	5.21	0.391	5	1.91	0.862	11	7.35	0.770

Table 2
Abundances of invertebrate settlers on shaded tiles. Values are given as means $\pm$ SE ($n = 4$) of sum of individuals settled to tiles of the same treatment over the 12 week study period.

Invertebrates	A: control	B: nutrient enrichment	C: herbivore exclusion	D: nutrient enrichment & herbivore exclusion
Total settlers	1882 $\pm$ 291	1698 $\pm$ 119	2966 $\pm$ 294	2155 $\pm$ 286
Ascidians	487 $\pm$ 386	384 $\pm$ 160	1503 $\pm$ 189	811 $\pm$ 247
Polychaetes	568 $\pm$ 46	608 $\pm$ 57	575 $\pm$ 44	679 $\pm$ 77
Bryozoans	502 $\pm$ 44	423 $\pm$ 58	478 $\pm$ 19	487 $\pm$ 69
Ciliates	294 $\pm$ 97	254 $\pm$ 95	384 $\pm$ 125	167 $\pm$ 53
Barnacles	14.8 $\pm$ 9.4	12.8 $\pm$ 5.1	7.3 $\pm$ 3.0	3.8 $\pm$ 1.2
Bivalves	13.5 $\pm$ 9.2	9.0 $\pm$ 3.5	10.8 $\pm$ 3.4	6.0 $\pm$ 1.4
Corals	3.8 $\pm$ 0.9	7.8 $\pm$ 5.4	6.5 $\pm$ 2.4	2.5 $\pm$ 1.3
Sponges	0.5 $\pm$ 0.3	0.8 $\pm$ 0.8	1.3 $\pm$ 0.3	0

Table 3
Results of 2-factorial generalized linear models (GLMs): influence of treatment and time on invertebrate settlement. Independent factors (1st column) are treatments (Tr) and time (T). Response variables (1st rows) are abundances of invertebrate settlers on shaded tiles. GLMs were performed in R and used negative binomial (total settlers and ascidians) or quasi-poisson (all other groups) distributions. Significant results are indicated by asterisks and displayed in bold. Tukey post hoc tests (function 'glht' of 'multcomp' package in R) were performed for groups of settlers experiencing significant influence of treatments (A: control, B: nutrient enrichment, C: herbivore exclusion, D: nutrient enrichment & herbivore exclusion).

GLM	Total settlers			Ascidians			Polychaetes			Bryozoans		
	df	Chi ²	p	df	Chi ²	p	df	F	p	df	F	p
Tr	3	23.37	*<0.001	3	13.97	*0.003	3	1.89	0.133	3	1.82	0.146
T	11	185.48	*<0.001	11	57.57	*<0.001	11	8.32	*<0.001	11	25.15	*<0.001
Tukey		z value	p		z value	p						
B-A		−0.350	0.985		−0.433	0.973						
C-A		3.946	*<0.001		3.377	*0.004						
D-A		1.932	0.215		1.924	0.218						
C-B		4.296	*<0.001		3.808	*<0.001						
D-B		2.281	0.102		2.357	0.086						
D-C		−2.015	0.182		−1.458	0.463						
GLM	Ciliates			Bivalves			Barnacles			Corals		
	df	F	p	df	F	p	df	F	p	df	F	p
Tr	3	1.73	0.163	3	2.21	0.088	3	4.69	*0.004	3	2.63	0.051
T	11	5.25	*<0.001	11	1.77	0.062	11	1.12	0.344	11	1.11	0.352
Tukey								z value	p			
B-A								−0.488	0.961			
C-A								−2.004	0.181			
D-A								−3.030	*0.013			
C-B								−1.553	0.398			
D-B								−2.666	*0.037			
D-C								−1.326	0.538			

