

# Increased Terrestrial Disturbances Modify Skeletal Properties and Mechanical Strength of Hard Corals

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Received: September 13, 2016

Accepted: September 29, 2016

Online Published: November 30, 2016

doi:10.5539/enrr.v6n4p153

URL: <http://dx.doi.org/10.5539/enrr.v6n4p153>

## Abstract

Skeleton properties determine coral survival by influencing the range of hydraulic conditions colonies can withstand, selection of suitable habitat, ability to compete for space and light, repair damage and the overall fitness and ecological success of scleractinian corals. Skeletal properties of 16 coral species comprising 3 growth forms collected from Kenyan coral reef lagoons were investigated and found to vary considerably not only between species but between reefs as well, with corals exposed to both sediment and nutrients showing consistent lower skeleton density and strength but high porosity compared to those from sediment-unaffected reefs. Further, high skeletal density and strength but low porosity values were measured in branching relative to other growth forms. The present findings also suggest that the negative effects of nutrients on skeleton properties may be counteracted by high hydrodynamic energy, resulting in stronger skeletons in high hydrodynamic energy-nutrient-polluted reef habitats relative to pristine reefs. These findings have important ecological and management implications with regard to the existence, persistence, productivity and protective value of reefs, damage risks, maintenance and conservation of biological diversity with respect to future global climate change events. Consequently, appropriate watershed, reef and fisheries management options that address the impacts of local anthropogenic stresses (sediments, nutrients, overexploitation) would be expected to alleviate the effects of these disturbances and have the potential to minimize future large-scale coral reef damage resulting from increased and frequent global climate change events, such as increased ocean acidification (due to elevated atmospheric CO<sub>2</sub>) and sea surface temperature.

**Keyword:** coral skeleton, density, growth form, porosity, sediment, strength, anthropogenic disturbances

## 1. Introduction

### 1.1 Impacts of Disturbances on Coral Reef

Coral reefs are maintained by the close balance between constructive (by carbonate-producing corals and coralline algae) and destructive (carbonate-removal by physicochemical and biological factors) processes (McKibben, 2012; McClanahan & Abunge, 2014). However, disturbances that impair carbonate production (calcification) or facilitate carbonate destruction (erosion) can potentially push coral reefs into 'phase shifts' and states of degradation (Tribollet & Golubic, 2011; Doropoulos, Ward, Diaz-Pullido, Hoegh-Guldberg, & Mumby, 2012). There is growing concern that rapid changes in global and local environmental factors are increasing the severity of reef damage (Hoegh-Guldberg et al., 2007; Selig, Casey, & Bruno, 2012; McClanahan, Starger, & Baker, 2014) therefore threatening the ecology of reefs and the livelihood of coastal inhabitants (McKibben, 2012), particularly in tropical and sub-tropical shallow nearshore reefs adjacent to highly modified catchment areas (De'ath, Fabricius, Sweatman, & Puotinen, 2012; Maina et al., 2013; Bartley et al., 2014; Ramos-Sharrón, Terres-Pulliza, & Hernandez-Delgado, 2015). Predicted increases in SST and atmospheric carbon dioxide (ocean acidification) and water quality changes (Cooper, De'ath, Fabricius, & Lough, 2008; Doropoulos et al., 2012) will likely combine to cause significant negative effects on calcification, carbonate production and reef framework integrity (Kleypas et al., 1999; Hoegh-Guldberg et al., 2007; McClanahan, Atewebanhan, & Omukoto,

2008; Godinot, Tribollet, Grover & Ferrier-Pagés, 2012) therefore undermining individual coral fitness and skeleton characteristics (Pisapia, Anderson, & Pratchett, 2014). Compromised coral skeleton integrity could adversely impact the mechanical properties of corals with severe consequences on resistance and resilience of coral reefs (Madin, Hughes & Connolly, 2012; Reyes-Nivia, Diaz-Pullido, Kline, Hoegh-Guldberg & Dove, 2013), ultimately affecting reef productivity and services.

### 1.2 Why Coral Skeletal Properties?

Skeletal material deposition and properties have important ecological and economic implications in coral fitness and the subsequent formation and maintenance of coral reef structures (Chamberlain, 1978; Schuhmacher & Plewka, 1981a; Cordero, 2013) as well as the socio-economics of coastal inhabitants (McClanahan and Cinner, 2012). Skeletal properties also play a significant role in the ability of corals to repair damage, withstand impacts of bioeroding organisms (Pisapia et al., 2014; Chen, Li, & Yu, 2013; Cameron & Edmunds, 2014) and the maintenance and structuring of coral assemblages. Apart from preventing assemblage dominance by small subsets of species, skeleton characteristics may also be of significance in (i) determining boulder movements and damage during high hydrodynamic energy events (Spiske et al., 2008), (ii) explaining the differential mortality of corals (Roughael & Inglis, 1998) and (iii) understanding maintenance mechanisms of biological diversity, patchiness and changes in community composition in reefs after physical disturbance events (Yost et al., 2013). Mechanical properties of coral skeletons are also important determinants in the survival of corals by limiting colony or branch size, range of hydraulic conditions colonies can withstand, influencing competition for space and light, selection of suitable habitat as well as affecting growth form characteristics (Allemand, E. Tambutté, Ziccola, & S. Tambutté, 2011; Yost et al. Chindapol et al., 2013; 2014). Previous studies have shed some light on the consequences of skeleton property characteristics and morphological modifications (Chamberlain, 1978; Schuhmacher & Plewka 1981a; Madin et al., 2012; Reyes-Nivia et al., 2013), importance of skeletal strength through geological time (Schumacher & Plewka, 1981b; Tomiak et al., 2013; Robinson et al., 2014) as well as changes in colony and reef framework strength (Caroselli et al., 2011; Chen et al., 2013). However, few studies have been undertaken to elucidate the influence of water quality parameters on coral skeleton modifications, especially the effects of increased sediment and nutrient concentrations on coral skeleton mechanical properties.

### 1.3 Terrestrial Run-Off and Coral Skeleton Properties

Anthropogenically enhanced delivery of sediments and nutrients represents a well-recognized threat to nearshore coral reef communities globally (Mellela, Perry, & Haley, 2004; Ramos-Sharrón et al., 2015). Increased levels of terrestrial inputs have not only been reported to cause modified coral growth and poor health conditions, but have also been shown to be trapped and incorporated into coral skeletons (Edinger et al., 2000; Mellela, Lewis, & Croke, 2013; Shirai et al., 2014; Risk, 2014) through various mechanisms (Corrège, 2006; Prouty et al., 2013; Risk, 2014). Although incorporated materials have been used to infer a variety of information relating to past environmental changes (Fleitmann et al., 2007; Lewis et al., 2012; Inoue et al., 2014), their effects on coral skeleton structure, level of coral architectural modification and overall skeleton mechanical properties have scantily been investigated. Moreover, studies undertaken so far have reported conflicting results with Buddemeier, Maragos, & Knudson, 1974; Barnes & Devereaux, 1988; Motai et al., 2012 implicating skeletal property changes to the packing of  $\text{CaCO}_3$  crystals (micro-architecture) while others have linked skeleton changes to the arrangements of corallite septa, thecae and dissepiments (Dodge et al. 1993; Bucher, Harriot & Roberts, 1998; Cordero, 2013) or meso-architecture. Further, Buddemeier and Kinze (1975) failed to ascertain whether observed variations in *Porites lobata* skeleton properties resulted from micro- or meso-architectural changes. More case studies are thus needed to increase our understanding on the impacts of terrestrial-derived disturbances on coral skeleton properties. This is important in the identification, formulation and implementation of appropriate measures for the management and conservation of shallow nearshore reefs impacted by terrestrially derived disturbance, measures that will potentially minimize and/or mitigate the impacts of future climate change events on coral reef communities.

Corals reefs in the northern end of Kenya's fringing reef are located in an ecotone between the seasonal influence of river discharge and Somali current/upwelling in the north, and low river discharge/runoff in the south. The Malindi fringing reef has, for many years, experienced the influx of sediment and nutrient input from the Sabaki River (McClanahan & Obura, 1997; Fleitmann et al, 2007) but only a few studies of the effects of this disturbance have been undertaken (Giesen & van der Kerkhof, 1984; van der Kerkhof and Giesen, 1984; van Katwijk et al., 1993; Obura, 1995; McClanahan & Obura, 1997). River Sabaki discharge has increased from  $28 \text{ m}^3 \text{ s}^{-1}$  in the 1950s through  $49 \text{ m}^3 \text{ s}^{-1}$  during the period 1957-1970 to about  $73 \text{ m}^3 \text{ s}^{-1}$  in the period 2001-2004 (Kithaka, Nthenge & Obiero, 2003) with potential severe consequences on nearby coral reef communities. The synergy between this and future global climate change is potentially alarming in that it could damage reefs, impede reef recovery, interfere with natural regeneration and accelerate the destruction of reefs. Consequently, a

study of the effect posed by river discharge in the Malindi coral reef system was undertaken and compared to other unfished reefs along the Kenyan coast in order to evaluate the response of coral skeleton properties and mechanical strength to the influence of land-derived disturbances.

