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Growth and corallite characteristics of Kenyan scleractinian corals under the influence of sediment discharge

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Disturbances of terrestrial origin are important determinants in the growth, carbonate production and well-being coral reefs. In this study, coral growth (density, linear extension and calcification rates) and corallite (diameter and density) variables were determined for selected species from four Kenyan protected reef lagoons, with one receiving a pulse of sediment discharge. Variable coral growth responses were observed, with some species showing higher growth rates while others exhibited low growth rates within the sediment impacted reef. Species corallite characteristics also showed variable responses, though corallite diameters were found to be larger in the sediment impacted reef with low corallite densities generally being observed in the mangrove-fringed reef. Coral bulk density was found to be poorly correlated to calcification and extension rate but calcification and extension rates were found to be highly correlated (R values 0.84 to 0.98). The variable responses observed in the current study have important implications and applications in coral reef health and management by providing information on the susceptibility of different corals species to local stressors, and together with coral distribution and composition data this information may be useful in the formulation of suitable and scientific based reef management strategies and also in predicting reef performance under future climate change scenarios.

Key words: Calcification, corals, climate change, density, linear extension, sediments, terrestrial disturbances.

INTRODUCTION

Coral reefs, the most complex and diverse ecosystems of the world, are the product of interaction between calcium

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carbonate constructive and destructive processes with environmental conditions. Coral reefs are known to be the most prolific biomineralising ecosystems in nature with calcification rates of ~2-6 kg $CaCO_3$ m^{-2} yr^{-1} as testament to the evolutionary success of the association between corals and the dinoflagellates algae, *zooxanthellae* (Barnes and Devereux, 1984). However, coral reefs are increasingly threatened by local and global environmental disturbances leading to progressive declines in reef-building potential and ultimately to states of net reef erosion. Changes in water quality due to modification of catchment areas through various human activities (Fabricius et al., 2011; Golbuu et al., 2011; Nakajima et al., 2013; Chen et al., 2015) are considered major factors in the degradation of coral reef worldwide. Increased human activities such as farming, coastal development and deforestation have elevated the rate of soil erosion and sediment input into rivers with subsequent increase in levels of turbidity, sediments and nutrients in coral reef areas (GESAMP, 2001; Rotmann and Thomas, 2012; D'Olivo et al 2014; Kumara et al., 2015). Recently, the number of reports on reef degradation due to land based stressors has increased (Crabbe and Carlin, 2007; Padilla-Gamiňo et al., 2012; Shantz and Burkepile, 2014; Prouty et al., 2014) with model estimates indicating that 22% of coral reefs worldwide (Bryant et al., 1998) and ~50% in countries with widespread land clearing are threatened by inland pollution and erosion.

Disturbances of terrestrial origin affect regeneration, recovery and calcium carbonate production processes of coral reefs (McCulloch et al., 2003) and have been recognized as significant controlling forces in the growth and skeletal properties of reef corals (Padilla-Gamino et al., 2012; Bartley et al., 2013; Kumara et al., 2015). Further, although sediments and turbidity play a significant role in marine geochemical processes and food webs, studies have shown that high sediment levels and turbidity have deleterious effects on coral reefs at the colony level (Golbuu et al., 2011) including reduced recruitment, photosynthesis, tissue thickness and increased mucus production. At the community level, high sediment levels lead to reduced coral cover, richness and diversity, coral colony abundance as well as increased disease incidences and mortality (Kuta and Richardson, 2002; Ruiz-Moreno et al., 2012).

Previous studies have provided insights into the effects of sediments on coral growth (Carricart-Gavinet and Merino, 2001; McDonald and Perry, 2003; Larsson et al., 2013; Kumara et al., 2015) with results suggesting complex, variable and even contradictory findings. Coral subjected to high sediment levels have shown declines in skeleton density, extension and calcification rates (Crabbe and Smith, 2005; D'Olivio et al., 2013; Nakajima et al., 2013; Larsson et al., 2013), though higher extension rates have also been measured in corals under terrestrial influence (Carricart-Ganivet and Merino, 2001; Edinger et al., 2000; Cruz-Piňón el al., 2003). Still, other studies reported

no effect on coral growth parameters as a result of high sediment concentrations (Edinger et al., 2000; Torres and Morelock, 2002; Golbuu et al., 2011). These contrasting findings may be of particular significance in future survival, existence and conservation of reefs (Kleypass et al., 1999; Kružić et al., 2012; Chen et al., 2015; Klein et al., 2015). Therefore, there is need for further studies to highlight these conflicting findings, this increase our understanding on the effects of sediments on coral growth and also provide information useful in the management of sediment disturbed reefs. This study was undertaken to investigate the response of coral growth rates (linear extension, density and calcification) and skeletal charac-teristics (corallite diameter or size and density) of scleractinian corals from Kenyan reef lagoons to increased sediment levels and the implication and application to coral reef management and conservation.

MATERIALS AND METHODS

Description of study areas

Four reef lagoons (Figure 1a to d) were chosen due to their accessibility, type of exploitation, influence of river discharge in addition to previous studies conducted. The study was undertaken in Mombasa, Watamu, Malindi and Shimoni's Kisite Marine National Parks (MNP), all reefs receiving protection from fishing and shell collection for over 15 years. Malindi reefs experience a pulse of land derived discharge during the short rain period (Sept-Nov, North East Monsoon, NEM season) from the nearby Sabaki River, potentially supplying sediments and nutrients. Watamu reef forms part of the Watamu Marine National Park and Reserve including the expansive (360 km^2), highly ramified, groundwater sustained Mida mangrove creek to its west (van Katwijk et al., 1993). Mombasa MNP is a long stretch of lagoonal fringing reef ~ 6 km long and 1 km from the shore situated in the Bamburi area about 5 km north of Mombasa town. This reef experiences water exchange with the Tudor and Mtwapa mangrove creeks on either end of the reef and the ocean via a depression (channel) through the reef. The fourth reef is in the Shimoni area within the Kisite Marine National Park in the southernmost part of the Kenyan coast close to the Tanzania border. The park is ~ 8 km offshore from the small town of Shimoni and on the seaward side of Wasini Island. This reef was chosen because of its remote location hence minimal influence from any anthropogenic disturbances. Three study sites were chosen from Malindi and Shimoni and two sites for each of the smaller (area) Mombasa and Watamu reefs.

Measurement of environmental factors

Measurements of environment parameters were conducted twice a month over a 3 year period between 2005 and 2007. Seawater surface temperature (SST) and salinity were taken (in triplicate) and measured in the field with an automated temperature-salinity probe. Triplicate current speed measurements were taken in the field from a rubber boat using a hand-held current meter. Chlorophyll *a,* nutrients and total suspended sediments (TSS) measurements and analyses were done on three 1-L water samples collected from each site. Chlorophyll *a* and nutrients (nitrates and phosphates) were determined by filtering water samples through 0.45 μm pore size filters into acid-washed vials and chlorophyll *a* and nutrients (nitrates and phosphates) determined through measurements of absorbance, spectrophoto-
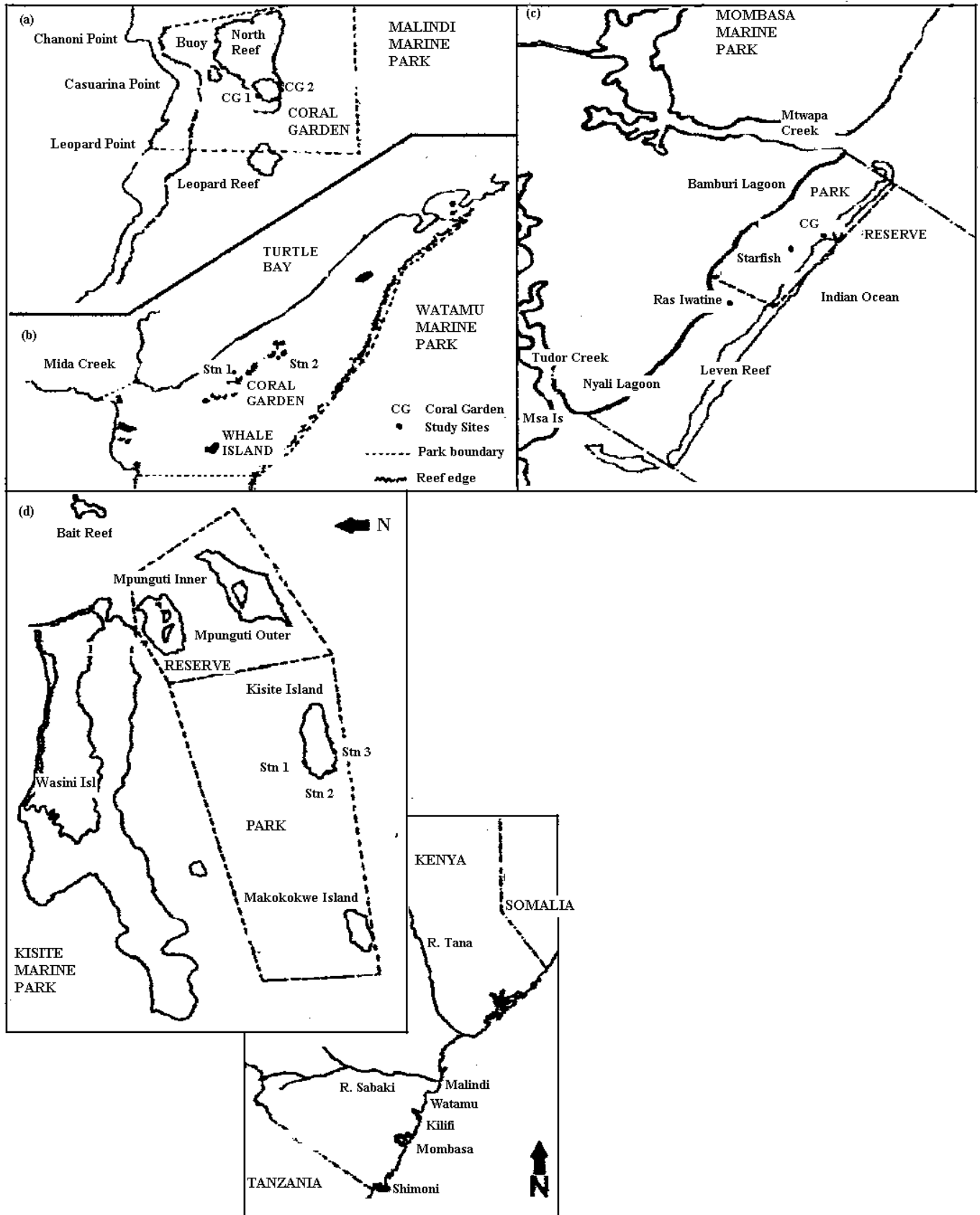
Figure 1. Map of southern Kenya's MPAs showing Malindi, Watamu, Mombasa and Shimoni reefs and location of study sites.

