



Research papers

Coral reef degradation and metabolic performance of the scleractinian coral *Porites lutea* under anthropogenic impact along the NE coast of Hainan Island, South China Sea

Cornelia Roder^{a,b,*}, Zhongjie Wu^c, Claudio Richter^{a,d}, Jing Zhang^e^a Leibniz Center for Tropical Marine Ecology (ZMT), 28359 Bremen, Germany^b King Abdullah University of Science and Technology, 23955-6900 Thuwal, Saudi Arabia^c Hainan Maritime and Fishery Department and Hainan Provincial Marine Development Plan and Design Research Institute, Haikou, (HPMDDI), China^d Alfred Wegener Institute for Polar and Marine Research, 27568 Bremerhaven, Germany^e State Key Laboratory of Estuarine and Coastal Research, East China Normal University, 3663 Zhongshan Road North, Shanghai 200062, China

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ABSTRACT

Hainan's coast provides favorable climatic, geochemical and biogeographic conditions for the development of extensive coral reefs in China. Observations in five reefs along the NE coast of Hainan showed, however, that the overall density of mobile macrofauna is low and key functional groups such as browsing, scraping or excavating herbivore fish are missing altogether. Coral diseases, partial mortality or tissue degradation are abundant and growth of macroalgal space competitors extensive. Signs of eutrophication, siltation and destructive fishing practices are evident resulting in a strongly altered environment unfavorable for coral recruitment success and survival. Acclimation to the anthropogenically altered conditions in the massive coral *Porites lutea* occurs at the cost of a decreased photosynthesis: respiration ratio reducing the regenerative capacity of these key framebuilding organisms. Even though, on the organismal level, corals are able to cope with these stressful conditions, a shift is imminent on the ecosystem level from a coral reef to a macroalgae-dominated community if land-based disturbance prevails unabated.

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1. Introduction

It is estimated that one third of all reef-building coral species are at risk of being extinct as a result of climate change and local ecosystem impacts (Carpenter et al., 2008). Amongst the most severe and acute local threats to coral reefs are the impacts of overfishing and pollution (Hodgson, 1999; Wilkinson, 2004; Hughes et al., 2007), which significantly lower a reef's resilience hence making it more subjected towards global changes in temperature and acidification (Carpenter et al., 2008). In places where they co-occur reef degradation has been shown to have deleterious impacts on coral communities (Lapointe et al., 1997; Littler et al., 2006; Mumby et al., 2007). Corals and algae are important primary producers co-occurring in tropical shallow water reefs (Crossland et al., 1991; Hatcher, 1997). As space competitors (Littler and Littler, 1985; Lapointe et al., 1997), their co-existence is balanced by nutrient supply (bottom-up control)

and grazing (top-down control), where the competitive advantage of fleshy macroalgae in terms of nutrient-enhanced growth is opposed by their greater grazing susceptibility. Changes in nutrient status and grazing can therefore have deleterious effects tilting the balance of corals to algae in reefs (Hughes, 1994; Bellwood et al., 2004), however, the rates and kinds of change are difficult to predict, as the interplay of direct and indirect effects is complex (Glynn, 1988), feedback loops result in non-linear system responses, and coral- or algal dominated communities are only two out of several possible alternate states (Rogers, 1990; Bellwood et al., 2004; Pandolfi et al., 2005).

Before phase shifts occur, changes in water quality already impact coral physiology, and corals have shown a wide range of responses to disturbances including self-cleaning via mucus production in waters subjected to sedimentation (Schuhmacher, 1977; Rublee et al., 1980), proliferation of the corals' symbionts and photosynthetic pigments in nutrient rich and turbid waters (Roder et al., 2011; Sawall et al., 2011), or the shift from autotrophic to mixotrophic or even heterotrophic nutrition if photosynthesis is not sufficient to maintain energy demands (Muscatine et al., 1989; Roder et al., 2010). Further responses to human induced ecosystem changes comprise reduced coral

* Corresponding author at: King Abdullah University of Science and Technology, 23955-6900 Thuwal, Saudi Arabia. Tel.: +966 28082542.

E-mail address: cornelia.roder@kaust.edu.sa (C. Roder).

growth (Bak, 1978; Marubini and Davies, 1996; Ferrier-Pagès et al., 2000), and declines in reproduction (Loya et al., 2004).

Corals have been shown to resist competition with macroalgae even in eutrophied waters, when sufficient grazing pressure on algae is present (Aronson and Precht, 2001; Aronson et al., 2002). Sometimes, the original grazers might not even be present any more, but replaced by other species such as sea urchins (McClanahan and Muthiga, 1988; Steneck, 1998). They can in cases of extensive overfishing become the only grazing control of algae (Ogden et al., 1973; Levitan, 1988) and may, when not antagonized by predators, become themselves a pest not only grazing on macroalgae, but finally also on corals and rock, and so eroding the total reef base (Glynn, 1984; Bellwood et al., 2004). When these grazers die off or migrate, they leave barren substrate behind which may be the base for extensive algal growth due to their efficient resettlement capabilities compared to that of corals (Hughes, 1994; Gardner et al., 2003), especially when coral recruitment is low (Aronson et al., 2002). Coral reefs threatened by a combination of anthropogenic stressors, such as eutrophication together with overfishing and mechanical habitat destruction due to the use of explosives (McManus et al., 1997), are at particularly high risk of imminent phase shift (Rogers, 1990; Hughes, 1994; Bellwood et al., 2004).

