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REPORT

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

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

Keywords Metabolism · Acclimatization · Photosynthesis · Nutritional status · Eutrophication · *Stylophora subseriata*

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Introduction

Eutrophication is one of the major threats to coral reefs (Jackson et al. 2001) affecting coral health and community composition (McCook 1999; Nyström et al. 2000; Fabricius 2005) and the ecological balance between corals and space-competing macroalgae (McCook 1999; Costa et al. 2008). The ability of coastal corals to adapt to changing nutrient and sediment loads can be highly variable between species (Fabricius 2005). The coral holobiont consists of

the coral animal and endosymbiotic unicellular algae (zooxanthellae of the genus *Symbiodinium*) and is therefore potentially mixotrophic, subsisting to varying degrees on hetero- and autotrophy. Heterotrophy contributes most to the material needs (nitrogen compounds), while photoautotrophy contributes to the energy and carbon demand of the coral (Anthony and Fabricius 2000; Piniak et al. 2003; Houlbrèque and Ferrier-Pagès 2008). The intense recycling and exchange of nutrients between the coral animal and the zooxanthellae make corals particularly adapted to life in nutrient-limited waters (Muscatine and Porter 1977; Furla et al. 2005; Yellowlees et al. 2008).

Nutrient and sediment runoff change the water quality and light environment in coastal waters. The increased organic and inorganic nutrient and particle loads, turbidity and sedimentation rates may affect coral metabolism (Tomascik and Sander 1985; Telesnicki and Goldberg 1995; Anthony and Fabricius 2000). While higher concentrations of organic matter may be beneficial for some corals by enhancing heterotrophy (Anthony and Fabricius 2000; Ferrier-Pagès et al. 2003), increased sediment loads have mostly been shown to smother, damage, or stress corals (Rogers 1990; Stafford-Smith 1993; Wesseling et al. 2001). This is often reflected in increased respiration rates (Abdel-Salam et al. 1988), decreased P/R ratios (Riegl and Branch 1995; Anthony and Fabricius 2000), decreased photophysiological performance (Philipp and Fabricius 2003), and/or decreased calcification rates (Cortes and Risk 1985; Rogers 1990). Increased particle loads may also enhance coral mucus production in response to particles settling on the coral surface (Stafford-Smith 1993; Riegl and Branch 1995; Brown and Bythell 2005). In spite of significant inputs of riverine nutrients, the associated changes in inorganic nutrient concentrations are often insignificant due to their rapid incorporation by nutrient-starved plankton in reefs (Furnas et al. 2005).

Increased heterotrophy in response to enhanced availability of organic matter, including dissolved and particulate organic matter and nano- to mesoplankton, may also foster photosynthesis in corals (Ferrier-Pagès et al. 2003; Borell et al. 2008) through the transfer of nitrogen from the host to the zooxanthellae and by enhanced zooxanthellae division rates (Piniak and Lipschultz 2004; Houlbrèque and Ferrier-Pagès 2008). Further, increased feeding might be associated with increased respiration (Houlbrèque et al. 2003) and leads often to an increase in biomass, lipids (Anthony 2006), and proteins (Houlbrèque and Ferrier-Pagès 2008).

In low light and nutrient-replete conditions, photoacclimation increases the photosynthetic efficiency in corals (Dustan 1982; Mass et al. 2007; Hoogenboom et al. 2009) by increasing the areal pigment (e.g., chl *a*) and light harvesting protein concentrations (Dubinsky et al. 1990; Titlyanov et al. 2001). The efficiency of the photosystem is proportional to the light absorbed by the photosystem II in the chloroplasts. It may be expressed as the maximum quantum yield (F_v/F_m) after dark adaptation or as the effective quantum yield (Φ PS II) at a given ambient light intensity, when neglecting interfering effects, e.g., photorespiration (Maxwell and Johnson 2000; Ralph et al. 2005).

Both heterotrophy and photosynthesis have a positive effect on coral growth, while heterotrophy may support calcification directly (e.g., increased amount of biomass and consequently enzymes that are involved in calcification) or indirectly by supporting zooxanthellae functioning (Allemand et al. 1998; Furla et al. 2000; Houlbrèque et al. 2003; Houlbrèque and Ferrier-Pagès 2008). The influence of photosynthesis on calcification was recognized early (Goreau and Goreau 1959), and the theory of light-enhanced calcification is widely accepted; the underlying mechanism, however, is still strongly debated (Gattuso et al. 1999; Furla et al. 2000; Allemand et al. 2004; Colombo-Pallotta et al. 2010). Calcification is not only dependent on the metabolic behavior of the holobiont but also directly affected by environmental factors. In particular, inorganic nutrients were found to have a negative effect on calcium carbonate precipitation (Marubini and Davies 1996; Ferrier-Pagès et al. 2000).

The effects of land runoff on corals have been extensively studied in laboratory experiments (reviewed in Fabricius 2005) to determine the roles of individual stressors on the metabolism of shallow water corals. Very few studies have been done on the interacting effects of stressors, and field data are available mainly from well-studied US and Australian reefs. The most biodiverse coral reefs in Southeast Asia, which are subject to the highest risks of land-based sources of pollution, have so far been neglected. Although the ecosystem level responses—losses in diversity, structural complexity, shifts in trophic structure—have been documented (Edinger et al. 2000), the nutritional status, trophic plasticity, and acclimatization potential of the frame-building corals are still largely unknown. While most species appear to be sensitive, some corals occupying a wider physiological niche are considered to be more resistant to eutrophication and sedimentation. This resistance usually coincides with a higher trophic plasticity, which for example, can be found in *Galaxea retiformis* and *Turbinaria mesenterina* in contrast to *Porites cylindrica* and *Acropora valida* (Anthony and Fabricius 2000; Anthony and Connolly 2004; Houlbrèque and Ferrier-Pagès 2008).

In situ measurements are needed to identify the main stressors, quantify their effects on the metabolic response of corals, and assess their plasticity and tolerance to anthropogenic changes in their coastal environment. In the present study, the metabolic response of the common

scleractinian coral *Stylophora subseriata* to an eutrophication gradient was investigated in situ in Spermonde Archipelago, Indonesia, with regard to changes in (1) zooxanthellae characteristics, including their photosystem, (2) the coral tissue, and (3) the metabolic rates, including photosynthesis, respiration, and calcification.