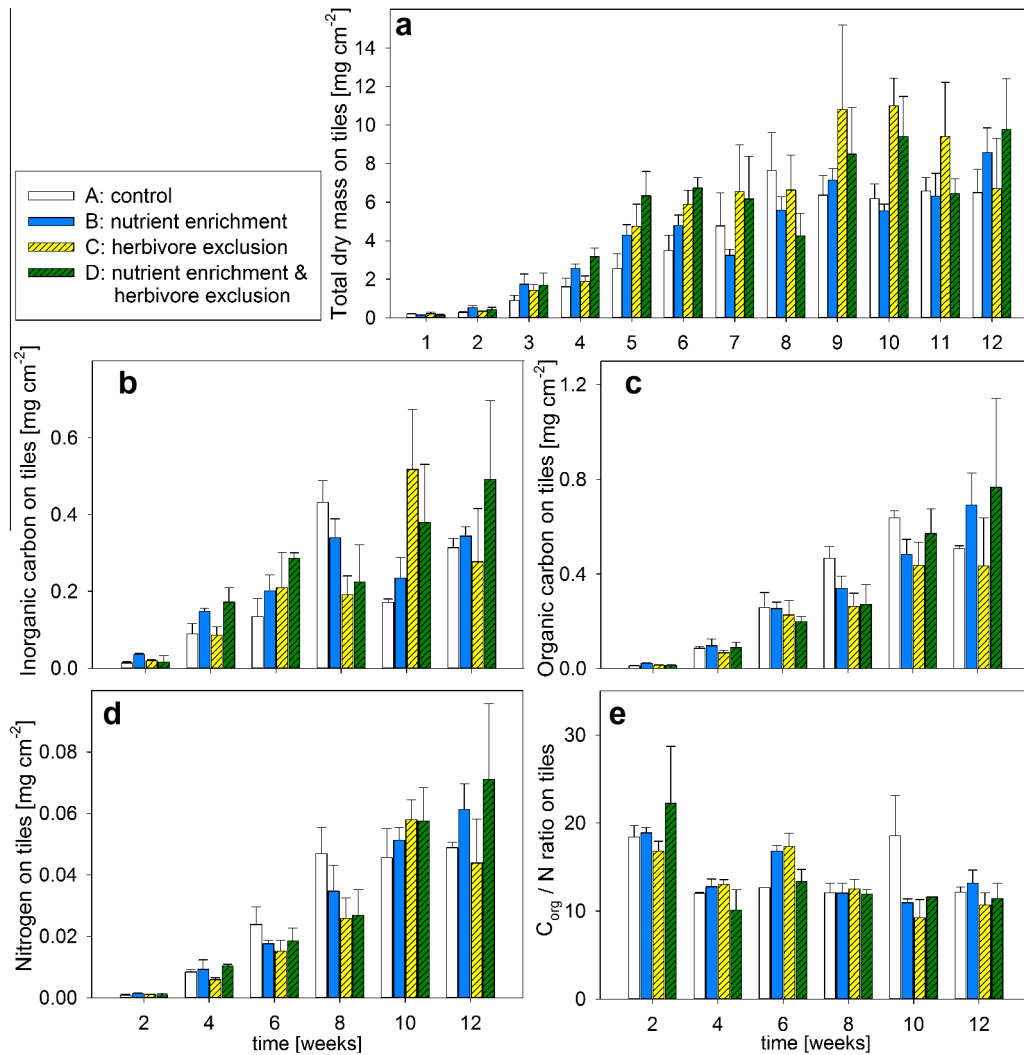


Fig. 4. Response parameters on light-exposed tiles. Development of (a) total dry mass, (b) inorganic carbon content, (c) organic carbon content, (d) nitrogen content and (e) C_{org}/N ratio over the sampling period of 12 weeks. Values are presented as means + SE. Replicates for analysis were $n = 4$ for dry mass and $n = 3$ for other parameters.

response to nutrient enrichment (Smith et al. 2001; Lapointe et al. 2004; Littler et al., 2006a). Also, nutrients may increase the abundances of filter feeding invertebrates like polychaetes, sponges, tunicates and bryozoans through the stimulation of plankton growth (Hallock and Schlager 1986; Hunte and Wittenberg 1992), while settlement of coral larvae usually decreases in response to eutrophication (Tomascik 1991; Hunte and Wittenberg 1992; Jessen et al. 2014). Simulated eutrophication did not affect algae growth or invertebrate abundances in the present study, either because simulated eutrophication was too weak or because benthic and pelagic algae were nutrient replete due to generally high availability of nutrients in the surrounding water.