Located in the vicinity of the coral triangle, which is recognized as the epicenter of coral reef biodiversity (Briggs, 2005; Hoeksema, 2007), Hainan features environmental settings considered optimal for reef growth. Shallow water depths, tropical temperatures and sufficient sunlight are considered to be main drivers in reef development and persistence (Kleypas et al., 1999) and are all given in the island's adjacent coast. However, the coral reefs of Hainan are yet poorly investigated. Descriptions from the 1950s focus on distribution and diversity of coral communities (Yu and Zou., 1996a,1996b), while later studies on coral diversity investigated anthropogenic effects (Yu and Zou, 1996a,1996b; Shi and Zhang, 2004). The findings raised concerns that the rapid economic growth and associated fishing, agriculture and aquaculture development had taken their toll, causing heavy eutrophication, pollution, and a demise of coral reefs in coastal waters. Reefs on the south coast of Hainan saw decreases in live coral cover from 60% in 1983, to 41.5% in 1998, and to 21.51% in 2002 (Yu and Zou, 1996a,1996b), one evidence that the foundation of the Sanya National Coral Reef Reserve in 1990 has not been a sufficient measure. During a reef and seagrass monitoring project in 2002 (Status of China Marine Ecology Report, 2002), coral, seagrass and fish species distribution, biomass and recruitment was assessed along the east coast of Hainan. The results revealed that live coral cover and coral recruitment, as well as coral reef associated fish and invertebrate density were very low, while macro-algal abundance, especially that of the brown algae *Sargassum* spp. was high (Hainan east coast coral reef and seagrass monitoring report, 2005). Therefore, further information on the status of Hainan's coral reefs and their potential threats is urgently needed to provide the base for a more sustainable coastal management. Here, we describe five coral reef ecosystems along the NE coast of Hainan and investigate the metabolic status of the massive coral *Porites lutea*, a wide-spread, abundant, and well-studied reef builder (Veron, 2000), to determine present reef condition and set a baseline for further studies in the area.

2. Material and methods

2.1. Assessment of study sites

In 2007 and 2008 field trips were conducted to the NE reef sites of Hainan (Fig. 1). Five reefs were sampled (from north to

south): Tongguling, Dongjiao Yelin, Changqi, Qinggeand Tanmen. Representative photographs displaying typical site characteristics for each reef are given in Fig. 2. Due to constraints in time, logistics and sampling, rapid assessments of the status of each reef were carried out and documented photographically. In detail, the study sites were examined in terms of coral cover, macroalgal cover, remaining substrate cover, grazer abundance, and general conspicuous factors such as visibility, recruit abundance, fish abundance, and diversity. Herein, estimates were either performed by recording percentages or in categories (excellent, sound, fair, poor). All estimates were independently recorded by two or three divers swimming U-search patterns of 100 m × 10 m in size at speeds of < 1 m s⁻¹ for 40 min. Records were subsequently collated and used if the estimate was congruent or if differences did not exceed 5%. An overview on differences between reef sites is given in Table 1. All fringing reefs along the NE-coast of Hainan are located in shallow waters (2–8 m) relatively close to shore (200–1000 m) and consist of a reef flat, crest and slope. The first inspection of the working areas revealed only fragmentary reefs with extensive overgrowth by macroalgae, coral rubble fields and only marginal live coral cover (often less than 1%). Higher and more diverse coral cover (up to 15%) was found along the reef crests where wave and surge action was strongest resulting in constant removal of sediments. Most (60%) of the living colonies were, however, small and partly affected by disease or mortality and often threatened by algal overgrowth or snail predation. By contrast, we documented a high abundance of crustose coralline algae and of fleshy macro-algae, the latter especially on the reef slopes, but almost a total lack of mobile macrofauna, especially of key functional groups of herbivorous and predatory fish or grazing echinoderms. Visibility was low (between 0.5 and 8 m) and coral rubble fields were generally covered with thick layers of sediment. A more detailed description of each site is given in the following:

Tongguling—The shallow reef flat of Tongguling (2–5 m) consisted of extensive coral rubble fields. The unsorted fragments suggest they originate from destructive bomb fishing, not storms, where the waxing and waning of waves result in well-sorted coral fragments (Dollár, 1982). The coral rubble was cemented together by encrusting algae, indicating that the destruction of the reef has not happened recently. Live coral cover was low (5–10%), but increased to 40% on the reef crest and diversity was highest compared to all other reefs observed. In the area of low cover, mainly small branching species could be observed, and diversity rose with increasing cover. Algae were present, but were less abundant than at other reef sites. Fish abundance was negligible and most individuals were juvenile.