#### 1.4 Hypotheses and Research Design

The presence of reefs under different forms of management (protected or unprotected) as well as reefs under the influence of various forms of terrestrially derived disturbances (river discharge, nutrients, sediments) along the Kenya coast offers a natural experimental design and unique opportunity to study the effects of these disturbances. The study was designed to investigate the impact of terrestrial input on mechanical properties and strength of hard corals in Kenyan protected reef lagoons in order to test the following three (3) main hypotheses

- 1) Reefs impacted by terrestrial run-off will show reduced coral skeleton matrix volume and bulk density
- 2) Terrestrial run-off impacted reefs will be dominated by corals with porous and weaker skeletons
- 3) Terrestrial run-off will modify the mechanical properties and strength of coral growth forms.

## 2. Materials and Methods

### 2.1 Study Sites

Four study reefs, Mombasa, Watamu, Shimoni and Malindi (Figure 1) were chosen for this investigation based on their accessibility, type of exploitation, terrestrial influence and study history. All reefs are fully protected, effectively excluding fishing and shell collection for over 15 years. Malindi reef experiences a pulse of land-derived sediments and nutrients during the September-November short rain period (NE monsoon season) via the Sabaki River. Watamu reef forms part of the Watamu Marine Park and Reserve including the highly ramified 360 km<sup>2</sup> groundwater-water sustained Mida mangrove creek. Mombasa MNP is a long stretch of lagoonal fringing reef ~ 6 km long and 1 km from the shore, and experiences occasional water exchange with the ocean via a depression/channel across and through the reef and two creeks (Tudor and Mtwapa) on either side. Shimoni reef lies within the Kisite/Mpunguti Marine Park situated on the southernmost part of the Kenyan coast ~ 8 km offshore from Shimoni town and on the seaward side of Wasini Island.

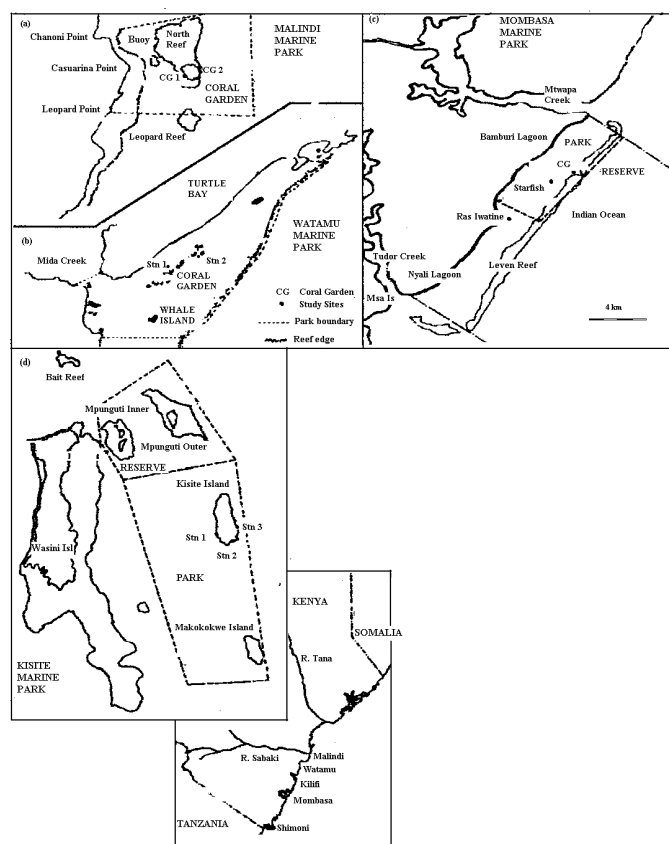


Figure 1. Map of the Kenya coast showing the position of (a) Malindi (b) Watamu (c) Mombasa and (d) Kisite Marine Parks, park boundaries and the location of the study sites

## 2.2 Oceanographic Studies

Environmental sampling was conducted twice per month. Triplicate temperature and salinity measurements were taken using an automatic probe and current velocity with a modified current drogue. Chlorophyll *a*, phosphate and nitrate concentrations were determined spectrophotometrically after filtration of triplicate 1L water samples through 0.45 µm pore size glass filters. Nitrates were first reduced to nitrites by passing water samples through a column containing copper coated cadmium fillings followed by diazotization with sulfanilamide and coupling with N (1-naphthyl)-ethylenediamine. For phosphate analysis, samples were reacted with a composite reagent containing molybdc acid, ascorbic acid and trivalent antimony. The absorbances of the resultant colored complexes were then measured with a spectrophotometer. Analytical grade potassium nitrate and potassium dihydrogen phosphates were used as standards for nitrates and phosphates analysis, respectively, standard curves were then generated for each nutrient species and the concentrations calculated using the slope and y-intercept of these graphs.

Sedimentation (deposition) rates were measured using replicate sediment traps retrieved from the sites every two (2) weeks, sediment then dried, weighed and sedimentation rates calculated. Total suspended sediment (TSS) concentration was determined by filtering triplicate 1-litre seawater samples through pre-weighed 0.45µm pore size glass filters, filters oven dried overnight at 60 °C and weighed after drying for gravimetric determination of TSS. Additionally, trapped and bottom sediments (collected using sediments corers) were analyzed for acid-insoluble residue (acid insolubles) and all sediment categories thereafter analyzed for organic matter. Briefly, organic matter was determined as loss in weight after sample combustion in a furnace at 500 °C for 4 hrs and acid-insoluble fraction was determined by digesting 5-10g sediment samples with dilute (5 %) hydrochloric acid (HCl) and weighing the residue after drying.

## 2.3 Coral Skeleton Characteristics

### 2.3.1 Bulk Density

Two concepts of coral skeletal density have been described in the literature; bulk-density or the variation in thickness and spacing of the principal skeleton components i.e. meso-architecture and microdensity or the arrangement and packing of calcium carbonate crystals (Barnes & Devereux, 1988; Bucher et al., 1998). These can be measured using methods that either preserve (direct volume measurements, X-ray and CT densitometry) or destroy (density of powdered coral skeleton) meso-architecture of skeleton (Buddemeier et al. 1974; Bucher et al., 1998; Barnes & Devereux, 1988; Cordero, 2013). Water displacement methods also provide microdensity estimates (Barnes & Devereux, 1988; Bucher et al., 1998; Cordero, 2013) when the voids in the skeleton are not allowed to fill with water. Coral density was obtained from coral pieces collected and transported immersed in sea water to avoid air entering the skeleton pores. At the laboratory sea water was gradually replaced with distilled water over a period of two (2) weeks, thereafter corals were soaked in bleach and acetone to remove organic matter. Corals were then washed in distilled water to remove bleach and acetone, care being taken to ensure complete immersion of samples throughout the procedure. Thereafter, saturated coral weight was determined by weighing samples in distilled water using a thin (~ 0.4-0.5 mm diameter) copper wire and a spring balance and sample volume then calculated by employing Archimedean techniques. Corals pieces were later dried in an oven at 100 °C to constant weight. After measurement of the dry weight of coral pieces, a water-proof coating was applied by quickly dipping coral samples in molten wax (at 105-110 °C) so that a thin wax layer prevented the ingress of water into the coral sample. Waxed corals were then weighed in air and then in water (buoyant weight) and the bulk density (dry weight/enclosed volume) calculated as

$$\text{wt in air} \div [(\text{waxed wt in air} - \text{waxed wt in water}) \times \text{water density}]. \quad (1)$$

### 2.3.2 Matrix Volume, Microdensity and Porosity

From the above data, skeletal matrix volume and volume of skeletal voids were calculated according to Bucher et al (1998) for the determination of porosity and microdensity. Bulk and microdensity were then treated as measures of meso- and micro-architecture respectively (Barnes & Devereux, 1988; Bucher et al., 1998; Cordero, 2013).