The median C_{org}/N ratio for communities on algae dominated light-exposed tiles (12.6 ± 2.8) was relatively low compared to the average value for benthic algae (18.3 , Atkinson and Smith 1983). The comparison suggests that the algae at the study site were not limited by nutrient availability, as the C:N ratio in algal biomass usually decreases with increasing ambient dissolved inorganic nitrogen concentrations (Lapointe et al. 1976; Atkinson and Smith 1983). Nitrogen concentrations in the reef could not be measured, but analysis of river-water discharging into the bay revealed very high water phosphate concentrations, likely caused by untreated gray water from bungalow resorts along the river.

However, phosphate concentrations in the experimental plots on the reef ($0.16 \pm 0.04 \mu\text{mol PO}_4^{3-} \text{L}^{-1}$) were similar to mean concentrations reported for 1000 coral reefs worldwide ($0.13 \pm 0.08 \mu\text{mol PO}_4^{3-} \text{L}^{-1}$, Kleypas et al. 1999) and therefore did not indicate a highly eutrophic system.

4.2. Effects of herbivore exclusion

Herbivore exclusion enabled the growth of macroalgae and decreased settlement of CCA in caged treatments. Fleishy macroalgae are particularly attractive to herbivores and only become abundant where grazing pressure is low (Hay 1984; Littler and Littler 1984). They may therefore be considered early warning indicators for reef degradation by overfishing. Although the herbivore biomass at the study site was 53% lower than mean herbivorous fish biomass in Indo-Pacific reefs ($29.0 \pm 4.1 \text{ g m}^{-2}$, Roff and Mumby 2012) and also lower compared to a nearby Marine Protected Area (Pusch, unpublished data), local fish populations were still able to control macroalgal growth in the open experimental treatments and in the reef (only 4% fleshy macroalgae cover compared to $10 \pm 12\%$ in the Indo-Pacific (Roff and Mumby 2012)). Moreover, herbivory significantly maintained cover of CCA and short algal turfs on settlement tiles – both characteristic