Materials and methods

Study site

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

Six islands, ranging between 1.2 and 17 km distance from shore and varying in intensity of eutrophication and turbidity, were selected as study sites (Fig. 1): Kayangan (KAY), Lae Lae (LL), Samalona (SAM), Lankadea (LAN), Bonebatang (BBA), and Bonetambung (BTA). An eutrophication gradient decreasing from near-shore to outer-shelf reefs was previously described by Edinger et al. (1998) and Renema and Troelstra (2001). (1) Southern near-shore reefs (KAY, LL) are impacted by sewage, sedimentation, and harbor activities, featuring silt-like high nutrient sediment, a visibility between 0.5 and 5 m, chl *a* concentrations between 1.5 and 2.9 μg l^{-1}, and suspended particulate matter (SPM) of about 20 mg l^{-1}. (2) Northern near-shore reefs (LAN) and mid-shelf reefs (SAM, BBA) are slightly impacted by pollution from the city in the wet season (mainly SAM), featuring a visibility between 10 and 18 m (<10 m in wet season), chl *a* concentrations between 0.5 and 0.8 μg l^{-1}, and SPM of about 8.2 mg l^{-1}. (3) Outer-shelf reefs (BTA) are not impacted by the effluents of the city, they feature a visibility from 10 to 30 m (7.5–20 m in wet season) and chl *a* concentrations of about 1.0 mg l^{-1}. Sea surface temperature varies little around 28.5°C in all sites throughout the year, and salinity is about 33‰; however, it can be lower in the near-shore reefs during the wet season.

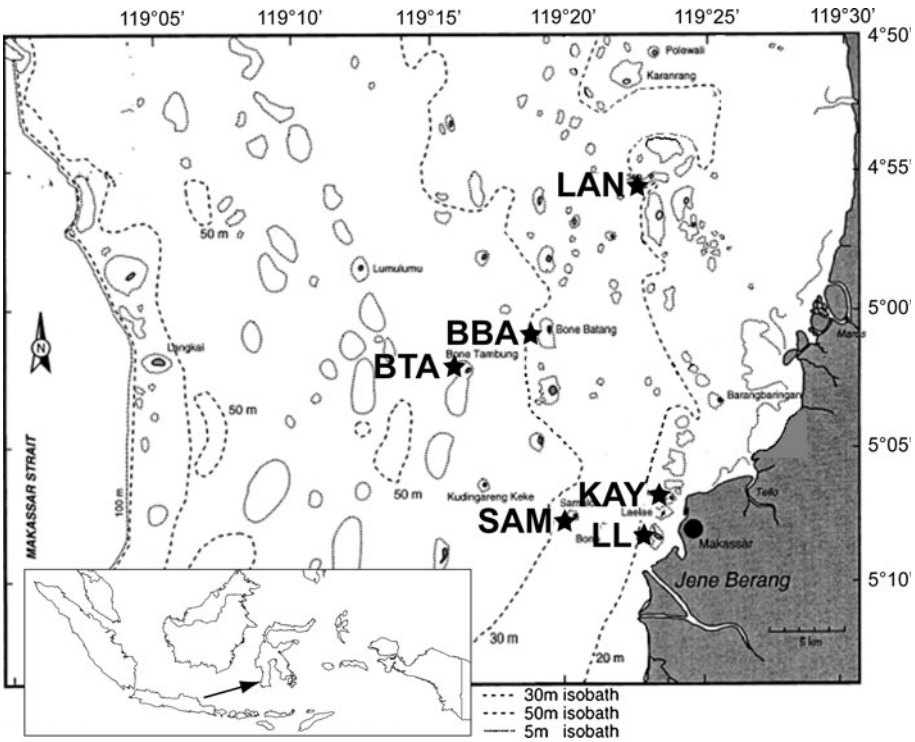

Fig. 1 Map of the Spermonde Archipelago, SW Sulawesi. Study sites: *KAY* Kayangan, *LL* Lae Lae, *SAM* Samalona, *LAN* Lankadea, *BBA* Bonebatang, *BTA* Bonetambung. Map adapted from Renema and Troelstra (2001)

Environmental parameters

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

Light intensity (PAR) was measured during the incubation period (1,300–1,400 h) with an underwater light meter (LiCor Li-192SA, Lincoln, USA) above the ocean surface (PAR_{air}), just below the surface and every 1 m down to 6 m. The light attenuation coefficient (K_d) was calculated from the light profile as a measure of turbidity (Dennison et al. 1993) by fitting a linear regression to the ln-transformed PAR data (slope = K_d) using the software CurveExpert 1.4. Note that K_d reflects the ratio in light intensities between surface and depth and is hence independent of insolation, which varied considerably between days, and hence sites, due to differences in cloudiness.

Coral collection and preparation

For the incubation experiments, 15 fragments from different *S. subseriata* colonies were collected from each site along the reef slope from a depth of 3 m. The 5- to 8-cm-high fragments were carefully removed from the middle part of the colonies and fixed to a plastic screw with underwater epoxy. The screws with the fragments were further fixed to a basket, in 3 m depth and were left for recovery for 2–3 weeks prior to the experiments. All of the fragments survived, showing re-sheeting of tissue across the exposed skeleton within 2 weeks.

Experimental design

In situ incubations were conducted at all sites within 3 weeks at the end of the dry season (September–October 2008). Sixteen (8 light and 8 dark) cylindrical acrylic chambers (1.8 l) were randomly distributed onto 4 plastic frames suspended at 3 m depth, 1 m above the bottom (Fig. 2). Chambers were filled with the surrounding seawater. Five of the light and dark chambers were fitted with one coral fragment each (screw cleaned from fouling organisms). The remaining three light and three dark chambers served as coral-free controls. Glass marbles introduced into the chambers ensured mixing of the incubation water, due to the motion of the marbles on the chamber bottom in the swaying motion of the suspended racks. Corals were fixed out of reach of chamber walls or marbles. The incubations started at 1,300 h local time and lasted between 1 and 1.5 h. One experiment was carried out per site and day resulting in 5 (3) replicates for light/dark (control) each.