metrically. Total suspended sediments (TSS) were quantified by filtering triplicate 1 L water samples from each site through pre-weighed 0.45 µm pore size glass filters, filters then oven dried overnight at 60 °C and TSS concentration obtained gravimetrically.

Sedimentation (sediment deposition or trapped sediments) rates were measured using replicate sediment traps deployed and retrieved biweekly from the study reefs. Each set of sediment traps consisted of four cylindrical plastic cups, 13.5 cm long and 7 cm in diameter tied to a PVC pipe firmly fixed to the bottom of the reef, the open end of the cups being ~ 50 cm from the sea bottom. Each reef had three sets of traps except Mombasa which had only two traps. After collection sediments were washed with freshwater, small animals and plant material removed and sediments oven dried at 60°C overnight, weighed and sedimentation rates computed in g cm^{-2}day^{-1}. Organic content in TSS and deposited sediment was determined as loss in weight after combusting 3 replicate (5 g) sediment samples in a furnace at 500°C for 4 h. Acid-insoluble fraction was determined by digesting five 5 to 10 g sediment samples with dilute (5%) hydrochloric acid (HCl) and weighing the residue after drying, assuming non-carbonate (acid insoluble) fraction to entirely be of terrestrial origin. All data are averages of sample collection and measurements conducted over 3 months during each of the SE (March to October) and NE, (October to March) monsoon (McClanahan, 1988) periods.

Linear extension rates

Coral species for extension rate studies were selected based on their common occurrence in the study reefs as well as ease of identification. Linear extension rates of selected corals were studied by measuring the diameters of labeled massive forms, height/length of branching corals and distance between the edge of encrusting forms and fixed points (not less than three) around the colony (lateral growth) using calipers. Ten different individual coral colonies or branches were chosen for each coral species and labeled with cable ties numbered with holes (1 to 10) and changes in extension measured after 2 months. At the end of the experimental period, algae were scraped off the numbered end of the cable tie to reveal the identity of the coral and the height, distance from fixed point or diameter of coral to the nearest mm and later converted to annual linear extension rates (mm yr^{-1}).

Skeletal density and calcification rates

Five sample corals per species were collected from each site and small pieces (3 to 5 g) cut from each for density and calcification determination. Bulk density was determined by suspending a small basket from a spring balance using a thin copper wire into an aquarium filled with distilled water. Coral samples kept immersed in water from collection and throughout the experiment were weighed in air (wet) and then in distilled water and later dried in an oven to constant weight. Bulk density was measured by determination of total enclosed volume by weighing samples while preventing the filling of skeletal voids with the weighing medium (Bucher et al., 1998). After measurement of the dry weight, a water-proof coating was applied by quickly dipping samples in molten paraffin wax (at 105 to 110°C), waxed coral pieces were then weighed in air and then in water and the bulk density calculated as

wt in air ÷ [(waxed wt in air - waxed wt in water) × water density]

Coral calcification rates (g CaCO$_3$ cm^{-2} yr^{-1}) were then calculated as the product of bulky density (g cm^{-3}) and extension rate (mm yr^{-1}) for each individual coral sample and averaged for each coral species.

Corallite characteristics

Corallite (diameter and density) characteristics were studies as

described by Sabater and Yap (2004). Briefly, a stereo microscope equipped with a micrometer eyepiece and a net micrometer was used. Corallites were selected from three randomly chosen parts of a 5 g coral piece (with branch tips being avoided), counted and their diameters measured. Measurements of corallite diameter were estimated by measuring the distance between the two opposite walls of each corallite. Corallites were counted within an area bounded by the net micrometer of the microscope eyepiece for estimation of the corallite density, the magnification employed depending on corallite sizes. Corallite density (number of corallites per unit area, #/unit area) was then computed from the value of corallite counts and its corresponding area.

Data analysis

The study was intended to investigate seasonality in coral growth, however loss of samples during the rough SEM season prevented this, therefore, all analyses were conductor on pooled data. Averages for environment data, growth parameters and corallite characteristics were compared between reefs using one-way ANOVA and post-hoc multiple comparison tests undertaken using STATISTICA version 6.0. Transformation of data was performed where necessary after tests for homogeneity and homoscedasticity. Tukey's HSD test was used to find which means were different after detecting significant differences. Relationships between the three growth parameters (extension rates, density and calcification) were then investigated for all the data from the four reefs together as well as for each individual reef.

RESULTS

Environmental factors

No significant differences in temperature, salinity and current velocity were detected between study reefs though current velocity was found to be high in Malindi compared to the other sites (Table 1). Chlorophyll *a* concentration was found to be significantly higher in Malindi and Watamu compared to Mombasa and Shimoni, however, phosphates and nitrates concentration did not differ between reefs. Significant high total suspended sediment (TSS) and sedimentation (deposition) rates were measured in Watamu and Malindi compared to Shimoni and Mombasa. No significant differences between reefs were detected for TSS organic content, however, Watamu reef exhibited low bottom sediment organic content compared to the rest of the study reefs. The percent organic content of trapped sediments (sediment deposition) in Malindi was found to be significantly higher relative to all other reefs. Additionally, acid insoluble residue content for bottom and deposited sediments was found to be high in Malindi compared to all other reefs (MLD>WTM=MSA>SHM).

Linear extension rates

Only one species, *Pocillopora damicornis* was observed to exhibit significant higher extension rates in the Malindi sediment impacted reef compared to all other reefs (Table 2). On the other hand, *Acropora robusta, Porites*

Table 1. Environmental parameters measured for each reef from the study.

Parameter	Malindi	Watamu	Mombasa	Shimoni	ANOVA	
					F	p
SST (˚C)	28.1±1.42	27.6 ±1.53	27.8 ±1.13	27.7±1.26	1.18	ns
Salinity (‰)	34.2±0.67	34.7±0.69	33.9±0.82	34.5±0.66	1.13	ns
Current velocity (m s^{-1})	0.22±0.03	0.18±0.07	0.16±0.06	0.17±0.07	1.86	ns
Chlorophyll a (µg l^{-1})	0.62±0.22	0.67±0.24	0.33±0.25	0.41±0.25	4.13	*
Nitrates (mg l^{-1})	1.46±0.48	1.19±0.28	0.89±0.39	0.80±0.37	2.35	ns
Phosphates (mg l^{-1})	0.66±0.26	0.75±0.42	0.68±0.35	0.54±0.25	0.44	ns
TSS (g l^{-1})	28.5±4.75	28.1±4.33	23.9±1.13	21.5±0.55	7.03	*
TSS Organics (%) 5.01±2.88		4.31±2.19	4.72±1.90	4.17±1.05	1.76	ns
Deposition (g m^{-2} day^{-1})	8.99±1.78	7.05±1.45	1.99±0.68	3.17±0.40	11.46	*
Deposition Organics (%)	7.57±0.99	4.14±0.68	5.65±2.29	3.91±1.75	7.52	*
Deposited Insolubles (%)	9.71±0.85	7.18±0.91	6.48±1.50	8.28±1.12	7.52	ns
Bottom organics (%)	3.52±2.08	2.31±0.59	3.64±1.55	3.59±1.14	4.74	*
Bottom Insolubles (%)	8.34±0.53	6.37±0.55	5.74±0.54	3.56±0.53	4.74	*

All values are averages (and standard deviations) from the NE and SE monsoon periods with significant levels indicated by * < 0.05, ns = non-significant.

Table 2. Linear extension rates (mm yr^{-1}) of selected coral species from Kenyan protected reefs and a summary of statistical analysis.