### 2.3.3 Skeletal Strength

Strength of coral skeletons was estimated using the porosity values obtained from Archimedes Principle and wax techniques according to the formula of Ryshkewitch (1953) for crystalline ceramic materials.

$$\sigma_P = \sigma_0 e^{-nP} \quad (2)$$

where  $\sigma_0$  represents the strength of a solid material; P is porosity; n is a constant between 4 (maximum strength) and seven (minimum strength) and  $\sigma_P$  is strength at porosity = P. The compressive strength of nonporous engineering/construction limestone (45-140 MPa) was used as  $\sigma_0$  due to its similar composition and crystal size with coral skeleton, the lower constant being used since the fine grained variety of limestone gives the highest value in compressive strength and was therefore deemed closer to that of nonporous coral skeletons (Chamberlain, 1978). Compressive strength of carbonate materials is typically an order of magnitude greater than tensile strength and both scale well and similarly with density (Chamberlain, 1978), thus the present skeleton strength estimates can still be useful in comparing the vulnerability of coral skeletons despite being derived from the compressive strength formula. The relationship between skeletal parameters was then explored through regression and correlation analysis with the aim of defining their relationship with skeletal strength and sedimentation.

### 2.3.4 Statistical and Data Analysis

Data was analyzed using JMP 7 and coral skeleton properties were compared between reefs using one-way ANOVA, a 2-way ANOVA was used to investigate the interaction between reefs and growth forms and post-hoc multiple comparison tests. Transformation of data was performed after tests for homogeneity and homoscedasticity using Bartlett's test. Tukey's HSD test was used to find differences between means after detecting significant differences through ANOVA tests. Relationships between coral strength growth parameters were assessed with correlations analysis using average values for whole reefs. Relationships between the three strength parameters (strength, bulk density and microdensity) were investigated for all the data from the four reefs together as well as for each individual reef.

## 3. Results

### 3.1 Oceanographic Studies

No significant differences in temperature, salinity and phosphates were detected between reefs but chlorophyll *a*, current velocity and nitrates were all found to be significantly high in Malindi but low in Shimoni compared to the rest of the study reefs. Higher TSS and sedimentation (trapped sediments) rates were measured in Malindi and Watamu relative to the other study reefs however no differences in TSS organics and trapped sediment (deposition) insoluble residue were detected between reefs (Table 1). Trapped sediment organic content, bottom sediment insoluble residue and organic matter content were all found to be higher in Malindi but low in Shimoni compared to the rest of the study reefs. Chlorophyll *a* also differed significantly between reefs and was found to be higher in Watamu and Malindi but lower in Mombasa and Shimoni.

Table 1. Environmental parameters measured for each reef from the study. All values are averages (and standard deviations) from the NE and SE monsoon periods

Parameter	Malindi	Watamu	Mombasa	Shimoni	F	p
SST (°C)	28.01±1.42	27.58 ±1.53	27.83 ±1.13	27.71±1.26	1.18	ns
Salinity (‰)	34.18±0.67	34.68±0.69	33.98±0.82	34.48±0.66	1.13	ns
Current (m s <sup>-1</sup> )	0.26±0.03	0.17±0.04	0.17±0.04	0.15±0.04	1.86	*
Chlorophyll <i>a</i> (µg l <sup>-1</sup> )	0.62±0.22	0.69±0.24	0.33±0.25	0.41±0.25	4.13	*
Nitrates (mg l <sup>-1</sup> )	1.46±0.48	1.19±0.28	0.89±0.39	0.80±0.37	2.35	*
Phosphates (mg l <sup>-1</sup> )	0.97±0.08	0.83±0.08	0.76±0.07	0.69±0.11	0.44	ns
TSS (g l <sup>-1</sup> )	28.45±4.75	28.10±4.33	23.88±1.13	21.48±0.55	7.00	*
TSS Organics (%)	5.01±2.88	4.31±2.19	4.72±1.90	4.17±1.05	1.76	ns
Trapped (g m <sup>-2</sup> day <sup>-1</sup> )	10.08±1.78	7.05±1.45	2.29±0.68	3.12±0.40	11.5	*
Trapped Insolubles (%)	9.66±0.81	7.07±0.91	6.43±1.48	8.22±1.11	7.52	ns
Traped Organics (%)	7.57±0.99	4.14±0.76	5.65±2.29	3.91±1.75	7.52	*
Bottom Insolubles (%)	8.32±0.45	6.28±0.54	5.69±0.50	3.47±0.48	4.74	*
Bottom organics (%)	3.52±2.08	2.31±0.59	2.64±1.55	2.59±1.14	4.74	*

significant levels indicated by \* < 0.05, ns = non significant.

### 3.2 Coral Skeleton Characteristics

#### 3.2.1 Bulk Density

Bulk density was observed to be low in Malindi corals compared to all other reefs, Tables 2&3 and Figure 2 (Watamu >Mombasa > Shimoni > Malindi) and was found to be high in branching forms compared to both massive and encrusting forms (branching > massive > encrusting, Figure 3). Malindi reef exhibited the lowest bulk density values for all the growth forms except for massive corals (Figure 3a). Species comparison revealed that *Alveopora fenestrata* ( $0.9\pm 0.1 \text{ g cm}^{-3}$ ) and *Echinopora gemmacea* ( $1.7\pm 0.1 \text{ g cm}^{-3}$ ) had the lowest and highest bulk densities, respectively, and both values were measured in the Malindi reef impacted by river discharge (Table 4).

Table 2. Analysis of variance for the influence of reef, species and interactions on skeletal bulk density, porosity, microdensity and strength of selected corals from Malindi, Watamu, Mombasa and Shimoni protected reef lagoons

Parameter	Factor	df	SS	F	p	Tukey's HSD
Bulk density	Reef	3	0.36	6.77	*	SHM > MLD/WTM < MSA
	Species	14	6.41	25.7	*	<i>P.eydouxi</i> , <i>Acropora sp</i> >all,
	R x S	42	2.68	3.57	*	see Table 4
Microdensity	Reef (R)	3	1.86	17.26	*	MSA/WTM <MLD/SHM
	Species(S)	14	1.49	2.99	*	<i>P.rus</i> >all, <i>A.humilis</i> <all
	R x S	42	6.34	4.27	*	see Table 5
Matrix Volume	Reef (S)	3	2.95	3.27	**	SHM >MLD, WTM > MSA
	Species (R)	14	38.71	9.20	*	<i>P. eydouxi</i> , <i>Acropora sp</i> >all
	R x S	42	54.47	4.31	*	see Table 6
Porosity	Reef (R)	3	2783.3	20.53	*	MSA/WTM < MLD, SHM
	Species (S)	14	11232.6	17.76	*	<i>P. daedelea</i> > all
	R x S	42	7386.2	63.89	*	see Table 7
Strength	Reef	3	8822.9	12.81	*	MSA>WTM< SHM>MLD
	Species	15	2606.4	18.93	*	<i>A. humilis</i> > all
	R x S	45	7882.6	3.82	*	see Table 8

\*denote significance at 0.01) with Tukey's HSD multiple.

Table 3. Analysis of variance for the influence of reef, growth form and interactions on bulk density, porosity and microdensity of selected corals from Malindi, Watamu, Mombasa and Shimoni protected reef lagoons

Parameter	Factor	df	SS	F	p	Tukey's HSD
Bulk density	Reef	3	0.84	3.7	*	WTM>MSA/SHM>MLD
	Growth form	2	2.58	17.1	**	b>e/m
	R x G	6	0.67	1.48	0.19	ns
Matrix Volume	Reef	3	4.82	2.5	0.06	ns
	Growth form	2	20.0	15.6	**	e>m/b
	R x G	6	10.0	2.6	*	See Figure 3b
Porosity	Reef (R)	3	3702	10.0	**	MLD>WTM>SHM>MSA
	Growth form	2	7633	31.1	**	m>e>b
	R x G	6	169.4	0.23	0.96	ns
Microdensity	Reef	3	33.8	14.2	**	SHM/MLD>WTM/MSA
	Growth form	2	82.2	51.9	**	e/m>b
	R x G	6	11.6	2.43	*	see Figure 3c
Strength	Reef	3	2309	8.4	**	MSA>WTM>SHM>MLD
	Growth form	2	5291	28.9	**	b>e>m
	R x G	6	791.5	1.45	0.19	ns

\* and \*\*denote significance at 0.05 and 0.001, respectively, ns=not significant) with Tukey's HSD multiple.