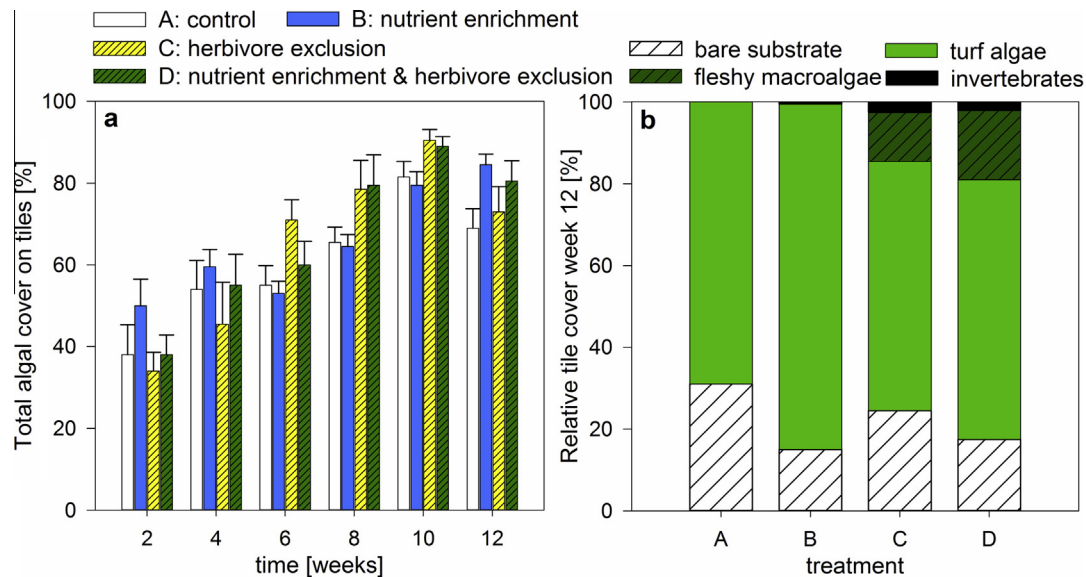


Fig. 5. Algal cover on light exposed tiles. Development of (a) total algal cover over time and (b) relative cover of benthic groups under different treatments in week 12. Values are presented as (a) means + SE or (b) means.

components of healthy reefs. Enhanced settlement of corals and CCA in the presence of herbivores has been observed in other studies (Smith et al. 2001; Sotka and Hay 2009; Rasher et al. 2012; Jessen et al. 2014) and suggests that top-down control by herbivores feeding on competing algae, rather than eutrophication as a direct bottom-up factor, is the more important factor influencing settlement of organisms. Abundances of ascidians on the other hand were higher in caged compared to open treatments, which suggests that this group exhibits high competitive advantages toward turf algae, or that they are preferentially grazed from accessible reef substrate. Supportively, previous studies found increased settlement of polychaetes and ascidians in response to simulated overfishing as post-settlement mortality due to predation was low (Vine 1974; Osman and Whitlatch 1998, 2004; Jessen et al. 2014). Other groups, like bryozoans, are more resilient to predation and can dominate communities also in open areas (Osman and Whitlatch 2004). Accordingly, abundances of bryozoans were equally high in all treatments in the present study. From these results, macroalgae and ascidians can be used as bioindicators of overfishing in a reef, as abundances only increased if predation pressure was lowered.

Although the herbivore community at the study site was obviously effective in limiting fleshy macroalgal growth, the overall algal growth response to caging was small compared to other studies, which together with the relatively low fish abundance suggests some effects of overfishing at the study site. Previous manipulation experiments showed highly significant increases in algal mass or cover in response to herbivore removal (Hughes 1994; Miller et al. 1999; Smith et al. 2010; Thacker et al. 2001; Smith et al. 2001; Belliveau and Paul 2002; Jompa and McCook 2002; Hughes et al. 2007; Gruner et al. 2008; Burkepile and Hay 2009; Rasher et al. 2012; Jessen and Wild 2013), e.g. 300-fold increased algal dry mass compared to controls after only 4 weeks of exposure (Jessen et al. 2013). The small differences between herbivore exclusion treatments and controls in the present study were due to the ineffectiveness of turf algal removal in uncaged treatments ($82 \pm 4\%$ turf algal cover in week 10), although accessible to grazing. The most important consumers of algae in a healthy coral reef are herbivorous fish (Hughes 1994; Bellwood et al. 2004). The herbivorous fish community at the study site (0.088 ± 0.031 ind. m^{-2}) was small, with only few large individuals, suggesting some effects

of overfishing at the study site which leads to insufficient control of turf algal proliferation ($42 \pm 6\%$ benthic cover). Turf algae can trap high amounts of sediments, and long filaments in nongrazed areas are likely even more efficient than grazed turfs. This is of concern as sediment loads in algal turfs can strongly suppress herbivory (Bellwood and Fulton 2008), leading to positive feedbacks on algal proliferation.