Species	Malindi	Watamu	Mombasa	Shimoni	ANOVA	
					F	p
Acropora sp	25.7 ± 5.38	7.48 ± 1.48	6.80 ± 3.35	31.2 ± 3.97	90.7	*
Acropora humilis	1.42 ± 0.29	3.53 ± 1.45	14.9 ± 2.86	3.89 ± 1.12	66.9	*
Acropora robusta	25.9 ± 4.36	33.5 ± 5.06	45.6 ± 6.73	49.2 ± 7.02	17.8	*
Porites lutea	15.2 ± 3.11	12.8 ± 2.13	13.9 ± 3.86	11.9 ± 1.11	1.09	ns
Porites rus	14.2 ± 5.68		22.3 ± 7.46	31.9 ± 9.87	7.53	*
Porites cylindrica	18.4 ± 5.74	6.93 ± 2.30	13.2 ± 2.08	30.1 ± 6.76	27.9	**
Pocillopora eydouxi	11.0 ± 5.57	14.8 ± 1.78	26.9 ± 3.28	21.6 ± 4.31	22.4	*
Pocillopora damicornis	60.9 ± 4.77	58.1 ±11.6	37.9 ± 9.73	39.9 ± 5.05	10.1	*
Favia sp	27.2 ± 6.32	24.8 ± 4.67	22.5 ± 8.32	21.1 ± 6.31	1.05	ns
Favites sp	27.2 ± 5.41	27.1 ± 7.24	27.1 ± 5.68	18.9 ± 5.29	2.37	ns
Pavona decussata	39.9 ± 9.45		17.3 ± 9.67	31.6 ± 7.85	8.04	*
Montipora digitata	22.9 ± 4.89		19.2 ± 4.28	28.9 ± 7.17	3.92	**
Alveopora fenestrate	30.8 ± 6.56		31.0 ± 9.94	21.9 ± 7.60	3.09	ns
Galaxea fascicularis	55.4 ± 11.9	16.9 ± 4.82	31.8 ± 9.21	88.2 ± 24.5	23.8	*
Echinopora gemmacea	10.5 ± 3.46	54.7 ± 8.19	26.2 ± 5.45	24.7 ± 6.19	48.9	*

Values are means and standard deviations. Significant levels are indicated by * < 0.01, ** < 0.05, ns-not significant.

rus, Porites cylindrica, Pocillopora eydouxi, *Galaxea fascicularis* and *Echinopora gemmacea,* all showed higher extension rates in Shimoni reference reef compared to Malindi sediment-impacted reefs. The following species exhibited no differences in extension rates between reefs, *Porites lutea, Favia sp, Favites sp* and *Alveopora fenestrata.* Extension rates for *Acropora humilis, A. fenestrata* and *P. eydouxi* were found to be higher in Mombasa compared to all other reefs. No differences in

extension rates were detected between the reference and sediment impacted reefs for *Acropora humilis, Acropora sp, Montipora digitata* and *Pavona decusatta.*

Bulk density and calcification rates

Bulk density data revealed low values for all species in Malindi (except *Acropora sp, P. cylindrica, P. damicornis*

Table 3. Bulk density values (g cm^{-3}) for selected coral species from Kenyan protected reefs and a summary of statistical analysis.

Species	Malindi	Watamu	Mombasa	Shimoni	ANOVA	
					F	p
Acropora sp	1.55 ± 0.07	1.00 ± 0.00	1.52 ± 0.45	1.00 ± 0.00	3.30	ns
Acropora humilis	1.12 ± 0.06	1.75 ± 0.04	1.73 ± 0.09	1.21 ± 0.01	55.7	*
Acropora robusta	1.08 ± 0.03	1.62 ± 0.07	1.46 ± 0.05	1.2 1± 0.16	42.1	*
Porites lutea	1.41 ± 0.08	1.70 ± 0.00	1.51 ± 0.03	175 ± 0.10	11.2	*
Porites rus	1.19 ± 0.09		1.20 ± 0.00	1.28 ± 0.16	0.46	ns
Porites cylindrica	1.50 ± 0.00	1.13 ± 0.18	1.36 ± 0.10	1.65 ± 0.19	5.20	ns
Pocillopora eydouxi	1.47 ± 0.43	1.70 ± 0.11	1.69 ± 0.08	1.84 ± 0.13	0.80	ns
Pocillopora damicornis	1.84 ± 0.07	1.06 ± 0.09	1.66 ± 0.12	1.42 ± 0.38	5.33	ns
Favia sp	1.26 ± 0.13	1.47 ± 0.16	1.43 ± 0.04	1.38 ± 0.26	0.62	ns
Favites sp	1.23 ± 0.05	1.44 ± 0.05	1.10 ± 0.03	1.41 ± 0.17	5.58	ns
Pavona decussata	1.50 ± 0.00		1.88 ± 0.18	1.52 ± 0.33	1.93	ns
Montipora digitata	1.10 ± 0.14		1.43 ± 0.33	1.20 ± 0.08	1.31	ns
Alveopora fenestrata	1.08 ± 0.12		2.37 ± 1.37	1.06 ± 0.09	0.40	ns
Galaxea fascicularis	1.04 ± 0.15	1.17 ± 0.24	1.55 ± 0.07	1.52 ± 0.21	5.56	ns
Echinopora gemmacea	1.42 ± 0.08	1.71 ± 0.06		1.56 ± 0.07	8.69	ns

Values are means and standard deviations. Significant levels are indicated by * < 0.01, ** < 0.05, ns-not significant.

and *A. fenestrata*) compared to Shimoni but only the difference for *A. humilis*, *A. robusta* and *P lutea,* were significant (Table 3). *Acropora sp, A. fenestrata* and *P. damicornis* showed non-significant higher bulk densities in Malindi compared to the Shimoni reference reef. Bulk density for *A. humilis, A. robusta, P. lutea, Favia sp, Favites sp* and *E. gemmacea* were found to be higher in Watamu compared to other reefs. Generally, high bulk densities were measured for corals from Mombasa reef relative to other reefs including the Shimoni reference reef. Coral calcification rates were found to be around 3.5 gm^{-2}yr^{-1} (Figure 2). *Acropora sp, P. damicornis, Favia sp* and *Favites sp*, *P. decusatta, M. digitata* and *A. fenestrata* had higher calcification rates in sediment exposed Malindi reef than in the Shimoni reference reef. By contrast, *A. robusta, E. gemmacea, P eydouxi, P. rus, P. cylindrica* and *G. fascicularis* showed higher calcification rates in Shimoni compared in Malindi. *A. humilis* and *P. lutea* showed no differences in calcification rates between reefs in the present study. On average calcification rates were found to be higher in Mombasa and lower in Watamu compared to the rest of the reefs.

Corallite characteristics

All species showed significant differences in corallite density between reefs but only *A. humilis, P. lutea* and *A. fenestrata* had significantly higher corallite density (numbers of corallites per unit area) in Malindi relative to all other reefs (Table 4) whereas *Acropora sp, P. rus, P. cylindrica, P. eydouxi* and *P. damicornis,* exhibited significant higher corallite density in Shimoni compared to

the rest of the study reefs. High corallite density was measured for *P. eydouxi, Favia sp* and *Favites sp* in Mombasa compared to all other study reefs. Low corallite densities were generally found in Watamu for all species relative to all other reefs except *Acropora sp, A. humilis, A. robusta* and *E. gemmacea*. Corallite diameter studies revealed larger corallites for *Acropora* sp, *A. humilis, A. robusta, P. lutea, P. eydouxi, P. damicornis, M. digitata, A. fenestrata* in Malindi compared to all other study reefs (Table 5) and were generally low in Mombasa reefs. *Favia sp* and *Favites sp* had significantly larger corallite diameters in Shimoni relative to all reefs while *P. decussata* had larger corallites in Mombasa compared to all other reefs.

Correlation between growth parameters

Relationships between the growth parameters were investigated with simple regression analysis for all data from the four reefs combined (Figure 3) as well as for each individual reef (Figure 4). For the combined data the relationships were variable being strong between calcification and extension rates, but bulk density was again found to be poorly correlated with the other two coral growth variables. For individual reefs, bulk density was weakly correlated to the other two growth parameters, however, calcification rate and linear extension were strongly correlated. This strong relationship between calcification rate and linear extension in all the studied reefs suggests that variations in calcification rates are more closely related to extension rate variations rather than with variations in bulk density.
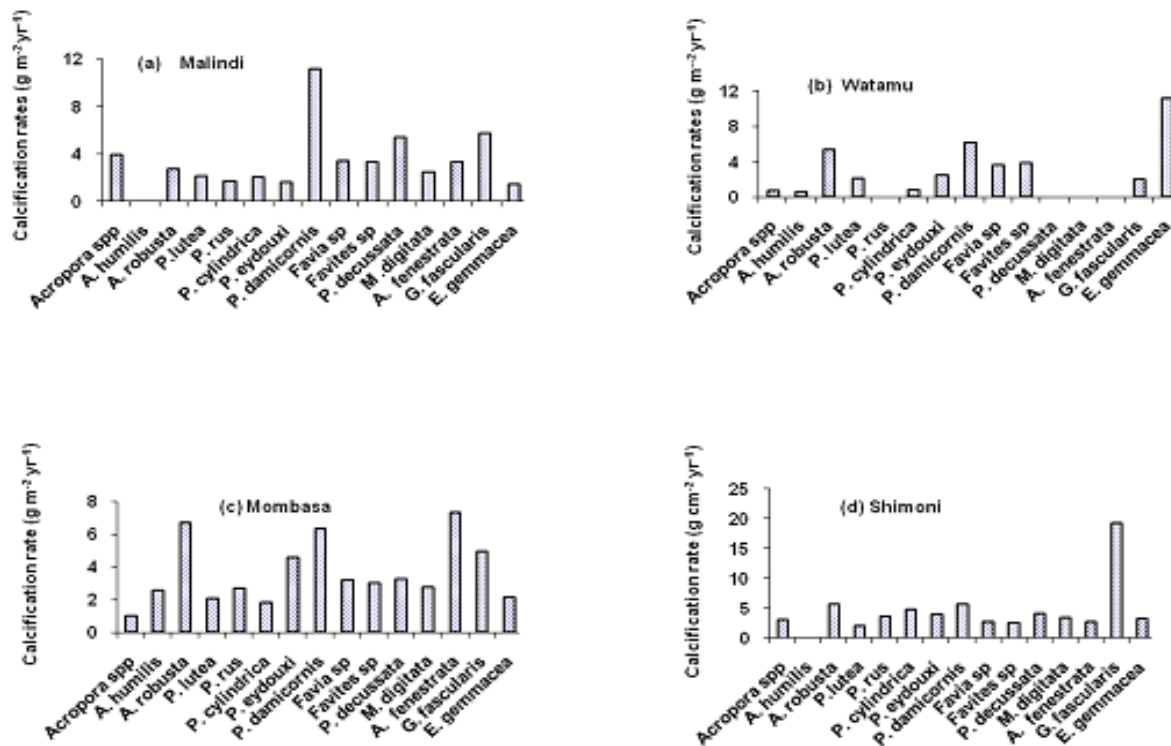
Figure 2. Calcification rates ($g\ m^{-2}\ yr^{-1}$) for selected coral species from Kenyan protected reefs.