Initial water samples were taken with sealable beakers and syringes (both 50 ml) at the time of chamber sealing from the surrounding water. Final water samples were taken with syringes directly from the chamber after opening on board. Dissolved oxygen (precision ± 3 µmol O_2 l^{-1}) was measured with an oxygen sensor (IntelliCal LDO™ Sensor HACH Lange GmbH, Germany) in the beakers ($n = 3$) and postincubation in each chamber immediately after opening. The samples in the syringes (initial: $n = 5$, final: $n = 2$ per

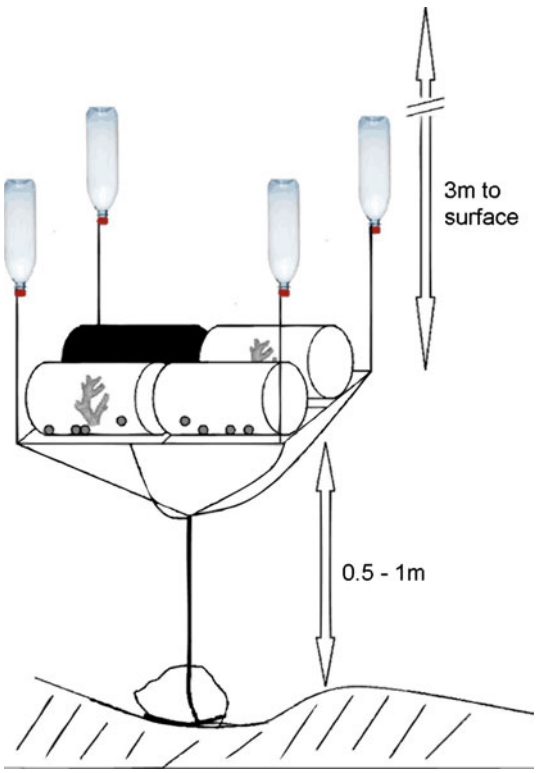

Fig. 2 Schematic drawing of the in situ incubation set-up for one of four racks with four chambers randomly distributed on the rack. Respiration chamber in *black*, photosynthesis chambers transparent, while the empty chamber is a control chamber. The rack is floating and can move with the waves and/or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

chamber) were filtered through Whatman GF/F glass fiber filters, pore size 0.7 μm, and stored in airtight tubes in a cooler until measurement of Total Alkalinity (TA).

Coral metabolism

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

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

TA is given in μeqv kg^{-1}, which corresponds to 1 μmol and is divided by two, since Ca^{2+} is divalent meaning that a change in TA of 2 μeqv corresponds to 1 μmol $CaCO_3$.

Photophysiological measurements were conducted on the coral fragments with a pulse amplitude modulation (PAM, Walz, Germany) fluorometer to assess the efficiency of the photosystem II (Maxwell and Johnson 2000; Borell and Bischof 2008). Maximum quantum yield (F_v/F_m) was measured after incubation from all fragments of the dark chamber (dark adapted) onboard. Later, dark-adapted corals were gradually light-adapted over 3 min until 985 μmol photons m^{-2} s^{-1} PAR, and the effective quantum yield (Φ PS II = $[F'_m - F_t]/F'_m$) was measured (Maxwell and Johnson 2000; Ralph et al. 2005). This light intensity represents roughly the measured light intensity in 3 m depth on a bright sunny day.

Coral nutritional status

Coral tissue was removed from the skeleton with an air gun and ~30 ml filtered seawater. The volume of the tissue slurry was measured and subsamples stored at −20°C until further analyses. Zooxanthellae were counted with a haemocytometer (Fuchs-Rosenthal) under the light microscope, and the zooxanthellae density was determined. Chl a was measured fluorometrically (Boto and Bunt 1978) by adding 4.5 ml 100% acetone to 0.5 ml of the slurry (final concentration 90%), extracting over night at 4°C, centrifuging the slurry for 5 min at 4,000 rpm, and measuring the dissolved chl a with a fluorometer (10-AU Fluorometer, Turner Design, CA) in a glass cuvette. The fluorometer was calibrated with chl a standard (Fluka, Sigma–Aldrich, Switzerland). For the gravimetric determination of tissue biomass (dry weight [DW]), 3 ml of tissue slurry was filtered on a preweighted GF/F filter. The salt was removed by shortly rinsing with distilled water, and the filter was dried at 40°C for at least 24 h prior weighing again. The protein content was determined photometrically (Coomassie Blue, λ 595 nm) after Bradford with bovine serum albumin as a standard (BioRad Protein Assay kit II, Munich, Germany). Protein was measured separately in the tissue ($prot_T$) and in zooxanthellae ($prot_Z$) after the cells were "opened" by ultrasonic maceration to release intracellular protein.

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

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

Data analyses

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

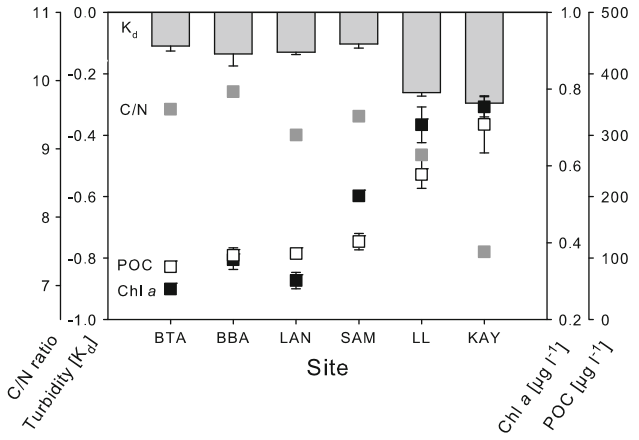

Fig. 3 Environmental parameters: C/N ratio of total particulate matter (POC), chl *a,* and POC concentration ($n = 3$); turbidity (K_d) ($n = 2$–8). The sites follow the distance from shore from furthest (BTA) to closest (KAY) distance. Mean ± SE