Table 4. Bulk density data (g cm<sup>-3</sup>, measured without exposure to air) for selected coral species from Kenyan protected reefs and a summary of statistical analysis

Species	Malindi	Watamu	Mombasa	Shimoni	F	p
Acropora sp	1.29±0.13	1.68±0.19	1.26±0.14	1.61±0.17	18.2	*
Acropora humilis	1.26±0.12	1.41±0.07	1.49±0.06	1.36±0.04	4.22	*
Acropora robusta	1.24±0.19	1.29±0.18	1.29±0.06	1.64±0.07	5.38	*
Porites lutea	1.26±0.27	1.27±0.07	1.13±0.02	1.04±0.04	11.2	*
Porites rus	1.03±0.07	1.29±0.04	1.29±0.28	1.10±0.13	0.68	ns
Porites cylindrica	1.06±0.23		1.09±0.05	0.99±0.12	0.36	ns
Pocillopora eydouxi	1.37±0.11	1.57±0.03	1.50±0.22	1.63±0.18	1.53	ns
Pocillopora damicornis	1.32±0.20	1.42±0.12	1.34±0.09	1.53±0.15	1.35	ns
Montipora digitata	1.00±0.07		1.43±0.33	1.05±0.04	8.89	*
Favia sp	0.99±0.12	1.15±0.17	1.13±0.19	0.93±0.04	2.23	ns
Favites sp	1.21±0.07	1.56±0.04	1.34±0.04	1.26±0.09	5.79	*
Pavona clavus	1.27±0.26	1.49±0.05	1.07±0.06	1.27±0.04	5.17	*
Pavona decussata	1.09±0.05		1.53±0.08	1.13±0.13	19.6	*
Alveopora fenestrata	0.76±0.09	2.14±1.04	0.92±0.18	0.85±0.13	86.4	*
Galaxea fascicularis	0.91±0.06	1.18±0.20	1.46±0.10	1.02±0.21	4.38	*
Echinopora gemmacea	1.72±0.10	1.38±0.12	1.41±0.04	1.55±0.16	5.47	*

Values are means (with standard deviations) and significance levels are indicated by: \* < 0.05, ns = not significant.

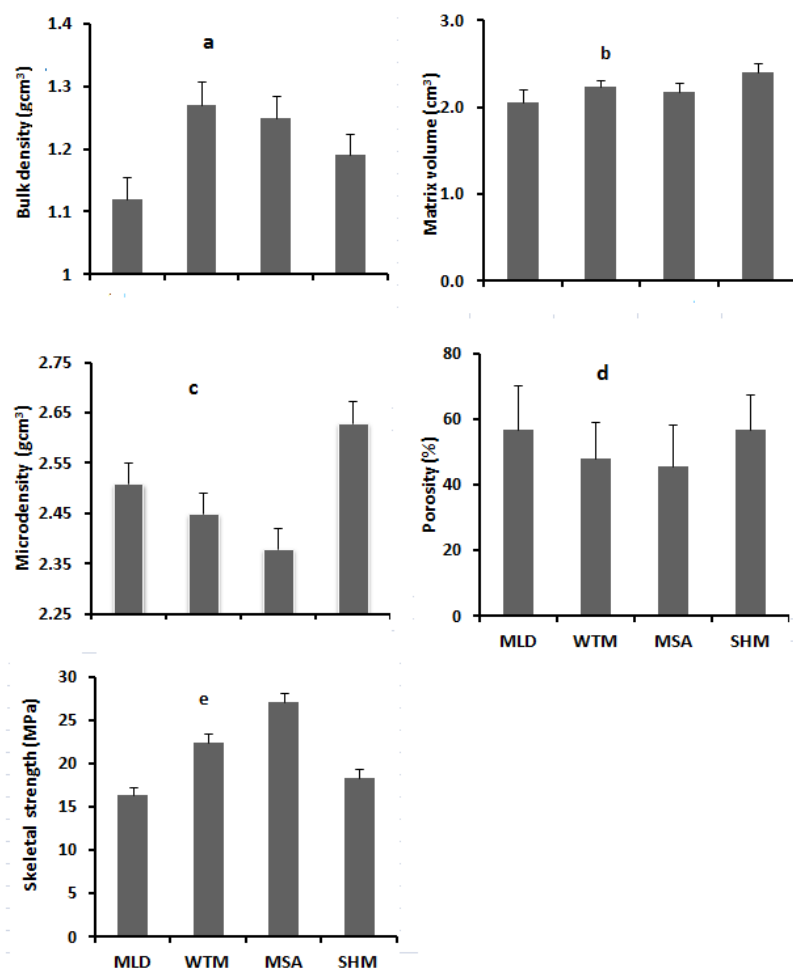


Figure 2. Coral skeleton property means from Malindi, Watamu, Mombasa and Shimoni coral reefs (a) bulk density (b) matrix volume (c) microdensity (d) porosity and (e) skeletal strength

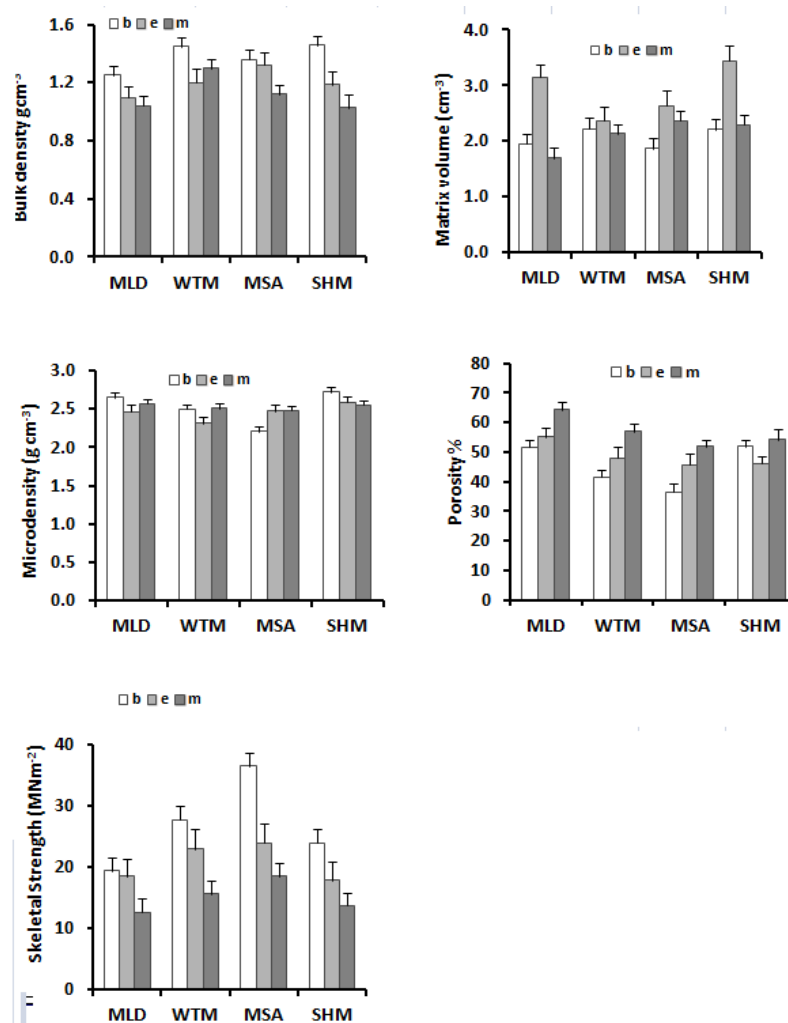


Figure 3. Skeletal characteristics of coral growth forms (b, branching, m, massive and e, encrusting) from Kenyan protected reef lagoons (a) bulk density, (b) matrix volume, (c) microdensity, (d) porosity and (e) skeletal strength

### 3.2.2 Matrix Volume, Microdensity and Porosity

Low matrix volume was measured in Malindi relative to other reefs (Figure 2b, Table 2) but was high in encrusting compared to other growth forms (Table 3). The highest and lowest matrix volume values were both measured in Malindi from *E. gemmacea* ( $5.6 \pm 0.4$ ) and *Favia sp* ( $1.00 \pm 0.25$ ), respectively (Table 5). High matrix volume was measured in Shimoni for all species except *A. robusta* and *E. gemmacea*. Like bulk density, microdensity also showed significant differences between reef and species and between growth forms ( $p < 0.001$ , Table 2) with the highest and lowest microdensity being recorded for *Pocillopora eydouxi* (Shimoni) and *M. digitata* (Malindi), respectively (Table 6). Low microdensity was measured in Mombasa ( $2.4 \pm 0.1 \text{ g cm}^{-3}$ ) relative to all other reefs (Mombasa < Watamu < Malindi < Shimon, Figure 2c). In fact Mombasa reef exhibited low microdensity values for all coral species except *P. rus*, *M. digitata*, *Favia sp* and *Pavona clavus*. Within reefs, the general trend was that massive and the encrusting forms showed lower microdensity compared to branching types (Figure 3c) except in the Watamu reefs.