Table 4. Corallite densities ($\#\ cm^{-2}$) of coral species from Malindi, Watamu, Mombasa and Shimoni and a summary of statistical analysis.

Species	Malindi	Watamu	Mombasa	Shimoni	ANOVA	
					F	p
Acropora sp	18.4 ± 2.19	21.2 ± 2.49	17.6 ± 2.19	26.4 ± 3.57	11.1	*
Acropora humilis	43.2 ± 5.93	27.8 ± 3.11	14.9 ± 4.95	24.8 ± 5.21	17.6	*
Acropora robusta	39.2 ± 3.34	20.8 ± 1.79	19.2 ±1.79	44.8 ±10.4	26.8	*
Porites lutea	100.8 ± 9.54	64.0 ± 2.83	70.4 ± 6.09	81.6 ±10.0	22.0	*
Porites rus	90.4 ± 5.37		101.6 ± 11.5	150.4 ± 2.19	91.8	*
Porites cylindrica	18.4 ± 5.74	6.93 ± 2.30	13.2 ± 2.08	30.1 ± 6.76	30.3	*
Pocillopora eydouxi	11.0 ± 5.57	14.8 ± 1.78	26.9 ± 3.28	21.6 ± 4.31	35.8	*
Pocillopora damicornis	90.4 ± 11.5	85.6 ± 40.4	113.6 ± 4.56	117.6 ± 5.37	17.9	*
Favia sp	1.09 ± 0.13	1.25 ± 0.00	1.80 ± 0.45	1.05 ± 0.11	3.73	*
Favites sp	2.85 ± 0.22	2.85 ± 0.38	3.16 ± 0.29	2.25 ± 0.71	10.3	*
Pavona decussata	365.6 ± 35.2		311.2 ± 44.1	410.8 ± 41.6	7.59	**
Montipora digitata	75.2 ± 7.16		44.8 ± 3.35	72.0 ± 7.48	35.4	*
Alveopora fenestrata	5.20 ± 0.84		3.9 0± 0.74	3.85 ± 0.34	6.45	**
Galaxea fascicularis	55.4 ± 12.0	17.0 ± 4.82	31.8 ± 9.21	88.2 ± 24.5	4.93	**
Echinopora gemmacea	1.45 ± 0.3	2.80 ± 0.45		1.30 ± 0.21	29.2	*

Values are means and standard deviations. Significant levels are indicated by * < 0.01, ** < 0.05, ns-not significant.

DISCUSSION

The influence of the Sabaki River on Malindi reef system's

water quality was evident from the high sediment, chlorophyll a and nutrient levels measured in the present study results. Sedimentation rates observed in Malindi (9.0

Table 5. Corallite diameters (mm) of selected coral species from Kenyan protected reefs and a summary of statistical analysis. Values are means and standard deviations. Significant levels are indicated by * < 0.01, ** < 0.05, ns-not significant.

Species	Malindi	Watamu	Mombasa	Shimoni	ANOVA	
					F	p
Acropora sp	1.50 ± 0.14	0.76 ± 0.09	0.98 ± 0.04	1.20 ± 0.07	66.09	*
Acropora humilis	1.74 ± 0.19	1.38 ± 0.18	1.04 ± 0.24	1.22 ± 0.16	63.94	*
Acropora robusta	1.78 ± 0.14	0.94 ± 0.11	0.92 ± 0.08	0.86 ± 0.13	11.43	*
Porites lutea	1.58 ± 0.13	1.12 ± 0.08	1.14 ± 0.11	1.12 ± 0.04	26.3	*
Porites rus	1.24 ± 0.11		0.72 ± 0.08	1.22 ± 0.08	48.22	*
Porites cylindrica	2.68 ± 0.13	1.52 ± 0.33	0.92 ± 0.13		85.16	*
Pocillopora eydouxi	1.52 ± 0.13	1.04 ± 0.11	1.10 ± 0.19	0.68 ± 0.08	32.92	*
Pocillopora damicornis	1.60 ± 0.10	0.86 ± 0.19	1.56 ± 0.29	0.74 ± 0.11	28.53	*
Favia sp	7.34 ± 0.61	7.90 ± 1.66	7.88 ± 0.99	10.1 ± 1.18	5.27	**
Favites sp	5.40 ± 0.89	5.74 ± 0.19	6.09 ± 0.40	6.60 ± 1.47	1.65	ns
Pavona decussata	0.70 ± 0.27		1.00 ± 0.32	0.48 ± 0.10	5.32	**
Montipora digitata	2.14 ± 0.24		1.56 ± 0.11	1.22 ± 0.15	34.90	*
Alveopora fenestrata	5.24 ± 1.00		2.52 ± 0.61	3.50 ± 0.83	13.66	*
Galaxea fascicularis	6.48 ± 1.34	6.41 ± 1.12	4.22 ± 0.99	1.22 ± 0.15	30.13	*
Echinopora gemmacea	3.10 ± 0.18	6.70 ± 0.84		5.98 ± 0.84	37.25	*
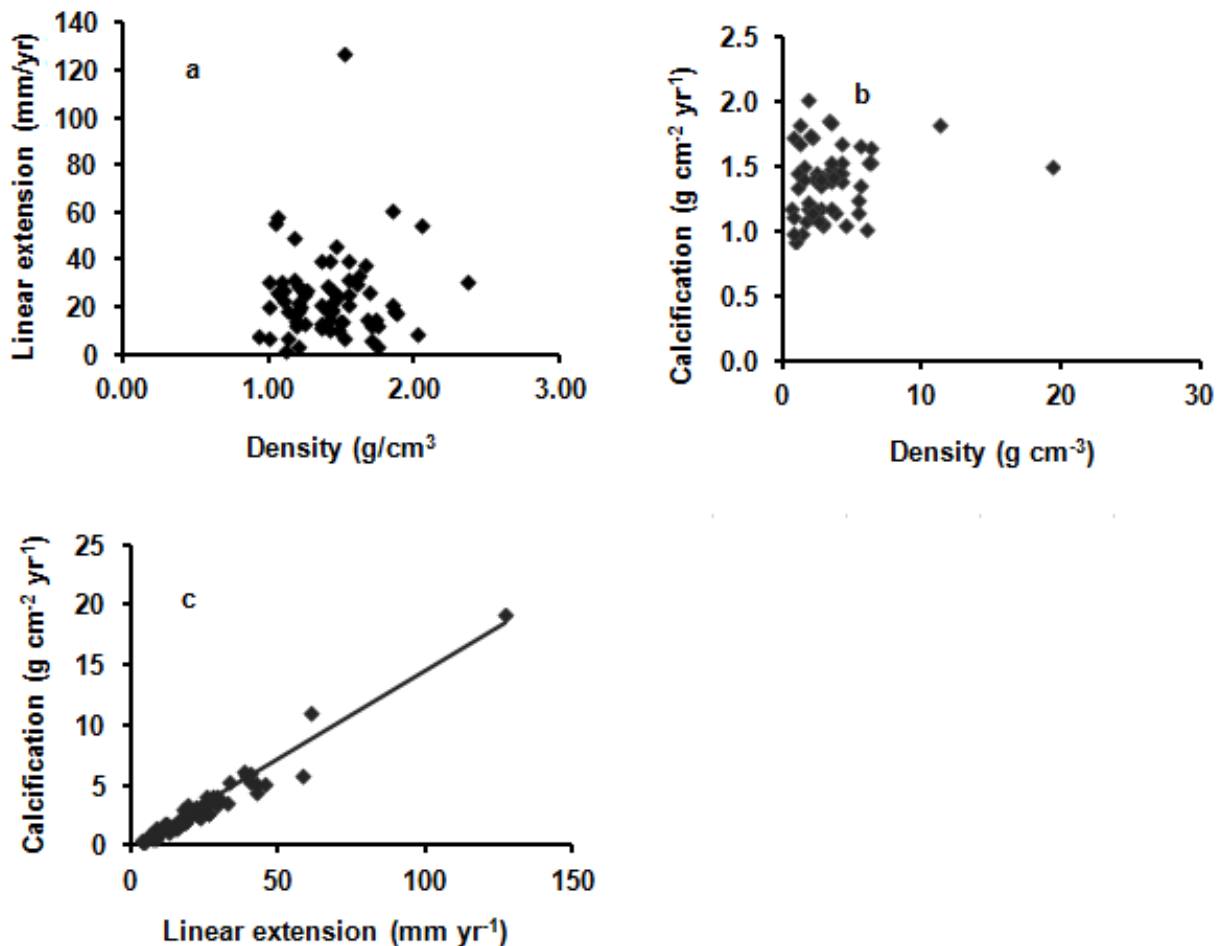
Figure 3. Relationship between calcification rates, bulk density and growth rates of selected coral species for all reefs combined.
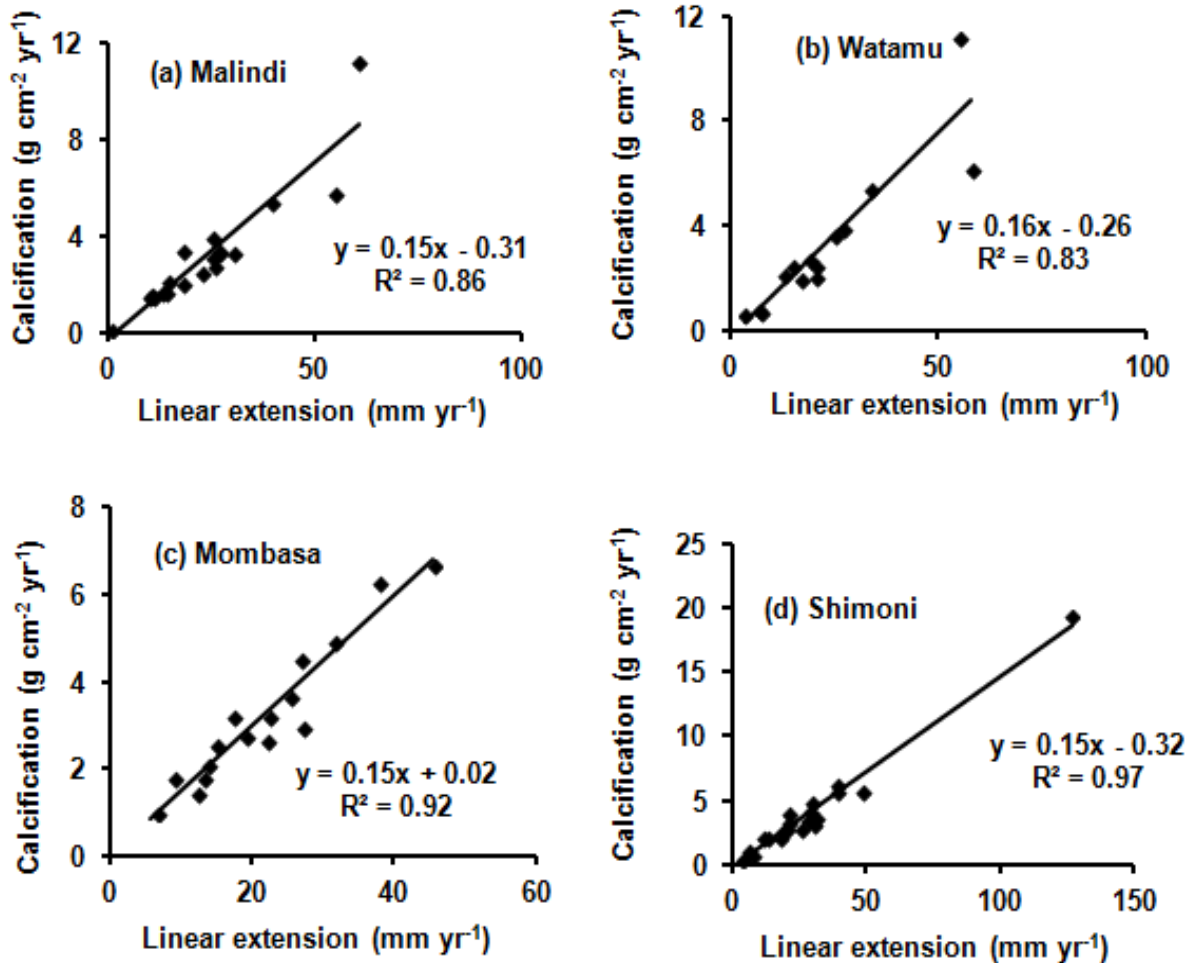
Figure 4. Relationship between calcification rates, bulk density and growth rates of selected coral species for individual reefs.