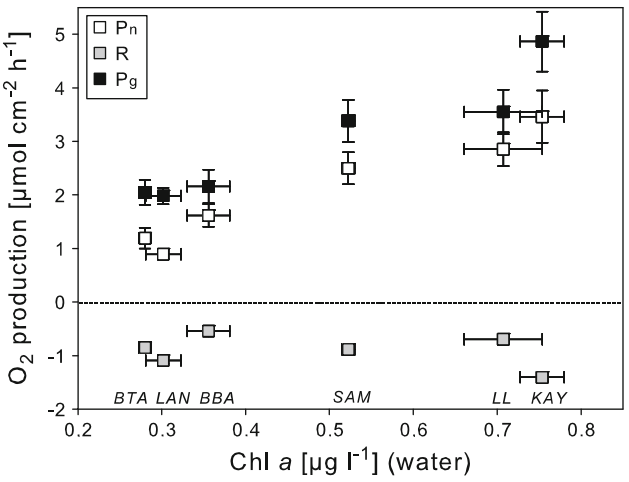

Fig. 4 Net photosynthesis (P_n), respiration (R), and gross photosynthesis (P_g) along the eutrophication gradient (chl *a* (water)). $N = 5$, mean ± SE

Results

Environmental data

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

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

Photosynthesis and zooxanthellae characteristics

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

Although the photophysiological measurements revealed no relationship between F_v/F_m and the environmental gradient, there was a weak positive relationship between Φ PS II and the gradient (Fig. 5c). Consequently, Φ PS II is correlated to areal chl *a* (Pearson, $r = 0.416$, $P < 0.05$); however, it is not related to zooxanthellar chl *a* (Pearson,

Table 1 Weather condition, light availability [µmol photons m^{-2} s^{-1}] in the air (PAR_{air}) and in 3 m depth (PAR_{-3m}), and turbidity (K_d) during the time of incubation

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

Sunny* indicates a very clear day. Mean ± SE

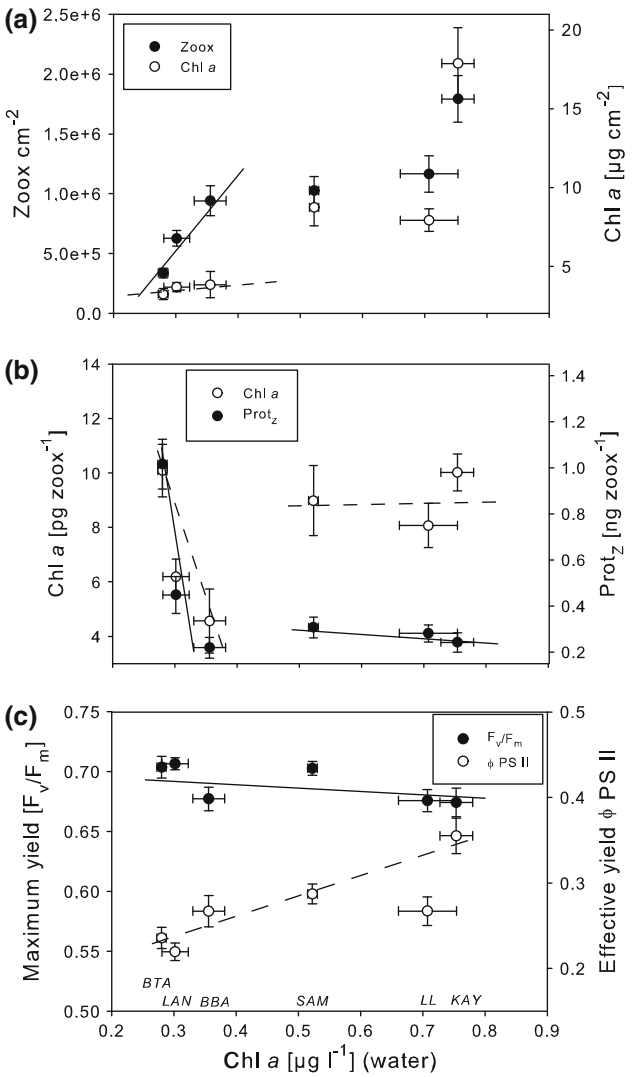

Fig. 5 Zooxanthellae characteristics along the eutrophication gradient (chl *a* (water)). **a** Zooxanthellae (zoox) density and tissue chl *a* concentration, *black* (zoox) and *dashed* (chl *a*) *line* indicate the differential pattern of increase in the mid-shelf reefs. **b** Cell-specific chl *a*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

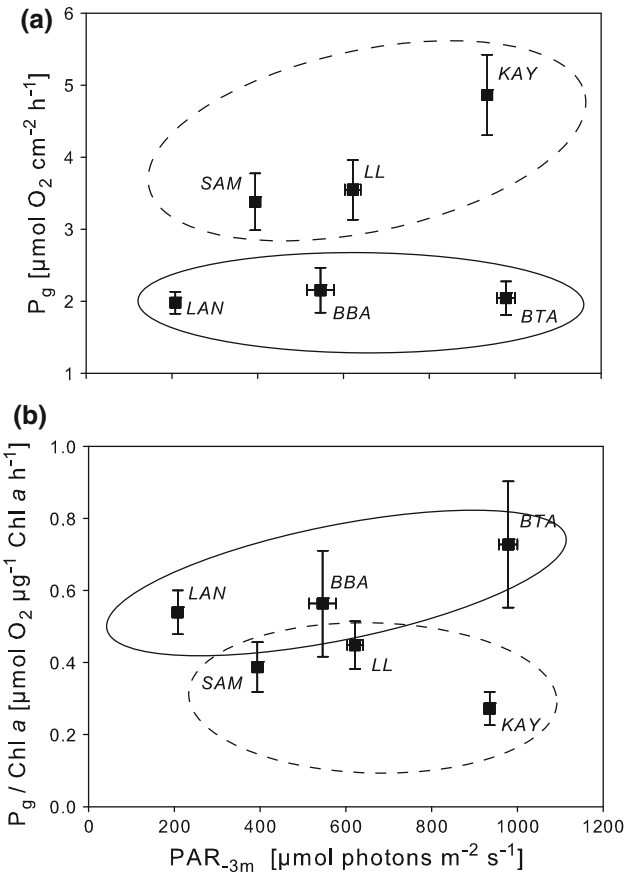

Fig. 6 **a** Gross photosynthesis (P_g) and **b** P_g per unit chl *a* versus light intensity in 3 m depth during the time of incubation (PAR_{-3m}). Mid-shelf reefs (*black circle*) and near-shore reefs (*dashed circle*). $N = 5$, mean ± SE

$r = 0.029$, $P > 0.05$) and slightly negatively correlated to zooxanthellar protein (Pearson, $r = -0.278$, $P < 0.05$).