4.3. Combined effects

Communities in combined treatments resembled the ones in caged treatments both on light-exposed and shaded tiles, and no significant differences between combined and single manipulations were found in any response parameter. In contrast, several studies reported highest algae mass or dominance of fleshy macroalgae on settlement surfaces exposed to both nutrient enrichment and herbivore exclusion (Smith et al. 2001, 2010; Burkepile and Hay 2006; Jessen et al. 2013). Often, nutrients had an effect on algal abundance only when herbivores were excluded (Russ and McCook 1999; Thacker et al. 2001; Jompa and McCook 2002). In general, studies testing factorial combinations of nutrients and herbivory on algae have varied in terms of nutrient effects, but have all emphasized the importance of herbivory (Miller et al. 1999; Smith et al. 2001; Thacker et al. 2001; Belliveau and Paul 2002; Burkepile and Hay 2006; Heck and Valentine 2007; Rasher et al. 2012). Likewise, results from the present study suggest that the top-down control herbivory is the actual key factor controlling reef algal growth and settlement of invertebrates at the study site.

5. Conclusion

These results to our knowledge for the first time describe responses to *in situ* eutrophication and herbivore exclusion in a South East Asian reef which is impacted by overfishing and pollution from land. Findings revealed that herbivorous fish limited the establishment of macroalgae, promoted the establishment of CCA and likely decreased sediment accumulation, all of which are critical to successful coral recruitment and growth. The relatively small herbivorous community was able to control fleshy macroalgal abundances at the study site while turf algae cover was hardly suppressed, indicating some impacts on the reef by overfishing. As

herbivory was identified as the main controlling factor for local benthic communities, we suggest that regional management efforts focus on measures to reduce the removal of herbivorous fishes to slow reef decline and facilitate coral recovery.