g m^{-2} day^{-1}) were lower than those measured using tiles (Obura, 1995), comparable to those from tubular traps (McClanahan and Obura, 1997) in the same site and close to values suggested by Rodgers (1990) to be detrimental to reef-building corals (10 g/m^2/day). However, observed suspended sediment (TSS) concentrations were higher than those previously measured by other workers (Brakel, 1984; van Katwijk et al., 1993; McClanahan and Obura, 1997) suggesting possible sediment increase with time. This increase may be attributed to changes along the Sabaki catchment areas due to increased population and agricultural activities, inappropriate farming methods and poor or failed soil conservation measures (Dunne, 1979; Bartley et al., 2013; Prouty et al., 2014). Changes in land use practices and population growth have previously been implicated in increasing the transport of sediments into the marine environment (Bartley et al., 2013; Prouty et al., 2014) with subsequent detrimental effects on coral reefs. In an earlier study, van Katwijk et al. (1993) reported presence of R. Sabaki sediments in Watamu reefs; however this was not in agreement with satellite and field study results (Brakel, 1984; McClanahan and Obura, 1997) we therefore suggest that high sedimentation rates observed in Watamu are likely the result of bottom sediment re-suspension especially during rough SEM conditions. As a nutrients proxy, elevated levels of chlorophyll a concentration measured in Malindi and Watamu relative to Mombasa and Shimoni may be due to (1) Sabaki River discharge enhancing phytoplankton productivity, (2) disturbed sediments releasing nutrients into the water column (3) upwelling off southern Somali and northern Kenya coast and (4) seapage of nutrient-rich ground water and runoff from Mida mangrove creek for the case of Watamu (McClanahan, 1988; Ohowa, 1996). High chlorophyll a (=increased phytoplankton) interferes with light penetration and exacerbates the negative effects of elevated sediment concentrations and this should be of concern to Watamu and Malindi reefs in light of predicted impacts of global climate change events.

High sediment organic and acid insoluble fractions from

Malindi confirm terrestrial influence. Although, stress levels on corals have been linked directly to the organic content of sediments (Bartley et al., 2013), nevertheless, we observed a thriving coral community in Malindi possibly due to East Africa's high tidal range (~4 m), site hydrodynamics, likely presence of sediment acclimatized/tolerant coral species and tolerable organic fraction levels. The above first two factors enhance flushing rates and therefore minimize accumulation and detrimental effects of sediments on reef communities. However, continued increases in land-based pollutants posse future concerns to the ecology of reefs and are of great significance for the Malindi reef areas in terms of park revenue and local community earnings since the highest turbid conditions occur during the NEM period (peak tourist and fishing season). There is therefore need to reverse or mitigated these conditions through robust soil conservation measures and land use practices upstream of the Sabaki as well as understanding the response of corals to sedimentation.

Combined reef growth data from all species revealed three contrasting groups: those with linear extension and calcification rates (1) positively (*A. fenestrata, Favites sp, Favia sp, P. lutea, P. damicornis and P. decusatta*) or (2) negatively (*Acropora sp, A. humilis, Acropora robusta, P. cylindrica, P. eydouxi and G. fascicularis*) affected by sediment concentrations and (3) those with growth parameters un-affected by sediment levels. The variable response of corals to sediments levels observed in the current study is similar to that found in previous studies (Bucher and Harrison, 2000; Carricart-Ganivet et al., 2000; Cruz-Pinon et al., 2003; Crabbe and Smith, 2005; Golbuu et al., 2011) and confirms the species-specificity of coral response to sediment exposure and other disturbances. This has been linked to individual coral species life history strategies of adaptation/tolerance to increased sedimentation and turbidity levels (Obura, 1995; Edinger et al., 2000; Fabricius, 2005) including physiological (mucus production, trophic level, P:R ratio), mechanical (cilliary action) as well as morphological modifications (corallite size and density, geometry). For example, Wooldridge (2014) concluded that in sediment-laden waters, reduced light penetration lowers photo-synthesis and disrupts autotrophy forcing species with thick tissue layers such as *Porites* to become heterotrophic as well as utilize energy reserves. Further, Padilla-Gamino et al. (2012) showed that some corals such as *Porites rus* change whole-colony morphologies from a plate-like to branching forms depending on the light conditions. This morphological and physiological plasticity is important in enabling a number of coral species to diversify strategies for energy acquisition and sediment rejection in order to facilitate persistence in turbid environments.