To determine whether there was a direct effect of light intensity on P_g occurring at the sites on different days, P_g was plotted against PAR prevalent at 3 m depth (PAR_{-3m}) (Fig. 6). There was no apparent relationship between the light intensity and oxygen production, due to the little change in P_g over the different light intensities within the categories mid-shelf and near-shore. This is evident for P_g cm^{-2} as well as for P_g (µg chl *a*)$^{-1}$ (Fig. 6). To determine the effect of chl *a* concentration on photosynthesis, P_g was standardized to chl *a* (Fig. 6b). Here, it becomes evident that the chl *a* concentration has a large impact on P_g visible in an inversion of the oxygen production rate of mid-shelf and near-shore corals (Fig. 6). This was further supported by multiple regression analyses, where areal chl *a* explained 66% of the variation of P_g, followed by Φ PS II, which explained 8%, and light intensity that explained only 2% of the variation (Table 2).

To summarize, the range of zooxanthellae characteristics and their relation to P_g, the two most dissimilar reefs in terms of environmental conditions are directly compared in Table 3.

Respiration and tissue nutritional status

In contrast to photosynthesis, *R* did not show a clear trend along the eutrophication gradient, although highest *R* occurred at the most eutrophied reef KAY (Fig. 4). Nevertheless, a threefold increase in tissue protein (BTA: 0.18 ± 0.02/LAN: 0.16 ± 0.02 to KAY: 0.48 ± 0.04 mg cm^{-2}) and almost a doubling in biomass (BTA: 5.59 ± 0.35/

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

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

$P < 0.05$ (bold)

Table 3 Contrasting the eutrophication gradient (chl *a* water), zooxanthellae (zoox) characteristics including areal zoox density and chl *a*, as well as the effective quantum yield at 985 PAR µmol photons m^{-2} s^{-1} (Φ PS II) and metabolic output in terms of areal gross photosynthesis (P_g) and P_g per unit tissue chl *a* at the two most dissimilar study sites Bonetambung (BTA) and Kayangan (KAY)

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

Mean ± SE

LAN: 4.85 ± 0.31 to KAY: 8.80 ± 0.80 mg DW cm^{-2}) (Fig. 7) were found from mid-shelf to near-shore. In consequence, only a weak relationship was found between R and tissue protein, and no relationship was found between R and tissue biomass and POC, the latter serving as a potential food source (Table 4).

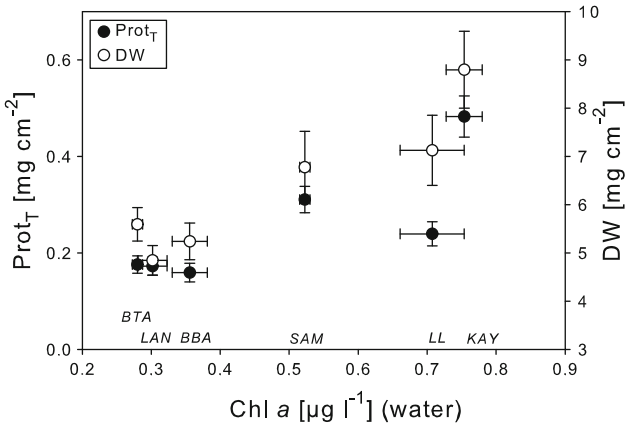

Fig. 7 Coral tissue parameter along the eutrophication gradient (chl *a* (water)). Tissue protein ($Prot_T$) and dry weight of biomass (DW). $N = 10$, mean ± SE

Calcification

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

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

Discussion

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

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

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

$P < 0.05$ (bold)

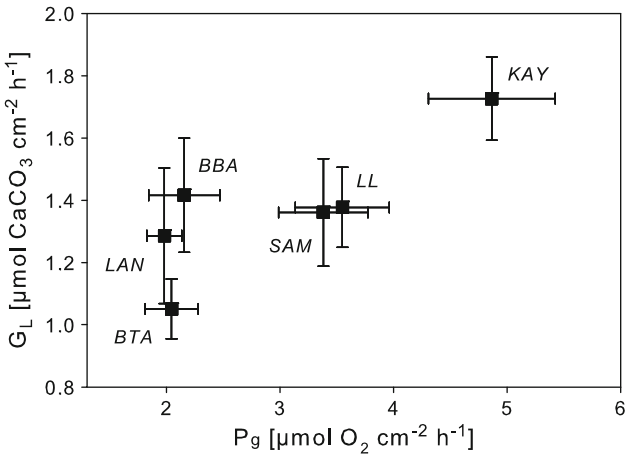

Fig. 8 Light calcification (G_L) versus gross photosynthesis (P_g). $N = 5$, mean ± SE

Over the last few years, there has been an intense debate about the varying effects of nutrification on corals (Szmant 2002; Loya and Kramarsky-Winter 2003; Rinkevich et al. 2003). While most authors agree that coastal nutrification and sedimentation are deleterious at the ecosystem level (reviewed in Fabricius 2005) by shifting the ecological balance between corals and space-competing macroalgae (Fabricius et al. 2005; Costa et al. 2008) in the absence of herbivores (McCook 1999; Jompa and McCook 2002), some suggest increased nutrient levels may, paradoxically, have positive effects on the metabolic performance of some corals (Bongiorni et al. 2003). Here, near-shore individuals of the common *S. subseriata* were found to outperform mid-shelf specimens in terms of nutritional status, P_g and G, and withstand adverse conditions of increased suspended sediment loads with no signs of respiratory and photophysiological stress.