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

Changqi—The reef area of Changqi is further offshore (~800 m) and depth ranges from 4 to 8 m. The site seemed to be heavily fished as indicated by high amounts of fishing boats in the reef area and audible as well as visible reoccurring explosions. Few large (several meters in diameter) massive *Porites* colonies represented the main part of live coral cover sustaining the damaged reef framework. However, many of them were affected

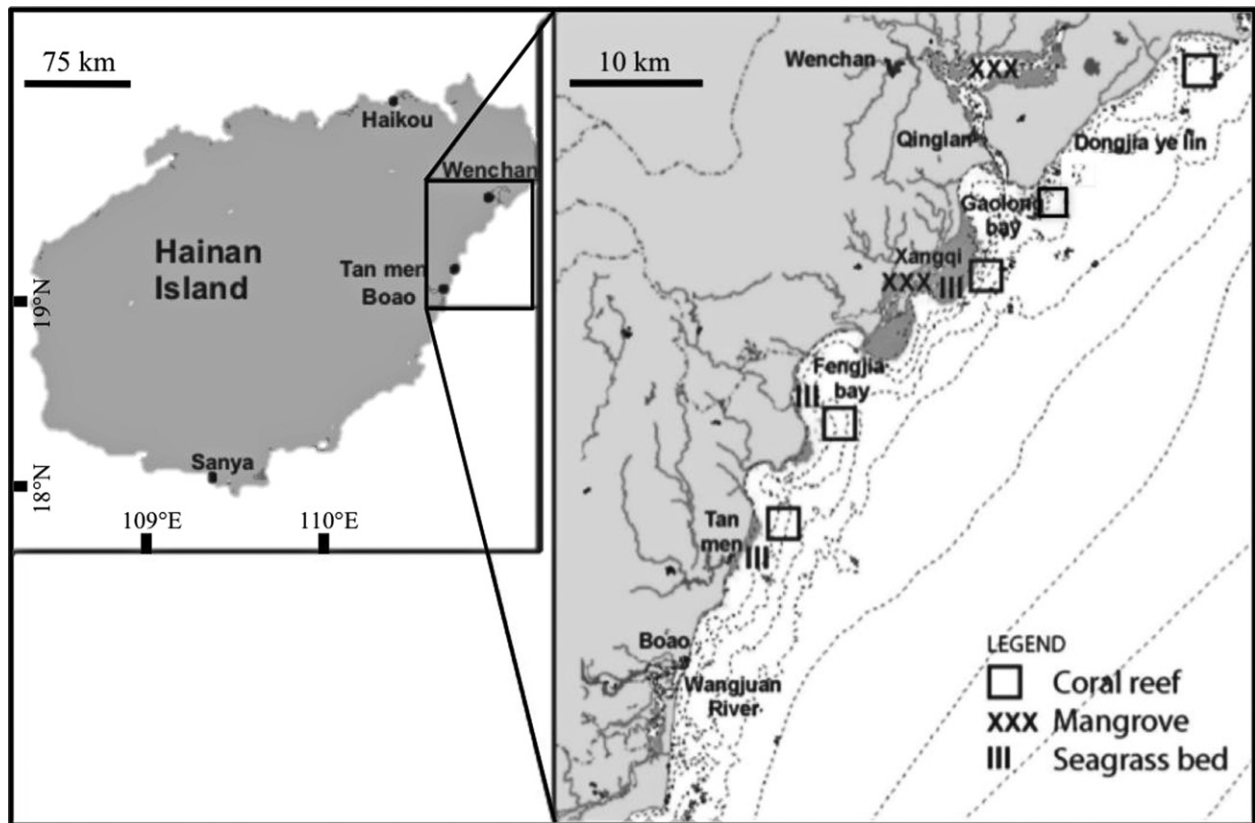


Fig. 1. Hainan Island located in the South China Sea and a close-up of the NE-coast indicating the five reef sampling sites (squares), from N to S: Tongguling, Dongjiao Yelin, Changqi, Qingge and Tanmen.

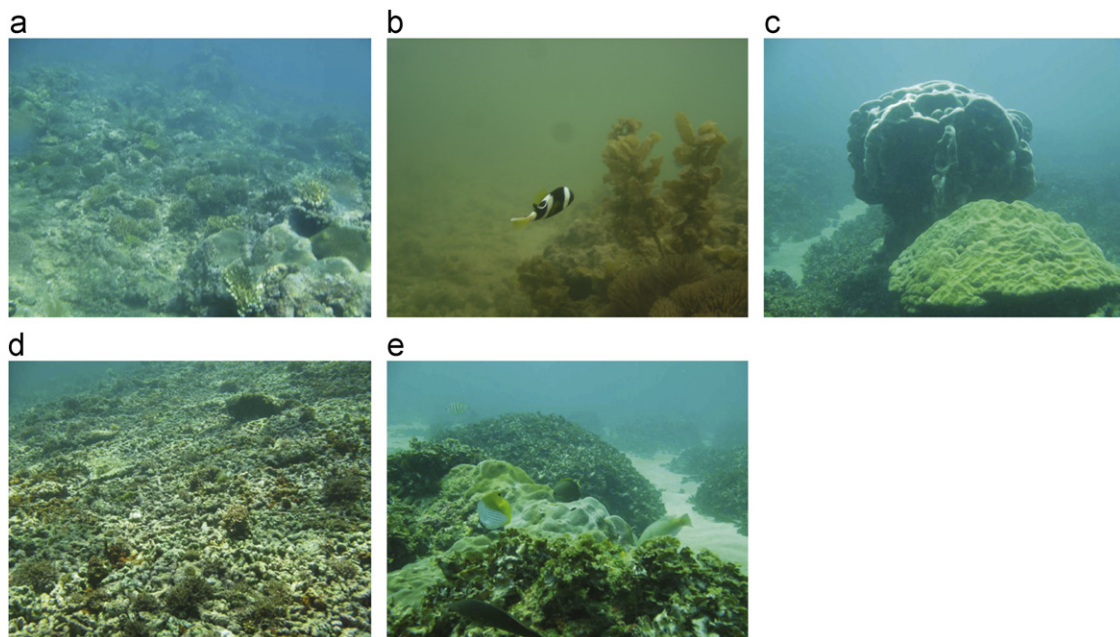


Fig. 2. (a) Tongguling reef, (b) Dongjiao Yelin reef, (c) Changqi reef, (d) Qingge reef, (e) Tanmen reef.