At a first glance the pattern of increased extension rate in the sediment-exposed reefs seemed anomalous since high sediment (and nutrient) levels have been associated with lowered extension rates. Such increases may be attributed to elevated zooxanthellae activity and increased heterotrophy that enhance coral metabolism and growth (Edinger et al., 2000; Fabricius, 2005). For example, *P. damicornis* has been reported to feed readily on sediments and therefore able to compensate for the low photosynthesis-respiration ratio at elevated turbidity levels (Anthony, 2000) explaining the high prevalence and enhanced growth rates of this species in the sediment impacted Malindi site in the present study. However, continued increase in sediments or nutrients influx has been implicated in diminishing extension owing to enhanced levels of phytoplankton and sediments interfering with light penetration (Edinger et al., 2000) and therefore lowering photosynthesis and calcification rates. Enhanced coral extension rates in stressful environments has also been associated with the utilization of stored (tissue) energy reserves (lipids, carbohydrates), however this capacity is not equally effectual in all coral species. The observed response pattern (increased extension rate) has been suggested to be a metabolic response pattern of corals with compromised health status and reduced probability to persist in the future as a reef-building and reproductive entities (Hughes and Grottoli, 2013; Woodridge, 2014). Such coral species would therefore be highly vulnerable to synergistic effects of local and global climate stressors.

Our results also show diminished linear extension rates in Watamu relative to the other mangrove fringed reef (Mombasa) and in Malindi compared to all other reefs. Observed reduction in coral growth parameters are similar to earlier findings (Rodgers, 1990; Edinger et al., 2000; Crabbe and Smith, 2005) and can be associated with reduced light penetration (due to increased sediment and phytoplankton concentration) and metabolic stress associated with energy expenditure in sediment rejection (ciliary action, polyp distension and mucus production), indicating low tolerance to increased sediments levels. We suggest that differences in extension rates observed between the two mangrove-fringed reefs likely resulted from different levels of nutrients in Mombasa relative to Watamu due to (1) volume of water reaching respective reef from creeks, (2) the distance of Mombasa reefs from the Tudor and Mtwapa creeks or (3) diluting effect due to mixing of lagoonal and oceanic waters through the depression in the Mombasa reef (Ohowa, 1996; Mwashote et al., 2005). The observed of lack of a coral extension rate response to elevated sediment level in some species (*P. lutea, Favia sp. Favites sp* and *A. fenestrata*) is unclear but may either be due to (1) counteracting effects of nutrients (enhanced extension rates) and sediments (reduced extension) canceling out each other, (2) individual coral species adaptations and tolerance to sediment levels, (3) lack of genetic capability to utilize particulate organic matter or (4) presence of low energy reserves available for growth (Veron, 2000; Padilla-Gamino et al., 2012). Moreover, Anthony (2006)

suggested that no-growth response to high sediment levels show that adverse impacts of sediments operate at the community or population level rather than at the individual level. The present study results thus confirm earlier reports of variable coral growth responses in polluted environments (Anthony and Fabricius, 2000; Fabricius, 2005) caused by changes in coral trophic status, morphological adaptations (Padilla-Gamino et al., 2012) and sediment tolerance, with some species becoming mixotrophic in high turbidity conditions while others remain phototrophic gaining only a small proportion of energy from particulate feeding.

Further, in the present study corals growing in the turbidreef showed larger diameters and calcification rates similar to the other findings (Todd et al., 2001; Todd, 2008). Increase in corallite size (diameter) has been associated with the efficient removal/rejection of sediment, though larger corallites have also been implicated in causing low reproductive output (Lauzinger et al., 2003). Large corallites also mean low corallite and skeleton density but such re-modeling interferes with the coal's ability to feed, compete for space and resist hydro-dynamic forces, therefore such modifications may not be ecologically 'cost' effective. Diminished corallite diameters measured in the mangrove-fringed reefs suggest that nutrients may have a negative effect on corallite size or that the reduction in corallite size is a strategy to survive in unfavourable conditions. Todd et al. (2001) contend that coral genotypes with phenotypic advantages enable corals to survive in environmental conditions normally perceived as unfavourable. Our results are preliminary and further studies and experi-ments are therefore needed to confirm and further understand how coral species respond to sediment and turbidity, especially with the use of reciprocal transplants experiments (RTEs).

Bulk density values in the current study ranged between 1.00 and 1.88 g cm^{-3}. Normally, coral density is restrained between an upper limit of 2.94 g cm^{-3} (pure aragonite) and a lower threshold value necessary to offer corals structural resistance against mechanical and hydrodynamic damage. Consistent low skeletal bulk density values were generally observed in the sediment exposed consisted with previous results (Carricart-Ganivet and Merino, 2001; Cooper et al., 2008). The observed low bulk density in polluted waters may be linked to either one or a combination of the following: (1)Heterotrophy and nutrient uptake increasing extension rates with the same or lower calcification rates (Carricart-Ganivet and Merino, 2001), (2) The uptake of terrestrial organic matter increasing the growth of soft tissue (Fabricius, 2005) with concomitant increase in porosity to the detriment of skeletal density or (3) Trapped particles within coral skeleton acting as crystallization inhibitors in the calcium deposition process (Belda, 1993; Atkinson et al., 1995).

Although incorporated sediments were not measured in the present study, evidence of sediment incorporation in corals from the Malindi area has previously been reported (Fleitmann et al., 2007). Surprisingly, bulk density values in the mangrove-fringed reefs were generally found to be higher than the offshore reef despite low density and high extension rates being associated with increased levels of nutrients in inshore waters (Belda et al., 1993; Atkinson et al., 1995). Here, we suggest that temperature differences between reef could be the likely cause of this observation, similar to the observations of Carricart-Ganivet (2004).

Calcification is an energy dependent process and maximum calcification occurs when conditions are optimum for energy uptake (Carricart-Ganivet, 2007; Allemand et al., 2011). However, in stressful environments energy allocation for calcification is considerably reduced (Allemand et al., 2011; Cabra-Tera et al., 2013; Wooldridge 2014) by diversion to sediment rejection and removal mechanisms leading to diminished coral calcification rates. Average coral calcification rates measured in the present study were comparable to those from previous studies (Carricart-Ganivet and Merino, 2000; De'ath, 2009; Carricart-Ganivet, 2011). Diminished calcification rates in turbid reefs result from increased energy expenditure required in sediment removal and rejection mechanisms through cilliary action and mucus production, with subsequent reduction in energy allocation to the calcification process (Kumara et al., 2015). However, high calcification rates were measured for *Acropora sp, P. damicornis, P. decussata, G. fascicularis* and *A. fenestrata* in the sediment impacted reef implying sediment tolerance and heterotrophic capabilities in these species. Corals have been shown to employ different coral growth strategies in disturbed environments with some investing increased calcification in linear extension while others use increased calcification to construct denser skeletons (Cruz-Piñón et al., 2003; Carricart-Ganivet, 2007).

The present study results also show that high extension rates do not necessarily translate into high calcification rates contrary to the findings of Carricart-Ganivet and Merino (2001). For example, in Watamu, the fastest growing coral was *P. darmicornis* (58.1 mm yr^{-1}) with a calcification rate of 6.2 g cm^{-2} yr^{-1}, a value lower than for *E. gemmacea* (11.2 g cm^{-2} yr^{-1}) with extension rates of 54.7 mm yr^{-1}. Also, in Shimoni *P. eydouxi* had extension rates of 21.6 mm yr^{-1} and a calcification rate of ~4.0 g cm^{-2} yr^{-1} compared to growth rates of 26.1 mm yr^{-1} and calcification rates of 2.8 g cm^{-2} yr^{-1} for *A. fenestrata*. Individual species differences in density coupled with the fact that calcification rate is a function of linear extension rate and density may be the likely cause of these observed findings. Further, species-specific abilities to utilize energy reserves and particulate matter as an energy source may also contribute to these variable and contrasting coral species responses. Low calcification rates measured in turbid waters have also been attributed to the cost of reproduction (egg and larval development)

especially in brooding corals (Cabra-Tena, 2013), mode of sediment removal (Larsson et al., 2013) and reduced light capture (for photosynthetic rates) due to diminished photosynthetic rates.

Coral growth, reef health and reef management implications

The present study documents variable coral species growth responses (increased and decreased growth characteristics) to the influence of sediments and turbidity. Coral growth strategy of enhanced or diminished extension rates in sediment impacted reefs has important implications and applications in coral reef health and management by providing information on the performance of corals in polluted environments (Cabra-Tena et al., 2013). Such information may be useful in the formulation of coral reef management and conservation strategies. Rapid extension rates have been linked to the instability of the coral-algae relationship and therefore a proxy for bleaching sensitivity as well as an indicator of the vulnerability to bleaching, reproductive capacity and likelihood of disease attack during stress (Wooldridge, 2014). This is of major importance in inshore polluted reefs considering future predicted increases in global environmental factors. Local stress factors will likely interact with ocean acidification and/or SST potentially shifting the calcification-erosion balance leading to coral reef degradation, habitat loss and decline in reef structure, ecosystem function and services (Ruiz-Moreno et al., 2012; Wisshak et al., 2013). This will have severe consequences on the reef ecology and livelihood of coastal communities. Moreover, the lack of expected coral extension rates response observed in the current study (Rodgers, 1990; Edinger et al., 2000) does not necessarily point towards absence of impact since extension rates may only be evident long after other signs of environmental stress and serious reef degradation have already occurred. Further, since low density skeletons and high bioerosion rates have been associated with inshore terrigenous influenced reefs (Tribollet et al., 2002; Tribollet and Golubic, 2005), with individual corals employing different growth strategies in response to water quality changes (Carricart-Ganivet, 2007; Golbuu et al., 2011; Nakajima et al., 2013) any options for the management of reefs experiencing local disturbances must take these aforementioned facts into consideration.