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

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

$P < 0.05$ (bold)

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

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

$P < 0.05$ (bold)

Environmental gradient

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

Photosynthesis and photoacclimation

The increase in P_g from mid-shelf to the near-shore reefs was almost linear with increasing eutrophication (water chl *a*) (Fig. 4), contrasting the nonlinear changes in the areal tissue chl *a* and zooxanthellae concentrations (Fig. 5a). These findings suggest the following mechanistic model linking the impact of eutrophication (nutrients and turbidity) to the coral nutritional status and to P_g: (1) Riverine nutrients were incorporated by the planktonic food web (hence the cross-shore water chl *a* gradient); and (2) incorporation of this plankton by corals fueled propagation of nutrient-limited zooxanthellae (linear increase between BTA and BBA, Fig. 5a). Getting closer to shore, (3) excess nutrients and increased turbidity promoted zoox-chl *a* synthesis (zoox-chl *a* increase between BBA and SAM, Fig. 5a) (Dubinsky et al. 1990); and (4) further increase in external nutrients near-shore (organic and inorganic) stimulated the concomitant increase in both zooxanthellae and chl *a* (LL and KAY, Fig. 5a) (Dubinsky et al. 1990; Ferrier-Pagès et al. 2003; Houlbrèque et al. 2003). Initially, zooxanthellar protein, as an important component of the photosynthetic apparatus (Dubinsky et al. 1990; Zonneveld 1997), followed the pattern of zooxanthellar chl *a* due to nutrient limitation (between BTA and BBA, Fig. 5b). However, the nutrient and energy investment into cell-specific protein was relatively low compared with chl *a* in near-shore reefs (SAM to KAY, Fig. 5b). A likely reason for this is that the coral invests energy into chl *a* synthesis to optimize light harvesting of the photosystem in turbid environments rather than into build-up of proteins important in the processing of light. An optimization of the photosystem is further supported by increased Φ PS II near-shore, in particular at KAY, which can be attributed to the increase in areal chl *a*. Another explanation for the different zooxanthellae characteristics may be found in adaptive processes, such as a change in zooxanthellae genotypes from mid-shelf to near-shore. Although this could not be found for the congener *S. pistillata* (van Oppen et al. 2005; Lampert-Karako et al. 2008), other coral species, e.g., of the genus *Acropora,* changed their genotypes with distance from shore (van Oppen et al. 2005). Overall, these possible mechanisms reveal a high acclimatization potential of the coral to nutrient enrichment and turbidity, which lead to the increasing P_g with proximity to shore.

The highly variable light intensities prevalent at the different days of incubation in our study were unfavorable and could have been minimized by replicate measurements over several days. This was not done, however, due to logistical constrains. Nonetheless, the results of the P_g measurements are representative because the different light intensities revealed only a low impact on P_g, as evident in similar P_g rates within near-shore or mid-shelf reefs despite strong variations in light intensities. These findings are supported by photosynthesis-irradiance curves (P–E curves) of previous studies with the congener *S. pistillata* featuring a similar distribution pattern as *S. subseriata*. Field and laboratory experiment found values of saturation irradiance (E_k) at 80–270 μmol quanta m^{-2} s^{-1} PAR in light-adapted corals (Porter et al. 1984, Ferrier-Pagès et al. 1998), indicating that the light intensities measured in our study (PAR_{-3m}) were in the plateau region of maximum photosynthesis (P_{max}). Furthermore, *Stylophora* is found in a wide range of light intensities (Falkowski and Dubinsky 1981) and, therefore, seems to feature a comparatively high phenotypic plasticity with low sensitivity to changes in light availability.

There was no evidence of a stress response of *S. subseriata,* in terms of decreased maximum quantum yield of zooxanthellae, to increased sedimentation or pollutants toward the coast (Philipp and Fabricius 2003).

Respiration, nutritional status, and stress

Although it is known that *R* increases with feeding (Houlbrèque et al. 2003) and stress (Telesnicki and Goldberg 1995), *R* was not influenced by the increased food availability and higher sedimentation that increased along the eutrophication gradient. *R* varied between the sites, and only the corals in the most near-shore reef KAY showed a distinct increase in *R*. This suggests that heterotrophy and/or stress may have exceeded a threshold in the most enriched coastal waters, enhancing *R* to approximately 50% above background levels. However, an overall increase in heterotrophy at KAY and the other near-shore sites was supported by the nutritional status of the

coral host, revealing an increase in biomass and protein levels toward the coast. This shows that the use of *R* as an indicator for feeding is limited, as previously demonstrated by Anthony and Fabricius (2000).

Calcification

Land runoff was shown to have a differential effect on *G* depending on the concentrations of inserted substances and the sensitivity of different coral species (Fabricius 2005). Here, G_L slightly increased toward the coast and even peaked in the most near-shore reef KAY. The correlation between G_L and P_g indicates that calcification is dependent on photosynthesis (Colombo-Pallotta et al. 2010). At the same time, elevated inorganic nutrient input and sedimentation in near-shore reefs hamper G_L, explaining the overall low increase in G_L with respect to P_g. Reasons for decreased G_L under high nutrient levels are found in a decoupling of symbiont and host (Dubinsky et al. 1990; Ferrier-Pagès et al. 2000; Allemand et al. 2004) or a direct inhibition of carbonate crystallization by inorganic nutrients (Simkiss 1964; Gattuso et al. 1999). A support of G (light and dark) by either *R* or elevated nutritional status of the coral host (Houlbrèque et al. 2003; Houlbrèque and Ferrier-Pagès 2008) was not evident in this study, except possibly at KAY, where highest R, tissue protein and biomass occurred together with highest *G*.

Interaction between photosynthesis, respiration, and calcification

In general, healthy corals under high light conditions provide more than 70% of the corals' energy demand by photosynthesis (Muscatine et al. 1981; Edmunds and Davies 1989). The host respires a large portion of photosynthates, and the acquired ATP is used inter alia for *G* (Al-Horani et al. 2003; Allemand et al. 2004) and mucus production (Brown and Bythell 2005), while the other portion provides compounds for the synthesis of cellular proteins, lipids (Muscatine and Cernichiari 1969; Dubinsky and Jokiel 1994), and mucus (Crossland 1987). The latter can account for 20–45% of the net photosynthate production (Brown and Bythell 2005).

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

In conclusion, this study demonstrates that there are corals that are able to tolerate and even take advantage of eutrophication. Increased inorganic and organic nutrition enhanced autotrophy and, most likely, heterotrophy of *S. subseriata*. This is partly used for *G* and partly for mucus production involved in sediment removal. Symptoms of stress usually reflected in decreased photosynthetic efficiency and increased *R* were not evident.

Due to its high trophic plasticity and photoacclimative potential *S. subseriata* is a highly flexible species compared with other coral species in the area. For the vast majority of less-tolerant coral species, however, human-induced pollution and degradation of coastal water quality has caused a dramatic loss in coral reef biodiversity and complexity in Spermonde Archipelago, the wider Southeast Asia, and beyond (Edinger et al. 1998; Wilkinson 2008).