by disease, partial mortality or competition with algae. Mucus excretion in most of these colonies was high with thick sheets covering the colonies, in response to the high sediment load. Branching species could only be rarely found as small recruits. Again, only low numbers of fish were present, most of them being juveniles.

Qingge—In Qingge the reef is close to the shore (~200 m) and depth does not exceed 4 m. Coral rubble cemented together by encrusting algae dominated the reef area. Further offshore, a mix of branching and foliose coral recruits and mid-sized massive colonies built the reef framework. Coral species diversity in this reef was second highest (after Tongguling) of all investigated reef

Table 1
Reef characteristics of the study sites along the NE coast of Hainan.

	Tongguling	Dongjiao Yelin	Changqi	Qingge	Tanmen
Distance from shore (m)	400	400	800	200	100
River impact	–	Wenchang/Wenjiao estuary	Wenchang/Wenjiao vicinity	–	Tanmen river delta
Fishing boats present in reef area per day	< 10	20–50	> 50	10–20	> 50
Depth (m)	2–5	2–4	4–8	1–4	5–8
Live coral cover (%)	5–10, up to 40	< 5	5	5–10	< 5
Macroalgal presence	Medium	High	Medium	Medium	High
Main substrate	Cemented rubble	Silted rubble	Dead massive coral	Cemented rubble	Dead massive coral
Diversity	Fair	Poor	Poor	Fair	Poor
Visibility	Good	Poor	Fair	Fair	Poor

sites, however, live coral cover was low and most colonies were rather small (mainly < 40 cm²). Algae were present in high amounts, but not as abundant as in Dongjiao Yelin or Tanmen. As in all other reefs, only few juvenile fish could be observed.

Tanmen—The reef of Tanmen is located directly outside the river estuary and the Tanmen harbor. It is slightly deeper than the other reefs (5–8 m) and characterized by high sediment loads and heavy algal growth. The living part of the coral reef consisted of mainly massive boulder colonies of *Porites*, which showed strong mucus secretion and were often affected by disease. The intense ship traffic and density of fishing boats in the area reflects the combined impacts of overfishing, pollution and mechanical destruction in this area. Not surprisingly, the reef was almost entirely devoid of fish.

2.2. Metabolic investigations

As a measure of coral condition at each site, five corals were investigated in terms of photosynthetic performance and biochemical composition. Photosynthetic performance was analyzed in situ with rapid light curves (RLC, Ralph et al., 1999; Ralph and Gademann, 2005) of the massive coral *P. lutea*. Triplicate RLC were carried out before noon (between 11 and 12 h local time) on cloud-free days using a submersible pulse amplitude modulated fluorometer (DivingPAM, Heinz Waltz Ltd., Germany) with a universal sample holder ('DIVING-USH') with a standardized distance of 1 cm between the fiber optics and the coral surface (Schreiber, 1986). The internal settings of the diving PAM were set to a range of photosynthetic active radiation (PAR) between 0 and 2896 $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$. Effective quantum yield of photosystem II ($\Delta F/F_m'$) and electron transport rates (ETR) were stored in the instruments internal memory (Ralph et al., 1999; Ralph and Gademann, 2005). Ambient light intensities were measured concomitantly with the light sensor of the DivingPAM. The resulting light curves are a good measure of the present photosynthetic performance and the short-term light history of the investigated colony (Schreiber et al., 1997). The ETR is calculated as $\Delta F/F_m' \times \text{PAR} \times 0.5 \times \text{ETR factor}$, where the factor 0.5 accounts for the assumed equal distribution of electrons between the two photosystems (Ralph et al., 1999), and the ETR factor for the light absorbance by the sample. The latter is unknown for *P. lutea* and was thus set to unity (i.e., assuming full absorbance of light by the tissue) yielding relative ETR (rETR) (Hoegh-Guldberg and Jones, 1999), a commonly used parameter allowing comparisons between different coral colonies of one species (Schreiber, 1986). Descriptions of the reefs were accomplished prior to examinations of light curves or analyses of collected fragments in order to obtain unprejudiced records.

Tissue samples ($n=3$ per colony) were taken from the non-shaded upper surface of the colony using hammer and chisel for subsequent biogeochemical analyses in the lab. Samples were

stored in ziploc plastic bags (< 3 ml residual water) on ice and transported to the laboratory for processing.