Coral skeletons in Malindi reef showed higher porosity compared to all other reefs (Malindi > Shimoni > Watamu > Mombasa, Figure 2d). Individually, all species studied had higher porosity in Malindi compared to all other studied reefs except *Acropora humilis*, *M. digitata*, *Pavona decusatta* and *Pavona clavus* (Table 7). Species-reef comparisons revealed that the most porous species was *Galaxea fuscicularis* in Watamu ( $74.5 \pm 10.5\%$ ) and the least porous was *Acropora humilis* ( $22.8 \pm 1.4\%$ ) in Mombasa. Massive corals were found to be the most porous ( $58.1 \pm 1.2\%$ ) relative to other growth forms. Highest and lowest porosity were measured in massive (Malindi,  $64.5 \pm 2.6\%$ ) and branching (Mombasa,  $36.5 \pm 2.6\%$ ) corals, respectively (Figure 3d).



### 3.2.3 Skeleton Strength

Significant differences in coral skeletal strength between reefs and species as well as reef-species interactions were detected. Stronger coral skeletons were observed in Mombasa (except *Pavona clavus*) compared to all other reefs, with corals from the Malindi reef impacted by river discharge generally showing weaker skeletons (Mombasa>Watamu>Shimoni>Malindi, Figure 2e). Higher coral strength values were also measured in branching corals relative to massive and encrusting forms, (Figure 3e, Table 8). Reef-species interaction showed that *Montipora digitata* (Mombasa) had the strongest skeleton whereas the lowest strength was measured in *G. fascicularis* from Malindi.

Table 5. Matrix volume (cm<sup>3</sup>) for selected coral species from Kenyan protected reefs and a summary of statistical analysis. Values are means (with standard deviations)

Species	Malindi	Watamu	Mombasa	Shimoni	F	p
<i>Acropora</i> sp	2.24±0.09	2.17±0.29	1.91±0.72	2.67±0.63	0.65	ns
<i>Acropora humilis</i>	1.83±0.14	1.83±0.14	2.08±0.30	2.17±0.52	0.77	ns
<i>Acropora robusta</i>	2.67±0.12	1.83±0.14	1.92±0.38	1.92±0.38	1.07	ns
<i>Porites lutea</i>	1.67±1.23	2.08±0.29	1.92±0.14	2.00±0.66	0.19	ns
<i>Porites rus</i>	1.42±0.14	1.92±0.72	1.08±0.14	1.33±0.38	2.07	ns
<i>Porites cylindrica</i>	1.25±0.50		1.92±0.52	1.58±0.38	1.50	ns
<i>Pocillopora eydouxi</i>	1.75±0.25	3.17±0.14	2.42±0.80	2.17±0.52	4.25	*
<i>Pocillopora damicornis</i>	1.67±0.58	2.42±0.29	1.75±0.25	3.00±0.25	8.67	*
<i>Montipora digitata</i>	1.50±0.25		1.13±0.18	2.08±0.58	4.53	*
<i>Favia</i> sp	1.00±0.25	2.58±0.52	2.92±0.76	2.75±0.25	9.61	*
<i>Favites</i> sp	2.67±1.53	2.00±0.50	1.50±0.25	3.25±0.25	2.41	ns
<i>Pavona clavus</i>	2.65±1.35	2.42±0.76	2.00±0.25	2.50±0.43	0.56	ns
<i>Pavona decussata</i>	1.83±0.52		2.33±0.14	2.25±0.90	0.58	ns
<i>Alveopora fenestrata</i>	1.42±0.14	1.83±1.51	2.83±0.76	1.75±0.50	5.78	*
<i>Galaxea fascicularis</i>	1.25±0.66	2.00±0.66	3.00±0.25	1.83±0.14	6.63	*
<i>Echinopora gemmacea</i>	5.58±0.38	2.33±0.14	2.08±0.80	4.25±1.64	9.43	*

Significance levels are indicated measured at p = 0.05, ns = not significant.

Table 6. Microdensity (g cm<sup>-3</sup>) for selected coral species from Kenyan protected reefs and a summary of statistical analysis. Values are means (with standard deviations)

Species	Malindi	Watamu	Mombasa	Shimoni	F	p
<i>Acropora</i> sp	2.66±0.31	2.63±0.13	2.06±0.10	2.58±0.15	1.25	ns
<i>Acropora humilis</i>	2.42±0.26	2.68±0.09	2.28±0.38	2.65±0.09	1.95	ns
<i>Acropora robusta</i>	2.62±0.21	2.81±0.16	2.13±0.15	2.75±0.08	26.1	*
<i>Porites lutea</i>	2.79±0.01	2.55±0.12	2.33±0.49	2.65±0.18	1.14	ns
<i>Porites rus</i>	2.73±0.08	2.12±0.10	2.85±0.13	2.87±0.13	30.5	*
<i>Porites cylindrica</i>	2.70±0.45		2.41±0.10	2.81±0.19	1.56	ns
<i>Pocillopora eydouxi</i>	2.42±0.14	2.45±0.06	2.40±0.04	2.90±0.21	10.7	*
<i>Pocillopora damicornis</i>	2.67±0.47	2.31±0.12	2.26±0.21	2.56±0.20	1.46	ns
<i>Montipora digitata</i>	2.03±0.06		2.45±0.07	2.59±0.25	9.93	*
<i>Favia</i> sp	2.74±0.07	2.49±0.35	2.55±0.11	2.31±0.08	2.54	ns
<i>Favites</i> sp	2.60±0.17	2.59±0.09	2.38±0.20	2.64±0.07	1.97	ns
<i>Pavona clavus</i>	2.33±0.22	2.51±0.32	2.67±0.26	2.49±0.08	0.99	ns
<i>Pavona decussata</i>	2.54±0.23		2.57±0.11	2.67±0.21	1.59	ns
<i>Alveopora fenestrata</i>	2.56±0.39	2.41±0.39	1.63±0.15	2.32±0.29	5.45	*
<i>Galaxea fascicularis</i>	2.58±0.21	2.51±0.06	2.54±0.11	2.77±0.07	2.51	ns
<i>Echinopora gemmacea</i>	2.57±0.11	2.57±0.22	2.37±0.39	2.61±0.01	0.59	ns

Significance levels are indicated measured at p = 0.05, ns = not significant.

Table 7. Porosity (%) for selected coral species from Kenyan protected reefs and a summary of statistical analysis. Values are means (with standard deviations)

Species	Malindi	Watamu	Mombasa	Shimoni	F	p
Acropora sp	50.5±9.5	35.9±4.5	39.0±7.2	37.1±10.0	2.01	ns
Acropora humilis	47.3±7.8	47.2±4.8	22.8±10.4	48.7±2.2	9.35	*
Acropora robusta	52.1±9.1	53.7±3.9	26.1±6.7	45.4±9.1	8.49	*
Porites lutea	68.2±23.4	45.9±2.8	46.5±7.0	60.5±3.6	5.76	*
Porites rus	67.3±1.01	38.5±4.6	54.6±9.6	61.7±2.9	15.1	*
Porites cylindrica	63.9±12.7		54.5±3.9	64.5±6.8	1.28	ns
Pocillopora eydouxi	43.2±3.3	35.6±1.1	36.7±8.1	43.7±9.0	1.71	ns
Pocillopora damicornis	48.9±15.2	38.3±6.4	39.9±8.9	40.0±5.0	0.75	ns
Montipora digitata	52.8±6.2		22.1±2.9	59.5±4.7	43.8	*
Favia sp	65.9±3.5	53.9±3.3	56.1±5.7	59.8±2.9	4.15	*
Favites sp	68.9±16.8	61.1±11.2	39.9±5.3	52.4±2.8	4.42	*
Pavona clavus	45.4±11.0	43.9±5.9	63.3±3.9	49.0±1.7	5.35	*
Pavona decussata	56.6±4.5		40.4±3.1	61.8±6.31	5.88	*
Alveopora fenestrata	66.1±2.3	72.1±10.1	45.7±5.8	62.7±9.2	8.77	*
Galaxea fascicularis	74.5±10.5	52.7±9.2	48.5±4.5	63.2±8.5	5.65	*
Echinopora gemmacea	33.0±2.9	46.2±1.5	39.9±8.9	40.5±6.0	2.77	ns

Significance levels are indicated by: \* < 0.05, ns = not significant.