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References

Abdel-Salam H, Porter JW, Hatcher BG (1988) Physiological effects of sediment rejection on photosynthesis and respiration in three Caribbean reef corals. Proc 6th Int Coral Reef Symp 2:189–194

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

Allemand D, Tambutté E, Girard JP, Jaubert J (1998) 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 E, Tambutté S, Zoccola D (2004) Biomineralisation in reef-building corals: from molecular mechanisms to environmental control. Comptes Rendus Palevol 3:453–467

Anthony KRN (2006) Enhanced energy status of corals on coastal, high-turbidity reefs. Mar Ecol Prog Ser 319:111–116

Anthony KRN, Connolly SR (2004) Environmental limits to growth: physiological niche boundaries of corals along turbidity-light gradients. Oecologia 141:373–384

Anthony KRN, Fabricius KE (2000) Shifting roles of heterotrophy and autotrophy in coral energetics under varying turbidity. J Exp Mar Biol Ecol 252:221–253

Bell PRF (1992) Eutrophication and coral reefs - some examples in the Great Barrier Reef lagoon. Water Res 26:553–568

Bongiorni L, Shafir S, Angel D, Rinkevich B (2003) Survival, growth and gonad development of two hermatypic corals subjected to in situ fish-farm nutrient enrichment. Mar Ecol Prog Ser 253:137–144

Borell EM, Bischof K (2008) Feeding sustains photosynthetic quantum yield of a scleractinian coral during thermal stress. Oecologia 157:593–601

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

Boto KG, Bunt JS (1978) Selective excitation fluorometry for the determination of chlorophylls and pheophytins. Anal Chem 50:392–395

Brown BE, Bythell JC (2005) Perspectives on mucus secretion in reef corals. Mar Ecol Prog Ser 296:291–309

Colombo-Pallotta M, Rodríguez-Román A, Iglesias-Prieto R (2010) Calcification in bleached and unbleached *Montastraea faveolata*: evaluating the role of oxygen and glycerol. Coral Reefs 29:899–907

Cortes JN, Risk MJ (1985) A reef under siltation stress: Cahuita, Costa Rica. Bull Mar Sci 36:339–356

Costa OS Jr, Nimmo M, Attrill MJ (2008) Coastal nutrification in Brazil: a review of the role of nutrient excess on coral reef demise. J South Am Earth Sci 25:257–270

Crossland CJ (1987) In situ release of mucus and DOC-lipid from the corals *Acropora variabilis* and *Stylophora pistillata* in different light regimes. Coral Reefs 6:35–42

Dennison WC, Orth RJ, Moore KA, Stevenson JC, Carter V, Kollar S, Bergstrom PW, Batiuk RA (1993) Assessing water quality with submersed aquatic vegetation. Bioscience 43:86–94

Dubinsky Z, Jokiel PL (1994) Ratio of energy and nutrient fluxes regulates symbiosis between zooxanthellae and corals. Pac Sci 48:313–324

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 B 239:231–246

Dustan P (1982) Depth-dependent photoadaption by zooxanthellae of the reef coral *Montastrea annularis*. Mar Biol 68: 253–264

Edinger EN, Jompa J, Limmon GV, Widjatmoko W, Risk MJ (1998) Reef degradation and coral biodiversity in Indonesia: effects of land-based pollution, destructive fishing practices and changes over time. Mar Pollut Bull 36:617–630

Edinger EN, Kolasa J, Risk MJ (2000) Biogeographic variation in coral species diversity on coral reefs in three regions of Indonesia. Divers Distrib 6:113–127

Edmunds PJ, Davies PS (1989) An energy budget for *Porites porites* (Scleractinia), growing in a stressed environment. Coral Reefs 8:37–43

Fabricius KE (2005) Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. Mar Pollut Bull 50:125–146

Fabricius K, De'ath G, McCook L, Turak E, Williams DM (2005) Changes in algal, coral and fish assemblages along water quality gradients on the inshore Great Barrier Reef. Mar Pollut Bull 51:384–398

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, Allemand D, Gattuso JP, Jaubert J, Rassoulzadegan F (1998) Microheterotrophy in the zooxanthellate coral *Stylophora pistillata*: effects of light and ciliate density. Limnol Oceanogr 43:1639–1648

Ferrier-Pagès 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

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

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

Furla P, Allemand D, Shick JM, Ferrier-Pagès C, Richier S (2005) The symbiotic anthozoan: a physiological chimera between alga and animal. Integr Comp Biol 45:595–604

Furnas M, Mitchell A, Skuza M, Brodie J (2005) In the other 90%: phytoplankton responses to enhanced nutrient availability in the Great Barrier Reef Lagoon. Mar Pollut Bull 51:253–265

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. Am Zool 39:160–183

Goreau TF, Goreau NI (1959) The physiology of skeleton formation in corals. 2. Calcium deposition by hermatypic corals under various conditions in the reef. Biol Bull 117:239–250

Grasshoff K, Ehrhardt M, Kremling K (1983) Methods of seawater analysis. Verlag Chemie Weinheim, New York

Hoogenboom MO, Connolly SR, Anthony KRN (2009) Effects of photoacclimation on the light niche of corals: a process-based approach. Mar Biol 156:2493–2503

Houlbrèque F, Ferrier-Pagès C (2008) Heterotrophy in tropical scleractinian corals. Biol Rev 84:1–17

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*. J Exp Mar Biol Ecol 296:145–166

Jackson JBC, Kirby MX, Berger WH, Bjorndal KA, Botsford LW, Bourque BJ, Bradbury RH, Cooke R, Erlandson J, Estes JA, Hughes TP, Kidwell S, Lange CB, Lenihan HS, Pandolfi JM, Peterson CH, Steneck RS, Tegner MJ, Warner RR (2001) Historical overfishing and the recent collapse of coastal ecosystems. Science 293:629–637

Jameson SC, Kelty RA (2004) A review of indicators of land-based pollution stress on coral reefs. Joint EPA/NOAA/USGA/DOI Workshop on Assessing Pollution Stress on Coral Reefs, Honolulu Hawaii