The strong and significant impacts of sediments loading on coral reefs thus require appropriate mitigation and regulation measures in watershed areas as part of the strategies for the management and protection of reef ecosystems. This way the potential compounding effects of anthropogenic and climate change stressors (Maina et al., 2011) are likely to be minimized or alleviated. For example, increased nutrients and sediments have been linked to coral disease outbreaks (Pollock et al., 2014) and may negatively impact recovery and resilience from climate change impacts (Ateweberhan et al., 2013) and on the

other hand, anthropogenic stressors may increase the severity of climate change impacts (Wiedenmann et al., 2012). Atewerbahan et al. (2013) reported that recovery from bleaching is severely retarded by local environmental parameters and that reef organisms having calcification already compromised by local environmental conditions cease to grow or dissolve altogether as a result of increased pH. Thus the variable responses of corals to disturbances are key ingredients in the management of coral reefs by helping to understand how important coral characteristics are likely to change in response to current and future environmental stresses and how management interventions might assist in safeguarding coral reefs against long term negative changes. Given the mounting evidence of increased frequency and severity of climate change in future and the increased vulnerability of coral reefs to increases in chronic local stressors (Maina et al., 2011; Ateweberhan et al., 2013;), management and alleviation of local stressors, particularly sedimentation will play a critical role in enhancing reef resilience and acclimation under future climate change scenarios (Ateweberhan et al., 2013). Further, considering the economic and ecological importance of coral reefs, studies on water quality parameters coupled with experiments on interactive effects of climate related stressors and local environmental factors will be required in order to shed more light on response of corals to environmental change and for sustainable and scientifically inspired coral reef management options.

Conflict of interest

Authors did not declare any conflict of interest.

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REFERENCES

Allemand D, Tambutté É, Zoccola D, Tambutté S (2011). Coral calcification, cells to reefs. In Coral reefs: an ecosystem in transition. Springer, Netherlands pp. 119-150. http://dx.doi.org/10.1007/978-94-007-0114-4_9

Anthony K (2006). Enhanced energy status of corals on coastal, high-turbidity reefs Mar. Ecol. Prog. Ser, 319: 111-116. http://dx.doi.org/10.3354/meps319111

Anthony KRN (2000). Enhanced particle feeding capacity of corals on turbid reef (Great Barrier Reef, Australia) Coral Reefs 19: 59-67. http://dx.doi.org/10.1007/s003380050227

Anthony KN, Fabricius KE (2000). Shifting roles of heterotrophy and autotrophy in coral energetics under varying turbidity. J. Exp. Mar.

Biol. Ecol. 252:221-253. http://dx.doi.org/10.1016/S0022-0981(00)00237-9

Ateweberhan M, Feary DA, Keshavmurthy S, Chen A, Schleyer MH, Sheppard CRC (2013). Climate change impacts on coral reefs Synergies with local effects, possibilities for acclimation, and management implications. Mar. Pollut. Bull, http://dx.doi.org/10.1016/j.marpolbul.2013.06.011

Atkinson MJ, Carlson B., Crow GL (1995). Coral growth in high nutrient, low pH sea water: a case study of corals cultured at the Waikiki Aquarium, Honolulu Hawaii Coral Reefs 14:215-233. http://dx.doi.org/10.1007/BF00334344

Barnes DJ, Devereux M J (1984). Productivity and calcification on a coral reef: a survey using pH and oxygen electrode techniques. J. Exp. Mar. Biol. Ecol. 79(3): 213-231. http://dx.doi.org/10.1016/0022-0981(84)90196-5

Bartley R, Bainbridge ZT, Lewis SE, Kroon FJ, Wilkinson SN, Brodie, JE, Silburn DM (2013). Relating sediment impacts on coral reefs to watershed sources, processes and management: Rev. Sci.Total Environ. 468-469 (2014) 1138–1153. http://dx.doi.org/10.1016/j.scitotenv.2013.09.030

Belda CA, Cuff C, Yellowlees D (1993). Modification of shell formation in their giant clam Tridacna gigas at elevated nutrient levels in sea water Mar. Biol. 117:251-257. http://dx.doi.org/10.1007/BF00345670

Brakel W (1984). Seasonal dynamics in suspended sediments plumes from the Tana and Sabaki rivers, Kenya: analysis of landsat imagery. Remote Sens. Environ. 16: 165-173. http://dx.doi.org/10.1016/0034-4257(84)90060-9

Bryant D, Burke L, McManus JW, Spalding M (1998). Reefs at Risk: A Map-based Indicator of Threats to the World's Coral Reefs. World Resources Institute, Washington, DC, USA, 56pp.

Bucher DJ, Harrison PL (2000). Growth responses of reef coral Acropora longicyanthus to elevated inorganic nutrients: do response to nutrients vary among coral taxa? Proc, 9th Intl. Coral Reef Symp, Bali Indonesia.

Bucher D J, Harriot V J, Roberts L G (1998). Skeletal microdensity, porosity and bulk density acroporid corals. J. Exp. Mar. Biol. Ecol. 228:117-136. http://dx.doi.org/10.1016/S0022-0981(98)00020-3

Cabra-Tena RA, Reyes-Bonilla H, Lluch-Cota S, Paz-García DA, Calderón-Aguilera LE, Norzagaray-López O, Balart EF (2013). Different calcification rates in males and females of the coral Porites panamensis in the Gulf of California Mar. Ecol. Prog. Ser. 476:1-8, 2013. http://dx.doi.org/10.3354/meps10269

Carricart-Gavinet JP (2011). Coral skeletal extension rate: An environmental signal or a subject to inaccuracies? J. Exp. Mar. Biol. Ecol. 405:73-79. ttp://dx.doi.org/10.1016/j.jembe.2011.05.020

Carricart-Gavinet JP (2007). Annual density banding in massive coral skeletons: result of growth strategies to inhabit reefs with high microborers' activity? DOI 10.1007/s00227-007-0780-3

Carricart-Gavinet JP (2004). Sea surface temperature and the growth of the West Atlantic reef-building coral Montastraea annularis J. Exp. Mar. Biol. Ecol. 302: 249-260. http://dx.doi.org/10.1016/j.jembe.2003.10.015

Carricart-Gavinet JP, Merino M (2001). Growth response of the reef building coral Montastrea annularis along a gradient of continental influence in Southern Gulf of Mexico. Bull. Mar. Sci. 66 (1): 133-146.

Carricart-Gavinet JP, Beltrán-Torres AU, Merino M, Ruiz-Zárate MA (2000). Skeleton extension, density and calcification rate of the reef building coral Montastrea annularis (Ellis and Solander) in the Gulf of Mexico. Bull. Mar. Sci. 66(1):215-224.

Chen T, Li S, Yu K, Zheng Z, Wang L, Chen T (2015). Increasing temperature anomalies reduce coral growth in the Weizhou Island, northern South China Sea Estuar, Coast. Shelf Sci. 130:121e126.

Crabbe MJC, Carlin JP (2007). Industrial sedimentation lowers coral growth rates in turbid lagoon environment, Discovery Bay, Jamaica Intl. J. Integr. Biol. 1:37-40.

Crabbe MJC, Smith DJ (2005). Sediment impact on growth rates of Acropora and Porites corals from fringing reefs of Sulawesi, Indonesia. Coral Reefs 24:437-441. http://dx.doi.org/10.1007/s00338-005-0004-6

Cooper TF, De'ath G, Fabricius KA, Lough JM (2008). Declining coral calcification in massive Porites in two nearshore regions of the northern Great Barrier Reef. Glob. Chang. Biol. 14:529-538.

http://dx.doi.org/10.1111/j.1365-2486.2007.01520.x

Cruz-Pi-ón G, Carricart-Gavinet JP, Espinoza-Avalos J (2003). Monthly skeletal extension rates of the hermatypic corals Montastrea annularis and Montastrea faveolata: biological and environmental controls. Mar. Biol. 143:491-500. http://dx.doi.org/10.1007/s00227-003-1127-3

De'ath G, Lough JM, Fabricius KE (2009). Declining coral calcification on the Great Barrier Reef Science 323:116-119.

D'Olivo JP, McCulloch MT, Eggins SM, Trotter J (2014). Coral records of reef-water pH across the central Great Barrier Reef, Australia: assessing the influence of river runoff on inshore reefs Biogeosci. Discuss. 11: 11443-11479. http://dx.doi.org/10.5194/bgd-11-11443-2014

D'Olivo JP, McCulloch MT, Judd K (2013). Long-term records of coral calcification across the 30 central Great Barrier Reef: assessing the impacts of river runoff and climate change, Coral Reefs, 32, 999–1012, http://dx.doi.org/10.1007/s00338-013-1071-8

Dunne T (1979). Sediment yield and land use in tropical catchments J. Hydrol. 42: 281-300. http://dx.doi.org/10.1016/0022-1694(79)90052-0

Edinger EN, Jompa J, Limmon GV, Widjatmoko W, Heikoop JM, Risk MJ (2000). Normal coral growth rates on dying reefs: Are coral growth rates good indicators of reef health? Mar. Pollut. Bull. 5: 404-425. http://dx.doi.org/10.1016/S0025-326X(99)00237-4

Fabricius KE (2011). Factors determining the resilience of coral reefs to eutrophication: a review and conceptual model. In: Dubinsky Z and Stambler N (ends): Coral Reefs: An Ecosystem in Transition. Springer, pp.493-505. http://dx.doi.org/10.1007/978-94-007-0114-4_28

Fabricius KE (2005). Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis Mar. Pollut. Bull. 50: 125–146. http://dx.doi.org/10.1016/j.marpolbul.2004.11.028

Fleitmann D, Dunbar RB, McCulloch M, Mudelsee M, Vuille M, McClanahan TR, Cole JE, Eggins S (2007). East African soil erosion recorded in a 300 year old coral colony from Kenya. Geophy. Res. Lett. 34: 1-5. http://dx.doi.org/10.1029/2006GL028525

GESAMP (2001). Protecting the oceans from land based activities. Land based sources and activities affecting the quality and uses of the marine, coastal and associated freshwater environment. UNDP, Nairobi.