Table 8. Coral skeleton strength (MPa) for selected species from Kenyan protected reefs and a summary of statistical analysis. Values are means (with standard deviations)

Species	Malindi	Watamu	Mombasa	Shimoni	F	p
Acropora sp	19.4±6.5	33.6±5.7	30.2±8.9	33.4±13.5	1.58	ns
A. humilis	21.9±7.2	21.5±4.3	59.1±24.2	20.0±1.8	6.59	*
A. robusta	18.1±6.6	16.5±2.6	50.4±13.0	23.8±8.8	10.04	*
Porites lutea	11.5±7.4	19.1±2.1	20.4±9.0	12.5±1.7	1.70	ns
Porites rus	9.5±0.4	30.4±5.8	16.6±6.5	11.9±1.4	13.5	*
Porites cylindrica	11.8±6.2		15.9±2.6	10.8±2.9	1.22	*
Pocillopora. eydouxi	25.0±3.3	33.7±1.4	33.3±10.2	25.6±9.9	1.26	ns
Pocillopora. damicornis	22.3±13.3	30.9±8.2	29.5±9.4	28.6±5.7	0.21	ns
Montipora digitata	17.3±4.4		62.6±0.4	13.1±2.6	245.3	*
Favia sp	10.2±1.4	16.3±2.3	15.1±3.2	12.9±1.5	4.59	*
Favites sp	15.5±2.9	18.3±2.4	24.7±3.2	17.3±1.9	8.62	*
Pavona clavus	24.4±5.6	24.6±5.8	12.7±0.9	19.7±1.4	4.21	*
Pavona decussata	14.7±2.9		27.9±3.5	12.1±2.9	24.1	*
Alveopora fenestrata	9.9±0.9	8.3±3.5	23.0±5.5	11.9±4.6	8.44	*
Galaxea fascicularis	7.5±2.9	17.8±7.1	20.3±3.7	11.7±4.3	4.49	*
Echinopora. gemmacea	37.5±4.2	22.1±1.4	29.5±7.5	28.3±1.9	4.25	*

Significance levels are at  $p < 0.05$ . Values obtained from the relationship between porosity and strength of carbonate materials.

### 3.2.4 Coral Skeleton Properties and Environmental Factors

All skeletal parameters in the sediment-impacted reef were adversely affected by the presence of terrestrial input (sediments and nutrients) and there was a fairly strong inverse relationship between bulk density and porosity (Figure 4) but strong direct proportionality between skeleton strength with bulk density and matrix volume (Figure 5). Coral microdensity was however poorly correlated with coral matrix volume, porosity and skeletal strength (Table 9) suggesting that variations in coral strength found in this study were mostly and to a large extent mainly influenced by the variation in bulk density and matrix volume rather than by the variations in microdensity of coral skeleton. From these observations we can infer that the arrangement of fundamental coral skeleton elements were the main cause of density variations unlike other studies where skeletal chemistry was suggested as the main reason. Our results show that elevated sediment levels alone or in combination with nutrients negatively impact mechanical properties of coral skeleton and that water motion may play an important

role in mitigating these negative impacts. Overall, our study reveals that disturbances of terrestrial origin not only cause declines in calcification rates, but can also cause morphological and mechanical changes on coral skeletons to more porous and potentially weaker and fragile forms, consequently undermining the integrity and biodiversity of coral reefs.

Table 9. Correlation analysis between coral skeleton parameters from four Kenyan protected lagoons. Relationships were fitted to the model  $y=a+bx$  with sites arranged in order of decreasing sediment influence

Reef	Code	n	Variables		a	b	r <sup>2</sup>	r	p
			x	y					
Malindi	MLD	57	Density	Porosity	1.99	-0.02	0.64	0.80	*
			Density	Strength	0.71	0.03	0.73	0.86	*
			Microdensity	Strength	3.45	0.05	0.19	0.43	*
			Matrix vol	Microdensity	1.71	0.13	0.14	0.12	ns
			Microdensity	Porosity	3.96	6.70	0.25	0.50	*
Watamu	WTM	48	Density	Porosity	2.45	-0.02	0.82	0.91	*
			Density	Strength	0.80	0.02	0.64	0.79	*
			Microdensity	Strength	2.41	0.003	0.01	0.11	ns
			Matrix vol	Microdensity	0.41	0.69	0.20	0.04	ns
			Microdensity	Porosity	2.29	0.003	0.001	0.10	ns
Mombasa	MSA	48	Density	Porosity	1.95	-0.02	0.75	0.87	*
			Density	Strength	0.86	0.02	0.73	0.86	*
			Microdensity	Strength	2.73	0.02	0.39	0.63	*
			Matrix vol	Microdensity	3.30	-0.45	0.03	0.18	ns
			Microdensity	Porosity	1.4	0.2	0.44	0.67	*
Shimoni	SHM	48	Density	Porosity	2.62	-0.06	0.89	0.95	*
			Density	Strength	0.66	0.03	0.47	0.69	*
			Microdensity	Strength	2.59	0.001	0.001	0.03	ns
			Matrix vol	Microdensity	24.3	-0.71	0.02	0.14	ns
			Microdensity	Porosity	2.64	-0.002	0.02	0.04	ns

n = number of individuals, r<sup>2</sup>, Pearson’s coefficient of determination, r, Pearson’s correlation coefficient, ns not significant, \*, p < 0.001).

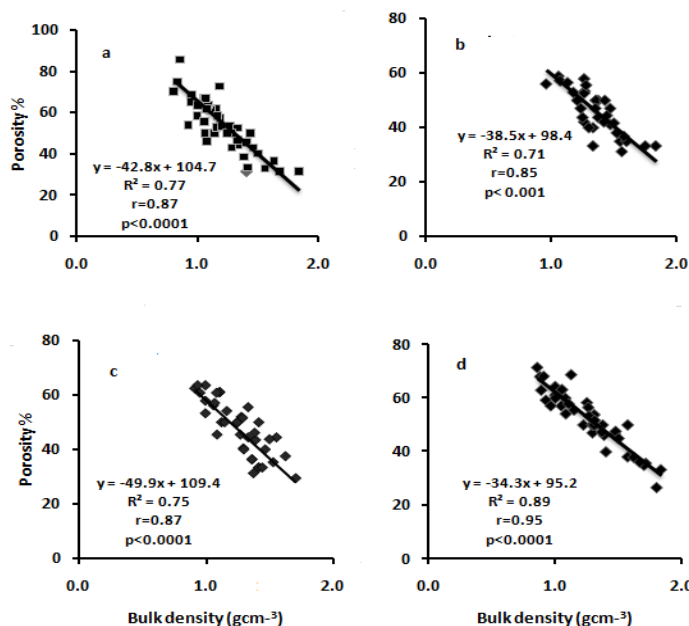


Figure 4. Relationship between coral skeleton porosity and bulk density for selected coral species from (a) Malindi, (b) Watamu, (c) Mombasa and (d) Shimoni protected reefs. Included are regression and correlation coefficients and significance tests

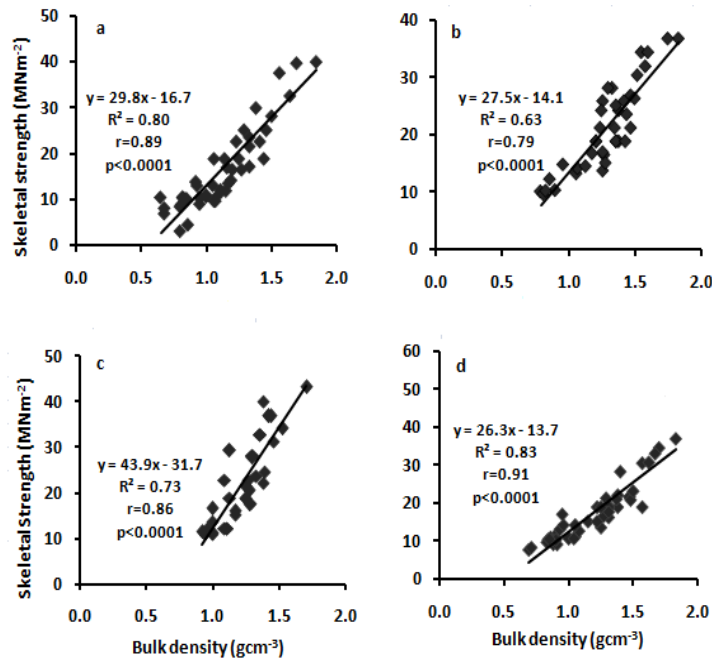


Figure 5. Relationship between strength and the bulk density of coral skeleton from (a) Malindi, (b) Watamu, (c) Mombasa and (d) Shimoni protected reefs, included regression and correlation coefficients and significance tests