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References

- Abelson, A., Olinsky, R., Gaines, S., 2005. Coral recruitment to the reefs of Eilat, Red Sea: temporal and spatial variation, and possible effects of anthropogenic disturbances. *Mar. Pollut. Bull.* 50, 576–582.
- Atkinson, M., Smith, S., 1983. C: N: P ratios of benthic marine plants. *Limnol. Oceanogr.* 28, 568–574.
- Bell, P.R.F., 1992. Eutrophication and coral reefs—some examples in the Great Barrier Reef Lagoon. *Water Res.* 26, 553–568.
- Belliveau, S., Paul, V., 2002. Effects of herbivory and nutrients on the early colonization of crustose coralline and fleshy algae. *Mar. Ecol. Prog. Ser.* 232, 105–114.
- Bellwood, D.R., Fulton, C.J., 2008. Sediment-mediated suppression of herbivory on coral reefs: decreasing resilience to rising sea levels and climate change? *Limnol. Oceanogr.* 53, 2695–2701.
- Bellwood, D.R., Hughes, T.P., Folke, C., Nyström, M., 2004. Confronting the coral reef crisis. *Nature* 429, 827–833.
- Burkpile, D., Hay, M., 2006. Herbivore vs. nutrient control of marine primary producers: context-dependent effects. *Ecology* 87, 3128–3139.
- Burkpile, D., Hay, M., 2009. Nutrient versus herbivore control of macroalgal community development and coral growth on a Caribbean reef. *Mar. Ecol. Prog. Ser.* 389, 71–84.
- Cheevaporn, V., Menasveta, P., 2003. Water pollution and habitat degradation in the Gulf of Thailand. *Mar. Pollut. Bull.* 47, 43–51.
- Chou, L.M., Tuan, V., Yeemin, T., Cabanban, A., 2002. Status of Southeast Asia coral reefs. In: *Status of coral reefs of the World: 2002*. Australian Institute of Marine Science, pp. 123–152.
- Diaz-Pulido, G., McCook, L.J., 2003. Relative roles of herbivory and nutrients in the recruitment of coral-reef seaweeds. *Ecology* 84, 2026–2033.
- Diaz-Pulido, G., McCook, L.J., 2005. Effects of nutrient enhancement on the fecundity of a coral reef macroalga. *J. Exp. Mar. Biol. Ecol.* 317, 13–24.
- Fabricius, K.E., 2005. Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. *Mar. Pollut. Bull.* 50, 125–146.
- FAO, 2011. Food and Agriculture Organization of the United Nations. FAO Statistical Databases. <www.fao.org>.
- Froese F, Pauly D (2012) FishBase. <www.fishbase.org>.
- Grasshoff, K., Kremling, K., Erhardt, M., 1999. *Methods of Seawater Analysis*, third ed. Wiley-VCH, Weinheim.
- Green, A.L., Bellwood, D.R., 2009. Monitoring functional groups of herbivorous fishes as indicators for coral reef resilience – A practical guide for coral reef managers in the Asia Pacific region. IUCN working group on climate change and coral reefs.
- Gruner, D.S., Smith, J.E., Seabloom, E.W., Sandin, S.A., Ngai, J.T., Hillebrand, H., Harpole, W.S., Elser, J.J., Cleland, E.E., Bracken, M.E.S., Borer, E.T., Bolker, B.M., 2008. A cross-system synthesis of consumer and nutrient resource control on producer biomass. *Ecol. Lett.* 11, 740–755.
- Hallock, P., Schlager, W., 1986. Nutrient excess and the demise of coral reefs and carbonate platforms. *Palaios* 1, 389–398.
- Hay, M.E., 1984. Predictable spatial escapes from herbivory: how do these affect the evolution of herbivore resistance in tropical marine communities? *Oecologia* 64, 396–407.
- Heck, J., Valentine, J., 2007. The primacy of top-down effects in shallow benthic ecosystems. *Estuar. Coasts* 30, 371–381.
- Houk, P., Musburger, C., Wiles, P., 2010. Water quality and herbivory interactively drive coral-reef recovery patterns in American Samoa. *PLoS One* 5, e13913.
- Hughes, T.P., 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* 265, 1547–1551.
- Hughes, T.P., Rodrigues, M.J., Bellwood, D.R., Ceccarelli, D., Hoegh-Guldberg, O., McCook, L.J., Moltschanowskyj, N., Pratchett, M.S., Steneck, R.S., Willis, B., 2007. Phase shifts, herbivory, and the resilience of coral reefs to climate change. *Curr. Biol.* 17, 360–365.
- Hunte, W., Wittenberg, M., 1992. Effects of eutrophication and sedimentation on juvenile corals. *Mar. Biol.* 114, 625–631.
- Jackson, J.B., Kirby, M.X., Berger, W.H., Bjorndal, K.A., Botsford, L.W., Bourque, B.J., Bradbury, R.H., Cooke, R., Erlandson, J., Estes, J.A., Hughes, T.P., Kidwell, S., Lange, C.B., Lenihan, H.S., Pandolfi, J.M., Peterson, C.H., Steneck, R.S., Tegner, M.J., Warner, R.R., 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293, 629–637.
- Jessen, C., Roder, C., Villa Lizcano, J.F., Voolstra, C.R., Wild, C., 2013. In-situ effects of simulated overfishing and eutrophication on benthic coral reef algae growth, succession, and composition in the Central Red Sea. *PLoS One* 8, e66992.
- Jessen, C., Voolstra, C.R., Wild, C., 2014. In situ effects of simulated overfishing and eutrophication on settlement of benthic coral reef invertebrates in the Central Red Sea. *PeerJ* 2, e339.