Golbuu Y, van Woesik R, Richmond RH, Harrison P, Fabricius KE (2011). River discharge reduces reef coral diversity in Palau Mar. Pollut. Bull. 62: 824–831. http://dx.doi.org/10.1016/j.marpolbul.2010.12.015

Hughes AD, Grottoli AG (2013). Heterotrophic compensation: a possible mechanism for resilience of coral reefs to global warming or a sign of prolonged stress? PLoS One 8: e8117. http://dx.doi.org/10.1371/journal.pone.0081172

Klein D Y, Barana MW, Obilor LA (2015). Coral growth under thermal stress and different levels of light intensity in Acropora aspera. Scholarly and Creative Works Conference. Paper 55.http://scholar.dominican.edu/scw/scw2015/Posters/55

Kleypas JA, Buddemmeir RW, Archer D, Gattuso J-P, Langdon C, Opdyke BN (1999). Geochemical consequences of increased atmospheric carbon dioxide on coral reefs. Science 284(5411): 118-120. http://dx.doi.org/10.1126/science.284.5411.118

Kumara WAAU, Kumara PBTP, Cumaranatunga PRT (2015). Spatial differences in the growth rates of Pocillopora damicornis associated with sedimentation rate and light intensity at Polhena patchy reef, southern Sri Lanka Sri Lanka J. Aquat. Sci. 20 (1):47-58. http://dx.doi.org/10.4038/sljas.v20i1.7455

Kuta KG, Richardson LL (2002). Ecological aspects of black band disease of corals: relationships between disease incidence and environmental. Coral Reefs 21:21:393-398

Kružić P, Sršen P, Benković L (2012). The impact of seawater temperature on coral growth parameters of the colonial coral Cladocora caespitosa (Anthozoa, Scleractinia) in the eastern Adriatic Sea DOI 10.1007/s10347-012-0306-4

Lauzinger S, Anthony KRN, Willis BL (2003). Reproductive energy investment in corals: scaling with module size. Oecologia 136: 524-531. http://dx.doi.org/10.1007/s00442-003-1305-5

Larsson AI, van Oevelen D, Purser A, Thomsen L (2013). Tolerance to long-term exposure of suspended benthic sediments and drill cuttings

in the cold-water coral Ophelia pertusa Mar. Pollut. Bull. http://dx.doi.org/10.1016/j.marpolbul.2013.02.033

Maina J, McClanahan TR, Venus V, Ateweberhan M, Madin J (2011). Global gradients of coral exposure to environmental stresses and implications for local management PLoS One, 6(8), e23064. http://dx.doi.org/10.1371/journal.pone.0023064

McClanahan TR, Obura DO (1997) Sedimentation effects on shallow coral communities in Kenya. J. Exp. Mar. Biol. Ecol. 209: 103-122. http://dx.doi.org/10.1016/S0022-0981(96)02663-9

McClanahan TR (1988). Seasonality in East Africa's coastal waters Mar. Ecol. Prog. Ser. 44(2):191-199. http://dx.doi.org/10.3354/meps044191

McCulloch M, Fallon S, Wyndha T, Hendy E, Lough J, Barnes D (2003). Coral records of increased sediment flux to the inner Barrier Reef since European settlement. Nature 421: 727-730. http://dx.doi.org/10.1038/nature01361

McDonald IA, Perry CT (2003). Biological degradation of coral reef framework in a turbid lagoon environment, Discovery Bay, Jamaica. Coral Reefs 22:523-535. http://dx.doi.org/10.1007/s00338-003-0340-3

Mwashote BM, Ohowa BO, Wawiye PO (2005). Spatial and temporal distribution of dissolved inorganic nutrients and phytoplankton in Mida Creek, Kenya. Wetl. Ecol. Manag, 13(6), 599-614. http://dx.doi.org/10.1007/s11273-003-5003-1

Nakajima R, Yoshida T, Fuchinoue Y, Okashita T, Maekawa T, Kushair MRM, Othman BHR, Toda T (2013). Sedimentation Impacts on the Growth Rates of the Scleractinian Coral Acropora formosa from Fringing Reefs of Tioman Island, Malaysia Sains Malaysiana 42(9): 1201–1205

Ohowa BO (1996). Seasonal variations of the nutrient fluxes into the Indian Ocean from the Sabaki River, Kenya. Disc. Innov. 8(3), 265-274.

Obura, DO (1995). Environmental stress and life history strategies, a case study of corals and river sediment from Malindi Kenya. PhD Thesis, University of Miami 326p.

Padilla-Gami-o JL, Hanson KM, Stat M, Gates RD (2012). Phenotypic plasticity of the coral Porites rus: Acclimatization responses to a turbid environment J. Exp. Mar. Biol. Ecol. 434–435: 71–80. http://dx.doi.org/10.1016/j.jembe.2012.08.006

Pollock F, Lamb JJB, Field ST, Heron SF, Schaffelke B, Shedraw G, Bourne DG, Willis BL (2014). Sediment and turbidity associated with offshore dredging increase coral disease prevalence on nearby reefs PlosOne. http://dx.doi.org/10.1371/journal.pone.0102498

Prouty NG, Storlazzi CD, McCutcheon AL, Jenson JW (2014). Historic impact of watershed change and sedimentation to reefs along west- http://dx.doi.org/10.1007/s00338-014-1166-x

Rodgers CS (1990). Response of coral reefs and reef organisms to sedimentation. Mar. Ecol. Prog. Ser. 62:185-202. http://dx.doi.org/10.3354/meps062185

Rotmann S, Thomas S (2012). Coral tissue thickness as a bioindicator of mine-related turbidity stress on coral reefs at Lihir Island, Papua New Guinea. Oceanography 25(4):52–63, http://dx.doi.org/10.5670/oceanog.2012.67

Ruiz-Moreno D, Willis BL, Page AC, Weil E, Cróquer A, Vargas-Angel Sabater MG, Yap HT (2004). Long-term effects of induced mineral accretion on growth, survival and corallite properties of Porites cylindrica Dana. J. Exp Mar. Biol. Ecol. 311(2):355-374. http://dx.doi.org/10.1016/j.jembe.2004.05.013

Shantz AA, Burkepile DE (2014). Context-dependent effects of nutrient loading on the coral-algal mutualism Ecology 95: 1995-2005. http://dx.doi.org/10.1890/13-1407.1

Todd PA (2008). Morphological plasticity in scleractinean corals. Biol. Rev. 83:315-337. http://dx.doi.org/10.1111/j.1469-185X.2008.00045.x

Todd PA, Sanderson PG, Chou LM (2001). Morphological variation in polyps of the scleractinean coral Favia speciosa (Dana) around Singapore. Hydrobiologia 444: 227-235. http://dx.doi.org/10.1023/A:1017570100029

Torres JL, Morelock J (2002). Effect of terrigenous sediment influx on coral cover and linear extension rates in three Caribbean massive coral species. Caribb. J. Sci. 38:222-229.

Tribollet A, Golubic S (2005). Cross-shelf differences in the pattern and pace of bioerosion of experimental carbonate substrates exposed for 3 years in the northern Great Barrier Reef, Australia. Coral Reefs 24:422-434. http://dx.doi.org/10.1007/s00338-005-0003-7

Tribollet A, Decherf G, Hutchings PA, Peyrot-Clausade M (2002). Large-scale spatial variability in bioerosion of experimental coral substrates on the Great Barrier Reef (Australia); importance of microborers. Coral Reefs 21:424-432.

Van Katwijk MM, Meier NF, Van Loon R, Van Hove EM, Giesen WBJT, Van der Velde G, Den Hartog C (1993). Sabaki River sediment load and coral stress: correlation between sediments and condition of the Malindi-Watamu reefs in Kenya (Indian Ocean). Mar. Biol. 117:675-683. http://dx.doi.org/10.1007/BF00349780

Veron J (2000). Corals of the World. Australian Institute of Marine Science, Townsville

Wiedenmann J, D'Angelo C, Smith EG, Hunt AN, Legiret F-E. Postle AD, Achterberg EP (2012) Nutrient enrichment can increase the susceptibility of reef corals to bleaching. Nat. Clim. Change 3, 160-164. http://dx.doi.org/10.1038/nclimate1661

Wisshak MC, Schönberg HL, Form A, Freiwald A (2013). Effects of ocean acidification and global warming on reef bioerosion-lessons from a clionaid sponge Aquat. Bio.l 19:111-127. http://dx.doi.org/10.3354/ab00527

Wooldridge SA (2014) Assessing coral health and resilience in a warming ocean: Why looks can be deceptive Bioassays DOI 10.1002/bies.201400074.