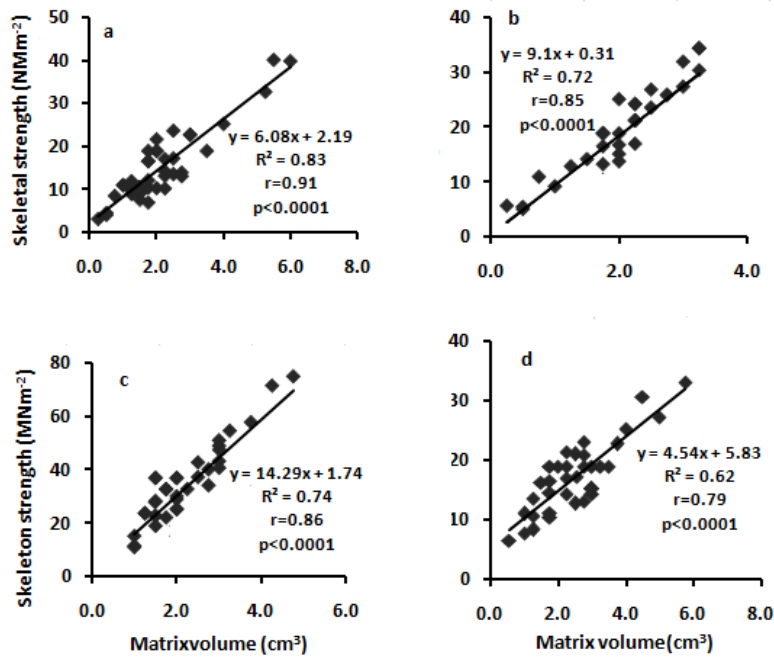


Figure 6. Relationship between strength and the matrix volume of coral skeleton from (a) Malindi, (b) Watamu, (c) Mombasa and (d) Shimoni protected reefs, included regression and correlation coefficients and significance tests

#### 4. Discussion

The future of corals reefs is threatened by global climate change events associated with increased ocean temperature, reduced seawater pH (ocean acidification) and local environmental degradation (Fantazzini et al., 2015; de Carlo, Gaetani, Holcomb & Cohen, 2015; Collard et al., 2016). Predicting the future existence and management of coral reefs therefore requires knowledge of the role played by (manageable) local environmental factors on coral calcification and the integrity of carbonate skeletons and reefs. In the present study significant variations were detected in coral skeletal properties as a consequence of increased terrestrial input. Skeleton

property variations found in this study are similar to those reported previously by other workers (Roche, Adel, Johnson & Perry, 2011; Cordero, 2013; Silbinger, Guadayol, Thomas, & Donahue, 2014; Tambutté et al., 2015; De Carlo et al., 2015). However, Walsh, Brading, Suggett and Smith. (2012) found no differences in coral skeleton characteristics from high and low turbid reefs and attributed this to branch orientation towards light (microhabitat characteristics).

Perhaps the most striking result from the present study is the consistently observed low bulk density, skeletal strength and high porosity of coral skeletons in the reef exposed to river discharge, similar to other reports on corals growing in disturbed sites (Carricart-Ganivet & Merino, 2001; Ammar, Mohammed & Mahmoud, 2005; Dunn, Sammarco & LaFleur Jr, 2012; Fantazzini et al., 2013). This may be attributed to compromised calcification process leading to the deposition of skeleton material of lower density and concomitant increase in linear growth (“stretching modulation” or Janus effect) as an adaptation to reduced resources, light and space (Carricart-Ganivet & Merino, 2001; Amman et al., 2005; Brahmi, Kopp, Domart-Coulon, Stolarski & Meibom, 2012; Cordero, 2013). Alternatively, this may also reflect growth-induced effects of higher levels of nutrients (Edinger et al., 2000). Several mechanisms have been proposed to explain the pathways involved in the detrimental effects of terrestrially derived disturbances and river discharge on coral skeletons (Edinger et al., 2000; Roche et al., 2011; Dunn et al., 2012; Cordero, 2013). Under optimum conditions of clear and oligotrophic waters, coral skeleton density approaches that of pure aragonite ( $2.94 \text{ gcm}^{-3}$ ) but skeletal material alterations e.g. from unstable aragonite ( $\rho = 2.95 \text{ gcm}^{-3}$ ) to stable calcite ( $\rho = 2.60\text{-}2.80 \text{ gcm}^{-3}$ ) or dolomitization ( $\rho = 2.90 \text{ gcm}^{-3}$ ) due to changing environmental variables has been shown to highly influence  $\text{CaCO}_3$  depositional cycles (Caroselli et al., 2011; Roche et al., 2011; Browne, Tay, Low, Larson, & Todd, 2015), skeletal architecture, structure and composition (Chamberlain 1978; Belda, Cuff & Yellowlees, 1993; Spiske, Böröcz, & Bahlburg 2008; Godinot et al., 2011; Dunn et al., 2012), overall calcification and carbonate production, (Lewis et al., 2012; Cordero, 2013). The resultant consequences of this on reef diversity and productivity as well as the livelihood of adjacent coastal communities have already been highlighted (McClanahan & Cinner, 2012).

The present results revealed three major environmental factors mediating changes in coral skeleton properties, namely; hydrodynamic energy, nutrient and sediment/turbidity levels. Malindi and Watamu reefs exhibited almost similar nutrient and TSS characteristics, however, terrestrial influence was greater in Malindi relative to all other reefs (high organic and acid insolubles content), possibly explaining the significantly compromised skeleton properties observed in Malindi corals. The combined effect of nutrient and sediment (Malindi reef) caused greater (negative) impact on coral mechanical properties relative to reefs impacted by either nutrients or high hydrodynamic energy alone. Stronger (less porous, denser) coral skeletons measured in Mombasa and Watamu relative to the Shimoni ‘pristine’ reefs likely resulted from the high hydrodynamic energy and low turbidity/sediment levels measured at these sites (Samuel and Monismith, 2013; Baldock et al., 2014, Lowe & Falter, 2015) compared to Shimoni reef despite the proximity to mangrove creeks and potential nutrient impacts. This is similar to the results of Sawall et al. (2011) who found that eutrophication was not always a major influence on coral performance although Dunn et al. (2012) measured reduced coral density under increased nutrient levels in a controlled laboratory experiment. Our results suggest that sediment-nutrient interaction is a major synergistic factor in influencing coral skeletal properties even in the presence of relatively high hydrodynamic energy although the impacts of nutrients levels seem to be counteracted by high hydrodynamics (Mombasa and Watamu data). However, Stambler, Popper, Dubinsky and Stimson (1991) observed no changes in the strength of carbonate skeletons in a water motion gradient probably because coral skeleton mechanical integrity is determined mainly by the strength of reef substrate to which corals are attached (J. Madin, Dell, E. Madin, & Nash, 2013).

High nutrient and sediment levels have both been reported to negatively impact calcification (Edinger et al., 2000; Dunn et al., 2012; Godinot, Ferrier-Pages, Montagna & Grover, 2011; Godinot et al., 2012) via their action as crystallization inhibitors (“crystal poison”) in the  $\text{CaCO}_3$  crystal production and arrangement process (Cuif, Dauphin, Nehrke, Nouet & Perez-Huerta, 2012; Venn et al. 2013; Mass et al., 2014). By distorting the orderly array of  $\text{CaCO}_3$  crystal packing (Venn et al. 2013; Mass et al., 2014), nutrients have been reported to modify the number and thickness of individual coral skeletal element as well as the arrangement, structure and chemistry of deposited calcium carbonate crystals (Belda et al., 1993; Mass, Drake, Peters, Jiang, & Falkowski, 2014) resulting in the production of less dense, more porous and structurally weaker calcium carbonate/calcium phosphate skeletons (Edinger et al., 2000; Godinot et al., 2011; Dunn et al., 2012; Madin et al., 2013) similar to present observation in Malindi reefs. Such skeleton pattern modifications have also been associated with increased soft tissue growth, zooxanthellae population and coral-zooxanthellae symbiotic activities (Edinger et

al., 2000; Dunn et al., 2012; Tanaka, Inoue, Nakamura, Suzuki, & Sakai, 2014), CO<sub>2</sub> utilization and production of OH<sup>-</sup> ions (Bednarz, Neumann, Niggel, & Wild, 2012). Increased photosynthetic activities not only reduce available energy for calcification but also disrupt the normal and stable intra-coelenteron pH.