- Jessen, C., Wild, C., 2013. Herbivory effects on benthic algal composition and growth on a coral reef flat in the Egyptian Red Sea. *Mar. Ecol. Prog. Ser.* 476, 9–21.
- Jokiell, P., Morrissey, J., 1993. Water motion on coral reefs: evaluation of the “clod card” technique. *Mar. Ecol. Prog. Ser.* 93, 175–181.
- Jompa, J., McCook, L.J., 2002. The effects of nutrients and herbivory on competition between a hard coral (*Porites cylindrica*) and a brown alga (*Lobophora variegata*). *Limnol. Oceanogr.* 47, 527–534.
- Kleypas, J.A., McManus, J.W., Meñez, L.A.B., 1999. Environmental limits to coral reef development: where do we draw the line? *Am. Zool.* 39, 146–159.
- Knight, M., Kushner, B., Starkhouse, B., Waite, R., White, A., 2012. Reefs at risk: revisited in the coral triangle. World Resources Institute, Washington DC.
- Kohler, K.E., Gill, S.M., 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. *Comput. Geosci.* 32, 1259–1269.
- Lapointe, B.E., 1997. Nutrient thresholds for bottom-up control of macroalgal blooms on coral reefs in Jamaica and southeast Florida. *Limnol. Oceanogr.* 42, 1119–1131.
- Lapointe, B.E., Barile, P.J., Matzie, W.R., 2004. Anthropogenic nutrient enrichment of seagrass and coral reef communities in the Lower Florida Keys: discrimination of local versus regional nitrogen sources. *J. Exp. Mar. Biol. Ecol.* 308, 23–58.
- Lapointe, B.E., Williams, L.D., Goldman, J.C., Ryther, J.H., 1976. The mass outdoor culture of macroscopic marine algae. *Aquaculture* 8, 9–21.
- Littler, M.M., Littler, D.S., 1984. Relationships between macroalgal functional form groups and substrata stability in a subtropical rocky-intertidal system. *J. Exp. Mar. Biol. Ecol.* 74, 13–34.
- Littler, M.M., Littler, D.S., Brooks, B.L., 2006a. Harmful algae on tropical coral reefs: bottom-up eutrophication and top-down herbivory. *Harmful algae* 5, 565–585.
- Littler, M.M., Littler, D.S., Brooks, B.L., Lapointe, B.E., 2006b. Nutrient manipulation methods for coral reef studies: a critical review and experimental field data. *J. Exp. Mar. Biol. Ecol.* 336, 242–253.
- McClanahan, T.R., Sala, E., Stickels, P.A., Cokos, B.A., Baker, A.C., Starger, C.J., Jones IV, S.H., 2003. Interaction between nutrients and herbivory in controlling algal communities and coral condition on Glover's Reef, Belize. *Mar. Ecol. Progr.* 261, 135–147.
- McCook, L.J., 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, L.J., Jompa, J., Diaz-Pulido, G., 2001. Competition between corals and algae on coral reefs: a review of evidence and mechanisms. *Coral reefs* 19, 400–417.
- Miller, M.W., 1998. Coral/seaweed competition and the control of reef community structure within and between latitudes. *Oceanogr. Mar. Biol. Annu. Rev.* 36, 65–96.
- Miller, M.W., Hay, M.E., Miller, S.L., Malone, D., Sotka, E.E., 1999. Effects of nutrients versus herbivores on reef algae: a new method for manipulating nutrients on coral reefs. *Limnol. Oceanogr.* 44, 1847–1861.
- Moberg, F., Folke, C., 1999. Ecological goods and services of coral reef ecosystems. *Ecol. Econ.* 29, 215–233.
- Murphy, J., Riley, J.P., 1962. A modified single solution method for the determination of phosphate in natural waters. *Anal. Chim. Acta.* 27, 31–36.
- Myers, R.A., Worm, B., 2003. Rapid worldwide depletion of predatory fish communities. *Nature* 423, 280–283.
- Nixon, S., 1995. Coastal marine eutrophication: a definition, social causes, and future concerns. *Ophelia* 41, 199–219.
- Nyström, M., Folke, C., Moberg, F., 2000. Coral reef disturbance and resilience in a human-dominated environment. *Trends Ecol. Evol.* 15, 413–417.
- Osman, R.W., Whitlatch, R.B., 1998. Local control of recruitment in an epifaunal community and the consequences to colonization processes. *Hydrobiologia* 375/376, 113–123.
- Osman, R.W., Whitlatch, R.B., 2004. The control of the development of a marine benthic community by predation on recruits. *J. Exp. Mar. Biol. Ecol.* 311, 117–145.
- Pauly, D., Chuenpagdee, R., 2003. Development of Fisheries in the Gulf of Thailand Large Marine Ecosystem: analysis of an unplanned experiment. In: Hempel, G., Sherman, K. (Eds.), *Large Marine Ecosystems of the world*. Elsevier, pp. 337–354.
- Paytan, A., Shellenbarger, G.G., Street, J.H., Gonneea, M.E., Davis, K., Young, M.B., Moore, W.S., 2006. Submarine groundwater discharge: an important source of new inorganic nitrogen to coral reef ecosystems. *Limnol. Oceanogr.* 51 (1), 343–348.
- Rasher, D.B., Engel, S., Bonito, V., Fraser, G.J., Montoya, J.P., Hay, M.E., 2012. Effects of herbivory, nutrients, and reef protection on algal proliferation and coral growth on a tropical reef. *Oecologia* 169, 187–198.