The following coral tissue parameters were evaluated to determine the metabolic status of the investigated colonies: zooxanthellae density, pigment concentration, dry mass as well as carbon and nitrogen content and isotopic carbon and nitrogen signatures of coral host and zooxanthellae. Two square centimeters of coral tissue were removed from the skeleton using an artist's airbrush and filtered seawater. The tissue slurry was subsequently homogenized and aliquots retained for zooxanthellae density counts using a Fuchs-Rosenthal haemocytometer and a microscope (Leitz, 260 \times magnification). 5 ml were filtered on glass fiber filters (Whatman GF/F) for pigment analysis using the standard procedure of Strickland and Parsons (1972) and frozen for later processing. The chlorophyll-a on the filters was extracted using 5 ml of acetone (90%) over 24 h in the dark at 4 $^\circ$ and determined spectrophotometrically (Lorenzen, 1967). In addition to chlorophyll-a content of its degradation product pheophytin was determined using the acidification method of Lorenzen (1967). The values for undegraded and degraded pigments were added to obtain the total chlorophyll-a content of the coral tissue (Hill et al., 1995, 2000).

15 ml of the slurry were centrifuged to separate zooxanthellae from coral host components (Muscatine et al., 1989; Swart et al., 2005) and (after several washing steps by rediluting the pelleted zooxanthellae in filtered seawater and repeated centrifugation) the two fractions were filtered on separate pre-combusted and pre-weighed glass fiber filters (Whatman GF/F) for further desiccation and determination of coral host and zooxanthellate dry weights on a microbalance (Mettler Toledo AB204-S, accuracy 0.1 mg). To determine possible the nutritional status and identify trophic level and sources of pollution (Heikoop et al., 2000), carbon and nitrogen contents and carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotopic signatures of zooxanthellae and coral host samples were determined using an isotope ratio mass spectrometer (Thermo Finnigan Delta Plus X/P and Flash EA 1112 Series in combination).

Appropriate tests for significant differences were conducted using the software Statistica (StatSoft).

3. Results

An overview of investigated tissue parameters is given in Table 2. We found significant differences between the five reef sites (Kruskal–Wallis; $p < 0.05$) in most of the coral parameters investigated (host and zooxanthellae dry weight, zooxanthellae densities or pigment concentrations, pigment concentrations per zooxanthellae, carbon and nitrogen contents and isotopic composition of host and symbionts), but no within-reef or within-coral differences (Table 2).

One to one comparisons between all reefs revealed that Tongguling had the highest zooxanthellate biomass, while

Table 2Means (SE) of tissue constituents of *Porites lutea* along the NE coast of Hainan and results from Kruskal–Wallis test (n.s. not significant).

	Units	Tongguling	Dongjiao Yelin	Changqi	Qingge	Tanmen	Kruskal–Wallis
Biomass coral host	mg cm ⁻²	8.78 (1.12)	4.83 (0.56)	6.47 (0.66)	5.54 (0.33)	5.61 (0.54)	n.s.
Carbon content coral host	μg cm ⁻²	409.10 (35.70)	1012.27 (464.23)	450.64 (36.03)	544.59 (31.47)	446.96 (18.29)	*
Nitrogen content coral host	μg cm ⁻²	92.48 (45.59)	149.77 (55.08)	127.41 (50.11)	292.58 (83.04)	57.94 (2.48)	*
δ ¹³ C coral host		-15.33 (0.60)	-15.03 (0.43)	-13.51 (0.52)	-13.27 (0.34)	-15.63 (0.23)	*
δ ¹⁵ N coral host		7.78 (0.26)	8.96 (0.32)	7.38 (0.41)	6.81 (0.14)	7.47 (0.11)	*
Biomass zooxanthellae	mg cm ⁻²	5.00 (0.54)	2.91 (0.26)	3.35 (0.43)	4.49 (0.28)	3.51 (0.24)	*
Zooxanthellae	10 ⁵ cm ⁻²	39.22 (4.29)	27.86 (2.23)	34.05 (3.66)	36.47 (3.83)	42.25 (3.71)	n.s.
Pigments	10 ⁻⁶ μg cm ⁻²	11.58 (1.22)	16.97 (2.09)	12.76 (1.39)	13.72 (1.43)	16.33 (2.12)	n.s.
Pigments per Zooxanthella	μg cell ⁻¹	3.02 (0.19)	5.87 (0.46)	4.06 (0.48)	4.17 (0.55)	4.17 (0.76)	*
Carbon content zooxanthellae	μg cm ⁻²	1544.99 (706.87)	2189.13 (849.07)	1469.02 (654.86)	1808.77 (461.45)	1877.57 (926.53)	*
Nitrogen content zooxanthellae	μg cm ⁻²	247.52 (94.64)	159.78 (55.04)	1364.33 (162.48)	425.21 (168.27)	472.58 (182.59)	*
δ ¹³ C zooxanthellae		-12.60 (0.37)	-13.81 (0.30)	-12.15 (0.35)	-11.33 (0.31)	-13.71 (0.27)	*
δ ¹⁵ N zooxanthellae		7.16 (0.51)	9.29 (0.96)	7.09 (0.47)	7.08 (0.21)	6.92 (0.28)	*

* Significant, $p < 0.05$.

zooxanthellate biomass was lowest in Dongjiao Yelin (Mann–Whitney U tests: $p < 0.05$). Although neither zooxanthellae densities nor pigment concentrations differed between the reefs, cell-specific pigment densities were highest in Dongjiao Yelin. The coral host and zooxanthellae carbon content also was significantly higher in Dongjiao Yelin compared to all other reefs. Nitrogen contents of the coral host were significantly higher in Qingge and lower in Tanmen compared with other sites, while nitrogen content of the zooxanthellae are significantly highest in Changqi and lowest in Dongjiao Yelin. Changqi and Qingge had significantly enriched carbon isotopic signatures of the coral host tissue, while those of the zooxanthellae were only significantly less negative in samples from Qingge. The nitrogen isotope ratios were significantly enriched in host tissue and zooxanthellae of corals from Dongjiao Yelin compared to the other reefs.