Jompa J, McCook LJ (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

Lampert-Karako S, Stambler N, Katcoff DJ, Achituv Y, Dubinsky Z, Simon-Blecher N (2008) Effects of depth and eutrophication on the zooxanthella clades of *Stylophora pistillata* from the Gulf of Eilat (Red Sea). Aquatic Conserv: Mar Freshw Ecosyst 18: 1039–1045

Loya Y, Kramarsky-Winter E (2003) In situ eutrophication caused by fish farms in the northern Gulf of Eilat (Aqaba) is beneficial for its coral reefs: a critique. Mar Ecol Prog Ser 261:299–303

Marubini F, Davies PS (1996) Nitrate increases zooxanthellae population density and reduces skeletogenesis in corals. Mar Biol 127:319–328

Mass T, Einbinder S, Brokovich E, Shashar N, Vago R, Erez J, Dubinsky Z (2007) Photoacclimation of *Stylophora pistillata* to

light extremes: metabolism and calcification. Mar Ecol Prog Ser 334:93–102
Maxwell K, Johnson GN (2000) Chlorophyll fluorescence - a practical guide. J Exp Bot 51:659–668
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
Moll H (1983) Zonation and diversity of scleractinia on reefs off S. W. Sulawesi, Indonesia. Ph.D thesis, Leiden University, p107
Muscatine L, Cernichiari E (1969) Assimilation of photosynthetic products of zooxanthellae by a reef coral. Biol Bull 137:506–523
Muscatine L, Porter JW (1977) Reef corals: Mutualistic symbioses adapted to nutrient-poor environments. Bioscience 27:454–460
Muscatine L, McCloskey LR, Marian RE (1981) Estimating the daily contribution of carbon from zooxanthellae to coral animal respiration. Limnol Oceanogr 26:601–611
Naumann MS, Niggl 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
Naumann M, Haas A, Struck U, Mayr C, el-Zibdah M, Wild C (2010) Organic matter release by dominant hermatypic corals of the Northern Red Sea. Coral Reefs 29:649–659
Nyström M, Folke C, Moberg F (2000) Coral reef disturbance and resilience in a human-dominated environment. Trends Ecol Evol 15:413–417
Philipp E, Fabricius K (2003) Photophysiological stress in scleractinian corals in response to short-term sedimentation. J Exp Mar Biol Ecol 287:57–78
Piniak GA, Lipschultz F (2004) Effects of nutritional history on nitrogen assimilation in congeneric temperate and tropical scleractinian corals. Mar Biol 145:1085–1096
Piniak GA, Lipschultz F, McClelland J (2003) Assimilation and partitioning of prey nitrogen within two anthozoans and their endosymbiotic zooxanthellae. Mar Ecol Prog Ser 262:125–136
Porter JW, Muscatine L, Dubinsky Z, Falkowski PG (1984) Primary production and photoadaptation in light- and shade-adapted colonies of the symbiotic coral, *Stylophora pistillata*. Proc R Soc Lond B 222:161–180
Ralph PJ, Larkum AWD, Kühl M (2005) Temporal patterns in effective quantum yield of individual zooxanthellae expelled during bleaching. J Exp Mar Biol Ecol 316:17–28
Renema W, Hoeksema B (2007) Delineation of the Indo-Malayan Centre of Maximum Marine Biodiversity: The Coral Triangle. In: Landman NH, Jones DS (eds) Biogeography, time, and place: Distributions, Barriers, and Islands, vol 29. Springer, Netherlands, pp 117–178
Renema W, Troelstra SR (2001) Larger foraminifera distribution on a mesotrophic carbonate shelf in SW Sulawesi (Indonesia). Palaeogeogr Palaeoclimatol Palaeoecol 175:125–146
Riegl B, Branch GM (1995) Effects of sediment on the energy budgets of four scleractinian (Bourne 1900) and five alcyonacean (Lamouroux 1816) corals. J Exp Mar Biol Ecol 186:259–275
Rinkevich B, Angel D, Shafir S, Bongiorni L (2003) 'Fair is foul and foul is fair': response to a critique. Mar Ecol Prog Ser 261: 305–309
Rogers CS (1990) Responses of coral reefs and reef organisms to sedimentation. Mar Ecol Prog Ser 62:185–202
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
Simkiss K (1964) Phosphates as crystal poison of calcification. Biol Rev 39:487–504
Stafford-Smith MG (1993) Sediment-rejection efficiency of 22 species of Australian scleractinian corals. Mar Biol 115:229–243
Szmant A (2002) Nutrient enrichment on coral reefs: Is it a major cause of coral reef decline? Estuaries 25:743–766
Tanaka Y, Ogawa H, Miyajima T (2010) Effects of nutrient enrichment on the release of dissolved organic carbon and nitrogen by the scleractinian coral *Montipora digitata*. Coral Reefs 29:675–682
Telesnicki GJ, Goldberg WM (1995) Effects of turbidity on the photosynthesis and respiration of two South Florida reef coral species. Bull Mar Sci 57:527–539
Titlyanov EA, Titlyanova TV, Yamazato K, van Woesik R (2001) Photo-acclimation of the hermatypic coral *Stylophora pistillata* while subjected to either starvation or food provisioning. J Exp Mar Biol Ecol 257:163–181
Tomascik T, Sander F (1985) Effects of eutrophication on reef-building corals I. Growth rate of the reef-building coral *Montastrea annularis*. Mar Biol 87:143–155
van Oppen MJH, Mahiny AJ, Done TJ (2005) Geographic distribution of zooxanthella types in three coral species on the Great Barrier Reef sampled after the 2002 bleaching event. Coral Reefs 24:482–487
Wesseling IJ, Uychiaoco AM, Aliño PE, Vermaat J (2001) Partial mortality in *Porites* corals: Variation among Philippine reefs. Int Rev Hydrobiol 86:77–85
Wilkinson C (2008) Status of coral reefs of the world: 2008. Global Coral Reef Monitoring Network and Reef and Rainforest Research Centre. Townsville, Australia p26
Yellowlees D, Rees TAV, Leggat W (2008) Metabolic interactions between algal symbionts and invertebrate hosts. Plant Cell Environ 31:679–694
Zonneveld C (1997) Modeling effects of photoadaption on the Photosynthesis-Irradiance curve. J Theor Biol 186:381–388