Accordingly, increased soft tissues growth must be accommodated by a similar increase in skeleton growth. If this happens without a concomitant increase in calcification rate, porous skeletons are thus produced to the detriment of skeleton density and strength (Belda et al., 1993; Dunn et al., 2012). Further, increased OH<sup>-</sup> ion concentration in coral's internal environment must be upregulated or counteracted by the generation of additional H<sup>+</sup> ions from increased calcification (Laurent, Tambutte S, Tambutte E, Allemand, & Venn, 2013; Venn et al., 2013) causing acidification of the coral internal environment and subsequent reduction in calcification and skeleton density and strength. This is of particular concern considering future raises in ocean acidification (Doropoulos et al., 2012; Tambutté et al., 2015), frequency and intensity of high energy hydrodynamic events (Spiske et al., 2008) and increases in bioeroders populations (De Carlo et al., 2015). However, the creation of complex 3-D internal habitats by bioeroders has been shown to be important in coral host-symbiot dynamics and ultimately on the survival of the coral holobiont (Yost et al., 2013). Although the specific nutrient species involved in the inhibition of CaCO<sub>3</sub> precipitation have not yet been identified, phosphate and polyphosphate groups have been suggested as the likely candidates (Belda et al., 1993; Osinga et al., 2011; Hoac, Kiffer-Moreira, Millan & McKee, 2013) due to their structural similarity with aragonite crystals. Depressed skeleton mechanical integrity observed in Malindi reefs are similar to those observed elsewhere in polluted waters (Edinger et al., 2000; Dunn et al., 2012; Ezzat, Towle, Irisson, Langdon & Ferrier-Pages, 2016 ) and may be similarly associated with (a) decreased light energy for photosynthesis and calcification, (b) metabolic drain on corals (photosynthesis versus respiration) causing reduced available energy for calcification and (c) heterotrophy on increased particulate matter enhancing skeletal and tissue growth without a corresponding increase in calcification rate (Edinger et al., 2000; Carricart-Ganivet and Merino, 2001; Fantazzini et al., 2015). These scenarios may possibly explain the observed differences between Malindi and Watamu reefs. Malindi reef sediments consistently exhibited high proportions of organic matter and acid insolubles compared to the rest of the studied reefs, a positive indicator of increased terrestrial influence as well as a potential heterotrophic energy source.

Despite the high hydrodynamic energy measured in Malindi reef, coral skeletons here were found to be relatively more porous contrary to previous results (Madin et al., 2013; Baldock et al., 2014). We hypothesize that the hydrodynamic energy levels in Malindi were not high enough to elicit reduction in skeleton porosity through thickening or counteract the (negative) impact imposed by high nutrient and sediment levels, hence the low skeleton porosity. On the other hand, improved skeleton properties measured in branching relative to other growth forms may be an adaptation to the comparatively greater bending forces experienced by branching corals (Chamberlain, 1978; Walsh et al., 2012) coupled with their ability to increase strength by filling skeletal voids with organic cement as they age (Roche et al., 2011), unlike massive corals that have their strength provided for mainly by their geometry. Further, Walsh et al. (2012) found massive corals to have greater variability within skeleton variables (skeletal density, porosity and microdensity) and also deposit aragonite of significantly lower density than that in the skeletons of branching corals. The effects of these three environmental factors on skeleton mechanical strength may be appreciated by comparing reef pairs; hydrodynamics (Mombasa and Shimoni), nutrients (Watamu and Mombasa) and sediment (Malindi and Watamu). These comparisons suggest that the coral skeleton modifications observed in sediment-exposed Malindi reef are to a greater extent the result of high sediment levels due to Sabaki River discharge other than any of the other factor measured in the present study. Our study revealed minimal influence of microdensity on skeletal properties compared to bulk density suggesting that variations in skeletal parameters observed were probably due to changes at the meso-architectural level. This is similar to the results of other workers (Dodge et al., 1993; Bucher et al., 1998; Cordero, 2013) implying that terrestrially-derived stressors affect the arrangements of coral colony fundamental units (corallites including septa, thecae and dissepiments).

Whereas inherent and environmental factors may induce species-specific and habitat variations in skeletal properties respectively, care should be exercised when comparing results from different studies due to a number of reasons. Sampling and measurement techniques employed, and the size and position of specimen on coral colony may affect estimated skeletal property values (Roche et al., 2011; Dunn et al, 2012). For example, although larger coral specimens usually produce low measurement errors they are also likely to give low density/high porosity values due to the presence of more borings. Differences between findings may also emanate from the specimen's relation to individual calices, seasonal banding or relative position on colony (Barnes & Devereaux, 1988; Cordero, 2013) as well as age difference in coral samples (Caroselli et al., 2011; Roche et al., 2011). Moreover, compared to other techniques, the wax method used presently has several sources

of limitation: (1) trapped air in skeleton voids during submersion tends to cause underestimation of porosity, (2) controlling viscosity of wax and size of wax coating on samples, (3) incomplete hydrated enclosed voids introduce errors in porosity calculations and (4) possible removal of acetone soluble skeletal structural compounds (Barnes & Devereux, 1988; Bucher et al., 1998).

Predicted increases in ocean pH (acidification) associated with increased atmospheric CO<sub>2</sub> levels and other climate change events (such as high SST and sea level) will likely cause weaker and more vulnerable coral skeletons (Kleypas et al., 1999; Doropolous et al., 2012; Tambutté et al., 2015; Collard et al., 2016) in future, immensely interfering with reef ecology and the provision of goods and services. Although declines in density and strength may sometimes be beneficial at the species level (Chamberlain, 1978; Schuhmacher 1984; Walsh et al., 2012), however, at the community level this may cause nearshore reefs, where local stresses are already a great concern, to be of reduced biodiversity, productivity and protective value (De Carlo et al., 2015; Ezzat et al., 2016). It is also worth noting that the relationship between porosity and strength is exponential (Roche et al., 2011; Dunn et al. 2012) hence coral skeletons in the low porosity-high strength end of the spectrum would be more vulnerable to synergistic effects of boring organisms and hydrodynamic forces (Chamberlain 1978; Maina et al., 2013; Bartley et al., 2014; Ramos-Sharrón et al., 2015) posing great concern to reef areas already weakened by anthropogenic perturbations.

This study results indicate that near shore reefs are under severe threat from local environmental factors and are likely to suffer most in future from climate change events such as ocean acidification, increased SST and high energy hydrodynamic events. However, it should be noted that not all reefs are at risk of degradation from disturbances, since exposure and site-specific conditions also determine susceptibility. Poorly flushed and shallow reefs close to river mouths, with disturbance history and low abundances of herbivores are the most vulnerable (Wooldridge et al., 2011). Disturbance vulnerability may also depend on the species composition of a reef as a result of the species-specific response of skeleton properties to environmental change. These species-specific responses have been attributed to different clades of *Symbiodinium sp* or other potential factors including the presence or absence of known or unknown enzymes e.g., Ca<sup>2+</sup>-ATPase or carbonic anhydrase (Lesser, Weis, Patterson, & Jokiel, 1994, Goiran Al-Moghrabi, Allemand, & Jaubert, 1996, McClanahan et al., 2014). Previous studies have shown that reefs dominated by corals with weaker skeletons will suffer the severest losses in the event of hydrodynamic disturbances, elevated SST, CO<sub>2</sub> or increased bioeroder populations (Spiske et al., 2008; Reyes-Nivia et al., 2013; Madin et al., 2013; Wiedenmann et al. 2013; D'Angelo & Wiedenmann, 2013; Perry et al., 2014; Perry & Harborne, 2016). Understanding the dynamics and interactions of environmental disturbances, their impact mechanisms and the tolerance/adaptability as well as resilience among coral species is therefore key in deriving focused and effective management plans for the future of healthy and productive reefs. For instance, the average strength, composition and abundance of species may be useful in ranking reefs according to their relative susceptibility and overall risk of damage (Craik, Kenchington, & Kelleher, 1990). Exposure, type and stress frequency data and the proportion of colonies impacted, combined with information on injury regeneration and fragment survival would in turn aid in evaluating the recovery process of reef assemblages. Identification of the susceptibility of corals to local stresses via proxies such as skeletal characteristics will therefore enable coral managers and conservationist to direct attention toward areas most at need and those with potential to become refugia in the future (Walsh et al 2012; Wiedenmann et al., 2013) providing shelter and maintenance of genetic diversity. This is especially important since it is projected that only minor benefits will accrue from current carbon emission reduction strategies to coral reef health, and will be noticeable only in the long term, probably 50-60 years after drastically reducing emissions (Donner, Skirving, Little, Oppenheimer, Hoegh-Guldberg, 2005; Ortiz et al., 2013; 2014). Consequently, appropriate watershed management strategies combined with reef and fisheries management options would be expected to alleviate the effects of terrestrially derived disturbances and have the potential to minimize predicted large-scale coral reef degradations arising from intense and frequent global climate change events.

### Acknowledgement

This research was kindly and generously supported by grants from the British Ecological Society (BES), the World Wildlife Fund (WWF), the International Development Research Centre (IDRC) Doctoral Research Award and the Simon Fraser University (SFU) President's Award to the first author in support of his PhD program. Permission for research in the marine parks was provided by the Kenya Wildlife Service (KWS). We are also grateful to the logistic support provided by KWS rangers and laboratory and field assistance from the staff of Kenya Marine and Fisheries Research Institute (KMFRI). Excellent fieldwork was provided by Masudi J. Zamu and Anthony M. Nzioka. All authors participated in the birth of the concept, project and experimental design and development of manuscript. Data collection was done by the first author.

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