Spearman correlations (Table 3) of all coral parameters showed significant positive correlations between coral host and zooxanthellae biomass. Both were also significantly correlated with zooxanthellae densities, but not with pigment concentrations. However, zooxanthellae densities were correlated with cell-specific pigment content and, thus, total pigment concentrations, resulting in a negative correlation between total pigment concentrations and zooxanthellae densities. Carbon contents of zooxanthellae and host are significantly correlated to pigment concentrations and the carbon content of the zooxanthellae additionally to zooxanthellae biomass and densities. While the nitrogen content of the coral host only correlated with the corresponding carbon content, the nitrogen content of the zooxanthellae was also positively correlated with zooxanthellae densities and biomass as well as to carbon and nitrogen content of the coral host. Carbon isotopic ratios were correlated between zooxanthellae and host, whereas carbon content showed a negative correlation between host and symbiont. The nitrogen isotopic signatures of host and symbiont also correlated significantly and the signature of the coral host increased with decreasing zooxanthellae and host biomass, while the nitrogen isotopic signatures of the zooxanthellae decreased with increasing zooxanthellae biomass, density and nitrogen content. The higher the signature of the host tissue or the zooxanthellae became, the lower was the nitrogen content of the zooxanthellae.

The general photosynthetic performance as illustrated by the rapid light curves (RLCs, Fig. 3) is similar for all reefs except Dongjiao Yelin where colonies of *P. lutea* reached only rETR maximum rates of < 100 ($\mu\text{mol electrons m}^{-2} \text{s}^{-1}$) and were hence less efficient. Most colonies (*P. lutea*) reached a saturation plateau with maximum rETR of 50–150 $\mu\text{mol electrons m}^{-2} \text{s}^{-1}$ at a photosynthetic active radiation (PAR) of about 1000 μmol

quanta $\text{m}^{-2} \text{s}^{-1}$. Only coral colonies from Tongguling did not reach saturation levels.

4. Discussion

The surveys along the NE coast of Hainan revealed a degraded status of coral reefs in the whole area, compounding the earlier studies of Yu and Zou., 1996a,1996b, who described that the once flourishing coral reefs of Luhuitou, in the southern part of Hainan, have suffered combined impacts of fishing, mining and land-based sources of pollution. This includes in particular severe sediment run-off via rivers to coastal waters, construction and alteration of land use near the coastline, comprising discharge of untreated human sewage, agriculture fertilizers and heavily polluted and eutrophied wastewater from land based aquaculture during the last decades. While all investigated reefs are obviously impacted, the reefs of Dongjiao Yelin and Tanmen can be seen as the ones facing the most severe threat due to their exposure to river runoff.

Previous reports have described concentrations of $< 10 \text{ mg l}^{-1}$ total suspended matter (TSM) (Rogers, 1990), and about $3 \mu\text{M}$ inorganic nitrogen and $0.5 \mu\text{M}$ phosphate as upper limits for reef environments (Kleypas et al., 1999). Coastal waters along the NE coast of Hainan are contaminated with high loads of TSM and nutrient concentrations, reaching up to 42 mg l^{-1} (TSM) and up to $40 \mu\text{M}$ inorganic nitrogenous compounds or $3 \mu\text{M}$ phosphate, especially during times of high precipitation (Liu et al., 2011; Herbeck, 2012; Herbeck et al., 2012). Highest amounts of TSM and nutrient loads were found at the reefs of Dongjiao Yelin and Tanmen (Herbeck, 2012), directly outside the river plumes of the Wenchang and the Wenjiao rivers. This is manifested by the low visibility at the investigated reefs, caused by the chronic nutrient- and sediment-loaded runoff and resulting in reduced light availability and stress caused by sedimentation (Fabricius, 2005). The dark coloration of the scattered living corals is further indication of reduced light levels and eutrophication. Additionally the extensive mucus sheets excreted by many corals in the area are known to be a cost-intensive technique to remove sediments (Schuhmacher, 1977), combat bio-fouling (Ducklow and Mitchell, 1979) as well as a general particle load protection (Ruble et al., 1980). Further human induced stresses are overfishing and the use of destructive fishing techniques (McManus et al., 1997). Altogether this indicates strong fertilization and degradation of all reef sites along the NE coast of Hainan as a result of an anthropogenic altered coastal system. The nitrogenous compounds suspended in the water column revealed high $\delta^{15}\text{N}$ values and could accordingly be ascribed to shrimp ponds as nitrogen

Table 3
Correlation of tissue and zooxanthellae parameters from *Porites lutea* colonies sampled along the NE coast of Hainan (n.s. not significant).