- Roff, G., Mumby, P.J., 2012. Global disparity in the resilience of coral reefs. *Trends Ecol. Evol.* 27, 404–413.
- Russ, G.R., McCook, L.J., 1999. Potential effects of a cyclone on benthic algal production and yield to grazers on coral reefs across the central Great Barrier Reef. *J. Exp. Mar. Bio. Ecol.* 235, 237–254.
- Smith, J.E., Hunter, C.L., Smith, C.M., 2010. The effects of top-down versus bottom-up control on benthic coral reef community structure. *Oecologia* 163, 497–507.
- Smith, S., Kimmerer, W., Laws, E., Brock, R.E., Walsh, T., 1981. Kaneohe Bay sewage diversion experiment: perspectives on ecosystem responses to nutritional perturbation. *Pacific Sci.* 35, 279–394.
- Smith, J.E., Smith, C.M., Hunter, C.L., 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.
- Sotka, E.E., Hay, M.E., 2009. Effects of herbivores, nutrient enrichment, and their interactions on macroalgal proliferation and coral growth. *Coral Reefs* 28, 555–568.
- Stobutzki, I.C., Silvestre, G.T., Garces, L.R., 2006. Key issues in coastal fisheries in South and Southeast Asia, outcomes of a regional initiative. *Fish Res.* 78, 109–118.
- Teichberg, M., Marinetto, P., Fox, S., 2012. Bottom-up versus top-down control of macroalgal blooms. In: Wiencke, C., Bischof, K. (Eds.), *Seaweed Biology: novel insights into ecophysiology, ecology and utilization*. Springer, pp. 449–467.
- Thacker, R., Ginsburg, D., Paul, V., 2001. Effects of herbivore exclusion and nutrient enrichment on coral reef macroalgae and cyanobacteria. *Coral Reefs* 19, 318–329.
- Todd, P.A., Ong, X., Chou, L.M., 2010. Impacts of pollution on marine life in Southeast Asia. *Biodivers. Conserv.* 19, 1063–1082.
- 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, M.J.A., Van Moorselaar, I., Engelhard, S., Hörnlein, C., Vonk, S.M., Visser, P.M., 2010. The effects of nutrient enrichment and herbivore abundance on the ability of turf algae to overgrow coral in the Caribbean. *PLoS One* 5, 1–8.
- Vine, P.J., 1974. Effects of algal grazing and aggressive behaviour of the fishes *Pomacentrus lividus* and *Acanthurus sohal* on coral-reef ecology. *Mar. Biol.* 24, 131–136.
- Yeemin, T., Ruengsawang, N., Buaruang, J., 2001. Coral reef management strategy policies in Thailand: lessons learnt for a decade. In: 5th International Conference on the Environmental Management of Enclosed Coastal Seas, Kobe, Japan.
- Yeemin, T., Sutthacheep, M., Somkleeb, N., 2006. Status of Coral Reefs in Thailand. In: 10th International Coral Reef Symposium. pp. 1062–1067.
- Zhang, J.-Z., Fischer, C.J., 2006. A simplified resorcinol method for direct spectrophotometric determination of nitrate in seawater. *Mar. Chem.* 99, 220–226.