	Biomass zooxanthellae	Zooxanthellae	Pigments	Pigments per zooxanthella	$\delta^{13}\text{C}$ coral host	$\delta^{15}\text{N}$ coral host	Nitrogen content coral host	$\delta^{13}\text{C}$ zooxanthellae	Carbon content zooxanthellae	$\delta^{15}\text{N}$ zooxanthellae	Nitrogen content zooxanthellae
Biomass coral host	0.676**	0.319**	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Biomass zooxanthellae		0.37**	n.s.	n.s.	n.s.	-0.346**	n.s.	0.549**	n.s.	n.s.	0.471**
Zooxanthellae			n.s.	n.s.	n.s.	-0.401**	n.s.	n.s.	n.s.	n.s.	n.s.
Pigments			0.458**	-0.381**	n.s.	n.s.	n.s.	0.338**	n.s.	n.s.	0.265*
Pigments per zooxanthella			n.s.	0.593**	n.s.	n.s.	n.s.	0.228*	n.s.	n.s.	n.s.
$\delta^{13}\text{C}$ coral host					n.s.	0.227*	n.s.	n.s.	n.s.	0.341**	n.s.
Carbon content coral host					0.303**	n.s.	n.s.	0.321**	n.s.	n.s.	n.s.
$\delta^{15}\text{N}$ coral host					n.s.	0.460**	n.s.	0.35**	n.s.	n.s.	0.375**
Nitrogen content coral host					n.s.	n.s.	n.s.	n.s.	n.s.	0.309**	-0.242*
$\delta^{13}\text{C}$ zooxanthellae							-0.279*	0.249*	n.s.	n.s.	0.295*
Carbon content zooxanthellae							n.s.	0.296**	n.s.	n.s.	n.s.
$\delta^{15}\text{N}$ zooxanthellae											0.719**
											-0.241*

* Significant, $p < 0.05$.

** Significant, $p < 0.01$.

sources (Herbeck et al., 2012). These high signatures can be found in zooxanthellae and tissue of corals, especially in Dongjiao Yelin, where the reef is close to the shore and unsheltered facing the river plume. As the signature of consumers is only slightly heavier compared to their diet (Yamamoto et al., 1995), $\delta^{15}\text{N}$ can indicate possible sources of nitrogen (Sammarco et al., 1999) and hence serve as a tracer of sewage pollution (Heikoop et al., 2000) such as aquacultural runoff.

The $\delta^{13}\text{C}$ values of the samples collected in Changqi and Qingge were less negative compared to the other reefs investigated in this study indicating a higher share of photosynthesis and lower share of heterotrophic inputs from allochthonous food sources (Muscatine et al., 1989) in coral nutrition. That the corals from Tongguling did not display such low $\delta^{13}\text{C}$ values despite the fair appearance of this reef site compared to Dongjiao Yelin and Tanmen might be explained by their higher photosynthetic efficiency leading to a depleted internal carbon pool with reduced selectivity for the lighter carbon isotope (Muscatine et al., 1989; Swart et al., 2005).

The lower zooxanthellae densities in Dongjiao Yelin counterbalanced by higher pigment concentrations are furthermore indicative of a lack of energy to harbor higher amounts of zooxanthellae that are more energy consuming to maintain suggesting costly acclimatization to a low-light environment (Falkowski and Dubinsky, 1981; Iglesias-Prieto and Trench, 1994). Another sign for deprived metabolic status indicating reduced health of the present corals (Fabricius, 2005), is the high content of carbon compared to nitrogen in corals from Dongjiao Yelin suggesting poor biomass quality as a result of low photosynthetic and low quality food input compared to reef such as Qingge and Changqi where biomass content is richer in organic nitrogen. This is further supported by the fact that coral colonies from Dongjiao Yelin had lowest photosynthetic capacities which is typical for corals chronically exposed to reduced light levels (Beer et al., 1998). While zooxanthellae densities of *P. lutea* are in the range of those shown for the same species in Chinese waters of Sanya (South Hainan) and Daya Bay (Guangdong Province, South China mainland) (Li et al., 2008), the investigated photosynthetic performance with saturation potentials are in the lower range of those reported (i.e., Beer et al., 1998; Ralph et al., 1999). The latter incidence deflects from the fact that all corals were shallow water specimens (< 6 m), but rather resembled efficiencies of deep or turbid water, i.e., low light specimens (Iglesias-Prieto and Trench, 1994; Jantzen et al., 2008). Besides changes in coral community structure (Loya, 1976; Tomascik and Sander, 1987; Rogers, 1990), or alterations of photosynthesis and coral metabolism (Riegl and Branch, 1995; Telesnicki and Goldberg, 1995), extensive amounts of suspended sediment and eutrophication have also been shown to decelerate coral growth (Bak, 1978; Tomascik and Sander, 1985; Marubini and Davies, 1996; Ferrier-Pagès et al., 2000), and negatively impact fertilization, larval settlement, and survival (Gilmour, 1999). Given the observed ecosystem degradation, such changes are likely to take place at the sites of this study. Further investigations are needed to determine whether and/or to which degree net reef development is currently maintained through growth and reproduction.

In general it seems that corals that still outlive these unfavorable conditions have arranged to respond to eutrophication and reduced light levels by adjusting their metabolic performance to the given conditions. Concomitant increases of coral host and zooxanthellae biomass and their densities can be explained as a result of mutual fostering of the symbiotic partners (Osinga et al., 2011) and high carbon reserves of host and algae might be photosynthetically derived due to high pigment concentrations. Nitrogen content, by contrast, was only high when zooxanthellae densities were high, supporting the assumption that better off

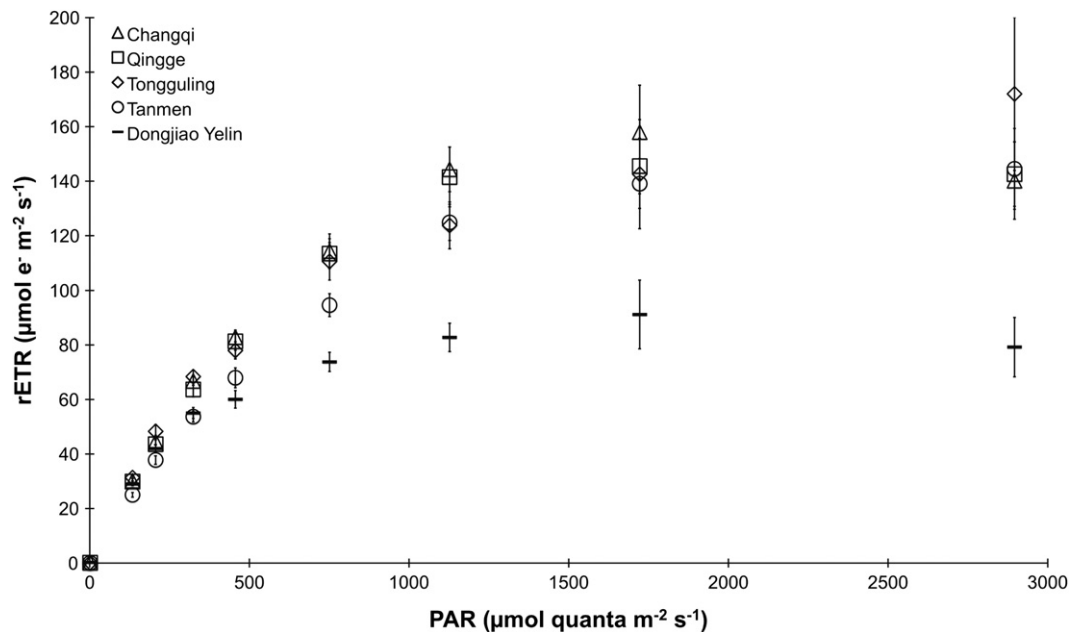


Fig. 3. Rapid light curves of *Porites lutea* colonies from various reefs along NE-Hainan. Error bars show standard deviations.

colonies would yield higher zooxanthellae numbers and possess higher quality biomass. Additionally, lower $\delta^{13}\text{C}$ values combined with increased carbon contents (as a result of decrease in photosynthetic and hence increase in heterotrophic share in nutrition) would lead to an accumulation of biomass. This assumption is further supported by the increase of zooxanthellae nitrogen content, biomass and density when $\delta^{15}\text{N}$ values are low indicative of establishment of rich biomass in areas exposed to less pollution (Heikoop et al., 2000).

Correlations between isotopic signatures of carbon and nitrogen from coral host and zooxanthellae, however, suggest a close cycling of material within the coral holobiont (Muscatine et al., 1989). However, it can be assumed that the fitness of *P. lutea* and most likely all other corals in the area is impacted to a degree where their own survival may still be possible, but, if conditions prevail or even deteriorate, the energetic costs necessary to cope with the disturbance are too high resulting in mortality of the coral community (Kirkwood, 1992). A glimmer of hope for the NE coral reefs of Hainan are the frequently noticed small sized coral colonies, mainly occurring along the reef crests which may signify recovery potential (Dustan, 1977), however, their survival may be uncertain because coral rubble, being the main substrate, especially on the reef flats, poses unfavorable conditions for settling and longer-term persistence (Hodgson, 1990) as it is easily turned by waves or surge and hence extremely unstable. Additionally, recruitment and larval destiny has been shown to be altered under anthropogenic impact (Guzman and Holst, 1993; Gilmour, 1999).

It appears that in previous decades, particularly during the rapid economic development in the 1990s, human activities have taken their toll on the coastal marine environment and at present all coral reefs along the NE coast of Hainan are suffering from eutrophication, siltation as well as disease to greater or lesser extent. The subsistence of scleractinian corals nevertheless indicates that reproduction is existent and, at least, in parts the top-down control of algae still holds as well as that reproduction is existent. Data on the abundance and grazing activity of herbivores or on coral reproduction is however wanting. Obviously, the importance to gain insights on the interactive consequences of high nutrient and sediment inputs from land-based runoff, the

low fish and invertebrate grazer abundances and the altered environment due to destructive fishing on coral health and reef status is crucial in the area to implement proper management strategies for the coral reefs of NE Hainan. Contiguous to in-depth monitoring of ecosystem status, immediate management actions should include the precise calculation of aquaculture and destructive fishing impacts, which are certain to play the major roles in reef degradation along the NE coast of Hainan.

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